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Research Paper

On the North American invasion of the House Sparrow and its absence in the Yucatan Peninsula

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ABSTRACT. Biological invasions occur when individuals of alien species establish and colonize new locations. The House Sparrow (*Passer domesticus*) is one of the most widespread invasive birds, native to Eurasia and North Africa, and has successfully invaded many regions from across the world. The House Sparrow was successfully introduced in 1852 into North America and quickly invaded most of the North American continent, except the Florida Peninsula. Currently, the species is found throughout agricultural and urban landscapes of North America except the Yucatan Peninsula. We analyzed the invasion process of the House Sparrow in order to determine why it is absent from the Yucatan Peninsula. For this, we focused our assessment on historical records of the species together with climatic variables. Using an ordination analysis, we compared the climatic space of the North American records for the House Sparrow with that of the Yucatan Peninsula, as well as those before and after the Florida Peninsula invasion, which took sparrows longer to fully colonize. We found that climate may represent an important driver in the process of invasion in the North American invasion of House Sparrows, probably delaying the Florida invasion, and so far, preventing the Yucatan Peninsula invasion. Our results suggest that the absence of the House Sparrow in the Yucatan Peninsula could be a temporal delay, as occurred in the Florida Peninsula; yet, climatic conditions in the Yucatan Peninsula show important differences from those of the Florida Peninsula. Given the species' plasticity and generalist life history traits, it is possible that the House Sparrow may overcome present climatic restrictions and invade the Yucatan Peninsula if proper management is not set in action.

À propos de l'invasion du moineau domestique en Amérique du Nord et de son absence dans la péninsule du Yucatan

RÉSUMÉ. Les invasions biologiques se produisent lorsque des individus d'espèces étrangères s'établissent et colonisent de nouveaux territoires. Natif d'Eurasie et d'Afrique du Nord, le moineau domestique (*Passer domesticus*) est l'un des oiseaux invasifs les plus répandus et a envahi avec succès de nombreuses régions du monde. Le moineau domestique a été introduit avec succès en Amérique du Nord en 1852 et a rapidement envahi la plus grande partie du continent nord-américain, à l'exception de la péninsule de Floride. Cette espèce est actuellement présente dans tous les paysages agricoles et urbains d'Amérique du Nord, à l'exception de la péninsule du Yucatan. Nous avons analysé le processus d'invasion du moineau domestique afin de déterminer les raisons de son absence dans la péninsule du Yucatan. Pour ce faire, nous avons concentré notre évaluation sur les dossiers historiques de l'espèce ainsi que sur les variables climatiques. Par une analyse d'ordination, nous avons comparé l'espace climatique des registres d'Amérique du Nord concernant le moineau domestique avec celui de la péninsule du Yucatan, ainsi que ceux qui ont précédé et suivi l'invasion de la péninsule de Floride, où la colonisation du moineau domestique a demandé plus de temps. Nous avons constaté que le climat pourrait constituer un facteur majeur du processus d'invasion de l'Amérique du Nord par le moineau domestique, ce qui a probablement retardé l'invasion de la Floride et jusqu'à présent, a empêché l'invasion de la péninsule du Yucatan. Nos résultats suggèrent que l'absence de moineaux domestiques dans la péninsule du Yucatan pourrait résulter d'un retard temporaire, comme ce fut le cas dans la péninsule de Floride ; pourtant, les conditions climatiques dans la péninsule du Yucatan présentent d'importantes différences par rapport à celles de la péninsule de Floride. Compte tenu de la plasticité de l'espèce et des caractéristiques historiques de la vie généraliste, il est possible que le moineau domestique parvienne à surmonter les restrictions climatiques actuelles et à envahir la péninsule du Yucatan si une gestion adéquate n'est pas mise en place.

Key Words: *Bird; climatic limit; distribution; invasive species; Passer domesticus*

