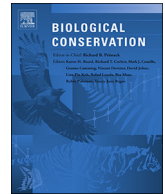




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When the winners are the losers: Invasive alien bird species outcompete the native winners in the biotic homogenization process

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ABSTRACT

Species are declining worldwide, but while some are becoming threatened, few others thrive under novel environmental conditions. Land use changes and biological invasion are the main drivers of this 'biotic homogenization' (BH) that increasingly occurs in human-dominated landscapes. Among birds, several groups of species have been identified as 'winners' in this process (e.g. invasive and native urban specialists and generalist species). Yet, as populations continue to grow, competition can appear between those groups and it is not yet clear who are the primary 'winners' in the BH process. Here, we analyze trends of common native and non-native birds during the last 15 years across Israel, where large populations of very destructive invasive alien bird species were introduced towards the end of the previous century, using a nation-wide citizen-science program, and two local standardized surveys. Community and population analyses showed that the non-native species are the primary 'winners' of the BH process. Native urban specialists and generalist species that were previously considered as 'winners' are now among the 'losers'. For instance, populations of the invasive common myna increased dramatically, while populations of the previously widespread house sparrow strongly decreased. Previous studies conducted in Israel have shed light on the mechanisms through which invasive bird species can impact native species, notably competition. We show that these processes are among the key factors that drive population declines and changes in bird communities. This highlights the importance of acting now, especially since non-native species are currently spreading from human-dominated areas to more natural environments.

1. Introduction

Land use changes, mainly agricultural intensification and urbanization, shape biodiversity through deletion and degradation of natural habitats, and modify community structures and species interactions (Foley et al., 2005). These changes have thus precipitated a global biodiversity crisis, resulting in worldwide species declines (Sala et al., 2000). However, these declines are not uniform (Sax and Gaines, 2003). Changes in species composition can result in either increased or reduced turnover of species, while some species are pushed away or going extinct, and others benefit from the new environmental conditions (Clavel et al., 2010). Habitat simplification and fragmentation is more likely to affect specialist species (i.e. species with specific habitat requirements), and to benefit generalist species (i.e. widespread and broadly tolerant species) and few native and non-native synanthropic species (Blair, 2004). This process, in which "few winners replace many losers", was described as the biotic homogenization (McKinney and Lockwood, 1999).

The biotic homogenization results in increased genetic, taxonomic

and functional similarities of regional biotas over time (Olden and Rooney, 2006). Impacts of this process have been particularly studied for bird populations (e.g., Devictor et al., 2008, 2007; Julliard et al., 2006). For instance, agricultural intensification reduces the suitability of habitats and the availability of food for birds (Donal et al., 2001), and erodes β -diversity (i.e. changes in community composition between sites) for birds at large scales (Karp et al., 2012). Urbanization causes habitat fragmentation that reduces specialization index of bird communities and thus destabilize communities over time (Clavel et al., 2010). Rapid declines of many common birds, including one of the most common species, the house sparrow (*Passer domesticus*), have been documented in Europe (Inger et al., 2015). Until recently common species have received considerably less attention than less abundant species at greater risk of extinction (Gaston, 2010). Declines in those species are particularly alarming, as they play key roles in terrestrial ecosystems, contributing much of the structure, biomass and energy turnover of many terrestrial systems. They are also likely to indirectly affect the human population, as many common species are urban, and urban biodiversity provides a wide range of ecosystem services (Gaston,

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2010; MEA, 2005) and is a key element for connecting people with nature (Miller and Hobbs, 2002), for instance through bird feeding (Cox and Gaston, 2016).

Common species can also be ‘winners’ of the biotic homogenization process, as some often thrive under the novel conditions humans form (Faeth et al., 2011). Anthropogenic habitats provide additional food and nesting sources, whether intentionally (bird food, nesting boxes) or unintentionally (e.g. through ornamental plants or garbage) (Kowarik, 2011). Additionally, urban sprawl, the unrestricted growth of urban areas, promotes habitat diversity, through homeowners’ individual choices in the plants they cultivate in their private gardens. Accordingly, urban bird species richness increases with the diversity of habitats (Evans et al., 2009). More recently, Paker et al. (2014) also found a positive relationship between shrubs species richness and bird species diversity in urban environments. The urban bird community was classified into three groups regarding their relation to the urban ecosystem: urban exploiters, urban adapters, and urban avoiders (Blair, 1996; Kark et al., 2007). Urban exploiters are native species that adapt to exploit the urban environment, and are characterized by high densities in urban settings; urban adapters are native species that can exploit green urban resources (e.g. ornamental vegetation) and thrive in green spaces; urban avoiders are native species that do not adapt (or are not pre-adapted) to intensive urbanization (Kark et al., 2007). Urban exploiters, and, to a lower extent, urban adapters, are thus likely to benefit from urbanization.

