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Vacant lands as refuges for native birds: An opportunity for biodiversity conservation in cities



Nélida R. Villaseñor^{a,*}, Luna A. Chiang^a, H. Jaime Hernández^a, Martín A.H. Escobar^b

- a Geomatics and Landscape Ecology Lab, Facultad de Ciencias Forestales y de la Conservación de la Naturaleza, Universidad de Chile, Santiago, 8820808, Chile
- b Escuela de Pregrado, Facultad de Ciencias Agronómicas, Universidad de Chile, Santiago, 8820808, Chile

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ABSTRACT

Vacant land in growing cities is commonly targeted for development because it is perceived as wasted land that provides no benefit for people or nature. However, vacant sites might contribute to biodiversity conservation. To help inform biodiversity-sensitive urban development, we examined whether vacant land provided suitable habitat for birds in the Latin American city of Santiago, Chile - a growing capital city located in a Mediterranean ecosystem identified as a global biodiversity hotspot. We posed the following questions: How do species richness and abundance of native and exotic birds vary among vacant lands, urban parks and residential areas? And does vacant land support a different bird community compared with urban parks and residential areas? We found that vacant lands helped conserve local birds. Vacant lands exhibited high species richness and abundance of native birds, and maintained significantly fewer exotic species than urban parks and residential areas. In addition, vacant lands supported a different bird community than urban parks and residential areas, including several native birds associated with grasslands and rural areas that are rare in the city. Although vegetation in vacant land was dominated by exotic herbaceous plants, they provided important resources for native birds. Our findings demonstrate that vacant land covered by spontaneous vegetation provides habitat for native birds. Given that vacant lands offer opportunities for biodiversity conservation and to connect urban residents with nature close to home, we discuss strategies to help maintain the benefits provided by vacant lands through urban design, land use planning and urban growth policies.

1. Introduction

Urban lands are expanding worldwide, highlighting the key role of landscape and urban planners in adopting strategies to achieve sustainable cities and reduce the impacts of urbanization on biodiversity. By 2050, 68 % of the world population will live in urban areas (United Nations, 2018). Urban lands are predicted to triple their area in only 30 years, leading to habitat loss in different regions, including biodiversity hotspots (Seto et al., 2012). Land development threatens several species with extinction, due to marked environmental change and the loss and degradation of habitats (McKinney, 2006). In the face of the rapid loss of global biodiversity, it is important to plan and manage urban land-scapes to help conserve local biodiversity.

Greenspaces are important for conserving biodiversity in urban landscapes. Greenspace supports a variety of plants, provides habitat for wildlife and increases functional connectivity for local fauna. A wide variety of greenspace exists, comprising different habitat types. They

range from heavily maintained patches of planted vegetation, such as pocket gardens created in heavily built-up areas, to remnants of native vegetation (Lepczyk et al., 2017). However, most research on biodiversity in greenspaces has been performed in urban parks, gardens and remnants of native vegetation, which comprise few habitat types (Rupprecht et al., 2015). Little research has investigated how spontaneously vegetated spaces - or informal greenspaces - support native species in urban environments.

Informal greenspaces, such as vacant land, can contribute to preserving biodiversity in urban landscapes. For instance, they can maintain a variety of plants and animals (reviewed by Bonthoux et al., 2014; Rupprecht et al., 2015). They can also provide habitats for nationally rare and scarce species, and support species that are more common in natural areas than on urban land (Eyre et al., 2003). Furthermore, they may present greater species richness than formal greenspaces or rural sites (Uno et al., 2010; Robinson and Lundholm, 2012).

A large number of species in informal greenspaces may be a result of

E-mail addresses: villasenor@uchile.cl (N.R. Villaseñor), luna.chiang.paisaje@gmail.com (L.A. Chiang), jhernand@uchile.cl (H.J. Hernández), mescobar@renare.uchile.cl (M.A.H. Escobar).

^{*} Corresponding author.

a large proportion of exotic species; however, findings are not consistent in the literature. Research from the USA, China and New Zealand has reported high numbers of exotic species in informal greenspaces, in contrast with findings of low numbers of exotic species in informal greenspaces in research mainly from Europe and South Africa (reviewed by Rupprecht et al., 2015). Knowing the origin of the species that greenspaces support (native or exotic) is important to understanding whether they contribute to preserving local biodiversity.

Among informal greenspaces, vacant lands – either abandoned or never developed – are common in cities worldwide. In the USA, about 15 % of city lands are vacant, which corresponds to roughly 3 million hectares, or an area about the size of Switzerland (Branas et al., 2018). In Latin American cities, the extent of vacant lands is reported to be as high as 40 % in cities located in tropical climates, such as Rio de Janeiro (Brazil) and Guayaquil (Ecuador); whereas this figure only reaches about 10 % in the Mediterranean city of Santiago (Chile) (de Araujo Larangeira, 2003).

