White Storks nest at high densities near landfills changing stork nesting distributions in the last four decades in Central Spain

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ABSTRACT

Human-induced environmental changes are the main drivers of the ongoing redistribution of biodiversity. The millions of tons of organic waste that is added daily to landfills can increase the carrying capacity of ecological systems with direct effects on species´ population sizes and/or distributions. Understanding the effect of landfills on bird distribution is essential to assess management decisions. Our aim was to determine the role of landfills in the distribution of the breeding population of White Storks (*Ciconia ciconia*) in the last 4 decades. For that purpose, we used historical and current census data of breeding pairs before and after landfill exploitation. In this study, we found that landfills have altered the distribution of the breeding population over the last 4 decades in the province of Madrid, Spain. We found that birds occupied new nesting sites near landfills independently of habitat quality as defined by prey abundance and quality according to previous studies. Nest density was higher near landfills and increased after the landfills began to be utilized by this species. Population growth and extremely high breeding densities may translate into conflicts with humans, particularly when new nesting sites are in urban areas, and possibly alter the perception of this bird species by the human population. Landfill closures, mandated by the European Landfill legislation, is an opportunity to reduce the effects of landfills on animal populations, and reduce human–wildlife conflicts. However, there must be a process of transition and a preliminary evaluation of habitat quality and suitability in the region to avoid a dramatic decline of the White Stork population.

Keywords: Ciconia ciconia, historical distribution, landfill, population dynamics, predictable anthropogenic food subsidies, urbanization, White Stork

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LAY SUMMARY

- Landfills attract wildlife in high numbers since they are an abundant and predictable anthropogenic food source. This may have an impact on species´ population sizes and/or distributions and an increase human–wildlife conflicts.
- We use historical and current data from breeding population census in Madrid region to assess changes in the population distribution of White Storks in the last four decades.
- Density of nests increased near landfills after White Storks started exploiting these facilities. In addition, breeding pairs occupied good-quality habitats and urban areas near landfills from 1984 to 2004, sifting to sub-optimal areas closer to the landfills in the later years.
- Landfill's closure can be an opportunity to reduce the health, security and safety risks of this facilities for birds and return to former population size numbers. However, this change on landfill management needs to be a gradual process and we recover and manage suitable habitats.

Las cigüeñas blancas (*Ciconia ciconia*) nidifican en altas densidades en las proximidades de los vertederos cambiando la distribución de la población reproductora en las últimas cuatro décadas en España central.

RESUMEN
Los cambios inducidos por los seres humanos son los principales factores subyacentes de la redistribución de la biodiversidad. Millones de toneladas de basura orgánica dispuesta diariamente en los vertederos puede desembocar en un incremento de la capacidad de carga de los ecosistemas con repercusiones directas en el tamaño y/o distribución de la población. Comprender el efecto de los vertederos en la distribución de las aves es esencial para evaluar las decisiones de gestión de fauna. Nuestro objetivo era determinar el papel de los vertederos en la distribución de la población reproductora de cigüeñas blancas (*Ciconia ciconia*) en las últimas cuatro décadas. Para este fin usamos datos de censos históricos y actuales de reproductores antes y después de la explotación de los vertederos. En este estudio, hemos encontrado que los vertederos han alterado la distribución de la población reproductora de cigüeña blanca a lo largo de las últimas cuatro décadas en la provincia de Madrid, España. Encontramos que las aves ocupaban nuevos sitios de cría cerca de los vertederos independientemente de la calidad del hábitat, definido por la abundancia y calidad del alimento. La densidad de los nidos fue mayor cerca de los vertederos y se incrementó tras el uso del vertedero por parte de esta especie en la región. El crecimiento poblacional y la extremadamente elevada densidad de parejas reproductoras puede dar lugar a conflictos con los seres humanos, particularmente cuando las nuevas zonas de cría se localizan en áreas urbanas y posiblemente cambie la percepción de las personas sobre esta especie. El cierre de vertederos tras la implementación obligatoria de la legislación Europea sobre Vertederos es una oportunidad para reducir los potenciales efectos negativos de los vertederos en las poblaciones animales y reducir los conflictos entre la fauna y los seres humanos. Sin embargo, debe existir un proceso de transición, así como una evaluación previa de la calidad e idoneidad del hábitat en la región para evitar una dramática disminución de la población de cigüeña blanca.

Palabras clave: Ciconia ciconia, distribución histórica, vertedero, dinámica de población, fuentes de alimentación antrópica predecibles, urbanización.

INTRODUCTION

Humans have deeply modified the size and distribution of species populations around the world (Boivin et al. 2016, Bar-On et al. 2018). Habitat fragmentation, overexploitation of natural resources, land-use change, and increasing human global pollution are behind dramatic population declines and shrinking distributions of many species (Dirzo et al. 2014, Ceballos et al. 2015). However, some anthropogenic activities have triggered spectacular population explosions of a small group of species. In addition to land-use transformation and climate change, predictable anthropogenic food subsidies (PAFS) have altered population dynamics by increasing food availability in particular locations (Oro et al. 2013).

Landfills are the main unintentional PAFS in terrestrial ecosystems. The continuous and abundant generation of organic waste attracts the attention of several species (Plaza and Lambertucci 2017). Animals cover long distances and modify their movement patterns to reach these PAFS (Soriano-Redondo et al. 2021, Spelt et al. 2021). White Storks (*Ciconia ciconia*) use these facilities as important stop-over sites and/or shorten their migrations both in time and distance (Gilbert et al. 2016, Arizaga et al. 2018, Cheng et al. 2019).

Food availability also encourages opportunistic bird species (i.e., gulls and vultures) to breed near landfills (Duhem et al. 2008, Monsarrat et al. 2013, Tauler-Ametller et al. 2017). During the breeding season, foraging on a predictable anthropogenic resource reduces foraging costs associated with seeking food and increases parental care of offspring (Moritzi et al. 2001, Soriano-Redondo et al. 2021). For instance, foraging at landfills increases clutch size and egg size, and enhances body condition and survival of offspring (Tortosa et al. 2002, Steigerwald et al. 2015, Djerdali et al. 2016a, Pineda-Pampliega et al. 2020). The increase in breeding success and survival may promote population growth that results in a higher density of individuals, an expansion of population range, or both. In addition, an elevated aggregation of breeding pairs may lead to an increase in intra-specific competition (Gilchrist and Otali 2002, Denac 2006, Djerdali et al. 2016b) and conflicts with humans (Belant 1997). This human-induced increase in population numbers is often considered to be a negative impact in the so-called overabundant species (Bino et al. 2010, Payo-Payo et al. 2015), but positive in endangered species (Tauler-Ametller et al. 2017, Plaza and Lambertucci 2018) with direct impact on population management. Thus, understanding the effects of landfills on population dynamics is essential to accurately address the management and conservation of both endangered and overabundant species.