Invasive alien species, the subset of non-native species that have detrimental environmental or social impacts (Blackburn et al., 2014), are often among the ‘winners’ of the biotic homogenization process (McKinney and Lockwood, 1999). Successful invaders are typically ecological generalists with wide distributional ranges, which are common in their native range (Pyšek et al., 2009). They are often introduced in urban areas, where they establish founder population that serve as a basis for expansion to more natural areas (McKinney, 2006). As they spread, they can displace or reduce the populations of several native species through processes including competition, predation and hybridization (Blackburn et al., 2014), resulting in reduced species diversity across urban areas. However, empirical evidence of the impact of non-native species on native communities remains poorly documented (Strubbe et al., 2011). This is due in part to the paucity of long-term studies monitoring both native and invasive alien species, especially pre- and post-invasion (Simberloff et al., 2013). In addition, the direct effects of competition between species are difficult to assess, partly because changes in species abundance is often slow and gradual, and effects of competition can be confounded with those of environmental change (Davis, 2003). For instance, in Israel there is evidence that two non-native birds, the common myna (*Acridotheres tristis*) and the rose-ringed parakeet (*Psittacula krameri*), are competing for nesting sites with local cavity nesters (Charter et al., 2016; Orchan et al., 2013). Yet long term evidence of impacts on populations or communities is still lacking. In Australia, Grarock and colleagues (2012) first showed a negative correlation between the abundance of the common myna and native species using long-term monitoring data. However, this correlation disappeared when they accounted for environmental change (Grarock et al., 2014).

In this study, we explore temporal trends in common native and non-native bird populations in Israel to understand who are the ‘winners’ and the ‘losers’ in the biotic homogenization process. Israel represents an ideal case study to explore this question for several reasons. First, since the changes this country has been undergoing during the 20th century have dramatically impacted bird populations, causing major changes for more than 70 % of the breeding bird species and resulting several local ‘winners’ (Yom-Tov et al., 2012). This includes the house sparrow, great tit (*Parus major*), white-spectacled bulbul (*Pycnonotus xanthopygos*), hooded crow (*Corvus cornix*) or Eurasian blackbird (*Turdus merula*). Second, mostly towards the end of the 20th century 13 non-native bird species were introduced (Shwartz et al.,

2008). For instance, the rose-ringed parakeet was raised as pet from the late 1960s and established large populations in Israel from the 1980s (Hatzofe and Yom-Tov, 2002). Another parakeet, the monk parakeet (*Myiopsitta monachus*) established its population at the late 1990s in the Tel-Aviv area and is rapidly spreading across Israel (Postigo et al., 2017). Several other bird species, including the common myna and the vinous-breasted starling (*Sturnus burmannicus*), were released by the owners of an aviary in the Yarkon Park, the metropolitan park of Tel-Aviv, during the late 1990s (Hatzofe and Yom-Tov, 2002; Holzapfel et al., 2006). The common myna has spread and established large populations across Israel. Both the common myna and the rose-ringed parakeet are considered among the 100 most destructive invasive alien species globally and in Europe (Lowe et al., 2000; Turbé et al., 2017).

The goal of this study is thus to explore how the recent introductions of few non-native birds influenced the populations of common and widespread urban adapters and exploiters that are considered among the winners of the biotic homogenization process in Israel (Shwartz et al., 2008). To test these hypotheses, we explored changes in common bird community and populations during the last 15 years, (1) all over Israel (using citizen science data), (2) in the Yarkon Park, origin of many invasions, and with documented evidence of a competition mechanism (Charter et al., 2016) and (3) in a natural protected area.

2. Methods

2.1. Bird data

Israel is a small and narrow country (ca. 20,500 km²) located in the eastern Mediterranean. We used three independent databases to investigate changes in bird communities across Israel in the last 15 years. First, we analyzed data from a nation-wide citizen science program, the winter backyard bird survey, a program that is conducted across Israel every year since 2006 (Fig. 1). This citizen science project is the longest bird monitoring program available in Israel. The surveys last for three weeks (mid-January), during which volunteers perform bird counts in public or private green spaces in the vicinity of their homes. In this program, only common species are monitored (see list of species in Table 1 and further details in Text S1).

Second, to explore the long-term impacts of competition between non-native and native species, we analyzed data from two longitudinal surveys in the Yarkon Park, the largest urban park in Israel (262 ha), located at the heart of the Tel-Aviv metropolis (Fig. 1). The first survey was originally conducted in 2003 (Shwartz et al., 2008), and was replicated in summer 2017 for the purpose of this analysis, using the same methodology (10 min point counts, for further details see Text S1). Because sampling effort differed between points and years (6–14 times in 2003 and 8–11 times in 2017) due to some operational constraints, it was standardized by randomly excluding surplus point counts in the survey with the higher sampling effort.

Finally, we analyzed a third dataset, from the Long-Term Ecological Research Station (LTER) located in “Ramat Hanadiv” natural reserve (Fig. 1), to compare trends in urban areas with a more natural setting. Ramat Hanadiv is a publicly accessible nature reserve comprising approximately 455 ha of typical natural Mediterranean vegetation combined with planted pine and cypress groves (Bashan and Bar-Massada, 2017). The LTER has an on-going breeding bird survey, which was initiated in 1988, but standardized in 2001. The survey is performed every three years from Mars to June (e.g. 2001, 2004 etc.). The sample array consists of three transects, each was visited 3–5 times between years. Sampling effort was therefore standardized for each transect, by randomly selecting three data replicates (per year) for each transect.

