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Demographic and spatial responses of resident bird populations to the arrival of migratory birds within an urban environment

Gonzalo A. Ramírez-Cruz¹ | Israel Solano-Zavaleta² | Marcela Méndez-Janovitz³ | J. Jaime Zúñiga-Vega²

¹Posgrado en Ciencias Biológicas, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico

²Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico

³Posgrado en Ciencias Biológicas, Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico

Correspondence

J. Jaime Zúñiga-Vega, Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, Mexico. Email: jzuniga@ciencias.unam.mx

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Abstract

Long-distance migration allows many bird species to overcome the severe climatic changes that occur in seasonal environments. Migration is highly demanding, and given its cyclical nature, we currently know that it has substantial effects on the population parameters of migratory birds during both breeding and wintering seasons. However, the potential effects of the presence of migratory birds in their wintering grounds on populations of resident birds have remain largely unexplored. Here, we propose the hypothesis that migratory birds negatively affect the habitat occupancy and population abundance of resident birds because of the arrival of numerous individuals during the most limiting months of the year. Here, we studied different species of migratory and resident birds that coexist during winter in an urban ecological reserve located within Mexico City. We used single-species multiseason occupancy models, two-species occupancy models, and distance sampling techniques to evaluate changes in occupancy and population density of resident bird species during three consecutive winters. We found an aggregation pattern between two resident species (*Psaltriparus minimus* and *Thryomanes bewickii*) with three migratory warblers (*Cardellina pusilla*, *Setophaga coronata* and *Setophaga townsendi*). Thus, our results provide evidence of the formation of mixed-species flocks in our study area. We also conclude that resident birds experience different demographic and behavioral processes during winter that not necessarily result from interspecific interactions with migratory birds.

KEYWORDS

distance sampling, long-distance migration, occupancy models, population density, resident birds

1 | INTRODUCTION

Long-distance migration evolved as one of many mechanisms to cope with temporal and spatial fluctuations of resources, and has been the subject of intensive attention

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by biologists (Bowlin et al., 2010; Faaborg et al., 2010). In the case of birds, our understanding about how they carry out long-distance movements is still expanding. Currently, we know that this phenomenon imposes substantial physiological costs on migratory species (Åkesson & Hedenström, 2007; Dingle, 2006; Sahashi & Morita, 2013). For instance, we know that migratory birds need to effectively catabolize adipose and even lean tissue to maintain their performance during long flights (Karasov & Pinshow, 2000; McWilliams, Guglielmo, Pierce, & Klaassen, 2004). To deal with such heavy costs, migratory birds must refuel both during their travel and immediately after their arrival to wintering grounds in order to recover from muscle damage and sleep deprivation (Guglielmo, Piersma, & Williams, 2001; Rattenborg et al., 2004). However, events such as habitat loss and fragmentation in the wintering grounds are likely to have a negative impact on the population parameters of migratory birds once they return to their breeding territories (Bowlin et al., 2010; Briedis, Krist, Král, Voigt, & Adamík, 2018; Marra et al., 2015; Norris & Marra, 2007; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004; Taylor & Stutchbury, 2016).

The studies on long-distance migration often focus on the ecological and physiological processes experienced by migrants, and thus, our knowledge about the potential ecological consequences of long-distance migration on resident bird populations is far more limited (Rodewald & Brittingham, 2002). The potential interactions between migrants and residents have been studied with a conservation focus, mainly in cases in which different pathogens are known to be transported by migratory birds and transmitted to residents and/or vice versa (Figuerola et al., 2008; Viana, Santamaría, & Figuerola, 2016; Waldenström, Bensch, Kiboi, et al., 2002). Other studies have evaluated interspecific competition between resident and migrant birds within their breeding grounds (Ahola, Laaksonen, Eeva, & Lehikoinen, 2007; Forsman, Thomson, & Seppänen, 2007; Wittwer, RB, Caplat, et al., 2015). Intraspecific competition in species with both resident and migratory populations has also been studied, confirming that resident individuals seem to have some advantages over newcomers (De la Hera, Pérez-Tris, & Tellería, 2012; Fudickar, Schmidt, Hau, Quetting, & Partecke, 2013; Ketterson & Nolan, 1976; Morganti, Assandri, Aguirre, et al., 2017). However, the possibility that migratory birds may have a negative impact on resident bird populations within wintering grounds has not been fully explored (but see Bensusan, Shorrock, & Hamer, 2011).

In this study, we propose the hypothesis that the massive arrival of migratory birds affects the local distribution of resident birds within their wintering grounds by reducing the area that residents can occupy. A reduction in the occupied area may result from the residents being forced to congregate into smaller and denser clusters of

individuals, or because of many residents moving to nearby areas to avoid competition with the arriving individuals with similar habits. This reduction could also be due to residents experiencing greater mortality, possibly as a consequence of negative interactions with migratory birds. Alternatively, if the occupancy of residents does not change, or increases during winter, it could mean that migratory and resident birds are able to form mixed flocks that offer benefits to both migrants and residents (Sridhar, Beauchamp, & Shanker, 2009).

