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Relationship between the presence of House Sparrows (*Passer domesticus*) and Neotropical bird community structure and diversity

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Abstract Invasive exotic species pose an important threat to biodiversity worldwide. However, there is little information on the effects that specific exotic bird species have on native biota. The House Sparrow is an excellent ecological model to evaluate the effect that an invasive exotic species has on native bird communities. Our study describes the relationship of the presence and abundance of House Sparrows with the structure, diversity, and composition of native bird communities in West Mexico. We used two approaches to compare House Sparrow invaded and non-invaded bird communities: (1) at a small geographic-scale that allowed us to evaluate shifts in avian communities with presence of the House Sparrow under similar environmental conditions; and (2) at the landscape-level to evaluate the effect of this species under a scenario of greater environmental heterogeneity. Results from both approaches show that areas invaded by House Sparrows have heavily-dominated avian communities with low species richness, while non-invaded areas exhibit highly-even and species-rich bird communities. Species turnover analysis indicates that the decrease in the number of bird species in House Sparrow invaded areas is caused by species loss, rather than a shift in species composition. Our results indicate that the invasion of an area by the House Sparrow, through synergistic interactions with human activities, determines the composition, structure, and diversity of native bird communities.

Keywords House Sparrow · Exotic species · Human-altered ecosystems · Urban ecology · Bird communities · Biodiversity

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Introduction

The anthropogenic introduction of exotic species represents a significant component of global change (Zaret and Paine 1973; Vitousek et al. 1997; Smith and Knapp 2001). Successful invasions of exotic species often cause major changes to native ecosystems (Wilson and Belcher 1989; Hawkes et al. 2005; Gritti et al. 2006). Exotic species can affect native biota at different ecological levels, modifying species population dynamics, community structure, or even ecosystems level processes (Kalinoski 1975; Gowaty 1984; Fritts and Rodda 1998). Humans have frequently introduced bird species into new areas (e.g., House Sparrows, Rock Pigeons, European Starlings, Monk Parakeets), yet our knowledge of their effects on native bird communities is limited (Chace and Walsh 2006).

The House Sparrow (*Passer domesticus*) is a good biological model to study human-caused bird species invasions. This sparrow, native to Europe and North Africa, was introduced to North America in 1850 from England and Germany (Baker 1995; Bull and Farrand 1997). Originally introduced to Brooklyn, New York, the House Sparrow has broadened its distributional range within urban and suburban areas throughout North America (Sibley 2001).

The success of the House Sparrow as an invasive species has been attributed to four natural-history traits that make it an excellent urban exploiter species (sensu Blair 1996; Kark et al. 2007): (1) it is an aggressive species that attacks birds of similar, or smaller size at feeding sites, and actively destroys nests of other species (McGillivray 1980; Gowaty 1984; Kimball 1997); (2) it is a dietary generalist that feeds on grain, insects, fruit and even human litter (Gavett and Wakeley 1986; Kimball 1997); (3) it has colonial-communal nesting strategies that allows its abundance to increase at an accelerated rate once it has invaded a new area (Kalinoski 1975; McGillivray 1980; Gowaty 1984); and (4) it can effectively expand its limits through human-altered landscapes (Kark et al. 2007). The House Sparrow is reported to negatively affect some North American native species such as the House Finch (*Carpodacus mexicanus*) and Eastern Bluebird (*Sialia sialis*) (Kalinoski 1975; Gowaty 1984), though the effects that the House Sparrow may have on native bird communities has not been evaluated. The aim of this study is to describe the relationship between the presence of House Sparrows presence and the structure and diversity of Neotropical bird communities. For this, we used two approaches: (1) a small geographic-scale study that allowed us to compare House Sparrow-invaded and non-invaded bird communities under the same environmental conditions. And (2) a landscape-scale study that allowed us to evaluate: (a) if the community structure of invaded and non-invade sites is related to environmental variation, and (b) if the presence of House Sparrows, regardless of habitat structure and environmental attributes, is related to bird communities with similar structures.