2.2. Statistical analyses

Analyses of bird communities in the Yarkon Park and Ramat Hanadiv were conducted for all non-migratory species sampled. For the

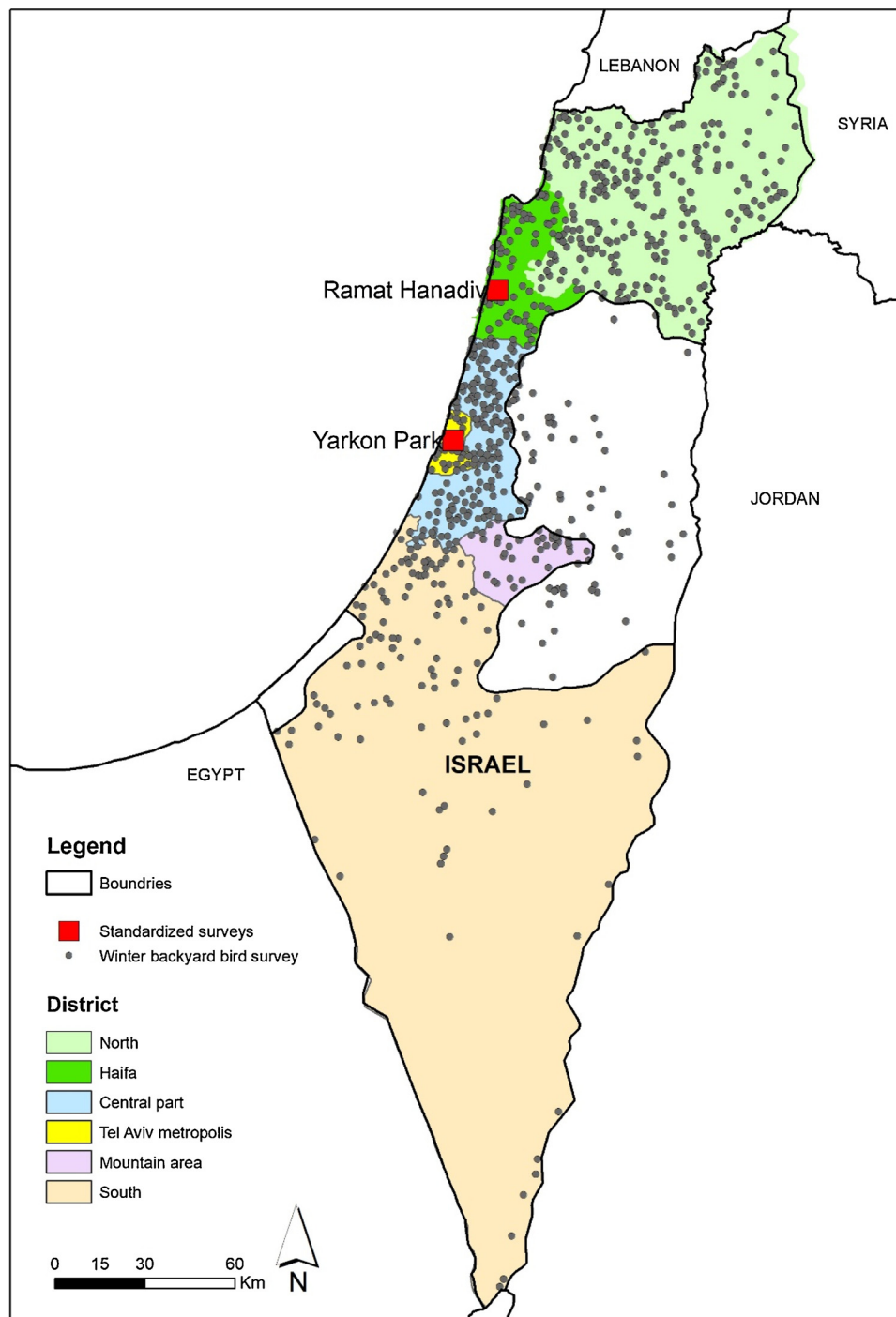


Fig. 1. Study sites of the two standardized surveys (Yarkon Park and Ramat Hanadiv) and locations of sampling from the winter backyard bird survey in Israel.

backyard bird survey, reliable longitudinal data were available only for the 14 most common resident and charismatic species, for most of which reliability between experts and non-experts was demonstrated (for details see [Lipschitz, 2014](#)). Population level analyses were conducted for those 14 common species for each database. We added analyses for 15th species, non-native, the monk parakeet, which was not surveyed in the backyard bird project, but could be observed in the two standardized surveys (Yarkon Park and Ramat Hanadiv surveys). Of the 15 common species we focused on, three were urban exploiters, eight urban adapters, and four non-native species.

2.2.1. Community analyses

We calculated species richness per visit and used linear mixed-effect models (nlme package; [Pinheiro and Bates, 2016](#)) with point/transect as a random effect and Gaussian error structure to compare differences in richness between years in the Yarkon Park and in Ramat Hanadiv. For each survey, we also calculated the abundance of native and non-native birds per visit and used mixed-effect models with point/transect as random effect to explore differences in abundance between years. These models were fitted with a negative binomial error structure because the data comprised many zeros, since many species were not seen in each visit. For each model, we tested for homoscedasticity with the Levene's test and normality of residuals to ensure model assumptions.

Table 1
 Classification of bird species, effect sizes for bird abundance all over Israel from 2006 to 2018, in Yarkon Park between 2003 and 2017 and in Ramat Hanadiv from 2001–2017; proportions of change (%) between first and last year of observation, for each database; and tendencies shown in Yom-Tov et al. (2012)'s paper looking at changes across the 20th century. Sample size of the three datasets for the 15 species are provided in brackets. Significance levels are displayed: * p < 0.05, ** p < 0.01 and *** p < 0.001.