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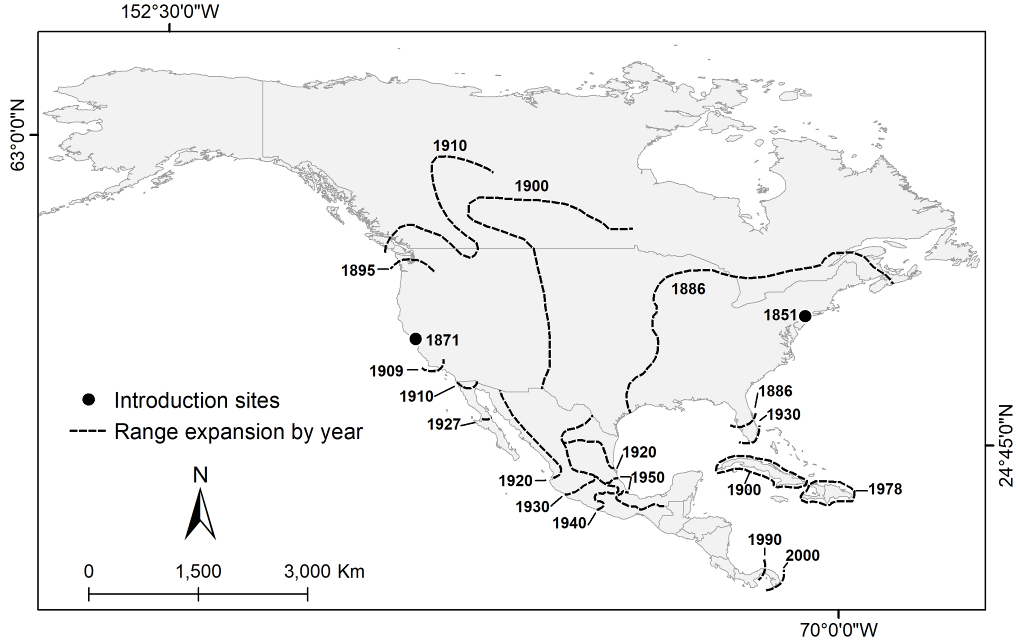
Fig. 1. Geographical representation of the historic invasion of the House Sparrow in North America. Range expansion isoclines represent first records.



INTRODUCTION

Biological invasions occur when individuals of exotic species establish and colonize new locations (Blackburn et al. 2009). This phenomenon comprises one of the main components of contemporary human-driven global change and has been considered one of the most important factors behind species extinction (Bellard et al. 2016). Furthermore, invasive species can re-structure local wildlife communities and even alter ecosystem processes, which can result in important economic losses and/or health problems (Pimentel et al. 2005, Simberloff et al. 2013, Booy et al. 2017).

Invasive birds are abundant throughout the globe, with a noteworthy urban representation (Blackburn et al. 2009). Cities are important centers for biological invasions, as urbanization often promotes the establishment and spread of invasive bird species because of their highly predictable conditions and resources that tend to be underused by native species (Shochat et al. 2010). One of the most widespread invasive birds, the House Sparrow (*Passer domesticus*), is a human-commensal considered to be native to Eurasia and northern Africa. It has successfully invaded most of the American Continent and other regions across the globe (e.g., Australia, New Zealand, South of Africa; Anderson 2006). Among the traits that make the House Sparrow a successful range expanding invader, its ecological and physiological plasticity head the list (Gavett and Wakeley 1986, Anderson 2006, Peach et al. 2008).

The House Sparrow was successfully introduced to North America in 1852 with individuals from Britain and Germany. After initial breeding populations established in the Bronx (NY, USA) (Robbins 1973), the North American invasion completed its transcontinental colonization around 1910 (Anderson 2006), with the notable exception of the Miami area (Florida Peninsula), which was not colonized until 1930 (Baughman 2003). This sparrow arrived in Mexico from the Pacific Coast invasion, where its populations reached Mazatlán (Sinaloa) by 1916 (Wagner 1959). These populations expanded across the Trans-Mexican Volcanic Belt during subsequent decades, arriving in Mexico City in 1933 and in Veracruz (Veracruz) by 1942 (Wagner 1959). Along the Atlantic Coast, the sparrow arrived in Monterrey (Nuevo León) by 1916, and only two years later in Tampico (Tamaulipas), which is 460 km to the southeast, where their spread came to a halt (Wagner 1959).

It is important to point out that the individuals established in Veracruz are presumed to have come from the Pacific Coast invasion and not the Atlantic Coast one, despite being only 380 km away from the latter. In fact, Wagner (1959) hypothesized that well preserved tropical forest in that area could have acted as a barrier for the sparrow, together with the high temperatures relative to elsewhere within the occupied range in North America. Finally, House Sparrows reached southern Mexico, Tuxtla Gutierrez, by 1948 (Wagner 1959). Although the North American invasion has currently reached Panama (Fig. 1), the most southerly reach of the North American invasion (Anderson 2006), it is absent in the Yucatan Peninsula, where only sporadic records of the species exist (presumably from cruises), but no breeding populations are known.

Based on the history of the North American invasion of the House Sparrow, in this study we addressed potential bioclimatic drivers for the House Sparrow being absent in the Yucatan Peninsula. For this, we used records for the species from open-source databases to describe the bioclimatic niche of the species and contrasted it with that from where it is absent in the Yucatan

Peninsula. We predicted that the bioclimatic, scenopoetic, nature of the Yucatan Peninsula could be a driver behind the absence of House Sparrows in that region, based on the slow expansion of the species' range in the Florida Peninsula, where similar conditions exist.

