UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE INVESTIGACIONES EN
ECOSISTEMA Y SUSTENTABILIDAD

RESPUESTAS DE LAS AVES MIGRATORIAS DE INVIERNO A GRADIENTES DE HÁBITAT EN REGIONES URBANAS NEOTROPICALES.

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR(A) EN CIENCIAS

PRESENTA:

RODRIGO PACHECO MUÑOZ

TUTOR(A) PRINCIPAL DE TESIS: DR. JORGE ERNESTO SCHÖNDUBE FRIEDEWOLD
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MÉXICO, CD. MX. MAYO, 2024.

HOJA EN BLANCO

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COORDINACIÓN GENERAL DE ESTUDIOS DE POSGRADO
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M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **19 de febrero de 2024** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **PACHECO MUÑÓZ RODRIGO,** con número de cuenta **305585589** con la tesis titulada **"RESPUESTAS DE LAS AVES MIGRATORIAS DE INVIERNO A GRADIENTES DE HÁBITAT EN REGIONES URBANAS NEOTROPICALES",** realizada bajo la dirección del **DR. JORGE E. SCHONDUBE FRIEDEWOLD**, quedando integrado de la siguiente manera:

Presidente: DR. ROBERTO ANTONIO LINDING CISNEROS
Vocal: DR. ZENÓN CANO SANTANA
Secretaria: DR. LUIS ZAMBRANO GONZÁLEZ
Vocal: DR. JOSÉ JAIME ZÚÑIGA VEGA
Vocal: DR. JAVIER SALGADO ORTIZ

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
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COORDINADOR DEL PROGRAMA

DR. ARTURO CARLOS II BECERRA BRACHO

c. c. p. Expediente del alumno

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Dedicatoria

A Karen y a mi bandada

Índice

Resumen

Las aves migratorias neárticas-neotropicales realizan dos migraciones anuales. Se reproducen en la región templada durante primavera-verano. En verano-otoño migran a la región tropical, donde invernan. Luego regresar a la región templada. Es por eso que requieren hábitats de calidad a lo largo de su migración. La conversión de áreas de vegetación nativa a zonas agrícolas o urbanas en sus zonas de invernada se vincula con una dramática disminución de sus poblaciones en las últimas décadas. La urbanización ha sido un proceso clave de transformación del suelo a lo largo de los siglos XXI y XXI. Los ambientes urbanos presentan desafíos y oportunidades para la biodiversidad, que incluyen a las aves migratorias. Durante la etapa reproductiva, pocas especies toleran la urbanización. Fuera de esta etapa, sus requisitos de hábitat se relajan y su asociación con ambientes urbanos incrementa. En su etapa de invernación, las ciudades neotropicales pueden albergar ensambles abundantes y diversos de aves migratorias. La presencia y abundancia de aves migratorias en ciudades neotropicales se asocia estrechamente con el arbolado urbano. Sin embargo, no es claro el papel que las ciudades juegan como hábitat invernal para las aves migratorias. En este proyecto doctoral evalúo las asociaciones entre las aves migratorias y las ciudades mexicanas. Los capítulos se centran en: 1) entender los factores que caracterizan al ambiente urbano y su efecto sobre los vertebrados que lo habitan; 2) evaluar el papel de las ciudades como hábitat para los ensambles regionales de aves migratorias, 3) discernir el papel de las áreas verdes urbanas y su arbolado para mantener ensambles diversos de aves migratorias en grandes ciudades y 4) evaluar la calidad de hábitat urbano para las aves migratorias invernantes, al contrastar poblaciones urbanas con no urbanas. Mi trabajo muestra que las ciudades reducen la diversidad taxonómica y funcional de las aves migratorias. Las aves migratorias que dominan los ambientes urbanos son comunes a escala regional pero son menos abundantes, relativo a ambientes silvestres. Esto lo asocio con una menor abundancia de recursos en el ambiente urbano. También sugiero que el ambiente urbano promueve un proceso de filtrado ambiental asociado a los rasgos funcionales de las aves migratorias. En el ambiente urbano generalmente son especies insectívoras con preferencias por la vegetación densa y los estratos vegetales altos. En consecuencia, su riqueza de especies y abundancias en áreas verdes urbanas está estrechamente asociada con la cobertura y densidad de sus árboles. Además, la posición geográfica de las áreas verdes urbanas en la ciudad les es irrelevante. Finalmente, demostré que la áreas verdes urbanas ofertan una buena calidad de hábitat para algunas especies, las cuales deben considerarse habitantes urbanos de invierno. Los resultados demuestran que las ciudades neotropicales contribuyen al ciclo anual de las aves migratorias. Sugiero que las ciudades pueden promover positivamente a las aves migratorias al considerar un manejo del hábitat urbano que fomente un arbolado amplio, denso y complejo, que se centre en las asociaciones positivas con los rasgos funcionales de las aves.

Abstract

Nearctic-Neotropical migratory birds undertake two annual migrations. They breed in the temperate region during spring-summer. In summer-autumn, they migrate to the tropical region, where they overwinter. They then return to the temperate region. This is why they require quality habitats throughout their migration. The conversion of native vegetation areas to agricultural or urban areas in their overwintering grounds has been linked to a dramatic decline in their populations in recent decades. Urbanization has been a key process of land transformation throughout the 21st and 22nd centuries. Urban environments present challenges and opportunities for biodiversity, including migratory birds. During the reproductive stage, few species tolerate urbanization. Outside this stage, their habitat requirements relax and their association with urban environments increases. In their overwintering stage, Neotropical cities can harbor abundant and diverse assemblages of migratory birds. The presence and abundance of migratory birds in Neotropical cities is closely associated with urban trees. However, the role that cities play as winter habitat for migratory birds is not clear. In this doctoral project, I evaluate the associations between migratory birds and Mexican cities. The chapters focus on: 1) understanding the factors that characterize the urban environment and its effect on the vertebrates that inhabit it; 2) evaluating the role of cities as habitat for regional assemblages of migratory birds; 3) discerning the role of urban green areas and their trees in maintaining diverse assemblages of migratory birds in large cities; and 4) evaluating the quality of urban habitat for wintering migratory birds by contrasting urban with non-urban populations. My work shows that cities reduce the taxonomic and functional diversity of migratory birds. The migratory birds that dominate urban environments are common at the regional scale but are less abundant, relative to wild environments. I associate this with a lower abundance of resources in the urban environment. I also suggest that the urban environment promotes an environmental filtering process associated with the functional traits of migratory birds. In the urban environment, insectivorous species with preferences for dense vegetation and high vegetation strata are common found. Consequently, their species richness and abundance in urban green areas is closely associated with the cover and density of their trees. In addition, the geographic position of urban green areas in the city is irrelevant to them. Finally, I showed that urban green areas offer good habitat quality for some species, which should be considered as winter urban dwellers. The results demonstrate that neotropical cities contribute to the annual cycle of migratory birds. I suggest that cities can promote migratory bir-

ds positively by considering urban habitat management that promotes a broad, dense, and complex tree cover, which focuses on positive associations with the functional traits of birds.

Introducción

Las aves migratorias neárticas-neotropicales (a partir de ahora referidas como “aves migratorias”) son un grupo polifilético de aves exclusivas al continente americano caracterizadas por presentar un ciclo anual con dos migraciones de larga distancia (Hayes, 1995; Winger et al., 2014; Somveille et al., 2020). Durante primavera-verano se reproducen en la región templada y el invierno lo pasan en la región tropical (Hayes, 1995; Faaborg et al., 2010). Entre ambas etapas, durante verano-otoño e invierno-primavera, cruzan el trópico de Cáncer a través de sus movimientos de larga distancia hacia sus territorios de invernada y reproductivos, respectivamente (La Sorte et al., 2016; Bayly et al., 2018). La mayor parte de su ciclo anual ocurre en sus territorios tropicales de invernada (Sherry y Holmes, 1996; Albert et al., 2020). Estas aves suelen requerir territorios extensos en hábitats de buena calidad tanto en sus zonas de reproducción como de invernación para lograr cumplir su ciclo anual exitosamente (Donovan et al., 2002; Faaborg et al., 2010; Albert et al., 2020). Es por ello que la transformación de zonas con vegetación nativa a sitios de uso antrópico es considerada la principal causa del declive sus tamaños poblacionales de las últimas décadas (Rosenberg et al., 2019; Schuster et al., 2019; Wilson et al., 2019).

La transformación del suelo en áreas urbanas ha crecido en importancia en los siglos XX y XXI (Balvanera et al., 2019). Aunque las áreas productivas ocupan gran parte del suelo modificado por humanos, las áreas urbanas crecen rápidamente en algunos lugares del planeta (Seto et al., 2012; Elmqvist et al., 2019; McDonald et al., 2020). La urbanización es el proceso por el cual la especie humana modifica la cobertura de suelo para crear, extender o intensificar áreas urbanas, con el fin de sostener altas densidades poblacionales dedicadas principalmente a actividades terciarias (MacGregor-Fors et al., 2012; Forman, 2014; United Nations et al., 2019). Este proceso implica la transformación del tipo de suelo a través de reducir y fragmentar la cobertura de vegetación nativa o productiva por medio de incluir elementos de gran complejidad estructural como construcciones, calles y elementos artificiales (MacGregor-Fors y Schondube, 2011; Barbosa et al., 2020). De este modo, los elementos vegetales presentes dentro de las zonas urbanas pueden ser parches remanentes o planeados, constituidos tanto por especies nativas como exóticas (Forman, 2014; Faggi y Caula, 2017; P. Barbosa, 2020). La urbanización genera condiciones ambientales únicas como el ruido, el tipo y la intensidad de las actividades humanas, la luz artificial nocturna, altas concentraciones de alimento y agua, fenómenos climáticos como la isla de calor y procesos biogeoquímicos alterados como las altas concentraciones de nitrógeno presentes en suelos urbanos (Pickett et al., 2001; Grimm et al., 2008; Gaston y Sánchez de Miguel, 2022). Estas diferencias estructurales y funcionales caracterizan a las áreas urbanas como un tipo de ecosistema distinto. Así, entender la relación de las aves migratorias con las áreas urbanas durante su ciclo anual se vuelve necesario para un manejo efectivo de sus poblaciones a futuro.

Las áreas urbanas se reconocen como una amenaza particular, generalizada y sustancial para la biodiversidad (United Nations et al., 2019; McDonald et al., 2020; Simkin et al., 2022). No obstante, esto depende tanto del contexto ambiental en que se encuentra la ciudad, como de los procesos de urbanización que esta experimenta (McDonald et al., 2020; Simkin et al., 2022). De este modo, los ecosistemas urbanos pueden contar con comunidades biológicas complejas (McDonald et al., 2020; Knapp et al., 2021; Spotswood et al., 2021). La persistencia de los organismos en ambientes urbanos depende en gran medida del conjunto de rasgos funcionales, que les permiten aprovechar las oportunidades que ofrece el hábitat urbano (Aronson et al., 2016; Neate-Clegg et al., 2023), como de sus interacciones con otros organismos capaces de sobrevivir dentro de las ciudades (MacGregor-Fors y Schondube, 2012).

A lo largo del año, las áreas urbanas tienen menos aves migratorias que entornos nativos y productivos (Stratford y Robinson, 2005; MacGregor-Fors et al., 2010; La Sorte et al., 2014). Durante la reproducción, pocas especies toleran la urbanización (Stratford y Robinson, 2005; Heide et al., 2023). Hay excepciones como *Dummetela carolinensis* que prospera en entornos urbanos (Evans et al., 2015; Ladin et al., 2018). Fuera de la etapa reproductiva, muchas especies de aves migratorias relajan sus requisitos de hábitat (Hutto, 1980; Greenberg, 1995; Sherry y Holmes, 1996; Gómez et al., 2016), lo que fomenta que incrementen su asociación con áreas urbanas durante el periodo invernal (Zuckerberg et al., 2016).

Durante las migraciones norte-sur y sur-norte, varias especies usan áreas urbanas para realizar escalas de descanso (Zuckerberg et al., 2016; La Sorte et al., 2020). Su presencia y abundancia se asocian con el arbolado urbano (Zuckerberg et al., 2016; Wood y Esaian, 2020; La Sorte et al., 2020; La Sorte y Horton, 2021; Buron et al., 2022). También los atrae la oferta de recursos hídricos (Barbosa et al., 2022). Además, Las áreas verdes urbanas pueden funcionar como un hábitat de buena calidad que les permite reponer las reservas de grasa durante sus escalas de descanso (Seewagen y Slayton, 2008). No obstante, condiciones del hábitat urbano como la luz artificial nocturna pueden desorientar, atraer y afectar negativamente a las aves migratorias (La Sorte et al., 2017; McLaren et al., 2018) Además de obstáculos donde pueden estrellarse como ventanas, o de una mayor presión de depredación por gatos domésticos (Cusa et al., 2015; Loss et al., 2019).

Una buena parte del ensamble de aves urbanas tropicales en el invierno esta formado por aves migratorias (Carbó-Ramírez y Zuria, 2011; Charre et al., 2013). La presencia de especies e individuos de aves migratorias en ambientes urbanos durante el invierno ha sido asociado con varios factores: 1) un incremento en la superficie del país cubierta por ambientes urbanos; 2) abundancia constante de recursos alimenticios e hídricos en el ambiente urbano durante la época seca-fría del año; y 3) la presencia de condiciones ambientales como la isla de calor urbana, que puede reducir el estrés térmico en estas aves en zonas de invernación más templadas (Barbosa et al., 2020; La Sorte y Horton, 2021). No obstante, el factor que mejor explica la riqueza de especies y abundancia de aves migratorias en zonas urbanas neotropicales son las áreas verdes con elementos arbóreos abundantes (MacGregor-Fors et al., 2010; Leveau, 2021; Amaya-Espinel y Hostetler, 2019). Incluso hay registros de de aves migratorias que presenta fidelidad de sitio invernal en zonas verdes urbanas entre años(Monroy-Ojeda et al., 2013). En el desarrollo de esta tesis también se confirmó la fidelidad de sitios en áreas verdes urbanas (Pacheco-Muñoz et al., 2022).

Al iniciar esta tesis había pocos estudios que abordan el uso de las áreas urbanas neotropicales por las aves migratorias invernantes (ver Carbó-Ramírez y Zuria, 2011; Charre et al., 2013). MacGregor-Fors et al., (2010) y Monroy-Ojeda et al., (2013) son los únicos trabajos enfocados exclusivamente a este fenómeno. Por ello, el propósito de esta tesis de doctorado es entender el papel que las áreas urbanas juegan como hábitat para las aves migratorias durante su etapa de invernada. Además, su alta capacidad de dispersión espacial las hace un modelo ideal para evaluar cómo la distribución de los hábitats urbanos afecta su presencia (Aronson et al., 2016). Esto se aborda a través de cuatro capítulos.

En el primer capítulo estudié el efecto que diferentes factores, que conforman y emergen de lo urbano, tienen sobre los vertebrados que habitan este tipo de ecosistemas. Para ello, realizaré una revisión de la literatura sobre los diversos factores que afectan la interacciones entre vertebrados y ambientes urbanos, sin considerar al grupo de los peces. Mi revisión consideró 1,127 artículos obtenidos con el motor de búsqueda de literatura académica Web of Science publicados hasta el año 2020. A los artículos seleccionados los evalué con el método de revisión sistemática por investigación de tejido y de agrupación por palabras conjuntas utilizando sus palabras clave (Aria y Cuccurullo, 2017; Nakagawa et al., 2019). Luego realicé una síntesis de las asociaciones reportadas para los distintos factores, con un enfoque jerárquico de las escalas espaciales y el nivel organizacional (ensamble, especie y población) utilizado para cada estudio. Finalmente, evalué la direccionalidad de la literatura académica sobre el tema. Resalté las características que se cuantifican en ambientes urbanos, sus asociaciones con los rasgos funcionales de los organismos y las métricas utilizadas para evaluar el rendimiento de los vertebrados en este contexto.

El segundo, tercero y cuarto capítulos de esta tesis se enfocan en abordar la relación de las aves migratorias con ambientes urbanos neotropicales. Para ello, estudié ciudades de la región centro-occidente de México. Los estudios los llevé a cabo a escala regional, de ciudad y de hábitat.

Para lograr lo anterior, en el segundo capítulo pregunté: ¿qué papel juegan las áreas urbanas para mantener la diversidad taxonómica y funcional de aves migratorias en una región, relativo a ambientes silvestres y productivos? Esto lo llevé a cabo en la región biocultural de “El Bajío”, en el Occidente de México, que es un área de invernación clave para las aves migratorias (Hutto, 1980; Wilson et al., 2019; Albert et al., 2020). Utilicé puntos de conteo con estimación de distancias para describir a los ensambles de aves migratorias en 13 localidades. En cada localidad registré a las aves migratorias en ambientes urbanos, productivos y silvestres. La categorización de la región en estos tres ambientes la realizamos con base en MacGregor-Fors y Vázquez (2020). La categorización tiene el propósito de resumir ampliamente la región, relativo a la presencia humana y sus actividades, considerando la infraestructura, los asentamientos y las actividades económicas que se realizan. Esta aproximación me permitió diferenciar las oportunidades y limitaciones particulares que ofrece el ambiente urbano a través de ciertos rasgos funcionales presentes en las aves migratorias, relativo a lo que ocurre en ambientes de vegetación nativa y productivos.

En el tercer capítulo me pregunté ¿cuál es la importancia de las áreas verdes urbanas de una megaurbe como la Ciudad de México para mantener la diversidad taxonómica y funcional de aves migratorias de su región sur? Esto lo abordé en áreas verdes remanentes del ecosistema del Pedregal de San Ángel, al sur del área urbana de la Ciudad de México (Lot y Camarena, 2009). Realicé registros estandarizados de aves migratorias en 12 áreas verdes. Luego, para cada área verde evalué sus características espaciales y los elementos de hábitat grises y verdes presentes tanto en su interior como a su alrededor. La información me permitió entender cuáles características de las áreas verdes tienen un mayor efecto sobre las aves migratorias. Así, establecí que las áreas verdes urbanas pueden albergar ensambles de aves migratorias taxonómica y funcionalmente complejos. También determiné que las densidad y cobertura arbórea de las áreas verdes es la única característica que las fomenta.

En el cuarto y último capítulo determiné si las áreas verdes de una ciudad neotropical ofrecen hábitat de calidad para las aves migratorias. Para ello contrasté la calidad corporal de las poblaciones de dos especies de chipes migratorios entre sitios de invernación tanto dentro como fuera de la ciudad *(Setophaga coronata y Leiothlypis ruficapilla)*. A las especies las seleccioné como modelos por ser abundantes en ambientes urbanos y silvestres. Luego comparé a las poblaciones de las áreas verdes de la ciudad de Morelia con ambientes con vegetación silvestres alrededor de la ciudad, a través de su captura por medio de redes de niebla en estaciones de monitoreo. A las poblaciones de ambas especies las comparé por sus abundancias en puntos de conteo, sus tasas de captura por el método de redes de niebla, sus estructuras poblacionales por sexos y por su calidad corporal individual. No encontré diferencias entre las poblaciones que invernan en las áreas verdes urbanas y los parches de vegetación nativa. Mis resultados mostraron que las áreas verdes de ciudades neotropicales pueden contribuir como hábitat de calidad para algunas especies de aves migratorias, lo que mantiene sus poblaciones durante el invierno.

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Capítulo I. Los vertebrados y lo urbano: una evaluación de sus relaciones

En el siglo XXI las áreas urbanas se transformaron en el hogar de la mayoría de los individuos de la especie *Homo sapiens* (United Nations et al., 2014). Este cambio ha acelerado la transformación de la cobertura del suelo natural a una cobertura modificada, relacionado a nuestro crecimiento y consumo de recursos. Actualmente la cobertura urbana representa el 4% de la superficie terrestre (Forman, 2014), su tasa de crecimiento es mayor al de la poblacional y su impacto afecta más allá del territorio que abarca (Balvanera et al., 2020; Elmqvist et al., 2019). Este proceso es considerado uno de los principales impulsores negativos de los ecosistemas, sólo superado por la expansión agrícola (Díaz et al., 2019). Ambos cambios se vinculan con la disminución del 40% de las especies de vertebrados terrestres a nivel global (Díaz et al., 2019). Sin embargo, el planteamiento teórico para entender la relevancia ecológica de lo urbano sobre los vertebrados a partir del trabajo de McDonnell y Pickett, (1990), se plantea una valoración distinta del ecosistema urbano (Pickett et al., 2016). Actualmente se reconoce el impacto negativo y generalizado de la urbanización sobre la biodiversidad (Fischer et al., 2015). No obstante, también es posible aumentar la cantidad, la calidad y la disponibilidad del hábitat urbano para aumentar su potencial de albergar biodiversidad (McDonnell y MacGregor-Fors, 2016).

En vertebrados la urbanización puede promover respuestas generalizables, pero también existen respuestas particulares a cierto nivel taxonómico o agrupación por rasgos funcionales. Para promover sinergias y oportunidades de investigación es necesario contrastar las respuestas de diversos grupos taxonómicos y funcionales. Por ello, conocer el estado del arte sobre cuáles son los factores que conforman y emergen de la urbanización, y de que forma afectan al grupo de los vertebrados, es importante para precisar oportunidades para un manejo integral del hábitat urbano.

El ecosistema urbano

Históricamente nuestra vida urbana lleva más de 5,000 años al considerar a las *polis* griegas o las ciudades antiguas de Egipto y Mesopotamia (Forman, 2014). No obstante, tanto el desarrollo de las ciudades como sus dinámicas sociales han cambiado con el tiempo. Durante la Revolución Industrial concentraron a la población rural alrededor de los centros de trabajo y más tarde los trenes permitieron el espaciamiento entre el hogar y los centros productivos (Murayana y Estoque, 2020). Durante la década que inició en 1970, la accesibilidad de la población al transporte fomentó la migración del centro hacia las áreas suburbanas, seguido por las oficinas y las nuevas actividades comerciales (Murayana y Estoque, 2020). La urbanización se retroalimenta con el crecimiento económico (Hare, 1999). Actualmente, las áreas urbanas contribuyen al 75% del PIB (Elmqvist et al., 2019) y la urbanización ocurre principalmente en los países en desarrollo (Murayana y Estoque, 2020), por lo que es necesario considerar su contexto histórico, social y económico.

La urbanización da lo urbano y se vincula con ciudades. Las características de lo urbano puede extenderse desde los pequeños pueblos hasta las megaciudades de más de 10 millones de habitantes (Balvanera et al., 2020; Forman, 2014). La sociología considera a la urbanización como un proceso que cambia la actitud y el estilo de vida de las personas; en economía es un cambio de la base económica primaria agrícola a la manufactura o al sector terciario (Murayana y Estoque, 2020). Para Forman (2014) es «*el cambio de densificación del suelo y/o expansión hacia el exterior*». McDonnell y Pickett (1990) lo definen como *«el incremento en la habitación humana, junto con el incremento en el consumo per cápita de energía y la modificación extensiva del paisaje, lo que crea un sistema que no depende de los recursos locales como fuente principal de recursos para persistir*».

Desde la ecología y para entender las consecuencias de lo urbano en los vertebrados, el proceso de urbanización requiere hacer explícito su origen en el Homo sapiens y, en este sentido, a nuestra especie como una ingeniera del ambiente físico (Jones y Gutiérrez, 2007). Bajo este concepto, la urbanización constituye nuestro proceso de ingeniería del ecosistema físico. Los cambios que mediamos estructuralmente son alogénicos. Es decir, que los cambios son externos a la especie, a través del cambio biótico y abiótico del hábitat. El conjunto de cambios resulta en el ecosistema urbano, que se caracteriza por estar dominado por nosotros y por las particularidades en sus consecuencias resultantes de nuestra ingeniería del ecosistema.

En este trabajo, defino urbanización como el proceso alogénico de ingeniería del ecosistema físico que ejerce la especie humana sobre el paisaje, en donde la cobertura nativa del suelo se sustituye por construcciones, caminos y estructuras artificiales, que satisfacen la intensificación de actividades que emergen de la densificación de los humanos y de su estructura socioeconómica. Su progreso fragmenta el paisaje, de modo que la cobertura vegetal del suelo puede estar conformada por parches de vegetación nativa remanente o por vegetación planeada por humanos y puede o no incluir especies exóticas. Este proceso da origen a lo urbano, se puede extender y densificar espaciotemporalmente, el consumo de energía per cápita de sus habitantes aumenta y su persistencia como sistema no depende de recursos locales. Esta consideración centraliza el origen intrínseco de la urbanización como parte de nuestra especie y hace explícito que el humano modifica el hábitat para la biota nativa. En este trabajo uso la definición hábitat de Hall et al. (1997) *«a los recursos y condiciones presentes en un área que producen ocupación, que incluye tanto a la sobrevivencia como a la reproducción, dado un organismo específico*». Los organismos regularmente ocupan hábitats que no permiten la persistencia individual o poblacional. Por ello, para describir el hábitat es necesario considerar su abundancia (su cantidad, independientemente de los organismos presentes) y calidad (su capacidad para proporcionar condiciones apropiadas para la persistencia individual y poblacional). Por lo tanto, el hábitat del ecosistema urbano puede contrastar con el hábitat nativo en los patrones de comunidades ecológicas en sus procesos de dispersión (el movimiento de individuos y especies, dentro y fuera de las comunidades locales), la selección (el éxito relativo de las especies dentro de una comunidad local), la deriva (cambios en la abundancia relativa de las especies debido al azar u otros efectos aleatorios), o la especiación a escala local y regional (McKinney, 2002; Mcgill et al., 2006; Vellend, 2010).

Los vertebrados y el hábitat urbano

Una característica del ecosistema urbano es la heterogeneidad en la abundancia, calidad y disponibilidad de hábitat (Pickett et al., 2016). Para estudiarla, desde un inicio se planteó la evaluación de la la relación de los factores urbanos con la biota con base en el paradigma de gradiente propuesto por Whittaker (1967). Su planteamiento consiste enmedir gradientes ambientales para asociarlos a cambios biológicos (McDonnell y Pickett, 1990; Whittaker, 1967). Por otro lado, la ecología urbana también ha incorporado y extendido tres paradigmas locales para abordar el estudio de ciudades: 1) la ecología *en* la ciudad, 2) la ecología *de* la ciudad y 3) la ecología *para* la ciudad (Pickett et al., 2016). Para evaluar qué factores afectan a los vertebrados y cómo lo hacen, en este trabajo me basé en los primeros dos paradigmas.

En el paradigma de la ecología *en* la ciudad los ecólogos cuantifican las variables que describen el hábitat urbano de los vertebrados en el contexto de parches y de coberturas del suelo. Se consideran las coberturas de caminos, de construcciones con su actividad dominante y su nivel de densificación, de cobertura de construcciones de forma general, de suelo desnudo, de densidad poblacional y la cobertura vegetal dominante: remanente o de origen antrópico (McDonnell y Pickett, 1990; McKinney, 2002; Pickett et al., 2016). A nivel local al ecosistema urbano se le puede categorizar en distintos tipos de hábitats. Las categorías son familiares al contexto urbano y permiten abordar los estudios hacia tipos de hábitats particulares del ecosistema (ej. jardines privados, parques o plazas). Sin embargo, en este paradigma la matriz urbana se considera un área inhóspita y las áreas con cobertura vegetal como parches fragmentados con vegetación remanente, parques, cementerios, jardines, lotes baldíos y yermos, ríos y humedales son un hábitat "verde" que alberga a la biodiversidad. Al hacer evaluaciones a escala regional, la ecología *en* ciudades considera a lo urbano como un hábitat general de los organismos y se contrasta con un hábitat no urbano (Pickett et al., 2016). Los hábitats que generalmente son usados para contrastar lo urbano son áreas silvestres y productivas, y hay quien incluye áreas periurbanas (McKinney, 2002).

En el paradigma de la ecología *de* ciudades el hábitat se extiende a la matriz urbana como un continuo pero se requiere una descripción rigurosa de las condiciones y las estructuras bióticas y abióticas que lo constituyen (Pickett et al., 2016). También se requiere considerar que el hábitat urbano se entrelaza con procesos que pueden entenderse desde las ciencias sociales, la geografía y la economía, por ejemplo (McDonnell y MacGregor-Fors, 2016). En la ecología *de* ciudades lo urbano es un mosaico en donde sus componentes se pretenden entender de una forma amplia y holística.

Los vertebrados son el grupo más estudiado en el ecosistema urbano y las aves son el grupo que concentra la mayor cantidad de las investigaciones (Aronson et al., 2014; Hedblom y Murgui, 2017), pero los estudios de vertebrados sobre mamíferos, reptiles y anfibios han ido en aumento (Bateman y Fleming, 2012; French et al., 2018; Hamer y McDonnell, 2008). Estas investigaciones nos permiten entender algunas respuestas generales de los vertebrados y es aceptado que las respuestas de las especies al disturbio urbano se pueden agrupar en tres categorías que las caracterizan: las *habitantes urbanas*, las *utilizadoras urbanas* y las *evitadoras urbanas* (Fischer et al., 2015). De acuerdo con Fischer et al. (2015), las especies *habitantes urbanas* pueden contar con poblaciones viables en lo urbano y pueden o no estar limitadas a otros hábitats no urbanos; las especies *utilizadoras urbanas*, por su parte, se caracterizan por hacer uso del hábitat y hasta contar con eventos reproductivos dentro del hábitat; finalmente, las especies *evitadoras urbanas* no son frecuentes en las áreas urbanas sin importar la progresión de su densificación pero pueden sustentarse en parches con cobertura vegetal. Esta clasificación depende del gradiente en la respuesta general de las especies a lo urbano y responde a la selección de hábitat de las especies (Fischer et al., 2015; Krausman y Morrison, 2016). Esta categorización, en parte, se basa en sus respuestas a la evaluación del hábitat y considera su abundancia, su calidad y su disponibilidad. No obstante, en la respuesta de los vertebrados ante la urbanización es muy importante considerar la amplitud y diversidad de sus rasgos funcionales. Es necesario entender el sentido biológico de la relación del desempeño evaluado de las especies, relativo a su nicho fundamental y realizado (Mcgill et al., 2006).

Las revisiones que han evaluado el efecto diferencial de los parámetros urbanos sobre los vertebrados normalmente abordan una sola clase taxonómica y sus respuestas rara vez se contrastan con otros grupos taxonómicos. Al respecto, la urbanización afecta mayoritariamente al sistema terrestre y por tal motivo limitaré esta revisión a los vertebrados cuyas historias de vida tengan una relación directa con este sistema: a las aves, a los mamíferos, a los reptiles y a los anfibios. Las aves son el grupo que cuenta con la mayor cantidad de estudios en el tema. La razón se vincula con el desarrollo histórico de la rama pero también porque es un grupo diverso las áreas urbanas a nivel global y los métodos para evaluarlos son económicos en tiempo y recursos, relativo a los otros grupos (Hedblom y Murgui, 2017; Lepczyk et al., 2017). El segundo grupo con más estudios son los mamíferos (Bateman y Fleming, 2012), el tercer lugar lo ocupan los reptiles (French et al., 2018) y el cuarto los anfibios (Hamer y McDonnell, 2008).
El objetivo principal de esta revisión es evaluar el estado del arte del conocimiento del efecto diferencial de los factores que conforman y emergen de lo urbano sobre los vertebrados que lo habitan, a través de tres objetivos particulares. El primero es ampliar la revisión del tema mediante una revisión sistemática de la literatura. El segundo es sintetizar los efectos de los parámetros urbanos sobre los vertebrados, con énfasis en los efectos sinérgicos. Los resultados seguirán una jerarquía taxonómica que irá de lo general a lo particular y se enfocarán en dos aspectos: 1) las distintas escalas espaciales de lo urbano, junto con los distintos tipos de hábitats y sus componentes que se consideran en la literatura y 2) el nivel taxonómico en el que se enfocan los estudios: comunidad, ensambles y poblaciones. En el tercer objetivo particular, realizaré una evaluación de la direccionalidad del tema y los tipos de estudios que se han realizado en el tiempo. Esta evaluación incluirá los los componentes que cuantificaron en el hábitat urbano, así como los rasgos funcionales y la medida de rendimiento que evaluaron en los vertebrados.

Un vistazo a la literatura

Mediante la búsqueda de investigaciones en el motor de búsqueda *Web of Science* y con los criterios de selección obtuve un total de 1127 artículos entre los cuatro grupos de vertebrados y sólo 28 de ellos abordaron a más de una clase. Estos registros los evalué con el método de revisión sistemática por investigación de tejido y seleccioné los trabajos con base en un análisis y agrupación por palabras conjuntas con base en palabras clave (Aria y Cuccurullo, 2017; Nakagawa et al., 2019). Los métodos de selección y revisión se detallan en el material suplementario. En la figura 1 muestro el total de investigaciones seleccionadas por cada clase de vertebrado, su intervalo temporal, registros totales en los dos periodos temporales considerados (previo al año 2015 y 2015–2020), y el número acumulado por países. El número total de investigaciones en aves fue de 509, en mamíferos fue de 221, en reptiles fue de 192 y en anfibios fue de 177. En reptiles y anfibios la búsqueda tuvo un límite menor al máximo (1000) de registros revisados por cada clase. Los trabajos más antiguos fueron de 1993. En todos los grupos el periodo 2015–2020 contó con más investigaciones. La selección contó con trabajos de todos los continentes habitados pero la gran mayoría son de países de regiones templadas como Estados Unidos, principalmente, y países europeos. La figura 2 muestra cada diagrama estratégico por clase y periodo con base en Cobo et al. (2011). El análisis con base en los registros obtenidos de cada grupo de vertebrados, así como la selección final de temas e investigaciones se encuentran como monografía en el material suplementario.

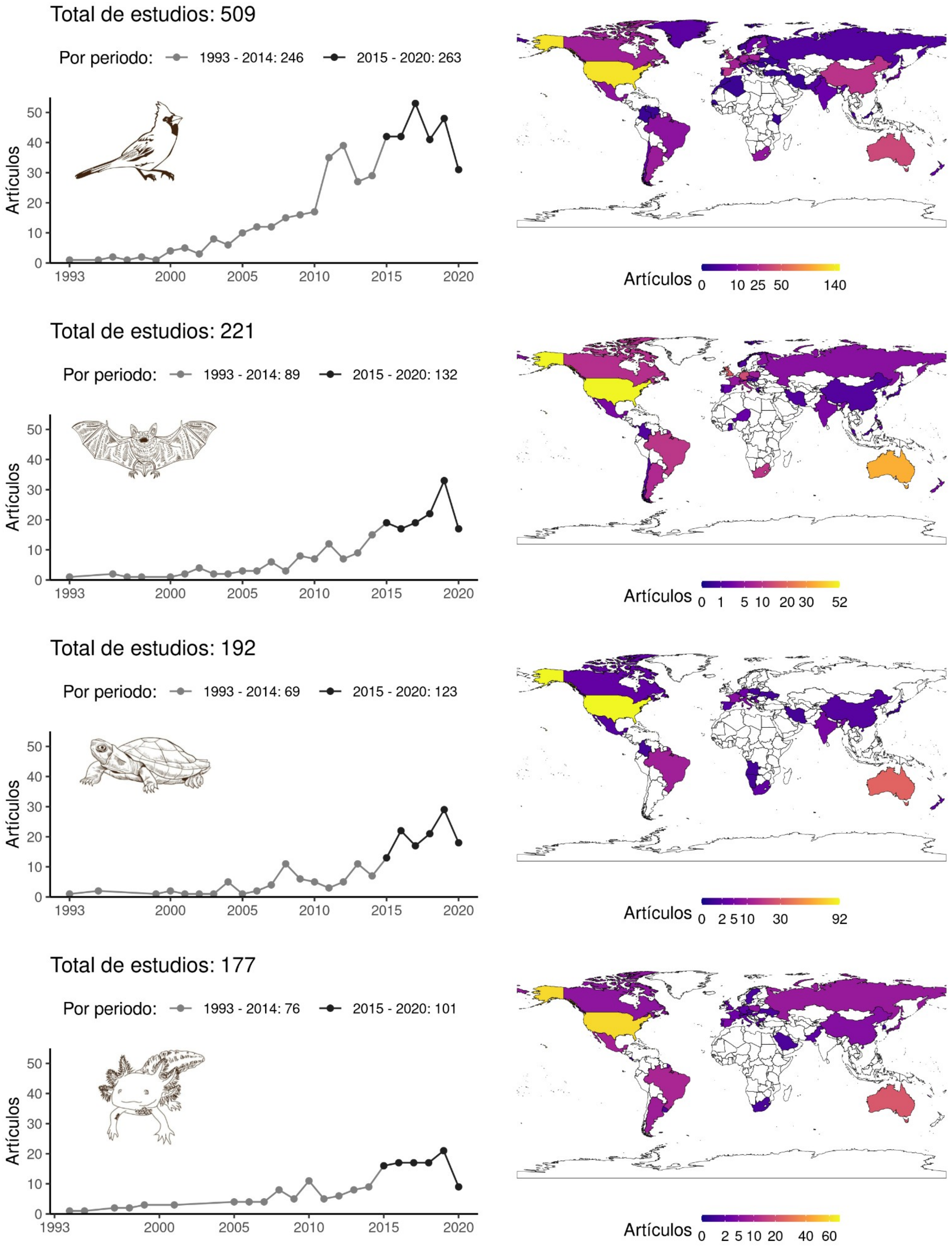

Figura 1. Selección de estudios por cada clase de vertebrado considerado. La columna izquierda indica el intervalo temporal y la columna derecha indica el número acumulado de artículos por país.

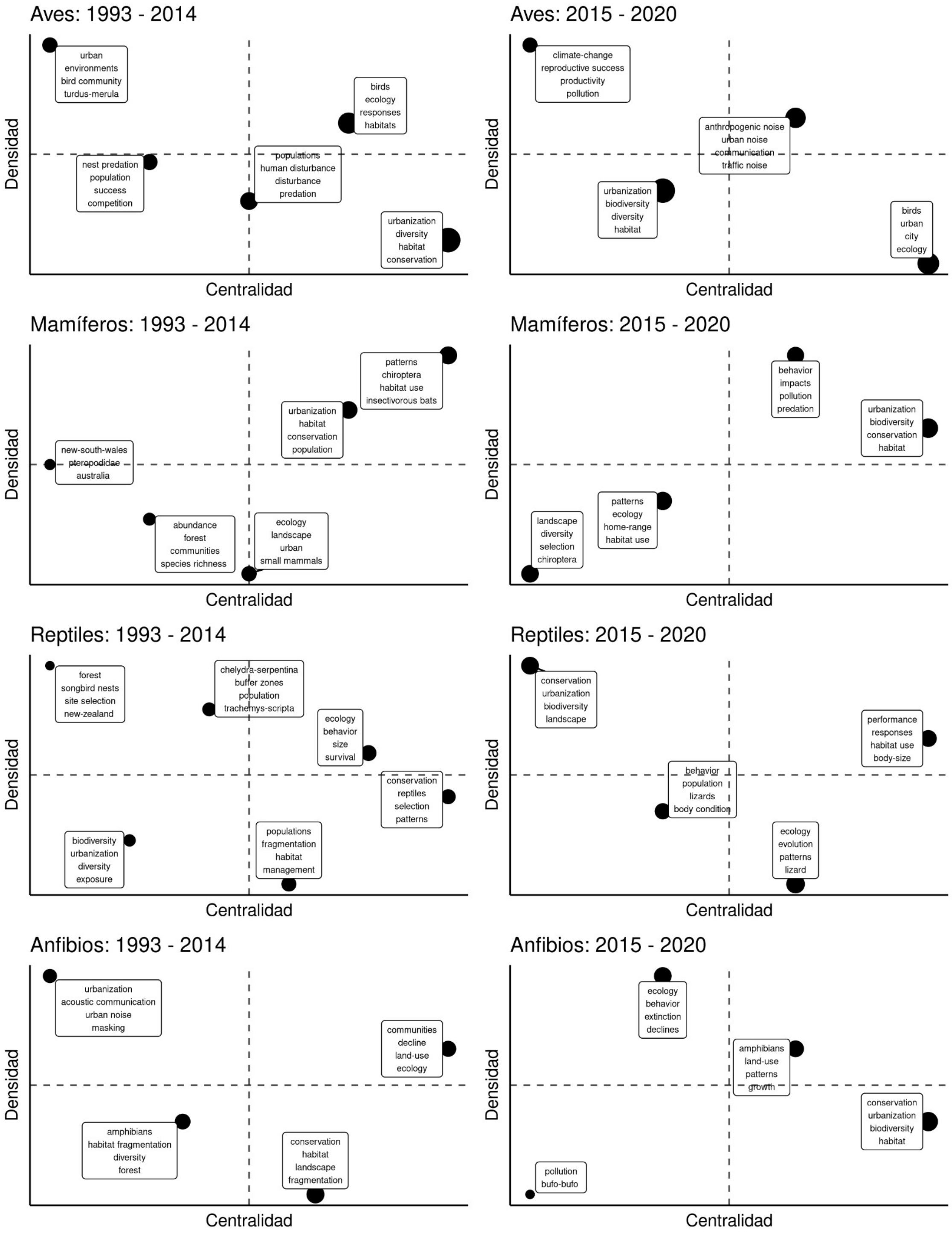

Figura 2. Diagrama estratégico con base en palabras clave por periodo y clase de vertebrado. Temas por cuadrante: Superior derecho: temas motores; Superior izquierdo: altamente desarrollado o aislado; Inferior izquierdo: emergentes o de relevancia decreciente; Inferior derecho: básicos y transversales.