Methods

Study area and field methods

We conducted our study in the Cuitzeo watershed, located in the state of Michoacán in West Mexico. This watershed is highly heterogeneous due to its topography, with an altitudinal range of 1,800–3,500 m asl, and associated habitats of fir forests, pine forests, oak forests, pine-oak forests, and subtropical shrublands. In addition, human activities have created several anthropogenic habitats: crop-fields, plantations, cattle-grazing grasslands, and urban sites. To understand the possible negative effects of House Sparrow invasions on Neotropical bird communities we used two approaches: (1) a small geographic-scale study in the peri-urban belt of the city of Morelia; and (2) a landscape-level analysis of bird communities within the watershed.

For the small geographic-scale study, we sampled 20 sites on the peri-urban belt of this rapidly growing city. Ten sites, located within the city perimeter, were invaded by the House Sparrow in the last 5 years. This invasion was the result of House Sparrows using peri-urban habitats affected by the most recent expansion of the city of Morelia (López et al. 2001). The other ten sites, which have not yet been invaded by the House Sparrow, were located 2–2.5 km away from invaded sites. Both invaded and non-invaded areas were similar in relation to their habitat characteristics. All of our sampling sites were located in plantations dominated by trees of the genus *Eucalyptus* with no difference in herbaceous plant ($t_{18} = 0.11$, $P = 0.92$), shrub ($t_{18} = 0.10$, $P = 0.91$), tree ($t_{18} = 0.91$, $P = 0.37$), and construction cover ($t_{18} = 0.24$, $P = 0.80$). This allowed us to control most habitat structure attributes, and thus, to evaluate the influence of House Sparrow presence on the structure, diversity, and composition of the native bird community.

At the landscape-level we surveyed a total of 574 sites distributed among eight habitat types in an area of $\sim$2,000 km^2. Of these, 204 sites were located within the city of Morelia, 30 in small human settlements, 30 in pine-oak forests, 30 in conifer forests, 30 in oak forests, 90 in subtropical shrub-lands, 90 in cropfields, and 70 in cattle-grazing grasslands. Altitude, climate, and habitat varied greatly among sites. Our goal was to compare bird community structure between sites were the House Sparrow was present and sites without this invasive species using a scenario of high environmental variation, to evaluate the relative roles that environmental variation and the invasion of House Sparrows may play on shaping native bird communities. We expected that if House Sparrow presence is a factor that molds native bird communities, all sites invaded by House Sparrows would have similar community structure, regardless of their environmental attributes. Furthermore, we expected that sites that were not invaded by this exotic species would show bird communities that differ in response to their environmental attributes. Finally, with this analysis we aimed to identify those habitat variables that where related to the House Sparrow's abundance.

To measure bird community structure, we carried out 10 min unlimited radius point-counts (following Ralph et al. 1996). We conducted all our sampling from 0700 to 1100 h visiting $\sim$20 sites per day. Point counts were located at a minimum distance of 250 m from each other to ensure survey independence (Ralph et al. 1996; Huff et al. 2000). To understand temporal variation in bird communities each site was surveyed in September 2006, and again in July 2007.