White Storks have utilized landfills in the Iberian Peninsula since the 1980s (Blanco 1996, Tortosa et al. 2002), when the southwestern breeding population reached the minimum number registered after a period of constant decline (Bernis 1981, Barlein 1991). First, they were observed wintering or roosting in the surrounding areas (Blanco 1996, Archaux et al. 2004). As the breeding population of White Stork continued to grow, this growth was associated with the use of landfills and implementation of conservation measures (Schulz 1999, Tortosa et al. 2002, Massemin-Challet et al. 2006). Although many studies have analyzed the positive effect of landfills on population size, which include an increase in juvenile survival by shortening migration (Flack et al. 2016, Rotics et al. 2017, Cheng et al. 2019), improvement to body condition (Pineda-Pampliega et al. 2021), and changes in reproductive parameters (Tortosa et al. 2002, Massemin-Challet et al. 2006, López-García et al. 2021)), few studies have explored the effects of landfills on the distribution of the breeding population and the occupation of new sites (Bialas et al. 2020). However, it is possible that the most suitable breeding areas and/or feeding areas overlap with the new anthropogenic food source, just by chance. This is particularly important in the case of species with a marked nest-site fidelity (Barbraud et al. 1999, Vergara et al. 2006) and philopatry (Del Hoyo et al. 2014), such as the White Stork, where the previous distribution is a determinant factor in the future expansion of the species. Previous studies focused on the effects of landfills on White Stork distribution often overlooked the potential effects of historical distribution due to the lack of available data before the use of the new feeding resources began (Djerdali et al. 2016b, Bialas et al. 2020, Hmamouchi et al. 2020a,b).

Our main objective was to evaluate the effects of landfills on the distribution of the growing population of White Storks over the nearly last 40 years. In this study we took into account the historical distribution of the breeding population. Our first purpose was to analyze which variables were associated with the probability of nest occupation before the use of landfills. We then evaluated the effects of landfills on the aggregability of this species, controlling for other potential confounding variables. Our final aim was to characterize the expansion process by identifying the differences between previous nesting sites and the new nesting sites. We hypothesized that landfills attracted White Stork pairs which bred nearer these facilities independently of the habitat quality as defined by prey abundance and quality according to previous studies (Alonso et al. 1991, Olsson and Bolin 2014, Zurell et al. 2018, Orłowski et al. 2019). Moreover, we proposed that the abundance of food provided by landfills would support higher densities of breeding pairs.

MATERIALS AND METHODS

Study Area and Data Collection

We surveyed the entire province of Madrid (8,030 km^2, Figure 1), Spain, searching for White Stork occupied nests during the 2021 breeding season (López-García and Aguirre 2023). The areas in the north and west of this region are characterized by mountain ranges, forests, and pastures usually devoted to cattle. The eastern area of the region is characterized by arable lands and crop fields. The south is similar to the east, but with more mixed habitats, water, and permanent crops associated with rivers. Madrid city has around 3.5 million inhabitants and is located at the center of this region. The White Stork has never bred in the southeastern area of Madrid (Molina and Del Moral 2005).

To evaluate the effects of landfills on the White Stork distribution, we also compiled data on nest occupancy from two previous censuses in 1984 (Lázaro et al. 1986) and 2004 (Molina and Del Moral 2005). The nest location accuracy in 1984 was less precise, as some locations were based on description only, and not on GPS locations. Because the precision error was between tens to a hundred of meters in 1984, we standardized resolution across sampling periods to a 1-km grid. All the censuses in our study area were based on the same methodology of direct assessment that was used in all the White Stork European censuses (Schulz 1999, Aguirre and Vergara 2009). This involved 3 visits to each location with nests to determine the occupancy of them between March to June. We made at least 1 visit in May wherever it was not possible to visit the location 3 times. A nest was considered as an occupied nest when we observed an adult, a pair or fledglings on the surface of the nest. All the municipalities were covered by car and/or walking. Also, we gathered information from local people and local authorities. In total, we had 215 occupied nests in 1984, 1,220 in 2004 and 2,327 in 2021.

In the Madrid region, White Storks were first observed feeding on the landfills in the 1980s (Manuel Fernández Cruz personal observations; Chozas 1983, Blanco 1996). The 4 main landfills in this region were first opened in the 1980s and were still active in 2021. The use of these 4 landfills (Alcalá de Henares, 40.457619°N, 3.36308°W; Colmenar Viejo, 40.664071°N, 3.72797°W; Pinto, 40.257118°N, 3.63755°W; and Valdemingomez also named Las Dehesas, 40.336427°N, 3.590375°W) by White Storks was confirmed in situ by Manuel Fernández Cruz and the authors in several visits between 1986 to 2021 (see localization in Figure 2). Two smaller landfills (Nueva Rendija and Colmenar de Oreja), were closed at the beginning of 2000. They were not included in our analysis due to the absence of observations of White Stork feeding at these sites. Therefore, the distribution of nests in 1984 was defined as the distribution of the breeding population in the region before White Storks started using the landfills.

It was not possible to identify individual nest re-occupation between the censuses due to the time elapsed between censuses and differences in the location accuracy (Barbraud et al. 1999). Instead, we classified the occupied nests into 2 variables to explore the direction of the expansion of the breeding population in relation to the spatial distribution of the nests. The nearest occupied nest to a nest recorded in the previous census, at maximum distance of 1 km (0). We considered new nests as all other nests (1). Therefore, new nesting sites' occupation (hereafter "new nesting sites") represent areas of population expansion.

To evaluate the effects of landfills and other environmental variables on the probability of a nesting site being abandoned between censuses, we defined an analogous binomial variable, following Bialas et al. (2020): either the nest was occupied in one census and also occupied in the next census (0), versus the nest was occupied in the first census but unoccupied in the following census (1). This variable was called probability of nesting sites abandonment (hereafter "abandoned nesting sites"). Both variables represent changes in two periods of time 1984–2004 and 2004–2021.

Spatial Analysis

We selected the following environmental variables from Corine Land Cover (CLC, https://centrodedescargas.cnig.es) known to affect the distribution of breeding White Stork populations (Carrascal et al. 1993, Radović et al. 2015, Orłowski et al. 2019, Hmamouchi et al. 2020a, Bialas et al. 2021): percentage of land covered by arable lands (CLC class 21), percentage of land covered by other agricultural areas (CLC class 22 and 24, except 244), percentage of land covered by forestry areas (CLC class 31 and 32, except 321), percentage of land covered by pastures, meadows & dehesas (i.e., Agro-forestry areas based on pastures with some trees and human management with livestock in the Mediterranean area) (CLC class 231, 321 and 244), distance to the nearest water body, and degree of urbanization. Because of the collinearity with the rest of the variables, we did not include the percentage of water bodies (CLC class 41 and 51) or percentage of highly altered urban areas (CLC class 1). As their resolution is better, we used distance to the nearest water body and degree of urbanization instead of percentage of water bodies (CLC class 41 and 51) or percentage of highly altered urban areas (CLC class 1)

These land cover types were obtained by grouping the original Corine Land Cover classes based on previous accumulated knowledge on this species, following the methodology used in Bialas et al. (2021). We calculated the percentage of each land cover type in each grid cell of 1 × 1 km.

We obtained the dataset of the degree of urbanization in a resolution of 30 arc-seconds (equivalent to 1 × 1 km) from the first hierarchical level of the Global Human Settlement Layer - Settlement Model Grid (GHSL-SMOD) from the Socioeconomic Data and Applications Center (https://sedac.ciesin.columbia.edu/data/set/ghsl-population-built-up-estimates-degree-urban-smod). This layer classifies each grid cell as rural, periurban, or urban areas, as a function of population density and the percentage of built-up areas (Florczyk et al. 2019). We used this information as a representation of the imperviousness of ground and potential food scarcity in cities, and human disturbance.

