

Article

Seasonal Dynamics of Woodland Insectivorous Mixed-Species Flocks in Urban Green Areas of Buenos Aires City, Argentina

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Simple Summary

The effects of urbanization on woodland insectivorous mixed-species flocks have been little studied, and no seasonal studies are known. This study aimed to describe the structure and seasonal dynamics of insectivorous mixed flocks in urban green areas of Buenos Aires City, Argentina. A total of 82 visits were conducted from April 2025 to March 2026. The most frequent and abundant bird species in flocks were the White-crested Tyrannulet (*Serpophaga subcristata*), the Greyish Baywing (*Agelaioides badius*), the Masked Gnatcatcher (*Poliophtila dumicola*), and the Tropical Parula (*Setophaga pitiayumi*). *Serpophaga subcristata*, *Poliophtila dumicola*, and *Setophaga pitiayumi* tended to occur together in flocks. Flock occurrence was significantly associated with Julian day and peaked in autumn and during the early winter, coinciding with the non-breeding season. The results suggest that mixed flocking behavior helps individuals and pairs of different bird species by likely improving access to food and reducing predation risk as they move outside their breeding territories.

Abstract

The effects of urbanization on woodland insectivorous mixed-species flocks have been little studied, and no seasonal studies have been conducted. This study aimed to describe the structure and seasonal dynamics of insectivorous mixed flocks in urban green areas of Buenos Aires City, Argentina. A total of 82 visits were conducted from April 2025 to March 2026. The potential effects of temperature, precipitation, humidity, and Julian day on flock occurrence were analyzed. The most frequent and abundant bird species in flocks were the White-crested Tyrannulet (*Serpophaga subcristata*), the Greyish Baywing (*Agelaioides badius*), the Masked Gnatcatcher (*Poliophtila dumicola*), and the Tropical Parula (*Setophaga pitiayumi*). *Serpophaga subcristata*, *Poliophtila dumicola*, and *Setophaga pitiayumi* tended to occur together in flocks. Flocks were observed in both native and exotic tree species. Flock occurrence was significantly associated with Julian day and peaked in autumn and during the early winter, coinciding with the non-breeding season. These results align with other studies conducted in subtropical and temperate regions. The significant relationship between flock occurrence and Julian day during the non-breeding season suggests that mixed flocking behavior helps individuals and pairs of different bird species by likely improving access to food and reducing predation risk as they move outside their breeding territories. A better understanding of the effects of urbanization on mixed flocks would be gained by comparing the spatial and temporal dynamics of flocking behavior in insectivorous birds in urban green areas with those in the region's native woodlands.



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Keywords: avian; behavior; invertivore; gregarious; Latin America; Argentina; neotropical region; urban

1. Introduction

Mixed-species flocks are conspicuous groups of different bird species that forage together [1]. These flocks have been studied in forest insectivorous birds in tropical and temperate regions (see reviews of Powell [2], Tubelis [3], Sridhar et al. [4], Goodale et al. [5,6], Beauchamp and Mangini [7], and Wu et al. [8]) and are associated with several benefits. On the one hand, the group of birds helps detect predators and reduces the risk of predation through the dilution effect [9]. Different species in the flock may ensure the presence of sentinel species and diverse alarm systems and vigilance [6,10]. On the other hand, different diets and foraging strategies among species in the flock may help reduce competition [11], while foraging efficiency is enhanced by reduced individual investment in vigilance [12–15].

Mixed flocks have shown two types of assembly, open membership and structured [16]. Open membership has been recorded in tropical and subtropical forests, and flock composition is variable, changing according to local bird community composition [17,18]. In contrast, structured mixed flocks have been recorded in understory evergreen forests and have a stable bird composition, which is independent of the variation in the relative abundances of bird species in the local community [19–21].

Mixed-flock size, diversity, and composition are expected to vary spatially along natural and anthropogenic gradients [5,8,22,23]. For example, Wu et al. [8] found that mixed-flock species richness increased toward the tropics, likely reflecting richer species pools. In addition, Montaña-Centellas and Jones [18] have found changes in the species richness and composition of bird flocks along altitudinal gradients in the Bolivian Andes in response to temperature and vegetation structure. On the other hand, anthropogenic forest loss and fragmentation have been linked to shifts in species composition and declines in species richness in tropical and temperate forests [24,25].

However, the temporal dynamics of mixed flocks have been much less explored [26]. For instance, the patterns of seasonal variation in mixed-flock behavior are unclear at the global scale, although some regional patterns have been identified [26]. In the tropics, flocks tend to be year-round [19,27], but see Rutt and Stouffer [28]. In contrast, mixed flocks in subtropical and temperate regions are seasonal, with higher flock occurrence and species richness during the non-breeding season [29–35]. Mangini and Areta [36] have suggested that seasonal changes in the occurrence of mixed flocks are driven by temperature variations, with low temperatures promoting mixed-flock formation due to increased energetic demands and food scarcity [37].

Urbanization is associated with habitat loss and fragmentation, as well as various forms of pollution and human disturbance that can alter bird behavior [38]. However, the impact of urbanization on woodland insectivorous mixed flocks has been little studied [39–41]. These studies have found that urban areas reduce insectivorous mixed-flocking behavior. For example, Fernández-Juricic [40] found that flock size increased in larger parks, in parks dominated by coniferous trees and large trees, and near other large parks in Madrid, Spain. The seasonal dynamics of flocks in urban environments have not yet been studied.

This study aimed to analyze the assembly and seasonal patterns of woodland insectivorous mixed-flock occurrence in urban green areas of Buenos Aires City, located in Argentina's temperate region. Given that urban areas buffer annual microclimatic and resource variations, which in turn buffer the seasonal dynamics of bird communities [42,43], we may expect

year-round activity of mixed flocks. Alternatively, mixed-flock occurrence may show strong seasonality linked to the non-breeding season or to low winter temperatures.