Data analysis

Small geographic-scale approach

Bird community structure (dominance/evenness) in invaded and non-invaded areas was analyzed using species rank/abundance plots (as suggested by Magurran 2004). In order to assess differences in dominance/evenness at invaded and non-invaded sites, and to test if the proportion of dominant and rare species varied among sites, we compared the slopes of the rank/abundance plots using analysis of covariance (ANCOVA). Because rank/abundance curves are not linear, abundance data was log transformed (Magurran 2004). We used a rarefaction analysis to compare bird species richness among sites (EstimateS platform; Colwell 2005). Rarefaction curves are computed species accumulation curves based on the repeated re-sampling of all pooled samples. These curves represent the statistical expectation for observed accumulation curves (Gotelli and Colwell 2001), enabling the comparison of the statistically expected species richness of each community at the same sampling effort or abundance (Moreno 2001). To facilitate comparisons with other studies, we also report Fisher's α diversity index values ($\alpha \pm 95\%$ confidence intervals). We applied a nested design GLM-ANOVA to determine whether bird abundances differed in presence or absence of the House Sparrow. To compare diversity values (interaction of species richness and abundances) between invaded and non-invaded areas, we computed a Bray-Curtis multivariate cluster analysis (BioDiversity Pro platform; McAleece 1997). We calculated species turnover between areas using β_{sim} (Lennon et al. 2001). This index quantifies the relative magnitude of species gains and losses in relation to the sample with the least number of unique species. This approach allowed us to evaluate whether bird communities in invaded areas may have exchanged species, or have simply lost them.

Landscape-level approach

To compare sites with and without House Sparrows at the landscape-level, we used all sites where House Sparrows were present ($n = 241$), and used a pseudo-random number generator (Wichman and Hill 1982) to randomly select 241 of the total 325 surveys where House Sparrows were absent. To evaluate bird community structure (dominance/evenness), we generated rank/abundance plots, and applied ANCOVA to compare plots between sites with and without House Sparrows. We also used ANCOVA to compare the bird community structure (dominance/evenness) of 20 randomly selected landscape-level surveys with those of the small geographic-scale approach. Finally, we conducted a stepwise multiple regression analysis to model House Sparrow abundance in relation to habitat attributes (height and cover of trees, shrubs, herbaceous plants, and buildings).

Results

Small geographic-scale approach

Bird community structure differed between House Sparrow invaded and non-invaded areas (ANCOVA of rank/abundance plots: $F_{1,54} = 6.10$, $P = 0.016$). All invaded sites exhibited communities that were dominated by the House Sparrow (Fig. 1). There were 175 more individuals of the most abundant species (House Sparrow), than the next ranked species (Barn Swallow—*Hirundo rustica*). House Sparrows represented almost one half of the total bird abundance at invaded sites (48.7 ± 3.9% SE of all individuals detected). Bird communities exhibited higher evenness at non-invaded sites (Fig. 1). The highest difference between the most abundant species at these sites (Lesser Goldfinch—*Carduelis psaltria*), and the next ranked species (House Finch—*Carpodacus mexicanus*), was of 19 individuals.

Community diversity values differed between invaded and non-invaded sites (Fig. 2). Bird species richness was significantly higher at non-invaded sites (34.0 ± 5.34 computed species at 247 individuals;