METHODS

We used published historical information to illustrate the advance of the House Sparrow invasion in North America (see Methods of Appendix 1). Additionally, we gathered unique dated and geo-referenced House Sparrow records (~5 km²) from the Global Biodiversity Information Facility (GBIF; https://www.doi.org/10.15468/dl.0jxnrc) from North America to Central America (from Canada to Panama). We also gathered House Sparrow records for the Yucatan Peninsula from the literature (Flota-Buñuelos et al. 2018) and the citizen science platform Naturalista (https://www.naturalista.mx).

We focused on the North American invasion area as it is known to be independent from the South American one, and because the House Sparrow is a highly plastic and adaptable species that has been shown to mold itself to the specific conditions of the areas that they invade. It has been suggested that this sparrow should be studied based on their regional invasive populations (Johnston and Selander 1964), as there is evidence that House Sparrows can rapidly adapt to new environments (Martin and Fitzgerald 2005). This, in turn, has been reflected in the changing morphological and physiological traits among their populations, mainly across the North American invasion range (Johnston and Selander 1964, 1971, Kendeigh 1976, Martin et al. 2004, 2005). Additionally, moderate genetic differentiation has been identified between North American House Sparrow populations and those from Eurasia and North Africa (Schrey et al. 2011, Liebl et al. 2015). Such differences have been claimed to be related to the individual response of these sparrows to novel environments (Riyahi et al. 2017, Cohen and Dor 2018), the reason why we considered the North American population of House Sparrows as an independent group to assess their climatic niche. Recent studies that incorporate intraspecific variation in species distribution models have improved distribution predictions when focusing on focal areas (Lecocq et al. 2019, Chardon et al. 2020). The latter is basically due to the local adaptations and local biotic interactions that the species have in each population and environmental scenario (Emery et al. 2015, Early and Keith 2019). Actually, recent evidence shows differentiation among regional House Sparrow populations (Hällfors et al. 2016, Marcer et al. 2016).

For the environmental characterization of the entire North American House Sparrow invasion, as well as the Florida and Yucatan Peninsulas, we used five bioclimatic variables (i.e., average daily range, temperature seasonality, average temperature of wettest quarter, annual precipitation and seasonality of precipitation), with a resolution of 0.416° from Wordclim (Version 1.4) (Hijmans et al. 2005). None of these variables were found to be highly correlated according to our Pearson correlation results ($r < 0.50$, $P < 0.05$; Fig. A1.1, A1.2) for the North American invasion area. Therefore, we used this set of non-correlated variables in further analyses sensitive to multicollinearity. Notably, we considered the delimitation of the Yucatan Peninsula based on the biotic provinces proposed by Barrera (Barrera 1962, Morrone 2005), which basically comprises the states of Campeche, Quintana Roo, and Yucatán, as well as the northernmost section of Belize and Guatemala (Duno-De Stefano et al. 2012). In the case of the Florida Peninsula, we delimited it according to the US ecoregions proposed by The Nature Conservancy (The Nature Conservancy 2008, Olson and Dinerstein 2002). We converted each cell from the raster file containing the climatic information of both peninsulas to vectorial points, which we assigned with values from the set of variables to construct climatic ellipsoids.

Although ecological niche models are helpful in reconstructing species niches (Peterson et al. 2011), having well represented areas or the accumulation of records, as we do for House Sparrow in its North American invasion, can bias the models due to the over-representation of environmental conditions (Kadmon et al. 2004, Anderson and Gonzalez 2011, Aiello-Lammens et al. 2015). Thus, we did not use ecological niche models in this study, mainly because the climatic space represented by the gathered records is more than sufficient to reconstruct the ecological niche of the House Sparrow in its North American invasion, avoiding all possible bias of ecological niche models (Jiménez-Valverde et al. 2008, García-Roselló et al. 2019).

To carry out the environmental analysis, we performed a principal components analysis (PCA) with the set of five aforementioned bioclimatic variables. Based on previous knowledge that shows that ordination approaches are useful in the assessment and comparison of ecological niches (Broennimann et al. 2012, Guisan et al. 2014), we used the resulting PC1-PC3 to generate spatial objects (i.e., rasters) for their further use as environmental variable proxies. Afterwards, we computed the ellipsoids that contained 95% of the data of PC1-PC3 of records for the entire North American invasion, as well as the geographic area of both the Yucatan and Florida Peninsulas (centroid and matrix of covariances method, *elipsem* package for R; Osorio-Olvera et al. 2016, Cobos et al. 2019).