Los ensambles de vertebrados urbanos

Considero como ensambles a un grupo de especies taxonómicamente relacionadas que se encuentran juntas en el espacio y el tiempo (Stroud et al., 2015). Aunque las diferencias inherentes entre los ensambles de vertebrados plantean estudiarlas con aproximaciones distintas, también pueden existen coincidencias. Por ejemplo, los ensambles de aves urbanas tienen una mayor capacidad de dispersión que los mamíferos, los reptiles y los anfibios, e incluso en estos últimos tres grupos su presencia en lo urbano se puede limitar únicamente a áreas con vegetación o a cuerpos de agua. En lo general, tanto el aumento en la cobertura de construcciones y de caminos, así como su densificación y usos, afecta negativamente a la riqueza de especies, y solo pocas tienen abundancias por encima de sus poblaciones no urbanas, que dominan la estructura de los ensambles. Por el contrario, el incremento de la cobertura vegetal, así como su complejidad, afectan positivamente la riqueza de especies y contribuyen a una estructuras más equitativa en los ensambles, en términos de abundancia relativa (Blair, 1996; Knutson et al., 1999; Germaine y Wakeling, 2001; Baker et al., 2003; Avila-Flores y Fenton, 2005; Riley et al., 2005).

La cobertura de las construcciones también se pueden categorizar con base en su uso. En ensambles de aves la cobertura con uso comercial se ha relacionado con una menor riqueza de especies (Blair, 1996). Por otra parte, también se ha registrado que en coberturas con uso residencial hay un decremento del número de especies de aves (Blair, 1996; Sandström et al., 2006), así como en la riqueza y actividad acústica de murciélagos (Avila-Flores y Fenton, 2005). En los tres casos anteriores, esto ocurre al comparar los datos con los obtenidos. También se ha contrastado el centro urbanístico, lo suburbano y lo periurbano como tipos de hábitats distintos. Por ejemplo, la riqueza de especies y la abundancia de las aves disminuye con el aumento de la urbanización al asociarla con un gradiente de tipos de hábitat constituido por lo periurbano, lo suburbano y el centro urbano (Clergeau et al., 2006; Melles et al., 2003).

Las categorizaciones de tipos de hábitat resumen parámetros ambientales que cuantifican y que describen cada sitio, como la proporción de cobertura de distintos estratos vegetales y la descripción de su composición, estructura física y densidades (Avila-Flores y Fenton, 2005; Blair, 1996; Sandström et al., 2006). Generalmente también incluyen la descripción de la densidad de construcciones (Melles et al., 2003), de caminos (Germaine y Wakeling, 2001; Isaac et al., 2014), de recursos (Blair, 1996) y de condiciones como la densidad humana (Halfwerk et al., 2011; Randa y Yunger, 2006), así como el efecto de la isla de calor (Putman et al., 2019). Los cambios en los ensambles entre los hábitats también ocurren en su composición y se vinculan con sus rasgos funcionales y con la abundancia, calidad y disponibilidad del hábitat (Avila-Flores y Fenton, 2005; Blair, 1996). El centro de las áreas urbanas, por ejemplo, se vincula con aves omnívoras y carnívoras, por su abundancia en recursos energéticos alóctonos, y suelen ser especies invasoras (Blair, 1996 ; Clergeau et al., 1998, 2006). También se promueven especies de aves que forrajean en suelo, al beneficiarse de la remoción de la cobertura vegetal, relativo a áreas residenciales y suburbanas (Melles et al., 2003; Clergeau et al., 2006). Los murciélagos de áreas urbanas se vinculan con rasgos funcionales que les permiten una mayor eficiencia en su carga alar (la masa total de un avión o animal volador dividida por el área de su ala), asociado con las áreas abiertas con poca cobertura arbórea que caracteriza a los ambientes urbanos (Avila-Flores y Fenton, 2005). Las áreas con mayor cobertura vegetal, por ejemplo, promueven recursos alimenticios para aves insectívoras y que anidan en huecos o árboles (Clergeau et al., 2006, 1998; Melles et al., 2003). En este sentido el hábitat local y el del paisaje pueden afectar diferencialmente a los ensambles.

Escalas espaciotemporales

Las estructuras locales del hábitat urbano como el arbolado o los arbustos aumentan la riqueza de especies al ofrecer sustratos de anidamiento, refugio o alimento, pero su cercanía con áreas forestales o parques los afecta de forma independiente y la capacidad de dispersión de las especies juega un papel importante (Melles et al., 2003). Una comparación entre ensambles de aves de dos ciudades templadas de Europa y América indicó que en el centro comparten especies dominantes: *Passer domesticus* y *Sturnus vulgaris*, ambas con densidades similares entre ciudades y consideradas invasoras para América (Clergeau et al., 2006); *Turdus merula* y *T. migratorius*, consideradas especies insectívoras equivalentes en ambas ciudades, mostraron densidades similares (Clergeau et al., 1998). Clergeau et al., (2006) evaluó el efecto del gradiente latitudinal sobre los ensambles de aves a través de evaluarlas en distintas ciudades de una región europea. Sus resultados mostrarons que tanto las áreas suburbanas como los centros, en menor y mayor medida, respectivamente, amortiguan su efecto y también promueven la similitud entre ensambles de aves (Clergeau et al., 2006).

El tiempo es un factor muy importante para evaluar la persistencia de especies en ambientes urbanos. Un estudio realizado por Ree y McCarthy (2005) en Melbourne, Australia, analizó la persistencia de mamíferos nativos con base en registros históricos gubernamentales. Los resultados revelaron que más de la mitad de las especies de la región tenían altas probabilidades de desaparecer por la urbanización y los mamíferos pequeños fueron señalados como los más afectados (Ree y McCarthy, 2005). En contraste, Westgate et al., (2015) examinó la ocurrencia de ensambles de ranas urbanas en Camberra, Australia, durante un período de 13 años por medio de ciencia ciudadana. Este estudio encontró que al conservar la cobertura vegetal riparia de la ciudad, las especies de ranas urbanas mantienen poblaciones estables y tienen baja probabilidad de desaparecer en el mediano plazo (Westgate et al., 2015).

Contrastes con hábitats no urbanos

Los ensambles de vertebrados urbanos también se contrastan con otros hábitats aledaños al área urbana (Pickett et al., 2016). Un contraste común es el rural–urbano. Una comparación entre murciélagos rurales y urbanos de Norte América, no mostró cambios en su composición ni en la abundancia de insectos que consumen(Coleman y Barclay, 2013). Sí encontraron cambios en su actividad de forrajeo asociados con la temperatura urbana (Coleman y Barclay, 2013).

Otro contraste es el de vegetación silvestre–urbano. En Panamá, el ensamble de murciélagos insectívoros se contrastó con bosques, con el borde y con lo urbano (Jung y Kalko, 2011). Al evaluarlos, notaron patrones comunes de decremento en riqueza y el aumento de sus abundancias, ambos relacionados con la urbanización (Jung y Kalko, 2011). También encontraron más actividad en el borde que en los bosques y lo urbano, y que las especies menos afectadas por la urbanización tienen mayor su eficiencia energética en áreas abiertas, dada su carga alar, su poco peso y los pocos recursos energéticos en el hábitat (Jung y Kalko, 2011).

En Indiana, EE.UU. el ensamble de murciélagos se evaluó en un gradiente arbóreo–rural–urbano (Duchamp y Swihart, 2008). En este ensamble la urbanización también se relacionó con el decremento de la riqueza y el favorecimiento de especies con carga alar eficiente en áreas abiertas (Duchamp y Swihart, 2008). También se vinculó con el decremento de quirópteros que descansan en árboles y al aumento de aquellos que descansan en rocas.

En Australia, un constraste del ensamble de marsupiales arbóreos de bosques con los urbanos mostró la pérdida de todas las especies folívoras y el aumento de especies generalistas (Isaac et al., 2014).; Para el ensamble de marsupiales, la estructura y la cobertura riparia urbana resulta muy importante.

Parches urbanos

Los parches de vegetación remanente o vegetación inducida por humanos se complementan con construcciones o por usos diversos que les damos los humanos (Forman, 2014; McDonnell y Pickett, 1990). Además, pueden incluir cuerpos de agua, como humedales (Rubbo y Kiesecker, 2005; Pillsbury y Miller, 2008; Holzer, 2014), ríos (Riley et al., 2005), estanques artificiales y lagos (Holzer, 2014; Kruger et al., 2015).

Por lo general, hay más especies de vertebrados en parches con coberturas con vegetación nativa que las áreas con vegetación inducida. El aumento de especies se vincula con una estructura y composición de estratos arbustivos y arbóreos más complejos y por la presencia de especies nativas (Avila-Flores y Fenton, 2005; Crooks et al., 2004; Duchamp y Swihart, 2008; Jung y Kalko, 2011; Threlfall et al., 2016).

El incremento de la calidad y abundancia de hábitat por el incremento en la complejidad en los estratos vegetales urbanos fomenta una mayor diversidad de vertebrados. En el mismo sentido, los parques (Zhou y Chu, 2012), jardines (Baker y Harris, 2007), ríos (Riley et al., 2005) y cuerpos de agua contribuyen al fomento de la biodiversidad urbana (Holzer, 2014; Rubbo y Kiesecker, 2005). El área total de los parches promueve la riqueza de especies (Baker et al., 2003; Crooks et al., 2004; Kruger et al., 2015; Zhou y Chu, 2012). La conectividad entre parches puede limitar la disponibilidad del hábitat y afectar la dispersión de los vertebrados (Baker et al., 2003; Oprea et al., 2009; Pillsbury y Miller, 2008).

La progresión de la urbanización también reduce la diversidad general de los ensambles que habitan los parches urbanos (Crooks et al., 2004; Germaine y Wakeling, 2001; Riley et al., 2005). Con el incremento de la coberuta urbana, los grupos tróficos de aves que están más limitados son los frugívoros e insectívoros porque se favorecen del alimento que produce o fomenta la vegetación (Crooks et al., 2004). En contraste, los granívoros y omnívoros pueden aprovechar recursos suplementados por humanos y prosperar (Crooks et al., 2004; Zhou y Chu, 2012).

Las especies que persisten con el incremento de la urbanización cuentan con rasgos funcionales que les permite aprovechar el hábitat. Por ejemplo, en el ensamble de lagartijas de la ciudad de Tucson, Arizona, EE.UU, hay especies que se benefician del incremento de la complejidad que brindan los elementos artificiales y los árboles exóticos al poderlo trepar (Germaine y Wakeling, 2001).

Otro papel que juega el incremento de la complejidad del hábitat es el de limitar la entrada de depredadores. Baker y Harris (2007) reportaron que la abundancia de mamíferos pequeños en jardines de Gran Bretaña tuvo una asociación menor en fomentar la abundancia de frutos vegetales pero el incremento en la complejidad estructural sí la fomentó, al limitar la entrada de depredadores. Este papel del hábitat también lo reportó Riley et al., (2005) en el ensamble de anfibios de arroyos del sur de California, EE.UU, donde limitaba el acceso de cangrejos exóticos. Además, en un ensamble de anfibios de cuerpos de agua en Portland, Oregon, EE.UU, la vegetación les ofrece áreas de oviposición y refugio (Holzer, 2014). Por el contrario, se ha reportado que la construcción de muros artificiales alrededor del cuerpo de agua o la reducción de la costa del cuerpo de agua que habitan puede limitar a anfibios con historias de vida terrestres (Parris, 2006; Pillsbury y Miller, 2008).

Aproximaciones multiclase

Entender el efecto del hábitat urbano a través del estudio de múltiples ensambles contrastantes puede permitir profundizar en sus respuestas diferenciales. Barrett y Guyer, (2008) reportaron que el icremento de cobertura urbana afectó de forma similar tanto a anfibios como reptiles de hábitats riparios y de arroyos de Georgia, EE.UU. Sin embargo, la contribución de diversos tipos de cobertura vegetal fue distinta para cada grupo taxonómico. Croci et al., (2008), por otro lado, evaluó el gradiente rural-urbano con ensambles de aves, mamíferos pequeños y escarabajos Carabidae en la ciudad de Rennes, Britania, Francia. Ellos reportaron la importancia de las distintas capacidades de dispersión de cada grupo y la necesidad de entender sus diferencias con el propósito de incrementar la calidad de hábitat de cada grupo; no obstante, tanto la fragmentación a escala regional como las carreteras a escala local afectan por igual a los tres.

Hamer y McDonnell (2008), con base en datos gubernamentales sobre la ocurrencia de la herpetofauna en Melbourne, Australia, encontraron que las ranas tienen mejores probabilidades de persistir que los reptiles, y que los hábitats remanentes eran muy importantes para la persistencia de ambos grupos. Por su parte, Garden et al. (2007), reportaron la asociación positiva entre los fragmentos con ensambles de mamíferos y reptiles de Brisbane con ciertas especies arbóreas, pero los reptiles preferían coberturas vegetales distintas y cercanas a los montículos de termitas. No obstante, también reportaron que se asociaron negativamente a la compactación de suelo.

Los vertebrados en el hábitat urbano

La variedad de factores que componen el hábitat urbano afectan diferencialmente a las distintas clases de vertebrados, a diferentes especies de un mismo ensamble, e incluso a ciertas poblaciones de una misma especie, según se muestra a continuación. Por ejemplo, Randa y Yunger (2006) encontraron que, al estudias los mamíferos carnívoros de la ciudad de Illinois, EE.UU, reportaron que *Procyin lotor* y, en menor medida, *Canis latran,* son más abundante al interior de la ciudad. Sus abundancias se vinculan con áreas residenciales y los recursos alimenticios que ofrecen. Por otro lado,*Vulpes vulpes* fue más común en áreas exteriores con buen arbolado y sin presencia de coyotes.

Un patrón similar de densidad diferencial lo registran Matsyura et al. (2016) con los córvidos de Zhytomyr, Federación Rusa, pues la máxima densidad de individuos y especies está en los parques, en tanto que el centro urbano lo domina *Corvus frugilegus*. El centro se caracteriza por ofrecer pocos recursos energéticos y pocos elementos para el descanso y el anidamiento. Del mismo modo, Mgelwa et al. (2018) encontraron que dos aves del género *Ploceus* tienen abundancias distintas entre el ambiente urbano y el rural en Camerún. Estos autores notaron que estas especies son afectadas por el ruido y el tráfico, y también tienen preferencias diferenciales por ciertas especies arbóreas para anidar. Por otra parte, se ha encontrado que la ocurrencia de *Rattus novergicus* en la ciudad de Salzburgo, Austria, se relaciona positivamente con los cuerpos de agua y con distintos tipos de vegetación (Traweger et al., 2006). Asimismo, Li et al. (2019) encontraron patrones de distribución de actividad en especies de murciélagos de Carolina del Norte, EE.UU, asociados con el ingreso económico de los habitantes. En su estudio registraron siete especies de murciélagos pero solo dosmbas especies se sociaron positivamente con el ingreso económico, mientras que solo en una especie se asoció negativa con los patrones de distribución de actividad dos especies del ensamble. No obstante, los mecanísmos por los que ocurre no son claros.

En vertebrados acuáticos urbanos, la cobertura vegetal que rodea al cuerpo de agua es necesaria. Esto se ha registrado para tortugas (Hamer y McDonnell, 2008; Marchand y Litvaitis, 2004; Ryan et al., 2014; Santoro et al., 2020) y anfibios (Fuyuki et al., 2014; Cayuela et al., 2015). Es este caso, la vegetación brinda refugio (Ryan et al., 2014) y estructura de hábitat que utilizan para ovipositar (Fuyuki et al., 2014; Cayuela et al., 2015; Santoro et al., 2020) además, esta variable afecta positivamente con la supervivencia y a la condición fisiológica (Hamer y McDonnell, 2008).

Asimisimo, otra variable que afecta a los vertebrados acuáticos urbanos es la calidad de la conectividad entre cuerpos de agua, según se discute a continuación. Por ejemplo, Marchand y Litvaitis, (2004) evaluaron los cuerpos de agua en el sur de Nuevo Hampshire, EE.UU, y reportaon que aquellos con una mayor densidad de carreteras tenían más individuos adultos de la tortuga *Chrysemys picta*. Sin embargo, las hembras que viven tierra adentro presentaron héridas corporales. Los resultados sugieren que las vías de comunicación repercuten en su reclutamiento. La baja calidad de la conectividad entre cuerpos de agua también se vincula con una menor probabilidad de ocupación en anfibios de la llanura aluvial del Rin alsaciano, Francia (Cayuela et al., 2015). No obstante, en las poblaciones periurbanas de *Chelodina longicollis* de Camberra, Australalia, que cuentan con conexiones entre parches de buena calidad la supervivencia entre la población de ambientes urbanos y no urbanas son iguales, aunque en la población urbana reportaron una mayor vagilidad (Rees et al., 2009).

La conectividad entre poblaciones también se ha abordado a nivel genético y es común que se se reporte una reducción del flujo génico en las poblaciones urbanas (Hitchings y Beebee, 1997; Noël et al., 2007; Delaney et al., 2010; Lazić et al., 2015; Combs et al., 2018; Lourenço et al., 2017). Las carreteras (Delaney et al., 2010), la distancia (Hitchings y Beebee, 1997; Noël et al., 2007, p. 207) y el tiempo de urbanización (Lourenço et al., 2017) parecen tener un papel importante en la estructura genética de las poblaciones urbanas. Al respecto, también existen poblaciones urbanas con cambios morfológicos que contrastan con sus poblaciones no urbanas; por ejemplo, la población urbana de *Passer domesticus* es más chica en tamaño e relación con la rural, aún en ensayors expeimentales, por ejemplo, se ha reportado que la población urbana es más chica en tamaño, relativa a la rural, aún en ensayor experimentales (Liker et al., 2008).

Temporalidad

El hábitat urbano amortigua algunos efectos de la temporalidad anuales sobre los vertebrados, pero no en todos los casos. Por ejemplo, en la ciudad de Yitomir, Ucrania, la fluctuación anual de las especies y densidades de córvidos que habitan lo urbano es estable (Matsyura et al., 2016). En parches de vegetación de la región metropolitana de la ciudad de Phoenix, EE.UU, también se ha reportado estabilidad en la poblaciones de lagartijas (*Sauromalus ater*) con un contraste temporal (Sullivan y Sullivan, 2008). En el mismo sentiso, para algunas Psittacidae de Australia los ambientes urbanos también pueden ser un refugio de la temporada de incendios y la temporada seca, por la disponibilidad continua a lo largo del año de recursos hídricos (Davis et al., 2011). De hecho, este alargamiento de los hidroperiodos en las ciudades ocasiona que se anule la estivación en tortugar acuáticas urbanas durante la temporada seca (Ferronato et al., 2016; Rees et al., 2009); no obstante, su actividad suele ser más alta en lluvias que en secas (Ferronato et al., 2016 , 2017). Babini et al. (2015) reportó para anfibios de la ciudad Río Cuarto, Córdoba, Argentina el alargamiento de los hidroperiodos afectó a especies que ovipositan en suelo y se hipotetiza que así evitan los cambios temporales del medio acuático.

Elementos

Vegetación

En general una cobertura arbórea amplia, con estructura arbórea y arbustiva compleja y con árboles grandes es muy importante para que las poblaciones urbanas de aves y murciélagos mantengan una alta abundancia, por lo que son buenos indicadores de la calidad de su hábitat (Brunbjerg et al., 2019; Threlfall et al., 2016). Esto ocurre tanto en parches de vegetación urbana como en la matriz urbana que cuenta con elementos de hábitat arbóreos (James Barth et al., 2015; Oprea et al., 2009). No obstante, la función de estos rasgos, como elemento de conectividad en la matriz urbana parece ser diferencial entre ambos grupos de vertebrados (Oprea et al., 2009).

Elementos artificiales

Durante la urbanización también se remueven o colocan elementos de materiales naturales o artificiales que los vertebrados usan como refugio. La remoción de rocas en jardines se relaciona con menos refugios para reptiles, por lo que proporcionarles rocas naturales o artificiales les permite limitar encuentros directos con humanos, así como a mantener condiciones fisiológicas adecuadas (Pattishall y Cundall, 2009; Webb y Shine, 2000). En este sentido, lagartijas del género *Anolis* en la ciudad de Miami, EE.UU que usan estructuras artificiales tienen mejores posibilidades de sobrevivir y en ambientes urbanos (Battles et al., 2018). Las poblaciones urbanas de la lagartija *Sceloporus occidentalis* del área metropolitana de Los Ángeles, California, EE.UU también se diferencian por el uso de superficies artificiales, relativo a las poblaciones rurales, ya que cuentan con divergencias morfológicas, al poseer dedos y extremidades más cortos (Putman et al., 2019).

Recursos

El hábitat urbano ofrece recursos energéticos limitados, por lo cual la evaluación de este tipo de recursos es importante. Por ejemplo, la persistencia de la lagartija *Phrinosoma platyrhinos* en reservas urbanas del área metropolitana de Phoenix, EE.UU depende de la presencia de hormigueros (Sullivan et al., 2014). Otro estudio en la misma región urbana señala que la abundancia de *Sauromalus ater* en las reservas urbanas se asocian positiviamente con la presencia las seis especies de plantas que consumen (Sullivan y Williams, 2009). Los recursos con origen humano también repercuten, ya sea suplementados de forma voluntaria o por residuos. Tryjanowski et al. (2015) evaluó la abundancia de alimento con origen humano en 26 pueblos y ciudades de Polonia en relación con el ensamble de aves. El alimento con origen humano no modificó la riqueza de especies de aves, pero sí modificó su composición, al agruparse por gremio y tipo de recurso. La provisión de recursos tiene como consecuencia reducir la respuesta de las aves al riesgo y el efecto se exacerba en contextos más urbanizados (Møller et al., 2015). Sin embargo, especies como el búho *Strix aluco* muestran una amplia plasticidad en los recursos que consume a lo largo de todo el gradiente rural–urbano de la ciudad de Varsovia, Polonia (Gryz y Krauze-Gryz, 2019).

Condiciones

Temperatura

El efecto de la isla de calor puede repercutir en las poblaciones de los vertebrados. Por ejemplo, Putman et al. (2019) determiní que las lagartijas *Sceloporus occidentalis* de ambientes urbanos tienen menos escamas dorsales, al compararlas con sus contapartes no urbanas y esto se vincula a una mayor evapotranspiración. En constraste, Sprau et al. (2017) evaluaron el papel de la temperatura en otra especies del grupo de las aves como *Parus major* y no encontraron una asociación entre la condición ambiental con el desarrollo o reproducción. No obstante, tanto el desarrollo como la reproducción fue menor en áreas urbanas, relativo a áreas no urbanas y los mecanismos por los que ocurrió esta diferencia no fueron considerados en ese estudio.

Luz

La luz artificial nocturna (LAN) repercute en el comportamiento y la fisiología de los vertebrados. Doren et al., (2017) evaluó la luz del Memorial del 9/11 en Nueva York y encontró que afecta los vuelos nocturnos de aves migratorias. Se estima que en un periodo 7 años, el memorial afectó el trayecto de 1.1. millones de aves a alturas de vuelo de hasta 4 km.

El papel de la luz en las ciudades también se ha propuesto que es el de una barrera que limita la conectividad en murciélagos (Hale et al., 2015). Una mayor cobertura de arbolado y calles más anchas amortiguan los efectos de la LAN sobre los murcielagos pero apagarlas elimina su papel sobre los organismos (Hale et al., 2015; Straka et al., 2019)

Por otra parte, aunque la biomasa de insectos parece no cambiar con la LAN (Bolliger et al., 2020; Haddock et al., 2019), la LAN sí tiene un papel en polillas que son presas de los murciélagos, al decrecer la respuesta de evadir a murciélagos en algunas de sus presas (Minnaar et al., 2015).

La LAN puede afectar los ritmos circadianos de los vertebrados urbanos (Hoffmann et al., 2019). Por ejemplo, Dominoni et al. (2013) evaluó el papel de la LAN de la ciudad de Munich, Alemania, en el ritmo circadiano de las poblaciones de ambientes urbanos y no urbanos del ave *Turdus merula*. En su estudio reportaron que las poblaciones urbanas de *T. merula* se alteran con la LAN y sus poblaciones también cuentan con un ritmo de vida más rápido, relativo a las no urbanas. Asimismo, la luz suprime los niveles de melatonina y enmascara la señal de luz natural, que se vincula con un retraso en las señales reproductivas del mamífero *Macropus eugenii*.

Ruido

El ruido interfiere con la información vocal entre individuos y puede alterar el comportamiento de los vertebrados urbanos. Por ejemplo, el ruido del tráfico puede afectar las señales de apareamiento (Bee y Swanson, 2007). En el mismo sentido, en el ave urbana *Parus major* la intensidad del ruido de la se relaciona con una menor actividad, una menor puesta de huevos y una menor supervivencia de crías (Halfwerk et al., 2011; Dominoni et al., 2020).

En los ambientes urbanos el ruido y la luz pueden ocurrir al mismo tiempo. Dominoni et al., (2020), evaluó el papel del ruido sobre *P. major* en condiciones experimentales y reportó que la especie aumenta su actividad durante la noche durante la noche y se reducen en el día . El efecto conjunto de ambos factores fue mayor que la suma de sus partes.

Actividad humana

Los vertebrados ajustan su comportamiento ante la presencia de humanos a distintas escalas. La tolerancia al riesgo de los vertebrados a los humanos sugiere ser contexto dependiente (Stillfried et al., 2017; Tryjanowski et al., 2015). No obstante, en un experimento en condiciones de laboratorio realizado por Vincze et al. (2016) sobre la habituación a humanos de *Passer domesticus* reportaron que las poblaciones urbanas se habituaban más rápido que las poblaciones rurales.

La manera en que los vertebrados ajustan su comportamiento ante la convivencia con los humanos está asociada con sus rasgos funcionales. Por ejemplo, el tamaño corporal y los síndromes de comportamiento como mayor audacia y una menor aversión al riesgo parecen tener un papel importante en la capacidad de las especies en tolerar a los humanos (Lapiedra et al., 2017; Samia et al., 2015).

Compuestos contaminantes

La contaminación por diversos compuestos en cuerpos de agua urbanos es común (Bókony et al., 2018). Sievers et al., (2018) evaluó como contaminantes pueden repercutir en el ensamble de anfibios de la ciudad de Melbourne, Australia. Lo que reportó fue que los contaminantes repercuten en el número de crías y también a limita las respuestas de los anffibios a señales olfativas , aunque en otras especies urbanas no se ha encontrado que les repercuta (Bókony et al., 2018). No obstante, hay pocas evaluaciones sobre estas condiciones del hábitat urbano y su efecto en los vertebrados. No obstante, al ser un un hábitat de abundancia limitada es deseable evaluar los efectos de la calidad del agua en los vertebrados que las usan.

Interacciones

Las interacciones ecológicas que se establecen el el hábitat urbano son complejas y dinámicas. Para algunos vertebrados sus depredadores están ausentes (Riley et al., 2005 ; Baker y Harris., 2007) y para otros vertebrados hay nuevos depredadores, que en ocasiones suelen ser especies invasoras (van Heezik et al., 2010). Las lagartijas urbanas de Puerto Rico de la especie *Anolis cristatellus*, por ejemplo, a pesar de no contar con fisiología distinta a sus conespecíficos rurales, sí cuentan con más heridas (Winchell et al., 2016). Thorington y Bowman (2003) realizaron una evaluación de nidos artificiales de aves en la matriz urbana del sur de Florida. En su estudio reportaron que los principales depredadores eran en orden decreciente: otras aves y mamíferos, una dinámica que no cambió a la largo del gradiente urbano. Asimismo, una evaluación del éxito reproductivo de cuatro especies de aves en San Diego, EE.UU que usan dos tipos de sustratos de anidación, realizado por Patten y Bolger, 2003, encontró que tanto aves como serpientes depredaban en áreas periurbanas, y que estas últimas eran predictoras del éxito reproductivo de las especies con anidamiento en suelo. Estos autores también encontraron que en el centro urbano había pocas serpientes, por lo que la depredación por aves de las familias Corvidae o Mimidae era más alta. Un ejemplo de un depredador invasor común en lo urbano es el gato, que frecuenta jardines y depreda aves adultas, roedores y reptiles ; y su impacto sobre las poblaciones de aves es tal, que puede transformar el hábitat urbano de la ciudad de Dunedin, Nueva Zelanda, en un sumidero de poblaciones de aves (van Heezik et al., 2010). Por otra parte, la abundancia de depredadores invasorres limita los tamaños poblacionales En cuerpos de agua y en anfibios como el *Ambystoma mexicanum* o en *Pseudacris regilla* la abundancia de depredadores invasores los limita, a pesar de que el hábitat cuente con condiciones ambientales adecuadas (Riley et al., 2005; Zambrano et al., 2007; Selene Babini et al., 2015).

Otra interacción que se puede modificar en los ambientes urbanos es el parasitismo. Hegglin et al., (2007) evaluaron el cambio de dieta en individuos urbanos de *Vulpes vulpes* en Zúrich, Suiza, a recursos alóctonos. Lo que notaron fue que el cambio a ambientes urbanos limita la transmisión de *Echinococcus multilocularis*, por el cambio en las presas que consume. En otro realizado por McMahon et al., (2017) sobre el efecto de la luz y el ruido en la ciudad de Panamá, Panamá reportaron una asociación negativa y sinérgica con la presencia del parásito *Corethrella* spp y su prevalencia en su hospedero, la rana *Engystomops pustulosus*. El ruido interfiere la comunicación interespecífica del parásito y la luz le emite una señal de peligro engañosa.

Conclusiones

Los periodos temporales que dividieron los estudios y las clases de vertebrados muestran un progreso diferencial del tema . Antes de 2015 los estudios que abordan los patrones generales de ensambles en el hábitat urbano son frecuentes, principalmente en vertebrados voladores. Actualmente los estudios convergen en evaluar aspectos autoecológicos. Asimismo, la descripción y cuantificación de los componentes y tipos de hábitats urbanos ahora es más específica y se enfoca principalmente en parámetros como la luz, el ruido y la presencia humana.

La sinergia de la luz y el ruido tienen consecuencias considerables y sinérgicas. La evaluación del uso de hábitat también permite evaluar a los componentes del hábitat que promueven una mayor dispersión de la especie, así como sus recursos clave.

Existen oportunidades a nivel de especie al evaluar sus rasgos funcionales y sus poblaciones para reconocer factores clave que los afectan. Considero central entender el patrón de distribución y actividad. Asimismo, recomiendo evaluar si las especies son moduladas por interacciones bióticas o por las condiciones particulares que componen al hábitat urbano a través del uso específico que las especies o grupos funcionales hacen de los recursos bióticos y abióticos de interés en lo urbano. Por lo anterior, es importante evaluar con una aproximación experimental y con contrastes de hábitat los mecanismos y procesos que llevan a las especies y poblaciones a ocupar ambientes urbanos.

Finalmente, es necesario entender los distintos tipos de promotores sucesionales en los ecosistemas urbanos. La naturaleza de lo urbano permite realizar un manejo informado y requerimos aprovecharlo ahora que nos estamos desarrollando como una especie preponderantemente urbana.

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Capítulo II: Opportunities for migratory birds in a highly anthropized urban region of Western Mexico

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Abstract (250 max.)

Urbanization drives land use change, transforming ecosystems and social processes. However, urban environments can provide habitat opportunities for some species. In this study, we examined the opportunities urban areas offer to overwintering migratory birds in a highly anthropized Urban Region of Western Mexico known as “El Bajío.” In addition to urban areas, we also sampled this urban region's productive and wildland environments. We used Generalized Linear Models to compare species richness, abundance, and the functional space of the migratory bird assemblages among environments. Results revealed differences in species richness and composition and functional space occupied by migratory birds among environments. Despite wildlands showing medium to high levels of human disturbance, they presented the highest species richness and abundance of migratory birds, with the urban environment presenting the lowest values. Insectivorous and granivorous birds were dominant. Productive migratory bird assemblages had a higher number of grassland-associated granivorous birds. The urban bird assemblage was dominated by insectivorous birds with dense habitat preferences and short culmen lengths, and a few granivorous species. Productive and urban assemblages showed similar species richness and abundance of insectivorous birds, characterized by high vegetation stratum preferences. Our results reveal that urban environments function as simplified forests, with anthropized environments in this Urban Region having the untapped potential to support complex assemblages of migratory birds. To increase opportunities for migratory birds in human-modified environments, we emphasize the need to maintain areas of complex vegetation that allow the presence of birds with diverse functional traits.

Keywords: anthropized environments, bird assemblage, community ecology, functional traits, land use change, overwintering

Introduction

Historically, land-use change has been primarily driven by expanding human-productive systems over areas of native vegetation (i.e. wildlands from here on; Alexander et al., 2015; Bren d'Amour et al., 2017) . However, during the last century, urbanization has become one of the global leading land-use drivers (Simkin et al., 2022). Urban expansion typically transforms agricultural areas close to cities (Bren d'Amour et al., 2017). Nevertheless, wildlands can also be affected, resulting in regions covered by complex landscape mosaics that include urban, productive, and wild ecosystems (Forman, 2014; Khor et al., 2022; Simkin et al., 2022). Urban areas transform ecosystem processes over large spatial scales (Forman, 2014; Grimm et al., 2008a; Pickett et al., 2020), becoming crucial to understand the social, economic, and political drivers that affect regional ecosystem processes (Elmqvist et al., 2019; Pickett et al., 2020; Mansur et al., 2022).

Land-use change by urbanization is characterized by replacing non-human elements of the environment with built-in impermeable cover and infrastructure, creating a different ecological system (Grimm et al., 2008b; MacGregor-Fors et al., 2012). The urban ecosystem presents a high human population, and the buildings, infrastructure, and resources required to maintain it (Elmqvist et al., 2013; Forman, 2014). In addition to human-made structures, vegetation is a crucial element of urban ecosystems (Faggi & Caula, 2017). Urban vegetation tends to be composed of a limited number of fragmented remnants of native vegetation, enriched with de novo green areas where humans plant a diverse array of mainly exotic species (Faggi & Caula, 2017; Johnson et al., 2021; Threlfall et al., 2016) . The cultural tendency to maintain open grass lawns with low density and diversity of shrubs generates a simplified lower stratum in the urban vegetation (Croci et al., 2008; Pena et al., 2023). Additionally, trees tend to grow faster and larger inside cities (Pretzsch et al., 2017).

Other environmental characteristics particular to urban ecosystems include altered water regimes, with a year-round relatively secure availability of water, regardless of local seasonal changes in precipitation (Knapp et al., 2021); a surplus of food resources (Spotswood et al., 2021); higher temperatures given the urban heat island effect (Lahr et al., 2018); and the presence of constant human activity that is related to noise, light, and other forms of pollution (da Silva et al., 2020; Falcón et al., 2020). As a result, the replacement of productive and wild ecosystems by urban areas offers a novel array of ecological opportunities for the regional pool of species, including those using the area on a seasonal basis (Croci et al., 2008; Aronson et al., 2016; Evans et al., 2018). While we are beginning to understand how resident birds interact with cities, we lack information on urbanization's effects on migratory avifauna (Knapp et al., 2021).

The Nearctic-Neotropical migratory landbirds (hereafter referred to as migratory birds) are a polyphyletic group of species exclusive to the American continent (Hayes, 1995). Their annual cycle consists of a breeding stage in the Nearctic region during spring and summer, and a non-breeding overwintering stage in the Neotropical region from late autumn until early spring. Between those stages, they conduct southbound and northbound long-distance movements (La Sorte et al., 2017; Albert et al., 2020). The survival of migratory birds is notably dependent on the quality of their overwintering habitats, given that they spend most of their annual cycle in them (Rappole & McDonald, 1994; Sherry & Holmes, 1996; Albert et al., 2020). Most populations of migratory bird species have been declining, with the transformation of wildlands to agricultural areas and urban ecosystems in their overwintering region representing the main threat to their populations (La Sorte et al., 2017; Rosenberg et al., 2019; Albert et al., 2020).

Generally, urban bird assemblages comprise species with a large tolerance to human activity (Møller et al., 2015; Sol et al., 2018). Their responses to the urban environment vary according to each species' life history and functional traits (Croci et al., 2008; Sol et al., 2018; Neate-Clegg et al., 2023). Migratory birds using cities are mainly comprised of insectivorous warblers associated with urban green areas with ample tree coverage (Zuckerberg et al., 2016; Amaya-Espinel & Hostetler, 2019; Pacheco-Muñoz, Aguilar-Gómez, et al., 2022). While the number of migrant bird species is lower in cities than in wild overwintering habitats (MacGregor-Fors et al., 2010), urban environments can act as critical regional refuges for migratory birds. This is especially important when areas surrounding the urban site present a high level of degradation, harsh environmental conditions, or limited critical resources (Pacheco-Muñoz, Ceja-Madrigal, et al., 2022).

While patterns of migratory birds species richness and abundance have been studied in the past in wildlands and productive environments of Western Mexico (Hutto, 1980; Villaseñor Gómez & Hutto, 1995; Malpica et al., 2017), urban areas in this region have been poorly studied (but see MacGregor-Fors et al., 2010; Monroy-Ojeda et al., 2013; Pacheco-Muñoz et al., 2022). Due to the global role of urbanization as a driver of regional ecosiystem processes, this lack of information is problematic for an adequate management framework (Knapp et al., 2021; Oke et al., 2021; Spotswood et al., 2021). In this study, we assessed the role played by urban areas to maintain the regional pool of migratory birds in a highly anthropized urban region of Western Mexico known as "El Bajío." To do this, we contrasted migratory birds' taxonomic and functional diversity among the three main environmental conditions present in this region: urban, productive (agriculture), and wildlands (native vegetation; following MacGregor-Fors & Vázquez, 2020; Fig. 1). We classified the regional landscape used this approach because it allows us to separate environmental conditions by combining habitat structure and human activities (MacGregor-Fors & Vázquez, 2020). We expect that wildlands will act as the main reservoir for the regional pool of these birds, while urban environments will show migratory bird assemblages with lower species richness and abundance than the two non-urban environments (Blair, 1996; MacGregor-Fors et al., 2010; La Sorte et al., 2014). We also expect that migratory bird assemblages will show contrasting functional traits among environments, with a higher functional diversity in non-urban environments (Aronson et al., 2016; Evans et al., 2018; La Sorte et al., 2014).