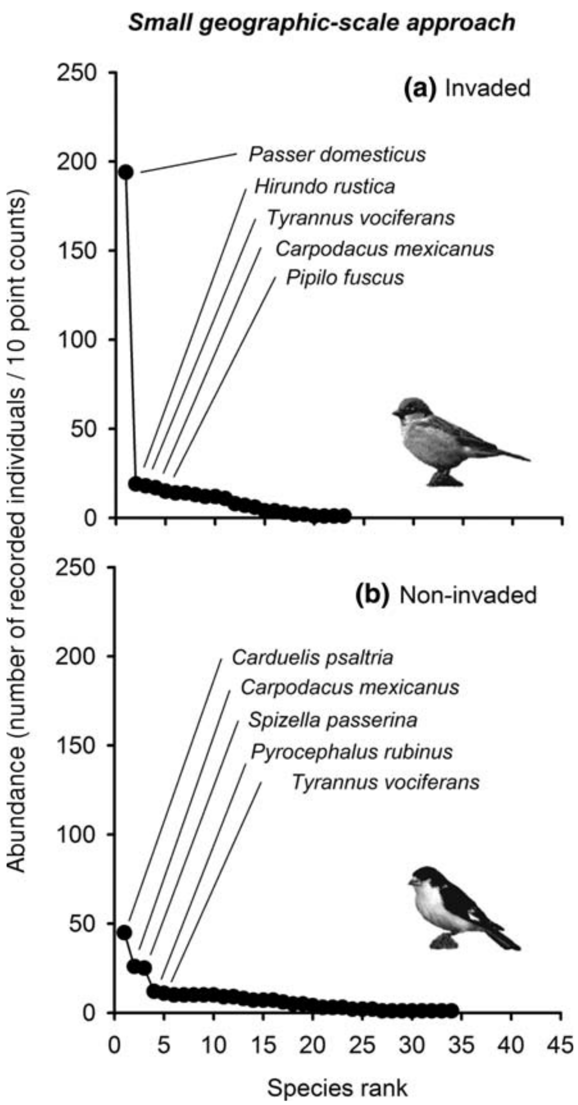

Fig. 1 Structure of bird communities at a small geographic-scale in the peri-urban belt of Morelia city. Rank/abundance plots for invaded and non-invaded bird communities show that invaded areas were highly dominated by the House Sparrow. The sparrow's presence was associated with lower species richness and changes in the species ranking order. Illustrations show the most abundant species for each community

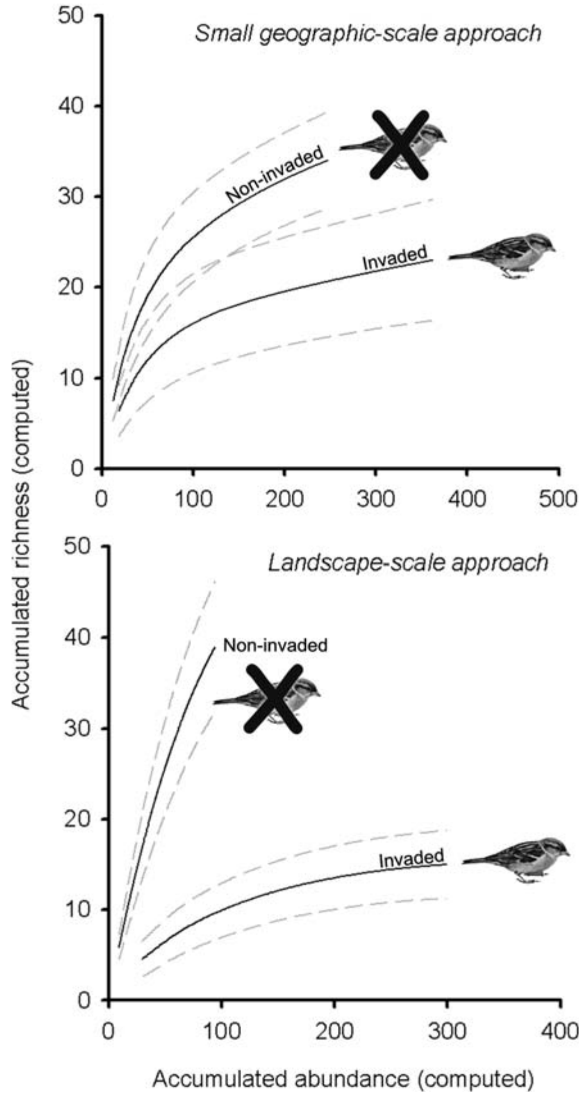

Fig. 2 Diversity differences in bird communities between House Sparrow invaded and non-invaded sites, at both the small geographic-scale and the landscape-level. Regardless of the spatial analysis used, invaded areas showed lower species richness than non-invaded ones, while total bird abundances were higher at invaded areas due to the large number of House Sparrows present in them. *Solid lines* represent mean accumulated species (computed) while *dashed lines* correspond to their 95% confidence intervals