2. Methods

2.1. Study Area

The study was conducted in three urban green spaces in Buenos Aires City, Argentina ($34^{\circ}35'59''$ S $58^{\circ}22'55''$ W; 3,121,707 inhabitants [44]; 25 m.a.s.l.; Figure 1). The city lies within an ecotone between the grasslands of the Pampean Phytogeographic Province, the semi-open woodlands of the Espinal Phytogeographic Province, and the woodlands of the Paranaense Phytogeographic Province [45,46]. The Pampean Phytogeographic Province of the study area comprises a mesophytic pseudosteppe dominated by *Bothriochloa lagurioides* and *Nassella* spp. [46]. The semi-open woodlands of the Espinal Phytogeographic Province comprise *Celtis ehrenbergiana*, *Zanthoxylum rhoifolium*, *Zanthoxylum fagara*, *Prosopis alba*, *Jodina rhombifolia*, and *Aspidosperma quebracho-blanco*. The woodlands of the Paranaense Phytogeographic Province of the study area comprise *Baccharis salicifolia*, *Tessaria integrifolia*, and *Salix humboldtiana*. However, the region has been heavily disturbed by agriculture, livestock grazing, and urban expansion. The climate is classified as subtropical humid (Cfa, Koppen-Geiger classification, [47], with a mean annual temperature of 18.25°C and annual precipitation of 1236.3 mm (National Meteorological Service). Seasons are marked by cold winters and hot, wet summers (Figure S1).

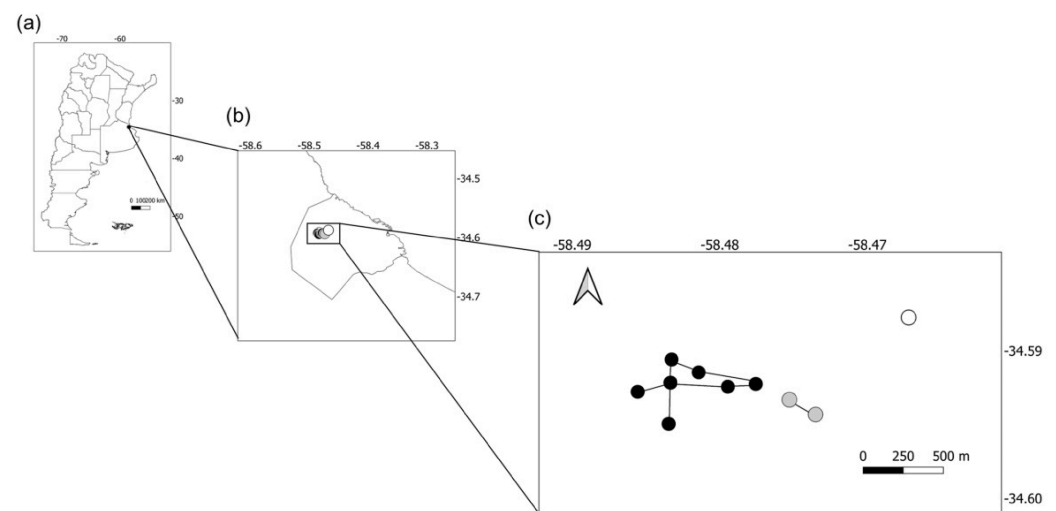


Figure 1. Location of Buenos Aires City in Argentina (a), point counts in Buenos Aires City (b), and point counts in the three urban green spaces surveyed (c). Black points are at the Faculty of Agronomy of Buenos Aires University, gray points are at the Isla de la Paternal park, and the white point is at the Antonio Malaver park. Black lines connecting points indicate the pathways where flocks were surveyed in addition.

2.2. Flock Surveys

Flock surveys were conducted in three urban green areas: (1) Faculty of Agronomy of Buenos Aires University (74 ha, seven point counts); (2) park Isla de la Paternal (7.82 ha, two point counts); and (3) park Antonio Malaver (1.18 ha, one point count) (Figure 1). The number of points in each green area varied by area size and accessibility. The general habitat structure of the green areas consisted of lawns with trees and some shrubs. Five-minute point counts with a 50 m radius, separated by at least 200 m, were conducted during the first four hours after sunrise [48]. In addition, flocks were surveyed on transects connecting points in the Faculty of Agronomy and Isla de la Paternal (Figure 1c).

Surveys were conducted over an annual cycle, from April 2025 to March 2026. Points in the Faculty of Agronomy were surveyed on one morning, totaling 45 visits during the annual cycle. Point counts in Isla de la Paternal and Malaver were conducted on another morning, totaling 37 visits. Each green area was visited between two and four times per month.

I defined a mixed flock as two or more individuals of different species moving in close proximity, within 10 m of the nearest individual [33]. However, I did not track flocks for longer than five minutes to avoid double counting of individuals in the same park and humans disturbing the flocks [49]. The time spent following flocks is similar to that reported in other studies conducted in urban areas [40,50]. In addition, I recorded the tree species used by each flock. Several studies have emphasized the role of native trees supporting bird diversity in urban areas [51–54]. Thus, the tree species was classified as native to the study area, native to the country but exotic in the study area (original to the country), or exotic. This study focused primarily on insectivorous bird species that forage in trees.

The use of mixed flocks by bird species was characterized as their frequency and association between species. Frequency was the number of flocks used by each bird species. Species association in flocks was analyzed through multivariate statistics (see below). In addition, I analyzed the relationship between the relative abundance of species in mixed flocks and their abundance in the study area.

2.3. Bird Species Surveys

Bird surveys were conducted during point counts to relate species' relative abundances to those in the flocks. Only individual birds foraging or perching in the green areas were recorded. The surveys were conducted simultaneously with those of bird flocks.

2.4. Environmental Variables

At the start of each survey, temperature and relative humidity were obtained from the local meteorological station's online data (<https://ws2.smn.gob.ar/>). The Julian day for each survey was also recorded. Thus, I had data on temperature, humidity, and the Julian day for each survey day ($n = 82$ visits). Total monthly precipitation was obtained from the National Meteorological Service.

2.5. Statistical Analysis

The relative abundance of bird species in flocks was correlated with their relative abundance in point counts using Pearson correlation. In addition, species associations within flocks were analyzed using ordination and cluster analyses based on the Jaccard dissimilarity index for presence/absence species data. Non-metric multidimensional scaling (NMDS) is a multivariate ordination technique that allows visualization of associations between species and flocks in a small number of dimensions using dissimilarity indices [55]. Hierarchical clustering was used to group species within the flocks based on the Jaccard dissimilarity matrix. Groups were obtained using the average-linkage method. NMDS was performed using the metaMDS function in the vegan package in R (version 4.4.2) [56,57], whereas the hierarchical clustering was performed using the hclust function in R.