Methods

Study area and sampling locations

We conducted our study in thirteen localities of the region known as "El Bajío". El Bajío is an urban region (*sensu* Forman, 2014), which, apart from presenting shared eco-physiographic characteristics (Calderon de Rzedowski, 1991), delimits a Mexican territory with a common socioeconomic history (Ramírez Velázquez & Tapia Blanco, 2000). It is located within the biocultural region of Western Mexico (*sensu* Schöndube 1969) in the Mexican states of Guanajuato and Michoacán and is considered the southern border of Chihuahua's Desert biogeographic province (Morrone, 2019; 101.4077–100.8015° W; 19.63878–20.73814° N; Fig. 1). It has been described as an area of valleys of silt accumulation created from diluvial runoffs of Pliocene and Quaternary volcanic activity (Sánchez Rodríguez, 2001), presenting an altitude range from 1721 to 2181 masl (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team, 2019). This urban region presents a dry-winter subtropical highland climate (Köppen climate type: Cwb). The average annual precipitation measures 723.7 ± 92.5 mm, while the mean annual temperature stands at 17.8 ± 1.1 °C (Fick & Hijmans, 2017). Annual temperatures vary from a maximum of 32.4 to a minimum of 2.8 °C (Fick & Hijmans, 2017).

El Bajío has been an important agricultural region for the last 3000 years. This process started after the introduction of maize to the region by the Chupicuaro culture (Schöndube, 1969; Cárdenas-García, 1999). Later in the 17th century, it was transformed under Spanish colonial rule by intense mining and cereal production (Sánchez Rodríguez, 2001). The quality of this region's soils generates high grain productivity, which earned this region the name of "Mexico's granary" since the colonial period (Sánchez Rodríguez, 2001). In the mid 20th century, government subsidies and programs incentivized agro-industrial farming, with maize and sorghum being the most common crops (Ramírez Velázquez & Tapia Blanco, 2000; Sánchez Rodríguez, 2001). In the 21st century, agro-industrial activities are still prevalent.

However, human activities have diversified, focusing on the commerce and manufacturing industry, with a dramatic increase in urban population and land covered by urban environments (Tagle-Zamora et al., 2016; Fig. 1). This urban growth has occurred mainly in productive areas. Nowadays and during the second decade of this century, *El Bajío* urban region substantially contributed to the economic and urban growth in the central region of Mexico (Tagle Zamora et al., 2016).

Wildlands in our studied urban region are scattered patches of subtropical xerophytic scrubland, pine-oak forests, and transition stages among these vegetation types (Cram et al., 2010; Sánchez-Blanco & Guevara-Féfer, 2013), covering 35.4% of the territory of our study area (Zanaga et al., 2022). Wildlands patches have the most complex vegetation structure in the region, mainly occurring in steep slopes and ravines, where agricultural activities are limited by topography and water availability (Hernández-Oria, 2007; Cram et al., 2010;). The most common native species of trees and shrubs include: *Bursera fagaroides*, *Casimiroa edulis*, *Celtis pallida, Ehretia latifolia, Fraxinus uhdei, Ipomea murucoides, Opuntia* spp*., Pinus* spp*., Prosopis laevigata, Quercus* spp*., Salix humboldtiana, Stenocereus queretaroensis, Vachellia farnesiana*, *Vackellia pannatula*, *Yucca filifera* (Cram et al., 2010) . Human pressure on this environmental condition includes illegal logging; wood gathering for fuel; free-ranging livestock (goats and cows); human-generated fires; the introduction of exotic plant species (*Casuarina equisetifolia*, *Eucalyptus* spp., *Morus alba*, and *Schinus molle*; and land-use change into agricultural and urban conditions (Hernández-Oria, 2007; López-Miguel & Ávila-Flores, 2010). Most wildlands remnants do not have a protection status, with only a few protected areas existing in the region (i.e., cerro del Punguato, cerro de Arandas, Siete Luminarias; CONABIO, 2020).

The productive environment comprises agricultural activities (crops, greenhouses, plantations, and livestock (Cram et al., 2010; Tagle-Zamora et al., 2016), covering 49% of the territory (Zanaga et al., 2022). Most cultivars are produced using irrigation (open channels with flooding or aspersion systems), with seasonal crops being produced on slopes during the rainy season (Cram Heydrich et al., 2010). Traditional crops include alfalfa, berries, corn, legumes, sorghum, wheat, and vegetables like asparagus, broccoli, cauliflower, and tomatoes (Sánchez-Rodríguez, 2001; Tagle-Zamora et al., 2016). However, in the last decade, several of these cultivars have been replaced with blue agave (*Agave tequilana*) plantations to produce tequila and mezcal. Crop fields tend to be divided by living fences of both native and exotic tree species (*Vachellia spp.*, *Eucalyptus spp.*, *Casuarina equisetifolia*, *Salix humboldtiana*, *Fraxinus uhdei*, *Celtis pallida*, *Morus alba*, and *Schinus molle*; personal observation R. P-M).

Finally, the urban environment is constituted by human settlements of different sizes (0.28—115 km^2) and human densities (1,067—9,687 hab/km^2; META, 2019) that cover 6.8% of our study area (Zanaga et al., 2022). The human settlements included in our study were: Colonia Guadalupe, San Pedro de los Sauces, José María Morelos, San Lucas Pío, Belisario Domínguez, Francisco Villa, Indaparapeo, Queréndaro, Zinapécuaro, Moroleon-Uriangato, Salamanca, Irapuato and Morelia (Fig. 1). The majority of these can be classified as residential towns with agricultural pursuits. However, the large urban centers (size ≥ 10 km^2; Salamanca, Moroleon-Uriangato, Irapuato, and Morelia) include important commercial and industrial activities (Ramírez-Velázquez & Tapia-Blanco, 2000; Tagle-Zamora et al., 2016). Residential areas display mostly one or two-story houses with little gardens or patios, while several-story buildings are rare and only present in large urban centers. Streets tend to be well illuminated, with exposed electric and communication infrastructure (poles and cables). This often limits the presence of trees and their size when they are planted on the streets (Dupras et al., 2016). Urban vegetation include both native (i.e. *Celtis pallida, Cupressus lusitanica, Fraxinus uhdei*, *Salix humboldtiana*, and *Taxodium mucronatum*) and exotic species (*Casuarina equisetifolia, Eriobotrya japonica*, *Eucalyptus* spp.*, Ficus benjamina, Grevillea robusta, Jacaranda mimosifolia, Ligustrum lucidum*, *Magnolia grandiflora*, *Schinus molle*). It is important to acknowledge that urban vegetated areas lack or present an oversimplified understory relative to wildlands (Pacheco-Muñoz et al., 2022).

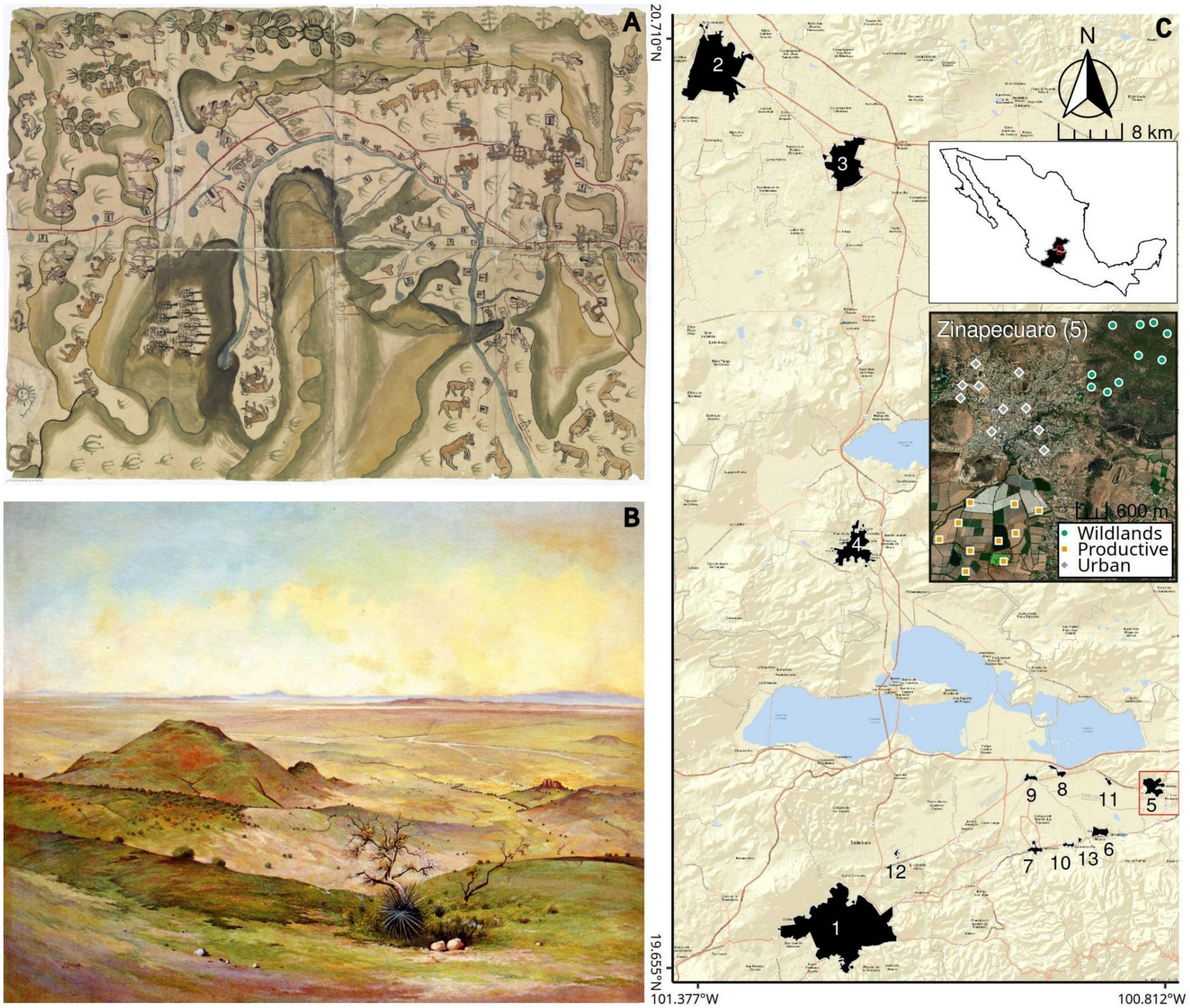

Figure 1. El Bajío is part of the biocultural region known as Western Mexico (Schöndube, 1969). *El Bajío* had continuous human occupation with agricultural activities for the last 3,000 years. Nowadays, it has become an urban region, highly modified by human activities. A) The cartographic codex "*Mapa de las villas de San Miguel y San Felipe de los Chichimecas y el pueblo de San Francisco Chamacuer*o" (1578–1580) shows the human-modified landscape and human settlements of an area of El Bajío in Guanajuato at the end of the XVI century. The codex depicts the native population (Chichimecas), fauna, vegetation (xerophytic shrubland, grasslands, and forests), and the introduction of cattle to the region, synthesizing information for a priority region for the Hispanic monarchy. B) Painting "*Paisajes del Bajío*" (1960) by the landscape artist Jesús Gallardo™ Carrillo (Courtesy by the owners of Jesús Gallardo™). The painting shows the long-term anthropogenic transformation that El Bajío region has undergone, with large open areas of lowlands used for agricultural purposes with few remnant areas of native vegetation, generally contained at hills. C) Map of our studied localities in El Bajío urban region. We sampled thirteen human settlements: Morelia (1), Irapuato (2), Salamanca (3), Moroleon-Uriangato (4), Zinapécuaro (5),

Queréndaro (6), Indaparapeo (7), Francisco Villa (8), Belisario Domínguez (9), San Lucas Pío (10), José María Morelos (11), San Pedro de los Sauces (12) and Colonia Guadalupe (13). The inserted satellite image shows the location of sampling points for Zinapécuaro to exemplify their general arrangement in the three environments for each location. In addition to each surveyed human settlement (gray), we surveyed the wildlands (green) and productive (orange) environments that surrounded them.

Bird surveys

We surveyed migratory birds in thirteen localities of El Bajío. Each sampling locality included a human settlement and its adjacent productive, and wildland environments (*sensu* MacGregor-Fors & Vázquez, 2020); see our survey example in Fig. 1). To determine bird species richness and abundances, we conducted 10 min long point counts with distance estimations (Bibby, 2000). All birds detected during the surveys were included in our species richness analyses. Only birds detected within a 40 m radius of the observer were included in our relative abundance analyses. This distance was selected based on the area that included ≥75% of all detections (37.5 m radius). We sampled during the winter months after migratory birds had established their overwintering territories in this urban region (November 2018 to February 2019).

To conduct bird surveys we delimited the areas occupied by each environment on the landscape using a geographical information system (QGIS Development Team, 2021). We randomly deployed up to 10 points inside the delimited area of each environment, with the total number of point counts sampled being proportional to the available area. A minimum distance of 250 m separated point counts. We sampled more point counts in urban settlements larger than 10 km^2 (20 in Salamanca, Moroleon-Uriangato, and Irapuato, and 30 in Morelia). Point counts were located at a minimum distance of 500 m in these human settlements. All points deployed within inaccessible zones were relocated to the closest accessible public area. The total point counts deployed were 106 in wildlands, 130 in productive, and 175 in the urban environment. The same observer performed all the bird surveys (A. C.-M.).

Bird characteristics

All bird species recorded were assigned residence status and functional characteristics. We classified residence status following Berlanga et al. (2008). Additionally, bird species that presented both migratory and resident populations (i.e., *Poleoptila caerulea, Troglodites aedon*) were considered migratory if they were absent during summer or their abundance doubled during the winter (R.P-M. and J.E.S. unpublished data). We did not include waterfowl and raptors in our analyses.

The functional traits of each species were assigned using categorical and continuous variables. Categorical variables included: 1) their primary trophic guild (Carnivore, Frugivore, Granivore, Insectivore, Nectarivore, Omnivore, and Scavenger (González-Salazar et al., 2014), 2) their primary foraging behavior (hawking, excavating, gleaning, and hovering; González-Salazar et al., 2014), and 3) their preferred habitat density (open, semi-open and dense habitats (Tobias et al., 2022). Continuous variables included: culmen (mm), beak width (mm), beak depth (mm), tarsus length (mm), tail length (mm), hand-wing index, and body mass (g). These variables were collected from the AVONET database (Tobias et al., 2022). We also included foraging strata mainly used as a continuous variable in our analyses (1 - ground, 2 - understory, 3 - mid-high, 4 -canopy, and 5-aerial). We determined each species' Principal Foraging Stratum by utilizing the percentages of use for each stratum category in the Elton traits database (Wilman et al., 2014). The value for each species was equal to the strata at which it accumulated more than 50% of its time, going from the lowest to the highest stratum.

Data processing and analysis

We contrasted the migratory bird assemblages among the three sampled environments of El Bajío urban region. We compared assemblages' species richness, abundance, structure, composition, and functional traits. We calculated migrant bird species richness by interpolating point-count incidence-based rarefactions to 106 points. This number represents the minimum point-count effort for one of our sampled environments (wildlands; Chao et al., 2014). We conducted this analysis using iNext package in R (Hsieh et al., 2016). Estimated species richness values were calculated with asymmetric confidence intervals of 84%. These confidence intervals allowed us to determine non-overlapping comparisons with a $p(\alpha) \leq 0.05$ (MacGregor-Fors & Payton, 2013). We contrasted migrant bird abundance among habitat types using a negative-binomial generalized linear model. This family model was chosen over a Poisson one due to the overdispersion found in the latter. We performed pairwise Tukey tests for each model through the "emmeans" R package (Lenth, 2022).

We also conducted analyses by trophic guild. We focused on the two dominant trophic guilds of migratory birds in our study urban region: insectivores and granivores (see below in the results section). Our trophic guild analyses included 1) a comparison of bird species richness, relative abundance, and functional diversity for each trophic guild in the three environments; and 2) a comparison of species richness and abundances between the two tropic guilds in the three environments. These comparisons were conducted similarly to those mentioned above for all migratory birds.

We evaluated the structure and composition of migratory bird assemblages by calculating the effort-based relative abundance of each species in each environment. We standardized all species' relative abundances to individuals per point count to achieve this. We used these abundance values to generate rank-abundance plots following Whittaker (1965). Briefly, a rank-abundance plot displays the assemblage evenness by ordering the species on the horizontal axis by their relative abundances from highest to lowest and displaying their relative abundances on the vertical axis. We use rank-abundance plots to compare the assemblage's evenness among environments. To do this, we logarithmically scaled the relative abundances. We compared them using a linear model with the log transform relative abundances as the response variable and the environment and their species ranks as interacting factors.

We assessed the migrant bird assemblage composition by calculating the Bray-Curtis dissimilarity index considering all locations (Magurran & McGill, 2011). We subsequently processed them by using a non-metric multidimensional scaling (MDS) on "vegan" R package (Oksanen et al., 2020). Then, we compared the assemblages from the three environments with a Multivariate Analysis of Variance for Assemblage Composition (MANOVAC), known as Adonis test (Oksanen et al., 2020). We considered the environment as the only factor, and we performed a subsequent pairwise posthoc test (Oksanen et al., 2020). We also assessed each bird species association with the three environments by calculating phi coefficients with all recorded species (Tichy & Chytry, 2006). The phi coefficient ranges from -1 to 1, where 0 represents no species association with the environment type, a positive coefficient reflects a positive association, and a negative coefficient reflects a negative one (Tichy & Chytry, 2006). The obtained phi coefficient is independent of sample size and was calculated using "indicspecies" package in R (De Cáceres & Legendre, 2009).

We assessed differences in functional traits among our environments using multitrait Gower distance and community-weighted mean values (CWM). These variables were weighted by the species' relative abundances per location for each environment (de Bello et al., 2021; Carmona et al., 2021). We considered all functional traits. Given that the Gower distance can give disproportional weight to certain variables, we calculated it following de Bello et al., (2021) and their "gawdis" R function to ensure balanced weight variables. Afterward, we used the calculated Gower distance to obtain the FEve, FDiv, and FDis functional diversity indexes (Córdova-Tapia & Zambrano, 2015; de Bello et al., 2021; Carmona et al., 2021). We calculated CWM with “FD” package in R (Laliberté & Legendre, 2010). The CWM for categorical values calculates the proportion of individuals in each category. We calculated CWM traits in all locations considering all migratory birds, and also for selected continuous CWM traits only considering insectivorous birds. The functional diversity index values obtained from functional traits comprised of continuous values were compared using generalized linear models considering the environment as the only factor. Categorical functional traits were also contrasted with generalized linear models considering the environment and the categorical trait as two interacting factors. In both cases, we assessed the differences given by the model using a posthoc pairwise Tukey test by their estimated marginal means, performed with the “emmeans” package in R (Lenth, 2022). We assumed relevant contrasts at a $p(\alpha) = 0.05$.

Results

We found a total of 43 migratory bird species in our studied urban region. This species assemblage includes members of 13 families of birds located in the orders Passeriformes (12 families, 39 species) and Apodiformes (one family, four species). The most important migratory bird trophic guilds were insectivorous (26 species) and granivorous (9 species), followed by nectarivorous and omnivorous (4 species each).

The wildland environment had the highest estimated species richness of migratory birds (32, 29.8 –34.2, ĉ: 0.99, 84% CI; see Fig. 2). These values did not differ from the regional species richness (31.2, 29.8–32.7, ĉ: 0.96, 84% CI). Migratory bird species richness was lower in the productive environment (26.7, 24.5–29, ĉ: 0.97, 84% CI) than in the wildlands, with the urban environment presenting the lowest species richness of the three environments (18.6, 16–21.1, ĉ: 0.95, 84% CI). Migratory birds' relative abundance differed among environments. The highest relative abundance occurred in the wildland environment, followed by the productive and the urban one (Table 1; Fig. 2).

Migratory bird assemblage structures differed among environments (Table 2; Fig. 3). *Setophaga coronata* and *Polioptila caerulea* were among the five most dominant species in the three environments of the urban region (Fig. 3). Wildlands and urban environments shared most of their dominant species identities and ranks (4 out of five from higuer to lower dominance: *Setophaga coronata*, *Polioptila caerulea*, *Leiothlypis ruficapilla* and *Spizella passerina*). These four shared species represented 52.1% and 79.3% of the total bird individuals in the wildland and the urban environments respectively (Fig. 3). Despite this peculiar similarity between these environments, wildlands presented a less dominated assemblage than urban areas, due to the different number of rare species (26 vs. 17 species, respectively). The productive environment differed in the composition and rank order of its most abundant species from the other two environments, with its five most dominant species standing for 73.6% of the abundance (Fig. 3). Of those, the most dominant species was *Tachycineta bicolor*, followed by *Spizella passerina*, *S etophaga coronata*, *Polioptila caerulea*, and *Passerculus sandwichensis* (Fig. 3).

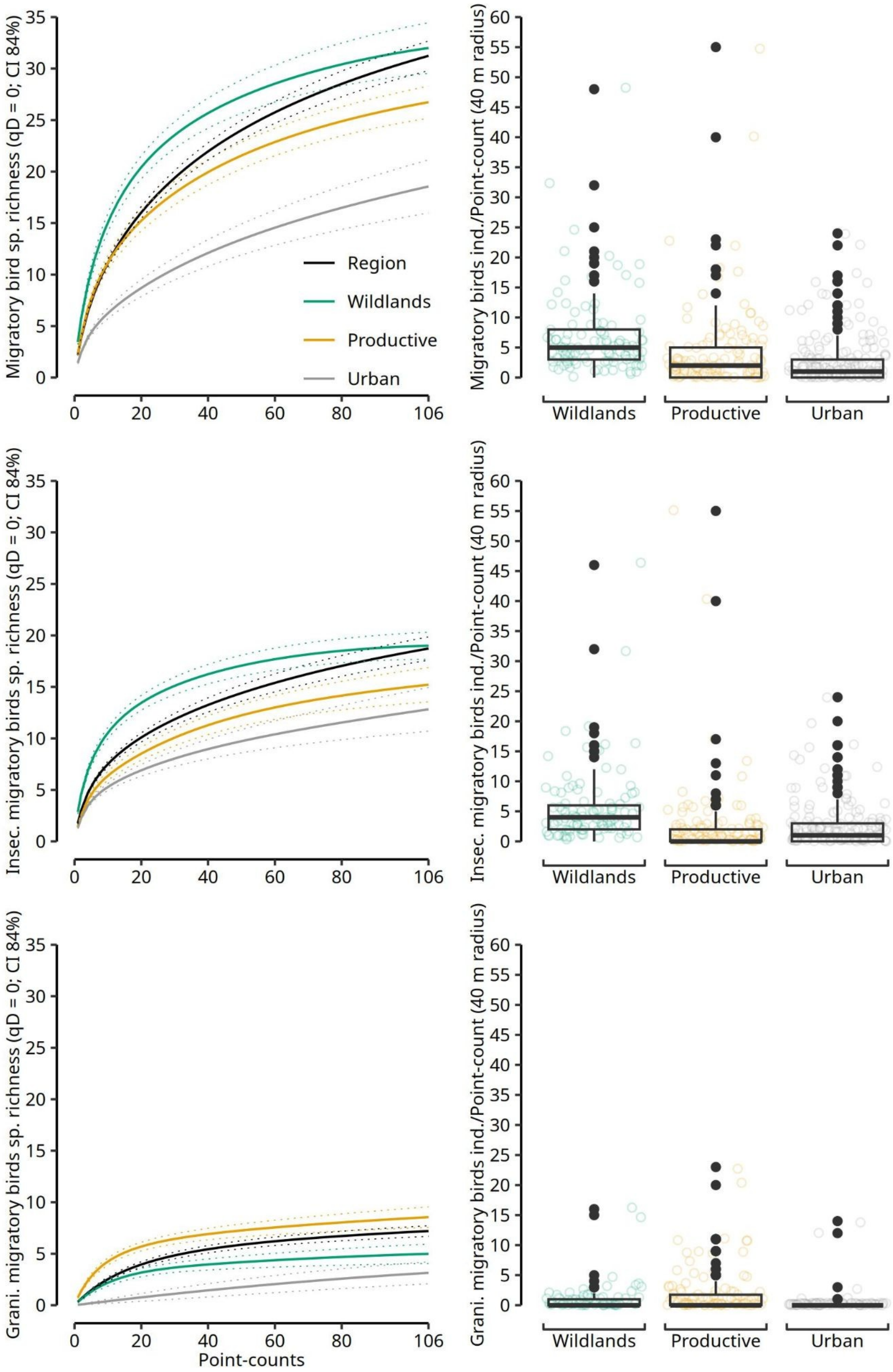

Figure 2. Migratory bird species richness and abundance in the three environments of *El Bajío* Urban Region. Left panels show incidence-based rarefaction estimated species richness with their 84% confidence intervals for the region (black), and the three environments: wildlands (green), productive (yellow), and urban (gray). The right panels show boxplots comparing the abundance of migratory birds (ind./point count) among the three environments. Jittered points represent the abundance recorded at each point count. The top row of figures includes all migratory bird species, the central row presents only insectivorous bird data, and the bottom row shows data on granivorous migratory birds only.

Table 1. Comparison of migratory bird relative abundance among the three environments: wildlands, productive, and urban. Data is presented for the whole migratory bird assemblage, and for insectivorous and granivorous birds separately. The values are a Posthoc Pairwise Tukey test for each assessed set of relative abundances with a negative-binomial generalized linear model: all migratory birds, insectivorous and granivorous migratory birds. An extended summary of the models is provided in Supplementary Materials 1.1. [$p < 0.05$; *, $p < 0.01$; **, $p < 0.001$ as "***"].

Response	Pairs	ratio (CI 95%)	SE	z ratio	*p* value
Mean individuals/point-count (40 m. radius-10 min.)	Wildlands / (Productive)	1.68 (1.15–2.45)	0.27	3.20	<0.01 **
	Wildlands / Urban	2.5 (1.74–3.58)	0.38	5.94	<0.001 ***
	Productive / Urban	1.49 (1.05–2.11)	0.22	2.69	<0.05 *
Mean insectivorous ind./point-count (40 m. radius-10 min.)	Wildlands / Productive	2.46 (0.44–1.61)	0.44	5.00	<0.001 **
	Wildlands / Urban	2.25 (1.52–3.33)	0.38	4.83	<0.001 ***
	Productive / Urban	0.91 (0.62–1.34)	0.15	-0.55	0.848
Mean granivorous ind./point-count (40 m. radius-10 min.)	Wildlands / Productive	0.45 (0.19–1.02)	0.16	-2.28	0.059
	Wildlands / Urban	4.31 (1.79–10.41)	1.62	3.89	<0.001 ***
	Productive / Urban	9.68 (4.27–21.97)	3.39	6.50	<0.001 ***

Table 2. Comparison of rank-abundance plots among environments to assess differences in the assemblages' evenness. The values shown were obtained by posthoc pairwise Tukey test on the linear model, with a log-transformed relative abundance. An extended summary of the model is provided in Supplementary Materials 1.2. [$p < 0.05$; *, $p < 0.01$; **, $p < 0.001$ as "***"].

Contrast	Estimate (CI 95 %)	SE	df	t ratio	*p* value
Wildlands-Productive	0.358 (0.245–0.47)	0.047	71	7.59	<0.001 ***
Wildlands-Urban	0.878 (0.76–0.996)	0.049	71	17.78	<0.001 ***
Productive-Urban	0.52 (0.397–0.644)	0.052	71	10.06	<0.001 ***

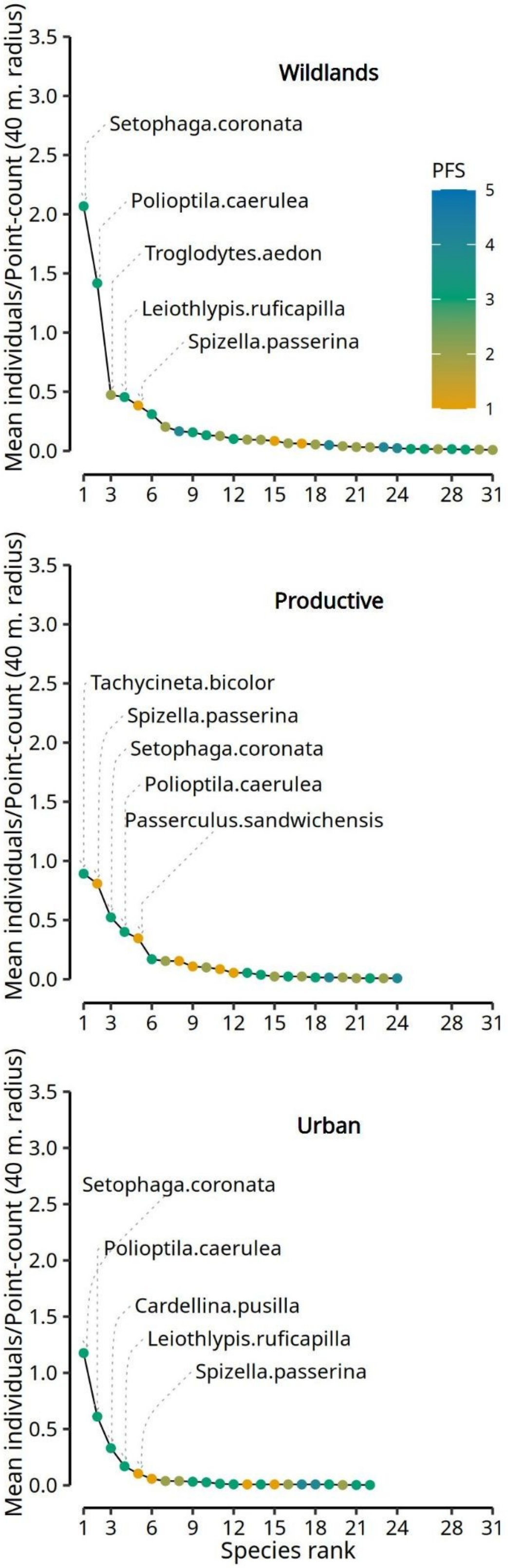

Figure 3. Rank-abundance plots of migratory bird assemblages in wildlands (green), productive (yellow), and urban environments (gray). Assemblage structure varied among environments, with the wildlands migratory bird assemblage being more diverse and even than those present in the other two

environments. Species rank values were given in ascending order using each species' mean abundance per point count (ind./40 m radius point count). Names of the five most dominant species are shown for each environment.

Migratory bird assemblage composition also differed among the three environments (Table 3; Fig. 4). The MDS and the adonis test showed the existence of three clusters. Each cluster was related to one environment, and while there is some overlap among the three clusters, each assemblage is different (Table 3; Fig. 4). Wildlands have unique species that did not occur in the other two environments, such as two hummingbirds (*Archilochus alexandri* and *Calothorax lucifer*). However, this environment also shared some species with the productive and the urban environments. These species were related to the granivore and insectivore trophic guilds, respectively.

The phi coefficient analysis determined relevant associations of particular migratory bird species to our three environments (Table 4). Six species were associated with wildlands (*Geothlypis tolmiei*, *Leiothlypis celata*, *L. ruficapilla*, *Piranga ludoviciana*, *Polioptila caerulea*, and *Troglodytes aedon*). Three were associated with the productive environment (*Passerculus sandwichensis*, *Spizella pallida*, and *S. passerina*). Furthermore, one species was associated with both former environments (*Melospiza lincolnii*; Table 4). No species were associated with the urban environment.

Insectivorous and granivorous were the most diverse migratory bird trophic guilds. The estimated species richness of the insectivorous tropic guild reached its highest value in wildlands (19, 17.5–20.5, ĉ: 1, CI: 84 %; Fig. 2), being similar to the estimated species richness of this trophic guild in the regional pool (18.7, 17.6–19.9, ĉ: 0.97, CI: 84 %). The productive and urban environments had statistically similar migratory birds' insectivorous species richness (15.2, 13.1–17.4, ĉ: 0.98 and 12.8, 10.8–14.9, ĉ: 0.96, CI: 84 %, respectively; Fig. 2) and abundances (Fig. 2; Table 1).

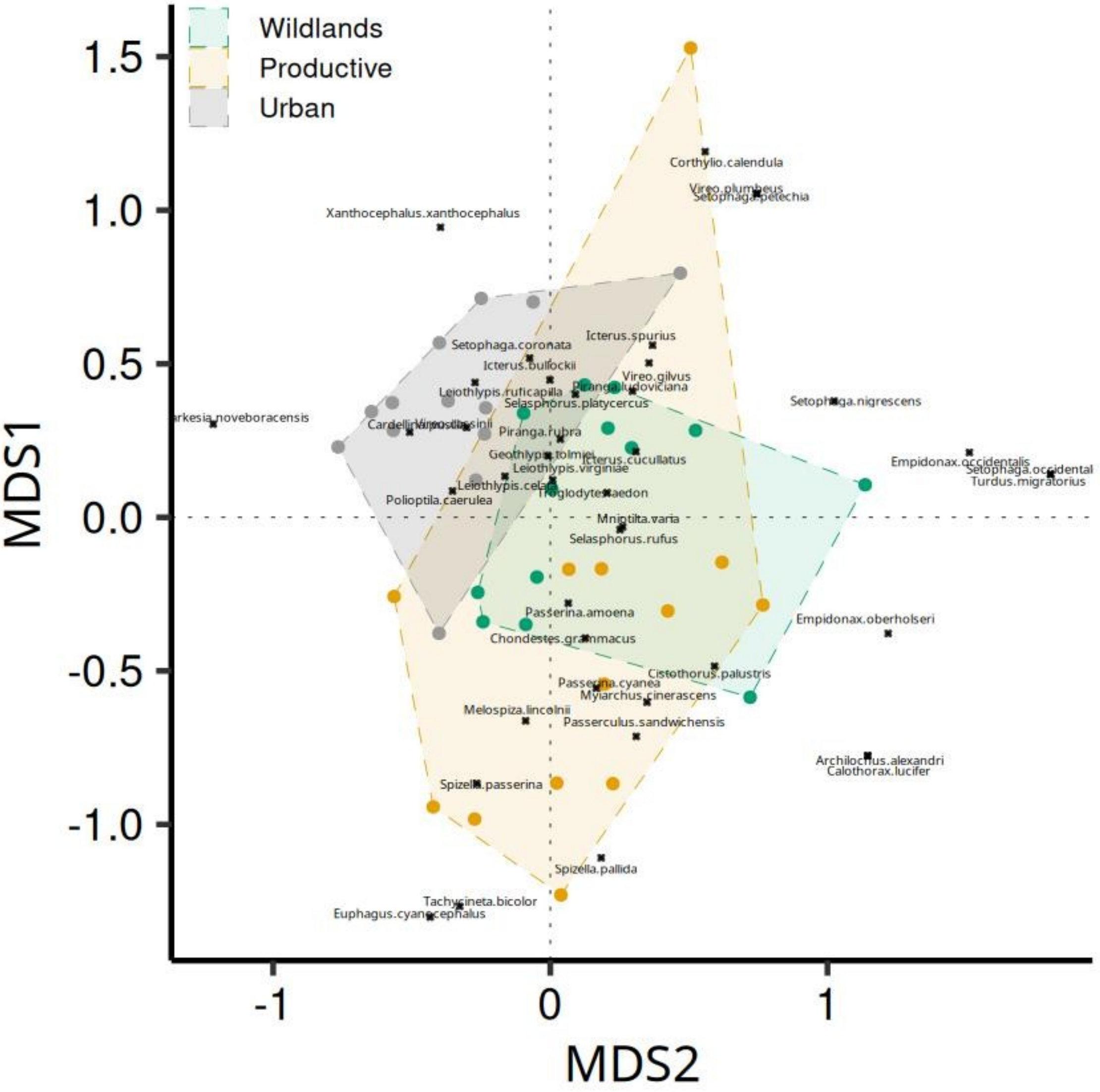

Figure 4. Multidimensional analysis of migratory bird assemblages composition in each environment (wildlands: green, productive: yellow, and urban: gray). Each point represents the assemblage found in one of our thirteen localities. Composition of migratory bird assemblages was assessed using the Bray-Curtis beta diversity index processed by an MDS analysis. Black squares represent migratory bird species. An Adonis analysis showed that assemblage composition differed among the three environments

Table 3. Comparison of the migratory bird assemblage composition in all our locations of the three studied environments. We show the values of the adonis pairwise posthoc test, over the processed Bray-Curtis index by the MDS. [$p < 0.05$; *, $p < 0.01$; **, $p < 0.001$ as "***"].

Pairs	SumsOfSqs	F value	*p* value
Wildlands / Productive	1.146	5.066	<0.01 **
Wildlands / Urban	1.125	6.414	<0.01 **
Productive / Urban	1.005	5.262	<0.01 **

Table 4. Phi coefficient relevant associations of migratory bird species to our three studied environments. There were no relevant associations of species to urban environments. [$p < 0.05$; *, $p < 0.01$; **, $p < 0.001$ as "***"].

OWMB species	Wildlands	Productive	Urban	stat	p.value
Geothlypis tolmiei	X			0.535	<0.05 *
Leiothlypis celata	X			0.411	<0.05 *
Leiothlypis ruficapilla	X			0.466	<0.05 *
Piranga ludoviciana	X			0.503	<0.05 *
Polioptila caerulea	X			0.715	<0.05 *
Troglodytes aedon	X			0.717	<0.05 *
Melospiza lincolnii	X	X		0.409	<0.05 *
Passerculus sandwichensis		X		0.57	<0.05 *
Spizella pallida		X		0.404	<0.05 *
Spizella passerina		X		0.409	<0.05 *

In the case of the granivorous trophic guild, its estimated species richness reached its highest value in the productive environment (8.6; 7.4–9.7; ĉ: 0.98; CI: 84%), being similar to the estimated species richness value for the regional pool for this trophic guild (7.2; 6.6–7.8; ĉ: 0.95; CI: 84 %; Fig. 2). The estimated granivorous species richness was similar between the wildlands and urban environments (5; 3.9–6.1; ĉ: 0.97 and 3.1; 2.1–4.2; ĉ: 0.52; CI: 84 %; Fig. 2). Migratory granivorous species abundance reached its highest in both wildlands and productive environments and its lowest value in the urban one (Fig. 2; Table 1).

The Gower distance-based values on migratory bird functional traits did not show differences among environments in FDiv and FEve, but they did in FDis (Table 5; Fig. 5). The difference in FDis was due to a higher value of trait dispersion in wildlands, relative to the urban environment (Table 5). The proportion of insectivorous individuals in the assemblage was higher in wildlands and urban environments, with the other trophic guilds occupying similarly low proportions of the assemblage (Fig. 6; Table 6). The productive environment had a similar proportion of insectivorous and granivorous bird individuals in its migratory bird assemblage (Fig. 6; Table 6). Gleaning was the dominant foraging behavior in all environments.

The proportion of individuals by their preferred habitat density (dense, semi-open, and open) showed differences among environments (Fig. 6; Table 6). In wildlands, the proportions of individuals with dense and semi-open habitat preferences were equal and higher than those with open habitat preferences (Table 6). In the productive environment, there were no differences in preferred habitat densities among bird individuals. However, this environment exhibited the highest values of individual proportions for preferences for semi-open and open habitats. In the urban environment, the three categories of preferred habitat densities had different proportions of individuals; the preference for dense habitat had the highest value, followed by the preference for semi-open and open habitats. Moreover, the proportion of individuals with dense habitat preference was highest in urban areas relative to the wildlands and productive environments. Preference for semi-open and open habitat densities were similar among environments (Fig. 6; Table 6).