We first assessed how the range of environmental conditions in locations where the North American House Sparrows can be present has changed across time. For this, we estimated and compared the volumes of the ellipsoids of House Sparrow records in periods of 50 years. For this, we divided the House Sparrow record into four periods (1850-1900, 1901-1950, 1951-2000, 2001-2019) and estimated and compared the ellipsoids for each record group using the previously generated PC1-PC3. Then, we assessed the degree of overlap of ellipsoids to determine the climatic similarity between the entire North American invasion and the Yucatan and Florida Peninsulas. Notably, for the ellipsoid for the Florida Peninsula, we used records spanning from 1850-1950, representing the period when the sparrow had not yet invaded the region. Finally, we evaluated the overlap of ellipsoids between both peninsulas to determine their climatic similarity. We ran all analyses in R 3.6 (R Core Team 2020).

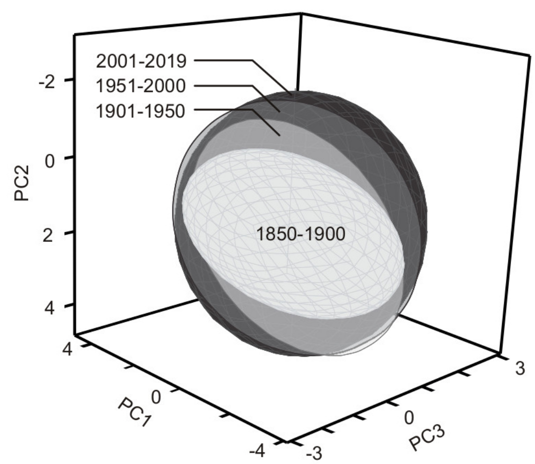
RESULTS

Based on historic and current House Sparrow records, we were able to construct the first comprehensive temporal map of the invasion of the species across its North American invasion (Fig.

1). The invasion process started in Brooklyn (NY, USA) in 1852. By 1910 House Sparrows had invaded central Canada, by 1950 they were present in southern Mexico, and by 1990 they had arrived in Panama. Regarding punctual information, we gathered a total of 101,415 records of House Sparrows along the current North American invasion path spanning 1850-2019, covering an area from central Canada to Panama. The number of collected records varied across time, as follows: 1850-1900: 199 records; 1901-1950: 1,188 records, 1951-2000: 25,559 records, 2001-2019: 74,469 records (Fig. A1.3).

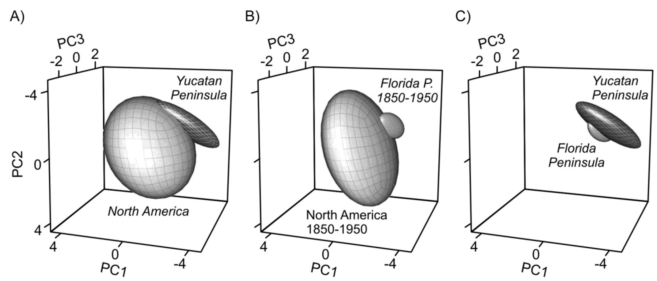
The first three components of the PCA explained 85% of the variance of the assessed environmental variables. The most important variables for PC1-PC3 were as follows: seasonality precipitation for PC1, annual precipitation for PC2, and mean temperature of wettest quarter for PC3 (Table A1; Fig. A1.4). The ellipsoid for the 1850-1900 period had a volume of 44.06, the one for the 1901-1950 period had a volume of 70.19, the one for the 1951-2000 period had a volume of 87.12, and the one from the 2001-2019 period had a volume of 88.71 (Fig. 2).

Fig. 2. Representation of the ecological space (PCA ellipsoids) of House Sparrow records for four time periods.



The climatic ellipsoid for the entire North American invasion was 18 times larger (niche volume = 78.36), than the one for the Yucatan Peninsula (niche volume = 4.26). Only 45% of the climatic ellipsoid of the Yucatan Peninsula overlapped with the one for the entire North American invasion (Fig. 3 panel A). Regarding the climatic ellipsoid of the Florida Peninsula before House Sparrow colonization (niche volume = 0.87), it was smaller than the ellipsoid for the North American before the invasion of the Florida Peninsula (niche volume = 64.8). Only 28% of that ellipsoid overlapped with that of the North American invasion between 1850 and 1950 (niche volume = 69.94, Fig. 3 panel B). The percentage of overlap between the Yucatan and Florida Peninsulas was only 17%, which means that 83% of the Yucatan Peninsula differs from the conditions of the Florida Peninsula (Fig. 3 panel C).