Mixed-flock presence was modeled as a function of environmental variables using Generalized Additive Models (GAMs) with a binomial error structure. GAMs are non-parametric regression models that allow the evaluation of nonlinear relationships between variables [58]. The response variable was the presence of flocks during each morning survey. The environmental variables were Julian day, temperature, humidity, and monthly precipitation for each weekly survey. Because each survey had a different number of point counts, this variable was included in the model to control for sampling effort. Because

multiple visits were made to each green area, which constituted temporal pseudoreplicates, each site was included in the model using the bs “re” function [59]. The sites corresponded to the green areas visited each morning, namely the Faculty of Agronomy, Isla de la Paternal, and Malaver parks. Model selection was based on Akaike’s Information Criterion (AIC), with models having lower AIC values chosen [60]. I used AICc due to the small sample size and obtained AICc values for all possible models using the dredge function in the MuMIn package [61]. The normality and heteroscedasticity of the model residuals were tested using the DHARMA package [62]. The best model (lowest AICc) was plotted with the visreg package [63].

3. Results

A total of 13 bird species and 86 individuals were detected across 14 flocks (Table 1). Flocks had a mean species richness of 3.14 species (range = 2–5 species) and a mean abundance of 6.14 (range = 2–13 birds). The most frequent and abundant species in flocks were the White-crested Tyrannulet (*Serpophaga subcristata*), the Greyish Baywing (*Agelaioides badius*), the Masked Gnatcatcher (*Poliophtila dumicola*), and the Tropical Parula (*Setophaga pitaiayumi*). Most species were resident and belonged to invertivore guilds. Flocks were observed in two native tree species from the study area [64,65], including *Enterolobium contortisiliquum* ($n = 4$) and *Erythrina crista-galli* ($n = 2$), *Tipuana tipu* ($n = 2$) exotic from the study area but native from northwestern Argentina [66], as well as in exotic tree species, including *Quercus robur* ($n = 4$) and *Ficus aurea* ($n = 2$).

The relative abundance of species in flocks was positively correlated with their relative abundance in point counts (Pearson correlation, $r = 0.749$, $n = 13$, $p = 0.003$; Figure 2). The relative abundance of *Poliophtila dumicola*, *Setophaga pitaiayumi*, *Serpophaga subcristata*, and *Agelaioides badius* tended to be overrepresented in flocks compared with their abundances in point counts. In contrast, the Rufous-collared Sparrow (*Zonotrichia capensis*) and the House Wren (*Troglodytes musculus*) were underrepresented.

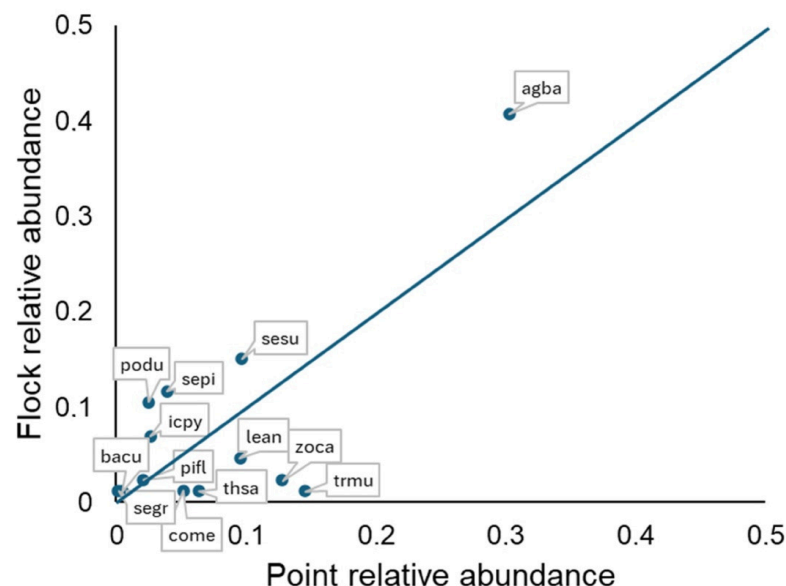


Figure 2. Relationship between the relative abundance of bird species in mixed flocks (y-axis) and in point counts (x-axis) during autumn and winter in urban green areas of Buenos Aires City, Argentina (see Table 1 for total individuals). The blue line indicates exact correspondence between the two relative abundances. Species names: agba, *Agelaioides badius*; bacu, *Basileuterus culicivorus*; come, *Colaptes melanochloros*; icpy, *Icterus pyrrhopterus*; lean, *Lepidocolaptes angustirostris*; pifl, *Piranga flava*; podu, *Poliophtila dumicola*; segr, *Serpophaga griseicapilla*; sepi, *Setophaga pitaiayumi*; sesu, *Serpophaga subcristata*; thsa, *Thraupis sayaca*; trmu, *Troglodytes musculus*; zoca, *Zonotrichia capensis*.

Table 1. List of species detected in mixed-species flocks of urban green areas of Buenos Aires City, Argentina. Numbers are the amount and percentage of flocks occupied by each species (n flocks = 14) and the total individuals of each bird species in flocks. Guild classification based on Wilman et al. [67]. * Winter migrant. ** Individuals surveyed during autumn and winter, simultaneously to flock occurrence.