Fisher's $\alpha = 10.68 \pm 0.52$), than at invaded sites (23 ± 6.67 computed species at 247 individuals; Fisher's $\alpha = 5.47 \pm 0.26$). However, bird abundances were higher at invaded sites (18.95 ± 2.76 individuals/point count), than at non-invaded sites (13.00 ± 1.55 individuals/point count). Differences in abundance values were significantly related to the presence of House Sparrows in both the 2006 and the 2007 surveys (GLM-ANOVA: $F_{1,36} = 14.8$, $P < 0.001$). The Bray-Curtis multivariate cluster analysis demonstrated high similarity between surveys in 2006 and 2007 at invaded sites (80.2%), followed by non-invaded sites (60.2%). However, there was low similarity in surveys between invaded and non-invaded sites ($36.4 \pm 3.12\%$). Of the 36 recorded bird species, 21 were shared by both areas, two were exclusive to invaded sites, and 13 were exclusive to non-invaded sites (Table 1). Thus, the β_{sim} value for the invaded and non-invaded areas was very low (0.08 dissimilarity), showing that invaded sites lost a great proportion of species rather than shifting their community composition.

Landscape-level approach

House Sparrows were recorded in two habitats: human settlements and cropfields. Urban sites with House Sparrows were highly heterogeneous in habitat attributes: 0–80% tree cover, 0–18 m tree height, 0–40% shrub cover, 0–7 m shrub height, 0–80% herbaceous plant cover, 0–3 m herbaceous plant height, and 0–100% built cover. Cropfields in which House Sparrows were recorded were located at a maximum distance of 609 m from any human settlement, and up to 14 km from Morelia city. Two bird species were only present in House Sparrow invaded areas: the Rock Pigeon—*Columba livia* and the Vaux's Swift—*Chaetura vauxi*. On the other hand, 32 native species were only recorded in non-invaded sites (Table 2).

Comparison of the 241 invaded and the 241 non-invaded sites showed significant differences in bird community dominance/evenness. Invaded sites had highly dominated communities, while non-invaded sites presented fairly even ones (Fig. 3). The slopes of the rank abundance plots for invaded and non-invaded sites were different (ANCOVA: $F_{1,53} = 4.46$, $P < 0.001$). To separate the potential impact of human activities (urbanization, agriculture), we compared bird community evenness at House Sparrow invaded and non-invaded sites for only urban and cropfield areas. We found that in both urban and agricultural sites, non-invaded communities were different from those invaded by House Sparrows (ANCOVA urban:

Table 1 Bird species recorded in invaded and non-invaded areas at the peri-urban belt of Morelia (small geographic-scale approach)

Species	Abundance (ind./10 point counts)	
	Invaded	Non-invaded
Columbina inca	12	5
Leptotila verreauxi	0	1
Cynanthus latirostris	8	9
Amazilia beryllina	7	7
Amazilia violiceps	0	1
Melanerpes formicivorus	0	3
Melanerpes aurifrons	6	7
Contopus pertinax	2	9
Contopus sordidulus	0	2
Empidonax sp.	0	1
Pyrocephalus rubinus	14	12
Tyrannus vociferans	18	11
Hirundo rustica	19	7
Psaltriparus minimus	3	0
Campylorhynchus gularis	11	7
Catherpes mexicanus	12	2
Thryomanes bewickii	4	6
Troglodytes aedon	1	5
Polioptila caerulea	1	10
Sialia sialis	2	9
Turdus rufopalliatus	1	1
Ptilogonys cinereus	0	2
Vermivora celata	0	3
Vermivora ruficapilla	0	1
Dendroica coronata	0	6
Dendroica nigrescens	0	3
Wilsonia pusilla	0	1
Piranga flava	0	1
Sporophila torqueola	14	9
Pipilo fuscus	15	10
Spizella passerina	1	25
Melospiza lincolnii	0	1
Passerina caerulea	4	4
Carpodacus mexicanus	17	23
Carduelis psaltria	13	43
Passer domesticus	194	0

Table 2 List of native species ($n = 32$) recorded exclusively in non-invaded sites at the landscape level