Distance to water bodies information was obtained from a database of topographical items in the 1:100000 scale, the BTN100 database of Organismo Autónomo Centro Nacional de Información Geográfica (https://centrodedescargas.cnig.es).

Our grid resolution was constrained by the lowest accuracy data on occupied nest locations in the census of 1984. We measured distance from centroids of each cell of the grid to the nearest landfill and nearest body of water using *st_distance* function in the *sf* package (Sumner et al. 2022). To obtain the nest density, we counted the number of nests in each grid cell (nests km^{-2}).

We defined the occupied nests identified in the 1984 census as presences and the random points generated in the study area as pseudoabsences. We generated the same number of pseudoabsences than presences to balance the statistical models. We used the *randomPoints* function in the *dismo* package (Hijmans et al. 2017) to generate the pseudoabsences within the area of Community of Madrid. We generated as many pseudoabsences as nests were found in 1984. Pseudoabsences were generated up to 1 km from each nest, according to the lowest accuracy data on occupied nest locations in the census of 1984.

Given that land cover and human population density have changed over the last 40 years, we chose the layer temporally closest to each year of census data (i.e., CLC 1990 to 1984 census, CLC 2006 to 2004 census, and 2018 CLC to 2021 census).

Spatial analyses were performed with QGIS 3.16.11 open-source software (QGIS

Development Team 2022) and 4.1.2 R version (R Core Team 2020).

Statistical Analysis

We built a linear model (LM) with a gaussian error structure to assess the variation in the distance from nests to the nearest landfill over the last 37 years. We included landfill distance and the year of the census (as factor) as predictor variables.

To identify which of several environmental variables determined the distribution of White Stork breeding populations in 1984, before this species used landfills in our study region, we used a generalized linear model (GLM) with a binomial response (pseudoabsence = 0, occupied nest = 1) and logit link function. We included the percentage of other agricultural areas (Agri), percentage of arable lands (Arable lands), percentage of forestry areas (Forest), percentage of pasture & dehesas (Pasture & Dehesas), degree of urbanization (Urbanization), and the distance to the nearest body of water (Water) as predictors.

We performed a GLM with a negative binomial error structure and log link function to evaluate the differences in nest density (nests km^{-2}) in relation to the distance to landfills and the census year (i.e., 1984, 2004 and 2021). We also evaluated the interaction of year and landfill distance, as well as interaction of year and environmental variables (Agri, Arable lands, Forest, Pasture & Dehesas and Water) in this analysis. To control for their potential confounding effects, we include the following predictor variables: Agri, Arable, Forest, Pasture & Dehesas, Urbanization, and Water. We also evaluated landfill distance and Pastures & Dehesas as a quadratic term.

In order to consider terms which may not have a linear relationship with the outcomes in our GLMs, we also included quadratic terms in the GLMs for both the probability of nest occupation and nest density. Although we tried all the different combination of quadratic terms for all the continuous variables (Agri, Arable, Forest, Pasture & Dehesas and Water), only the ones that improved the Akaike's Information Criterion corrected (AIC_c < 2 units of the previous best model) in the model selection process were included.

To analyze the relationships between distance to landfills and various environmental variables on new nesting sites and abandoned nesting sites we built GLMs with binomial error structures and logit link functions. We built those separate models for each period of time 1984–2004 and 2004–2021, named 2004 and 2021 for the new nesting sites and for the abandoned nesting sites. Besides distance to landfill, the following predictor variables were included in the analyses: Agri, Arable, Forest, Pasture & Dehesas, Urbanization, and Water.

We used the Akaike's Information Criterion corrected for small sample size (AIC_c) for model selection (Burnham and Anderson 2002). We generated models with all possible combinations of our predictor variables and ranked them based on the differences between the AIC_c of a given model and the AIC_c of the model with the lowest AIC_c (ΔAIC_c). The model with the lowest AIC_c was considered to be the best model. When there were two or more equally plausible models with less than 2 units of AIC_c of difference, we applied model averaging among these equivalent models using the *model.avg* function in the *MuMIn* package (Barton 2022).

We conducted pairwise comparisons with Tukey post hoc tests to explore differences in urbanization degree, or years in the case of the mean distance to landfill and nest density statistical analysis. We report the results of the post-hoc analysis only when the analysis of variance (ANOVA) tests used first were significant.

Collinearity was evaluated using variance inflation factor (VIF) statistics and it was acceptable in all of the models (VIF < 3). All statical analysis were performed with R version 4.1.2 (R Core Team 2020).

RESULTS

The mean ± SE distance of occupied nests to the nearest landfill was 17.51 ± 0.89 km in 1984, 15.10 ± 0.31 km in 2004, and 14.06 ± 0.22 km in 2021. On average, nests were significantly closer to the landfills in 2021 than in 2004 (Tukey HSD test, estimate ± SE = 2.42 ± 0.81, *T*-student = 3.45, P = 0.007) and 1984 (Tukey HSD test, estimate ± SE = 3.45 ± 0.78, *T*-student = 4.44, $P < 0.001$). Similarly, we found that nests were closer to landfills in 2004 than in 1984 (Tukey HSD test, estimate ± SE = 1.03 ± 0.39, *T*-student = 1.03, $P = 0.02$).

According to the model selection the following variables predicted the nest occupation in 1984: a low percentage of agricultural areas, arable lands, and forest areas; more than 25% coverage of pastures & dehesas; and proximity to water bodies (Table 1). The probability of nesting in 1984 in rural areas was significantly higher than in urban areas (Tukey HSD test, estimate ± SE = 1.34 ± 0.55, Wald = 2.43, $P = 0.04$) (Figure 3).

Landfill distance negatively affected nest density depending on the year of the census (Table 2). The nest density increased near landfills in 2004 and 2021 compared to 1984 (both Tukey HSD test, $P < 0.001$) (Fig. 4). Moreover, nest density had a negative relationship with the percent coverage of agricultural fields and arable lands, and increased near water bodies (Table 2). In addition, nest density was lower in periurban areas than in rural areas (Tukey HSD test, estimate= –0.52 ± 0.14, Wald = 3.746, $P < 0.001$) independently of the year (Table 2, Figure 5).

Model selection of new nesting sites in 2004 resulted in two equally good models ($AIC_c < 2$) (Supplementary Material Table S1). Selected models include all variables (Supplementary Material Table S1). Both models included agricultural areas, forest areas, landfill distance, pastures & dehesas, degree of urbanization, and distance to water bodies (Table 3). In 2004, new nesting sites were closer to landfills and in areas with a higher percentage of: agricultural coverage, forest, and pastures & dehesas, and in closer proximities to water bodies (Table 3, Figure 6). Moreover, new nesting sites were ubicated in a higher proportion in urban areas than in rural areas (Tukey HSD test, estimate = –1.12 ± 0.39, Wald = –2.90, $P = 0.011$) (Figure 6).