Group	Scientific name	Latin name	Backyard bird survey – 2006 to 2018 (N = 9480)			Yarkon Park survey – 2003 & 2017 (N = 5070)			LTER in Ramat Hanadiv – 2001 to 2017 (N = 756)			Trend
			Estimate ± SE	Proportion of change (%)	Estimate ± SE	Proportion of change (%)	Estimate ± SE	Proportion of change (%)				
Native species – urban exploiters	Feral pigeon	<i>Columba livia</i>	0.22 ± 0.07***	43.16	-0.19 ± 0.16	-36.70	0.005 ± 0.005	100.00 ^a	0.005 ± 0.005	100.00 ^a	Decreasing	
	Hooded crow	<i>Corvus corone cornix</i>	0.06 ± 0.04**	14.22	-0.25 ± 0.06***	-57.47	0.05 ± 0.03	15.00	0.05 ± 0.03	15.00	Increasing	
Native species – urban adapters	House sparrow	<i>Passer domesticus</i>	-0.10 ± 0.10 *	-28.45	-0.32 ± 0.05***	-83.86	-0.03 ± 0.01 *	-75.00	-0.03 ± 0.01 *	-75.00	Increasing	
	Eurasian blackbird	<i>Turdus merula</i>	-0.02 ± 0.01***	-39.51	0.001 ± 0.004	9.38	0.23 ± 0.08**	12.96	0.23 ± 0.08**	12.96	Increasing	
	Eurasian hoopoe	<i>Upupa epops</i>	-0.007 ± 0.004*	-38.37	0.001 ± 0.007	4.05	-0.04 ± 0.01 *	-90.91	-0.04 ± 0.01 *	-90.91	Increasing	
	Eurasian jay	<i>Garrulus glandarius</i>	-0.01 ± 0.01 (p = 0.08)	-30.13	0.01 ± 0.004*	135.00	0.27 ± 0.04***	108.33	0.27 ± 0.04***	108.33	Increasing	
	Great tit	<i>Parus major</i>	-0.009 ± 0.008 (p = 0.06)	-29.83	0.02 ± 0.004***	527.27	-0.01 ± 0.05	-11.36	-0.01 ± 0.05	-11.36	Increasing	
Non-native species	Graceful prinia	<i>Prinia gracilis</i>	-0.03 ± 0.006***	-35.45	-0.06 ± 0.007***	-64.86	-0.04 ± 0.11	-14.77	-0.04 ± 0.11	-14.77	Increasing	
	Palestine sunbird	<i>Nectarinia osea</i>	-0.05 ± 0.01***	-57.74	-0.008 ± 0.006	-27.03	-0.07 ± 0.05	-30.61	-0.07 ± 0.05	-30.61	Increasing	
	Syrian woodpecker	<i>Dendrocopos syriacus</i>	-0.01 ± 0.003***	-51.12	0.000 ± 0.000	0.00	-0.001 ± 0.01	-25.00	-0.001 ± 0.01	-25.00	Increasing	
	White-spectacled bulbul	<i>Pycnonotus xanthopygus</i>	-0.09 ± 0.01***	-44.91	-0.14 ± 0.02***	-67.99	-0.38 ± 0.08***	-51.94	-0.38 ± 0.08***	-51.94	Increasing	
	Laughing dove	<i>Streptopelia senegalensis</i>	0.05 ± 0.03***	21.20	-0.02 ± 0.005***	-79.73	0.04 ± 0.04	35.71	0.04 ± 0.04	35.71	Introduced	
	Common myna	<i>Acridotheres tristis</i>	0.30 ± 0.02***	843.50	0.58 ± 0.08***	243.74	0.08 ± 0.01***	1300.00 ^a	0.08 ± 0.01***	1300.00 ^a	Introduced	
	Monk parakeet	<i>Myiopsitta monachus</i>	Not surveyed	Not surveyed	0.74 ± 0.09***	481.32	Not observed	Not observed	Not observed	Not observed	Introduced	
	Rose-ringed parakeet	<i>Psittacula krameri</i>	0.13 ± 0.03***	250.81	0.18 ± 0.03***	221.88	0.03 ± 0.01**	400.00 ^a	0.03 ± 0.01**	400.00 ^a	Introduced	

^a Those three species were not observed in 2001, so to calculate the percentage of change, we added one individual observed in 2001 and one observed in 2017.

All analyses were performed using R version 3.3.3 (R Core Team, 2013). For the Yarkon Park survey, we also compared community composition between years, as our community indicator analysis showed large differences in this survey. We used non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance using Bray-Curtis distance matrices (vegan package; Oksanen et al., 2017) with 100 iterations, and analysis of similarities with 999 permutations.

For the backyard bird survey, we calculated species richness, abundance of native and non-native, respectively, per visit and used generalized linear models with a Poisson error structure to compare differences in richness and abundances between years all over Israel. We used bootstrapping to test the effect of year (following Spiegel et al., 2016). Such an approach was chosen since sampling effort was not standardized across years, and since we could not obtain participants' ID and exact location, and there was a risk of dependency. We performed random permutations and built null models with 1000 iterations to control for these biases: for species richness, we first randomized data between years 1000 times, keeping sampling effort constant, then ran linear models and plotted distribution of slope estimates. Finally, we compared observed slope estimates to the distribution of those of the null model to determine whether richness significantly differed across time compared to as would be expected by chance. The significance level was obtained by measuring the number of values of the null-model coefficients below (if negative coefficient) or above (if positive coefficient) the value of the observed coefficient. We proceeded similarly for abundances of native and non-native species.

2.2.2. Population analyses

To explore how population size varied with time in the Yarkon Park and Ramat Hanadiv, we calculated the abundance per visit for each of the 15 common species and built 30 linear mixed-effect models with point/transect as a random effect. For the backyard bird survey, we assessed temporal changes of average abundance per year for each of the 14 species surveyed using generalized linear models. We used the average abundance per species per year ($n = 13$) in the models, as for some sampling points we could only identify locations at the neighborhood or town scale. We used the same bootstrapping approach described above to determine significance levels.