English Name	Scientific Name	Guild	Flock Numbers (%)	Total Individuals in Flocks	Total Individuals in Points **
Green-barred Woodpecker	<i>Colaptes melanochloros</i>	Invertebrate	1 (7)	1	33
Narrow-billed Woodcreeper	<i>Lepidocolaptes angustirostris</i>	Invertebrate	4 (29)	4	61
White-crested Tyrannulet	<i>Serpophaga subcristata</i>	Invertebrate	9 (64)	13	62
Straneck's Tyrannulet	<i>Serpophaga griseicapilla</i> *	Invertebrate	1 (7)	1	1
House Wren	<i>Troglodytes musculus</i>	Invertebrate	1 (7)	1	93
Masked Gnatcatcher	<i>Polioptila dumicola</i>	Invertebrate	6 (43)	9	16
Tropical Parula	<i>Setophaga pitaiayumi</i>	Invertebrate	6 (43)	10	25
Golden-crowned Warbler	<i>Basileuterus culicivorus</i>	Invertebrate	1 (7)	1	3
Hepatic Tanager	<i>Piranga flava</i>	Invertebrate	1 (7)	2	13
Sayaca Tanager	<i>Thraupis sayaca</i>	Omnivore	1 (7)	1	41
Rufous-collared Sparrow	<i>Zonotrichia capensis</i>	Plant and Seeds	2 (14)	2	82
Greyish Baywing	<i>Agelaioides badius</i>	Invertebrate	7 (50)	35	194
Variable Oriole	<i>Icterus pyrrhopterus</i>	Invertebrate	4 (29)	6	17

Ordination analyses and hierarchical clustering based on Jaccard dissimilarity indicated that *Polioptila dumicola*, *Setophaga pitaiayumi*, and *Serpophaga subcristata* tended to occur together in flocks (Figure 3). The Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), *Zonotrichia capensis*, the Green-barred Woodpecker (*Colaptes melanochloros*) and *Agelaioides badius* formed another association.

The best model predicting flock occurrence included the Julian day (estimated degrees of freedom = 1.904, Chi-square = 7.232, $p = 0.030$, pseudo- $r^2 = 0.105$; Table S1). The predicted probability of flock occurrence peaked between Julian days 100 and 200, corresponding to the austral autumn, the beginning of winter, and the non-breeding season for bird species (Figure 4). No flocks were recorded from spring through much of the summer.

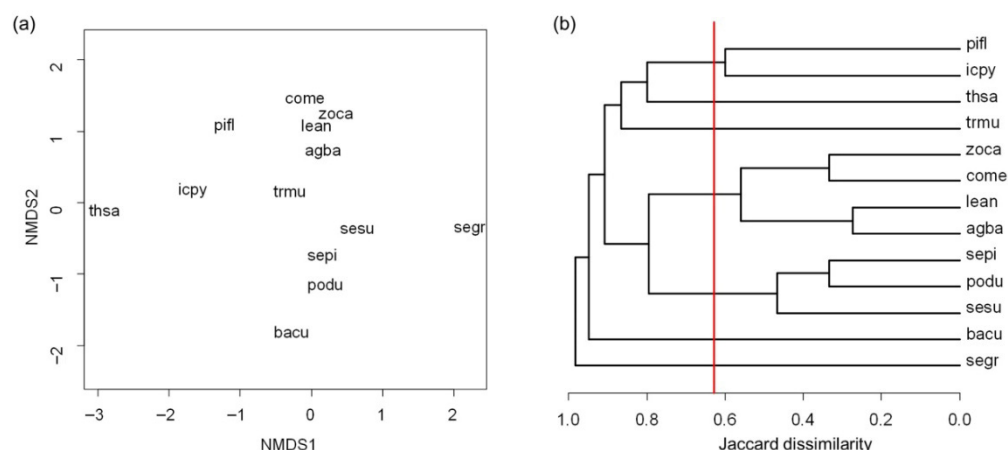


Figure 3. (a) Non-metric multidimensional scaling (NMDS, stress = 0.076) based on Jaccard dissimilarity showing bird species associations in mixed flocks, and (b) cluster analysis showing groups of species in flocks. The vertical red line indicates a median cut-off of 0.628 dissimilarity. Species names: agba, *Agelaioides badius*; bacu, *Basileuterus culicivorus*; come, *Colaptes melanochloros*; icpy, *Icterus pyrrhopterus*; lean, *Lepidocolaptes angustirostris*; pifl, *Piranga flava*; podu, *Poliophtila dumicola*; segr, *Serpophaga griseicapilla*; sepi, *Setophaga pitiayumi*; sesu, *Serpophaga subcristata*; thsa, *Thraupis sayaca*; trmu, *Troglodytes musculus*; zoca, *Zonotrichia capensis*.

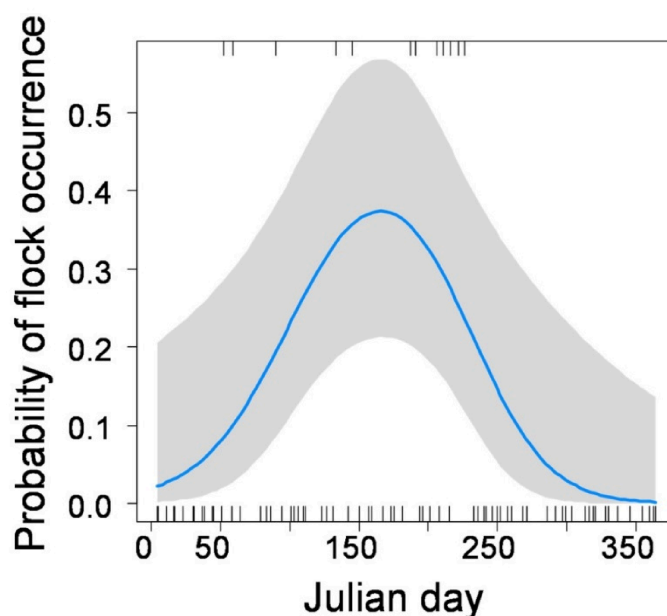


Figure 4. Predicted probability of bird mixed-species flock occurrence (y-axis) in relation to the Julian days (x-axis) in urban green areas of Buenos Aires City, Argentina. The solid line shows the fitted model and the shading represents 95% confidence intervals.

4. Discussion

The results showed that mixed-species flocks of woodland insectivorous birds in urban green spaces support the open-membership hypothesis, as flock species composition was positively related to their abundance in green areas. Flock formation was highly seasonal, predominantly during the non-breeding season.

In general, the relative abundance of bird species in mixed flocks was positively correlated with their relative abundance during bird surveys in the green areas. Therefore, flock composition varies with that of local communities, supporting the idea of open membership in flocks [18,68]. This variable flock formation contrasts with other studies in

which species composition is stable and flocks are usually dominated by nuclear species that contribute to flock formation and cohesion [20,26,69].