In 2021, new nesting sites were significantly further away from landfills and water bodies than abandoned nesting sites, and in areas with a higher proportion of arable lands (Table 3, Figure 6). In the period between 1984 and 2004, abandoned nesting sites (2004) increased near areas with a higher percentage of agricultural land, but this relationship was not found for any of the other variables ($p > 0.05$) (Table 3). However, the number of abandoned nesting sites (2021) during the period of 2004–2021 increased with the distance to landfills (Figure 7). Abandoned nesting sites in this period also increased with the percentage of arable lands, forest, and in urban areas (Table 3, Figure 7).

DISCUSSION

This study suggested that the increase of the breeding population of White Storks was associated with the exploitation of landfills as feeding resources, which has also been found in other species, such as gulls and vultures (Duhem et al. 2008, Tauler-Ametller et al. 2017). The distribution of the expanding breeding population has not been random. After landfill exploitation began, pairs gradually nested near these facilities in spite of being poor-quality habitat (i.e., low availability and abundance of prey) such as agricultural fields, forests or urban areas.

As it has been observed in other species such as gulls and vultures (Belant et al. 1998, Monsarrat et al. 2013, Tauler-Ametller et al. 2017), White Storks are attracted by the large amount of organic waste and the constant renewal of resources in landfills. These almost unlimited anthropogenic food sources reduce the dependency on prey availability (Payo-Payo et al. 2015, Evans and Gawlik 2020), therefore reducing intraspecific competition and conflicts over feeding resources (Restani et al. 2001, Corman et al. 2016). White Storks not only breed near landfills, but they are also more aggregated around these facilities since 1984 (Figure 2). This situation may favor aggregability that often results in colony formation in the Mediterranean region (Carrascal et al. 1990, Massemin-Challet et al. 2006, Djerdali et al. 2016b). Thus, the probability and number of interactions between individuals are exponentially elevated in a colony as well as in places where food is concentrated in a limited area (i.e., landfills or vulture restaurants). Since pathogens proliferate in landfills and aggregation of individuals enhances infectious disease transmission (Bradley and Altizer 2007, Moyers et al. 2018), the proliferation of potential avian species associated with these facilities raises public health issues (Hatch 1996, Navarro et al. 2019, Höfle et al. 2020). The increase of nesting density in periurban and urban areas in the last 4 decades (Figure 5) also could result in greater wildlife–human conflicts, such as nuisance by noise or dirtiness, and damage to buildings and other human structures (Belant 1997, Vergara et al. 2007, Zbyryt et al. 2021). This situation may change the human perception of this species from an iconic bird to a pest species (Belant 1997, Belant et al. 1998).

The high nest density and low occurence of abandoned nesting sites in rural areas indicate that typically White Storks avoid areas with high human densities and a high percentage of land cover transformation to impervious ground. This may be explained by the higher physiological stress associated with an elevated degree of urbanization and human population density (Ellenberg et al. 2007, Strasser and Heath 2013) and risks for nestling survival such as collision with electricity poles, nesting deterrents, or nest removal which are abundant in urban areas (Garrido and Fernandéz-Cruz 2003, Moreira et al. 2018, Marcelino et al. 2021). Moreover, the highest nest densities in rural areas were possibly associated with proximity to landfills in 2004 and 2021, or possibly because of farms and zoos in 1984, where human food supply or the presence of cows increase feeding rates (Tryjanowski et al. 2005, Massemin-Challet et al. 2006, Hilgartner et al. 2014, Zbyryt et al. 2020). In contrast, two opposite forces underlie the wide range of nest density that we found in urban areas. Breeding pairs avoid urban areas because of the human disturbance to the nestlings and the scarcity of natural feeding resources (Strasser and Heath 2013, Seress et al. 2020). As long as landfills allow birds to occupy nests in urban areas, but limited to certain sites such as the highest structures (i.e., churches, antennas, electricity poles), nest density will increase primarily at particular buildings or sites (Bialas et al. 2020).

In accord with previous studies, we found this species preferentially breeds in areas with pastures and dehesas, near water bodies and in rural areas while avoiding agricultural fields, arable lands, forests and urban areas (Alonso et al. 1991, Carrascal et al. 1993, Zurell et al. 2018, Hmamouchi et al. 2020a). However, these preferences changed over the last four decades as shown through our analysis of new and abandoned nesting sites. In the period between 1984 and 2004, birds primarily expanded to areas close to landfills, independently of the habitat quality, because it was not related to any land cover variable. Besides landfill distance, it is possible that several strategies converged to determine the occupation of new nesting sites in 2004. On the one hand, the astonishing population increase in this period led to a process of expansion to high-quality areas, with a high percentage of pastures and dehesas and near water bodies, while breeding pairs disappeared from areas with a high percentage of agricultural usage (Figure 6). On the other hand, inexperienced young pairs might have been forced to breed in poor-quality areas in this expanding population, which resulted in a high percentage of occupied nests in other agricultural fields, forests, and in urban areas (Newton 1992, Vergara and Aguirre 2006). Future research should explore this question further.

The expansion process continued in the period between 2004 and 2021. After the occupation of the most favorable areas near landfills, it seems that new nesting sites were located in equivalent or suboptimal quality patches in this period (Table 3, Figure 2). These areas farther from landfills and water bodies with a high percentage of arable lands are possibly being utilized by young or low-quality individuals (Newton 1992, Vergara and Aguirre 2006). Arable lands may constitute an alternative and suboptimal feeding area in recent decades due to habitat degradation in Europe, which has been supported in previous studies (Orłowski et al. 2019, Bialas et al. 2021). In agreement with these previous studies (Orłowski et al. 2019, Bialas et al. 2021), we found that birds abandoned suboptimal areas, with a higher percentage of arable lands, forests, urban areas, and areas far away from landfills in 2021, showing the poor-quality of these areas to pairs nested there in 2004.

Nevertheless, our findings show that the new food resource at landfills allows White Storks to colonize new and previously unsuitable areas. Previous research has indicated that the breeding success of these pairs is lower (López-García et al. in press, Bialas et al. 2021), and the extra food from landfills primarily increases the density of breeding pairs in the surrounding areas.

In conclusion, the use of landfills by White Storks has played an important role in the distribution of this species in the Community of Madrid. The reduction of organic waste because of the closure of current landfills following the European directive (Directive 1999/31/EC and 2018/850/EC) provides an opportunity to reduce nearby nest density, thus reducing potential wildlife-human conflicts (Belant 1997) as well as reducing potential risks to wildlife associated with an intensive use of landfills (Plaza and Lambertucci 2018, López-García et al. 2021). However, this should be a gradual process and managers must evaluate the nearby habitat quality and possibly support expanding suitable habitat in the region. Otherwise, White Storks might in future decades be in the same critical situation as they were in 1950–1980.

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Ethics statement
All methods and procedures adhere to Complutense University Guidelines and we have permits for fieldwork from the Dirección General de Biodiversidad y Recursos Naturales Área de Conservación de Flora y Fauna (Consejería de Medio Ambiente, Vivienda y Agricultura).

Conflict of interest statement
The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability
Data are available in the Supplementary Material.

LITERATURE CITED

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Figure 1. Map of Mediterranean area with our study region (Madrid) highlighted in black.