Fig. 3. Representation of the ecological space (PCA ellipsoids) of House Sparrows records in different regions and periods of time. (A) North America and Yucatan peninsula, (B) records from 1850–1950 of North America and the Florida peninsula, (C) Comparison between both peninsulas.



DISCUSSION

The House Sparrow is an outstanding example of an avian invader, not only due to the amount of invaded territory, but because of the speed of its invasion rates (Clergeau et al. 2004, Liebl et al. 2015), and the negative implications it has for native avifauna (MacGregor-Fors et al. 2010, García-Arroyo et al. 2020, but see González-Oreja et al. 2018). Originally from Eurasia and North Africa and introduced to northeastern USA in the mid-1800s, no apparent barrier has been identified to prevent its invasion across North and Central America yet. However, our results show that there seems to be a climatic restriction that limited its invasion rate in the Florida Peninsula and could be behind its current absence in the Yucatan Peninsula.

The North American invasion of the House Sparrow, that now extends to Central America, has occurred in only 169 years (Moulton et al. 2010), with the first 35 years being enough to invade all eastern and part of central USA (from eastern Iowa to southern Texas). However, it took almost 80 years for the sparrow to get to southern Florida (Baughman 2003). Although the species was initially recorded in south Florida in the 1930s (Howell 1932), it took 40 years for it to fully invade the territory.

Our results show that the climatic conditions of the Florida Peninsula by 1950 could have represented a climatic barrier that slowed down the invasion rate of the North American House Sparrow. It is possible that further adaptation in the subsequent 20 years was necessary for the sparrow to fully colonize the region (Johnston and Selander 1964, Schrey et al. 2011). A similar process seems to be happening in the Yucatan Peninsula. Our results show that the climatic conditions in the current North American House Sparrow invasion and that of the Yucatan Peninsula differ importantly, with approximately 55% of the conditions for the peninsula being unique to it. The environmental conditions that show a differentiation pattern between the records for the species in the Yucatan Peninsula were determined mainly by two temperature variables (i.e., mean temperature of the wettest quarter-Bio 8, temperature seasonality-Bio 4), and one precipitation variable (i.e., annual precipitation-Bio 12; Fig. A1.4). Thus, in the Florida Peninsula relative humidity was high for most of the year (given the combination of the temperature and precipitation variables) in comparison to the environmental conditions of the locations with the majority of the species' records.

The aforementioned environmental conditions of the Florida Peninsula are also typical of tropical forests which are well conserved in the southwest of the Yucatan Peninsula (Rzedowski 2006). These factors could also be restricting the presence of House Sparrows in the region and access to the rest of the peninsula (Fig. A1.3). Similarly, the presence of House Sparrows across North America has been related to the presence of urban settlements and human activities (Riyahi et al. 2013), which are relatively small and sparsely distributed in the southwest of the Yucatan Peninsula. However, the northwestern section of the Yucatan Peninsula has well developed urban areas with a population of over 2 million inhabitants and a considerable population density of (53 inhab./km^2). Moreover, the state capital Merida is among the 10 most populated cities in Mexico. Additionally, the State of Quintana Roo has 1.5 million inhabitants and population density of 34 inhabitants per km^2, and in the north of the state there are the cities of Cancun and Ciudad Playa del Carmen which constitute an important urban continuum in the region (INEGI 2020). Actually, there are isolated House Sparrow reports for the Yucatan Peninsula (even considered "occasional"; MacKinnon 2005, Flota-Buñuelos et al. 2018), most likely related to the arrival of cruise ships that come from Florida or the Antilles. Yet, the individuals have not yet been able to establish stable populations, which is why we hypothesize that the restriction in this particular case is more closely related to a climatic factor, rather than the lack of immigrating individuals. It is notable that House Sparrows were already established in southern Mexico by 1950 and in four decades invaded Central America down to Panama. Despite the latter representing a 2,000 km straight line invasion, the sparrow is still absent (70 years after it arrived to southern Mexico) in the Yucatan Peninsula, which is only 200 km away from areas successfully colonized by 1950.