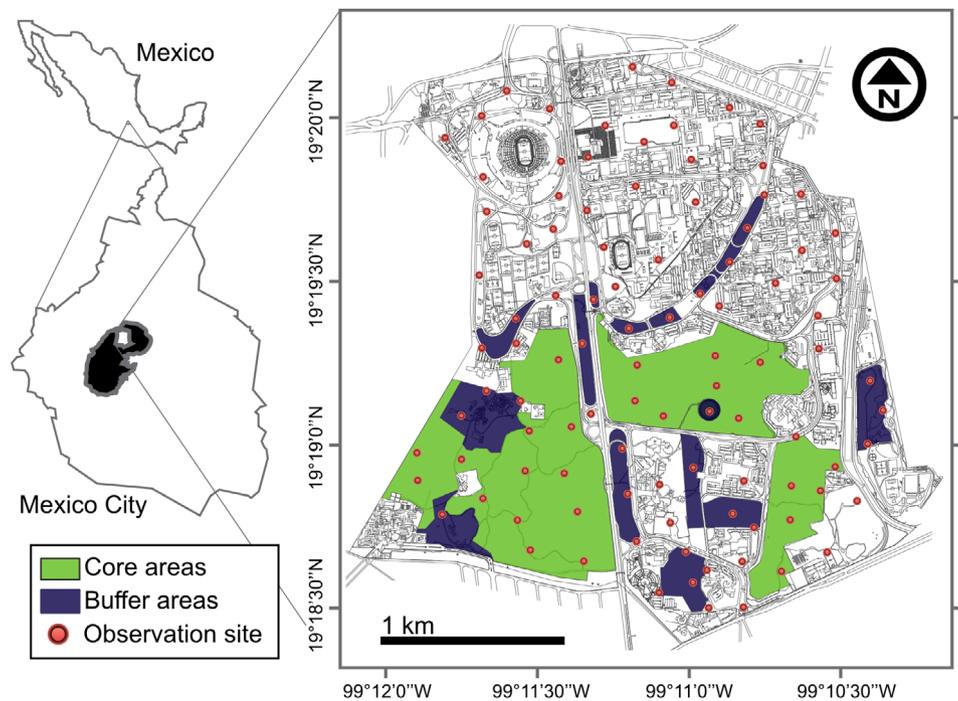
Here, we focused on different species of resident and migratory birds that coexist during the winter in an urban ecological reserve located within Mexico City. We used single-species multiseason occupancy models (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003; MacKenzie, Nichols, Royle, Pollock, Bailey, & Hines, 2018) to evaluate if the probability of presence of resident species decreased during the winter seasons of three consecutive years. We also used conditional two-species occupancy models (Richmond, Hines, & Beissinger, 2010) to examine potential spatial interactions between each resident species and each migratory species in an attempt to know if migratory birds had negative effects on the occupancy of resident birds during these winters. In addition, to know if the reduction in occupancy probability of residents was due to a reduction in their abundance during the winter, we used distance sampling techniques to estimate changes throughout the year in the population density of the residents (Buckland, 2001; Thomas et al., 2010). Our results reveal interesting dynamic patterns between resident and migratory bird populations that inhabit an urban ecosystem located within one of the largest cities in the world, and provide insight into the functioning of cyclic ecological phenomena such as the demographic interactions that occur between migratory and resident birds every year during the nonbreeding season.

2 | MATERIALS AND METHODS

2.1 | Study area

Despite the rapid urbanization of Mexico City, fragments of its original ecosystems are still present. In particular, the vestigial xerophytic scrubland in the southern part of the city is currently protected within the main campus of Universidad Nacional Autónoma de México (UNAM, Figure 1). Known as Reserva Ecológica del Pedregal de San Ángel (REPSA), this reserve preserves 237 ha of a unique vegetation dominated by *Pittocaulon praecox*, *Buddleja cordata*, *Dodonea viscosa*, and *Muhlenbergia robusta* among other native species (Castillo-Argüero,

FIGURE 1 Location of the Reserva Ecológica del Pedregal de San Ángel (REPSA) and Universidad Nacional Autónoma de México (UNAM) within Mexico City. *Note:* The three types of areas are shown: core, buffer, and urban. Circles correspond to each observation site. The black area within the insert of Mexico City depicts the original extension of the native scrubland



Martínez-Orea, Nava-López, & Almeida-Leñero, 2013; Lot & Cano-Santana, 2009). The REPSA is divided into three core conservation areas (171 ha), and 13 buffer areas (66 ha) surrounded by 48 ha of unprotected scrubland, 121 ha of green areas, 112 ha of streets, roads, and parking lots, 83 ha of buildings, and 129 ha of sidewalks and other urban structures, covering a total area of 730 ha (Zambrano, Rodríguez Palacios, Pérez Escobedo, et al., 2016). The main substrate consists of volcanic rock originated from the eruption of the Xitle volcano (Siebe, 2009). Altitude ranges from 2,270 to 2,349 m above sea level. Climate is temperate subhumid with abundant summer rains from June to October, with a mean annual precipitation and temperature of 870 mm and 15.6°C, respectively (Zambrano et al., 2016). The REPSA and the surrounding campus serve as wintering grounds for several migratory birds that use its scattered and mixed vegetation landscape during winter (from December to March) (Arizmendi, Del, Espinosa de los Monteros, & Ornelas, 1994; Howell & Webb, 1995).

2.2 | Field methods

We randomly selected 100 observation sites that spanned the 730 ha of the REPSA and UNAM: 25 observation sites within the core conservation areas, 27 within buffer areas, and 48 covering the surrounding urban landscape. The minimum distance between sites was 150 m. Each observation site was visited by a group of trained observers between five and seven occasions during 3 months of the year representing spring (May), fall (September), and winter