Additionally, we investigated whether temporal changes in abundance of the invasive myna, monk and rose-ringed parakeet and the native house sparrow, Syrian woodpecker and great tit varied between Tel-Aviv region and the other regions in Israel. This was done because Tel-Aviv metropolis is acknowledged as the center of invasion of the common myna, monk and rose-ringed parakeet, and since studies conducted in the Yarkon Park provided evidence of strong competition between those species (Charter et al., 2016; Orchan et al., 2013; Schwartz et al., 2008). Therefore, we repeated the previous analyses based on the backyard bird survey but proceeded per region: we first built linear models assessing temporal changes in the average abundance per year for each species, for each region separately. Then, a null model with 1000 iterations was created to control for sampling effort across years and regions (randomizing data between regions 1000 times, keeping sampling effort and years constant). We then compared observed differences in slope estimates between the Tel-Aviv region and other ones, to the ones of the null models. Significance level was obtained similarly as described above.

3. Results

3.1. Bird community significantly changed over the last 15 years

We found a significant decrease of bird species richness in Yarkon Park, from 2003 to 2017 (Table 2). Abundance of native species significantly decreased in Yarkon Park, while abundance of alien species significantly increased. Increase in abundance of alien species was also observed all over Israel (backyard bird survey) and in Ramat Hanadiv,

although only marginally significant. More specific community analysis in the Yarkon Park revealed observation of 33 bird species (see Table S1 for list of species) out of which six were aliens (18.2 %) and the remaining 27 were native (81.8 %). Community composition based on abundance of species significantly varied in Yarkon Park between 2003 and 2017 (ANOSIM, Global rho = 0.37, $p = 0.001$). The bird community in this park strongly changed from native based communities with the house sparrow, hooded crow, cattle egret and spur-winged lapwing as dominant species in 2003 to alien community dominated by the common myna, monk and rose-ringed parakeet in 2017 (Fig. 2).

3.2. Populations of common birds significantly changed over the last 15 years

Results from the three databases indicate significant changes in abundance of common bird species in the last 15 years (Table 1; Fig. 3). We observed significant declines in the abundance of almost all urban adapters at country scale. Abundance of the three non-native species and urban exploiters significantly increased, except for the house sparrow, for which it significantly decreased. These trends were confirmed for the house sparrow, graceful prinia, Palestine sunbird, Syrian woodpecker, white-spectacled bulbul, common myna and rose-ringed parakeet in the two standardized surveys in Yarkon Park and Ramat Hanadiv. While the monk parakeets were not observed in the natural reserve (Ramat Hanadiv), their numbers dramatically increased in the Yarkon Park. Most notably, the abundance of the common myna and the rose-ringed parakeet increased by 843 % and 250 %, respectively, from 2006 to 2018 across the country (Table 1). In contrast, the house sparrow and the white-spectacled bulbul, with significant declines in all three databases, decreased by 28 % and 44 %, respectively. We observed conflicting trends between databases for the hooded crow and the non-native laughing dove, which increased at the national scale but decreased in Yarkon Park, and for the Eurasian blackbird which decreased at the national scale but increased in Ramat Hanadiv (Table 1).

3.3. Regional trends for cavity nester species

Using the backyard bird survey, we identified differences in population growth trends between regions for the native and non-native cavity nesting species. We compared all regions to the Tel-Aviv region and found that while the house sparrow was decreasing in all regions, except the mountain region, the common myna and the rose-ringed parakeet were increasing (Table 3; Fig. S1). However, the estimates in the north region significantly differed from the estimates in Tel-Aviv region for the house sparrow, the rose-ringed parakeet and common myna, as well as the estimates in the mountain region compared to Tel-Aviv region for the house-sparrow and common myna (Table 3; Fig. S1). Weaker decline of the house sparrow was recorded in the north region, which was coinciding with weaker increases of the common myna and the rose-ringed parakeet in this region. Slight increase of the house sparrow in the mountain region matched with a weaker increase of the common myna in the mountains. The trend for the great tit was only marginally significant at the country scale, and we did not observe any significant differences in estimates between regions compared to Tel-Aviv one. The Syrian woodpecker decreased similarly in all regions; no significant difference was observed compared to Tel-Aviv region.

4. Discussion

Mounting empirical evidence demonstrates that biotic homogenization is on the rise all over the world, in several taxa, as a result of landscape changes, climate change and biological invasions (Blouin et al., 2019; Capinha et al., 2015; Hensley et al., 2019; Hodges and McKinney, 2018). Urbanization causes taxonomic, functional and evolutionary homogenization of bird communities, benefiting a small number of species while affecting many others (Devictor et al., 2007;

Table 2

Effects sizes and standard errors for variation of total species richness and abundance of native versus non-native species between 2003 and 2017 for the Yarkon Park survey, between 2001 and 2017 for the Ramat Hanadiv survey, and between 2006 and 2018 for the Backyard bird survey. Significance levels are displayed: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Estimate \pm SE Backyard bird survey	Yarkon Park survey	Ramat Hanadiv survey
<i>Bird species richness</i>			
Intercept	-13.48 \pm 1.14	159.40 \pm 35.75 ***	131.39 \pm 190.27
Year	0.01 \pm 0.01	-0.07 \pm 0.01 ***	-0.05 \pm 0.09
<i>Native species Abundance</i>			
Intercept	17.38 \pm 1.28	3.13 \pm 0.11 ***	1.80 \pm 0.03***
Year	-0.01 \pm 0.01	-0.27 \pm 0.03 ***	0.01 \pm 0.01
<i>Non-native species abundance</i>			
Intercept	-0.01 \pm 2.48	2.72 \pm 0.11 ***	-2.73 \pm 0.71***
Year	0.06 \pm 0.01 ($p = 0.07$)	0.56 \pm 0.05 ***	0.46 \pm 0.28 ($p = 0.09$)