Figure 2. Changes in nest density (nests km^{-2}) and distribution of the breeding population of White Storks in the province of Madrid. Location of landfills is marked by white triangles. Grid resolution is 1 km^2.

Figure 3. Probability of nest occupation in 1984 in relation to the percentage of (**A**) agricultural fields, (**B**) arable lands, (**C**) forest, (**D**) pastures and dehesas, (**E**) degree of urbanization, and (**F**) distance to water bodies. Shading is the 95% confidence intervals. In the degree of urbanization (**E**), the whiskers show the 95% CI and the asterisk (*) designates the groups with significant differences.

Figure 4. Effect of landfill distance on nest density. Nest density is higher in 2021 and 2004 than in 1984, before White Storks began utilizing landfills. Shaded areas represent the 95% confidence intervals.

Figure 5. Differences in nest density (nests km^{-2}) as a function of degree of urbanization (with 95% confidence intervals) independently of the year. Significant differences are marked with asterisks (*).

Figure 6. Relationship between the probability of new nesting sites in 2004 and 2021 and the percentage of other agricultural fields (Agri), percentage of arable lands (Arable), percentage of forest (Forest), percentage of pastures & dehesas (Pastures & dehesas), distance to the nearest landfill (Landfill distance), degree of urbanization, and distance to water bodies. In general, the probability of new nesting sites was higher in 2004 than in 2021. Shaded areas show the 95% confidence intervals. In the degree of urbanization plot, whiskers show the 95% CI and asterisks (*) represent significant differences. We only show significant differences.

Figure 7. Relationship between abandoned nesting sites in 2021 and the percentage of other (**A**) arable lands, (**B**) percentage of forest, (**C**) distance to the nearest landfill, and (**D**) degree of urbanization. Shaded areas represent the 95% confidence intervals. Asterisks (*) indicate significant differences.

Table 1. Output from the GLM for probability of nest occupation before White Storks began to use landfills (1984). Values are provided for the following predictors: percentage of other agricultural fields (Agri), arable lands (Arable), forest (Forest), pasture and dehesas (PD), degree of urbanization (Rural, Periurban or Urban), and distance to water bodies (Water). Estimates (Est), standard errors (SE) and 95% confidence intervals (CIs) were calculated by model averaging for models with a ΔAIC < 2.

	Est	**SE**	**Wald**	***p*-value**	**2.5% CI**	**97.5% CI**
Agri	−1.49	0.47	3.19	0.001***	−2.41	−0.58
Arable	−0.91	0.45	2.01	0.045*	−1.79	−0.02
Forest	−3.34	0.66	5.08	<0.001***	−4.63	−2.05
PD	2.46	1.06	2.34	0.019*	0.40	4.55
PD^2	−2.61	0.97	2.70	0.007**	−4.50	−0.72
Rural	0.65	0.33	1.99	0.046*	0.01	1.30
Periurban	0.30	0.23	1.30	0.195	−0.15	0.75
Water	−1.87	0.51	3.67	<0.001***	−2.87	−0.87

Note: Significance level: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Table 2. Nest density relationship to the landfill distance, controlling by year (as a factor), percentage of other agricultural fields (Agri), arable lands (Arable), forest (Forest), pasture and dehesas (PD), degree of urbanization (Rural, Periurban, or Urban), and distance to water bodies (Water). Estimates (Est), standard errors (SE) and 95% confidence intervals (CIs) were calculated by model averaging of models with a ΔAIC < 2.

	Est	SE	Wald	*p* value	2.5% CI	97.5% CI
Agri	−0.01	0.01	2.623	0.009**	−0.02	−0.03
Arable	−0.01	0.01	2.12	0.035*	−0.02	−0.01
Landfill	−0.07	0.01	6.10	<0.001***	−0.01	−0.05
Landfill^2	0.03	0.01	2.67	0.008**	0.01	0.05
PD	0.01	0.01	1.18	0.237	−0.01	0.02
Rural	0.01	0.01	3.06	0.002**	0.01	0.02
Periurban	−0.01	0.01	2.94	0.003**	−0.02	−0.01
Water	−0.02	0.01	4.45	<0.001***	−0.03	−0.01
1984	−0.04	0.01	3.10	0.002**	−0.07	−0.02
2004	0.01	0.01	0.85	0.394	−0.01	0.04
Arable*1984	0.01	0.01	1.40	0.161	−0.01	0.02
Arable*2004	0.01	0.01	0.66	0.513	−0.01	0.02
Landfill*1984	0.02	0.01	1.73	0.083	−0.01	0.04
Landfill*2004	−0.02	0.01	2.20	0.028**	−0.04	−0.01
PD*1984	0.01	0.01	0.48	0.631	−0.01	0.02
PD*2004	0.01	0.01	1.86	0.063	−0.01	0.03
Forest	0.01	0.01	0.91	0.365	−0.01	0.01

Note: Significance level: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Table 3. Probability of occurrence of new nesting sites and abandoned nesting sites. Values are provided for the following predictors: percentage of other agricultural fields (Agri), arable lands (Arable), forest (Forest), pasture and dehesas (PD), Landfill distance (Landfill), degree of urbanization (Rural, Periurban or Urban), and distance to water bodies (Water). Estimates (Est), standard error (SE) and 95% confidence intervals (CIs) were calculated by model averaging of models with a ΔAIC < 2.

	Est	SE	Wald	*p* value	2.5% CI	97.5% CI
New nesting sites 2004						
Agri	0.82	0.34	2.40	0.027*	0.15	1.50
Arable	0.06	0.20	0.31	0.758	−0.43	0.83
Forest	1.03	0.27	3.79	<0.001***	0.50	1.56
PD	1.02	0.34	2.96	0.003**	0.34	1.69
Landfill	−0.10	0.26	3.93	<0.001***	−1.50	−0.50
Rural	−1.03	0.34	3.04	0.002**	−1.69	−0.37
Periurban	0.01	0.26	0.02	0.986	−0.50	0.51
Water	−1.10	0.29	3.75	<0.001***	−1.68	−0.52
New nesting sites 2021						
Agri	−0.02	0.06	0.36	0.720	−0.27	0.09
Arable	0.65	0.10	6.39	<0.001***	0.45	0.85
Forest	0.01	0.04	0.09	0.930	−0.17	0.21
PD	−0.01	0.05	0.16	0.875	−0.28	0.19
Landfill	0.29	0.10	2.92	0.004**	0.10	0.49
Rural	0.15	0.11	1.38	0.169	−0.07	0.37
Periurban	0.84	0.10	8.75	<0.001***	0.65	1.03
Water	1.59	0.12	13.22	<0.001***	1.36	1.83
Abandoned nesting sites 2004						
Agri	1.24	0.46	2.71	0.007**	0.34	2.13
Arable	1.20	0.92	1.30	0.195	−0.15	3.05
Forest	−0.83	0.92	0.89	0.371	−2.97	0.37
PD	0.15	0.55	0.27	0.787	−1.26	2.82
Landfill	0.58	0.75	0.77	0.442	−0.34	2.48
Water	0.05	0.28	0.18	0.857	−0.95	1.78
Abandoned nesting sites 2021						
Agri	0.22	0.28	0.78	0.438	−0.08	0.94
Arable	2.76	0.47	5.81	<0.001***	1.83	3.69
Forest	0.84	0.28	3.00	0.003**	0.29	1.39
PD	0.57	0.66	0.87	0.385	−0.24	2.13
Landfill	0.88	0.33	2.64	0.008**	0.23	1.53
Rural	0.50	0.49	1.01	0.314	−0.47	1.47
Periurban	−2.16	0.50	4.33	<0.001***	−3.14	−1.18
Water	−0.38	0.43	0.89	0.374	−1.39	0.13