(January) seasons from 2015 to 2018. Specifically, we collected field data during May and September of 2015; January, May, and September of 2016; January, May, and September of 2017; and January 2018, for a total of nine sampling seasons. Despite our focus being on the winter seasons, the spring and fall surveys were conducted mainly to compare occupancy probabilities and population densities of the residents before and after the period during which the migratory birds are present. Each visit consisted of a 15-min period of observation. All visits took place either between sunrise and noon or between 5 p.m. and sunset. Observations were carried out within a 20-m radius from the center of the observation sites. Observers recorded species of migratory and resident birds by using binoculars. The average detection distance in the three types of areas was 21.3 m (24.2 m in core areas, 18.8 in buffer areas, and 20.8 m in urban areas). In the cases in which an observation site was located near the border of any type of area, we made sure that the observation radius was inside only one type of area. At each site, we visually estimated and registered the following environmental traits: percent vegetation cover at forb (<0.5 m), shrub (0.5–3 m), and tree (>3 m) layers, percent of exposed volcanic rock in the substrate, and percentage of urban land use. We made these estimations at the end of the observation round, after the observers had had a general view of the observation site. The five observers individually gave a category to each cover from 1 to 10 (total sum = 10). An average consensus was then reached between all observers to determine the percentage of each type of cover in the area adjusting extreme estimates (Klimeš, 2003). The sum of all vegetation covers, exposed rock, and urban substrate was always 100%. We also registered the number of shrub and

tree species, and the presence/absence of gardening activities (watering, pruning, and mowing), and measured the distance from each site to the nearest human-made structure (road, garden, building, etc.) using Google Earth (Google, 2017). In addition, we measured the distance from the center of the observation site to the spot where each bird was first detected perching with the use of a Nikon Aculon Laser Rangefinder.

2.3 | Study species

To avoid false positives (i.e., misidentification of species) and to ensure model convergence, we focused on migratory and resident bird species that were both common and easy to identify in the field. To evaluate the effect of the presence of migratory birds on the occupancy of resident birds, we paired four small migratory insectivorous birds: yellow-rumped warbler (*Setophaga coronata*), Townsend's warbler (*S. townsendi*), Wilson's warbler (*Cardellina pusilla*), and blue-gray gnatcatcher (*Poliophtila caerulea*) (Ammon & Gilbert, 1999; Hunt & Flaspohler, 1998; Wright, Hayward, Matsuoka, & Hayward, 1998), each with two small resident insectivorous birds with similar feeding strategies: bushtit (*Psaltriparus minimus*) and Bewick's wren (*Thryomanes bewickii*) (Kennedy & White, 2013; Sloane, 2001), for a total of eight migratory-resident pairs. We also studied two additional migratory-resident pairs. First, the migratory American robin (*Turdus migratorius*) and the resident rufous-backed robin (*Turdus rufopalliatus*), which are two closely related species that feed on fruits, seeds, litter, and invertebrates (Carbó-Ramírez et al., 2015; Pineda-López & Malagamba Rubio, 2009; Vanderhoff, Pyle, Patten, et al., 2016). Second, we paired two migratory sibling flycatcher species of the genus *Empidonax* (*E. hammondii* and *E. oberholseri*) whose morphological similarity makes their correct identification difficult (therefore, we refer to these two species as the complex *E. hammondii-oberholseri*) (Pereyra & Sedgwick, 1993; Sedgwick, 1994; Zink & Johnson, 1984), with the resident vermilion flycatcher (*Pyrocephalus rubinus*) (Ellison, Wolf & Jones, 2009). Flycatchers are known to use similar feeding strategies that may lead to interspecific competition (Fitzpatrick, 1980; Verbeek, 1975).

2.4 | Data analyses

2.4.1 | Occupancy estimation and species interaction factor

We used single-species multiseason occupancy models (MacKenzie et al., 2003, 2018) implemented in program MARK (White & Burnham, 1999) to estimate occupancy (ψ) and detection (p) probabilities of migratory and

resident birds and to compare occupancy of residents among May (spring), September (fall), and January (winter) of three different years. Therefore, we analyzed data from nine different seasons for resident species, and from three different winters for migratory species. These models can also estimate the local colonization (γ) and extinction (ϵ) probabilities for each species. However, for the purpose of this study we kept these parameters constant to reduce the number of parameters of each model. We used the detection histories containing the information of every detected and nondetected species at each observation site during our repeated visits to build competing linear models that tested the effects of relevant environmental covariates on p first, and then on ψ . We also considered null models in which we estimated a single intercept for both parameters. For all bird species we incorporated the following covariates to the linear models: percentage of forb, shrub, and tree cover, presence/absence of gardening activities, distance to the nearest human structure, percentage of urban land use, and the number of tree and shrub + tree species. In the case of the Bewick's wren, we also considered the percentage of exposed volcanic rock. In addition, we included models in which the type of area (core conservation, buffer, or urban areas) affected both detection and occupancy probabilities. Before fitting models, we standardized all environmental covariates to a mean of zero and variance of one. We started with a general model in which all parameters were affected by the type of area. Then, we modeled p by testing different covariates while maintaining ψ invariant. To secure model convergence, we only included additive models when more than one source of variation was supported by the best fitting models. For all species we used the R package unmarked (Fiske & Chandler, 2011; R Core Team, 2019) to calculate the variance inflation factor (\hat{c}), and adjust model selection according to the degree of overdispersion. Hence, to select the environmental covariates with the strongest influence on ψ and p , we used the quasi-likelihood of the Akaike's information criterion adjusted for small samples (QAICc, Burnham & Anderson, 2002), which takes into account the \hat{c} value to assess model fit. We considered models with a difference <2 QAICc units with respect to the best-fitting model (i.e., $\Delta\text{QAICc} < 2$) as having strong support in our data. We calculated model-averaged estimates of ψ and p based on Akaike weights, which are measures of the relative support for each model in the data (Burnham, Anderson, & Huyvaert, 2011). Model selection results from single-species multiseason occupancy models and detection probability (p) estimates can be found in Table S1, Table S2, and Table S3 in Supporting Information (SI).