Emergent research in shrinking cities (that have experienced strong human population declines) has found that abandoned urban lands promote plant and animal conservation, as well as the provision of ecosystem services (Kwok, 2018, and references therein). Although there is increasing awareness on the benefits to biodiversity of vacant land in shrinking cities, vacant lands are commonly perceived as "wasted" land and having negative social and economic value by residents, land use planners and local authorities. Vacant lands are associated with crime risk, violence, trash dumping and informal housing (e.g. Nassauer and Raskin, 2014; Branas et al., 2018), which might explain why vacant land is usually modified without assessment of environmental losses. Therefore, in cities where urban growth and urban infill is taking over the scarce open space left behind by past development, new empirical evidence on biodiversity in vacant lands will help to understand the benefits of these areas (if any), before modifying this land.

To help inform biodiversity-sensitive urban development, we investigated whether vacant land provides a suitable habitat for birds in the Mediterranean city of Santiago, Chile. For this, we posed the following questions: (1) How do species richness and abundance of native and exotic birds vary among vacant lands, urban parks and residential areas? and (2) Do vacant lands support a different bird community compared with urban parks and residential areas? We also explored seasonal variation in bird species richness and abundance due to seasonal movements of Neotropical birds (del Hoyo et al., 2019). Empirical evidence from this work will help improve our understanding of the value of vacant land for maintaining native birds in urban landscapes. In addition, scientific evidence from Latin America is highly needed, because this region is one of the most urbanized regions in the world, with more than 80 % of its population living in urban areas (United Nations, 2018). However, several critical knowledge gaps persist, limiting sustainable development (Magle et al., 2012; MacGregor-Fors and Escobar-Ibáñez, 2017).

2. Methods

2.1. Study area

The study area is located in the city of Santiago (33°27′ S-70°40′ W), Metropolitan Region, Chile. The city covers an area ca. 800 km² and is the home of more than 6 million inhabitants (INE, 2019). It is the most populated city in Chile and one of the most populated cities in Latin America. It lies in the Santiago Valley, an area of fertile land surrounded by hills (between the Chilean Coastal Range and The Andes). The climate is semi-arid Mediterranean, warm and dry in summer (December to March), while cool and humid in winter (June-September). Precipitation is concentrated in the winter months (ca. 300 mm/year) (INE, 2015). Vegetation in the city is largely dominated by exotic species: ca. 84 % of trees in Santiago are exotic (Hernández and

Villaseñor, 2018).

Santiago is located in central Chile, a global biodiversity hotspot: a biologically rich area that has lost more than 70 % of the extent of its original primary vegetation and where conservation actions should be prioritized (Myers et al., 2000). Despite the importance of central Chile for biological conservation, less than 2 % of the land is protected under the National System of State-Protected Areas (SNASPE, the Spanish acronym). Biodiversity conservation is harder in the Metropolitan Region, which has less than 1 % of land under protection (SNASPE) and concentrates approximately 40 % of the national human population (INE, 2015). Urban development is one of the main threats for biodiversity in this region. However, little empirical research exists in the area to effectively guide sustainable urbanization.

2.2. Study design

We investigated the influence on bird diversity of three land-use types: vacant land, urban park and residential areas. To select sites, we used a digital layer of vacant lands available for the capital city (Observatorio de ciudades, 2012). We focused on vacant lands where spontaneous vegetation covered > 50 % of the area and there was no evidence of current management. Vacant lands are commonly dominated by exotic annual herbaceous plants, such as Chamomilla suaveolens, Erodium moschatum, Hordeum murinum, Lepidium sp., and Poa annua (Figueroa et al., 2019); and presented a very low cover of trees and shrubs (e.g. Acacia caven) (Chiang, 2019). We disregarded vacant lands: (1) smaller than 1 ha in size to ensure bird surveys could be performed entirely inside the land use of interest (see section Bird surveys); (2) located less than 1 km inside the city limits to avoid additional variation on birds due to close proximity with the city's edge (e.g. Silva et al., 2015); and (3) without access (e.g. sites that were completely fenced and had no administrator or owner on the site).

For each vacant site that met our criteria, we defined a "neighborhood" (1 km radius) in which we searched for an urban park and a residential area. Urban parks corresponded to managed parks larger than 1 ha in size that offer green spaces for residents' recreation. They are commonly dominated by exotic vegetation, including herbaceous plants such as Oxalis corniculata, Taraxacum officinale, Cynodon dactylon, Dichondra repens, Trifolium repens and Poa annua (Figueroa et al., 2018); and exotic trees, such as Prunus cerasifera, Acer negundo, Acacia melanoxylon, Liquidambar styraciflua and Ligustrum lucidum (Figueroa et al., 2018; Chiang, 2019). Residential areas corresponded to built-up areas larger than 1 ha in size dominated by one-story or two-story houses. Residential areas usually present low vegetation cover, where dominant trees comprised exotic species, most of them planted by residents and local authorities, such as Acer negundo, Robinia pseudoacacia and Citrus limon (Chiang, 2019).

We randomly selected seven "neighborhoods" that comprised all three land-use types (Fig. 1). The selected "neighborhoods" were dominated by residential areas with a few areas of industrial land use. They were located in the western and southern part of the city because the vacant lands that met our criteria were located in these areas (Fig.1 in Supplementary Material). In each site (land-use type within the selected "neighborhood"), sampling was performed along two 50 m transects (7 "neighborhoods" x 3 land use-types x 2 transects = 42 transects).

