



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).

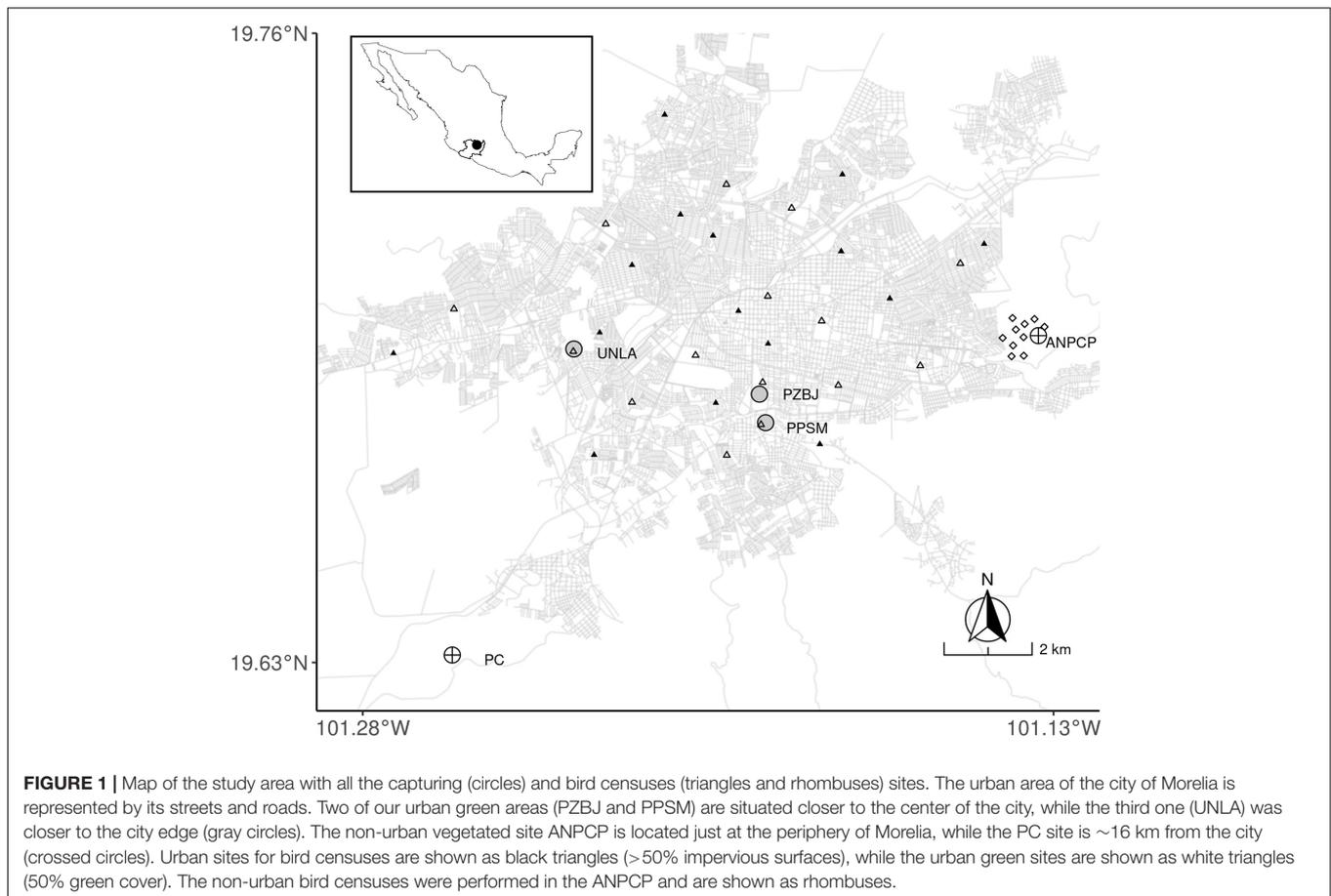
In this study, we focus on urban green areas' role in supporting the migrant bird populations of two species of warblers during their overwintering stage: *Setophaga coronata* and *Leiothlypis ruficapilla*. Migratory birds like these species need to rebuild their body condition after their long-distance 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°