The PFS index CWM was higher in wildland and urban environments, relative to the productive one (Table 5; Fig. 7). Culmen length was smaller in the urban environment relative to the wildlands (Table 5; Fig. 7). Beaks were wider in productive environments compared to the urban one. Beak depths were higher in productive environments (Table 5; Fig. 7). Among environments, migratory bird assemblages were similar in their body mass, tarsus length, hand wing index, and tail length (Table 5). The contrasts among environments only considering insectivorous migratory birds showed that the pattern of higher CWM PFS and shorter CWM beak lengths from culmen in urban environments, relative to wildland environments, persisted (Table 5; Fig. 7). Beak width values for insectivorous migratory birds were similar among environments (Table 5).

Table 5.1 Contrast among environments by their functional diversity multitrait Gower distance-related indexes and the Community Weighted Means (CWM) of continuous functional traits pairwise Posthoc Tukey tests. The tests were performed over their respective linear models. An extended summary of the model is provided in Supplementary Materials 1.3. [$p < 0.05$; *, $p < 0.01$; **, $p < 0.001$ as "***"].

Response	Contrast	Estimate (CI 95 %)	SE	df	t ratio	*p* value
FDiv	Wildlands-Productive	0.014 (-0.073–0.1)	0.035	35	0.385	0.922
	Wildlands-Urban	0.024 (-0.06–0.109)			0.7	0.765
	Productive-Urban	0.011 (-0.076–0.097)			0.301	0.951
FEve	Wildlands-Productive	-0.014 (-0.137–0.109)	0.05	35	-0.276	0.959
	Wildlands-Urban	-0.062 (-0.183–0.058)			-1.271	0.421
	Productive-Urban	-0.049 (-0.171–0.074)			-0.97	0.601
FDis	Wildlands-Productive	0.02 (-0.057–0.098)	0.032	36	0.641	0.799
	Wildlands-Urban	0.086 (0.009–0.164)			2.716	<0.05 *
	Productive-Urban	0.066 (-0.012–0.143)			2.075	0.109

Table 5.2. (Continues)

Response	Contrast	Estimate (CI 95 %)	SE	df	t ratio	p value
CWN-Primary Foraging Stratum (PFS)	Wildlands-Productive	0.545 (0.191–0.9)	0.145	36	3.757	<0.01 *
	Wildlands-Urban	-0.224 (-0.579–0.13)			-1.546	0.282
	Productive-Urban	-0.769 (-1.124–-0.415)			-5.303	<0.001 **
CWN-body mass (g)	Wildlands-Productive	-1.346 (-4.579–1.887)	1.323	36	-1.018	0.571
	Wildlands-Urban	1.237 (-1.996–4.469)			0.935	0.622
	Productive-Urban	2.583 (-0.65–5.815)			1.953	0.139
CWN-Beak length culmen (mm)	Wildlands-Productive	0.782 (-0.018–1.582)	0.327	36	2.388	0.057
	Wildlands-Urban	0.834 (0.034–1.635)			2.549	<0.05 *
	Productive-Urban	0.053 (-0.748–0.853)			0.161	0.986

Table 5.3. (Continues)

Response	Contrast	Estimate (CI 95 %)	SE	df	t ratio	p value
CWN-Beak width (mm)	Wildlands-Productive	-0.168 (-0.412–0.075)	0.099	36	-1.694	0.221
	Wildlands-Urban	0.206 (-0.037–0.449)			2.069	0.111
	Productive-Urban	0.374 (0.131–0.617)			3.763	<0.01 **
CWN-Beak depth (mm)	Wildlands-Productive	-0.448 (-0.866–-0.03)	0.171	36	-2.622	<0.05 *
	Wildlands-Urban	0.266 (-0.152–0.684)			1.556	0.277
	Productive-Urban	0.714 (0.296–1.132)			4.178	<0.01 **
CWN-Tarsus lenght (mm)	Wildlands-Productive	0.333 (-0.779–1.445)	0.455	36	0.732	0.746
	Wildlands-Urban	-0.224 (-1.336–0.888)			-0.492	0.875
	Productive-Urban	-0.557 (-1.669–0.555)			-1.224	0.447

Table 5.4. (Continues)

Response	Contrast	Estimate (CI 95 %)	SE	df	t ratio	p value
CWN-Hand wing index	Wildlands-Productive	-2.506 (-6.337–1.326)	1.568	36	-1.598	0.259
	Wildlands-Urban	0.389 (-3.443–4.22)			0.248	0.967
	Productive-Urban	2.894 (-0.938–6.726)			1.846	0.169
CWN-Tail lenght (mm)	Wildlands-Productive	-0.917 (-3.764–1.93)	1.165	36	-0.787	0.713
	Wildlands-Urban	-0.31 (-3.157–2.537)			-0.266	0.962
	Productive-Urban	0.607 (-2.239–3.454)			0.521	0.861
CWN-Insectivorous PFS	Wildlands-Productive	-0.043 (-0.151–0.064)	0.044	36	-0.988	0.589
	Wildlands-Urban	-0.112 (-0.22–-0.004)			-2.542	<0.05 *
	Productive-Urban	-0.068 (-0.176–0.039)			-1.554	0.279

Table 5.5. (Continues)

Response	Contrast	Estimate (CI 95 %)	SE	df	t ratio	p value
CWN-Insectivorous beak lenght culmen	Wildlands-Productive	0.669 (-0.01–1.349)	0.278	36	2.408	0.054
	Wildlands-Urban	0.715 (0.036–1.395)			2.574	<0.05 *
	Productive-Urban	0.046 (-0.633–0.725)			0.166	0.985
CWN-Insectivorous beak width culmen	Wildlands-Productive	0.117 (-0.094–0.329)	0.087	36	1.357	0.374
	Wildlands-Urban	0.186 (-0.026–0.398)			2.148	0.094
	Productive-Urban	0.068 (-0.143–0.28)			0.791	0.711

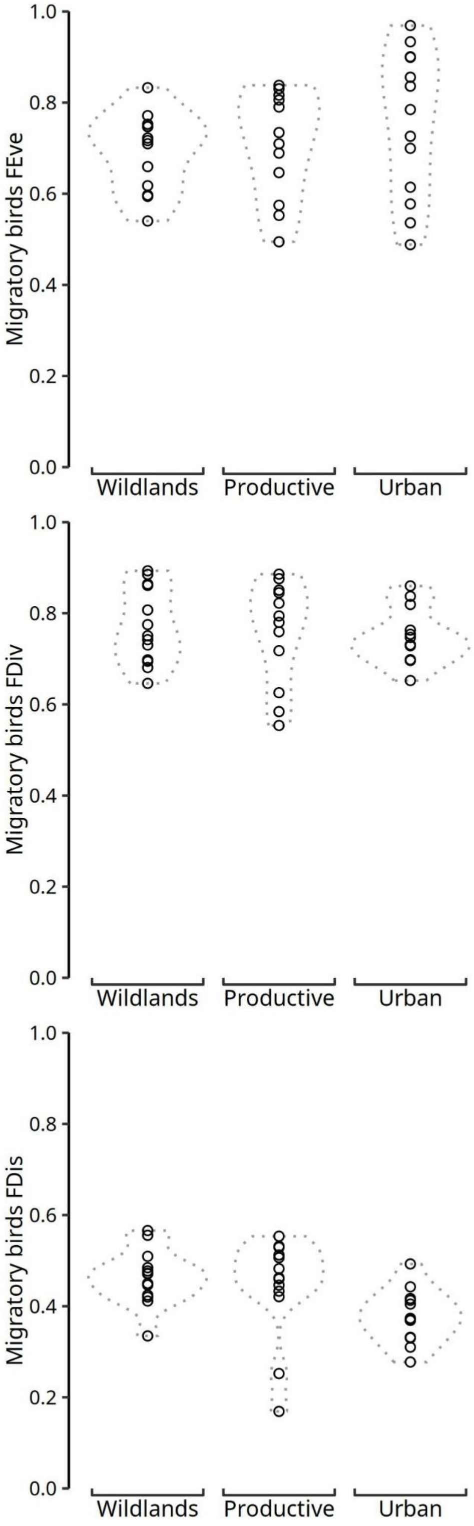

Figure 5. Migratory bird functional diversity indexes of all our locations contrasted among our three studied environments. The indexes FEve (top), FDiv (mid), and FDis (bottom) were calculated from categorical and continuous traits of each recorded species and processed by the Gower distance. We only found a difference in FDis values between wildlands and urban environments.

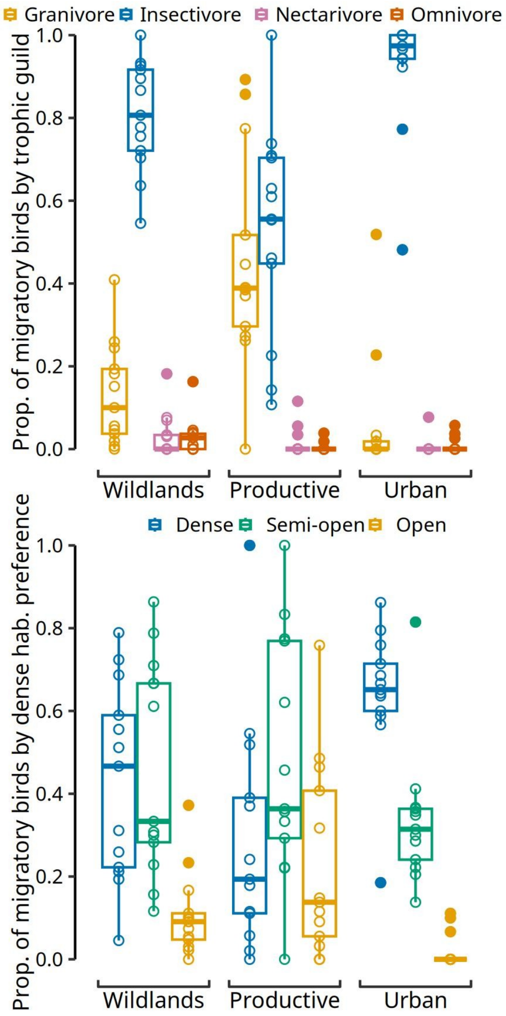

Figure 6. Proportions of individuals in each trophic guild (top) and foraging behavior categories (bottom) in the three environments of *El Bajío* Urban Region. Both trophic guild and foraging behavior were relevant categorical migratory bird functional traits. The insectivorous trophic guild was the one that presented a higher proportion of individuals, especially in the urban environment. In productive environments, granivorous and insectivorous birds had similar proportions of individuals. The proportion of individuals whose species associates with dense habitats was higher in the urban environment, while those species preferring open habitats showed a lower proportion of individuals in this environment and in wildlands. There were no differences among the proportion of individuals with preferences for different habitat densities in the productive environment.

Table 10.1. Assessment of trophic guild, Foraging behavior, and Habitat Density, functional categorical traits among environments. We show the estimated values of their linear models. [$p < 0.05$; *, $p < 0.01$; **, $p < 0.001$ as "***"].

Response	Term	Estimate	std.error	t value	*p* value
Trophic guild (proportion)	(Intercept)	0.131	0.037	3.544	<0.01 **
	Insectivorous	0.675	0.052	12.905	<0.001 ***
	Nectarivorous	-0.098	0.052	-1.881	0.062
	Omnivorous	-0.101	0.052	-1.937	0.055
	Productive	0.319	0.052	6.099	<0.001 ***
	Urban	-0.07	0.052	-1.333	0.185
	Insectivorous:Productive	-0.596	0.074	-8.052	<0.001 ***
	Nectarivorous:Productive	-0.336	0.074	-4.541	<0.001 ***
	Omnivorous:Productive	-0.345	0.074	-4.656	<0.001 ***
	Insectivorous:Urban	0.187	0.074	2.526	<0.01 **
	Nectarivorous:Urban	0.043	0.074	0.581	0.562
	Omnivorous:Urban	0.049	0.074	0.665	0.507
Foragin behaviour (proportion)	(Intercept)	0.028	0.029	0.96	0.339
	Gleaner	0.912	0.041	22.437	<0.001 ***
	Hovering	0.005	0.041	0.126	0.9
	Productive	0.051	0.041	1.26	0.21
	Urban	-0.028	0.041	-0.679	0.499
	Gleaner:Productive	-0.086	0.057	-1.488	0.14
	Hovering:Productive	-0.068	0.057	-1.186	0.238
	Gleaner:Urban	0.082	0.057	1.426	0.157
	Hovering:Urban	0.001	0.057	0.014	0.989

Table 10.2. (Continues)

Response	Term	Estimate	std.error	t value	p value
Habitat density (proportion)	(Intercept)	0.428	0.059	7.266	<0.001 ***
	Density Open	-0.32	0.083	-3.844	<0.001 ***
	Density Semi open	0.036	0.083	0.428	0.67
	Productive	-0.14	0.083	-1.684	0.095
	Urban	0.214	0.083	2.572	<0.05 *
	Density Open:Productive	0.264	0.118	2.242	<0.05 *
	Density Semi open:Productive	0.157	0.118	1.33	0.186
	Density Open:Urban	-0.301	0.118	-2.552	<0.05 *
	Density Semi open:Urban	-0.342	0.118	-2.903	<0.001 **

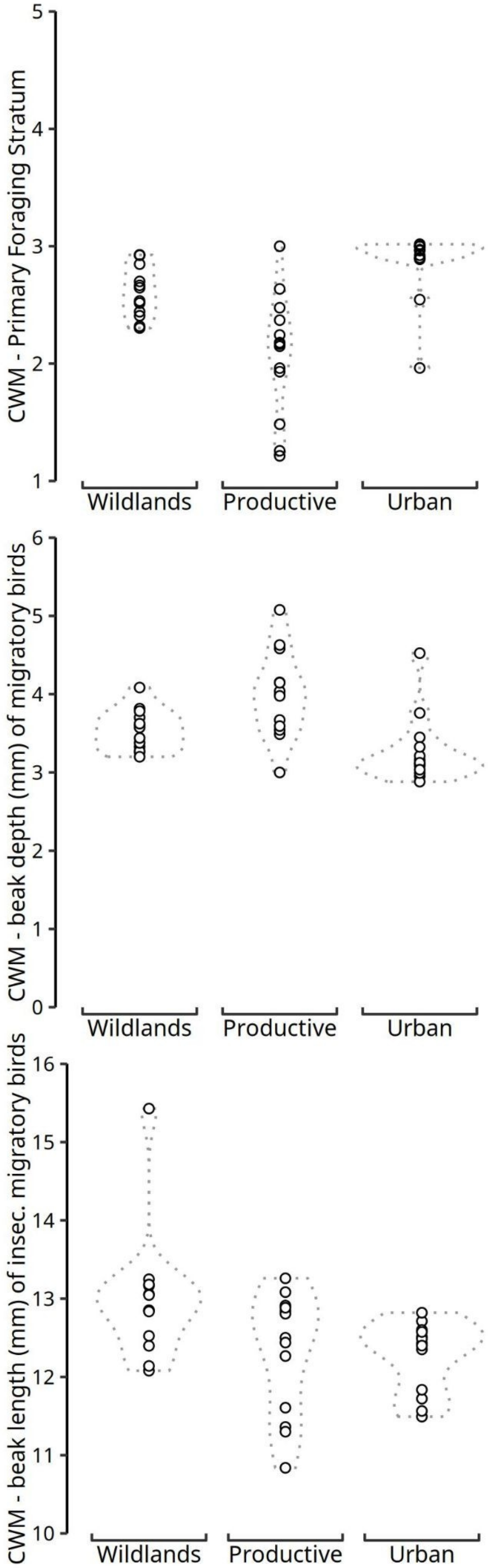

Figure 7. Community Weighted Mean (CWM) values of the Primary Foraging Stratum (PFS; top), beak depth (mm; mid), and beak length (mm; bottom) of insectivorous migratory birds in *El Bajío* Urban Region. PFS´values were higher in the wildland and urban areas than in productive environment. The bird

assemblages of productive environment had the highest beak depths. The beak length of insectivorous migratory birds was lower in urban environments relative to wildlands.

Discussion

Our study reveal that *El Bajío* supports a diverse assemblage of migratory birds during the winter months. This regional assemblage is dominated by a group of species that exhibit resilience to anthropogenic changes and are present across all three environments. Notably, there are significant differences in the species richness, abundance, and composition of migratory bird assemblages among the three environments. Wild areas host more complex migratory bird assemblages, whereas urban environments have the less complex ones. We propose that these differences in migratory bird assemblage characteristics result from a regional environmental filtering process. This filtering process is shaped by the functional traits of migratory bird species, the specific habitat characteristics of each environment, and resource constraints observed in both the productive and urban environments.

In this section, we first explore the impact that transforming wildlands into productive areas and later converting them into urban environments, has on migratory bird assemblages. When making these comparisons, we focused on species richness, abundance, and composition differences. Second, we examine the structure of migratory bird assemblages across the three types of environments, emphasizing the shared species. Third, we delve into the functional traits present in the assemblages of the three environments. Finally, we discuss the implications of our findings for conserving migratory birds in this critical overwintering region on the continent.

Changes in migratory bird ensembles associated with land-use change in El Bajío urban region.

The land use change experienced in this region for the last 3,000 years has transformed wildlands, generating a complex landscape that includes wildland remnants with intermediate to high levels of human disturbance inside a matrix of agricultural and urban areas. Although this region presents one of the lowest levels of ecosystem integrity in the country (CONABIO, 2019), the wildland habitat patches of El Bajío still contain a significant number of migratory bird species existing in other areas of Western Mexico with similar environmental characteristics (same altitudinal and latitudinal range; GBIF, 2022; see Supplementary materials). In this environment, we recorded a number of migratory bird species that did not differ from the calculated species richness for the regional pool. This indicates that despite its historical alteration by humans, the wildlands of El Bajo are still an essential habitat for overwintering migratory birds today (Hutto, 1980; Wilson et al., 2019).

El Bajío shows two different trajectories of land use change that have affected migratory bird assemblages. The first one is the transformation of wildlands into productive areas. This transformation started millennia ago with the arrival of agriculture (Schöndube Baumbach, 1969), and has undergone an important increment in recent centuries through the opening of extensive areas for intensive cultivation (Fig. 1; (Ramírez-Velázquez & Tapia-Blanco, 2000; Sánchez-Rodríguez, 2001). This first environmental change due to human activities generated essential changes in the communities of migratory birds, leading to a 40% species loss (13 species), with most of the missing species being those associated with semi-open and dense vegetation (Tobias et al., 2022). Yet, productive environments offered new habitat conditions that allowed the arrival of eight migratory species with open habitat preferences to this region (21.8% of the total observed in wild environments). These species could have invaded *El Bajío* from the grasslands of the Central Altiplano located north of it (≈100 km from our study area). The combination of species losses and turnover generated an assemblage that is 24% (0.22–0.26; CI 95 %) similar to the one present before this agricultural land-use change occurred.

The migratory bird assemblage of the productive environment also differed in its abundance in relation to wildlands, presenting 40% fewer individuals. This reduction in abundance was not associated with the loss of some species that accompanied the conversion of wildlands to productive environments. These species were already present in low abundances in wildlands, representing only 8.2% of the total migratory bird abundance in that environment. However, it was caused by a reduction in the number of individuals of two insectivorous species that were abundant in wildlands: *Setophaga coronata* and *Polyoptila caerulea* (51.7% to 22.9% of the total abundance in wildlands and productive environments, respectively; see Fig. 3). The abundance difference of these species suggests that crucial resources may limit their densities in the productive environment (Bock & Jones, 2004; Evans et al., 2018). Interestingly, while some open-habitat species were dominant in the productive environment, their numbers did not compensate for the abundance loss compared to wildlands. While the productive environments of *El Bajío* offer opportunities for the arrival of open habitat migrant birds, they harbor assemblages that present lower species richness and abundance values, limiting their conservation potential value in the region (Villaseñor-Gómez & Hutto, 1995).

The second trajectory of land use change in El Bajío is associated with urban growth replacing productive areas (Ramírez-Velázquez & Tapia Blanco, 2000; Mendoza-Ponce et al., 2019). This land-use transition modifies the assemblage of migratory birds by losing 42.3% of the species that use the open areas (11 species). These species represent 39.5% of the migratory bird abundance in the productive environments of the Urban Region, indicating that urban areas offer different habitat elements and food resources (Ortega-Álvarez & MacGregor-Fors, 2009; Evans et al., 2018). For example, migratory birds in urban environments are strongly associated with green infrastructure like large street trees, or parks where trees are essential habitat elements (MacGregor-Fors et al., 2010; Amaya-Espinel & Hostetler, 2019; Pacheco-Muñoz, Aguilar-Gómez, et al., 2022). The reduction in bird abundance caused by the urbanization of productive environments was mainly associated with the loss of two species of migratory birds from open areas that were exclusive to and abundant in productive environments. These two species were *Tachycineta bicolor* and *Passerculus sandwichensis*, which comprised 30.7% of the total abundance in productive environments. These results also suggest that the lower abundance of migratory birds in urban areas may be caused by limited food resources and reduced areas of quality habitat inside this environment (Blair, 1996; Ortega-Álvarez & MacGregor-Fors, 2009; Evans et al., 2018).

Urbanization processes have also occurred in areas that used to be covered by native vegetation (Mendoza-Ponce et al., 2019). While this land-use change occurs less frequently, in the last half century this process has generated housing suburbs of different socioeconomic levels around the largest cities in the region (e.g., Irapuato, Morelia, Moroleon-Uriangato, and Salamanca; Ramírez-Velázquez & Tapia-Blanco, 2000; Aguilar et al., 2022). This modification of wildlands due to urbanization represents a loss of 43% of the species of the migratory bird assembly. Their populations also declined, as wildlands had 250% more individuals. This species richness and abundance decline resembles the previously described by MacGregor-Fors et al., (2010) for de Morelia region.

Interestingly, the urban migratory bird assemblage recovered three of the 13 species present in wildlands that were absent in productive environments. This indicates that some migratory birds associated with wildlands can use urban environments (Amaya-Espinel & Hostetler, 2019). Zuckerberg et al., 2016) observed plasticity in the habitat choices of migratory birds while on migration or during the overwintering period, often favoring urban environments. Additionally, some migratory birds considered interior forest specialists overwinter in Neotropical cities (Amaya-Espinel & Hostetler, 2019). Our results, together with those from other studies, indicate that some green features of the urban environment, like large trees, can offer migratory birds some habitat opportunities present in wildlands.

Differences in assemblage structure among environments.

The differences in species richness, abundance, and composition that we have previously discussed generate different migratory bird assemblages in the three environments. The main differences among these migratory bird assemblages were associated with 1) changes in the abundances of common species shared among the three environments. And 2) the presence of some species that take advantage of the opportunities offered by productive and urban environments.

The set of migratory birds shared among the three environments consists of 15 species. This group constitutes 34% of the regional pool of migratory bird species; in wildlands, they constitute 47%; in productive environments, 57%; and in urban areas, 68%. Most of these species are small insectivorous birds, mainly warblers (e.g. *Setophaga coronata*, *Cardellina pusilla*, *Leiothlypis ruficapilla*, *L. celata*, *Mniotilta varia*, *Corthylio calendula*, *Polioptila caerulea*, *Troglodytes aedon*). These species have been stated to have a broad capacity to take advantage of a large diversity of habitats (Hutto, 1989; Greenberg, 1995; Villaseñor-Gómez & Hutto, 1995;). They have also commonly been mentioned as a familiar part of Neotropical urban bird assemblages (MacGregor-Fors et al., 2010; Amaya-Espinel & Hostetler, 2019; Pacheco-Muñoz, Aguilar-Gómez, et al., 2022).

The core group of migratory bird species shared among the three environments includes dominant species that represent 82% of the total regional abundance (Fig. 3). While the shared species include the most abundant species, it is essential to notice that they differed in their abundance among environments, defining the structure of the bird assemblages. Species abundance differences among habitats have been associated with a change in the abundance of food resources and quality of habitat patches in productive and urban environments (La Sorte et al., 2014; Amaya-Espinel & Hostetler, 2019). It has also been associated with a gradient of human activity (Sol et al., 2018). Sadly, our study did not evaluate the relative role that habitat elements and human activity played on the behavior of the migratory birds. We recommend future studies to evaluate the role that trees (species involved, their architecture, and food resources), crops (type and managing activities), and human activity (human presence, noise, mobility) play on the behavior and ecology of migratory birds in both productive and urban overwintering environments (Knapp et al., 2021; Smallwood & Wood, 2023).

Functional traits of migratory birds in El Bajío Urban Region

The regional migratory bird assemblage was primarily composed of insectivorous species, followed in importance by granivorous birds. This result is consistent with findings from other Neotropical overwintering regions (Hutto, 1980; Greenberg, 1995; Villaseñor-Gómez & Hutto, 1995). Migratory bird assemblages varied in specific functional traits in the region's three studied environments (Aronson et al., 2016). However, the core species shared among environments (see above) indicate critical common functional traits, suggesting that in today's landscape, any of the region's environments can maintain the most abundant functional traits of the regional pool of migratory birds.

These core species were characterized by being small body-size insectivorous birds that like to engage in gleaning foraging behavior, and show preferences for dense and semi-open habitats. These species have been reported as typical winter inhabitants of Neotropical wildlands (Hutto, 1980, 1986), urban areas (MacGregor-Fors et al., 2010; Charre et al., 2013; Pacheco-Muñoz et al., 2022), and productive environments (Villaseñor-Gómez & Hutto, 1995). Their presence and abundance in anthropogenic environments have been associated with a complex vegetation structure that includes dense trees, and an intricate lower stratum of bushes and herbs (Villaseñor-Gómez & Hutto, 1995; MacGregor-Fors et al., 2010; Pacheco-Muñoz et al., 2022). While this set of species has the potential to be perpetuate in anthropogenic environments (Wilson et al., 2019), it is crucial to understand their interactions with specific environmental elements, such as trees and shrub species, to maintain their populations in the future.

Other species in this core group included sparrows, cardinals, an icterid, and a hummingbird (see Supplementary Materials). This diverse collection of trophic groups of migratory birds in productive and urban environments highlights the broad spectrum of resources available to them in human-altered sites (Croci et al., 2008; Evans et al., 2018). This high trophic diversity could be related to the presence of flowers and fruits in urban sites and seeds in productive environments (Smith et al., 2005). Additionally, human-modified habitats present novel habitat features, like buildings, cables, poles, and other structures, that help support bird assemblages associated with structurally complex habitats (MacGregor-Fors & Schondube, 2011; Zúñiga-Vega et al., 2019). The presence of a surplus of water in human-altered environments during the cold-dry season of the year, when water is most limiting, could also promote the presence of a diverse array of trophic guilds in these environments (Barbosa et al., 2020; MacGregor-Fors et al., 2020).

The differences in migratory bird assemblages across environments, based on their functional traits, allow us to identify crucial environmental features that can act as opportunities or limitations for migratory birds. Wildlands presented abundant insectivorous birds, with our findings confirming the prevalence of this guild in wildland assemblages (Greenberg, 1995; Hutto, 1980; Villaseñor-Gómez & Hutto, 1995; Malpica et al., 2017). However, the ten migratory bird species we only recorded on wildlands were diverse in their diets (nectarivorous, insectivorous, and omnivorous) and presented semi-open and dense habitat preferences (Supplementary Material 2). Their presence indicates an affinity for a complex vegetation structure that includes mature trees and several layers of vegetation (herbs and shrubs) while simultaneously offering semi-open spaces combined with dense understory areas (Melo & Piratelli, 2023; Neate-Clegg et al., 2023).

The migratory bird assemblage of productive environments was functionally characterized by a balanced proportion of the abundance of insectivorous and granivorous birds, and balanced abundances by habitat preferences (dense, semi-open, and open habitats). However, the seven migratory birds exclusively recorded in productive environments had open and semi-open habitat preferences. Their functional traits underscore the importance of open spaces for aerial foraging in productive environments (i.e. *Tachycineta bicolor*) while also promoting birds that forage for seeds on the ground (i.e. *Passerculus sandwichensis*; Smith et al., 2005).

Our results indicate that the productive environment harbored the regional pool of migratory granivorous birds. Similarly, granivorous migratory birds have been described as abundant in intensively managed crops during their overwintering period in other regions of the continent (Smith et al., 2005). Associated with this, the migratory bird assemblage of productive environments had the highest beak depth and the lower primary foraging stratum of our studied Urban Region. These functional traits indicate the importance of crop-related food resources and habitat characteristics of productive environments for some migratory bird species (Smith et al., 2005, p. 200; Villaseñor-Gómez & Hutto, 1995). Moreover, our results indicate the importance of living fences in Western Mexico's productive environments, as they increase the vegetation complexity and offer opportunities for birds that do not feed on seeds or use the ground for foraging (Villaseñor-Gómez & Hutto, 1995).

We were surprised to find a lack of migratory granivorous species in the urban assemblage. This is remarkable if we consider that resident urban bird assemblages are typically dominated by granivorous species, suggesting the presence of abundant food resources for this trophic guild (Blair, 1996; MacGregor-Fors et al., 2012; Evans et al., 2018). We propose three non-mutually exclusive hypothesize to explain the absence of granivorous migratory birds in the urban environment of *El Bajío*: 1) competitive exclusion by abundant resident granivorous birds, which includes exotic species like the House sparrow (*Passer domesticus*) that tend to be aggressive towards smaller granivorous bird species (MacGregor-Fors et al., 2012; Mittelbach & Schemske, 2015; Supplementary Material 2); 2) the lack of understory vegetation in urban environments could limit grassland migratory granivorous species that tend to forage and hide from predators among dense herbs (Lakatos et al., 2022; Melo & Piratelli, 2023; Neate-Clegg et al., 2023); and 3) a possible lack of behavioral and physiological traits in migratory granivorous birds that allow them to abide the urban stressors generated by human activity (Sol et al., 2018; Zúñiga-Vega et al., 2019).

The lack of granivorous birds in the urban environment generates an assemblage dominated by insectivorous birds. Interestingly, the migratory insectivorous species using urban areas were characterized by presenting dense habitat preferences, higher Primary Foraging Stratum values, and smaller beak dimensions than those species using the other environments (Table 5; Fig. 6). As hypothesized by Greenberg's (1995) breeding currency hypothesis, the availability of small arthropods over the tree canopy and plant foliage could be enhanced in environments that presented depauperized bird assemblages, like urban areas (Stratford & Robinson, 2005; MacGregor-Fors et al., 2010; La Sorte et al., 2014). This could promote an abundance of insectivorous migratory birds with short culmens like the one we found. The three migratory birds exclusively recorded in urban environments had dense and semi-open habitat preferences and were associated to water related habitats (*Parkesia noveboracensis*, *Setophaga petechia* and *Vireo plumbeus*; Supplementary Material 2). This opportunity could arise by the urban year-round water surplus (MacGregor-Fors et al., 2020). The functional characteristics of the urban migratory bird assemblage of *El Bajío* suggests that urban areas can act as simplified forests with a high water surplus (Pacheco-Muñoz, Aguilar-Gómez, et al., 2022; Pacheco-Muñoz, Ceja-Madrigal, et al., 2022). Thus, our results indicate that offering water sources and increasing tree abundance and vegetation complexity is essential for enhancing migratory bird populations in urban environments.

Future opportunities for migratory birds in a Mexican Urban Region.

The high spatial dispersal ability of migratory birds makes them an ideal model for understanding how different factors mold their assemblages in the human-modified landscape of El Bajío Urban Region. Our results indicate species composition differences among environments, supporting the hypothesis that migratory species are filtered by their functional traits in anthropic environments (Croci et al., 2008; Aronson et al., 2016; Evans et al., 2018). Additionally, our results suggest that while some migratory species can use the three environments, their lower abundances in human-modified habitats are related to limited resource abundance in these environments (Rodenhouse et al., 2003; Bock & Jones, 2004; Ruiz-Sánchez et al., 2017; Planillo et al., 2021). The shared core of migratory bird species indicates that some habitat features, primarily tree density, and size, positively contribute to their presence and abundance in any environment. This shows a promising opportunity to manage this biological group in a highly modified Urban Region.

Sadly, human modification of the wildlands of El Bajío by agricultural activities like grain or legume production is not the worst scenario migratory birds face in West-central Mexico. In the last decade, traditional crops (alfalfa, beans, corn, oats, wheat, sorghum; Sánchez-Rodríguez, 2001; Cram et al., 2010) have been replaced by blue agave cultivars (*Agave tequilana*) used for the production of tequila (Romero Martínez, 2021; personal observations). Agave production is not only being conducted on flat areas that present irrigation, but also on the hillsides where the last remnants of wildlands are located (Romero Martínez, 2021). Agave cultivars have a low habitat complexity. This could generate additional negative impacts on the migratory bird populations of this region. As a result, we recommend conducting studies on the effects of the dramatic expansion of blue agave production in Mexico on migratory bird populations.

While conservation efforts for migratory birds in this region should focus on maintaining wildland patches (Hutto, 1986; Wilson et al., 2021), it is crucial to understand that both productive and urban environments offer opportunities to promote their conservation inside Urban Regions (Elmqvist et al., 2013; Schuster et al., 2019; Wilson et al., 2021). The accelerated rate of land-use change to agave cultivars experienced by this region (Romero-Martínez, 2021) suggests that urban areas can act as an essential habitat for migratory bird species as this productive system expands over the landscape. To achieve this, we need to manage cities so they can offer the best habitat available for migratory birds. The fact that several migratory birds can use urban areas for overwintering while maintaining good physical condition (Pacheco-Muñoz et al., 2022) indicates the need to integrate these birds into Neotropical urban planning. Our results indicate that increasing habitat quality for migratory birds in cities could become crucial for their conservation, considering the transformation suffered by wildlands and productive environments in the Anthropocene.

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Supplementary materials

Supplementary material 1.1. An extended summary of the models of Table 1. It shows the abundance estimates given the contrast among environments by the negative binomial generalized linear model.

Response	term	Estimate	Std. Error	z value	*p* value
Mean individuals/point-count (40 m. radius - 10 min.)	(Intercept)	1.91	0.12	16.16	<0.001 ***
	Productive	-0.52	0.16	-3.2	<0.01 **
	Urban	-0.92	0.15	-5.94	<0.001 ***
Mean insectivorous ind./point-count (40 m. radius - 10 min.)	(Intercept)	1.72	0.13	13.27	<0.001 ***
	Productive	-0.9	0.18	-5	<0.001 ***
	Urban	-0.81	0.17	-4.83	<0.001 ***
Mean granivorous ind./point-count (40 m. radius - 10 min.)	(Intercept)	-0.27	0.27	-1	0.318
	Productive	0.81	0.35	2.28	<0.05 ***
	Urban	-1.46	0.38	-3.89	<0.001 ***

Supplementary material 1.2. An extended summary of the models of Table 2. It shows the estimates calculated given the comparison of Rank-abundance plots among environments to assess differences in the assemblages' evenness. These estimates were calculated by using a linear model, with a log-transformed relative abundance.

Response	term	Estimate	Std. Error	t value	*p* value
Rank	(Intercept)	-0.069	0.062	-1.111	0.27
	rank	-0.066	0.003	-19.533	<0.001 ***
	Productive	0.006	0.095	0.066	0.947
	Urban	-0.302	0.097	-3.106	<0.01 **
	rank:Productive	-0.027	0.006	-4.424	<0.001 ***
	rank:Urban	-0.042	0.007	-6.379	<0.001 ***

Supplementary material 1.3.1 An extended summary of the models of Table 5. It shows the calculated estimates given the contrast among environments by their functional diversity multitrait Gower distance-related indexes and the Community Weighted Means (CWM) of continuous functional traits. These estimates were calculated by using linear models.

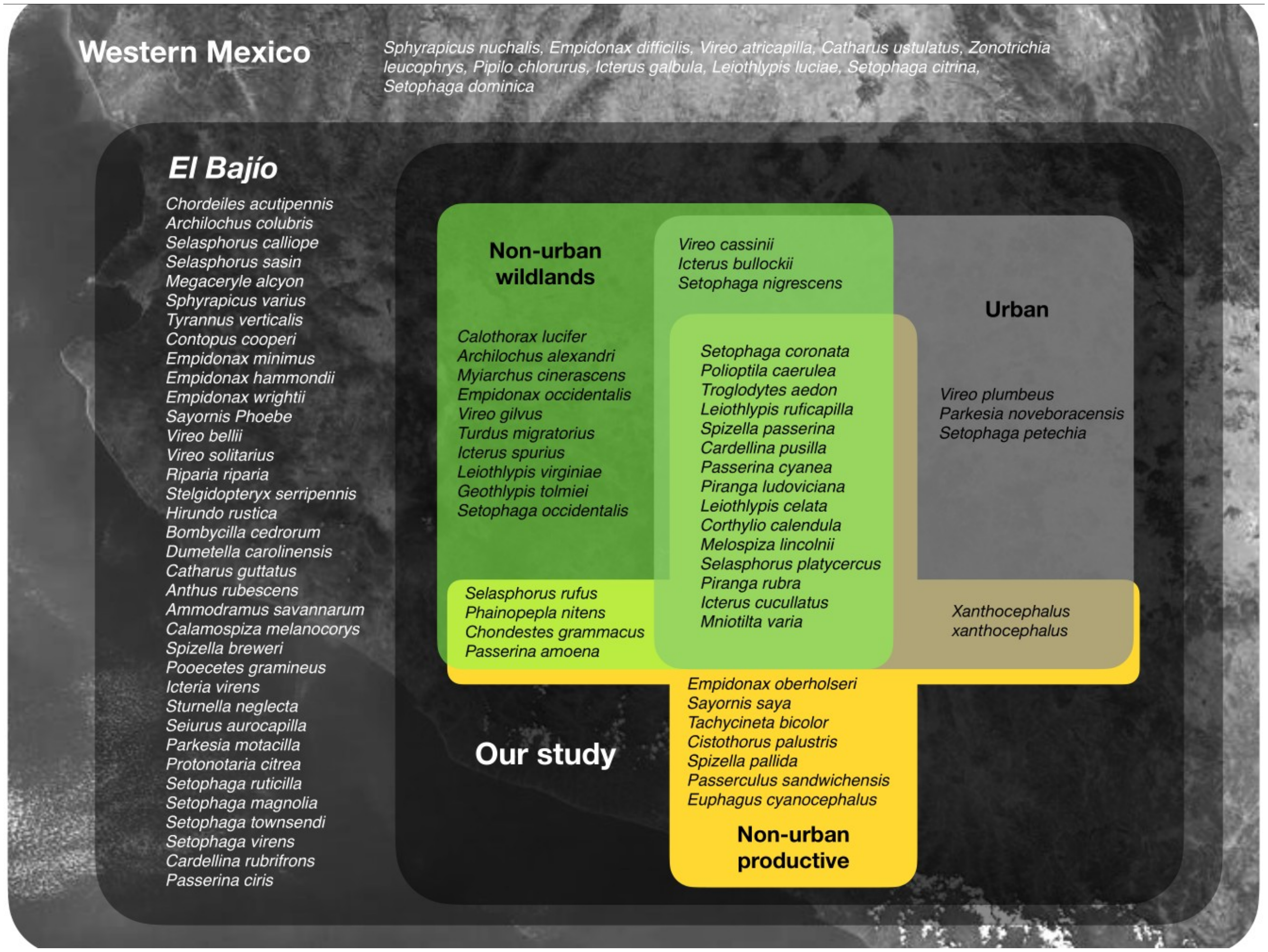
Response	Term	Estimate	Std. Error	t value	p value
FDiv	(Intercept)	0.771	0.024	31.613	<0.001 ***
	Productive	-0.014	0.035	-0.385	0.703
	Urban	-0.024	0.035	-0.7	0.489
FEve	(Intercept)	0.693	0.035	19.937	<0.001
	Productive	0.014	0.05	0.276	0.784
	Urban	0.062	0.049	1.271	0.212
FDis	(Intercept)	0.771	0.024	31.613	<0.001 ***
	Productive	-0.014	0.035	-0.385	0.703
	Urban	-0.024	0.035	-0.7	0.489
CWN - PFS	(Intercept)	2.627	0.103	25.609	<0.001 ***
	Productive	-0.545	0.145	-3.757	<0.01 **
	Urban	0.224	0.145	1.546	0.131
CWN - body mass (g)	(Intercept)	11.579	0.935	12.38	<0.001 ***
	Productive	1.346	1.323	1.018	0.316
	Urban	-1.237	1.323	-0.935	0.356
CWN - Beak length culmen (mm)	(Intercept)	13.469	0.231	58.185	<0.001 ***
	Productive	-0.782	0.327	-2.388	<0.05 *
	Urban	-0.834	0.327	-2.549	<0.05 *

Supplementary material 1.3.2 (Continues)

Response	Term	Estimate	Std. Error	t value	p value
CWN - Beak width (mm)	(Intercept)	3.432	0.07	48.812	<0.001 ***
	Productive	0.168	0.099	1.694	0.099
	Urban	-0.206	0.099	-2.069	0.046
CWN - Beak depth (mm)	(Intercept)	3.544	0.121	29.328	<0.001
	Productive	0.448	0.171	2.622	0.013
	Urban	-0.266	0.171	-1.556	0.128
CWN - Tarsus lenght (mm)	(Intercept)	17.574	0.322	54.621	<0.001
	Productive	-0.333	0.455	-0.732	0.469
	Urban	0.224	0.455	0.492	0.625
CWN - Hand wing index	(Intercept)	23.223	1.109	20.949	<0.001
	Productive	2.506	1.568	1.598	0.119
	Urban	-0.389	1.568	-0.248	0.806
CWN - Tail lenght (mm)	(Intercept)	52.134	0.824	63.304	<0.001
	Productive	0.917	1.165	0.787	0.436
	Urban	0.31	1.165	0.266	0.792

Supplementary material 1.3.3 (Continues)

Response	Term	Estimate	Std. Error	t value	p value
CWN - Insectivorous PFS	(Intercept)	2.866	0.031	92.044	<0.001
	Productive	0.043	0.044	0.988	0.33
	Urban	0.112	0.044	2.542	0.015
CWN - Insectivorous beak lenght culmen	(Intercept)	12.985	0.197	66.065	<0.001
	Productive	-0.669	0.278	-2.408	0.021
	Urban	-0.715	0.278	-2.574	0.014
CWN - Insectivorous beak width culmen	(Intercept)	3.295	0.061	53.818	<0.001
	Productive	-0.117	0.087	-1.357	0.183
	Urban	-0.186	0.087	-2.148	0.039



Suplemmentary material 2. A figure of that shows lists of recorded migratory species in Western Mexico. The species lists are shown grouped as Venn diagrams and each group shows a different spatial scales of their presence in Western Mexico, El Bajio and those recorded in our study. The migratory bird species shown for Western Mexico and El Bajio were obteined through citizen science records, given by GBIF (2022).