2.3. Bird surveys

To account for seasonal variation in bird diversity, all 42 transects were surveyed for birds three times in 2018: during austral summer (February), winter (August) and spring (October-November). These seasons provide a good understanding of bird dynamics in our region. On each 50 m transect, all birds seen and heard within 30 m from the transect line were recorded (Bibby et al., 2000); however, birds flying over the transect area were not recorded unless they were using the site

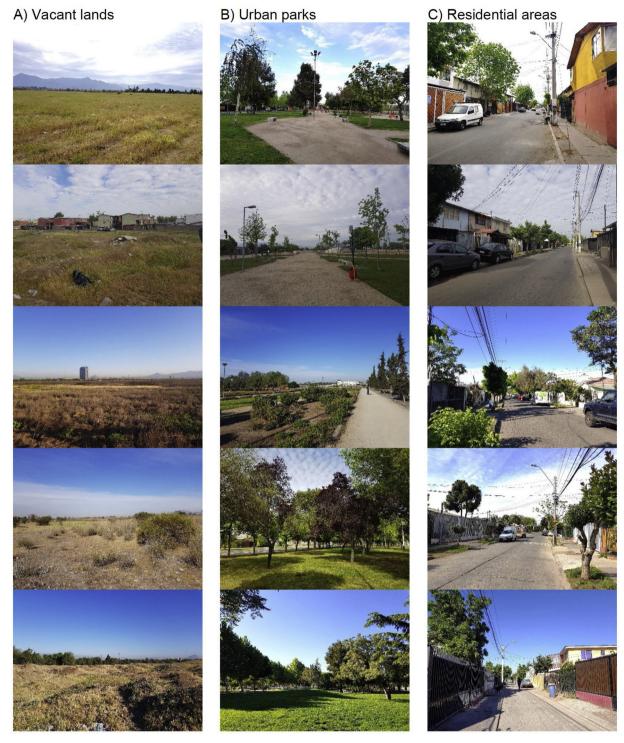


Fig. 1. Examples of sites surveyed in Santiago, Chile. (A) Vacant lands dominated by spontaneous vegetation mainly comprised of exotic annual herbaceous plants and very few trees and shrubs. (B) Urban parks highly managed and dominated by lawn and exotic trees. (C) Residential areas dominated by houses and impervious surfaces, with few trees (mainly exotic).

(e.g. swallows hunting insects). Detections > 30 m from the transect line were not included in our analyses (Villaseñor and Escobar, 2019) to sample the same area across land-use types. All transect counts were performed during mornings (from 7:00 am up to four hours after sunrise) to coincide with high bird activity. We did not survey transects on days with poor weather conditions (e.g. rain, strong wind or fog). To limit additional sources of variation, transect counts in different land-use types and seasons were performed by the same trained observer (NRV), and the three different land-use types that comprised a

"neighborhood" were surveyed on a same day. In residential areas, the 50 m transects were located along sidewalks, where the transect width of 60 m included sidewalk, street, houses and their gardens. For each transect, we calculated the number of native and exotic species (species/50-m transect) and their abundance (individuals/50-m transect). Native and exotic species were classified following Barros et al. (2015), except for species of uncertain origin (e.g. Marín, 2000).

Table 1

Total number of bird records by land-use type during transect surveys in Santiago, Chile. (x) Species recorded outside transects.

Scientific name	English name	Local name	Vacant land	Urban park	Residential area
Origin: exotic					
Callipepla californica	California quail	codorniz	4	6	0
Columba livia	Rock dove	paloma	11	30	56
Myiopsitta monachus	Monk parakeet	cotorra argentina	0	9	0
Nymphicus hollandicus	Cockatiel	cacatúa ninfa			X
Passer domesticus	House sparrow	gorrión	66	110	437
Origin: native					
Agelasticus thilius	Yellow-winged blackbird	trile	5	0	0
Anairetes parulus	Tufted tit-tyrant	cachudito	0	5	0
Anthus correndera	Correndera pipit	bailarín chico	53	0	0
Colorhamphus parvirostris	Patagonian tyrant	viudita	0	1	0
Columbina picui	Picui ground-dove	tortolita cuyana	16	11	16
Curaeus curaeus	Austral blackbird	tordo	4	1	0
Diuca diuca	Common diuca-finch	diuca	6	5	0
Elaenia albiceps	White-crested elaenia	fio-fio	0	14	5
Falco sparverius	American kestrel	cernícalo	1	0	0
Larus dominicanus	Kelp gull	gaviota dominicana	X		x
Leptasthenura aegithaloides	Plain-mantled tit spinetail	tijeral	6	4	1
Milvago chimango	Chimango caracara	tiuque	2	7	1
Mimus thenca	Chilean mockingbird	tenca	X		
Muscisaxicola maclovianus	Dark-faced ground-tyrant	dormilona tontita	2	0	0
Parabuteo unicinctus	Harris's hawk	peuco	X		
Phrygilus fruticeti	Mourning sierra-finch	yal	5	0	0
Pygochelidon cyanoleuca	Blue-and-white swallow	golondrina de dorso negro	1	0	0
Sephanoides sephaniodes	Green-backed firecrown	picaflor chico	0	7	2
Sicalis luteola	Grassland yellow-finch	chirihue	157	8	0
Sporagra barbata	Black-chinned siskin	jilguero	2	2	0
Sturnella loyca	Long-tailed meadowlark	loica	30	6	0
Tachycineta meyeni	Chilean swallow	golondrina chilena	80	18	17
Troglodytes aedon	House wren	chercán	14	32	14
Turdus falcklandii	Austral thrush	zorzal	30	245	26
Vanellus chilensis	Southern lapwing	queltehue	10	18	0
Xolmis pyrope	Fire-eyed diucon	diucón	1	2	0
Zenaida auriculata	Eared dove	tórtola	147	89	32
Zonotrichia capensis	Rufous-collared sparrow	chincol	132	83	17
Origin: uncertain					
Molothrus bonariensis	Shiny cowbird	mirlo	6	29	7