After identifying the environmental covariates with the most evident effect on ψ and p , we implemented conditional two-species occupancy models (Richmond et al., 2010) to

know if there was a nonindependent co-occurrence pattern between migratory and resident birds. This parameterization assumes dominance of a species A over a species B. We used the detection histories of the winter seasons to build conditional occupancy models for each pair of migratory (A) and resident (B) species. All these two-species models incorporated the previously selected environmental covariates affecting the following parameters: detection probability of the migratory species (p^A), detection probability of the resident species (p^B), occupancy probability of the migratory species (ψ^A), occupancy probability of the resident species given that the migratory species was also present (ψ^{BA}), and occupancy probability of the resident species given that the migratory species was absent (ψ^{Ba}). Then, we built an unconditional model with only one occupancy probability for species B ($\psi^{BA} = \psi^{Ba}$; i.e., assuming that occupancy of residents is not affected by the presence of migrants) and used AICc to compare the fit of this unconditional model against that of the conditional model in which we separately estimated both ψ^{BA} and ψ^{Ba} (i.e., assuming that occupancy of residents differs between sites where migrants are present versus sites where migrants are absent).

For all migratory-resident pairs and for all three winters (January of 2016, 2017, and 2018) we estimated the species interaction factor (SIF) to evaluate if the co-occurrence pattern between resident and migratory species reflects avoidance (i.e., a negative spatial interaction) or aggregation (i.e., a positive spatial interaction). A SIF value of 1 indicates that the occurrences of both species are independent from one another. When SIF is statistically different than 1, it indicates that the species are less or more likely to co-occur than expected under the hypothesis of independence. Specifically, $SIF < 1$ indicates avoidance and $SIF > 1$ indicates aggregation. Details on the calculation of SIF are given in Richmond et al. (2010).

If our hypothesis of a negative effect of the presence of migratory birds on the occupancy of resident birds is correct, we expect to observe three patterns. First, occupancy probability of residents (derived from the single-species models) must be lower during winter (when migratory birds are present) in comparison with the spring and fall seasons (when migratory birds are absent). Second, the conditional model must have stronger support than the unconditional model (i.e., the unconditional model must differ in more than 2 AICc units with respect to the conditional model; Burnham & Anderson, 2002). Third, the SIF value must be statistically lower than 1.

2.4.2 | Density estimation

To estimate density (number of individuals per hectare), we used variable-radius point counts (Buckland, 2001;

Buckland, Rexstad, Marques, & Oedekoven, 2015), as previously described (see field methods above). We considered only the information of perching individuals to ensure their actual use of the observation site in contrast to just flying over it. We modeled density of resident birds with program Distance 7.2 (Thomas et al., 2010). We used distance data from all 100 observation sites to estimate overall density of each resident species within the study area. We tested every model combination among the four key functions (half-normal, uniform, hazard rate, and negative exponential) and the three series expansions (cosine, simple-polynomial, and hermite-polynomial) implemented in Distance 7.2. Density estimates for all sampling seasons (spring, fall, and winter of 3 years) were obtained via model averaging based on the AICc weights of all models (Burnham & Anderson, 2002). Model selection results and detection probability (p) estimates can be found in Table S4 in SI.

The main purpose of estimating density of residents was to search for a consistent decrease in their abundance during the winter in comparison with spring and fall. Lower abundance of residents coinciding with both a decrease in their occupancy during winter and a SIF value < 1 would be indicative of higher mortality and/or emigration of residents as a consequence of a negative effect of the presence of the migratory species. Alternatively, if we detect a reduction in occupancy of residents and a $SIF < 1$ during winter with no change in their abundance, then this would indicate that the presence of migrants forced residents to occupy a smaller area, presumably by congregating into denser groups, with no effect on the total number of resident individuals.

3 | RESULTS

Occupancy probability of the rufous-backed robin showed a slight decrease during the winters of 2016, and 2017 as indicated by lower estimates and non-overlapping confidence intervals of at least one type of area with respect to the estimates from the spring seasons (Figure 2a). This decrease in ψ coincided with an evident decrease in density only during the second winter (Figure 2b). The unconditional model with the American robin had stronger support than the conditional model during all winter seasons (Table 1). The estimated SIF were not statistically different than 1 (Figure 3a).

Occupancy and density of the vermilion flycatcher did not decrease during the winters as indicated by overlapping confidence intervals with estimates derived from most other seasons (Figure 2c and d). In all winter seasons, the unconditional model had stronger support than the conditional model that suggested