Capítulo III. Overwintering in a megacity: Urban green areas and migratory birds in Mexico City

ANEXO MANUSCRITO PUBLICADO:

Pacheco-Muñoz, R., Aguilar-Gómez, M. Á., y Schondube, J. E. (2022). Overwintering in a megacity: Urban green areas and migratory birds in Mexico City. *Urban Forestry y Urban Greening*, *73*, 127614.

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Overwintering in a megacity: Urban green areas and migratory birds in Mexico City

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ABSTRACT

Nearctic-Neotropical migratory birds are threatened by land-use change throughout their complex annual cycles. While urbanization is an essential driver of land-use change, it is unclear how it affects migrant birds. Although migratory birds are more diverse in non-urban patches of native vegetation than in urban areas, neotropical cities can host diverse assemblages of overwintering migrant birds. Migratory birds in neotropical cities tend to be closely associated with urban green areas (UGAs). However, how their presence and abundance are affected by the habitat elements of UGAs and the urban matrix of neotropical cities is poorly understood. In this study, we compared the migratory bird species richness and abundances among UGAs and the urban matrix of the southern section of the megacity of Mexico City and native vegetation sites outside the city. Our results show that UGAs in neotropical cities provide habitats capable of maintaining complex overwintering migratory bird assemblages with local trees as critical features. We also assess the role that UGAs' characteristics play in determining migrant bird assemblages. We conducted bird censuses and measured habitat traits to determine how migrant bird assemblages are related to the habitat features of our study sites. We measured local, buffer, and spatial habitat features of each UGA. We found 23 overwintering migrant species in the three habitats, with 22 present within UGAs. Both UGAs and urban matrix sites had higher estimated species richness of migrant birds than non-urban native vegetation sites located outside the city. Only local features of UGAs affected migrant birds. While tree abundance in UGAs was positively associated with migratory bird species richness, the proportion of tree coverage was positively related to bird abundance. Our results show that UGAs in neotropical cities can maintain complex overwintering migratory bird assemblages, with trees being the most critical habitat feature. As a result, UGA management focused on maintaining trees and increasing their numbers can improve habitat conditions for migratory birds overwintering in neotropical cities.

1. Introduction

Nearctic-Nneotropical migratory birds (hereafter called "migrant birds") are a polyphyletic group that is characterized by an annual life cycle that includes a long-distance latitudinal migration through the Northern hemisphere of America (Hayes, 1995; Winger et al., 2014). Their annual cycle broadly consists of four stages, in which they: 1) breed in spring and summer north of the tropics; 2) migrate south to the tropics during autumn; 3) establish tropical overwintering territories; and 4) migrate north to their breeding territories during late winter and spring (Bayly et al., 2018; Hayes, 1995; La Sorte et al., 2016). This migratory long-distance behavior follows changes in resource availability and climatic conditions that occur at a continental scale (Gómez et al., 2016; Somveille et al., 2015; Youngflesh et al., 2021).

Migrant birds have experienced a significant decline in their abundance during the last 50 years (Rosenberg et al., 2019). This negative abundance trend is associated with land-use changes driven by human activities in breeding and overwintering areas. Because these birds spend at least two-thirds of their annual cycle migrating or overwintering in the tropics (8–9 months of the year; Albert et al., 2020; La Sorte et al., 2016), the anthropogenic transformation of stopover and overwintering sites can dramatically affect their conservation (Albert et al., 2020; Donovan et al., 2002; Rosenberg et al., 2019).

Urbanization has been one of the main drivers of land-use change in

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the last century (Balvanera and Ptaff, 2019; Forman, 2014; Grimm et al., 2008), and so it has become critical to understand how it affects migrant birds along the different stages in their annual cycle. In general, migrant bird abundances are lower in urban areas than in non-urban habitats, within native vegetation both in their breeding (Stratford and Robinson, 2005) and in their nonbreeding areas (MacGregor-Fors et al., 2010). However, their degree of association with urbanized sites varies throughout the year (Zuckerberg et al., 2016). Migrant birds are less associated with urban areas during their breeding season, increasing their use of cities during migration (Zuckerberg et al., 2016).

During southbound migration to their overwintering territories, certain bird species are associated with urban and peri-urban habitats (Evans et al., 2018; Zuckerberg et al., 2016). While migrating, their presence in cities has been strongly related to sites that exhibit a large amount of tree cover (Wood and Esaian, 2020; Zuckerberg et al., 2016). Furthermore, stopover sites in these urban green spaces have been found to allow energetic refueling processes similar to those occurring in non-urban native habitats, which allows them to continue their migration (Seewagen et al., 2011, 2010).

Once migratory birds arrive at their overwintering grounds, only a minority use urban areas. Most migrant birds using urban sites are insectivorous and granivorous passerines (Amaya-Espinel and Hostetler, 2019). Like what happens during the southbound and northbound migrations, overwintering migrant birds tend to concentrate in urban locations with high tree cover (MacGregor-Fors et al., 2010; Carbó-Ramírez and Zuria, 2011; Amaya-Espinel and Hostetler, 2019). Although migrant birds primarily use urban green areas (UGAs) inside cities, they are also found in the urban matrix. However, their occupancy decreases in response to the density of human-made structures (Zúñiga-Vega et al., 2019). Furthermore, the use of UGAs and their urban surroundings by migratory birds seems to be independent of their spatial location context inside the urban matrix (La Sorte et al., 2020; MacGregor-Fors et al., 2010).

In this study, we evaluated the role of UGAs as a habitat for overwintering migrant bird assemblages relative to non-urban native vegetated areas and urban matrix sites. We also assessed the association between migrant species richness and abundances and the habitat characteristics of UGAs. Given that: 1) overwintering migrant birds rely on small arthropods in trees that may remain unexploited in their absence in tropical regions (Greenberg, 1995; Malpica et al., 2017), 2) small arthropods increase in abundance in wetter environments (Greenberg, 1995), 3) urban trees can host abundant insects, relative to non-urban trees, and the heat island effect can increase abundance (Dale and Frank, 2014), and 4) that UGA management can promote tall and well-watered trees and grasses that offer abundant and stable foraging opportunities for birds to feed on insects and seeds (Barbosa et al., 2020), we expect that mainly insectivores and a few granivore species will dominate the overwintering migrant bird assemblages in UGAs. Consequently, we also expected a strong positive association between migrant bird species richness and abundances and the local tree density and coverage inside UGAs and their surrounding urban matrix areas (MacGregor-Fors et al., 2010; Wood and Esaian, 2020). Finally, because migrant birds move at larger spatial scales than most resident species, we expect that the spatial arrangement of UGAs inside the city will not affect the migratory bird assemblage. Instead, local habitat characteristics will be critical in determining the migrant bird assemblage.

2. Methods

2.1. Study area and sampling sites

We conducted our study in Mexico City (19°25′10″N 99°08′44″O; Fig. 1). The city has an area of approximately 1485 km^2 and harbors one of the largest human populations in the world (~9.2 million inhabitants; INEGI, 2020). Due to its size and environmental heterogeneity, we focused our study only on a section of this megacity. The selected section

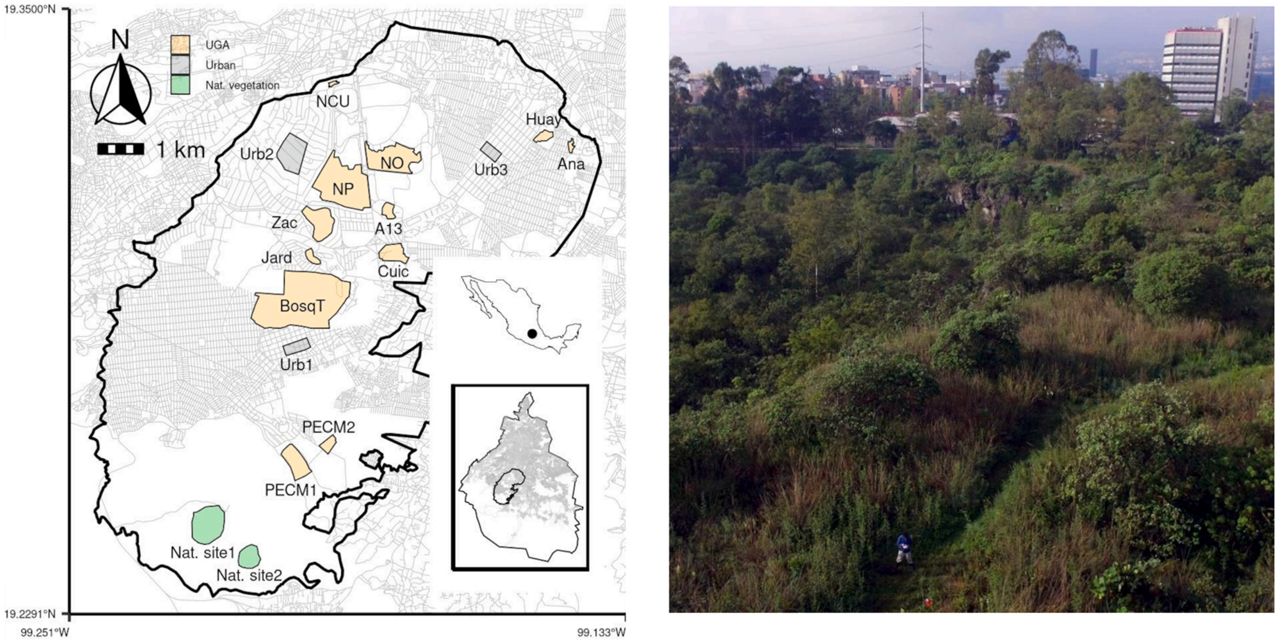


Fig. 1. (double). Location of Mexico City and its delimited territory of xerophytic shrubland vegetation known as the *Pedregal* (polygon defined with bold black line). Streets are highlighted to point out the urban matrix and its intensity. Our sampling sites are delimited by polygons and shown by name. Our sampling sites polygons are colored depicting habitat type: Urban Green Areas (UGAs) - yellow, Urban Infrastructure sites (Urb1, Urb2, Urb3) - gray, and Native Vegetation Sites (Nat. site1 and Nat. site2) - green. Complete names of UGAs are specified in the main text (see Methods section). The right panel shows an aerial picture of *Pedregal* habitat (UGA A13). This UGA is mostly covered by shrubs and grasses, but it also includes some trees. The first four trees at the front of the picture are *Buddleja cordata* and the tallest trees at the background and at the border of the area are *Eucalyptus sp.* The A13 UGA belongs to the Pedregal de San Ángel Ecological Reserve, administered by the National Autonomous University of Mexico. This UGA only has one unpaved trail, and only a few visitors. It is surrounded by university buildings. A person located at the central-bottom part of the picture provides scale (R. P-M).

was located in its southern region and exhibited UGAs with a unique native plant community of xerophytic shrubland known as "*Pedregal*" (Lot and Camarena, 2009; Fig. 1). This vegetation type grows on a volcanic rock formation that originated ~1700 years ago with the eruption of the Xitle volcano (Siebe, 2000). The altitude in this section of the city ranges from 2250 to 3000 m above sea level (Peralta and Prado, 2009). Climate is temperate sub-humid with summer rains (June-October), with an average annual precipitation of 833 mm, and a mean annual temperature of 15.6 °C (SEREPSA, 2020). The most common plant species in the *Pedregal* vegetation type are *Buddleja cordata*, *Echeveria gibbiflora*, *Bromus carinatus*, *Verbesina virgata,* and *Muhlenbergia robusta* (Catillo-Argüero et al., 2009). While xerophytic shrubs dominate this vegetation type, it can present ecotones with trees of the genera *Pinus, Quercus, Alnus,* and *Abies* (Lot and Camarena, 2009). Since the middle of the 20th century, the growth of Mexico City has fragmented this vegetation type replacing it with residential and commercial areas (Peralta and Prado, 2009). Additionally, exotic tree species such as *Eucalyptus globulus*, *Casuarina equisetifolia*, and *Schinus molle* have become established (Catillo-Argüero et al., 2009; Segura-Burciaga, 2009). Today, the remnants of this vegetation type constitute an irregular array of UGAs of different sizes with contrasting management practices and differences in habitat characteristics (Lot and Camarena, 2009; Peralta and Prado, 2009).

To conduct our study, we selected sampling sites in tree habitat types within our selected section of the city. Our sites included: 1) UGAs, 2) areas covered with urban infrastructure (urban matrix), and 3) areas with native *Pedregal* habitat located outside and at the edge of the city (Fig. 1). We used areas of urban infrastructure inside the city and native pedregal habitat sites outside the city as contrasting habitat types to understand how the migrant bird assemblage uses the UGAs. We selected 12 UGAs located within the limits of the *Pedregal* vegetation type (Fig. 1). We worked in all the UGAs that presented remnants of this vegetation type where we were granted permission to perform bird surveys. All selected UGAs were limited by surrounding streets and walls. From south to north, the twelve UGAs included in our study were: two areas within the urban natural protected area *Parque Ecológico de la Ciudad de México* (PECM1 and PECM2); the urban natural protected area of *Bosque de Tlalpan* (BosqT); a UGA inside a private residential cluster (Jard); the UGA within the archaeological site of Cuicuilco (Cuic); the urban natural protected area of *Cerro del Zacatepetl* (Zac); four areas within the urban *Pedregal* ecological reserve managed by the National Autonomous University of Mexico (UNAM: A13, NP, NO, and NCU); a public UGA within a residential area named *Huayamilpas* (Huay); and an UGA preserved by the Diego Rivera-Anahuacalli Museum (Ana). Most UGAs were visited and used by large numbers of people. However, Zac, Ana, Cuic, and NO have fewer visitors due to access restrictions. We selected our urban infrastructure sites by visiting urbanized areas located inside the *Pedregal* (see Fig. 1). We recognized the existence of an important environmental heterogeneity in the urban matrix given the intensity of the urbanization and the presence and abundance of green infrastructure. Thus, we choose three random areas located in the southern, western, and eastern sections of the urban matrix within the *Pedregal* to represent this heterogeneity. (Urb1, Urb2, and Urb3, respectively; Fig. 1). The three urban areas are residential, but Urb1 presents more vegetation and is located in a less densely populated area of the city than Urb2, and Urb3. Finally, the sites that we selected as non-urban habitat areas with native *Pedregal* vegetation outside the city (hereafter referred to as native vegetation sites) include the Xitle (Nat. area1) and the Cuautzontle (Nat. area2) remnant volcanic cones (Fig. 1). Both native vegetation sites with *Pedregal* habitat have low urban and agricultural land use coverage, harbor abundant native vegetation, and receive few visitors.

2.2. Field methods

2.2.1. Bird assemblages

To record the migrant bird assemblages, we visited each sampling site once during the winter of 2017 (February). We registered all migrant and resident birds seen or heard at each sampling area following the Standardized Search method (Watson, 2003). This method is a results-based stopping rule method "suited to comparing richnesses of terrestrial birds in patchy landscapes" (Watson, 2003). It maximizes completeness relative to other standard methods for bird records (Watson, 2004). It also allows contrasting the species richness of an area independently of its size (Watson, 2003). There are two fundamental aspects of the Standardized Search method: 1) a robust sampling stopping rule and 2) a time interval for sampling periods. Once the survey satisfies the stopping rule, it is considered complete. Our sampling period consisted of ten-minute intervals conducted immediately one after the other in the same sampling transect. Our sampling stopping rule consisted of not recording new species on three consecutive sampling periods (30 min).

We conducted the surveys by walking freely throughout the sites at a pace of ~2 km/hour, following a route to cover all accessible areas of the UGAs and native vegetation sites. In native *Pedregal* vegetation areas within lava fields where volcanic rocks are dominant, walking is difficult and dangerous so we were forced to conduct our sampling routes on trails. In urban sites, we conducted surveys by walking along the streets. We did pilot surveys to determine the transect width and sampling pace. The majority of our detections occurred at less than 50 m from the observer. Consequently, we designed our transects to be 100 m wide.

We conducted surveys from 7:00 am to 11:00 am. Our surveys started at sunrise and were performed during the following four hours, a period of the day in which bird activity remains relatively constant in our study sites. We planned for another visit to a site if the sampling stopping rule was not achieved in one visit. However, this never occurred. All sites were sampled by the same highly-trained professional bird observer (MAA-G).

We obtained the primary trophic guild of each bird species from González-Salazar et al. (2014). This classification includes five categories: omnivore, granivore, insectivore, nectarivore, and frugivore. We classified species residence status using two categories: a) residents: species that remain in the area year-round; and b) migrant birds: species that conduct a long-distance migration from their main reproductive habitats, located north of the Tropic of Cancer, to regions inside the tropics that they inhabit during their nonbreeding season (following Howell and Webb, 1995).

We used the total number of species found in each UGA as total species richness. Later we divided all recorded birds into migrant and resident categories. We considered their relative abundances as the rate of observed individuals per sampling period (individuals/10 min). We assumed no double-counting of individuals during our sampling. Because avoiding double-counting is tricky, we paid careful attention to where each detected bird was located, counted birds in groups carefully, and noted whether birds stayed in a place as we moved by or moved in a direction that meant they might be counted again (Bibby, 2000; Ralph et al., 1996). The relative abundance of all migratory birds recorded in each UGA was calculated with a least square regression line considering the cumulative number of individuals as the response variable and the sampling periods as a fixed factor. The resulting estimate of the model is the rate of observed individuals per ten minutes. We only calculated the relative abundance of migrant birds (see models in Supplementary Material 1). The relative abundance calculated as observed individuals/10 min provides insight into the data collection process. This method allowed us to indirectly assess the constancy of individual detectability during the standardized search surveys. It also provides an abundance value that can be contrasted with different timespans. In addition to the total relative abundance, we also obtained the proportion of migratory bird individuals for each trophic guild in our three sampled habitats.

2.2.2. Habitat features

To determine how migrant bird assemblages related to the habitat features of our study sites, we measured several local, buffer, and spatial habitat features of each UGA. Local features were those found inside each UGA, buffer habitat features were those found inside a 250 m buffer area surrounding each UGA, and spatial features allowed us to describe the UGAs spatial context inside the megacity. UGA local features included tree density, tree, shrub, herb, and built land cover proportions. Buffer habitat features also included: tree density and tree, shrub, herb, and built land cover proportion. Additionally, buffer features included the number of buildings, electric poles, light poles, the mean width of the streets, and the mean number of floors on the highest buildings. Our urban features were selected as variables that provide insight on urbanization intensity (see MacGregor-Fors et al., 2010 and MacGregor-Fors and Schondube, 2011) while at the same time acting as a critical habitat feature for birds. For example, poles indicate the presence of different urban services while acting as a habitat feature that provides shelter and roosting sites for birds (MacGregor-Fors and Schondube, 2011). Building density and height indicate urban habitat complexity and indirectly measure human density, while at the same time, they can limit bird dispersion (Gómez-Martínez et al., 2019). We also presumed that the number of streets and their maximum width indirectly show human activity. Spatial features of UGAs included their size, their distance in meters to the closest native vegetated site located outside the city, and their distance relative to all other UGAs.

We determined the tree, shrub, herb, and cover using spectral bands 1–6 of LANDSAT 8 satellite images of Mexico City with a 30 m resolution (USGS High-Level Data Products LC80260472015194LGN00). We used the images to create a training dataset of the four land cover categories to generate a supervised classification with an xgboost model and produce a raster image of the classified landscape. We later added the street cover by downscaling the image's resolution to 10 m and overlapping the roads and avenues in a GIS (INEGI, 2011). UGA local tree density was assessed by generating 5 cm resolution maps of all sites using a flying drone (DJI Phantom 3 Standard). The high definition maps were later processed by deploying four random polygons with a diameter of 20 m (0.031 ha) inside each map and manually counting the number of trees to obtain the mean tree density of all our sampled areas. We did not collect this data at the Cuicuilco archeological site (Cuic) due to drone-flying restrictions imposed by the National Institute of Anthropology (INAH). All buffer features were measured using Google Earth and Google Streetview and calculated by sampling ten 50 m diameter plots (0.196 ha) randomly deployed in each buffer area. We calculated the mean value of each measured feature from the ten plots. Finally, we determined the UGAs' total area and position using QGIS software (QGIS Development Team, 2021).

2.3. Data analysis

We performed all analyses in the R programming language (R Core Team, 2021). We contrasted the overwinter migrant estimated species richness of our three habitat types: UGAs, urban sites, and native vegetation sites. We performed an incidence-based rarefaction ($q = 0$; Chao et al., 2014) to conduct this comparison, considering the combined sampled periods of all surveys in each habitat type on the 'iNext' package (Hsieh et al., 2016). With 34 samples, the urban habitat had the lowest number of survey periods when combining all surveys. Thus, we limited the rarefaction interpolation to this sample limit and used 84% confidence intervals to allow statistically relevant comparisons (MacGregor-Fors and Payton, 2013). If 84% confidence intervals did not overlap, we considered the data to be statistically different with an $\alpha = 0.05$ (following Payton et al., 2003).

We assessed the relationships between migratory bird species richness, abundances, and habitat characteristics using generalized linear regressions (GLMs). To avoid multicollinearity among the habitat features in our GLMs models, we first constructed a correlation matrix considering each UGA as a unit and only including all measured local and buffer UGAs habitat features (Supplementary Material 2). As a result, we only considered tree density and the land coverage proportion of local and buffer trees, shrubs, herbs, and construction land as habitat variables to be included as fixed factors habitat variables in our models. We checked the data distribution through Shapiro-Wilk tests and visually through qqplots. We assessed migratory bird species richness relationships with Gaussian GLMs (Shapiro-Wilk test: $W = 0.94$, $p = 0.55$), while migratory bird abundance relationships were assessed through negative binomial models. Abundance data were not normally distributed (Shapiro-Wilk test: $W = 0.74$, $p < 0.01$), and Poisson models were overdispersed. As a result, negative binomial models were implemented with the 'MASS' package. For both response variables of migrant species richness and abundances, we considered five global models: area, distance to the city edge, local tree density, local land coverage proportion, and buffer land coverage proportionSupplementary Material. We excluded the UGA "Cui" from the models used to evaluate local tree density effects due to missing data. All other generated models include all UGAs. We generated the model pools considering a global model, subset models, and null models. We only considered additive models without considering interaction terms between predictors. We conducted model selection following the corrected Akaike Information Criterion (AICc). The results section only shows the selected models. All pools of models and their AICc ranking values are shown in the supplemental material (see Supplementary Materials 4 and 5).

2.4. The role of the spatial context of UGAs in bird beta diversity

Additionally, we assessed the migrant bird species beta diversity among UGAs using: 1) β-sor (dissimilarity), 2) β-sim (turnover), and 3) β-sne (nestedness) as proposed by Baselga (2010). β-sor considers all aspects of incidence-based beta diversity, and its additive partitions account for turnover and nestedness (Baselga, 2010). A species turnover occurs when species are replaced by others, while nestedness occurs when the species found on a site represent a subset of a site that hosts more species (Baselga, 2010). To determine how similar were the migrant bird assemblages present in UGAs, urban sites, and native vegetation sites outside the city, we generated a dendrogram using the β-sor dissimilarity with the average method for cluster arrangement (Baselga, 2010; Moreno, 2019). To determine nestedness or turnover patterns associated with the distance among the different UGAs, we implemented power models with the distance in meters between UGAs as a fixed effect for each beta diversity index (Baselga, 2012; Soininen et al., 2007).

3. Results

3.1. Bird species richness and abundance

We recorded 97 bird species in 721 records in all our sites during winter (see resident species in Supplementary Material 3). Of those, 23 species were overwintering migrant birds (23.7%). Of the recorded migrant bird species, 22 were found inside UGAs, 14 were present in the urban infrastructure sites, and six were present in the native habitat areas outside the city (Tables 1 and 2). The winter migrant bird assemblage was taxonomically constituted by ten families (Table 2). The migratory bird assemblage was functionally constituted of 20 insectivores, two granivores, and one frugivore species (Table 2). Native vegetation sites only presented insectivorous species. While in urban and UGAs, insectivorous species represented 93% and 86% of their respective local pool of migrant birds. Sampling sites that presented the highest migrant bird species richness were Bosq and NP, with 13 species. We registered the lowest number of migrant bird species at PECM2 (three species) and Urb3 (two species; Table 1).

Table 1
Migratory bird species richness and abundances, resident birds species richness, and habitat characteristics of each sampling site. The number of survey periods represents the sampling effort conducted at each site following the standardized search method (Note: area values signaled with * denote the surveyed sites that were not UGAs).

						Spatial features		Local features					Buffer features					
Site	Type	WMB richness	Resident bird richness	WMB abundance	Survey period	Area (ha)	Edge distance (m)	Trees density (0.1 ha)	Tree LC (prop.)	Shrubs LC (prop.)	Herbs LC (prop.)	Urban LC (prop.)	Trees density (0.1 ha)	Buffer tree LC (prop.)	Buffer shrubs LC (prop.)	Buffer herbs LC (prop.)	Buffer street LC (prop.)	Buffer urban LC (prop.)
A13	UGA	7	20	1.58	11	7.51	7.35	9.7 (± 0)	0.11	0.79	0	0.1	9 (± 7.1)	0.09	0.06	0.08	0.66	0.11
Ana	UGA	8	14	2.37	9	2.71	11.02	14.5 (± 1.9)	0.51	0	0.08	0.41	3.2 (± 2)	0.01	0	0.01	0.75	0.23
BosqT	UGA	13	21	12.34	14	199.78	04.04	24.2 (± 11.2)	0.73	0.25	0.01	0.01	7 (± 4.5)	0.09	0.08	0.03	0.63	0.17
Cuic	UGA	4	16	0.82	9	19.36	6.52		0.11	0.61	0.03	0.06	6.7 (± 5.6)	0.03	0	0.03	0.78	0.15
Huay	UGA	10	20	7.82	8	07.02	10.66	20.2 (± 8.5)	0.06	0	0	0.9	4.5 (± 2.4)	0.01	0	0	0.76	0.24
Jard	UGA	10	15	1.86	11	5.97	5.74	25 (± 4.1)	0.19	0.27	0.12	0.1	8.9 (± 4.8)	0.04	0.03	0.01	0.74	0.19
PECM1	UGA	5	18	0.67	8	26.79	1.71	11.3 (± 8.1)	0	0.97	0.02	0	10.5 (± 4.4)	0.05	0.8	0.01	0.08	0.06
PECM2	UGA	3	19	01.07	12	7.88	2.56	14.5 (± 6.7)	0	0.86	0.09	0	5.1 (± 3.3)	0.01	0.88	0.03	0.02	0.06
NCU	UGA	6	13	1.21	11	1.6	9.55	21.8 (± 8.1)	0.31	0.22	0	0.41	11 (± 7.6)	0.04	0.01	0.01	0.82	0.11
NO	UGA	5	23	1.67	13	56.29	8.14	13.7 (± 10.3)	0.04	0.91	0	0.03	17.1 (± 6.2)	0.11	0.19	0.08	0.52	0.1
NP	UGA	13	24	3.54	15	100.42	7.12	24.2 (± 7.7)	0.09	0.82	0.01	0.02	18.2 (± 10.2)	0.08	0.19	0.06	0.55	0.12
Zac	UGA	9	17	11.13	12	33.16	6.22	18.5 (± 10.7)	0.6	0.21	0.06	0.03	10.2 (± 8)	0.04	0.02	0.04	0.75	0.15
Urb1	Urban area	9	16	1.55	13	131.1 *		11.3 (± 4.2)										
Urb2	Urban area	9	17	3.32	14	387.5 *		14.5 (± 7.6)										
Urb3	Urban area	2	13	0.71	7	101.73 *		6.5 (± 12.9)										
Nat. site1	Native vegetation	6	34	1.77	21	499.23 *		42.7 (± 7.2)										
Nat. site2	Native vegetation	4	28	1.39	17	195.97 *		23.4 (± 3.1)										

Table 2
Migratory bird species found in the three surveyed habitats with their respective primary trophic guilds. Values show the number of occurrences of each bird species relative to the number of sampling sites in each habitat category.

Family	Species	Primary trophic group	UGA	Urban	Native
Parulidae	*Leiothlypis celata*	Insectivore	10/12	1/3	2/2
Polioptilidae	Polioptila caerulea	Insectivore	10/12	1/3	0/2
Regulidae	*Corthylio calendula*	Insectivore	10/12	2/3	2/2
Parulidae	*Setophaga coronata*	Insectivore	8/12	3/3	2/2
Parulidae	*Cardellina pusilla*	Insectivore	7/12	3/3	0/2
Parulidae	*Leiothlypis ruficapilla*	Insectivore	6/12	2/3	0/2
Icteridae	*Icterus bullockii*	Insectivore	5/12	1/3	0/2
Parulidae	*Mniotilta varia*	Insectivore	5/12	1/3	0/2
Cardinalidae	*Piranga rubra*	Insectivore	4/12	0/3	1/2
Vireonidae	*Vireo gilvus*	Insectivore	4/12	1/3	0/2
Emberizidae	*Melospiza lincolnii*	Granivore	3/12	0/3	0/2
Parulidae	*Geothlypis tolmiei*	Insectivore	3/12	0/3	0/2
Parulidae	*Setophaga nigrescens*	Insectivore	3/12	0/3	0/2
Tyrannidae	*Empidonax hammondii*	Insectivore	3/12	1/3	0/2
Tyrannidae	*Empidonax oberholseri*	Insectivore	3/12	0/3	0/2
Bombycillidae	*Bombycilla cedrorum*	Frugivore	2/12	1/3	0/2
Cardinalidae	*Piranga ludoviciana*	Insectivore	2/12	1/3	0/2
Cardinalidae	*Passerina cyanea*	Granivore	1/12	0/3	0/2
Parulidae	*Setophaga occidentalis*	Insectivore	1/12	0/3	1/2
Parulidae	*Setophaga townsendi*	Insectivore	1/12	1/3	2/2
Turdidae	*Catharus guttatus*	Insectivore	1/12	0/3	0/2
Vireonidae	*Vireo plumbeus*	Insectivore	1/12	0/3	0/2
Icteridae	*Icterus cucullatus*	Insectivore	0/12	1/3	0/2

The overwintering migrant bird species richness estimated for each habitat was similar between UGAs (16.4 species; 15.3–17.6, 84% CI; Fig. 2) and urban sites (14 species; 10.7–17.3, 84% CI; Fig. 2), while native vegetation sites showed a lower value (5.8 species; 5.4–6.2, 84% CI; Fig. 2). In UGAs and urban sites, most of the recorded migrant bird individuals were insectivores, while in native vegetation sites, we only recorded birds from this trophic guild (Fig. 2). While represented by only one species (*Bombycilla cedrorum*), frugivores were the second most important trophic guild and were limited to UGAs and urban sites *(*Fig. 2). Granivores were only recorded in UGAs and presented very low abundances *(*Fig. 2).

3.2. UGA habitat features affecting migratory birds

Migrant bird species richness and abundances were affected by local tree features of UGAs (Table 3; see Supplementary Material 4 and 5 to see model pool assessing overwintering bird richness and abundances ranked by AIC). Migrant bird species richness was positively related to tree density, while migrant bird abundance was positively related to tree density and tree land coverage (Table 3; Fig. 3). The buffer habitat characteristics and the spatial context features of UGAs did not affect migrant bird species richness and abundances (Table 3). While we did find a positive pattern between UGAs size and migrant bird species richness, this relationship was not statistically significant. However, we found a significant species richness/are relationship when considering migratory and resident species (Table 3 and Supplementary Material 4).

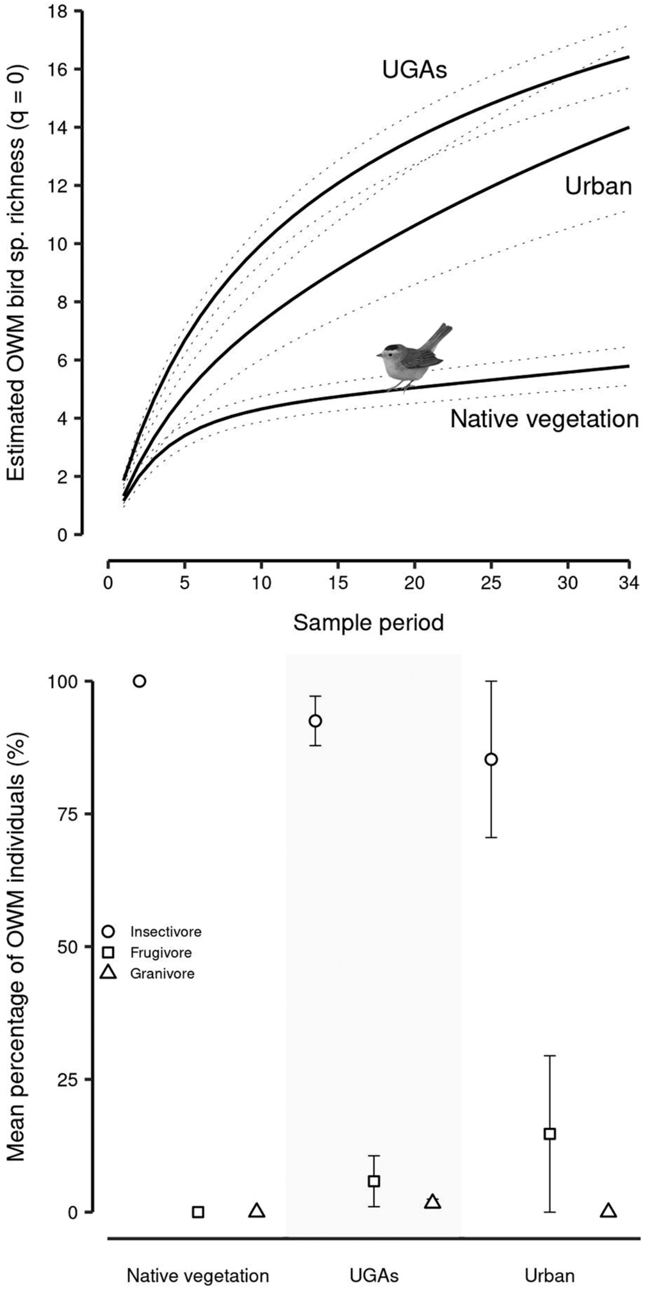


Fig. 2. (single). Upper panel: Estimated species richness of overwintering migrant birds (OWM) for the three sampled habitats. Values were estimated by incidence-based rarefaction limited at 34 sampling period. UGAs and urban matrix sites presented higher estimated species richness than natural vegetation sites located outside the city. Lower panel: Mean percentage (points) and standard deviation (error bars) of OWM individuals by habitat type (Native vegetation, urban green areas (UGAs) and urban infrastructure (Urban)) and trophic guilds (Insectivores, frugivores and granivores). Insectivorous birds dominated the three habitats. The perched bird in the upper panel is a Wilson's warbler (*Cardellina pusilla*), a species frequently found in UGAs and urban sites.

The existence of the species-area relationship considering all the bird species in the bird assemblage of each UGA suggests that our sampling methods allowed us to describe patterns of species richness in the sampled UGAs correctly.

Considering all bird surveys, including UGAs, urban infrastructure, and native vegetation sites, we did not find a clear grouping pattern among the migrant bird assemblages present in each habitat type (Fig. 4). The distance decay relationship among UGAs distances and beta

Table 3
Selected GLMs that show the species-area relationship for the total bird species richness (resident and migrant species), and associations between the overwintering migrant bird species richness and abundances and the habitat features of UGAs.

UGA characteristic	Term	Estimate	Std. error	Statistic	p. value
Total bird sp. Richness (Gaussian, link: log)					
Area (ha)	(Intercept)	2.96	0.11	27.83	0.000
	log(Area)	0.11	0.03	3.46	0.006
OWM sp. Richness (Gaussian)					
Trees/0.1 ha	(Intercept)	0.23	2.52	0.09	0.928
	Trees/0.1 ha	0.44	0.13	3.25	0.010
OWM abundance (Negative binomial)					
Local LUC	(Intercept)	0.59	0.33	1.80	0.072
	Arboreal prop.	2.40	0.81	2.96	0.003

diversity of their migrant bird assemblages assessed through the Sorensen family index (β-sor, β-sim, β-sne) showed no patterns (Table 4; Fig. 5).

4. Discussion

Our study shows that UGAs that present high tree densities and coverage can harbor a large number of migrant bird species. We detected more migrant bird species in UGAs (22 observed species) than in the areas with native vegetation sites located outside and at the city's edge (six observed species; Table 2; Fig. 2). The estimated species richness for UGAs and urban areas did not show statistically significant differences. However, the total observed species in urban matrix sites were 36% lower than in UGAs. All migrant bird species observed in the native vegetation sites were present inside the UGAs. Additionally, one migrant bird species was only recorded in one of our urban sites (*Icterus cucullatus*) but not in UGAs or the native vegetation sites outside the city (Table 2). The majority of our recorded migrant bird species were insectivores, which is similar to what has been found in other neotropical Mexican cities (Carbó-Ramírez and Zuria, 2011; Escobar-Ibáñez et al., 2020; MacGregor-Fors et al., 2010). As we expected, our analyses showed that migratory species richness and abundances were related to local tree features, as reported during both their migration through cities (La Sorte et al., 2020; La Sorte and Horton, 2021; Wood and Esaian, 2020) and their overwintering period inside urban areas in the Neotropics (Amaya-Espinel and Hostetler, 2019; Charre et al., 2013; MacGregor-Fors et al., 2010). We also found that the spatial attributes of UGAs, such as their location inside the urban matrix or their distance from each other, did not affect the composition of the migrant bird assemblages. This result is similar to previous studies that show that migrant birds use UGAs indistinctly of their position within urban areas (La Sorte et al., 2020; MacGregor-Fors et al., 2010).