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/km² (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/km² (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/km² (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. magnoliifolia*. Other dominant tree species are *Bursera cuneata*, *B. bipinnata*, *Ipomea mureocoides*, *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/km² (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 mureocoides*, *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 (~ 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),

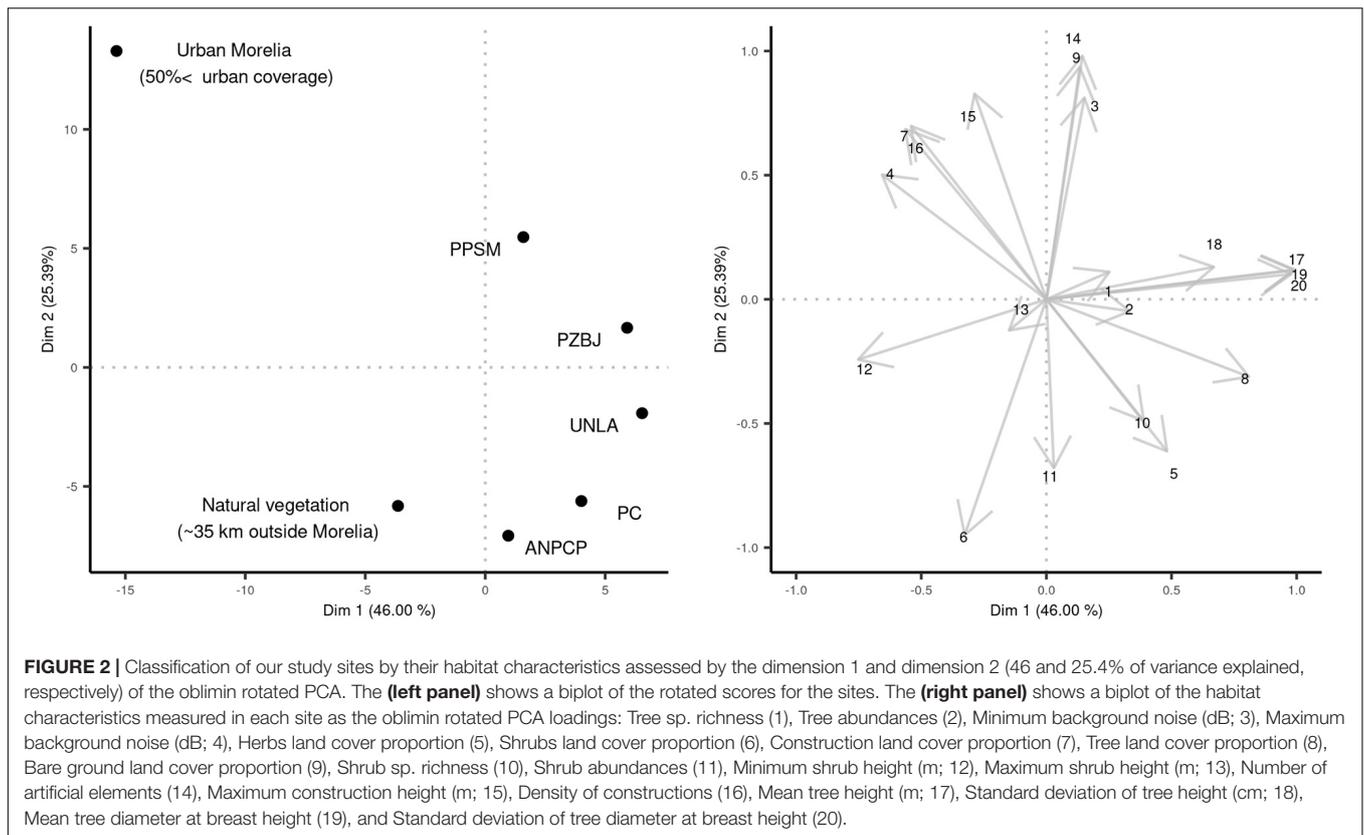
flight-feather wear, number of ectoparasites in its wing feathers, and levels of fat reserves (following Kaiser, 1993).