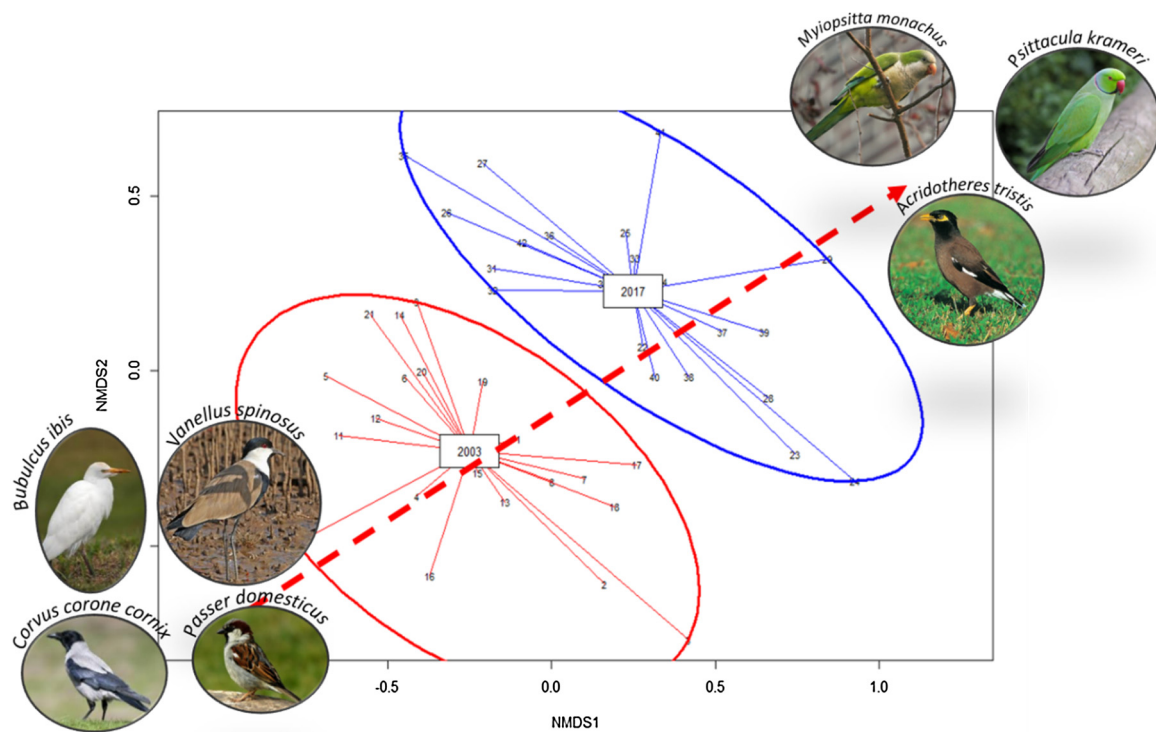


Fig. 2. Non-Metric Multidimensional Scaling showing changes in bird community in Yarkon Park, Israel, from 2003 (Red circle) to 2017 (Blue circle). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Morelli et al., 2016). Non-native and native urban specialists (i.e. urban exploiters) and generalist (i.e. urban adapters) are often considered as winners in the biotic homogenization process. Loss of specialist species to generalists can facilitate future species invasions (McKinney and Lockwood, 1999). This process simplifies biotic interactions, weakens the selection pressure in the homogenized communities and endangers the long-term success of native species (Olden et al., 2004). Here we show, for the first time, that non-native bird species outcompete most other urban specialist and generalist species that up until recently were among the winners in the biotic homogenization process (Yom-Tov et al., 2012). This process amplifies homogenization at a large-scale, resulting in globally similar communities dominated by very few successful non-native species confirming previous claims (McKinney and Lockwood, 1999).

Urban exploiters and adapters have adapted to exploit the grey and green resources (respectively) provided by urban environments (Blair, 1996). Consistently, the population size of two of the three urban exploiters species (hooded crow and feral pigeon) increased at the country

scale. In contrast, most of urban adapters declined across Israel in the last 15 years. Declines in common bird species have been recorded all over the world, mainly due to land use changes (Gross, 2015; Regan et al., 2015). In the last seventy years Israel has been undergoing fast development process, resulting in extensive changes in human population density and land uses (Shoshany and Goldshleger, 2002). This process has resulted in changes in more than 70 % of the breeding bird species in Israel, some positive, some negative (Yom-Tov et al., 2012). The changes were explained by Yom-tov et al. (2012) by the development of irrigated agriculture and gardening in urban settlements and in desert areas, as well as the development of aquaculture have created favorable conditions for many species. The inconsistent trends between this study and the previous trends (Yom-Tov et al., 2012) can be a result of the different methodologies used (expert assessment vs. monitoring data) and the time scale studied (15 vs. over 80 year). Alternatively, differences may reflect the true impacts of processes such as climate change (Julliard et al., 2004), illegal poaching (Yom-Tov, 2003) or the accelerated urban development Israel is undergoing since the 1990s,