Note: significance level: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Figure 1

Figure 2

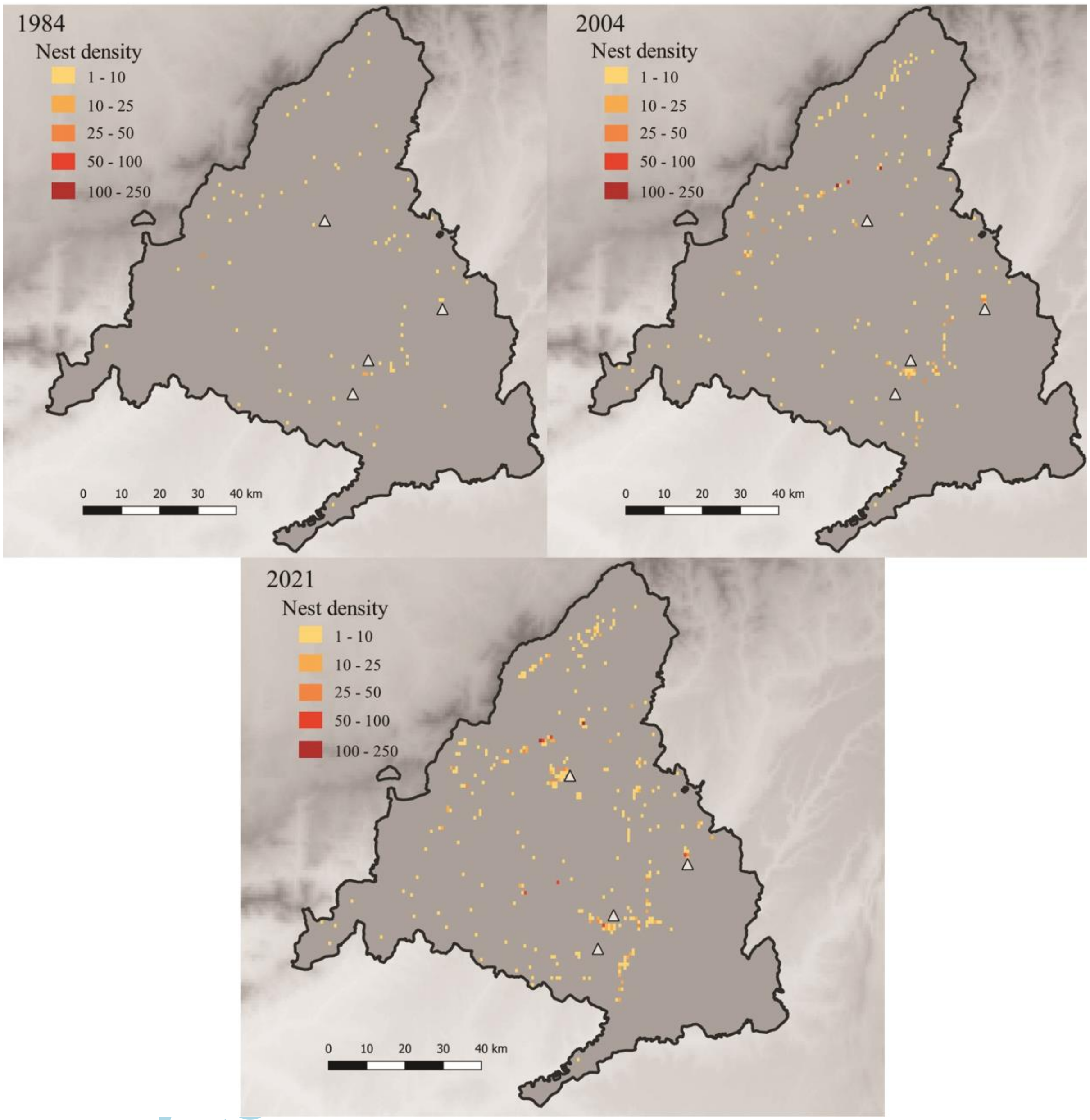

1984
Nest density
1 - 10
10 - 25
25 - 50
50 - 100
100 - 250
0 10 20 30 40 km
2004
Nest density
1 - 10
10 - 25
25 - 50
50 - 100
100 - 250
0 10 20 30 40 km
2021
Nest density
1 - 10
10 - 25
25 - 50
50 - 100
100 - 250
0 10 20 30 40 km