However, some species were overrepresented in flocks relative to their abundance in the study area. *Serpophaga subcristata*, *Polioptila dumicola*, and *Setophaga pitaiayumi* tended to occur together in flocks. In general, these species are highly insectivorous foliage foragers in the canopy of the region's native woodlands [67,70]. To my knowledge, there are no published records of mixed-species flocks in the region's native woodlands.

On the other hand, *Agelaioides badius* was also overrepresented in flocks and was associated with other underrepresented species in flocks, such as *Lepidocolaptes angustirostris*, *Zonotrichia capensis*, and *Colaptes melanochloros*. *Zonotrichia capensis* have a more varied diet and habitat use, foraging on plant material and seeds on the ground [67,71]. Moreover, *Colaptes melanochloros*, *Agelaioides badius*, and *Zonotrichia capensis* have also been recorded forming mixed ground flocks during spring and summer [49].

Therefore, two types of flocks were recorded in this study. A more stable mixed flock composed of foliage insectivore specialists, such as *Serpophaga subcristata*, *Polioptila dumicola*, and *Setophaga pitaiayumi*, and another less stable mixed flock composed of *Agelaioides badius* and other transient species, such as *Lepidocolaptes angustirostris*, *Zonotrichia capensis*, and *Colaptes melanochloros*. Further research is needed to analyze the distinct roles of species in mixed flocks, such as nuclear, leader, or sentinel [26].

Mixed flocks were observed in similar proportions across native and exotic tree species. Therefore, these patterns agree with other studies showing that both native and exotic tree species can support native birds by providing food resources [72,73]. However, this study only analyzed tree use by flocks, and a more detailed test of tree selection, comparing use and availability, is required.

Flocks were highly seasonal, peaking in autumn and early winter, which corresponds to the non-breeding season. This pattern aligns with other studies conducted in temperate and subtropical areas [29,30,33–35,74]. However, our results did not show a relationship between flock occurrence and temperature. The climatic fluctuations in our study area were likely not severe enough to trigger flocking behavior [36]. The urban heat island phenomenon in large cities such as Buenos Aires [75–77] may raise minimum winter temperatures, resulting in milder climatic conditions for birds. Instead, the significant relationship between flock occurrence and Julian days during the non-breeding season suggests that mixed flocking behavior likely helps individuals and pairs of different species find food and avoid predators as they move outside their breeding territories.

The number of flocks recorded in this study was lower than in other studies conducted in urban areas [39–41]. The differences may be related to sampling effort, although the number of sites and visits in this study appears similar to those in other studies [39,41]. Alternatively, the lower number of flocks in this study could reflect lower densities of the bird species that form flocks, such as *Serpophaga subcristata*, *Polioptila dumicola*, and *Setophaga pitaiayumi*. These species depend on native woodlands [70], which are scarce in the region due to the ecotone transition with natural grasslands (see Study Area) and are further reduced by deforestation, exotic tree invasion, cattle grazing, agriculture, and urban expansion [78]. In addition, tree species used in urban green spaces in the study area are mostly exotic, which can negatively affect bird species densities [79]. In contrast, the abundance of bird species that form flocks in other studies conducted in the Northern Hemisphere [39–41] may be higher because forested biomes naturally surround cities. Therefore, higher regional densities of bird species can promote greater flock formation compared with this study.

5. Conclusions

The relative abundance of bird species in flocks was positively related to their abundance in the study area. Therefore, habitat quality in urban green areas that support forest insectivorous bird species is fundamental to flocking behavior. On the other hand, the seasonal dynamics of flocks were similar to those reported in studies conducted in temperate and subtropical areas. Flocking behavior in insectivorous forest species is mainly observed outside the breeding season, probably favoring food search and minimizing predation risk. However, other factors, such as prey detectability, may influence mixed-species flock formation [80] and warrant further research. Given the limited data from this study, I recommend surveying additional urban green areas in winter to examine how green area size, isolation, and habitat structure affect flock behavior. In addition, a better understanding of the effects of urbanization on mixed flocks would be gained by comparing the spatial and temporal dynamics of flocking behavior in forest birds in urban green areas with those in the region's native woodlands.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/birds7030046/s1>, Figure S1: Climatic characteristics of flock surveys in green areas of Buenos Aires City, Argentina. Temperature (a) and humidity (b) data were retrieved from the National Meteorological Service online website (<https://ws2.smn.gob.ar/>) at the beginning of each survey during April 2025–March 2026. Precipitation data (c) are monthly values during the study period from the local station of the National Meteorological Service, related to the median Julian day of each month; Table S1: Generalized additive models showing the relationship between flock occurrence and environmental variables, sampling effort, and sampling site. Humidity, Julian day, precipitation, temperature, and site have smooth terms. df: degrees of freedom; logLik: log-likelihood; delta: difference of AICc between models; weight: represents the relative probability or support of each model in a candidate set.

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References

1. Morse, D.H. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.* **1970**, *40*, 119–168.
2. Powell, G.V. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. In *Ornithological Monographs*; American Ornithological Society: Chicago, IL, USA, 1985; pp. 713–732.
3. Tubelis, D.P. Mixed-species flocks of birds in the Cerrado, South America: A review. *Ornitol. Neotrop.* **2007**, *18*, 7.
4. Sridhar, H.; Beauchamp, G.; Shanker, K. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim. Behav.* **2009**, *78*, 337–347. [[CrossRef](#)]
5. Goodale, E.; Ding, P.; Liu, X.; Martínez, A.; Si, X.; Walters, M.; Robinson, S.K. The structure of mixed-species bird flocks, and their response to anthropogenic disturbance, with special reference to East Asia. *Avian Res.* **2015**, *6*, 14. [[CrossRef](#)]
6. Goodale, E.; Sridhar, H.; Sieving, K.E.; Bangal, P.; Colorado, Z.G.J.; Farine, D.R.; Heymann, E.W.; Jones, H.H.; Krams, I.; Martínez, A.E.; et al. Mixed company: A framework for understanding the composition and organization of mixed-species animal groups. *Biol. Rev.* **2020**, *95*, 889–910. [[CrossRef](#)] [[PubMed](#)]
7. Beauchamp, G.; Mangini, G.G. Body mass, diet, foraging strata and foraging behaviour predict variation in the propensity to join mixed-species flocks across birds. *Ibis* **2024**, *166*, 1384–1394. [[CrossRef](#)]