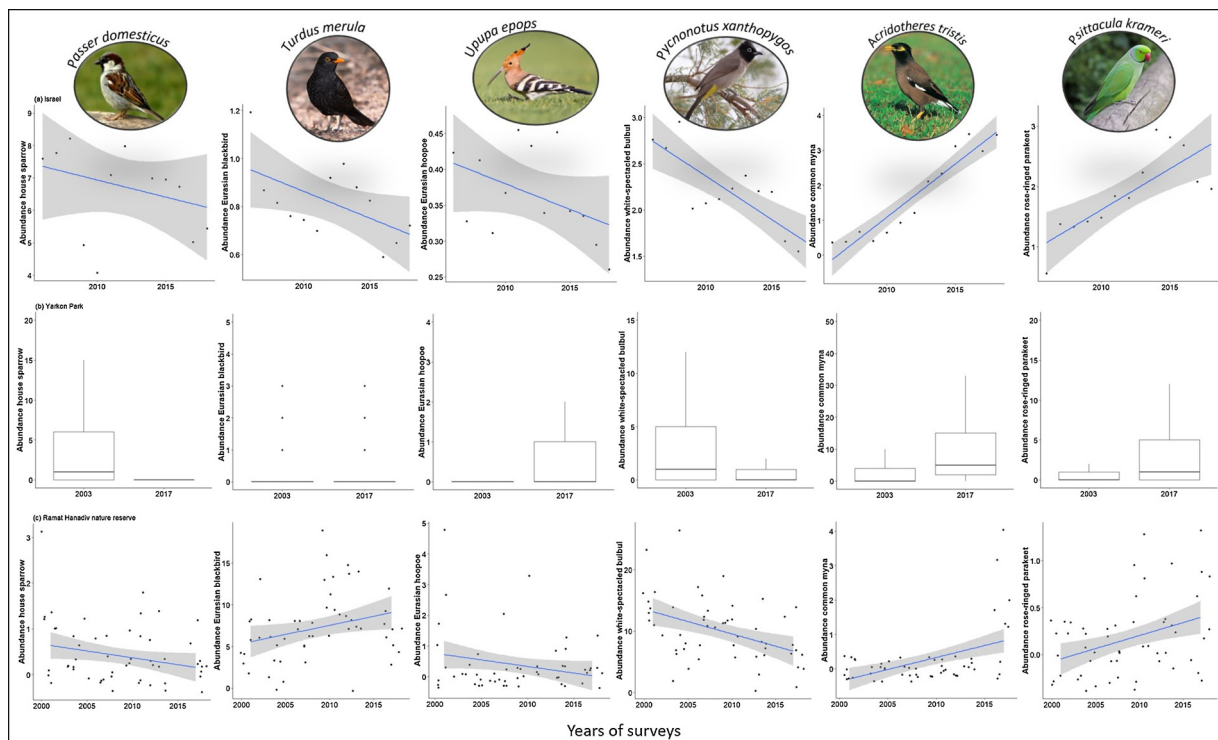


Fig. 3. Abundance of the house sparrow, Eurasian blackbird, Eurasian hoopoe, white-spectacled bulbul, common myna and rose-ringed parakeet across years, for (a) all over Israel (backyard bird survey) between 2006 and 2018, (b) in the Yarkon Park in 2003 and 2017, and (c) in Ramat Hanadiv nature reserve between 2001 and 2017.

which increased urban density and reduced extent of green spaces (Shoshany and Goldshleger, 2002). The scope of our study does not allow to determine whether and how these processes influence the community of birds across Israel. However, evidence from previous studies and the current one in the Yarkon Park indicate that non-native species may play an important role in species declines.

Yarkon Park is acknowledged as the main center of bird invasion in Israel. Bird richness and total abundance of local species strongly declined in the last 15 years, while the abundance of non-native ones increased significantly. The fact that the management of the Yarkon Park remained similar in the last 15 years, apart from few local interventions that aimed to improve the conditions for biodiversity (Liav Shalem, Yarkon Park ecologist, 2019, pers. comm.), suggests that species invasion is pivotal in affecting bird communities in this park. Furthermore, two species that were previously dominating (house sparrow and hooded crow) also declined significantly. Evidence for declines of house sparrows have been recorded elsewhere in Europe (Inger et al., 2015; Shaw et al., 2008). Suggested mechanisms driving the declines of urban populations of house sparrows include nutritional deficit affecting the development of juveniles (Meillère et al., 2017), or

increase of oxidative stress linked to the toxicity of pollution (Herrera-Dueñas et al., 2017). In Israel however, evidence for nest site competition between non-native cavity nesters and house sparrows was established in the Yarkon Park and impacts on house sparrow's population were predicted (Charter et al., 2016; Orchan, 2007; Orchan et al., 2013). Common mynas and rose-ringed parakeets displace house sparrows from nest sites and preyed on their chicks (Common mynas), hereby reducing their breeding success (Charter et al., 2016; Orchan et al., 2013). Consistently, our results showed that house sparrow populations are decreasing faster in Tel-Aviv district, the origin of invasions and where common myna's and parakeet's populations grow fast, compared to the north and mountain districts the front of myna invasion (Cohen et al., 2019). Hence, we have strong basis to argue that the population decline of the house sparrow is influenced by the introduction of non-native cavity nesters and especially the common myna in Yarkon Park area, and potentially elsewhere in the country.