2.4. Data analyses

We fitted generalized linear mixed models (GLMMs) to evaluate the influence of land-use type (a factor with three levels: vacant land, urban park and residential area) and season (a factor with three levels: summer, winter and spring) on species richness and total abundance of both native and exotic birds. Predictive models were fit with GLMMs with a Poisson distribution (log link) using "lme4" (Bates et al., 2015) in R 3.4.1 (R Core Team, 2017). All models included neighborhood as a random effect that accounted for the spatial dependence between samples within the same neighborhood (n = 7) (Bolker et al., 2009). We assessed overdispersion in all our models by comparing the sum of the squared Pearson residuals to the residual degrees of freedom. When a model was overdispersed, we included an observation-level random effect. We also checked model residuals to evaluate if the model was appropriate for the data. To evaluate the significance of terms in GLMMs, we used Wald tests. We estimated mean and standard error for each response variable in our models with "AICcmodavg" (Mazerolle, 2017) and plotted their expected mean values and 95 % confidence intervals.

Randomization tests were used to test for differences in cumulative species richness for native and exotic birds between vacant lands and both urban parks and residential areas. To perform randomization tests we used 1000 randomizations and the "rich" package (Rossi, 2011). In addition, we built species accumulation curves of native bird species for the three land-use types – total and by season – using the "vegan" package (Oksanen et al., 2016). To estimate the number of species with increasing sample size we used the sample-based rarefaction method

(Mao Tau estimate, Colwell et al., 2012). To find species richness by sampling individuals, we used the individual-based rarefaction method (Oksanen et al., 2016). We also estimated the number of native species present in the assemblage by land-use type, but not observed in the reference sample, using Chao2, which is a robust estimator of minimum richness based on incidence data (Gotelli and Colwell, 2011). We did not perform these analyses for exotic birds because few exotic bird species inhabit our study area (e.g. Gutiérrez-Tapia et al., 2018; Benito et al., 2019).

A multivariate ordination of beta diversity was performed to evaluate differences in bird communities. We used non-metric multidimensional scaling (NMDS, with two dimensions), which uses an iterative search for ranking and placement of the variables to find a solution that minimizes stress (i.e. mismatch between the rank order of distances in the data, and the rank order of distances in the ordination) (Minchin, 1987). For this analysis, we first calculated the average abundance of each bird species recorded in transect counts within a same site (n = 21 sites) (e.g. White et al., 2005). Then, we used the metaMDS function in the "vegan" package. This function performs NMDS, searches for a stable solution using several random starts, standardizes the scaling in the result, and adds species scores to the site ordination (Oksanen et al., 2018). Prior to performing NMDS, data were square root transformed, submitted to Wisconsin double standardization (because data had a large range of values), and the Bray-Curtis dissimilarity index was calculated (see Oksanen et al., 2018 for details).

We used a permutational multivariate analysis of variance (PERM-ANOVA, based on 999 permutations) (Anderson, 2001) to test for differences in avian composition among land-use types. We also

performed a permutational analysis of multivariate dispersions (Anderson, 2006), which tests whether groups differ in their withingroup dispersion (distance to group median). To identify species that contributed the most to the dissimilarity between land-use types we used the similarity percentage (SIMPER) with a cut-off value of 70 %. SIMPER performs pairwise comparisons of groups of sampling units and finds the average contributions of each species to the average overall Bray-Curtis dissimilarity (Clarke, 1993). To test for significance, permutation tests returned the probability of getting a larger or equal average contribution in random permutation of the group factor (999 permutations). These tests were performed with the "vegan" package (Oksanen et al., 2016).

3. Results

We observed 34 bird species during surveys in 126 transect counts. Thirty species were recorded within transects: 25 natives, four exotics and one species of uncertain origin - *Molothrus bonariensis* (the shiny cowbird), which was not included in our analyses because we focused on native and exotic birds. This led to a total of 2122 bird records (birds seen or heard). Most of these records corresponded to native birds (65.6%). Among native birds, the most abundant species were: *Turdus falcklandii* (austral thrush, comprising 14% of total records), *Zenaida auriculata* (eared dove, 12%) and *Zonotrichia capensis* (rufous-collared sparrow; 11%). Exotic birds comprised 34.4% of total records and were distributed in four species: *Passer domesticus* (house sparrow), *Columba livia* (rock dove), *Callipepla californica* (California quail) and *Myiopsitta monachus* (monk parakeet). *Passer domesticus* was the species with the largest number of records, representing 28% of total records (Table 1).