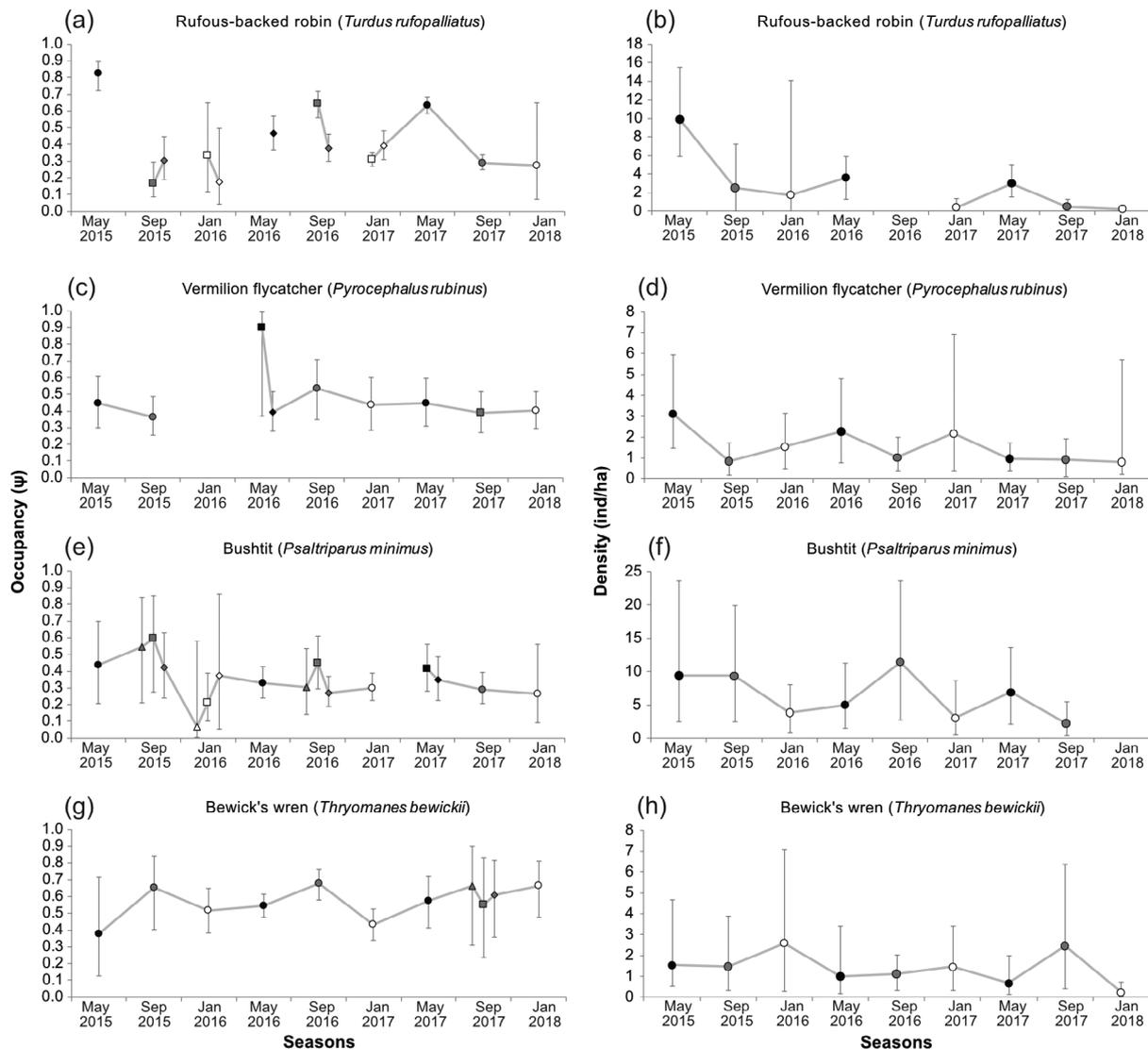


FIGURE 2 Occupancy probability and density estimates for four resident bird species during nine sampling periods. *Note:* Colors indicate different seasons: black = spring, gray = fall, white = winter. Shapes correspond to sampling periods in which we detected evident differences in occupancy among different types of areas: triangle = core areas, square = buffer areas, diamond = urban areas. Missing parameter estimates were not accurately estimated (i.e., their standard errors were too large). Error bars denote 95% confidence intervals

an effect of the migratory *E. hammondii-oberholseri* (Table 1). Consequently, all three SIF values were not statistically different than 1 (Figure 3b).

Occupancy and population density of the bushtit did not decrease during any of the three sampled winters (Figures 2e and f). Regarding potential spatial interactions with migratory birds, we found evidence of co-occurrence between this resident bird with the Wilson's warbler, the yellow-rumped warbler, and the Townsend's warbler during the winter of 2017. In these three cases the conditional model had stronger support than the unconditional model (Table 1). During this winter, the SIF values were statistically higher than 1 (Figure 3c, d, and e).

Finally, occupancy of the Bewick's wren decreased from fall of 2016 to the winter of 2017 (Figure 2g).

Whereas population density did not show any particular reduction during any season (Figure 2h). We found strong evidence of a spatial interaction between the Bewick's wren and the Townsend's warbler during winter of 2016. In this season, the conditional model had stronger support than the unconditional model (Table 1) and the estimated SIF was statistically higher than 1 (Figure 3i). In addition, we found some evidence of a spatial interaction between the Bewick's wren and the blue-gray gnatcatcher during winters of 2016 and 2017. In these cases, the unconditional model provided the best fit (Table 1), but the conditional model also had relatively strong support ($\Delta\text{AICc} < 2$ in both cases). However, the estimated SIF values were not statistically different than 1 (Figure 3j). The estimated SIF values for the potential

TABLE 1 Summary of model selection results for two-species occupancy models that tested the hypothesis that the presence of a migratory species (denoted as A) influences the occupancy of a resident species (denoted as B)