Although competition for nesting sites is expected to affect all native cavity nesters (Charter et al., 2016), our results showed no significant declines of populations of great tit and Syrian woodpecker in Yarkon Park. A previous study in which nest boxes were added and the size of

Table 3

Effect sizes for variation in bird abundance in each region of Israel, and proportion of changes from 2006 to 2018, based on the backyard bird survey. Number of plots per regions are provided in brackets. Significant differences between estimates of the Tel Aviv region (reference; origin of the bird invasion) and each of the other regions are displayed in bold: * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

Group	Scientific name	Latin name	Estimate \pm SE per region				
			Tel Aviv (reference) (N = 1675)	Central (N = 2965)	Mountain (N = 1161)	North (N = 2721)	South (N = 958)
Native species – urban exploiter	House sparrow	<i>Passer domesticus</i>	-0.20 \pm 0.08	-0.15 \pm 0.13	0.05 \pm 0.16*	-0.02 \pm 0.11*	-0.21 \pm 0.22
Native species – urban adapter	Great tit	<i>Parus major</i>	-0.01 \pm 0.01	-0.01 \pm 0.01	-0.01 \pm 0.02	-0.02 \pm 0.01	0.01 \pm 0.01
	Syrian woodpecker	<i>Dendrocopos syriacus</i>	-0.01 \pm 0.01	-0.01 \pm 0.01	-0.01 \pm 0.01	-0.01 \pm 0.004	-0.01 \pm 0.01
Non-native species	Common myna	<i>Acridotheres tristis</i>	0.39 \pm 0.08	0.39 \pm 0.04	0.29 \pm 0.05*	0.17 \pm 0.03***	0.34 \pm 0.04
	Rose-ringed parakeet	<i>Psittacula krameri</i>	0.20 \pm 0.05	0.17 \pm 0.05	0.15 \pm 0.04	0.08 \pm 0.04**	0.07 \pm 0.05**

entrance hole manipulated showed that great tits nested in small cavities successfully, but that when they attempted to nest in the large cavities, they were displaced by the common mynas (Charter et al., 2016). This could explain the significant increase in population of great tits, for which there is no niche overlap and they can even benefit from reduced competition with the house sparrow. Orchan et al. (2013) also demonstrated that there is no niche overlap in cavity preference between the Syrian woodpecker and non-native cavity nesters. In fact, the Syrian woodpecker excavate few cavities every year with entrance hole which is too small for the myna and parakeet, but with time parakeet can enlarge the entrance (Orchan et al., 2013). In accordance, we found that woodpecker populations in the park are stable and slightly decrease across Israel. Declines in other urban adapters such as, white-spectacled bulbul, cannot be explained by competition for nesting sites with non-native species. However, aggressive interactions have been previously documented between common mynas and rose-ringed parakeets and native species (Grarock et al., 2012; White et al., 2019). Understanding the impact of non-native species on non-cavity nesters is important, as well as other mechanisms that cause the declines of those species. For instance, Eurasian blackbird is declining in human dominated landscapes, but still increasing in natural remnants. In this case, land use change may potentially drive these declines. Declines of Eurasian blackbirds could also be caused by infection with Usutu virus, that was found in Israel (Mannasse et al., 2017), and for which there is evidence of negative impact on populations of blackbirds in Europe (Camp et al., 2019).

Disentangling the effect of invasion from the effect of land use changes is challenging, i.e. whether non-native species are the ‘drivers’ or ‘passengers’ of ecological change (MacDougall and Turkington, 2005). Direct evidence of impact of non-native species over native ones remains scarce. Although our large-scale temporal data does not allow to establish a direct causality link between the common myna invasion and declines of house sparrows, it joins other evidence on the mechanisms through which this invasive alien bird may directly affect native populations. Non-native species have particularly benefited from the biotic homogenization process in Israel, and we suggest that the invasion is, at least partly, driving the declines of native species that were previously considered ‘winners’. This is particularly concerning, given the role common species play in the functioning of ecosystems and the delivery of ecosystem services (Gaston, 2010). The global distribution of the common myna is alarmingly extensively expanding, and large areas worldwide are considered at risk of common myna invasion (Cohen et al., 2019). In our study, the bird community did not significantly change in the nature reserve, suggesting that effects of the invasion remain limited to human-dominated landscapes for now. There were less non-native species recorded, which suggest that currently natural areas are more resilient than urban areas, but if non-native populations continue to grow, they will spread to more natural areas (Cohen et al., 2019).

4.1. Conservation implication

This study showed increases of ca. 250 %–800 % in populations of non-native species, while abundance of common native species has been mostly decreasing. If no action will be taken, we predict that bird communities across Israel will become dominated by non-native species, like in the Yarkon Park. This flags the importance of setting appropriate management strategies, to halt or mitigate the spread of non-native birds, particularly the common myna. In Australia, large eradication campaigns have been used effectively to control common myna populations (e.g. see Yarra Indian Myna Action Group WWW Document, 2019). Implementation of artificial nesting sites that non-native species cannot enter (e.g., Charter et al., 2016) could also help. In Israel, interventions that have been mostly directed at the rose-ringed parakeet, in relation to agricultural damages (White et al., 2019) should be redirected towards the common myna that is putting many

areas at risk (Cohen et al., 2019). Since the common myna is a charismatic species, any mitigation attempts can suffer from public protest against lethal action (Lišková et al., 2015). Efforts should thus be made to learn from previous experience of mitigation effort and to identify non-lethal ways to control this populations. However, to implement effective policy, it is important to run cost-benefit analyses that explore the social, ecological, economic and consequences of different intervention prior to any mitigation campaign (Strubbe et al., 2011).

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Declaration of Competing Interest

There is no conflict of interest in this work.

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