8. Wu, J.; Goodale, E.; Li, W.; Zou, F.; Zhang, Q. Patterns in the global diversity of mixed-species bird flocks in relation to environmental factors. *Biol. Divers.* **2024**, *1*, 44–53. [\[CrossRef\]](#)
9. Whitfield, D.P. Redshank *Tringa totanus* flocking behaviour, distance from cover and vulnerability to sparrowhawk *Accipiter nisus* predation. *J. Avian Biol.* **2003**, *34*, 163–169. [\[CrossRef\]](#)
10. Colorado Zuluaga, G.J. Why animals come together, with the special case of mixed-species bird flocks. *Rev. EIA* **2013**, *10*, 49–66.
11. Bangal, P.; Sridhar, H.; Shanker, K. Phenotypic clumping decreases with flock richness in mixed-species bird flocks. *Front. Ecol. Evol.* **2021**, *8*, 537816. [\[CrossRef\]](#)
12. Caraco, T.; Martindale, S.; Pulliam, H.R. Avian flocking in the presence of a predator. *Nature* **1980**, *285*, 400–401. [\[CrossRef\]](#)
13. Elgar, M.A.; Catterall, C.P. Flocking and predator surveillance in house sparrows: Test of an hypothesis. *Anim. Behav.* **1981**, *29*, 868–872. [\[CrossRef\]](#)
14. Mangini, G.G.; Gandoy, F.A.; Areta, J.I.; Blendinger, P.G. Benefits of foraging in mixed-species flocks depend on species role and foraging strategy. *Ibis* **2023**, *165*, 629–646.
15. Mangini, G.G.; Gandoy, F.A. Social Dynamics and Foraging Strategies of Woodpeckers in Mixed-Species Flocks of Birds in Subtropical Forests. *Acta Ornithol.* **2026**, *60*, 91–102. [\[CrossRef\]](#)
16. Montaña-Centellas, F.A.; Muñoz, J.; Mangini, G.G.; Ausprey, I.J.; Newell, F.L.; Jones, H.H.; Fanjul, M.E.; Tinoco, B.A.; Cahill, J.R.A.; Arbeláez-Cortés, E.; et al. Network structure of avian mixed-species flocks decays with elevation and latitude across the Andes. *Philos. Trans. R. Soc. B Biol. Sci.* **2023**, *378*, 20220099. [\[CrossRef\]](#) [\[PubMed\]](#)
17. Muñoz, J. The Role of Facilitation in the Structure of Tropical Bird Communities: A Case Study of Mixed-Species Flocks. Doctoral Dissertation, University of British Columbia, Vancouver, BC, Canada, 2016.
18. Montaña-Centellas, F.A.; Jones, H.H. Temperature and vegetation complexity structure mixed-species flocks along a gradient of elevation in the tropical Andes. *Auk* **2021**, *138*, ukab027. [\[CrossRef\]](#)
19. Jullien, M.; Thiollay, J.M. Multi-species territoriality and dynamic of neotropical forest understorey bird flocks. *J. Anim. Ecol.* **1998**, *67*, 227–252. [\[CrossRef\]](#)
20. Maldonado-Coelho, M.; Marini, M.Â. Mixed-species bird flocks from Brazilian Atlantic forest: The effects of forest fragmentation and seasonality on their size, richness and stability. *Biol. Conserv.* **2004**, *116*, 19–26. [\[CrossRef\]](#)
21. Coddington, C.P.; Cooper, W.J.; Mokross, K.; Luther, D.A. Forest structure predicts species richness and functional diversity in Amazonian mixed-species bird flocks. *Biotropica* **2023**, *55*, 467–479. [\[CrossRef\]](#)
22. Kajiki, L.N.; Montaña-Centellas, F.; Mangini, G.; Colorado Z, G.J.; Fanjul, M.E. Ecology of mixed-species flocks of birds across gradients in the Neotropics. *Rev. Bras. Ornitol.* **2018**, *26*, 82–89. [\[CrossRef\]](#)
23. Fanjul, M.E.; Echevarria, A.L.; Martínez, M.V. Estructura y composición de las bandadas mixtas de aves invernales a lo largo del gradiente latitudinal en las selvas montañas de las Yungas, Argentina. *Acta Zool. Lilloana* **2021**, *65*, 268–286. [\[CrossRef\]](#)
24. Tellería, J.L.; Virgós, E.; Carbonell, R.; Pérez-Tris, J.; Santos, T. Behavioural responses to changing landscapes: Flock structure and anti-predator strategies of tits wintering in fragmented forests. *Oikos* **2001**, *95*, 253–264. [\[CrossRef\]](#)
25. Hariharan, P.; Bangal, P.; Sridhar, H.; Shanker, K. Habitat use by mixed-species bird flocks in tropical forests of the Western Ghats, India. *J. Trop. Ecol.* **2022**, *38*, 393–400. [\[CrossRef\]](#)
26. Mangini, G.G.; Rutt, C.L.; Sridhar, H.; Buitron, G.; Muñoz, J.; Robinson, S.K.; Montaña-Centellas, F.; Zarco, A.; Fanjul, M.E.; Fernández-Arellano, G.; et al. A classification scheme for mixed-species bird flocks. *Philos. Trans. R. Soc. B Biol. Sci.* **2023**, *378*, 20220100. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Jayarathna, A.; Kotagama, S.W.; Goodale, E. The seasonality of mixed-species bird flocks in a Sri Lankan rainforest in relation to the breeding of the nuclear species, Orange-billed Babbler *Turdoides rufescens*. *Forktail* **2013**, *29*, 138–139.
28. Rutt, C.L.; Stouffer, P.C. Seasonal dynamics of flock interaction networks across a human-modified landscape in lowland Amazonian rain forest. *Ecol. Appl.* **2021**, *31*, e02235. [\[CrossRef\]](#) [\[PubMed\]](#)
29. Davis, D.E. A seasonal analysis of mixed flocks of birds in Brazil. *Ecology* **1946**, *27*, 168–181. [\[CrossRef\]](#)
30. Dean, S. Composition and seasonality of mixed-species flocks of insectivorous birds. *Notornis* **1990**, *37*, 27–36. [\[CrossRef\]](#)
31. Alves, M.A.S.; Cavalcanti, R.S. Sentinel behavior, seasonality, and the structure of bird flocks in a Brazilian savanna. *Ornitol. Neotrop.* **1996**, *7*, 43–51. [\[CrossRef\]](#) [\[PubMed\]](#)
32. Develey, P.F.; Peres, C.A. Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil. *J. Trop. Ecol.* **2000**, *16*, 33–53. [\[CrossRef\]](#)
33. Ippi, S.; Trejo, A. Dinámica y estructura de bandadas mixtas de aves en un bosque de lenga (*Nothofagus pumilio*) del Noroeste de la Patagonia argentina. *Ornitol. Neotrop.* **2003**, *14*, 353–362. [\[CrossRef\]](#)
34. Tubelis, D.P.; Cowling, A.N.N.; Donnelly, C. Role of mixed-species flocks in the use of adjacent savannas by forest birds in the central Cerrado, Brazil. *Austral Ecol.* **2006**, *31*, 38–45. [\[CrossRef\]](#)
35. Fernández-Arellano, G.J.; Bonanomi, J.; Pinho, J.B. Seasonal drivers of mixed-species flocks from tropical savannas: Insights from the Pantanal wetland. *J. Field Ornithol.* **2023**, *94*, 3. [\[CrossRef\]](#)