Species pair	Winter	Model	AICc	Δ AICc	w	k
American robin	January 2016	U	7,316.36	0.00	0.96	9
<i>Turdus migratorius</i> (A)		C	7,322.86	6.50	0.04	12
Rufous-backed robin	January 2017	U	13,097.40	0.00	0.81	8
<i>Turdus rufopalliatu</i> s (B)		C	13,100.28	2.88	0.19	11
	January 2018	U	10,292.61	0.00	0.79	7
		C	10,295.29	2.67	0.21	9
Hammond's-dusky flycatcher	January 2016	U	3,359.56	0.00	0.99	10
<i>Empidonax hammondii-oberholseri</i> (A)		C	3,369.66	10.09	0.01	14
Vermilion flycatcher	January 2017	C	530.60	0.00	0.68	8
<i>Pyrocephalus rubinus</i> (B)		U	532.08	1.47	0.32	7
	January 2018	U	2036.58	0.00	0.88	8
		C	2040.57	4.00	0.12	10
Wilson's warbler	January 2016	U	621.87	0.00	0.50	9
<i>Cardellina pusilla</i> (A)		C	623.36	1.49	0.50	12
Bushtit	January 2017	C	801.47	0.00	0.86	9
<i>Psaltriparus minimus</i> (B)		U	805.14	3.67	0.14	8
	January 2018	U	701.04	0.00	0.92	11
		C	706.04	5.00	0.08	13
Yellow-rumped warbler	January 2016	U	719.86	0.00	0.84	10
<i>Setophaga coronata</i> (A)		C	723.19	3.33	0.16	13
Bushtit	January 2017	C	955.02	0.00	1.00	9
<i>Psaltriparus minimus</i> (B)		U	967.75	12.73	0.00	8
	January 2018	C	792.91	0.00	0.58	14
		U	793.59	0.68	0.42	12
Townsend's warbler	January 2016	U	465.44	0.00	0.92	11
<i>Setophaga townsendi</i> (A)		C	470.36	4.92	0.08	14
Bushtit	January 2017	C	3,416.63	0.00	0.78	9
<i>Psaltriparus minimus</i> (B)		U	3,419.10	2.48	0.22	8
	January 2018	U	375.23	0.00	0.79	10
		C	377.82	2.59	0.21	12
Blue-gray gnatcatcher	January 2016	U	381.17	0.00	0.79	10
<i>Polioptila caerulea</i> (A)		C	383.80	2.63	0.21	13
Bushtit	January 2017	U	551.02	0.00	0.75	10
<i>Psaltriparus minimus</i> (B)		C	553.24	2.23	0.25	11
	January 2018	U	723.59	0.00	0.68	9
		C	725.12	1.54	0.32	11
Wilson's warbler	January 2016	U	726.86	0.00	0.95	9
<i>Cardellina pusilla</i> (A)		C	732.57	5.71	0.05	12
Bewick's wren	January 2017	U	900.80	0.00	0.88	7
<i>Thryomanes bewickii</i> (B)		C	904.85	4.04	0.12	9
	January 2018	U	973.67	0.00	0.85	8
		C	977.20	3.53	0.15	10

(Continues)

TABLE 1 (Continued)

Species pair	Winter	Model	AICc	Δ AICc	w	k
Yellow-rumped warbler	January 2016	U	824.84	0.00	0.90	10
<i>Setophaga coronata</i> (A)		C	829.21	4.36	0.10	13
Bewick's wren	January 2017	U	1,063.42	0.00	0.82	7
<i>Thryomanes bewickii</i> (B)		C	1,066.49	3.08	0.18	9
	January 2018	U	1,066.04	0.00	0.87	9
		C	1,069.87	3.83	0.13	11
Townsend's warbler	January 2016	C	566.67	0.00	0.87	14
<i>Setophaga townsendi</i> (A)		U	570.43	3.76	0.13	11
Bewick's wren	January 2017	U	3,519.17	0.00	0.77	7
<i>Thryomanes bewickii</i> (B)		C	3,521.58	2.41	0.23	9
	January 2018	U	648.01	0.00	0.84	7
		C	651.27	3.26	0.16	9
Blue-gray gnatcatcher	January 2016	U	483.69	0.00	0.53	9
<i>Poliptila caerulea</i> (A)		C	483.91	0.22	0.47	10
Bewick's wren	January 2017	U	646.58	0.00	0.65	9
<i>Thryomanes bewickii</i> (B)		C	647.80	1.23	0.35	11
	January 2018	U	996.53	0.00	0.90	6
		C	1,000.89	4.36	0.10	8

Note: For each migratory-resident pair of species and for each season we used the Akaike's information criterion adjusted for small sample sizes (AICc) to compare a model in which the occupancy of the native species (ψ^B) depends on the presence (ψ^{BA}) or absence (ψ^{Ba}) of the exotic species (conditional model, denoted as "C") against a model in which the occupancy of the native species is independent of the presence of the exotic species (unconditional model, denoted as "U"). Models highlighted in bold type correspond to cases in which the conditional model had stronger support than the unconditional model (Δ AICc > 2).

interactions of the Bewick's wren with the Wilson's warbler and the yellow-rumped warbler were not statistically different than 1 (Figures 3g and h).

In summary, we found only two evident reductions in occupancy and population density throughout the sampled seasons. None of these was associated with negative spatial interactions, but we found four other cases in which a positive spatial interaction was detected (Table 2).

4 | DISCUSSION

Our results revealed two interesting general patterns. First, we found aggregation patterns between the resident bushtit and the migratory Wilson's warbler, the yellow-rumped warbler, and the Townsend's warbler as well as between the resident Bewick's wren and the migratory Townsend's warbler, which represent evidence of the formation of mixed-species flocks. Intriguingly, these positive spatial interactions were not consistent during all 3 years, but instead occurred only during one of the surveyed winters.