Invasive species can broaden or change their ecological niche in invaded areas (Broennimann et al. 2007, Rödder and Lötters 2009, Medley 2010, Strubbe et al. 2015), which happened with House Sparrows colonizing the USA, particularly the Florida Peninsula. In fact, changes in the climatic tolerance of invasive species and their establishment in new areas can also be driven by ecological interactions in the invaded regions (González-Moreno et al. 2015), along with other species traits such as capacity of dispersion, reproductive strategies, and ecological generalization (Sol et al. 2012, Estrada et al. 2016). Thus, based on our results and previous information, we consider two mutually exclusive future scenarios for the House Sparrow in the Yucatan Peninsula. First, the climatic conditions of the Yucatan Peninsula, together with other ecological factors (e.g., competitor species, not enough individuals to establish new reproductive populations) will represent a barrier that will not allow the successful invasion of House Sparrows. Second, the species will continue its adaptation process, eventually pass through its lag phase, and then be able to establish a population large enough to overcome the existing climatic and ecological restrictions, mainly due to some advantageous traits (e.g., ecological generalist, reproduction strategies; Sol et al. 2012) and eventually invade the Yucatan Peninsula, as happened in the Florida Peninsula. If the second scenario holds true and processes are similar to those that occurred in the Florida Peninsula invasion, we could expect the start of an invasion process in the Yucatan Peninsula in the short-to-medium term, which is why if the aim is to control the invasion, intensive monitoring and management plans are required.

Responses to this article can be read online at:
https://www.ace-eco.org/issues/responses.php/1835

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Appendix 1

On the North American invasion of the House Sparrow and its absence in the Yucatan Peninsula

Alexander Peña-Peniche, Claudio Mota-Vargas, Michelle García-Arroyo and Ian MacGregor-Fors*

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Figure A1.1. Correlation between the 19 bioclimatic variables extracted from Wordclim (Hijmans et al. 2005) within the region covered by the North American House Sparrow invasion.

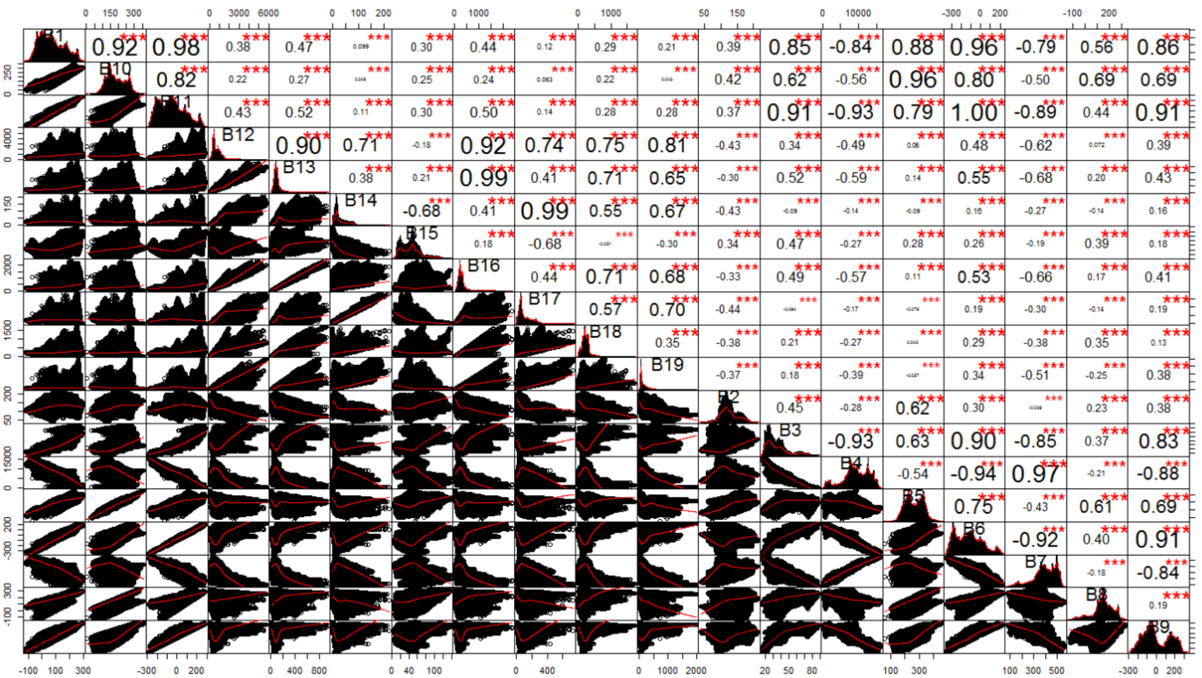

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Figure A1.2. Correlation between the variables selected to create the PCA variables.