36. Mangini, G.G.; Areta, J.I. Bird mixed-species flock formation is driven by low temperatures between and within seasons in a Subtropical Andean-foothill forest. *Biotropica* **2018**, *50*, 816–825. [\[CrossRef\]](#)
37. Caraco, T. Time budgeting and group size: A test of theory. *Ecology* **1979**, *60*, 618–627. [\[CrossRef\]](#)
38. Maune, A.L.; Caspers, B.A.; Damas-Moreira, I. The impact of urbanisation on social behaviour: A comprehensive review. *Biol. Rev.* **2026**, *101*, 1003–1035. [\[CrossRef\]](#) [\[PubMed\]](#)
39. Yaukey, P.H. Patterns of avian population density, habitat use, and flocking behavior in urban and rural habitats during winter. *Prof. Geogr.* **1996**, *48*, 70–81. [\[CrossRef\]](#)
40. Fernández-Juricic, E. Forest fragmentation affects winter flock formation of an insectivorous guild. *Ardea* **2000**, *88*, 235–241.
41. Lee, T.M.; Soh, M.C.; Sodhi, N.; Koh, L.P.; Lim, S.L.H. Effects of habitat disturbance on mixed species bird flocks in a tropical sub-montane rainforest. *Biol. Conserv.* **2005**, *122*, 193–204. [\[CrossRef\]](#)
42. Shochat, E.; Warren, P.S.; Faeth, S.H.; McIntyre, N.E.; Hope, D. From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* **2006**, *21*, 186–191. [\[CrossRef\]](#) [\[PubMed\]](#)
43. Leveau, L.M.; Jokimäki, J.; Kaisanlahti-Jokimäki, M.L. Urbanization buffers seasonal change in composition of bird communities: A multi-continental meta-analysis. *J. Biogeogr.* **2021**, *48*, 2391–2401. [\[CrossRef\]](#)
44. Instituto Nacional de Estadística y Censos. *Censo Nacional de Población, Hogares y Viviendas 2022: Resultados Definitivos: Indicadores Demográficos por Sexo y Edad*, 1st ed.; Instituto Nacional de Estadística y Censos—INDEC: Ciudad Autónoma de Buenos Aires, Argentina, 2023.
45. Cabrera, A.L.; Willink, A. *Biogeografía de América Latina*; Programa Regional de Desarrollo Científico y Tecnológico: Washington, DC, USA, 1973; Volume 13, pp. 1–117.
46. Oyarzabal, M.; Clavijo, J.; Oakley, L.; Biganzoli, F.; Tognetti, P.; Barberis, I.; Maturo, H.M.; Aragón, R.; Campanello, P.I.; Prado, D.; et al. Unidades de vegetación de la Argentina. *Ecol. Austral* **2018**, *28*, 40–63. [\[CrossRef\]](#)
47. Peel, M.C.; Finlayson, B.L.; McMahon, T.A. Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* **2007**, *11*, 1633–1644. [\[CrossRef\]](#)
48. Bibby, C.J.; Burgess, N.D.; Hill, D.A. *Bird Census Techniques*; Academic Press: London, UK, 1992.
49. Leveau, L.M. Local and landscape drivers of ground bird flocking behavior in urban parks of Buenos Aires City, Argentina. *Birds* **2025**, *6*, 23. [\[CrossRef\]](#)
50. Fernández-Juricic, E. Nested patterns of species distribution and winter flock occurrence of insectivorous birds in a fragmented landscape. *Ecoscience* **2002**, *9*, 450–485. [\[CrossRef\]](#)
51. Ikin, K.; Knight, E.; Lindenmayer, D.B.; Fischer, J.; Manning, A.D. The influence of native versus exotic streetscape vegetation on the spatial distribution of birds in suburbs and reserves. *Divers. Distrib.* **2013**, *19*, 294–306. [\[CrossRef\]](#)
52. Paker, Y.; Yom-Tov, Y.; Alon-Mozes, T.; Barnea, A. The effect of plant richness and urban garden structure on bird species richness, diversity and community structure. *Landsc. Urban Plan.* **2014**, *122*, 186–195. [\[CrossRef\]](#)
53. Pena, J.C.D.C.; Martello, F.; Ribeiro, M.C.; Armitage, R.A.; Young, R.J.; Rodrigues, M. Street trees reduce the negative effects of urbanization on birds. *PLoS ONE* **2017**, *12*, e0174484. [\[CrossRef\]](#) [\[PubMed\]](#)
54. Basile, M.; Augustinus, B.A.; Brockerhoff, E.G. Urban tree canopy cover over 30% and native trees enhance bird insectivory and tree biosecurity. *Biol. Conserv.* **2025**, *310*, 111387. [\[CrossRef\]](#)
55. McCune, B.; Grace, J.B. *Analysis of Ecological Communities*; MjM Software Design: Gleneden Beach, OR, USA, 2002.
56. Oksanen, J.; Simpson, G.; Blanchet, F.; Kindt, R.; Legendre, P.; Minchin, P.; O'Hara, R.; Solymos, P.; Stevens, M.; Szoecs, E.; et al. *Vegan: Community Ecology Package*. R Package, version 2.6-2; R Foundation for Statistical Computing: Vienna, Austria, 2022. Available online: <https://CRAN.R-project.org/package=vegan> (accessed on 19 June 2026).
57. R Development Core Team. *R: A Language and Environment for Statistical Computing*, version 4.4.2; R Foundation for Statistical Computing: Vienna, Austria, 2024.
58. Zuur, A.F.; Ieno, E.N.; Walker, N.J.; Saveliev, A.A.; Smith, G.M. *Mixed Effects Models and Extensions in Ecology with R*; Springer: New York, NY, USA, 2009; Volume 574, p. 574.
59. Wood, S. *Package mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation*, version 1.9-4; R Foundation for Statistical Computing: Vienna, Austria, 2021. Available online: <https://cran.r-project.org/web/packages/mgcv/mgcv.pdf> (accessed on 19 June 2026).
60. Burnham, K.P.; Anderson, D.R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed.; Springer: New York, NY, USA, 2002.
61. Bartoń, K. *Package 'MuMIn'*, version 1.48.19; CRAN: Windhoek, Namibia, 2026. Available online: <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf> (accessed on 19 June 2026).
62. Hartig, H.; Lohse, L.; de Souza, M. *Package 'DHARMA', Residual Diagnostics for Hierarchical (Mul-ti-Level/Mixed) Regression Models*, version 0.4.7; R Foundation for Statistical Computing: Vienna, Austria, 2025. Available online: <https://cran.r-project.org/web/packages/DHARMA/DHARMA.pdf> (accessed on 19 June 2026).
63. Breheny, P.; Burchett, W. Visualization of Regression Models Using visreg. *R J.* **2017**, *9*, 56–71. [\[CrossRef\]](#)