3.1. Native species richness and abundance

For native birds, our analyses revealed a highly significant effect of land-use type on both species richness ($\chi^2=42.38$, df = 2, P<0.0001) and abundance ($\chi^2=104.14$, df = 2, P<0.0001), with vacant lands and urban parks supporting greater species richness and abundance of native birds per transect than residential areas (Fig. 2A, Table 1 in Supplementary Material). Season also had a significant effect on species richness ($\chi^2=9.37$, df = 2, P<0.009) and abundance ($\chi^2=12.62$, df = 2, P<0.002), where summer surveys exhibited the lowest species richness and abundance of native birds per transect (Fig. 2A, Table 1 in Supplementary Material).

3.2. Exotic species richness and abundance

For exotic birds, our analyses revealed a highly significant effect of land-use type on both species richness ($\chi^2=21.15$, df = 2, P<0.0001) and abundance ($\chi^2=87.93$, df = 2, P<0.0001). Vacant lands supported significantly lower species richness and abundance of exotic birds per transect than urban parks and residential areas (Fig. 2B, Table 1 in Supplementary Material). There was no significant effect of season on species richness ($\chi^2=2.05$, df = 2, P=0.36), but we found a significant effect on abundance ($\chi^2=25.36$, df = 2, P<0.0001): summer surveys exhibited the lowest abundance of exotic birds per transect (Fig. 2B, Table 1 in Supplementary Material).

3.3. Cumulative number of species

Sample-based species accumulation curves showed that vacant lands and urban parks exhibited a similar cumulative number of native species (in total and by season, P > 0.1, Table 2A, Fig. 3A). In contrast, vacant lots exhibited higher cumulative species richness of native birds than residential areas (P < 0.007) – but the difference was not statistically significant during summer (P = 0.11). Individual-based species accumulation curves showed that native birds in residential areas not

only presented a low species richness, but also exhibited a very low abundance (Fig. 3B). The majority of species accumulation curves did not seem to reach an asymptote, but they were close to the minimum estimate of asymptotic species richness (Chao2 estimates, Fig. 3). Thus, we lacked a few (rare) species. We note these results must be interpreted with caution, as they might underestimate species richness (Gotelli and Colwell, 2011).

For exotic birds, we found significant differences in spring, where vacant lots exhibited lower cumulative species richness of exotic birds compared to urban parks (P = 0.02) and residential areas (P = 0.007; Table 2B).

3.4. Dissimilarity in community composition

Based on NMDS ordination, a change was observed in bird community composition on a gradient from vacant lands through urban parks to residential areas, where NMDS presented a fair goodness-of-fit (stress = 0.17; Fig. 4). Bird communities differed among land-use types $(F_{2.18} = 4.096, R^2 = 0.31, P = 0.001)$, but not in their within-group dispersion ($F_{2.18} = 0.2$, P = 0.8). The differences in bird community structure between land-use types were mainly due to changes in the relative contribution of seven species according to the SIMPER analysis (Table 3). Of these, five species exhibited their highest average abundance in vacant lands: Sicalis luteola (grassland yellow-finch), Zenaida auriculata, Zonotrichia capensis, Tachycineta meyeni (Chilean swallow), and Anthus correndera (correndera pipit), where an individual species contributed up to 11 % of the total dissimilarities between land-use types. Turdus falcklandii exhibited its highest average abundance in urban parks and explained up to 23 % of the total dissimilarities between land-use types. Passer domesticus exhibited its highest average abundance in residential areas and was the most important species explaining differences between residential areas and both vacant lands and urban parks, contributing with 35 % of total dissimilarities (Table 3).

4. Discussion

Vacant lands are widely perceived as "wasted" land with no benefits to people or nature, but here we demonstrate that vacant lands covered by spontaneous vegetation contribute to conserving local birds in a Latin American capital city. In our study, where we recorded ca. 80 % of the terrestrial bird species reported for Santiago (compiled by Gutiérrez-Tapia et al., 2018), three main findings demonstrate the value of vacant lands for birds: (1) vacant lands exhibited high species richness and abundance of native birds, similar to urban parks; (2) vacant lands maintained significantly fewer exotic species than urban parks and residential areas; and (3) vacant lands supported a different bird community than urban parks and residential areas, including birds that are not common in the urban environment. Opportunities to connect urban residents with nature provided by vacant lands should be recognized and considered in landscape planning and urban growth policies.