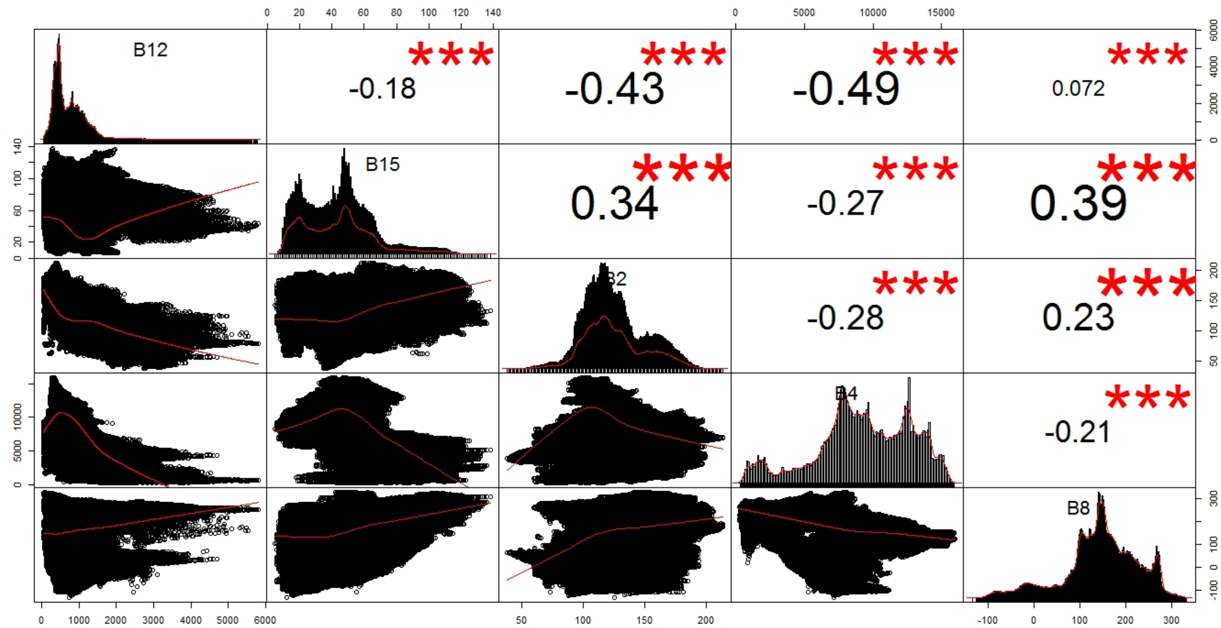

Figure A1.3 House Sparrow records in two periods (1850–1950 and 1951–2019) showing its scarce presence in the Florida Peninsula before 1951 and the present records of the Golf coast and part of the Caribbean.