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



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 ($\Delta AIC < 2$). 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

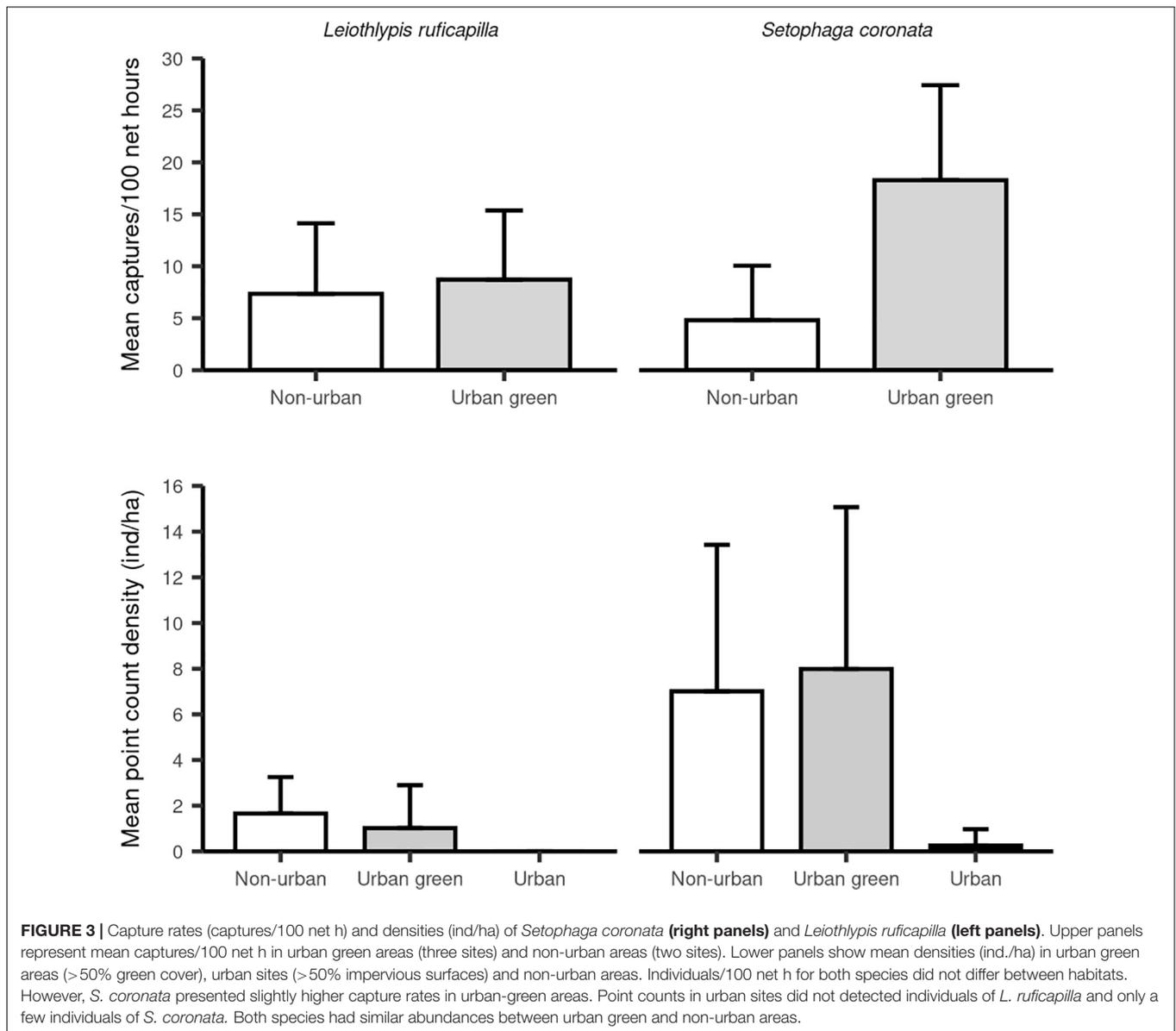
The classification of our sampling sites by their habitat characteristics (PCA oblimin rotated analysis) showed a clear separation of urban areas, UGAs, and non-urban areas by the values of dimension 1 and dimension 2 (71.4% of variance explained; **Figure 2**). Based on the oblimin rotated loadings (**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
<i>Setophaga coronata</i>	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
<i>Leiothlypis ruficapilla</i>	Non-urban/U	314014	7642928	0.01	1.00
	Non-urban/UG	385.80	08510.11		
	U/UG	1.63	0.65	1.21	0.45
		0.00	0.00	-0.01	1.00