The species richness of migratory species we found using UGAs was large relative to other studies in Mexican cities located at similar latitudes. MacGregor-Fors and collaborators (2010) reported 11 species of migrant birds for the entire city of Morelia, while a similar assessment of the avian assemblage for the city of Xalapa by Escobar-Ibáñez and collaborators (2020)found 19 migratory bird species. In UGAs in Pachuca, Carbó-Ramírez and Zuria (2011) reported 15 migratory bird species, and Charre and collaborators (2013) reported 40 migrant bird species inside UGAs in Mexico City. Only Charre and collaborators (2013) reported more migrant bird species than we did (22 species), and both studies were conducted inside Mexico City. The lower number of migratory species we found could be caused by the fact that we limited our study to the *Pedregal* habitat, while Charre and collaborators (2013) selected UGAs located throughout the city, including a more extensive diversity of environmental conditions.

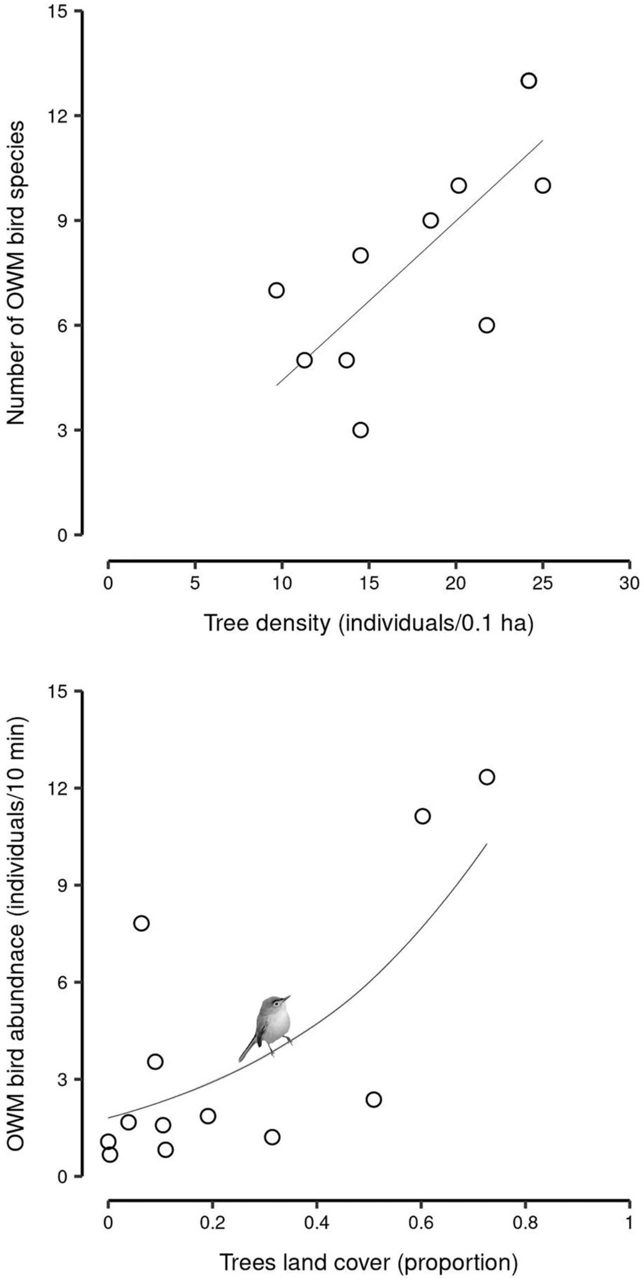


Fig. 3. (single). Positive association of migratory bird species richness and abundances with UGA local tree features. The upper panel shows the relationship between migratory bird species richness and tree density adjusted by a gaussian GLM. The lower panel shows the relationship between the abundance of migratory birds and the proportion of tree land cover adjusted by a negative binomial GLM. The lines in both figures depict the estimated values given by their respective fitted model. The perched bird in the lower panel is a Blue-grey gnatcatcher (*Polioptila caerulea)*, a species frequently found in UGAs.

Our study found that a section of Mexico City can harbor more migrant bird species than the entire cities of Morelia and Xalapa (Escobar-Ibáñez et al., 2020; MacGregor-Fors et al., 2010). These differences seem to be caused by each city's geographic location and environmental characteristics. To account for this, instead of comparing the total number of recorded migrant species in each study, we compared the proportion of migrant birds in the urban bird assemblages reported inside each city. Migrant species in the *Pedregal* constituted 29% of the bird species richness we found in our urban area (UGAs plus urban habitat; Supplementary Material 3), with a similar proportion being reported for Xalapa (28%; Escobar-Ibáñez et al., 2020). However, migratory bird species in UGAs in Pachuca and Mexico City constituted

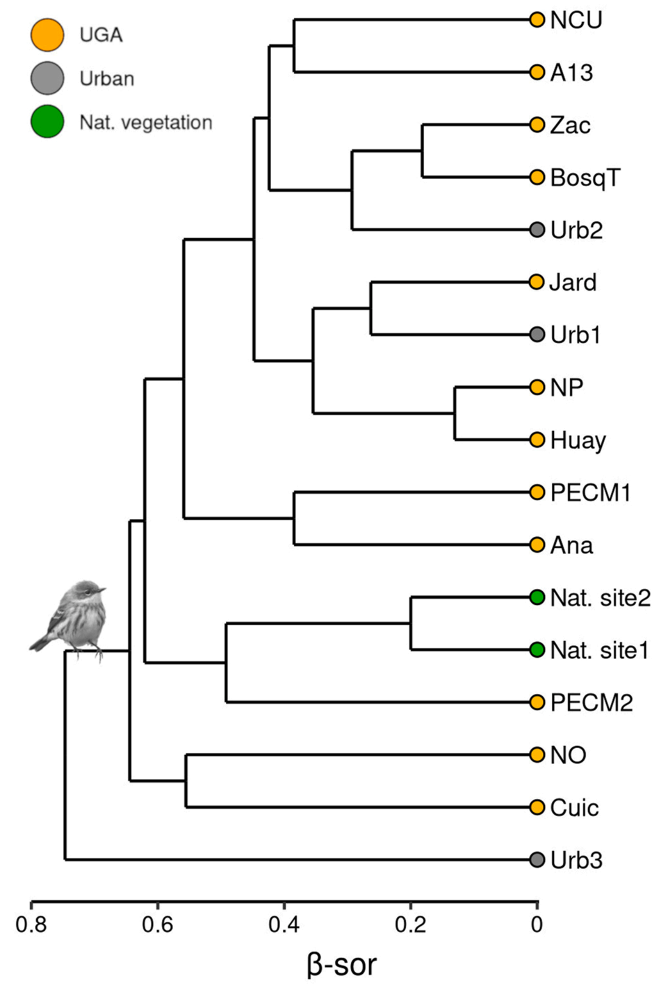


Fig. 4. (single). Dissimilarity analysis of the migrant bird composition considering all surveyed sites in the study (method = "average"). The composition dissimilarity was assessed with the β-sor index. Our assessment included our three habitat types and are depicted by color: Urban green areas (UGAs; orange), urban infrastructure sites (Urb1, Urb2, and Urb3; gray) and native vegetation sites (Nat. site1 and Nat. site2; green). We added urban infrastructure and vegetation sites as controls of urban intensity. Complete names of UGAs are specified in this article's main text (see Methods section). Our analysis did not show a pattern among sites. The perched bird is a Yellow-rumped Warbler (*Setopha coronata)*, a species found in all three habitat types.

Table 4
Distance decay assessment results by power models of the composition dissimilarity of UGAs in their migrant bird assemblage (using β-sor, β-sim, β-sne beta diversity indexes) and the minimum distances in meters between UGAs. We found that none of the beta diversity indexes assessed for the migrant bird assemblage were associated with a dissimilarity pattern, given the distances among all UGAs.

β index	Model structure	K	AICc	Δ AICc	AICcWt	Cum. Wt
β-sor	Null	2	-48.92	0.00	0.56	0.56
	~ log(Distance (m))	3	-48.47	0.45	0.44	1.00
β-sim	Null	2	-9.66	0.00	0.64	0.64
	~ log(Distance (m))	3	-8.50	1.16	0.36	1.00
β-sne	Null	2	-67.16	0.00	0.75	0.75
	~ log(Distance (m))	3	-64.97	2.20	0.25	1.00

41% and 42% of their urban bird species richness, respectively (Carbó-Ramírez and Zuria, 2011; Charre et al., 2013). The proportion of migrant bird species inside Mexican cities is equal to or higher than the proportion that migrant bird species occupying the assemblages found in non-urban vegetated areas considered Areas of Importance for Bird Conservation (AICAS) within similar latitudes to the latter cities (25–29%; Berlanga et al., 2007). These proportions are similar to the ones reported by Leveau (2021) in an urban global assessment of migratory birds. Thus, although the total migrant bird species richness is lower in urban areas relative to non-urban vegetated areas (Leveau, 2021; MacGregor-Fors et al., 2010), the proportion they occupied in urban bird assemblages suggests that urban habitats have a similar ecological space for migrant birds than non-urban vegetated areas (Leveau, 2021).

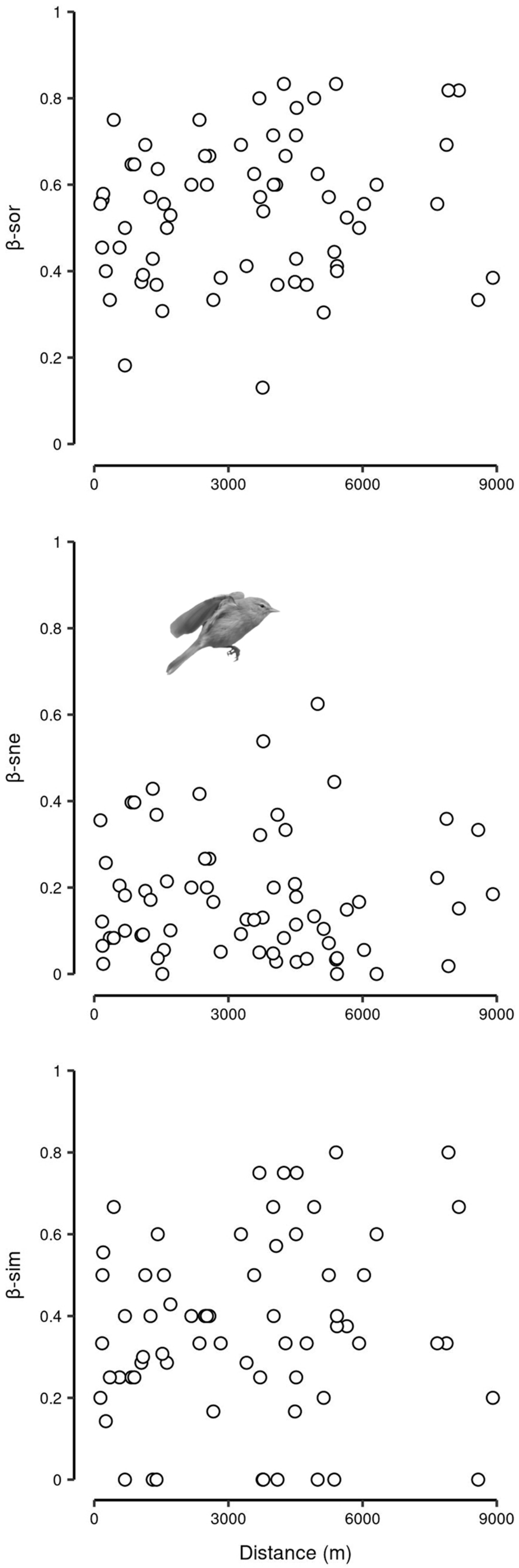
We provide two non-excluding hypotheses to explain this pattern:

1) Our results support the breeding currency hypothesis (Greenberg, 1995). This hypothesis states that overwintering grounds with depauperate resident bird assemblages or high arthropod abundance, such as urban areas (López-Flores et al., 2009; Dale and Frank, 2014), can have a higher proportion of insectivore migrant birds. This is caused by the high availability of food resources due to the reduced resident bird populations or the natural surplus of arthropod abundance present in the habitat (Greenberg, 1995; Hutto, 1980; Malpica et al., 2017). However, we lack information on this topic, and future studies should consider measuring arthropod abundance in urban trees and their association with migrant birds in neotropical cities.

And 2) Relative to non-urban native vegetation sites, urban areas offer more stable environmental conditions and fewer resource limitations than non-urban habitats (Leveau, 2018; La Sorte and Horton, 2021). Urban conditions, such as the heat island effect, can play an important role in relieving cold stress relative to non-urban areas (La Sorte and Horton, 2021; Leveau, 2021). Higher temperatures inside cities could ease the metabolic costs of overwintering at high altitudes in the tropics ($\geq$ 2500 m.a.s.l.), where minimal temperatures can reach $-$ 2 °C (SMN, 2021). Furthermore, cities can provide abundant water that can be limited outside of them during the dry season (September-May). This could be especially important in urban areas located in xeric conditions (Barbosa et al., 2020; MacGregor-Fors et al., 2020). Thus, UGAs may provide similar or even greater quality habitats for migrant birds during the winter than non-urban native vegetation sites.

The habitat quality that UGAs provide to migratory birds was only related to some of their local features, not to those present in their buffer area or their spatial context in the city. While we did find a positive pattern between UGAs size and migrant bird species richness, this relationship was not statistically significant. We offer two complementary hypotheses that could explain this result. First, we think the lack of a significant species-area relationship could be caused by the limited range of sizes found in our UGAs (1.7–200 ha), while Leveau et al. (2021) reported a more extensive range of UGAs sizes (1–350 ha). Although they found a positive relationship between these two variables, the pattern they report is exponential, with few differences in the number of migratory bird species found in UGAs that present sizes smaller than 150 ha.

Secondly, this result could be caused by a group of migratory bird species that use most UGAs (see below). Six species were found in 50% or more of the UGAs (*Leiothlypis celata*, *Polioptila caerulea*, *Corthylio calendula*, *Setophaga coronata*, *Cardellina pusilla*, and *Leiohlypis ruficapilla*, in order of importance based on their frequency of occurrence; Table 2). These species were also found in our urban sites and have also been reported as being abundant and dominant in the cities of Morelia, Pachuca and Xalapa (with minimal differences among these cities; Carbó-Ramírez and Zuria, 2011; Escobar-Ibáñez et al., 2020; MacGregor-Fors et al., 2010). Additionally, although not as frequently present, the majority of migrant bird species that we found in the UGAs of the Pedregal have also been reported in other neotropical cities (Carbó-Ramírez and Zuria, 2011; Escobar-Ibáñez et al., 2020; MacGregor-Fors et al., 2010). These results suggest the existence of a group of migratory bird species that respond similarly to the green and human-made features of the urban habitat is not affected by the size of green habitat elements in Neotropical cities. This supports the idea that



(caption on next column)

Fig. 5. (single). Scatterplot of the distance decay given the beta dissimilarity indices obtained from the migrant bird assemblage and the minimum distance (m) among all UGAs (Beta dissimilarity indexes: upper panel: β-sor; central panel: β-sne; and lower panel: β-sim). We did not find a relationship between any of the calculated beta diversity indexes and the distances among all UGAs assessed by power models (β-sim:turnover and β-sne: nestedness). The bird flying in the central panel is an Orange-crowned Warbler (*Leiothlypis celata)*, the most frequent migratory bird species found in UGAs.

urban areas can provide suitable habitats for complex and healthy migratory bird assemblages (Nava-Díaz et al., 2022; Pacheco-Muñoz et al., 2022).

The lack of a relationship between the migrant bird incidence-based composition and UGA spatial configuration suggests that this feature does not limit their use as wintering habitat. This use of tree-dominated habitat patches regardless of the landscape configuration is similar to findings by previous studies in which migrant birds were present in islands of habitat immersed in a sea of unusable habitats (MacGregor-Fors et al., 2010; La Sorte et al., 2020). We hypothesized that the absence of an effect of the spatial arrangement of the UGAs is associated with the flight behavior of migratory birds. Unlike most forest resident species, migratory birds tend to fly at greater altitudes while moving among areas (Gómez-Martínez et al., 2019).

The local habitat features of UGAs that affected migrant bird richness and abundances were those related to local trees. This is similar to findings from previous studies conducted on urban migratory birds during the migration (La Sorte et al., 2020; La Sorte and Horton, 2021; Wood and Esaian, 2020) and overwintering stages of their life cycle (Amaya-Espinel and Hostetler, 2019; Charre et al., 2013; MacGregor-Fors et al., 2010)**.** Our results add to evidence that trees are a crucial habitat feature to maintain the presence of migrant birds inside cities during the winter. This conclusion is expected, as most migrant bird species require forest patches to maintain their annual cycle (e.g., breed) and rely on tree canopy insects for food (Amaya-Espinel and Hostetler, 2019; Cusa et al., 2015). Additionally urban trees tend to grow faster and can be larger relative to non-urban areas due to a warmer environment and a stable provision of water (Pretzsch et al., 2017; Pacheco-Muñoz et al., 2022). Urban trees can also harbor greater arthropod abundance (Dale and Frank, 2014). We hypothesized that urban trees provide habitat quality for migrant birds mainly regarding habitat structure, foraging substrate, and food resources. Therefore, understanding the characteristics and identity of urban trees related to migrant birds could provide in-depth information for management to focus on their relationships.

Our findings demonstrate that UGAs in the *Pedregal* can provide overwintering habitat to migratory bird assemblages constituted mainly by insectivore species. We emphasize that increasing and conserving local tree features in UGAs can positively affect the migrant bird assemblages. Given the evidence that urban tree abundance has on human well-being, this is a win-win situation for human and migrant bird conservation. Furthermore, in megacities such as Mexico City, where opportunities to establish new UGAs or increase their size are rare, focusing on managing their vegetation elements and habitat structure becomes a feasible task. This is highlighted by the fact that UGA spatial location did not affect the migrant bird assemblage, allowing tree management actions (i.e., adding more trees) to benefit the migrant birds in all sampled UGAs.

CRediT authorship contribution statement

Rodrigo Pacheco-Muñoz: Conceptualization, Software, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration. **Miguel Ángel Aguilar-Gómez:** Methodology, Investigation, Data curation. **Jorge E. Schondube:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2022.127614.

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Capítulo IV. Wintering town: individual quality of migratory warblers using green urban areas in a Neotropical city

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Wintering Town: Individual Quality of Migratory Warblers Using Green Urban Areas in a Neotropical City

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Migratory birds can be familiar winter visitors of Neotropical cities. However, of the regional migrant species bird pool, only a few species are abundant in urban areas. Their presence inside cities has been positively related to green urban areas with high tree cover. However, urban elements like artificial lights can also attract them to cities. Habitat quality that enables energetic refueling for migrant birds is crucial in all their annual migratory stages. While some Nearctic cities offer a high-quality refueling habitat for migrant birds, we lack this information for Neotropical cities where migratory birds winter. In this study, we evaluate whether the urban green areas of a Neotropical city act as high-quality habitats for two abundant species of migratory warblers: *Setophaga coronata* and *Leiothlypis ruficapilla.* We assessed this by capturing birds inside three urban green areas and comparing their abundances, population structure, and individual quality (scaled-mass index—SMI) with individuals spending winter in natural vegetation habitats outside the city. We found that both species do not show differences in SMI between urban and non-urban sites. We also found that *Setophaga coronata* had a higher capture rate in urban than non-urban sites, while *Leiothlypis ruficapilla* had similar capture rates in both habitats. Our findings indicate that the urban green areas of cities can act as suitable quality habitat during winter for two abundant migrant birds. Our results indicate that cities can have a higher conservation potential for a declining and sensitive group such as the Nearctic-Neotropical migratory birds than previously thought. We also point out the need to acknowledge that migratory species can be urban dwellers.

Keywords: Nearctic-Neotropical migrant, mist netting, body condition, vertebrates, Mexico, avian, point-count, non-urban

INTRODUCTION

Urban areas have become the most important habitat for humans, harboring more than half of our worldwide population (Grimm et al., 2008; Elmqvist et al., 2019). Urbanization transforms local habitats by replacing natural features with human-made structures that maintain large resident human populations and their emergent activities (Grimm et al., 2008; Forman, 2014). They concentrate economic activities, pollution emissions, and a large diversity of resources with a local, regional or global origin (Forman, 2014; McPhearson et al., 2016). Cities modify biogeochemical and social processes and weather and biodiversity patterns at local and regional scales (McKinney, 2002; Grimm et al., 2008).

While the concept of urban ecosystem is not new (Stearns and Montag, 1974), cities tend to be perceived by their human inhabitants not as ecologically functional systems but as sites with high levels of environmental degradation caused by the human disturbance of natural processes (Grimm et al., 2017; Groffman et al., 2017). This negative perception of urban systems is reinforced by the fact that some animal species from the regional pool cannot maintain viable populations inside urban areas (Fischer et al., 2015; Aronson et al., 2016). Still, due to their high environmental heterogeneity and emergent properties, cities can offer crucial resources like food (Tryjanowski et al., 2015; Seress et al., 2020), water (Barbosa et al., 2020), and shelter (Davis et al., 2011), and limit predation to vertebrate species (Zuñiga-Palacios et al., 2021). They also offer more stable climatic conditions year-round than those present in the habitats that surround them (Leveau, 2018; Stewart and Waitayachart, 2020). Thus, they can act as critical habitats for many regional species (Aronson et al., 2014).

The importance that urban ecosystems have for different species of the regional fauna is species-specific. For some species, they can represent an ecological trap (Zuñiga-Palacios et al., 2021). At the same time, they can act as a suitable environment for others (Møller, 2009; Spotswood et al., 2021). The interaction between the functional characteristics of wildlife species and the local context of the urban habitat determines which species are filtered, given their phylogenetic and functional traits, and how their populations respond to urbanization (Aronson et al., 2016; Evans et al., 2018). Changes in wildlife behavior to cope with human presence can also be crucial at the species and the individual level (Sol et al., 2018). Furthermore, when the ecological systems surrounding a city become degraded, local fauna can perceive urban habitats as suitable places to survive (Davis et al., 2011; MacGregor-Fors et al., 2020; Zuñiga-Palacios et al., 2021). Consequently, the role of cities as ecological traps or as suitable habitats for regional fauna requires a species-specific assessment, focusing on the individual quality of organisms and their population attributes (Spotswood et al., 2021; Zuñiga-Palacios et al., 2021).

Nearctic-Neotropical migrant birds (hereafter referred to as migrant birds; Hayes, 1995) can be abundant winter visitors of Neotropical urban areas. However, only a few species tend to be present inside cities, occurring mainly in urban green areas with abundant tree features (MacGregor-Fors et al., 2010; Carbó-Ramírez and Zuria, 2011; Amaya-Espinel and Hostetler, 2019). As a result, urbanization has been considered harmful for this group of birds. Recent studies have shown that this view is not entirely accurate, with migratory birds being able to use urban habitats as stopover sites to refuel their fat reserves similarly to how they do it in non-urban habitats (Seewagen and Slayton, 2008; Seewagen et al., 2011). Due to their capacity to use an extensive array of habitats during their annual cycle and their flight and dispersal capacities, migrant birds can occupy and use cities more extensively than resident species (Zuckerberg et al., 2016; La Sorte et al., 2020).

In this study, we focus on urban green areas' role in supporting the migrant bird populations of two species of warblers during their overwintering stage: *Setophaga coronata* and *Leiothlypis ruficapilla*. Migratory birds like these species need to rebuild their body condition after their long-distance fall migration (Sherry and Holmes, 1996; Holmes, 2007). This requires good quality habitats that allow them to survive their overwintering period and prepare for their northbound spring migration (Schuster et al., 2019; Albert et al., 2020). As a result, these species are ideal models for evaluating the quality of green urban habitats compared to those present around cities. To evaluate the urban habitat quality, we principally focused on the bird's body condition because the first response of wildlife to disturbance occurs at the physiological level modifying their individual quality (Chávez-Zichinelli et al., 2013; Zuñiga-Palacios et al., 2021).

MATERIALS AND METHODS

Study Site

We studied migratory warblers in urban green areas (UGAs) of the city of Morelia, inside the urban matrix, and in native vegetation areas with low human disturbance located in the vicinity of the city (non-urban sites from hereafter; **Figure 1**). The city of Morelia is the capital of the state of Michoacán and presents a population of 850,000 inhabitants (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020). It is located in central-western Mexico (19° 42′08′′N 101° 11′34′′ W; **Figure 1**), within the biogeographic province known as the Trans-Mexican Volcanic Belt (Morrone, 2019). This biogeographic zone is considered a critical region for conserving overwintering migratory birds, as it has the highest winter densities of these birds in North America (Bayly et al., 2018). It is also a critical stopover region used by migrant birds during both their fall and spring migrations (La Sorte et al., 2016; Bayly et al., 2018).

We selected sites for capturing birds and for conducting bird censuses. Our field work took place during November and December 2020. Our study sites for capturing birds were based on their environmental characteristics such as abundant tree coverage, spatial location, the security level they presented for our team members to work there, and the presence of access limitations that control the number of visitors. We compared UGAs and non-urban sites with natural vegetation. Our selected sites acted as replicates of this two conditions. UGAs were represented by three replicates: (1) Santa María water treatment plant (Planta Potabilizadora Santa María: PPSM; 19° 40′46.0 "N, 101° 11′34.6′′W), 2) Morelia's Benito Juárez Zoo (Parque Zoológico Benito Juárez: PZBJ; 19° 41′08.3 "N, 101° 11′37.0′′ W), and 3) the vegetated grounds of a university (Universidad Latina de América: UNLA; 19° 41′42.1 "N, 101° 14′04.3′′ W). Non-urban vegetated sites were represented by two replicates: (1) Cerro Punhuato State Protected Natural Area (Area Natural Protegida Cerro Punhuato: ANPCP; 19° 41′53.0 "N, 101°

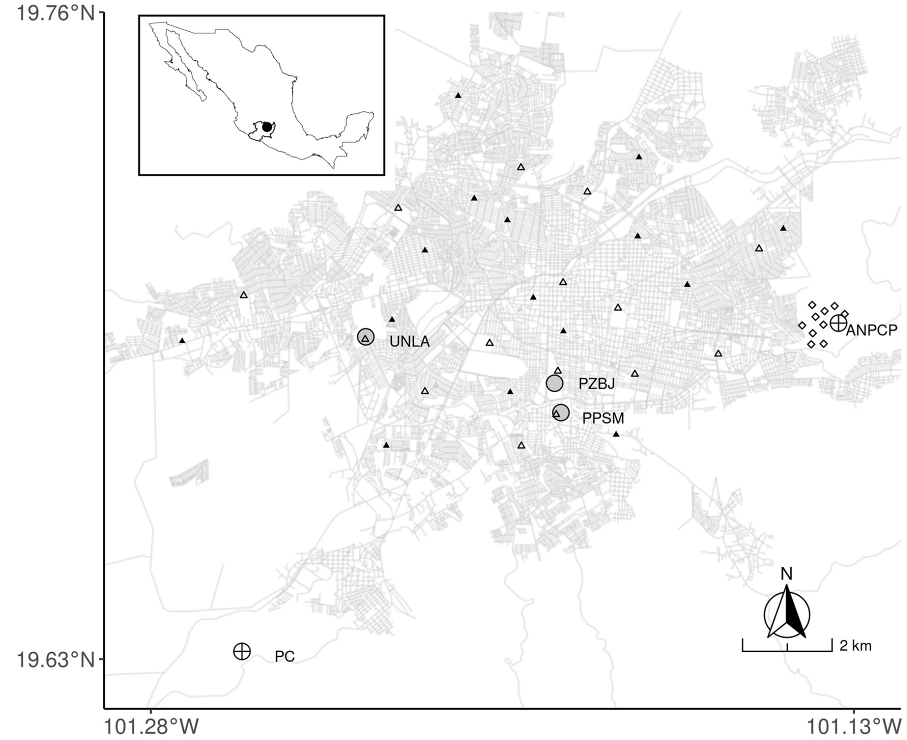

FIGURE 1 | Map of the study area with all the capturing (circles) and bird censuses (triangles and rhombuses) sites. The urban area of the city of Morelia is represented by its streets and roads. Two of our urban green areas (PZBJ and PPSM) are situated closer to the center of the city, while the third one (UNLA) was closer to the city edge (gray circles). The non-urban vegetated site ANPCP is located just at the periphery of Morelia, while the PC site is ∼16 km from the city (crossed circles). Urban sites for bird censuses are shown as black triangles (>50% impervious surfaces), while the urban green sites are shown as white triangles (50% green cover). The non-urban bird censuses were performed in the ANPCP and are shown as rhombuses.

08′09.4″ W); and (2) a patch of pine-oak vegetation located within the facilities of the Cointzio reservoir, administered by the National Water Commission (Presa Cointzio: PC; 19° 37′52.1 "N, 101° 15′37.3″ W). The spatial location of all sampling sites is shown in **Figure 1**. We were unable to include a third replica due to access limitations to other suitable sampling areas. The characteristics of all our bird capturing sites are the following:

Urban green areas:

- The PPSM site has an area of 4 ha. Vegetation covers 55% of the area (grasses 15%, and trees 40%). The rest of the area is covered by parking lots, concrete esplanades, roads, and buildings (25%), and water treatment infrastructure (20%). The most common tree species include both native (*Fraxinus uhdei*, *Salix bonplandiana*) and exotic species (*Eriobotrya japonica*, *Ficus benjamina*, *Eucalyptus camaldulensis*, and *Casuarina equisetifolia*). Shrub cover under the trees is low (10%) and includes several species. The area has permanent access to water resources in the form of water treatment ponds and channels. The human activities carried out in this area include maintaining gardens (grass areas) and the water treatment infrastructure. Residential areas surround the site with a population density of 4.13 people/km^2 (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020).
- The PZBJ site has 24 ha, with vegetation covering 60% of the area (pastures and open gardens 30%, and trees 30%). Shrub cover under trees and in open areas is low and mostly limited to ornamental species used as path walls. The urban infrastructure consists of roads and buildings, covering 30% of the area. The remaining 10% of the area is cover by an artificial lake. Trees are sparse and large, including native (*Fraxinus uhdei*) and exotic species (*Eucalyptus camaldulensis*, *Casuarina equisetifolia*, *Spathodea campanulata*, *Ficus benjamina*, and *Phoenix canariensis)*. Animals are exhibited in fenced enclosures, and their food is available to birds and other wildlife. The artificial lake, a small stream, and animal water troughs are abundant and permanent water sources. During our study, the zoo was closed due to the COVID-19 pandemic, and human activities were limited to essential maintenance by zoo staff. Nonetheless, this was the sampled UGA with the highest human activity. The zoo's surrounding urban area includes two main avenues, two educational institutions, a public park, and residential and commercial areas with a population density of 6.58 people/km^2 (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020).
- The vegetated grounds of the UNLA have a size of 20 ha. From this area, 20% was occupied by open areas with grass used for sports activities, 10% by a pond, and the rest (70%)

is an area with tree cover that is susceptible to flooding and part of the year acts as a wetland. The dominant tree species are the native species *Salix humboldtiana*, *S. bonplandiana*, *Fraxinus uhdei*, and *Taxodium mucronatum.* Also, there are some scattered individuals of non-native trees (*Eucalyptus camaldulensis* and *Casuarina equisetifolia)*. Shrub cover is low, with scattered individuals. Water resources are available all year long and include the pond, some water channels, and the wetland. The urban surroundings of the UNLA include the university buildings and parking lots, vegetated lots, and residential and commercial areas with a population density of 6.73 people/km^2 (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020). Human activities were restricted due to the COVID-19 pandemic and limited to maintenance activities by the university staff. Previously to the pandemic, various sports and cultural activities were carried out in this area regularly.

Non-urban sites:

- The ANPCP is located on the periphery of the city of Morelia and covers an area of 117 ha. Restoration activities have been carried out in this protected area for more than 20 years. The area presents patches of *Quercus* forest, gallery forest, subtropical scrub, and exotic vegetation. Dominant *Quercus* species are *Q. obtusata, Q. castanea, Q. deserticola,* and *Q. magnolifolia*. Other dominant tree species are *Bursera cuneata*, *B. bipinnata*, *Ipomea murocoides*, *Acacia farnesiana*, *A. pennatula*, *Condalia velutina,* and *Opuntia* spp. Tree species such as *Fraxinus uhdei* and non-native species such as *Eucalyptus camaldulensis* and *Casuarina equisetifolia* occurred scattered through the area and on its urban periphery. Shrub cover is diverse and abundant below the tree canopy. The site has two main buildings that serve as a managing station and a telecommunications station and cover less than 1% of the area. Some unpaved roads extended throughout the area, covering less than 5% of its surface. Human activity on the site is low and limited to individuals or small groups of people who visit the area to perform recreational or educational activities. The protected natural area is surrounded by patches of native vegetation (25%), non-intensive rainfed crops (25%), and the rest (50%) presents residential areas with a population density of 5.21 hab/km^2 (Instituto Nacional de Estadística, Geografía e Informática [INEGI], 2020) and a 4-lane highway.
- The PC site has an extension of 16 ha. It is located 4.5 km from the edge of the city of Morelia. The site is fenced and has restricted access. Nearly all the area is covered by remnant pine-oak vegetation. However, it has an open area with pastures (10%), a permanent water stream (5%), and a few buildings and a paved road covering less than 5% of the area. The vegetation structure of the shrub and tree layers is complex and diverse. Species of Pinus and Quercus characterize the arboreal vegetation. There are also individuals of *Fraxinus uhdei*, *Salix sp*., *Bursera cuneata*, *B. bipinnata*, *Ipomea murocoides*, *Acacia farnesiana*, *A. pennatula*, *Condalia velutina, Opuntia* spp., and a few individuals of the invasive tree species *Eucalyptus camaldulensis*. There is very little human activity in the area. The area is surrounded by native forest, cultivated areas, a few houses, and a reservoir.

We determined the density of our selected migrant bird species (see in the section above) using 10 min unlimited radius point counts with distance estimations (Ralph et al., 1996). All bird records were performed by the same observer (A. C-M). We only included in our analyses the birds we detected inside a 50 m radius. A minimum distance of 250 m separated all point counts. We deployed 30 random points within the city of Morelia: 15 points in urban green areas ($>$50% green cover) and 15 urban points ($>$50% impervious surface cover). The point count in urban green areas included one point count in each of the three UGAs where we capture birds. Due to the size of the UGAs where we captured birds, we were forced to sample several additional locations to have independence among our point counts. We also deployed ten points within the ANPCP non-urban site. Distances of bird records were obtained with a range-finder (*Nikon Rangefinder Forestry Pro 550*). We used these records to calculate the density of *S. coronata* and *L. ruficapilla* in the three habitat types. The location of our bird censuses sites is shown in **Figure 1**.

We described the habitat components of both our bird capture and bird censuses sites. We characterized both the green and gray habitat elements using 25 m radius sampling points located around each of the ten mist nets we used to capture birds and around all point count sites. The green elements quantified in both habitats were the number of arboreal and shrub morphospecies as their species richness, respectively, the densities of trees and shrubs, tree height (m), tree diameter at chest height (DBH; cm), and the minimum and maximum shrub height (m). The gray elements quantified in both habitats were the number of buildings, their maximum height, and the number of artificial elements that were not buildings. We measured the proportion of cover represented by the tree canopy, the shrub layer, herbaceous layer, bare soil, and buildings for each habitat sampling point. Additionally, we quantify the minimum and maximum background noise levels (dB) using a sound level meter (*EXTECH EN300*). We obtained all measured heights and distances with a range-finder.

To determine how similar our sampling sites were (for UGAs and non-urban sites), we compared the habitat elements of all sampling sites using a principal component analysis (PCA), followed by an oblimin rotation. Additionally, we included the ten most urbanized bird censuses point count sites ($\geq$50% of urban impervious and building coverage) and ten natural vegetation sites located away from the city ($\sim$35 km; Querendaro county) as a reference to compare our sites. A throughout explanation of our habitat characterization and their contrast using the oblimin rotated PCA is provided in **Supplementary Material**.

Focal Species

We focused on two selected migratory warblers: *Setophaga coronata* and *Leiothlypis ruficapilla*. Both species are abundant in urban and vegetated non-urban areas during winter in the city of Morelia (MacGregor-Fors et al., 2010; personal observations). *Setophaga coronata* is a migratory warbler that breeds in mature coniferous and mixed coniferous-deciduous forest habitats of temperate zones north of the continent, wintering in a large diversity of Neotropical habitats (oak-pine forests, forest edges, and open areas including anthropized habitats; Howell and Webb, 1995; Liu and Swanson, 2015). It forages for insects both in trees and open grass areas (Greenberg, 1979) and is considered the most opportunistic species within the *Setophaga* group due to its plasticity in foraging strategies (Greenberg, 1979). We evaluated the *Setophaga coronata auduboni* subspecies, because this is the only subspecies present in western Mexico. *Leiothlypis ruficapilla* is a species that breeds in second-growth, open deciduous, or mixed-species forests of temperate zones north of the continent and winters primarily in low deciduous open forest and urban residential areas (Howell and Webb, 1995). It forages for insects mainly in the shrub layer (Howell and Webb, 1995). Moreover, both birds respond to different habitat characteristics through changes in their abundances or body weight during migration (Rodewald and Brittingham, 2007) and in their overwintering territories (Greenberg et al., 1997; Murphy et al., 2001).

Habitat Quality for Migrant Birds

We evaluated how important UGAs are for wintering migrant warblers directly by evaluating the body condition of individuals of both species and indirectly by determining their abundances. We compared abundances because they tend to reflect habitat quality (Bock and Jones, 2004). We conducted both assessments relative to our sampled non-urban areas. To evaluate the individual body condition, we captured individuals using ten mist nets per site (12 × 2.5 m nets with a mesh size of 16 mm) for 4 weeks during the winter period. We capture birds from November 23 to December 19, 2020. During this period, migrant birds have established winter territories after their southbound migration, and their body condition is dependent on their wintering habitat (Sherry and Holmes, 1996; Bayly et al., 2018). Additionally, no migrant birds pass through the area during this period while migrating to other regions (La Sorte et al., 2016, 2017). We operated nets from sunrise to 11:30 a.m. with a team of 3–5 people, conducting net-rounds every 30 min (Ralph et al., 1996). All sites were sampled at least one time per week during the sampling period. Because our sampling effort differed slightly among sites, we calculated and standardized the catch-per-unit effort to the number of individual captured per 100 net h at each site (captures/100 net h). All captured migratory birds were identified and tagged with numbered aluminum rings from the BIRDS.MX system. We took the following data from each bird: age (only in *Setophaga coronata*: subadult and adult), sex (males or females), body mass (± 0.01 g: Ohaus digital Scout Pro electronic scale), wing chord length (± 0.5 mm: millimeter ruler with wing stop), tarsal length (± 0.01 mm: millimeter Vernier), flight-feather wear, number of ectoparasites in its wing feathers, and levels of fat reserves (following Kaiser, 1993).