Species
Accipiter cooperii
Zenaida macroura
Columbina passerina
Leptotila verreauxi
Lampornis amethystinus
Eugenes fulgens
Selasphorus platycercus
Trogon elegans
Melanerpes formicivorus
Colaptes auratus
Lepidocolaptes leucogaster
Attila spadiceus
Sayornis nigricans
Myiarchus tuberculifer
Myiarchus nuttingi
Vireo belli
Vireo atricapilla
Cyanocitta stelleri
Aphelocoma ultramarina
Poecile sclateri
Catharus occidentalis
Peucedramus taeniatus
Parula superciliosa
Dendroica occidentalis
Ergaticus ruber
Atlapetes pileatus
Melozone kieneri
Aimophila ruficeps
Oriturus superciliosus
Ammodramus savannarum
Euphonia elegantissima
Carduelis pinus

$F_{1,28} = 5.44$, $P = 0.026$; ANCOVA agricultural: $F_{1,21} = 66.37$, $P < 0.001$).

Results at the landscape-level were similar to those observed at the small geographic-scale. When we compared the community structure of invaded sites of the landscape-scale approach (20 randomly selected sites) with the data from the small geographic-scale we found no differences in the slopes of their rank/abundance plots (ANCOVA: $F_{1,40} = 0.24$, $P = 0.62$). Non-invaded sites at the landscape-level had rank/abundance plots that differed in their slope with invaded sites at the small geographic-scale (ANCOVA: $F_{1,82} = 4.23$, $P = 0.04$). Non-invaded sites at both the landscape and small geographic scales differed significantly in community evenness (ANCOVA: $F_{1,96} = 8.45$, $P < 0.001$). The stepwise multiple regression analysis showed that House Sparrow abundance had a positive relation with built cover and building height, and a negative relation with shrub cover (Table 3).

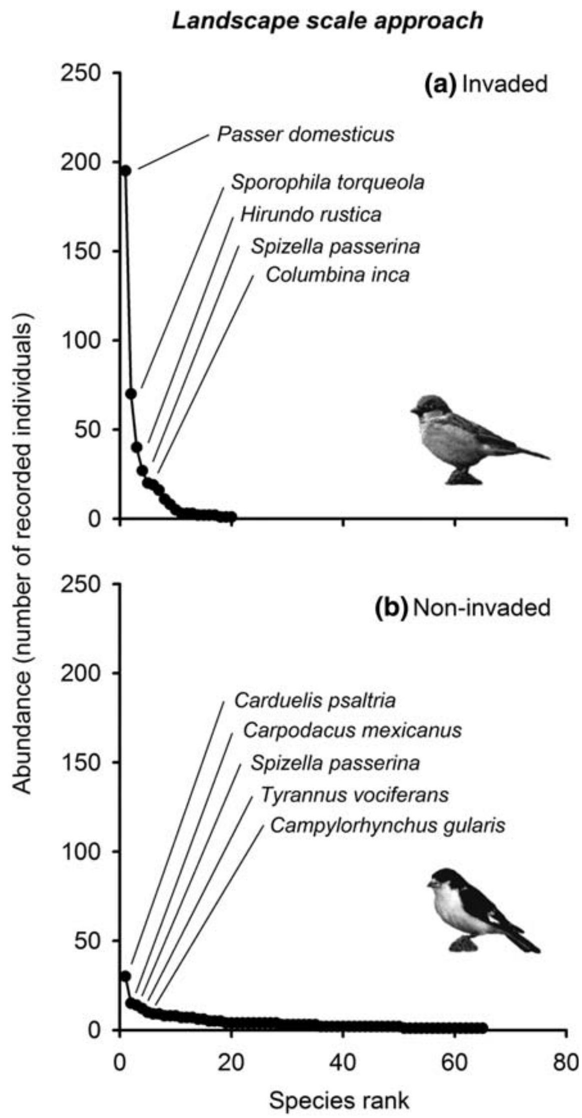

Fig. 3 Rank/abundance plots for House Sparrow invaded and non-invaded bird communities at the landscape-level. Rank/abundance plots for invaded and non-invaded bird communities show an almost identical pattern to the one found for the small geographic-scale approach (see Fig. 1). Bird communities of invaded areas at the landscape-scale approach were also highly dominated by the House Sparrow, regardless of the high environmental heterogeneity present in the sampled sites