Figure 3

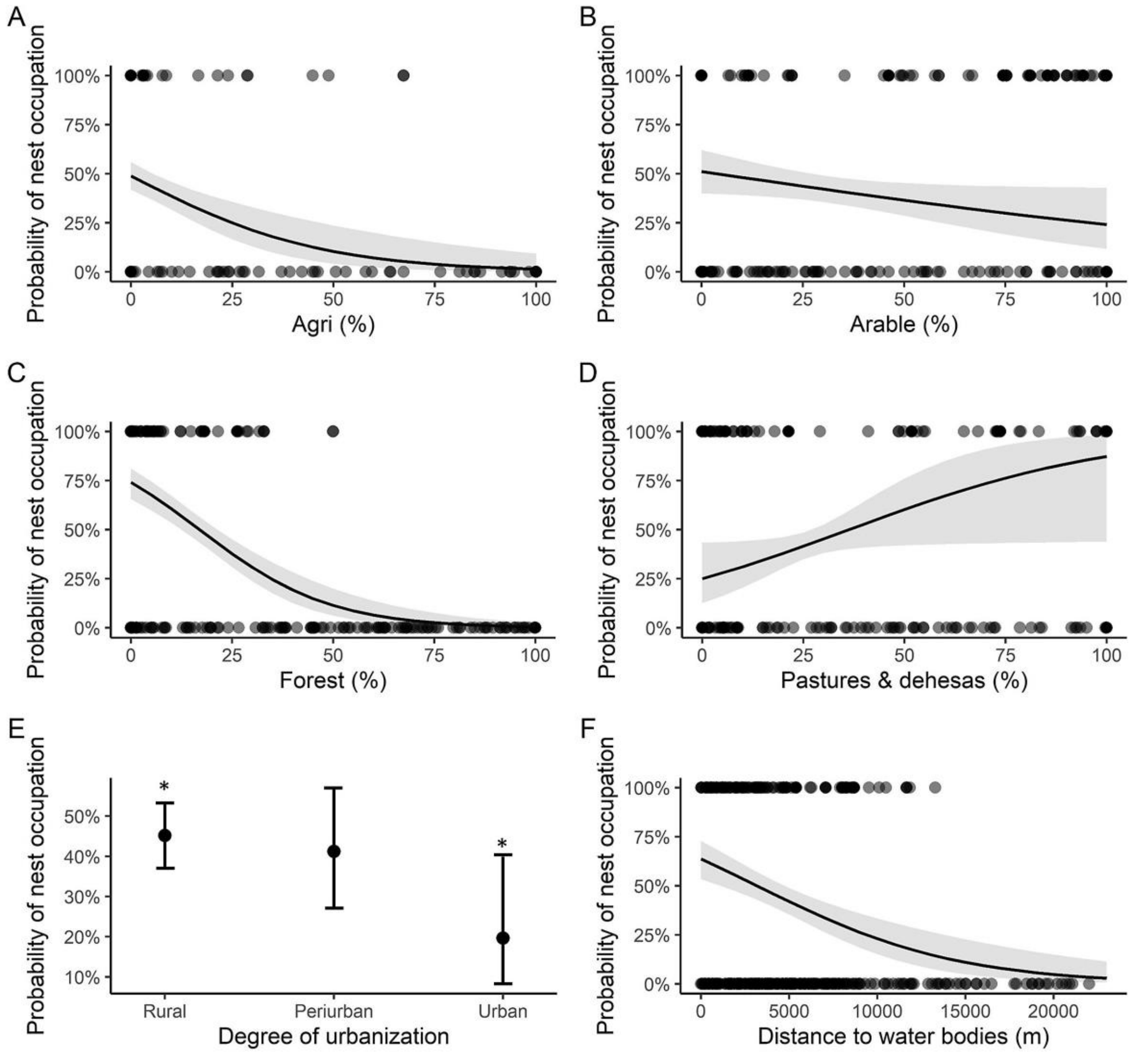

A
Probability of nest occupation
100%
75%
50%
25%
0%
0
25
50
75
100
Agri (%)
B
Probability of nest occupation
Arable (%)
C
Probability of nest occupation
Forest (%)
D
Probability of nest occupation
Pastures & dehesas (%)
E
Probability of nest occupation
50%
40%
30%
20%
10%
*
Rural
Periurban
Urban
Degree of urbanization
F
Probability of nest occupation
0
5000
10000
15000
20000
Distance to water bodies (m)

Figure 4

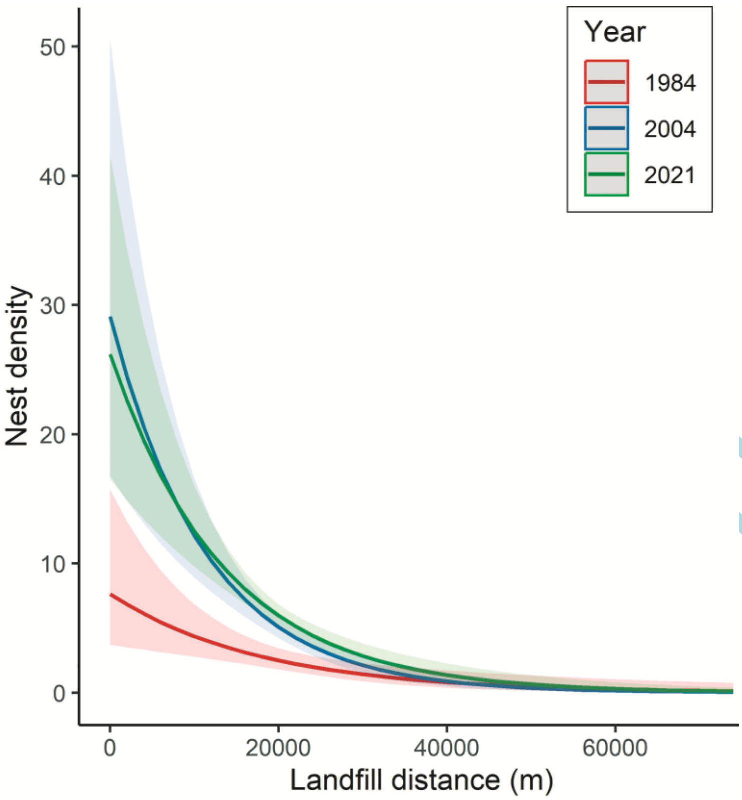
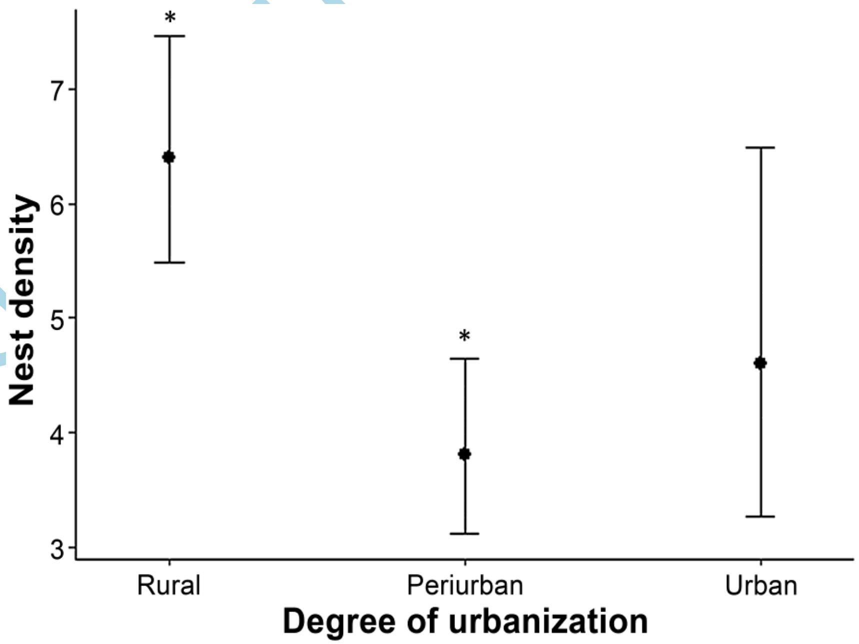
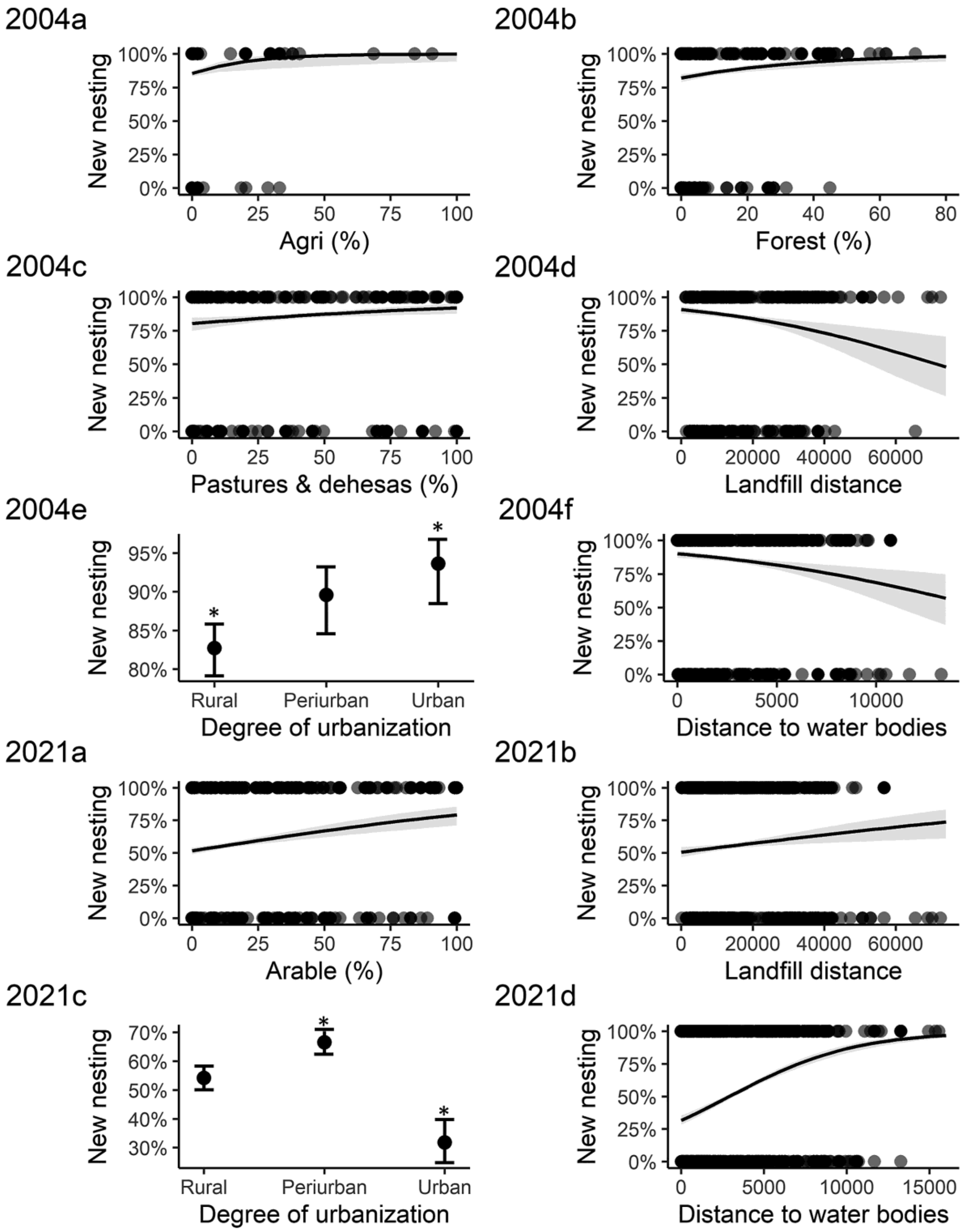