4.1. Vacant lands support mainly native birds and few exotic birds

Vacant lands can provide habitat for a variety of species in cities and towns, but, are these lands supporting part of the local biodiversity? We found that vacant lands as well as urban parks maintained high species richness and abundance of native birds. Both vacant lands and urban parks supported more native birds than residential areas, probably because they present greater vegetation cover, that provides foraging and nesting resources for birds (Leveau et al., 2018). An additional benefit of vacant lands is that they maintain significantly fewer exotic birds than urban parks and residential areas, likely due to the lack of built structures and paved surfaces. Exotic species such as *Passer domesticus* (house sparrow) and *Columba livia* (rock dove) nest in buildings

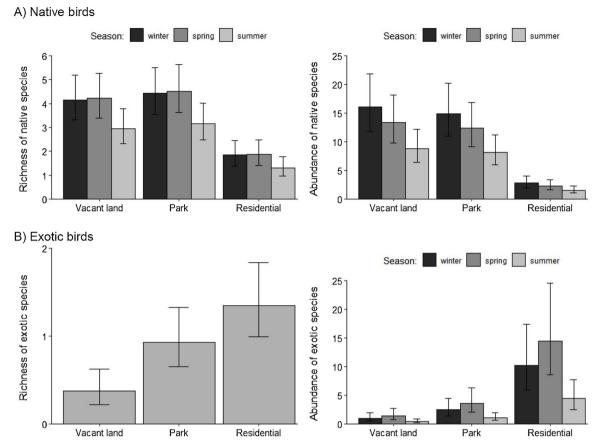


Fig. 2. Estimated mean species richness and abundance per transect count of (A) native and (B) exotic birds by land use type and season from Generalized Linear Mixed Models (GLMMs). Confidence limits at 95 % are shown.

Table 2Comparisons of cumulative species richness for (A) native and (B) exotic birds between vacant lands and urban parks, and vacant lands and residential areas (in total and for each season). *P-values* from randomization tests. Significant *P-values* are in bold.

	Total	Winter	Season Spring	Summer				
A. Cumulative species richness of native birds								
Vacant lot	21	17	15	10				
Urban park	19	14	17	10				
difference	2	3	-2	0				
P	0.28	0.14	0.32	_				
Vacant lot	21	17	15	10				
Residential area	10	8	8	7				
difference	11	9	7	3				
P	0.001	0.001	0.007	0.11				
B. Cumulative species ric	B. Cumulative species richness of exotic birds							
Vacant lot	3	2	1	2				
Urban park	4	4	2	3				
difference	-1	-2	-1	-1				
P	0.27	0.12	0.02	0.27				
Vacant lot	3	2	1	2				
Residential area	2	2	2	2				
difference	1	0	-1	0				
P	0.51	-	0.007	-				

and are commonly seen foraging on seeds and food scraps on paved surfaces, and thus, they reach high abundances in built-up areas (McKinney, 2006; Benito et al., 2019).

Our findings agree with a growing body of literature reporting the benefits of vacant land for fauna. For instance, when vegetation has reestablished naturally in formerly disturbed vacant sites, butterflies reach higher species richness than in parks and semi-natural habitats (Öckinger et al., 2009). Vacant lands are important habitats for beetles, sustaining species that are more common in natural than in urban land (Eyre et al., 2003). Thus, vacant lands maintain a diverse animal community, including pollinating and pest-controlling species, providing the urban landscape with ecological, educational and economic value (Robinson and Lundholm, 2012).

4.2. Vacant lands support a new bird community in the city

Our study reveals that vacant lands supported a different bird community than urban parks and residential areas, and comprised several birds that were not common in the urban environment. For instance, *Anthus correndera* (correndera pipit), *Agelasticus thilius* (yellow-winged blackbird), *Sicalis luteola* (grassland yellow-finch), and *Muscisaxicola maclovianus* (dark-faced ground-tyrant). These birds are commonly labeled "urban avoiders" (e.g. Leveau et al., 2018) and found in open habitats, such as grasslands and wetlands (del Hoyo et al., 2019). Because these habitats are rare inside the city, these birds occur mainly on rural land and rarely in urban areas. However, vacant lands provided grassland habitat for these native bird species within the city.

Grasslands in vacant lands are dominated by exotic annual herbaceous plants that are common in rural lands (Figueroa et al., 2019) and can provide important sources of food for native birds. Early-successional habitats offer plentiful seeds and insects (e.g. Öckinger et al., 2009; Robinson and Lundholm, 2012). This resource availability might explain the high abundances in vacant lands of five native species that contributed to differences between land-use types. Of these, three species are granivores: Sicalis luteola, Zenaida auriculata (eared dove), Zonotrichia capensis (rufous-collared sparrow); and two species are

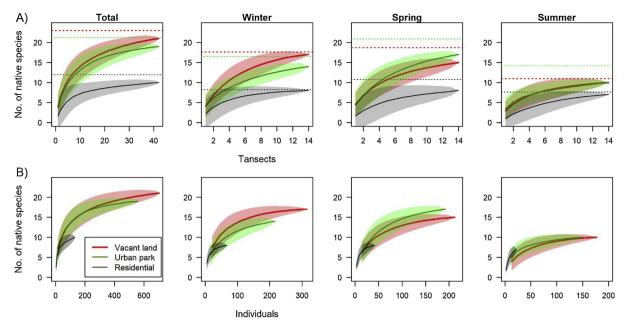


Fig. 3. Species accumulation curves for native birds recorded in total and by season in Santiago, Chile. (A) Sample-based and (B) individual-based species accumulation curves. Dotted lines show minimum species richness estimated by Chao2.