Table 3 Relationship between House Sparrow abundance and habitat structure variables

General model	$R = 0.44$	$F_{3,548} = 46.08$		$P = 0.001$
	Beta	SE	$t(548)$	P
Intercept			5.18538	0.000000
Shrub cover	−0.116999	0.040161	−2.91327	0.003723
Construction cover	0.155195	0.068247	2.27403	0.023350
Building height	0.260973	0.067942	3.84109	0.000137

Discussion

Our results show that areas invaded by the House Sparrow differ greatly from non-invaded areas, regardless of their environmental conditions or level of human disturbance (i.e., urbanization, agriculture). At the small geographic-scale we established a negative relationship between the presence of House Sparrows and native bird species richness. We also found a positive relationship between House Sparrow presence and total bird abundance. At the landscape-level, bird community diversity and structure exhibited patterns that did not differ from those found at the small geographic-scale. In this section we discuss shifts in bird community diversity, structure, and composition at House Sparrow invaded and non-invaded sites, focusing on the importance of the House Sparrow as a molder of native bird communities.

There was a dramatic decrease in the evenness of bird communities where House Sparrows were present. This was caused by a reduction in bird species richness and an increase in bird abundances at invaded sites. Our results are consistent with patterns of diversity generated by other invasive species of different taxa, such as plants, invertebrates, and fishes (Vitousek et al. 1997; Gritti et al. 2006). The increase in total bird abundance at invaded sites was caused by a dramatic increase in the number of House Sparrow individuals. This is not surprising, since House Sparrows have been found to be a dominant species in the communities where they occur all over the world (Emlen 1974; Gavareski 1976; Cupul-Magaña 1996; Clergeau et al. 1998; White et al. 2005), and are an excellent example of an invasive urban exploiter species.

The species turnover analysis at both scales showed that the bird composition of invaded and non-invaded sites was similar; however, invaded sites had low species richness due to the loss of several native species. Because our sampling sites for the small geographic-scale approach were environmentally very similar, our results suggest that the presence of the House Sparrow is the cause of native species loss. This was supported by our results from the landscape-level approach, where regardless of environmental variation, invaded sites exhibited simpler, more dominated communities. One of the possible explanations for these patterns is the House Sparrow's aggressiveness towards native species (Kalinoski 1975; Gowaty 1984). At our study sites we observed House Sparrows violently attacking some native species at feeding sites (e.g., Lesser Goldfinch, White-collared Seedeater, Golden-fronted Woodpecker). Similar aggressive interactions between the House Sparrow and local species have also been reported for other sites in North America (Kalinoski 1975; Grussing 1980; Gowaty 1984).

Bird communities of House Sparrow invaded sites at both the small geographic-scale and the landscape-level had similar structure and composition. This similarity could be generated by two urban-related forces: (1) shifts in the structure and composition of natural habitats to artificial impoverished systems; and (2) the attraction of exotic, invasive, and aggressive species that successfully exploit the resources and conditions of urban systems. As a result of these processes, a number of species may avoid the urban habitat due to the lack of appropriate habitat or their incapability to deal with aggressive urban exploiters. Other urban adaptable species that could live in urban conditions may also be limited by negative competition with urban exploiters. Alternatively, there may be an increase in the number of individuals of those species capable of exploiting urban conditions and resources (Blair 2001; McKinney 2002). Thus, the avifaunas of different cities are highly similar in comparison to the avifaunas of the adjacent habitats. Such a scenario makes urbanization a major cause of biotic homogenization, where animal communities are dominated by only a few species that are able to maintain healthy populations within urban habitats (Blair 2001; McKinney 2006).