We assessed the individual body condition for each migrant bird species by calculating a modified scaled-mass index (SMI; Peig and Green, 2009), following Brodeur et al. (2020). The modified SMI was calculated by substituting the scaling factor obtained by modeling a standardized major axis regression (SMA) to a scaling factor obtained by modeling a non-linear power function regression (Brodeur et al., 2020). The SMI adjusts the mass of all individuals of each species, given a scaling exponent from the relationship of mass and a body size measurement (Peig and Green, 2009). As recommended by Peig and Green (2009), we choose wing chord length as body size measurement as it was the best-correlated measurement of body size with the mass on a log-log scale for both species (*S. coronata*: $r = 0.51$, $P \leq 0.001$ and *L. ruficapilla*: $r = 0.4$, $P \leq 0.01$). The SMI must be independent of body size measurement (Brodeur et al., 2020). Our unmodified calculated SMIs for both species were negatively correlated with our selected body size measurement (*S. coronata*: $r = -0.49$, $P \leq 0.001$ and *L. ruficapilla*: $r = -0.56$, $P \leq 0.001$). However, our modified SMIs were uncorrelated to their respective body size measurements (*S. coronata*: $r = 0$, $P = 1$ and *L. ruficapilla*: $r = 0$, $P = 1$). Thus, we used the modified SMI (hereafter referred to as just SMI) as body condition index. To calculate the scaling factor, we removed three individuals of each migrant bird species due to mass measurement errors during processing. We also tested if individuals of each species grouped by sex or habitat had different slopes but they did not differ. We obtained the SMI scaling factor through the power function of mass and body length for both migrant bird species (*S. coronata*: $y = -0.66 \times \hat{}0.729$ and *L. ruficapilla*: $y = 0.51 \times\hat{}0.396$). Finally, we assessed the SMI association to energy stores in each migrant bird species, through their Pearson correlations with our fat category index with a confidence interval of 95%.

Data Analysis

The density of each species recorded by our survey point counts was contrasted between habitat types (urban, UGAs, and non-urban sites). We assessed this contrast by fitting a negative binomial and a Poisson generalized linear model (GLM) for *S. coronata* and *L. ruficapilla*, respectively, with habitat type as a fixed factor. Posteriorly, for each model, we computed the estimated marginal means and performed a pair-wise contrast of our factor categories considering a 95% confidence level.

We compared the individual captures/100 net h, the individual SMI, the flight-feather wear, and the ectoparasite load of each migrant warbler species between our two habitat conditions (UGAs and non-urban) and between sexes. We fitted GLMs to evaluate individual captures/100 net h, linear mixed models (LMM) to evaluate the individual SMI, and generalized linear mixed models (GLMM) to evaluate flight-feather wear and ectoparasite load. All models had habitat type and sex as a fixed factor, and mixed models had site as a random factor to allow for similarity of measurements from the same sites. For each of the four measurements of each species assessed, we fitted a pool of five models: a multiplicative, an additive, a single term

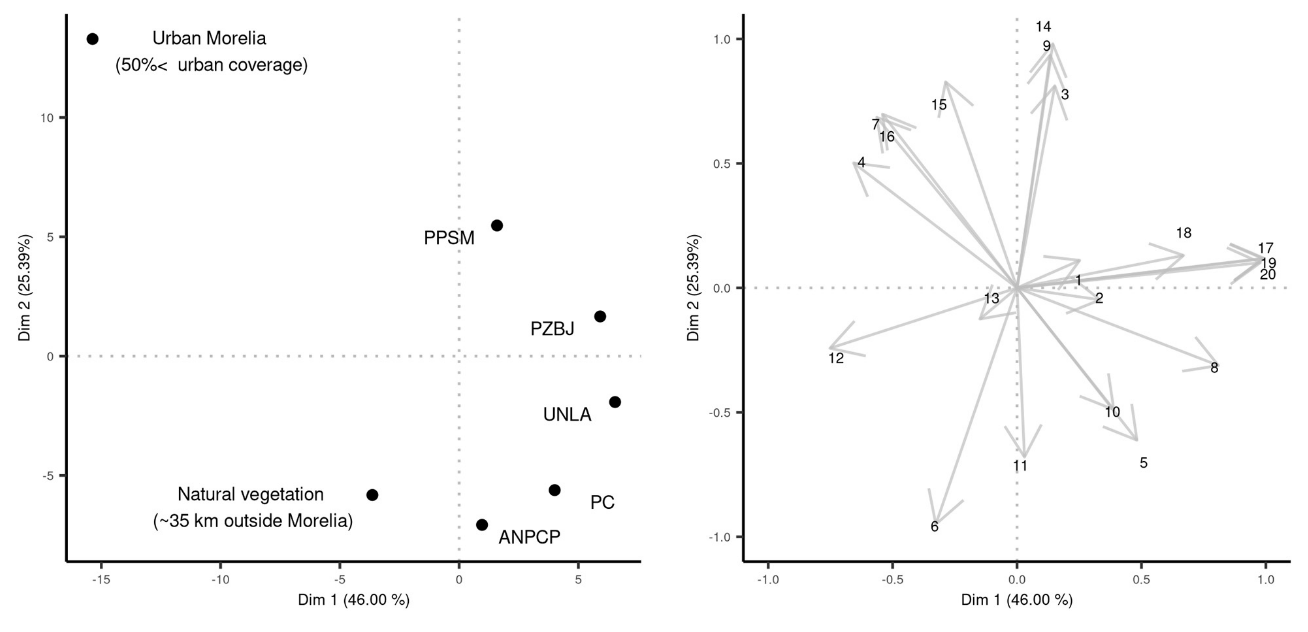

FIGURE 2 | Classification of our study sites by their habitat characteristics assessed by the dimension 1 and dimension 2 (46 and 25.4% of variance explained, respectively) of the oblimin rotated PCA. The **(left panel)** shows a biplot of the rotated scores for the sites. The **(right panel)** shows a biplot of the habitat characteristics measured in each site as the oblimin rotated PCA loadings: Tree sp. richness (1), Tree abundances (2), Minimum background noise (dB; 3), Maximum background noise (dB; 4), Herbs land cover proportion (5), Shrubs land cover proportion (6), Construction land cover proportion (7), Tree land cover proportion (8), Bare ground land cover proportion (9), Shrub sp. richness (10), Shrub abundances (11), Minimum shrub height (m; 12), Maximum shrub height (m; 13), Number of artificial elements (14), Maximum construction height (m; 15), Density of constructions (16), Mean tree height (m; 17), Standard deviation of tree height (cm; 18), Mean tree diameter at breast height (19), and Standard deviation of tree diameter at breast height (20).

structure of factors (one for sex and habitat, separately), and also a null model. Models evaluation was conducted through AICc. We selected models with the lowest AICc (Δ AIC < 2). We used Poisson and negative binomial models to assess the individual captures/100 net h, the flight-feather wear, and the ectoparasite load, given that the data was from counts and was non-normally distributed. We choose negative binomial models over Poisson models if overdispersion was detected in the latter. To perform our SMI analysis, we first checked the data for normality for each bird species through a Shapiro-Wilk test (*S. coronata*: $p > 0.05$ and *L. ruficapilla*: $p > 0.05$). We checked all selected models through Q-Q plots. Our analysis that assessed the individual captures/100 net h, the individual SMI, the flight-feather wear, and the ectoparasite load in both our selected bird species did not include data from recaptures. All analyses were performed through R language (R Core Team, 2021).

RESULTS

Habitat Differences Among Sites

The classification of our sampling sites by their habitat characteristics (PCA oblimin rotated analysis) showed a clear separation of urban areas, UGAs, and non-urban areas by the values of dimension 1 and dimension 2 (71.4% of variance explained; **Figure 2**). Based on the oblimin rotated loadings (**Figure 2**), the urban site negative values from dimension 1 and the positive values from dimension 2 were principally driven by the number of constructions, a dominant proportion of construction land cover, and the maximum background noise levels (max. dB). The Dimension 2 of our analysis separated UGAs from non-urban areas. UGAs showed higher minimum background noise levels (min. dB), a higher proportion of bare ground land cover, and a greater density of artificial elements (elements/area) relative to non-urban sites. Non-urban sites had a more significant proportion of land covered by herbs and greater values of shrub species richness, abundances, and land cover proportion (**Figure 2**). From all UGAs, UNLA showed habitat characteristics closest to non-urban sites, with the least

TABLE 1 | Differences of bird densities by habitat type (U, Urban and UG, urban green) of both overwintering warbler species, assessed by a pairwise contrast of the negative binomial (*S. coronata*) and the Poisson (*L. ruficapilla*) GLMs estimated marginal means.

Species	Contrast	Ratio	Std. error	*z*-ratio	Adj. *p*-value
Setophaga coronata	Non-urban/U	27.50	20.03	4.55	<0.001
	Non-urban/UG	0.88	0.40	–0.29	0.96
	UG/U	31.33	21.87	4.94	<0.001
Leiothlypis ruficapilla	Non-urban/U	314014385.80	764292808510.11	0.01	1.00
	Non-urban/UG	1.63	0.65	1.21	0.45
	U/UG	0.00	0.00	–0.01	1.00

The pairwise contrast is shown by the models' estimated ratio.

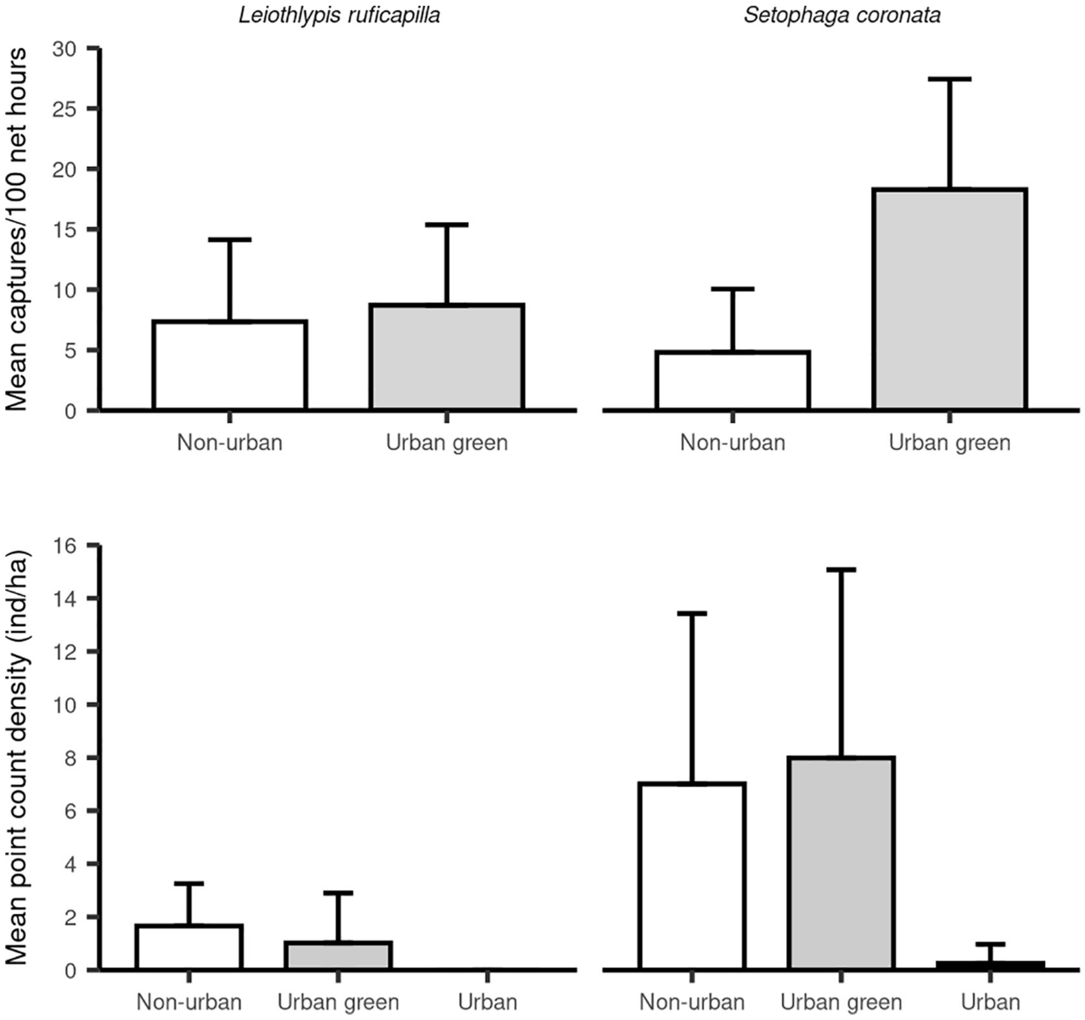

FIGURE 3 | Capture rates (captures/100 net h) and densities (ind/ha) of *Setophaga coronata* **(right panels)** and *Leiothlypis ruficapilla* **(left panels)**. Upper panels represent mean captures/100 net h in urban green areas (three sites) and non-urban areas (two sites). Lower panels show mean densities (ind./ha) in urban green areas (>50% green cover), urban sites (>50% impervious surfaces) and non-urban areas. Individuals/100 net h for both species did not differ between habitats. However, *S. coronata* presented slightly higher capture rates in urban-green areas. Point counts in urban sites did not detected individuals of *L. ruficapilla* and only a few individuals of *S. coronata.* Both species had similar abundances between urban green and non-urban areas.

amount of constructions and artificial elements. However, it did not have an abundant shrub layer. The loading values of the oblimin rotated PCA dimension 1 and dimension 2 are shown in **Supplementary Material**.

Points Count Records and Bird Captures

Our bird census for *S. coronata* recorded 94 individuals in urban green sites, 55 individuals in non-urban sites, and three in urban sites. For *L. ruficapilla* we recorded twelve individuals in UGAs, 13 individuals in non-urban sites, and none in urban sites. The point count density of both migrant species and their contrast among habitats showed that urban sites had fewer individuals of *S. coronata* than the non-urban and urban green habitat types (**Table 1** and **Figure 3**). Densities for *S. coronata* were similar between UGAs and non-urban sites (**Table 1** and **Figure 3**). For *L. ruficapilla*, our analyses show no differences in the densities among habitat types (**Table 1** and **Figure 3**).

In our banding sites, we captured a total of 95 individuals of *S. coronata* and 72 individuals of *L. ruficapilla*. For *S. coronata* we captured 48 females and 47 males, while for *L. ruficapilla* we captured 25 females, 39 males, and eight individuals whose sex was not identified. By habitat, we capture 82 individuals of *S. coronata* in UGAs, and 13 individuals in non-urban areas. In comparison, we captured 38 individuals of *L. ruficapilla* in UGAs and 34 individuals in non-urban areas. We recaptured two individuals of *S. coronata* and four individuals for *L. ruficapilla*. After their original capture day, two *S. coronata* were recaptured in UGAs 7 and 14 days later. We did not recapture any individual of *S. coronata* in a non-urban area. For *L. ruficapilla*, we recaptured two individuals 14 days after their original capture in UGAs. For non-urban areas, one individual of this species was recaptured 7 days after its capture and another 14 days later. Mean individual captures/100 net h for both species by habitat type and sex are presented in **Table 2**. Capture rates of *S. coronata* differ by habitat type, being slightly higher in UGAs relative to non-urban areas (**Tables 3**, **4** and **Figure 3**). Capture rates of *L. ruficapilla* did not differ between habitats, but they did by sex (**Table 3** and **Figure 3**), with males presenting higher capture rates than females (**Table 4** and **Figure 3**).

Evaluation of Individuals

Both species' body condition (SMI) did not differ between UGAs and non-urban areas (**Table 3** and **Figure 4**). *S. coronata* did not present differences by habitat type or sex in SMI, flight-feather wear, and ectoparasite load. For this species, the null model was indistinguishable from other models in their respective pool (**Table 3**). In *L. ruficapilla* our analyses indicate differences by sex in SMI, flight-feather wear, and ectoparasite load (**Table 3**). Furthermore, the pool of models of the SMI and the flight-feather wear in *L. ruficapilla* showed modest support for differences given by the interaction of habitat type and sex (Δ AICc < 2; **Table 3** and **Figure 4**), but showed an AICc weight lower than 50% (**Table 3**). Our selected models show that *L. ruficapilla* males had slightly lower SMI values, more flight-feather wear, and lower ectoparasite loads, regardless of habitat type (**Table 4**). SMI and values of fat categories were positively correlated in *S. coronata* ($r = 0.21$, df = 90, $p \leq 0.05$; **Figure 5**). However, while they were not correlated in *L. ruficapilla*, they showed a positive trend ($r = 0.21$, df = 64, $p = 0.08$; **Figure 5**).

DISCUSSION

The body condition, abundances, the proportion of sexes, and wintering residency of both of our studied species indicate that cities, through their green areas, can maintain viable winter populations of some species of migratory birds. In this section, we first compare the habitat characteristics of both UGAs and non-urban native vegetation areas. Second, we discuss how human management generates specific habitat elements in UGAs that favor migratory birds. Third, we compare the individual body condition of migratory birds in UGAs and non-urban native vegetation areas. Finally, we propose that migratory birds can be considered urban dwellers, and included in urban planning strategies.

Our UGAs and non-urban areas showed fundamental differences in their vegetation structure and the characteristics of

TABLE 2 | Captures rates (individuals/100 net h) of both focal migrant bird species, by sex (F, Females and M, Males) and by habitat type.

		Mean (ind/100 net h)	
Species	**Category**	**Non-urban $n = 2$**	**Urban green $n = 3$**
Setophaga coronata	F	2.5 (± 2.49)	9.13 (± 4.59)
	M	2.32 (± 2.75)	9.15 (± 5.93)
Leiothlypis ruficapilla	F	2.69 (± 1.4)	3.27 (± 2.37)
	M	3.55 (± 3.83)	4.79 (± 4.38)

TABLE 3 | *S. coronata* and *L. ruficapilla* GLM, LMM, and GLMMs' pools that evaluate the role of habitat type and sex on their capture rates (individuals/100 net h), body condition (SMI), flight-feather wear and ectoparasite load through the Akaike criteria.

Species	**Measurement**	**Model family**	**Model structure**	**K**	**AICc**	**Δ AICc**	**AICcWt**
Setophaga coronata	Individuals/100 net h	NBGLM	Hab. type	3	60.42	0.00	0.76
			NULL model	2	63.29	2.87	0.18
			Sex + hab. type	4	66.42	6.00	0.04
			Sex	3	67.58	7.16	0.02
			Sex * hab. type	5	75.41	14.99	0.00
	SMI	LMM	Sex	4	170.03	0.00	0.34
			Sex + hab. type	5	170.87	0.85	0.22
			Null model	3	170.89	0.87	0.22
			hab. type	4	171.61	1.58	0.15
			Sex * hab. type	6	173.04	03.02	0.07
	Feather wear	PGLMM	Null model	2	215.78	0.00	0.42
			Sex	3	216.69	0.92	0.27
			Hab. type	3	217.65	1.87	0.17
			Sex + hab. type	4	218.58	2.80	0.10
			Sex * hab. type	5	220.33	4.55	0.04
	Ectoparasite load	NBGLMM	Null model	3	502.99	0.00	0.49
			Hab. type	4	504.53	1.53	0.23
			Sex	4	505.01	02.01	0.18
			Sex + hab. type	5	506.54	3.54	0.08
			Sex * hab. type	6	508.75	5.75	0.03
Leiothlypis ruficapilla	Individuals/100 net h	NBMM	Sex	3	54.27	0.00	0.94
			Sex + hab. type	4	59.96	5.69	0.05
			Null model	2	64.67	10.40	0.01
			Hab. type	3	67.98	13.70	0.00
			Sex * hab. type	5	68.95	14.68	0.00
	SMI	LMM	Sex	4	65.61	0.00	0.54
			Sex * hab. type	6	67.35	1.74	0.23
			Sex + hab. type	5	67.43	1.82	0.22
			Null model	3	72.91	7.29	0.01
			Hab. type	4	74.39	8.77	0.01
	Feather wear	PMM	Sex	3	137.21	0.00	0.52

(Continued)

TABLE 3 | (Continued)

Species	Measurement	Model family	Model structure	K	AICc	Δ AICc	AICcWt
			Sex * hab. type	5	138.45	1.25	0.28
			Sex + hab. type	4	139.26	02.05	0.19
			Null model	2	145.59	8.38	0.01
			Hab. type	3	147.55	10.34	0.00
	Ectoparasite load	NBMM	Sex	4	323.69	0.00	0.68
			Sex + hab. type	5	326.06	2.38	0.21
			Sex * hab. type	6	327.24	3.55	0.11
			Null model	3	361.79	38.10	0.00
			Hab. type	4	363.69	40.00	0.00

NBGLM, negative binomial generalized model; NBGLMM, negative binomial generalized mixed effects model; LMM, linear mixed effects model; PGLMM, Poisson generalized linear mixed effects model.

TABLE 4 | Models with the lowest AICc selected from de model pool with an effect given by our fixed factors: habitat type (Urban green and non-urban areas) and sex.

Species	Measurement	Factor	Estimate	Std. error	Statistic
Setophaga coronata	Individuals/100 net h	(Intercept)	1.57	0.47	3.35
		Habitat—urban	1.34	0.56	2.38
Leiothlypis ruficapilla	Individuals/100 net h	(Intercept)	1.11	0.33	3.40
		Sex—males	0.35	0.44	0.79
	SMI	(Intercept)	8.48	0.08	101.10
		Sex—males	−0.01	0.10	−0.07
	Feather wear	(Intercept)	−0.32	0.25	−1.27
		Sex—males	0.01	0.31	0.04
	Ectoparasite load	(Intercept)	2.00	0.36	5.60
		Sex—males	−0.45	0.45	−1.00

The statistic for the LMM (SMI) model was the t-value, while for the rest of the models we used the z-value with log-transformed estimates.

their surrounding habitats. Both habitat categories were grouped apart from our urban sites reference (>50% impervious surfaces) due to their differences in habitat structure, principally by a greater urban intensity given by more construction features and high noise levels (**Figure 2**). The habitat differences between our UGAs and non-urban areas were principally driven by their vegetation complexity. Non-urban areas were characterized by presenting a greater grass and shrub land coverage proportion and higher values of shrub species richness and abundances. Additionally, they presented a lower number of artificial elements. This result is consistent with previous studies that show that UGAs generally exhibit less vegetation complexity in the shrub layer than forest habitats outside cities (Threlfall et al., 2016). The absence of a complex shrub layer in UGAs has been reported to reduce the habitat quality for resident birds (Savard et al., 2000). Interestingly, our results show that this is not the case for our studied migratory bird species.

Surprisingly, our studied UGAs presented a tree layer with greater complexity than the non-urban areas (**Figure 2**). This was related to the presence of broader and higher trees in UGAs. This structural difference in the tree layer was linked to dominant exotic trees that grow to larger sizes than most native species found outside the city (e.g., *Eucalyptus camaldulensis*, and *Casuarina equisetifolia*). Additionally, the management of the UGAs, which includes using large quantities of water for irrigation, and local changes in weather inside the city (e.g., reduced seasonality, urban heat island), allows urban trees to grow larger (Pretzsch et al., 2017). This more complex tree layer found in the UGAs seems to provide suitable habitat quality for insectivore migratory warblers, a group of birds associated to this habitat feature (Amaya-Espinel and Hostetler, 2019).

Previous studies showed that UGAs' tree species richness did not affect migratory birds (MacGregor-Fors et al., 2010; Carbó-Ramírez and Zuria, 2011). This seems to explain why both the presence and abundance of exotic and native tree species inside the UGAs of Morelia did not affect migratory birds' abundances and individual quality. Both *S. coronata* and *L. ruficapilla* showed similar body conditions in UGAs dominated by exotic trees (*Eucalyptus camaldulensis*, *Casuarina equisetifolia*, *Spathodea campanulata*, *Ficus benjamina*, and *Phoenix canariensis*; PZBJ) and in those that mainly presented native tree species (*Salix humboldtiana*, *S. bonplandiana*, *Fraxinus uhdei*, and *Taxodium mucronatum*; UNLA). However, while migrating through temperate urban areas, these birds have been associated with native trees (Wood and Esaian, 2020). This significant difference in their behavior during the migration and wintering periods indicates that the role of urban trees for migrant birds requires further investigation, considering aspects like tree identity, architecture, and biogeographic origin to understand their use by migratory bird species (Wood and Esaian, 2020).

The similarity of body condition of our study species between our UGAs and non-urban conditions indicates that UGAs can provide a habitat quality comparable to those of non-urban habitats. Our findings are similar to those from temperate cities, showing that migrant birds can replenish their fat reserves using UGAs as stopover sites (Seewagen, 2008; Seewagen and Slayton, 2008; Seewagen et al., 2011). These urban stopover sites allow migrant birds to generate similar amounts of fat than those individuals using areas of native vegetation with low human disturbance located away from cities (Liu and Swanson, 2014). The absence of differences in feather wear and ectoparasite load in both species also indicates that both UGAs and non-urban conditions have similar habitat quality (Delgado-V and French, 2012). Furthermore, the similar recorded densities and capture rates of both species in urban and non-urban sites also

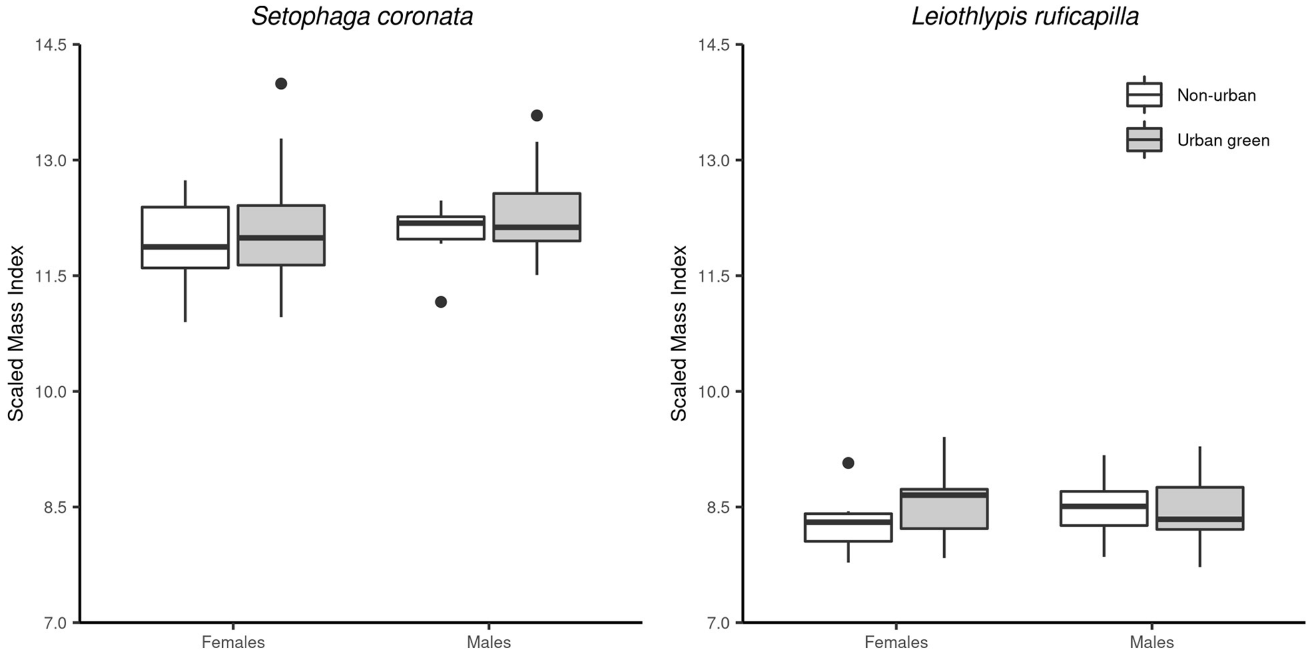

FIGURE 4 | Calculated standardized-mass index (SMI) for *S. coronata* **(left panel)** and *L. ruficapilla* **(right panel)** as a measurement of body condition. We show SMI values for both migrant bird species by sex in both habitat conditions. The SMI did not differ between sexes and habitats for both species.

support this claim (Bock and Jones, 2004). We found a slightly higher capture rate for *S. coronata* in UGAs relative to non-urban areas, which may represent an increment in capture rates due to compact bird densities in a limited space. However, it is important to notice that the absence of records or the low densities of both migrant species in our urban matrix sites indicate that they avoid urban habitats with high built cover and low abundance of trees as have been reported before (Zúñiga-Vega et al., 2019).

Overwintering migrant birds populations tend to present segregation by sex and age categories when they occupy areas with heterogeneous habitat quality (Sherry and Holmes, 1996; Albert et al., 2020). Adult males control better quality habitats, and females and juvenile males use lower quality habitats (Sherry and Holmes, 1996). We did not detect any differences by sex within habitat types, which indicates that UGAs offer resources that allow populations un-skewed by sex or with similar differences as in non-urban habitats (Sherry and Holmes, 1996; Liu and Swanson, 2014). Our result for *L. ruficapilla* suggests this is the case between their male and female population in the region, regardless of habitat type. Our selected SMI model for *L. ruficapilla* shows relevant statistical differences given by sex, but the effect might be biologically irrelevant [∼0.1% difference in *L. ruficapilla* mean mass (g); **Table 4**]. However, higher capture rates and more flight-feather wear in males may indicate accentuated territorial behavior (Murphy et al., 2001). Given that they are insect forage gleaners, more flight-feather wear in *L. ruficapilla* males can also reflect the use of denser vegetation. Furthermore, their lower ectoparasite load support that they occupy better quality habitats (Delgado-V and French, 2012). These differences by sex can also be attributed to the earlier arrival of males relative to females in overwintering, but this topic requires further research (Francis and Cooke, 1986).

The correlation between the body condition (SMI) and the fat categories in *S. coronata*, and the positive trend between these variables shown by *L. ruficapilla* indicate that the SMI reflects differences in the abundance of their energetic reserves (Peig and Green, 2009; Labocha and Hayes, 2012). Most of our captured birds for both focal species presented low-fat values (1–4 on a scale of 8; Kaiser, 1993; **Figure 5**). While this may be perceived as birds inhabiting low-quality habitats, we have a different interpretation. Our capture period encompassed the moment of the annual cycle of migrant warblers where they just established winter territories and are finishing their recovery from the fall migration (La Sorte et al., 2016, 2017; Albert et al., 2020). As a result, most migrant birds will show low or intermediate fat values because they have not reached the period of winter where they become hyperphagic in preparation for the spring northbound migration (Sherry and Holmes, 1996; Albert et al., 2020).

While our recapture data for both species in UGAs and non-urban areas was low, it was not different from those previously reported in different regions of the Neotropics (Ruiz-Gutiérrez et al., 2012; Monroy-Ojeda et al., 2013; Valdez-Juárez et al., 2018). Low recaptures rates in mist-nets are common for migratory warblers during the winter, even at sites where these birds present strong territoriality and philopatry (Monroy-Ojeda et al., 2013). Our data is very similar to that reported by Monroy-Ojeda et al. (2013) for an UGA in central Mexico. While running a winter banding station in the botanical garden of the city

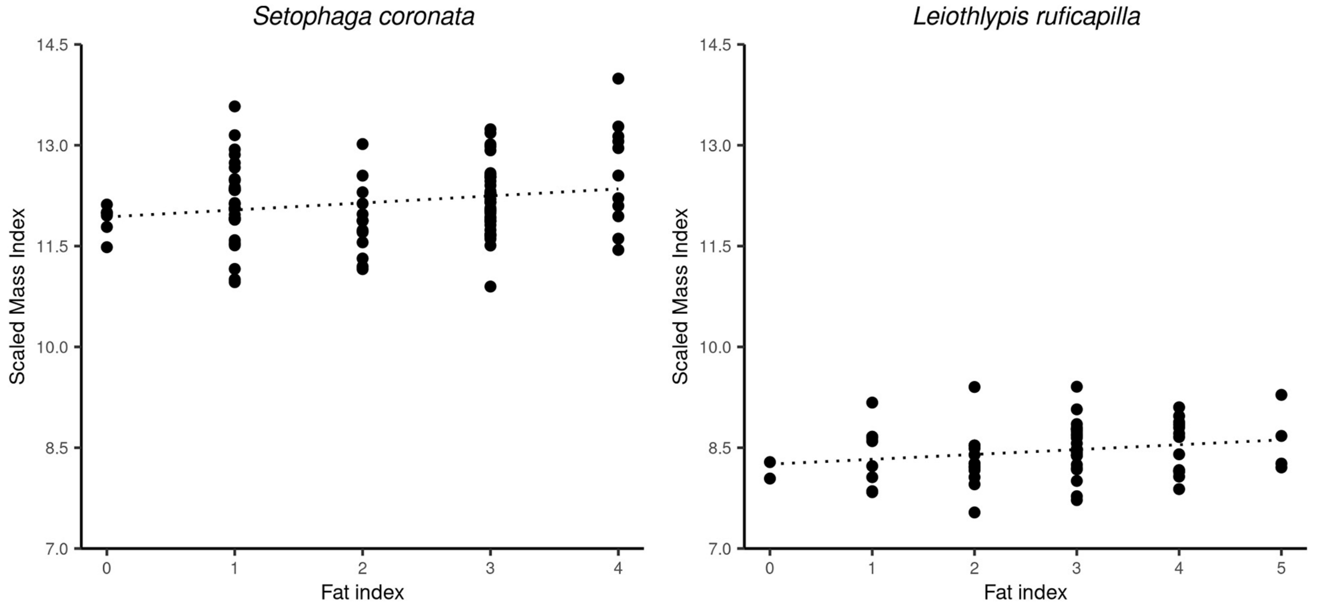

FIGURE 5 | Correlations between the calculated standardized mass index (SMI) and the measured fat index for individuals of *S. coronata* **(left panel)** and *L. ruficapilla* **(right panel)**. *S. coronata* showed a positive correlation, while *L. ruficapilla* did not. However, the latter presented a positive trend.

of Oaxaca for 10 years, these authors reported that recaptures from the same season for warblers (repeats that indicate winter residency) average 6.7% of all banded individuals. They also found that recaptures from different years, that indicate winter fidelity for a site, are higher than recaptures from the same season, suggesting that it is hard to recapture birds during the same wintering period. Our recapture data for only one season, along with the information reported by Monroy-Ojeda et al. (2013) and visual recaptures of some of our banded individuals by birdwatchers at our study sites, suggest that both species were maintaining winter residency both in urban green and non-urban areas at our study site. However, this topic requires further study.

To successfully survive their complex annual cycle, migratory birds require good habitat quality throughout all the geographic areas they use while breeding, migrating, and wintering (Schuster et al., 2019; Albert et al., 2020). Their probability of survival in one stage of their annual cycle can be overturned by cumulative carry-over effects from previous stages (Sherry and Holmes, 1996; Albert et al., 2020). Our data indicate that for *S. coronata* and *L. ruficapilla*, tropical cities can maintain overwintering bird populations with similar individual quality to those present in natural vegetation habitats located outside cities, acting as a habitat of sufficient quality to allow them to complete their complex annual cycle successfully.

Due to their use of urban areas during winter as non-breeders, these species would be categorized as urban utilizers under Fischer et al. (2015) classification. These authors apply this category to species that "occur in urban environments as non-breeders or as breeders that are present only because of dispersal from adjacent natural areas." However, since our data suggest that migratory species can overwinter successfully inside urban areas, being independent of non-urban natural vegetation habitats, they should be considered winter urban dwellers (species whose persistence in an urbanized landscape is independent of natural areas). Using this category will acknowledge the importance of urban areas for some species of this important group of birds and help to create urban management strategies that include migrant birds and their conservation.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because we complied with all legal requirements to capture birds. We also followed all the codes of conduct of the birds' capture network to which we belong (BIRDS.MX). Our institution acknowledges our animal management practices during fieldwork. Additionally, we followed "The guidelines to the use of wild birds in research." Ed. Fair, J. M. Third edition. 2010.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.779507/full#supplementary-material

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Conclusión

El uso de áreas urbanas neotropicales por las aves migratorias de invierno es el resultado de la asociación de los rasgos funcionales de las especies con las características del hábitat. Es evidente que la urbanización representa diversas fuentes de riesgo, al reducir la riqueza de especies y las abundancias de aves migratorias. No obstante, los resultados de esta tesis indican los ecosistemas urbanos neotropicales de México tienen el potencial para proporcionar un valioso hábitat de invernada para algunas aves migratorias.

La evaluación que realicé en la región urbana del Bajío, al oeste de México, mostró que el ensamble de aves migratorias está compuesto principalmente por gremios de aves insectívoras y granívoras (capítulo II). Al contrastar los ambientes silvestres, productivos y urbanos de la región urbana, los ambientes silvestres resultaron ser los más importantes como hábitat de invernada para las aves migratorias. Estos ambientes silvestres cuentan con la mayor riqueza de especies y las poblaciones más densas. Los ambientes agrícolas destacaron por albergar la mayor riqueza de especies y densidades poblacionales de aves granívoras. Los ambientes urbanos mostraron la menor riqueza de especies y de densidades poblacionales. Sin embargo, los ensambles de aves migratorias urbanas son complejos. El ensamble de aves migratorias urbanas estuvo dominado por individuos insectívoros cuyas especies se caracterizan por presentar rasgos funcionales asociados a hábitats boscosos, al tener preferencia por hábitats densos y forrajear alimento en el follaje de estratos vegetales elevados. Las diferencias que encontré entre los ensambles de aves migratorias de los tres ambientes refleja que los ambientes productivos y urbanos tienen procesos de filtrado ambiental distinto.

El contraste que hice entre los tres ambientes en la región urbana del Bajío también mostró que hay un conjunto de especies de aves migratorias que comparten y algunas especies de este conjunto suelen ser abundantes. La presencia de este grupo de aves señala que los tres ambientes comparten elementos de hábitat que promueven su presencia, pero las características como su estructura y densidad modulan sus abundancias poblacionales.

Mi investigación sobre el papel de las Áreas Verdes Urbanas (AVUs) neotropicales en la Ciudad de México mostró que son muy importantes para las aves migratorias (capítulo III). La principales características de las AVUs que promueven la riqueza de especies y las abundancias poblacionales de aves migratorias es la densidad y la cobertura de árboles.

También encontré que el contexto espacial en el que las AVUs se encuentran en la ciudad puede ser irrelevante en la similitud de especies que podemos encontrar. Sugerimos que esta irrelevancia entre el contexto espacial de las AVUs y el ensamble de aves migratorias se debe a su alta capacidad de movilidad. Además, el papel del arbolado urbano en el fomento de aves migratorias también ocurre fuera de las AVUs, por lo que su papel también es importante en esta función incluso en la matriz urbana. Estos hallazgos destacan el papel positivo de los elementos de hábitat arbóreos, tanto individualmente como en conjunto, en el hábitat a escala local de las aves migratorias. Por lo tanto, dado que el ensamble de aves migratorias urbanas se caracteriza por sus rasgos funcionales de hábitats boscosos y el arbolado urbano se asocia positivamente con su riqueza de especies y sus abundancias poblacionales, en este trabajo propongo que los ambientes urbanos funcionan como bosques simplificados para las aves migratorias.

Finalmente, también demostré que para dos especies de aves migratorias abundantes que usé como modelos, los ambientes urbanos les proporcionan hábitats de calidad similar al que les ofrecen los ambientes silvestres (capítulo IV). En ambas especies evalué la calidad del hábitat a través de su condición corporal individual y sus densidades poblacionales. Los valores de estas características los contrasté entre las poblaciones de ambientes urbanos y silvestres. Este estudio fue el primero en su tipo en evaluar la calidad del hábitat urbanos para aves migratorias invernantes. Por ello, recomiendo que ciertas especies de aves migratorias abundantes deben clasificarse como habitantes urbanos invernales, con el propóstiso de resaltar su consideración en el manejo urbano.

La evaluación de su condición corporal la realicé a través de establecer un programa de monitoreo de aves urbanas de invierno. Este monitoreo se constituyó de distintas estaciones de monitoreo que establecimos dentro de AVUs en la ciudad de Morelia, Michoacán, y en los ambientes silvestres de alrededor. El establecimiento de este programa de monitoreo lo desarrollé durante esta tesis y se pretende mantener indefinidamente. Hasta el momento se ha realizado por cuatro años consecutivos.

Los hallazgos de este proyecto doctoral resaltan la necesidad de estrategias de gestión urbana que prioricen el mantenimiento y mejora de estructuras de vegetación complejas, especialmente enfocada a los árboles. Integrar estas estrategias en la planificación y desarrollo urbanos puede aumentar la capacidad no aprovechada de las ciudades para fomentar poblaciones de aves migratorias, contribuyendo a objetivos más amplios de conservación de la biodiversidad.