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



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 ($\Delta AICc < 2$; **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 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	$\Delta AICc$	AICcWt		
<i>Setophaga coronata</i>	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			
<i>Leiothlypis ruficapilla</i>	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 2 | Captures rates (individuals/100 net h) of both focal migrant bird species, by sex (F, Females and M, Males) and by habitat type.

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

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
<i>Setophaga coronata</i>	Individuals/100 net h	(Intercept)	1.57	0.47	3.35
		Habitat—urban	1.34	0.56	2.38
<i>Leiothlypis ruficapilla</i>	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.

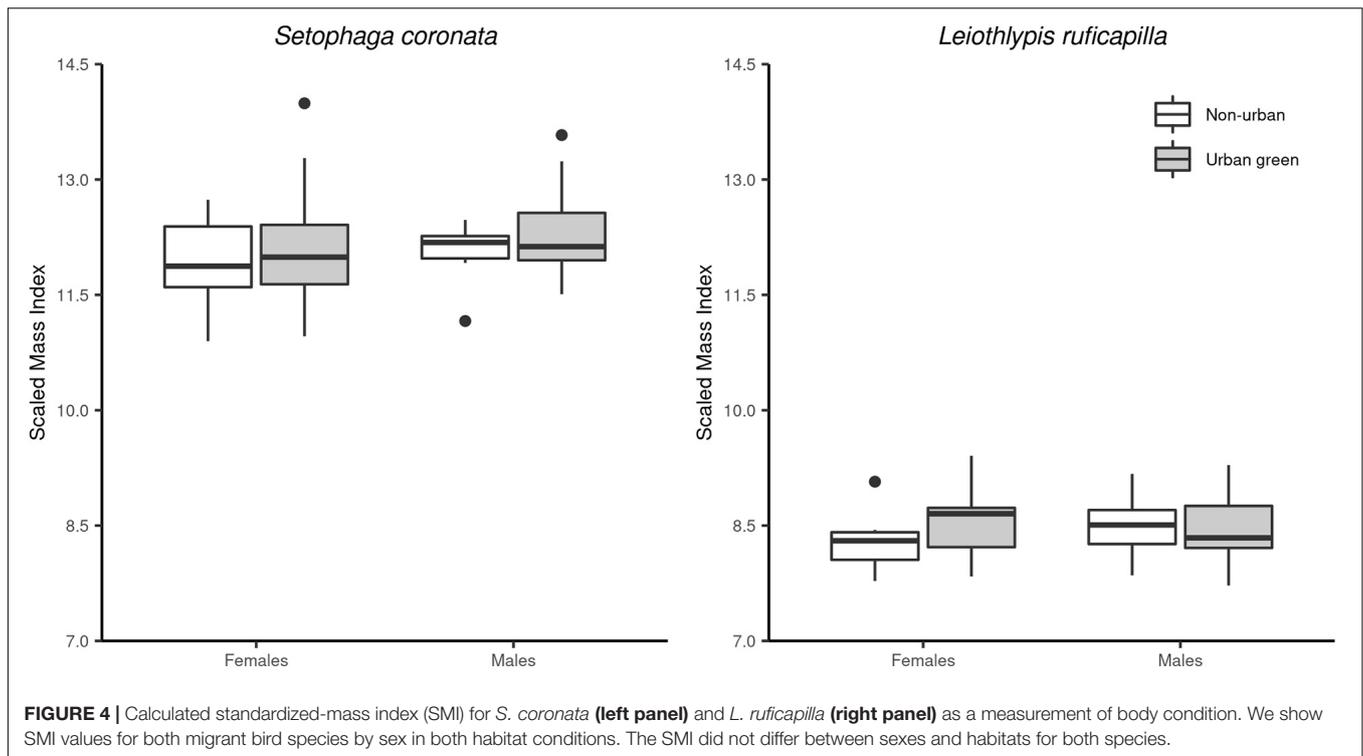
their surrounding habitats. Both habitat categories were grouped apart from our urban sites reference (> 50% impervious surfaces) due to their differences in habitat structure, principally by a greater urban intensity given by more construction features and high noise levels (Figure 2). The habitat differences 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