However, in the case of non-invaded sites, bird communities differed between the small geographic and landscape levels, and this appears to result from the environmental variation that exists between the homogeneous small geographic-scale sites, and the heterogeneous landscape-level sites. Our peri-urban sites, used at the small geographic-scale analysis, are extremely similar among them, and as a result, had almost identical bird communities. Because these sites are located in the area of influence of the city of Morelia, their bird communities are affected by urbanization processes and therefore present lower species richness than non-invaded sites with native vegetation in other areas of the watershed (MacGregor-Fors et al., in press). Bird communities inhabiting non-invaded sites at the landscape-scale approach overestimate species richness because they comprise the bird communities that exist in all the habitats present in the Cuitzeo watershed. Therefore, their high species richness is an artifact of our analysis that conglomerates the high environmental variation present in our study area.

At the landscape-level we only recorded House Sparrows within human-altered urban and agricultural systems. This is a factor that could obscure our findings by confounding the effects of human activity and House Sparrow presence on the structure and diversity of bird communities. Nevertheless, when considering only urban and agricultural areas, bird communities still differed between invaded and non-invaded sites. Non-invaded human-altered areas have communities that are richer and more even than human-altered areas invaded by House Sparrows. Non-invaded human-altered sites have bird communities that are intermediate in the slope of their rank/abundance plots between non-invaded natural sites and invaded-sites (all Newman-Keuls post hoc tests P values < 0.001; Fig. 4). This suggests that even though human alteration has an effect on bird community structure and diversity, House Sparrow invasion plays a crucial role in determining species richness and abundance of avian communities.

Our results show that House Sparrow abundance is related to urbanized and open areas with a low density of shrubs. This is a very common scenario within Latin-American cities, where the House Sparrow has invaded and become highly abundant. Curiously, while the House Sparrow has expanded its numbers and distribution range across the American continent, European populations are declining (Shaw et al. 2008). Robinson et al. (2005) have related these declines to the industrialization of agricultural activities that no longer allow the House Sparrow to exploit agricultural leftovers as food. Also, the fact that European cities have become cleaner in the last few years, reducing the availability of litter as a food resource, could have negative effects on this species' populations, although others factors such as the change in habitat structure in cities could also explain this negative trend (Shaw et al. 2008). These factors could be taken advantage of to limit House Sparrow populations in America, and reduce the negative effects of this species on native bird communities.

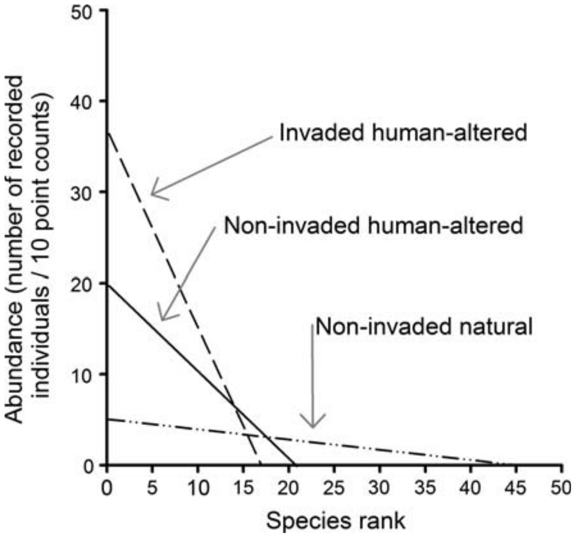

Fig. 4 Slopes from rank/abundance plots indicating the dominance/evenness of invaded and non-invaded bird communities: (1) House Sparrow invaded human-altered habitats (urban and agricultural sites; *segmented line*); (2) non-invaded human-altered habitats (urban and agricultural sites; *solid line*); and (3) non-invaded natural habitats (native forests and shrubland sites; *segmented-dotted line*). Our results indicate that although human activities modify the structure of bird communities, the presence of House Sparrows is crucial to determine the dominance/evenness values of the bird communities they invade

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