Year
1984
2004
2021
Nest density
50
40
30
20
10
0
0
20000
40000
60000
Landfill distance (m)

Figure 5



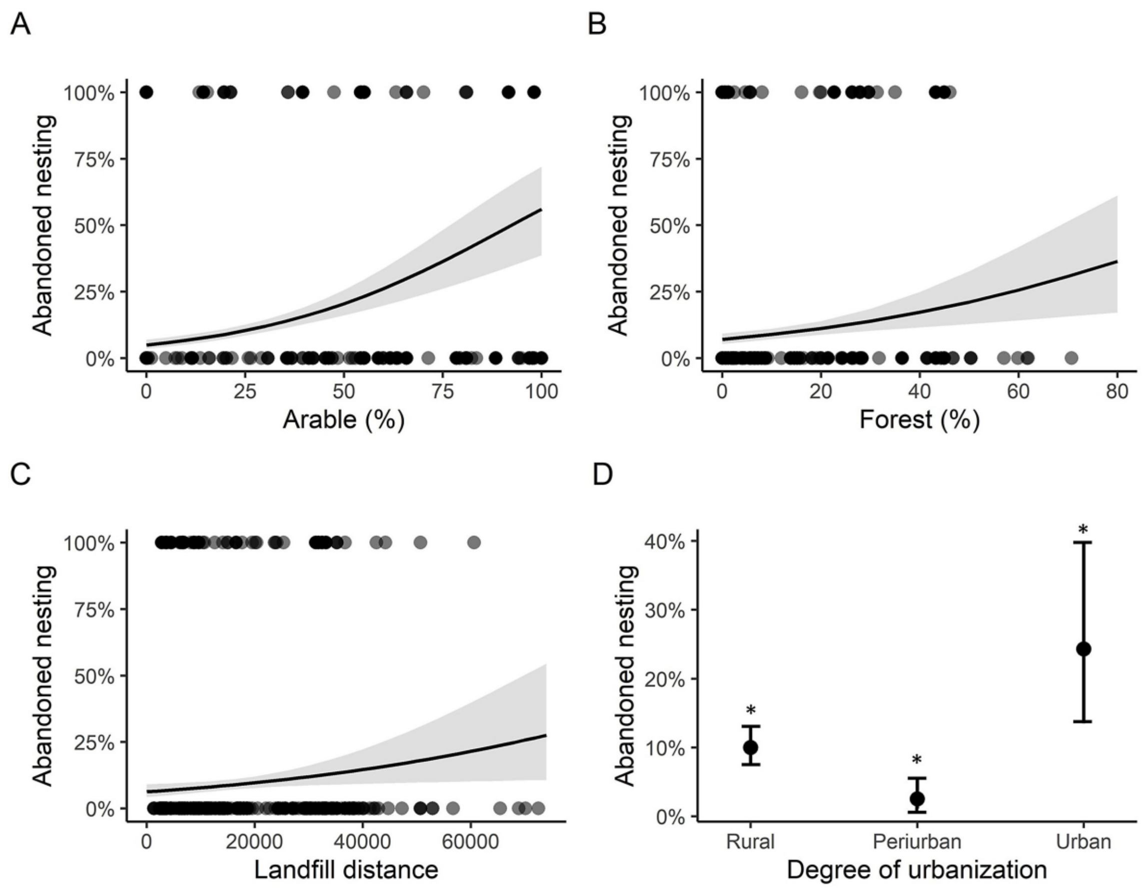
*
*
7
6
5
4
3
Nest density
Rural
Periurban
Urban
Degree of urbanization

Figure 6



2004a
New nesting
100%
75%
50%
25%
0%
0 25 50 75 100
Agri (%)
2004b
New nesting
0 20 40 60 80
Forest (%)
2004c
New nesting
0 25 50 75 100
Pastures & dehesas (%)
2004d
New nesting
0 20000 40000 60000
Landfill distance
2004e
New nesting
95%
90%
85%
80%
Rural Periurban Urban
Degree of urbanization
2004f
New nesting
0 5000 10000
Distance to water bodies
2021a
New nesting
0 25 50 75 100
Arable (%)
2021b
New nesting
0 20000 40000 60000
Landfill distance
2021c
New nesting
70%
60%
50%
40%
30%
Rural Periurban Urban
Degree of urbanization
2021d
New nesting
0 5000 10000 15000
Distance to water bodies

Figure 7


A
100%
75%
50%
25%
0%
Abandoned nesting
0
25
50
75
100
Arable (%)
B
Abandoned nesting
0
20
40
60
80
Forest (%)
C
Abandoned nesting
0
20000
40000
60000
Landfill distance
D
40%
30%
20%
10%
0%
Abandoned nesting
*
Rural
Periurban
Urban
Degree of urbanization