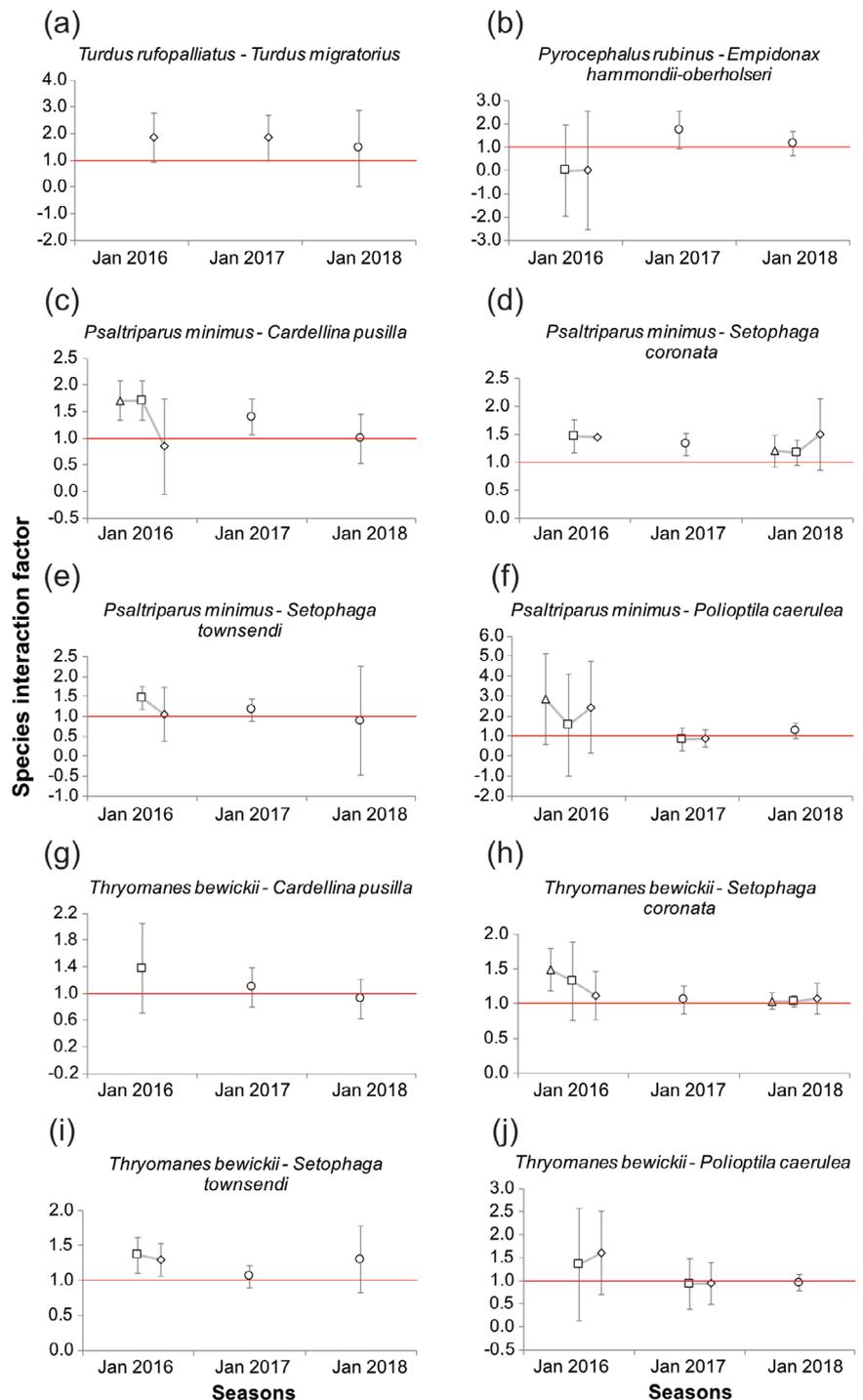
Second, we found indirect evidence of the mechanisms underlying spatial population changes within the

study area. During January of 2017, both occupancy and density of the rufous-backed robin decreased, as well as the area occupied by the Bewick's wren. In neither of these cases was this reduction associated with negative spatial interactions with migratory birds. In the case of the rufous-backed robin, the decrease in the area occupied may have resulted from the fact that fewer individuals were present in the area due to higher mortality or emigration out of the study area during this particular winter. In contrast, in the case of the Bewick's wren, the reduction in the occupied area did not coincide with a decrease in abundance during this same season. Hence, this change can be explained by behavioral mechanisms, meaning that the same number of individuals that were present throughout the entire year congregated within smaller patches during one winter.

4.1 | Negative spatial interaction between resident and migratory birds

We found no evidence to support our initial hypothesis that the arrival of migratory birds alters the local distribution of residents during the nonbreeding season. Some

FIGURE 3 Species interaction factor (SIF) calculated for 10 pairs of resident and migratory bird species. *Note:* Shapes correspond to sampling periods in which we detected evident differences in occupancy among different types of areas: triangle = core areas, square = buffer areas, diamond = urban areas. Missing parameter estimates were not accurately estimated (i.e., their standard errors were too large or close to zero). Error bars denote 95% confidence intervals



authors have pointed out the possibility that the rufous-backed robin and the American robin may compete for the same resources (Pineda-López & Malagamba Rubio, 2009). However, other authors have attributed the recent expansion of the distribution range of the rufous-backed robin from the Pacific slope to the Atlantic slope of Mexico to the lack of competitors (Martínez-Morales et al., 2010). According to our results, we found evidence that partially supports the second scenario. Regarding flycatchers from the genus *Empidonax*, many of them are

solitary, but occasional aggressive interactions with other flycatcher species have been observed (e.g., between *E. hammondi* and *E. occidentalis*; Sedgwick, 1994). In the case of the migratory warblers, some individuals of both sexes of the Wilson's warbler are territorial in the wintering grounds (Ammon & Gilbert, 1999), the yellow-rumped warbler is known to become territorial when food is scarce, and much like the Townsend's warbler it has been known to defend trees from other insectivorous birds during winter (Hunt & Flaspohler, 1998; Wright

TABLE 2 Summary of the overall spatial interactions detected

Species	American robin (<i>Turdus migratorius</i>)	Flycatchers (<i>Empidonax hammondi-oberholseri</i>)	Wilson's warbler (<i>Cardellina pusilla</i>)	Yellow-rumped warbler (<i>Setophaga coronata</i>)	Townsend's warbler (<i>Setophaga townsendi</i>)	Blue-gray gnatcatcher (<i>Poliophtila caerulea</i>)
Rufous-backed robin (<i>Turdus rufopalliatus</i>)	NE					
Vermilion flycatcher (<i>Pyrocephalus rubinus</i>)		NE				
Bushtit (<i>Psaltriparus minimus</i>)			+	+	+	NE
Bewick's wren (<i>Thryomanes bewickii</i>)			NE	NE	+	NE

Note: NE = no effect. "+" = positive spatial interaction.

et al., 1998). Last, it is still not clear if the blue-gray gnatcatcher exhibits territorial behavior during winter (Kershner & Ellison, 2012). However, we found no evidence of a negative spatial interaction between these migratory species and resident birds across all three winters. Likely, this is due to two possible explanations: (1) that the local environment provides enough resources for both migratory and resident birds during winter, and (2) that the accuracy of our occupancy and density estimations was insufficient to detect small effects across the three surveyed years.