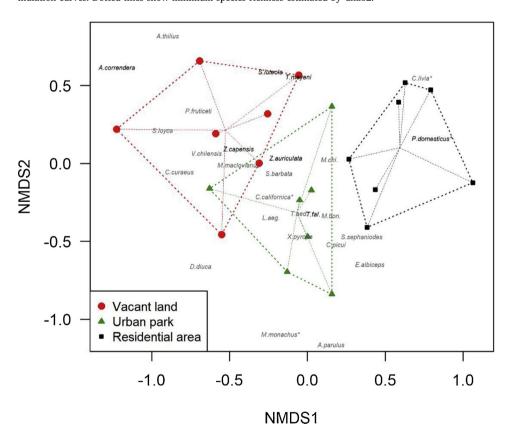


Fig. 4. Non-metric multidimensional scaling (NMDS) of sites based on Bray-Curtis dissimilarities representing the variation in bird community composition of tree land-use types in Santiago, Chile (see Methods). Species that contributed the most to group differences (according to SIMPER analysis) are shown in black. Species that were recorded only once are not displayed. (*) Exotic species. Stress = 0.17.

insectivores: *Tachycineta meyeni* (Chilean swallow) and *Anthus correndera* (del Hoyo et al., 2019). Bird species with specialized diets, such as these insectivores and granivores, tend to be less tolerant to urban development (Callaghan et al., 2019); here vacant lands contributed to high abundance of these birds in the city.

The bird community in urban parks corresponded to a transition between bird communities in vacant lands and residential areas. Several species found in urban parks are positively associated with wooded cover, such as *Troglodytes aedon* (house wren), *Anairetes parulus*

(tufted tit-tyrant), Elaenia albiceps (white-crested elaenia), Sephanoides sephaniodes (green-backed firecrown) and Turdus falcklandii (austral thrush) (Leveau and Leveau, 2004; Benito et al., 2019). Troglodytes aedon and Anairetes parulus search for insects on trees and shrubs, and Elaenia albiceps hunts for insects in the tree canopy. Sephanoides sephaniodes, a nectarivorous bird, is frequently seen feeding on flowering trees and shrubs. Turdus falcklandii was by far the most abundant species in urban parks, and thus, it was important in explaining total dissimilarities between land-use types. This species is commonly reported

Table 3

Percentage contribution of most important species to pairwise dissimilarities between land-use types based on the Bray-Curtis dissimilarity index (SIMPER). These species contribute at least to 70 % of the differences between land-use types. The average abundances of these species (individuals/transect count) by land-use type are displayed. For each species, it highest average abundance is in bold.

Scientific name	Dissimi	Dissimilarity (% contribution)					Average abundance		
	Vacant land vs. Urban park		Vacant land vs. Residential		Urban park vs. Residential		Vacant land	Urban park	Residential
Turdus falcklandii	22	***	-		23	***	0.7	5.8	0.6
Sicalis luteola	11		10	*			3.7	0.2	0
Zenaida auriculata	11		10		8		3.5	2.1	0.8
Passer domesticus	9		35	***	35	***	1.6	2.6	10.4
Zonotrichia capensis	8		11	**	7		3.1	2	0.4
Tachycineta meyeni	7	*	6	**			1.9	0.4	0.4
Anthus correndera	6	*					1.3	0	0
Cumulative contribution (%)	74		72		73				

Significance codes for permutation *P-value*. They show the probability of getting a larger or equal average contribution in random permutation of the group factor: ***P < 0.01; **P < 0.05; *P < 0.05; *P < 0.01.

as the most abundant native species in urban parks in Santiago (e.g. Estades, 1995; Amaya-Espinel et al., 2019), probably because urban parks offer abundant resources for this bird: several individuals of *Turdus falcklandii* were commonly sighted in urban parks searching for invertebrates in lawns and using trees for shelter, foraging and nesting.

Bird communities in residential areas were different from communities in vacant lands than those in urban parks. Residential areas exhibited a reduced number of bird species and their abundances were largely dominated by two exotic species: Passer domesticus and Columba livia. Among all birds, Passer domesticus was the most abundant bird, and explained most of the dissimilarities between land use types. Passer domesticus and Columba livia take advantage of foraging and nesting resources provided by humans, and thus, become more abundant with increasing built infrastructure and paved surfaces (White et al., 2005, Benito et al., 2019). These synanthropic species are commonly labeled as "urban exploiters" (e.g. Leveau et al., 2018) or "urban dwellers" (e.g. Amaya-Espinel et al., 2019), and they contribute to biotic homogenization of cities worldwide (McKinney, 2006). The dominance of these two exotic species is likely due to low tree and shrub cover in residential areas surveyed, because woody vegetation cover promotes a higher abundance of several native bird species in our study area (Benito et al., 2019). An increase in woody vegetation cover in urban areas might also result in greater bird species richness and improve environmental quality in cities (e.g. Pei et al., 2018).