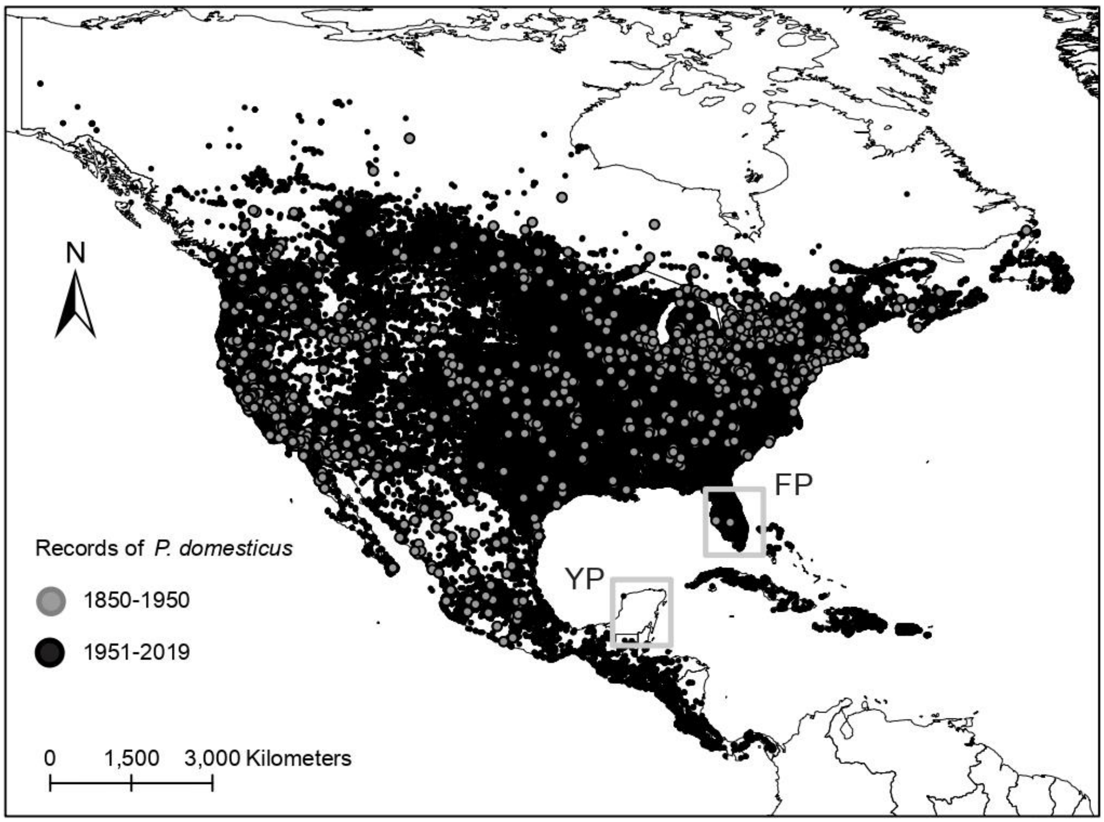

Figure A1.4. First two Principal Components showing House Sparrow records from North America (black dots) and the Florida Peninsula (grey dots). Bio_4 is temperature seasonality, Bio_8 is mean temperature of the wettest quarter, Bio_12 is mean annual precipitation, Bio_15 is precipitation seasonality and Bio_2 is mean diurnal range.

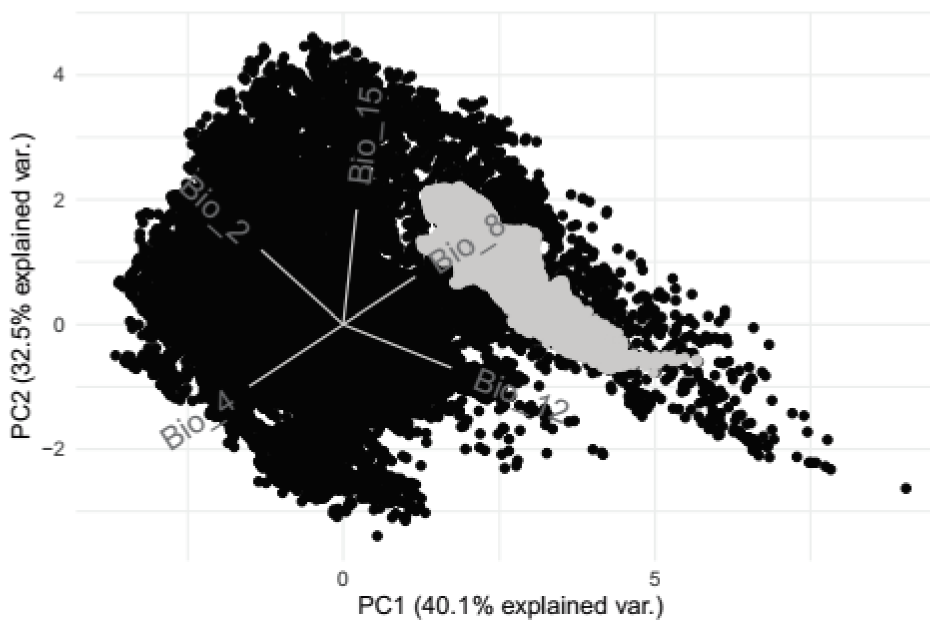

Table A1. Results from a PCA of 19 climatic variables extracted from Worldclim for the area invaded by House Sparrows within North America.

	PCA loadings				
	PC1	PC2	PC3	PC4	PC5
Bio 12	0.1162	*****-0.7635	0.0333	-0.0189	0.6341
Bio 15	*****-0.5673	0.0625	0.2334	0.7640	0.1897
Bio 2	*****-0.5289	0.3029	*****-0.5057	-0.3814	0.4768
Bio 4	0.3956	*****0.5493	0.4727	-0.0354	0.5630
Bio 8	-0.4779	-0.1403	*****0.6821	-0.5188	-0.1326

	PCA summary				
Standard deviation	1.3694	1.2465	0.9058	0.7626	0.4109
Proportion of Variance	0.3751	0.3108	0.1641	0.1163	0.0338
Cumulative Proportion	0.3751	0.6858	0.8499	0.9662	1.0000

*Indicates the most important variables for each component

Method followed to obtain Figure 1

We used the map information provided by Wagner (1959), Baughman (2003), and unique species records (~5 Km^2) obtained from the Global Biodiversity Information Facility (GBIF; DOI10.15468/dl.0jxnrc) to compile a database of the introduction and invasion of the House Sparrow in North America. We used a set of records associated to a location and a date to perform an inverse distance weighting (IDW) interpolation to generate a raster continuum of the presence of the species and their change in time. Our final map contains the redrawing of the range-expansion lines from Baughman (2003) and the lines of the invasion in the limits of the classes obtained through the interpolation, marked each with the year.

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