4.2 | Positive spatial interaction between resident and migratory birds

We found strong evidence of mixed-species flocks that contain both resident and migratory species. Specifically, the bushtit and the Bewick's wren aggregated with the Townsend's warbler, and the bushtit also aggregated with the Wilson's and yellow-rumped warblers. The formation of mixed-species flocks has two main benefits: improving foraging efficiency and decreasing mortality caused by predation (Morse, 1977; Sridhar et al., 2009). However, flocking behavior can also impose costs on birds such as intensification of intra and interspecific competition (Hutto, 1988; Sridhar & Guttal, 2018; Thomson, Forsman, & Mönkkönen, 2003). The dynamic balance between advantages and costs of forming mixed-species flocks, as well as other biotic and abiotic factors, may explain why we found inconsistent positive spatial interactions between migratory and resident birds across all three winters (Barbe, Morel, Yann, et al., 2018; Farley, Sieving, & Contreras, 2008). According to our results, some positive spatial interactions between migratory and resident birds were detected during the winter of 2017, which was particularly dry compared to the winters of 2016 and 2018 (0 mm of rainfall versus 9.4 and 10.8 mm,

respectively; RUOA 2018). Given that the bushtit, the Bewick's wren, and the three migratory warblers are largely insectivorous, their aggregation was more evident likely as a response to the decrease in arthropod abundance.

4.3 | Behavioral and demographic processes of resident birds

Our results also indicate that resident birds experience two interesting processes that are independent of the presence of migratory birds. First, the observed decrease in occupancy of the rufous-backed robin during the winter of 2017 occurred in parallel with a decrease in population density. Therefore, the reduction in the area occupied by this resident bird resulted from demographic changes. Presumably, the observed reduction in occupancy and density of rufous-backed robin was caused by an increase in mortality. Although bird survival is known to be generally higher in urban areas, the rufous-backed robin and other resident birds are still prone to window and vehicle collisions, and to predation by domestic animals in these areas (Leveau & Zuria, 2017). Alternatively, lower population density, and therefore lower occupancy, could have stemmed from short-distance migration to the urban areas that surround our study site. Other bird species such as the common raven (*Corvus corax*) are known to make more use of urban landscapes during winter because anthropogenic food sources and roost sites provide enhanced survival rates for these birds (Peebles & Conover, 2017). Particularly, Mexico City is located at a high altitude (on average 2,240 m of elevation) and, hence, has a mean temperature during the winter that is considerably lower compared to the surrounding states. Thus, some resident birds might prefer to travel short distances to spend the winter in warmer sites.

Second, the Bewick's wren experienced a reduction in its occupancy probability during the winter of 2017 that was not related to negative spatial interactions with migratory birds, or by reductions in the number of individuals. This reduction in the area occupied by this resident bird presumably arose from changes in its behavior. Similar population declines have been reported for other wren species in Great Britain during harsh winters (Peach, Du Feu, & McMeeking, 2008). Even though there is no previous evidence of flocking in this species (Kennedy & White, 2013), our study indicates that they may become somewhat more social during severe winter seasons in our study area. The result of this social and behavioral process was the reduction in the total area that these birds occupied during the driest winter that we surveyed. It is also worth mentioning that the Bewick's wren may be excluded from some areas by the migratory house wren (*Troglodytes aedon*; Verner & Purcell, 1999). Unfortunately, observations of the house wren during our fieldwork were extremely scarce. Thus, we were unable to test the effect of this known competitor on the presence of the Bewick's wren.

Finally, we must emphasize that our analytical approach that consisted in estimating simultaneously occupancy and density allowed us to disentangle the causes of the observed reductions in the area occupied by our focal species. A smaller occupied area may result from fewer individuals being present, such as we observed in the rufous-backed robin. In this case, lower occupancy results from demographic processes such as mortality or emigration. Alternatively, if the occupied area decreases with no evident reduction in population density, then individuals are congregating into denser groups that occupy less space, such as we observed in the Bewick's wren. In this case, lower occupancy results from a behavioral process. In addition, implementation of two-species occupancy models also allowed us to infer that, at least during the 3 years of our study, the reduction in occupancy and population density of the rufous-backed robin was not caused by a negative interaction with the congeneric American robin. The robustness of all these inferences relies to a great extent on the fact that all our analytical tools take into account our imperfect detectability of these species in the field (Buckland et al., 2015; MacKenzie et al., 2018).

4.4 | Future directions

Given our results, some additional possibilities about the ecology of birds in urban wintering grounds remain unexplored. First, that positive co-occurrence patterns similar to the ones we detected may be influenced by “syn-urbanization” (Luniak, 2004) of resident and migratory birds.

Second, that the resident bird populations are unaffected by the arrival of migratory birds because of the “prior residence effect” (Kokko, López-Sepulcre, & Morrell, 2006; Senar & Pascual, 2015; Snell-Rood & Cristol, 2005). And third, that migratory birds experience “heterospecific attraction” (Mönkkönen, Helle, & Soppela, 1990) toward some resident species, using them as a cue for valuable resources within the wintering grounds (Thomson et al., 2003). Future studies should address these possibilities through experimental approaches, carry out similar surveys for a longer time period to gather more data, and/or could also test for spatial interactions between several migratory birds during the nonbreeding season.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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