Future research should investigate species birth and death rates in vacant lands, urban parks and other lands in the city. Although some areas might be attractive for birds, they may be population sinks due to high mortality or low reproductive success, where immigrants compensate for an excess of deaths (Jokimaki et al., 2011).

4.3. Seasonal variation in Santiago's bird diversity

Our study reveals a seasonal effect on native birds. Native birds were more speciose and exhibited higher abundances in winter and spring than in summer, a pattern that has been described in the city (e.g. Villaseñor and Escobar, 2019). During autumn and winter, several birds immigrate to the city in their search for milder weather. Some bird species might move naturally from hills and the Andes mountain range to lower altitudes in the central valley (where Santiago is located), such as Sicalis luteola, Diuca diuca (common diuca-finch), and Sturnella loyca (long-tailed meadowlark) (Villaseñor and Escobar, 2019). Sephanoides sephaniodes is mostly absent in Santiago during the breeding season, but during winter was frequently observed foraging on flowering trees and shrubs in residential areas and urban parks. In addition, some bird species that reproduce in the south migrate north, such as Colorhamphus parvirostris (Patagonian tyrant) and Muscisaxicola macloviana (dark-faced ground-tyrant) (del Hoyo et al., 2019).

Cities provide a large amount of food available through the year (Jokimaki and Suhonen, 1993). A variety of exotic plant species in Santiago (Hernández and Villaseñor, 2018) provides flowers, fruits and seeds for different bird guilds across the year, and food scraps are constantly available for synanthropic birds (Estades, 1995; McKinney, 2006). The high abundance of food resources can be important to support a large abundance of birds during environmentally adverse seasons (winter) or during seasons of high food demand (spring).

4.4. Vacant lands and biodiversity-sensitive urban design and land-use planning

Our findings contribute to the growing body of evidence on the value of vacant land to preserve biodiversity. Vacant lands covered by spontaneous vegetation provide habitats that would otherwise be rare or absent in large cities, and can resemble ecosystems that have declined (Rupprecht et al., 2015). This may explain the common finding that vacant lands maintain a significant part of the diversity of plants and animals (Bonthoux et al., 2014) and present a special variety of species that makes them valuable for nature conservation (Maurer et al., 2000). Our study adds that these areas provide an important habitat for local birds and support a different bird community than parks and residential areas, including several bird species from rural lands that are rare in the city. Therefore, they help maintain different life history strategies. This scientific evidence highlights the importance of vacant lands for biodiversity and presents new opportunities for urban residents to experience and connect with nature close to home or work.

It is important to understand the environmental value of these areas and search for strategies to sustain the benefits they provide through urban design, land-use planning and urban growth policies. Among the different views on urban design, Clément (2004) proposes that residual and abandoned sites are part of "the third landscape", a landscape where biological diversity exists. This land is dynamic, seasonal changes in vegetation are respected, restoring ecosystem resilience and sustaining biodiversity. Maintaining large residual spaces allows for plant and animal life and education for people on the need for these refuges for biodiversity (Clément, 2004). During city planning, vacant lands can be maintained through different zoning. For example, wastelands in Berlin range from the inner city to the margins and provide a place where wild plants grow (Maurer et al., 2000). They can also be considered part of the green infrastructure along with formal greenspaces and green corridors because they contribute to maintaining natural cycles and deliver a variety of ecosystem services (Lepczyk et al., 2017; Ávila, 2018). Urban growth policies should attempt to maintain lands that are important for biodiversity and the provision of ecosystem services.

Successful consideration of vacant lands in biodiversity-sensitive urban design requires solutions to the social issues associated with these areas. Vacant lands are not only the target of urban development, but are also transformed into traditional parks (dominated by lawn) and community gardens (Kremer and Hamstead, 2015). They are also managed to reduce negative externalities, such as fear of residents, violence and crime (e.g. Branas et al., 2018). Transformations and common management practices on spontaneous vegetated lands, such as vegetation clearing, constant mowing and herbicide or pesticide applications, usually result in negative effects on biodiversity because they change the conditions that made them favorable to plants and animals (Rupprecht et al., 2015). Additional research and management solutions are needed to balance human needs and perceptions while maintaining biodiversity and ecological processes. In addition, good knowledge of vacant lands (e.g. land-use legacies) and the socioecological system are required in order to avoid unintended consequences (e.g. for human health and ecosystem services, Nassauer and Raskin, 2014).

5. Conclusion

Informal greenspaces are ubiquitous in urban landscapes around the world and might help conserve biodiversity in cities and towns. Here we demonstrate that vacant lands maintain native birds in a Latin American capital city. They also support a different bird community when compared to formal greenspace and residential areas and provide suitable habitats for birds of rural areas that are rare in the city, such as birds associated with grassland habitats. Our results highlight that vacant lands covered by spontaneous vegetation are important greenspaces that maintain a variety of native birds in a growing city; therefore, urban planners and designers need to consider the ecological consequences of developing or transforming these lands. Further attention should be placed on vacant lands, as they can contribute to conserving biodiversity and offer opportunities for urban sustainability and people-nature interactions.

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Declaration of Competing Interest

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

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Appendix A. Supplementary data

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