64. Burkart, A. Ojeada sinóptica sobre: La vegetación del Delta del Río Paraná. *Darwiniana* **1957**, *11*, 457–561.
65. Burgueño, G. *Restauración del Paisaje Metropolitano: Apuntes Para la Reflexión y Planificación en la Región Metropolitana de Buenos Aires*; Orientación Gráfica Editora: Buenos Aires, Argentina, 2014.
66. Lahitte, H.B.; Hurrell, J.A.; Valla, J.J.; Jankowski, L.S.; Bazzano, D.; Hernández, A.J. *Árboles Urbanos. Biota Rioplatense IV. Inventario de la Biota de la Región del Delta del Paraná, Isla Martín García y Ribera Platense*; L.O.L.A.: Buenos Aires, Argentina, 1999.
67. Wilman, H.; Belmaker, J.; Simpson, J.; De La Rosa, C.; Rivadeneira, M.M.; Jetz, W. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals: Ecological Archives E095-178. *Ecology* **2014**, *95*, 2027.
68. Jones, H.H.; Robinson, S.K. Patch size and vegetation structure drive changes to mixed-species flock diversity and composition across a gradient of fragment sizes in the Western Andes of Colombia. *Condor* **2020**, *122*, duaa006. [[CrossRef](#)]
69. Martínez, A.E.; Gomez, J.P. Are mixed-species bird flocks stable through two decades? *Am. Nat.* **2013**, *181*, E53–E59. [[CrossRef](#)] [[PubMed](#)]
70. Cueto, V.R.; De Casenave, J.L. Foraging behavior and microhabitat use of birds inhabiting coastal woodlands in east central Argentina. *Wilson Bull.* **2002**, *114*, 342–348. [[CrossRef](#)]
71. Leveau, L.M. Microhabitat Selection by Ground-Foraging Birds in Urban Parks. *Animals* **2025**, *15*, 1155. [[CrossRef](#)] [[PubMed](#)]
72. Gray, E.R.; van Heezik, Y. Exotic trees can sustain native birds in urban woodlands. *Urban Ecosyst.* **2016**, *19*, 315–329. [[CrossRef](#)]
73. Wood, E.M.; Esaian, S. The importance of street trees to urban avifauna. *Ecol. Appl.* **2020**, *30*, e02149. [[CrossRef](#)] [[PubMed](#)]
74. Jiang, D.; Sieving, K.E.; Meaux, E.; Goodale, E. Seasonal changes in mixed-species bird flocks and antipredator information. *Ecol. Evol.* **2020**, *10*, 5368–5382. [[CrossRef](#)] [[PubMed](#)]
75. Oke, T.R. City size and the urban heat island. *Atmos. Environ.* **1973**, *7*, 769–779. [[CrossRef](#)]
76. Camilloni, I.; Barrucand, M. Temporal variability of the Buenos Aires, Argentina, urban heat island. *Theor. Appl. Climatol.* **2012**, *107*, 47–58. [[CrossRef](#)]
77. Zhou, B.; Rybski, D.; Kropp, J.P. The role of city size and urban form in the surface urban heat island. *Sci. Rep.* **2017**, *7*, 4791. [[CrossRef](#)] [[PubMed](#)]
78. Mérida, E.; Athor, J. *Talares Bonaerenses y su Conservación*; Fundación de Historia Natural “Félix de Azara”: Buenos Aires, Argentina, 2006.
79. Curzel, F.E.; Bellocq, M.I.; Leveau, L.M. Local and landscape features of wooded streets influenced bird taxonomic and functional diversity. *Urban For. Urban Green.* **2021**, *66*, 127369. [[CrossRef](#)]
80. Mangini, G.; Mokross, K.; Gandoy, F.; Areta, J.I. Mixed-species flocking is associated with low arthropod detectability and increased foraging efficiency by Yungas forest birds in Argentina. *Ornithology* **2022**, *139*, ukab087. [[CrossRef](#)]

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