Los esfuerzos futuros de investigación en áreas urbanas deben centrarse en las características específicas del hábitat local dentro de la matriz urbana que impulsan la distribución y aptitud de diferentes especies de aves migratorias. Por ejemplo, entender la interacción de especies de aves migratorias específicas con especies de árboles específicas puede brindarnos información sobre los mecanismos por los cuáles se da el proceso de filtrado ambiental en ambientes urbanos. Comprender estas asociaciones a una escala local también permite intervenciones de conservación urbana dirigidas. Asimismo, también es muy importante conocer el papel de la urbanización en las poblaciones de aves migratorias a largo plazo, ya que no existe esta información en el país. Los programas de monitoreo dirigidos a entender las tendencias poblacionales a través del tiempo, como el desarrollado de este proyecto doctoral, son una herramienta muy útil para hacerlo.

Las áreas urbanas neotropicales presentan una oportunidad subutilizada para fomentar su uso por aves migratorias invernantes. Es necesario un esfuerzo interdisciplinario entre urbanistas, ecólogos y conservacionistas para diseñar e implementar planes de desarrollo urbano que consideren una perspectiva de su manejo como ecosistema urbano. Estos planes requieren una perspectiva que atienda las necesidades humanas, así como la protección y mejora de las condiciones ambientales para la vida silvestre que utiliza los ambientesáreas urbanos, como lo propongo en este proyecto doctoral con aves migratorias. Por ello, La asosiación de las aves migratorias con áreas urbanas representa una oportunidad factible para posicionar a las ciudades como áreas clave que inspiren y promuevan soluciones al cambio global actual.

Anexos

Capítulo I

Métodos

La revisión sistemática del estado del arte del tema [1] la realicé mediante el método de investigación de tejido o «*research weaving*» (ver [2]). La búsqueda de literatura la realicé entre el 26 y 28 de julio a través del motor *Web of Science* (WOS) (https://www.webofknowledge.com) bajo el criterio de tema (TS). Hice una búsqueda por cada clase taxonómica de vertebrado: aves, mamíferos, reptiles y anfibios. Para realizarlas combiné dos conjuntos de palabras clave: uno estático para todas las búsquedas y uno dinámico para cada una de las cuatro clases. Las palabras clave del conjunto estático eran las siguientes: (urban* OR city OR town) AND (habitat OR resource* OR environmental condition OR limiting resource OR interaction OR competition OR temperature OR heat OR water OR light OR humidity OR vegetation OR disturbance OR pollut* OR sound OR noise OR social OR econom* OR activit*) AND (relat* OR affect* OR drive OR modif* OR increas* OR decreas* OR influenc* OR assess* OR gradient OR induce OR determine). Las palabras clave de los cuatro conjuntos dinámicos fueron las siguientes: para aves (bird* OR avian); para mamiferos (mammal* OR rodent* OR chiropter* OR bat* OR Soricomor* OR primate* OR carnior* OR Artiodact* OR diprotodont* OR didelphimor* OR Dasyuromor* OR marsupial* OR lagomor* OR afromosor* OR Eulipot* OR Cingul* OR peramelemor* OR scandent* OR Perissodact* OR ungulate* OR macroscelid* OR pilos* OR monotrem* OR probosci* OR elephant* OR feral* OR domestic*); para reptiles (reptile* OR turtle* OR lizard* OR snake* OR crocodile* OR alligator*); y para anfibios (amphibian* OR caecilian* OR Salamander* OR Newt* OR Mudpuppie* OR Frog* OR Toad*). Con el método de investigación de tejido que usé para esta revisión de literatura no busqué una profundización intensiva del tema por cada clase de vertebrado, busqué generar un entendimiento amplio y general del tema a través de los distintos grupos taxonómicos. El criterio de inclusión de estudios en la revisión fue que se considerara uno o más parámetros del hábitat urbano, ya sea de forma cuantitativa o cualitativa, y que lo relacionen con algún parámetro de rendimiento medido en vertebrados. Otro criterio fue que no consideré un umbral temporal, ni artículos de revisión o de investigaciones teóricas, de acuerdo a la clasificación de WOS. Los resultados de la búsqueda se reordenaron por el criterio de relevancia y generé una lista con los estudios seleccionados dentro de los primeros 1000 registros.

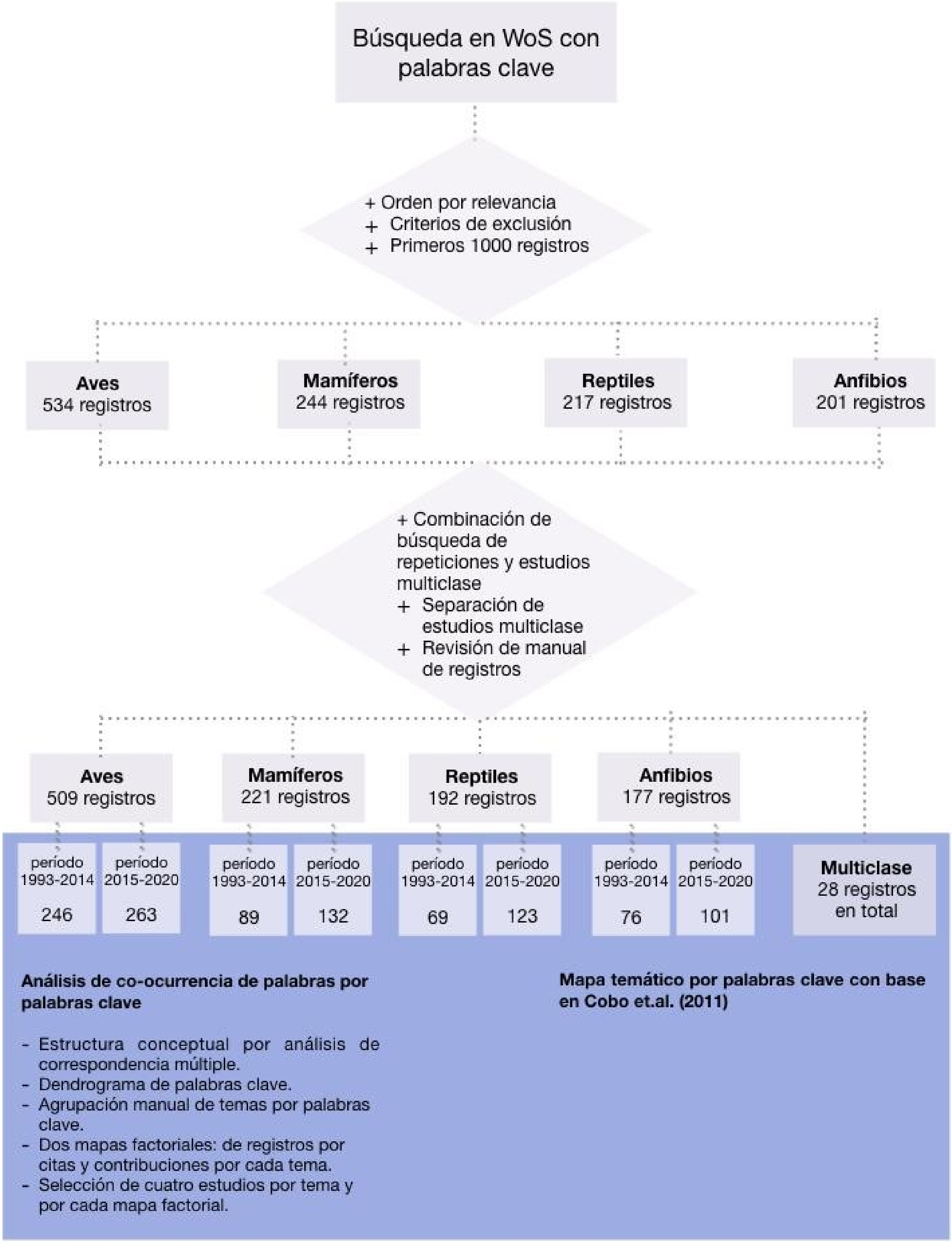
Las cuatro listas con las investigaciones que se obtuvieron por grupo de vertebrados se procesaron por medio del lenguaje de programación R-lang [3] y el paquete «*bibliometrix*» [4]. Los registros se filtraron y revisaron de acuerdo a los criterios de selección. Posteriormente se combinaron para identificar información repetida. Los registros repetidos se revisaron y las investigaciones que abordaban dos o más clases se removieron y se agruparon en una quinta lista independiente bajo la clasificación de investigaciones multi-clase. También se realizó una revisión manual de las listas de cada clase para buscar investigaciones similares e incluirlas en el nuevo listado. Ninguna lista contaba con registros repetidos.

Para evaluar el estado del arte del tema dividí cada lista con la selección de estudios por cada clases de vertebrados en dos periodos: antes del año 2015 y 2015-2020. Esta configuración dio un total de siete conjuntos de estudios seleccionados, incluyendo la lista multi-clase. Posteriormente cada una se procesó utilizando las palabras clave de sus investigaciones por medio de un análisis de co-palabras con el paquete «*bibliometrix*» [4]. El propósito de este análisis es generar una estructura conceptual con los registros de cada conjunto y con base en una red de co-ocurrencia de sus palabras clave [4]. Esto permite aplicar un Análisis de Correspondencia Múltiple en las palabras clave y evaluar su similitud por ocurrir en investigaciones similares [4]. La similitud entre conceptos la evalúo a través de un dendrograma y el número de agrupaciones resultantes entre cada lista las selecciono manualmente con base en mis observaciones y mi criterio. Cada agrupación puede considerarse como un conjunto de investigaciones que tratan temas similares dentro de la lista [4]. Posteriormente, de cada conjunto generé un mapa factorial con las investigaciones con el mayor número de citas y otro con las investigaciones que más contribuyeron a las agrupaciones. La selección de investigaciones se hizo con reemplazo para en ambos mapas factoriales. De cada grupo temático de cada conjunto seleccioné un máximo de cuatro estudios con el mayor número de citas y cuatro estudios relevantes para la agrupación . El total de estudios arrojados de cada conjunto por este procesamiento se revisaron y se seleccionaron manualmente bajo mis criterios, para obtener una visión amplia, heterogénea y relevante de los estudios de vertebrados en el hábitat urbano. Finalmente, para cada conjunto, excepto el multiclase, se generó un diagrama estratégico [5] con base en Cobo et al. (2011). Para generarlo también se procesaron las palabras clave de todos los estudios en cada conjunto por análisis de co-palabras, de acuerdo al protocolo de «*bibliometrix*» [4]. El diagrama de la figura 1 muestra un eje de densidad y otro de centralidad, y cada cuadrante representa temas específicos indicados en la figura.

Figura 1. Diagrama estratégico por análisis de co-ocurrencia de palabras. Modificado de Cobo et al., (2011).

Las principales ventajas del método de revisión por investigación de tejido es que permite una búsqueda flexible para realizar una revisión temática, que procura la transparencia, permite conocer equipos clave en el tema pero también otras contribuciones similares e importantes. También permite, de la mano de «*bibliometrix*» y R-lang, hacer transparente y reproducible el proceso de revisión a través de código [2,6].

El mapa conceptual de la búsqueda y revisión se muestra a continuación (Figura 2). También se anexan acompañando este material suplementario a las monografías resultantes del análisis de co-ocurrencia de palabras de cada conjunto y lista de registros bibliográficos. Las monografías contienen los diagramas estratégicos, los dendrogramas de agrupaciones de palabras y los mapas factoriales de selección de estudios por citas y contribuciones.



Análisis de co-ocurrencia de palabras por palabras clave

- Estructura conceptual por análisis de correspondencia múltiple.
- Dendrograma de palabras clave.
- Agrupación manual de temas por palabras clave.
- Dos mapas factoriales: de registros por citas y contribuciones por cada tema.
- Selección de cuatro estudios por tema y por cada mapa factorial.

Mapa temático por palabras clave con base en Cobo et.al. (2011)

Figura 2. Mapa conceptual del proceso de búsqueda y revisión

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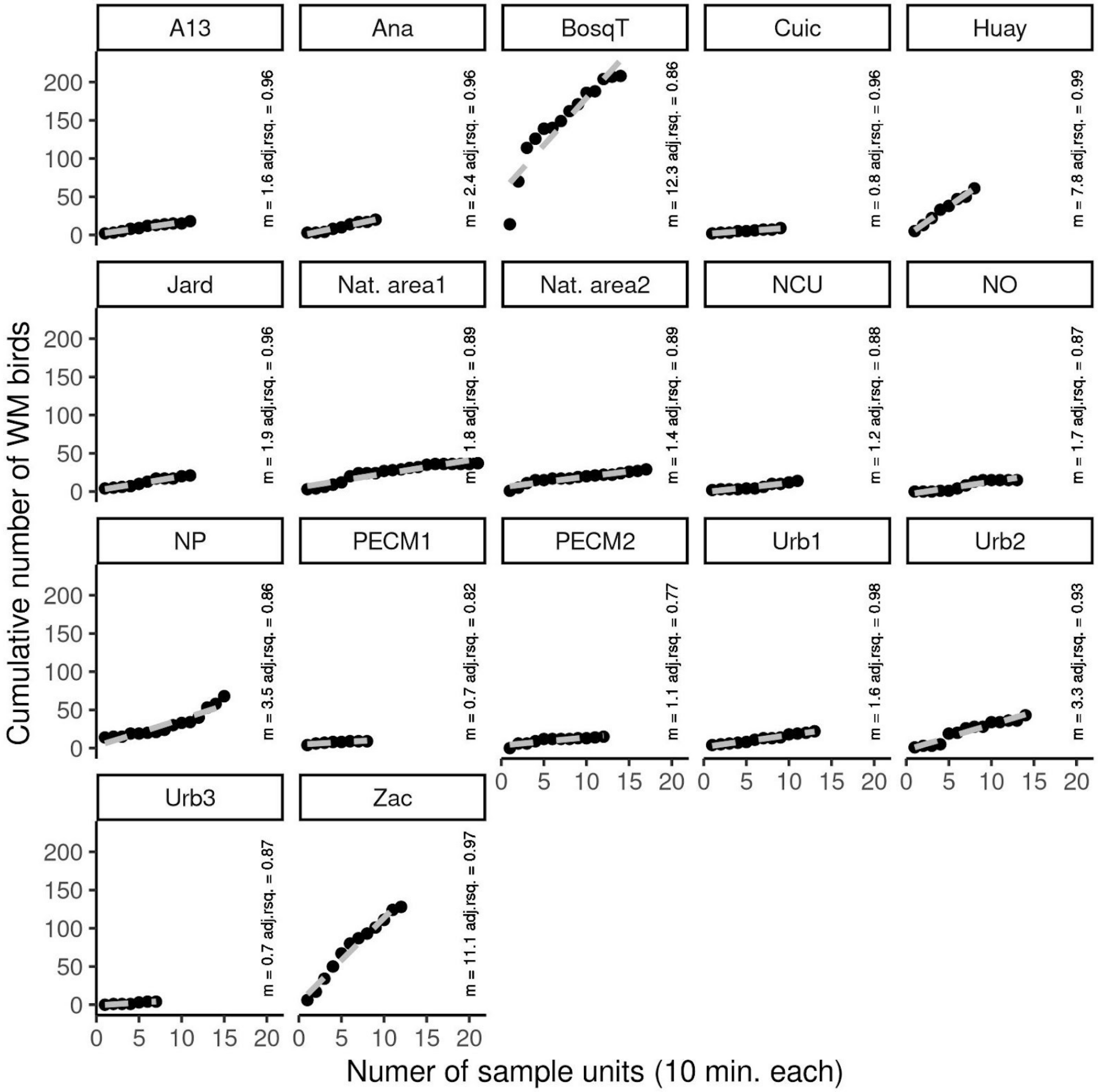
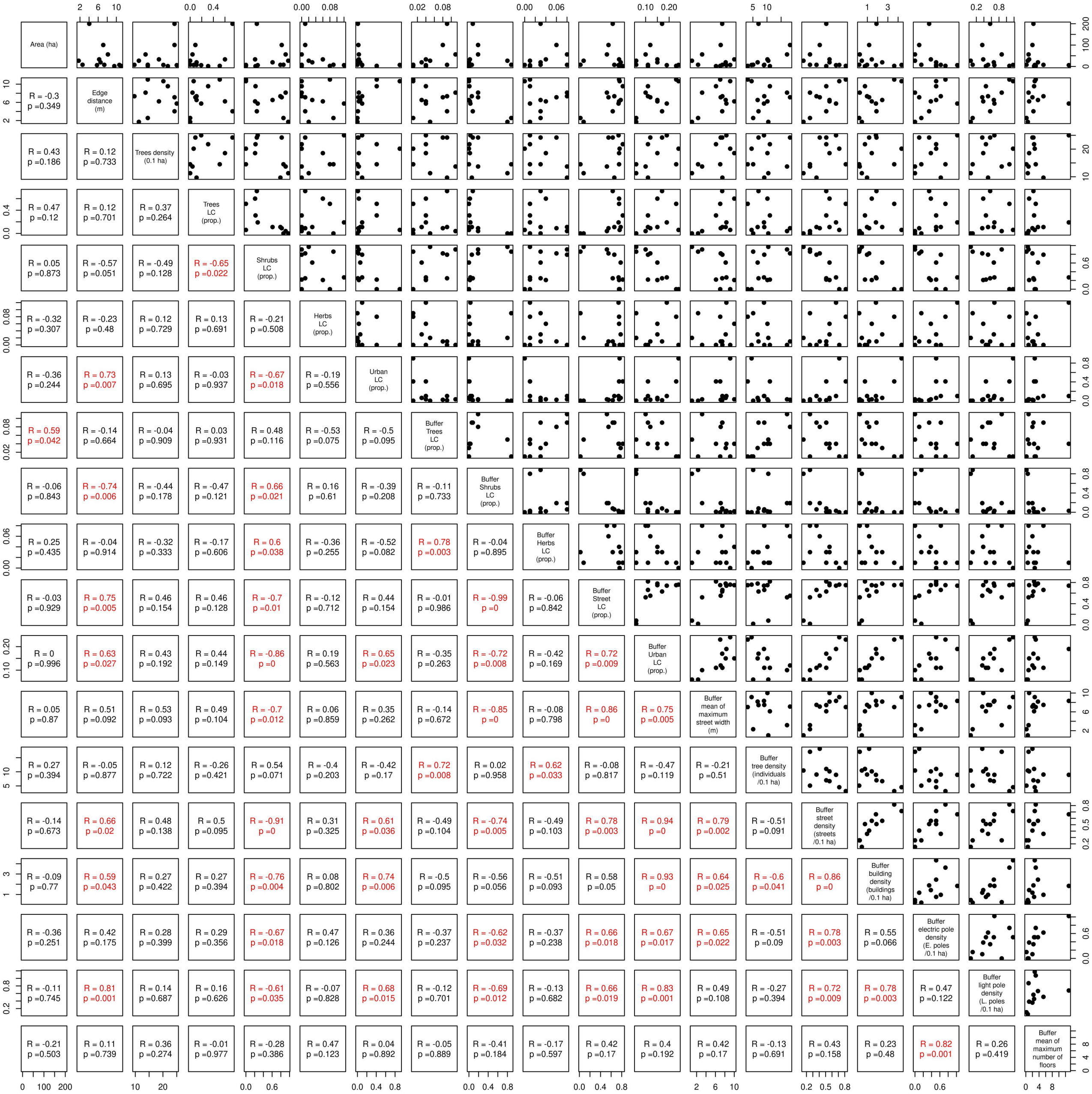
Capítulo III

Supplementary Material 1. Relative abundance of overwintering migrant birds as the rate of observed individuals per each sampling unit (individuals/10 min) in all our bird surveys. The rate is calculated through a linear model using the cumulative number of individuals as the response variable and the number of sampling units as a fixed factor. The slope and the adjustes R squared are shown for each panel.



Supplementary Material 2. Pearson correlation matrix that includes all UGAs quantified local and buffer habitat features. Correlations with $p < 0.05$ are indicated with the color red.



Supplementary Material 3. Presence-absece of Resident species recorded during our study in the three considered habitat types, with their respective trophic guild.

Family	Specie	Trophic guild	Na. area	UGA	Urb
Aegithalidae	*Psaltriparus minimus*	Insectivore	1	1	1
Cardinalidae	*Cardinalis cardinalis*	Granivore	0	1	0
Cardinalidae	*Passerina caerulea*	Insectivore	0	1	0
Cardinalidae	*Pheucticus melanocephalus*	Insectivore	1	1	1
Cardinalidae	*Piranga flava*	Insectivore	1	0	0
Certhiidae	*Certhia americana*	Insectivore	1	0	0
Columbidae	*Columba livia*	Granivore	0	1	1
Columbidae	*Columbina inca*	Granivore	0	1	1
Corvidae	*Aphelocoma woodhouseii*	Omnivore	0	1	0
Corvidae	*Cyanocitta stelleri*	Omnivore	1	0	0
Emberizidae	*Aimophila ruficeps*	Granivore	0	1	0
Emberizidae	*Arremon virenticeps*	Granivore	1	0	0
Emberizidae	*Atlapetes pileatus*	Granivore	1	1	0
Emberizidae	*Diglossa baritula*	Nectarivore	1	1	1
Emberizidae	*Junco phaeonotus*	Granivore	1	1	0
Emberizidae	*Melospiza melodia*	Granivore	0	1	1
Emberizidae	*Melozone fusca*	Granivore	0	1	1
Emberizidae	*Melozone kieneri*	Granivore	0	1	0
Emberizidae	*Oriturus superciliosus*	Granivore	1	0	0
Emberizidae	*Pipilo maculatus*	Granivore	1	1	0
Emberizidae	*Spizella atrogularis*	Granivore	0	1	0
Emberizidae	*Spizella passerina*	Granivore	1	1	0
Emberizidae	*Sporophila torqueola*	Granivore	0	1	0
Fringillidae	*Euphonia elegantissima*	Frugivore	1	0	0
Fringillidae	*Haemorhous mexicanus*	Granivore	0	1	1
Fringillidae	*Spinus pinus*	Granivore	0	1	0
Fringillidae	*Spinus psaltria*	Granivore	1	1	1
Hirundinidae	*Petrochelidon pyrrhonota*	Insectivore	0	1	0
Hirundinidae	*Tachycineta thalassina*	Insectivore	1	0	0
Icteridae	*Icterus abeillei*	Insectivore	0	1	1
Icteridae	*Icterus parisorum*	Insectivore	1	1	0
Icteridae	*Molothrus aeneus*	Granivore	0	0	1
Icteridae	*Quiscalus mexicanus*	Omnivore	0	1	1

Supplementary Material 4. (Continues)

Family	Specie	Trophic guild	Na. area	UGA	Urb
Mimidae	*Melanotis caerulescens*	Insectivore	1	1	0
Mimidae	*Mimus polyglottos*	Insectivore	0	1	0
Mimidae	*Toxostoma curvirostre*	Insectivore	0	1	1
Paridae	*Poecile sclateri*	Insectivore	1	0	0
Parulidae	*Basileuterus belli*	Insectivore	1	0	0
Parulidae	*Basileuterus rufifrons*	Insectivore	1	1	0
Parulidae	*Cardellina rubra*	Insectivore	1	0	0
Parulidae	*Geothlypis nelsoni*	Insectivore	0	1	0
Parulidae	*Myioborus miniatus*	Insectivore	1	0	0
Parulidae	*Oreothlypis superciliosa*	Insectivore	1	1	0
Passeridae	*Passer domesticus*	Omnivore	0	1	1
Peucedramidae	*Peucedramus taeniatus*	Insectivore	1	0	0
Picidae	*Colaptes auratus*	Insectivore	1	0	0
Picidae	*Melanerpes formicivorus*	Insectivore	1	1	0
Picidae	*Picoides scalaris*	Insectivore	0	1	1
Psittacidae	*Myiopsitta monachus*	Omnivore	0	1	0
Ptilogonatidae	*Ptilogonys cinereus*	Insectivore	1	1	1
Sittidae	*Sitta carolinensis*	Insectivore	1	1	0
Trochilidae	*Amazilia beryllina*	Nectarivore	0	1	1
Trochilidae	*Colibri thalassinus*	Nectarivore	1	0	0
Trochilidae	*Cynanthus latirostris*	Nectarivore	0	1	1
Trochilidae	*Eugenes fulgens*	Nectarivore	1	1	0
Trochilidae	*Hylocharis leucotis*	Nectarivore	1	1	0
Trochilidae	*Selasphorus platycercus*	Nectarivore	1	0	0
Troglodytidae	*Catherpes mexicanus*	Insectivore	0	1	0
Troglodytidae	*Thryomanes bewickii*	Insectivore	0	1	1
Troglodytidae	*Troglodytes aedon*	Insectivore	1	1	0
Turdidae	*Catharus occidentalis*	Insectivore	1	0	0
Turdidae	*Myadestes occidentalis*	Insectivore	1	1	0
Turdidae	*Turdus assimilis*	Insectivore	1	0	0
Turdidae	*Turdus migratorius*	Insectivore	1	1	1
Turdidae	*Turdus rufopalliatus*	Insectivore	0	1	1

Supplementary Material 5. (Continues)

Family	Specie	Trophic guild	Na. area	UGA	Urb
Tyrannidae	*Camptostoma imberbe*	Insectivore	0	1	0
Tyrannidae	*Contopus pertinax*	Insectivore	1	1	0
Tyrannidae	*Empidonax fulvifrons*	Insectivore	0	1	0
Tyrannidae	*Empidonax occidentalis*	Insectivore	0	1	0
Tyrannidae	*Myiarchus cinerascens*	Insectivore	0	1	0
Tyrannidae	*Myiopagis viridicata*	Insectivore	1	0	0
Tyrannidae	*Pyrocephalus rubinus*	Insectivore	0	1	0
Tyrannidae	*Tyrannus vociferans*	Insectivore	0	1	0
Vireonidae	*Vireo huttoni*	Insectivore	1	1	0

Supplementary Material 6. GLM pools that evaluate the role of UGA's habitat characteristics: Area, edge distance, tree density and both locan and buffer land use cover proportion (LUC) on the overwintering migrant bird species (OWM sp. richness). We only assessed the role of UGAs total area on the total number of bird species. We use gaussian GLMs to assess OWM sp. Richness and link: log, gaussian GLMs to assess the total bird species- area relationship. Models were selected using the Akaike criterion.

UGA characteristic	**Model structure**	**K**	**AICc**	**Δ AICc**	**AICcWt**	**Cum. Wt**
Total bird sp. richness						
Area	log(Sp. richness) ~ log(area)	3	73.76	0.00	0.51	0.51
	Sp. richness ~ area	3	73.96	0.20	0.46	0.97
	Null	2	79.26	5.50	0.03	1.00
OWM sp. richness						
Area	sp. richness ~ area	3	65.34	0.00	0.62	0.62
	Null	2	67.24	1.90	0.24	0.85
	log(sp. richness) ~ log(area)	3	68.21	2.87	0.15	1.00
Distance	Null	2	67.24	0.00	0.83	0.83
	OWM sp. richness ~ distance	3	70.48	3.24	0.17	1.00
Trees/0.1 ha	Sp. richness ~ Trees/0.1 ha	3	57.11	0.00	0.48	0.48
	log(Sp. richness) ~ log(Trees/0.1 ha)	3	57.12	0.01	0.48	0.95
	Null	2	61.73	4.62	0.05	1.00

Supplementary Material 7. (Continues)

UGA characteristic	Model structure	K	AICc	Δ AICc	AICcWt	Cum. Wt
Local LUC	Null	2	67.24	0.00	0.30	0.30
	Sp. richness ~ Arboreal prop.	3	67.47	0.23	0.26	0.56
	Sp. richness ~ Shrub prop.	3	68.22	0.97	0.18	0.74
	Sp. richness ~ Urban prop.	3	70.66	3.42	0.05	0.80
	Sp. richness ~ Herbs prop.	3	70.76	3.52	0.05	0.85
	Sp. richness ~ Arboreal prop. + Herbs prop.	4	71.72	4.48	0.03	0.88
	Sp. richness ~ Arboreal prop. + Shrub prop.	4	71.77	4.53	0.03	0.91
	Sp. richness ~ Arboreal prop. + Urban prop.	4	71.81	4.57	0.03	0.94
	Sp. richness ~ Urban prop. + Shrub prop.	4	72.26	5.02	0.02	0.96
	Sp. richness ~ Shrub prop. + Herbs prop.	4	72.31	5.07	0.02	0.99
	Sp. richness ~ Herbs prop. + Urban prop.	4	75.29	8.05	0.01	0.99
	Sp. richness ~ Herbs prop. + Urban prop. + Shrub prop.	5	76.70	9.45	0.00	1.00
	Sp. richness ~ Herbs prop. + Arboreal prop. + Shrub prop.	5	77.40	10.15	0.00	1.00
	Sp. richness ~ Herbs prop. + Arboreal prop. + Urban prop.	5	77.76	10.52	0.00	1.00
	Sp. richness ~ Shrub prop. + Arboreal prop. + Urban prop.	5	78.05	10.81	0.00	1.00
	Sp. richness ~ Arboreal prop. + Urban prop. + Shrub prop. + Herbs prop.	6	85.35	18.11	0.00	1.00

Supplementary Material 8. (Continues)

UGA characteristic	Model structure	K	AICc	Δ AICc	AICcWt	Cum. Wt
Buffer LUC	Sp. richness ~ Urban prop.	3	66.69	0.00	0.25	0.25
	Sp. richness ~ Arboreal prop. + Urban prop.	4	67.17	0.48	0.20	0.46
	Null	2	67.24	0.55	0.19	0.65
	Sp. richness ~ Shrub prop.	3	67.84	1.14	0.14	0.79
	Sp. richness ~ Arboreal prop.	3	70.27	3.58	0.04	0.84
	Sp. richness ~ Herbs prop. + Urban prop.	4	70.84	4.15	0.03	0.87
	Sp. richness ~ Herbs prop.	3	70.85	4.16	0.03	0.90
	Sp. richness ~ Urban prop. + Shrub prop.	4	71.14	4.44	0.03	0.93
	Sp. richness ~ Arboreal prop. + Shrub prop.	4	72.08	5.39	0.02	0.95
	Sp. richness ~ Shrub prop. + Herbs prop.	4	72.37	5.67	0.01	0.96
	Sp. richness ~ Herbs prop. + Arboreal prop. + Urban prop.	5	72.50	5.81	0.01	0.97
	Sp. richness ~ Shrub prop. + Arboreal prop. + Urban prop.	5	72.74	6.05	0.01	0.99
	Sp. richness ~ Arboreal prop. + Herbs prop.	4	73.26	6.56	0.01	1.00
	Sp. richness ~ Herbs prop. + Arboreal prop. + Shrub prop.	5	76.16	9.46	0.00	1.00
	Sp. richness ~ Herbs prop. + Urban prop. + Shrub prop.	5	77.12	10.43	0.00	1.00
	Sp. richness ~ Arboreal prop. + Urban prop. + Shrub prop. + Herbs prop.	6	80.99	14.30	0.00	1.00

Supplementary Material 9. Negative binomial GLM pools that evaluate the role of UGA's habitat characteristics: edge distance, tree density and both locan and buffer land use cover proportion (LUC) on the overwintering migrant bird abundance. We used negative binomial GLMs to assess them. Models were selected using the Akaike criterion.

UGA characteristic	Model structure	K	AICc	Δ AICc	AICcWt	Cum. Wt
Distance	Null	2	66.69	0.00	0.83	0.83
	Abundance ~ distance	3	69.92	3.23	0.17	1.00
Trees/0.1 ha	Null	2	60.37	0.00	0.55	0.55
	Abundance ~ Trees/0.1 ha	3	60.73	0.36	0.45	1.00

Supplementary Material 10. (Continues)

UGA characteristic	Model structure	K	AICc	Δ AICc	AICcWt	Cum. Wt
Local LUC	Abundance ~ Arboreal prop.	3	60.65	0.00	0.35	0.35
	Abundance ~ Shrub prop.	3	62.21	1.55	0.16	0.51
	Abundance ~ Arboreal prop. + Urban prop.	4	62.82	2.16	0.12	0.63
	Abundance ~ Arboreal prop. + Shrub prop.	4	63.53	2.87	0.08	0.72
	Abundance ~ Arboreal prop. + Herbs prop.	4	63.80	3.15	0.07	0.79
	Null	2	63.92	3.27	0.07	0.86
	Abundance ~ Urban prop. + Shrub prop.	4	65.41	4.76	0.03	0.89
	Abundance ~ Shrub prop. + Herbs prop.	4	65.76	5.11	0.03	0.92
	Abundance ~ Shrub prop. * Arboreal prop.	5	66.38	5.73	0.02	0.94
	Abundance ~ Herbs prop.	3	67.24	6.58	0.01	0.95
	Abundance ~ Urban prop.	3	67.45	6.79	0.01	0.96
	Abundance ~ Herbs prop. + Urban prop. + Shrub prop.	5	67.49	6.83	0.01	0.97
	Abundance ~ Herbs prop. + Arboreal prop. + Shrub prop.	5	67.74	7.09	0.01	0.98
	Abundance ~ Herbs prop. + Arboreal prop. + Urban prop.	5	68.18	7.52	0.01	0.99
	Abundance ~ Shrub prop. + Arboreal prop. + Urban prop.	5	69.01	8.35	0.01	1.00
	Abundance ~ Herbs prop. + Urban prop.	4	71.90	11.25	0.00	1.00
	Abundance ~ Arboreal prop. + Urban prop. + Shrub prop. + Herbs prop.	6	76.27	15.61	0.00	1.00

Supplementary Material 11. (Continues)

UGA characteristic	Model structure	K	AICc	Δ AICc	AICcWt	Cum. Wt
Buffer LUC	Null	2	63.92	0.00	0.27	0.27
	Abundance ~ Urban prop.	3	64.11	0.19	0.25	0.52
	Abundance ~ Shrub prop.	3	64.58	0.66	0.20	0.72
	Abundance ~ Arboreal prop. + Urban prop.	4	66.67	2.75	0.07	0.79
	Abundance ~ Arboreal prop.	3	67.40	3.48	0.05	0.83
	Abundance ~ Herbs prop.	3	67.45	3.53	0.05	0.88
	Abundance ~ Herbs prop. + Urban prop.	4	68.08	4.16	0.03	0.91
	Abundance ~ Urban prop. + Shrub prop.	4	68.36	4.44	0.03	0.94
	Abundance ~ Arboreal prop. + Shrub prop.	4	69.11	5.19	0.02	0.96
	Abundance ~ Shrub prop. + Herbs prop.	4	69.15	5.23	0.02	0.98
	Abundance ~ Arboreal prop. + Herbs prop.	4	71.40	7.48	0.01	0.99
	Abundance ~ Shrub prop. + Arboreal prop. + Urban prop.	5	72.94	9.02	0.00	0.99
	Abundance ~ Herbs prop. + Arboreal prop. + Urban prop.	5	72.94	9.02	0.00	1.00
	Abundance ~ Herbs prop. + Urban prop. + Shrub prop.	5	74.32	10.40	0.00	1.00
	Abundance ~ Herbs prop. + Arboreal prop. + Shrub prop.	5	74.61	10.69	0.00	1.00
	Abundance ~ Arboreal prop. + Urban prop. + Shrub prop. + Herbs prop.	6	81.74	17.82	0.00	1.00

Capítulo IV

We described the green and gray habitat components in both our selected sites for capturing birds and for conducting bird censuses records. In sites for capturing birds, we described the habitat components within a 25 m radius sampling point located around each of the ten mist nets deployed at each area. In the sampling points for conducting bird censuses records, we also described the habitat components within a 25 m radius. All sites were characterized by the same person (RP-M). The green elements were quantified as following: the number of morphospecies of trees and shrubs was considered as their species richness, respectively; we counted all individuals of trees and shrubs; the mean and the standard deviation of tree height (meters) and their breast height diamater (DBH; centimeters) was obtained by selecting up to 20 individuals, considering the biggest and the smallest tree, and 18 random individuals; we also measure shrubs' maximum and minimum height (meters). The gray elements were quantified as follows: the number of doors or the number of individual constructions was considered as the number of buildings or constructions; On building structure we only considered the maximum building height; the number of artificial elements was obtained by counting poles, light poles, benches or any other non-mobile artificial object. We estimated the land use cover proportion of the tree canopy, the shrub layer, the herbaceous layer, the bare soil, and buildings. Finally, the background noise levels were constituted by their minimum (min. dB) and maximum (max. dB) decibel measurement in a five minute period, using a sound level meter (*EXTECH EN300*).

To contrast how similar were our selected sites for capturing birds within each of their considered condition (urban green areas and non-urban sites), we compared the described habitat elements withi their respective sampling points. To do this we performed a principal component analysis (PCA), followed by an oblimin rotation. To enhance our analysis we also included the ten most urbanized bird censuses point count sites (≥50% of urban impervious and building coverage) and ten natural vegetation sites located away from the city (~35 km; Querendaro County) as a reference to compare our sites. To perform our PCA we first obtained a matrix with the seven selected sites along with the mean sampling point value of all the described habitat characteristics and the standard deviation (sd) of tree height and DBH. Then, all the values of the habitat components in the resulting matrix were mean-centered and scaled by their standard deviation. We latter performed the PCA. We only kept the principal component 1 and principal component 2, as they explained 71.4% of the cumulative percentage of variance (suplemmentary material 1). The resulting PCA loadings were followed by both a varimax (orthogonal) and an oblimin (oblique) rotation to obtained the rotated dimension 1 and dimension 2. We assessed the correlation of the varimax rotated loadings through Pearson correlations. Given the correlation of the varimax rotated loadings had an R of 0.3<, we opted for the oblimin rotated loadings for our site contrast assessment (suplemmentary material 2).

Supplementary material 1. Principal Component Analysis results of sites habitat components. We show the eigenvalues, their percentage of variance explained and the cumulative percentage of variance of the principal components from most to least explanatory.

	eigenvalue	percentage of variance	cumulative percentage of variance
comp 1	9.20	46.00	46.00
comp 2	5.08	25.39	71.40
comp 3	2.84	14.19	85.59
comp 4	1.26	6.30	91.88
comp 5	1.13	5.67	97.55
comp 6	0.49	2.45	100.00

Supplementary material 2. Oblimin rotated PCA loadings one and two (ORL 1 and ORL 2, respectively) of each described green and grayhabitat component for the seven sites within a 25 m radius point: the number of morphospecies (sp. Richness) and abundance of trees and shrubs; along the mean and standar deviation of tree height (meters) and breast diamater height(BDH; cetimeters); the minimum and maximum background noise levels measured as decibels (dB); the land use cover proportion (LCP) of the tree canopy, the shrub layer, the herbaceous layer, the bare ground, and buildings; the number of artificial elements; and the maximum height of constructions (meters).

Habitat component	**ORL 1**	**ORL 2**
Tree DBH s.d.	0.99	0.12
Mean tree height	0.99	0.12
Mean tree DBH	0.98	0.10
Tree LCP	0.81	-0.31

Supplementary material 3. (Continues)

Habitat component	**ORL 1**	**ORL 2**
Tree height s.d.	0.67	0.13
Herbs LCP	0.48	-0.61
Shrubs sp. richness	0.39	-0.49
Trees abundances	0.33	-0.05
Trees sp. richness	0.25	0.11
Min. noise (dB)	0.15	0.81
Num. artificial elements	0.14	0.98
Bare ground LCP	0.13	0.94
Shrubs abundances	0.03	-0.68
Max. shrub height	-0.15	-0.13
Max. constuction height	-0.29	0.83
Shrubs LCP	-0.33	-0.95
Construction LCP	-0.54	0.70
Num. constructions	-0.56	0.69
Max. noise (dB)	-0.66	0.50
Min. shrub height	-0.75	-0.24