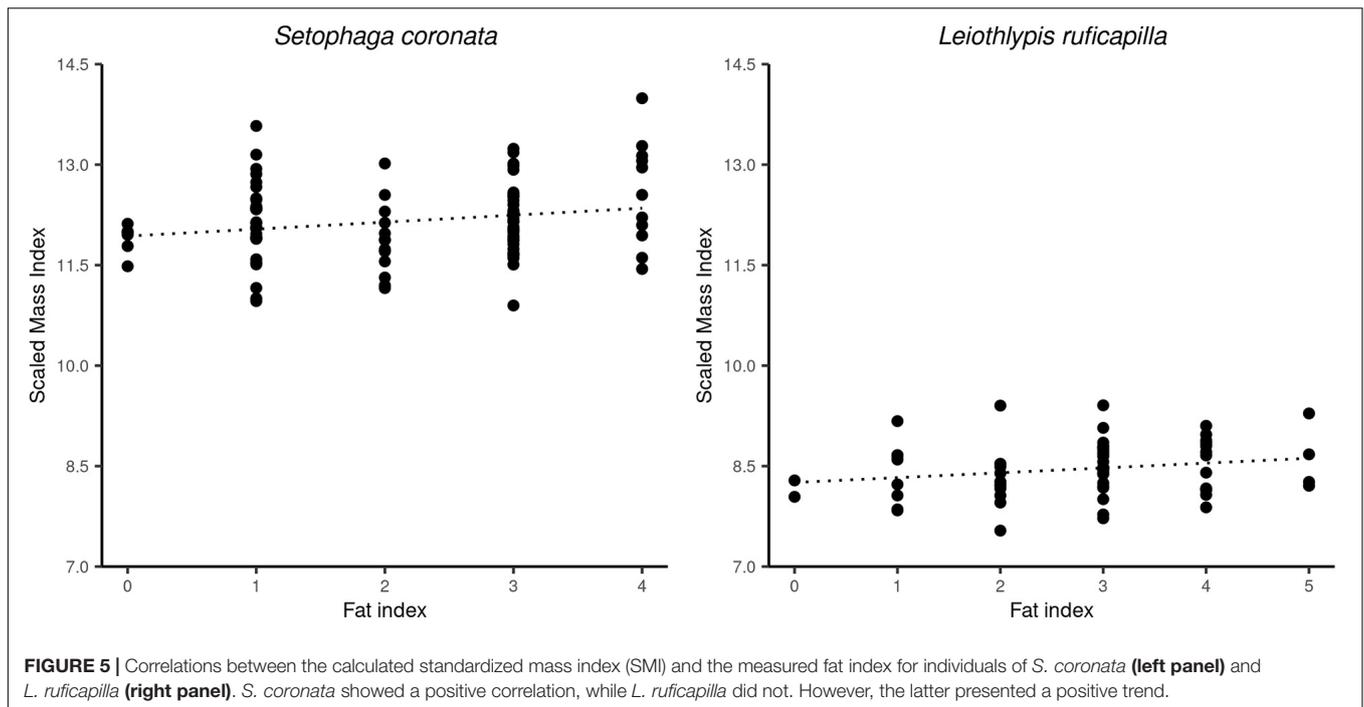
support this claim (Bock and Jones, 2004). We found a slightly higher capture rate for *S. coronata* in UGAs relative to non-urban areas, which may represent an increment in capture rates due to compact bird densities in a limited space. However, it is important to notice that the absence of records 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 [$\sim 0.1\%$ 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



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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