RESEARCH ARTICLE

Niche shifts over spread of a biological invasion: Unveiling the role of changing habitat preference and density-dependence

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Abstract

Aim: Anticipating the ultimate fraction of a landscape that might be susceptible to invasion is challenging as several species are able to expand the range of environmental conditions used over invasion. Despite its relevance, the more proximate processes underlying observed shifts are not sufficiently understood. Habitat selection theory predicts that as population density increases, individuals start using sub-optimal resources to compensate for the limitation of the preferred ones. However, niche shifts might also occur as result of changes in habitat preferences over time. Here, we tested these alternative hypotheses by investigating nesting resource use and selection over a biological invasion and the relative effect of density-dependence on such patterns.

Location: Barcelona, Spain.

Methods: We take advantage of a large dataset recording the occurrence of the invasive monk Parakeet, *Myiopsitta monachus* in Barcelona in the period 1975–2015. We apply generalized linear models to analyse changes in nesting habitat preferences and its interactive effect with conspecific presence.

Results: Temporal changes in nesting habitat use occurred. Palm species were the most commonly used nesting substrate since the beginning of the invasion but the diversity and frequency of use of other nesting substrates increased over time. Changes in nesting substrate use were consistent with a change in habitat selection, when accounting for habitat availability. Although a general role of conspecific aggregation on occupation patterns was found, it was mostly additive. That is, shifts in nesting substrate did not structure in relation to conspecific distribution.

Conclusions: Shifts in nesting resource selection can occur during the spread stage of biological invasions, probably related to innovation and learning, rather than to optimal habitat selection. These shifts present a significant challenge for forecasting efforts and management. However, changes do not happen rapidly over time, highlighting that there is a management opportunity window before significant shifts occur.

Zulema Núñez-Tobajas and Laura Cardador contributed equally to this study.

1 | INTRODUCTION

The anthropogenic transport of species beyond their native areas has accelerated the introduction, and subsequent establishment and spread of alien species worldwide (Dyer et al., 2017; Turbelin et al., 2017). The numbers of alien species have increased in the majority of taxa over time (Seebens et al., 2017), and future global spread is expected (Seebens et al., 2021). Awareness of the ecological and socioeconomic impacts of alien species (Blackburn et al., 2014; Evans et al., 2020) has generated much interest in understanding the factors leading to invasion success, as not all species are capable of breaking the barriers of different stages of the invasion process (i.e. transport, introduction, establishment and spread [Blackburn et al., 2011]). A great body of research has focused on the first stages of the invasion process (e.g. Case, 1996; Cassey et al., 2004; Lincoln et al., 2015; Redding et al., 2019). Comparatively, the patterns and mechanisms of spread are less well understood (Pietrek & González-Roglich, 2015).

Environmental characteristics of the recipient environment have been proved to be a fundamental factor explaining establishment success (Redding et al., 2019) and also proposed as a key environmental factor for spread (Abellán et al., 2017; Cardador et al., 2022; Lovell et al., 2021). In particular, similarity between environmental characteristics of the recipient and previously occupied areas has been demonstrated to be relevant (Abellán et al., 2017; Cardador et al., 2022). However, predicting the ultimate fraction of the landscape that might be susceptible to invasion based on environmental similarity continues to be challenging as increasing evidence suggest that several species are able to expand the range of environmental conditions used over the course of invasion (e.g. Cardador & Blackburn, 2020; Mori et al., 2020). Despite its relevance, the more proximate processes underlying observed shifts are not sufficiently understood.

Habitat selection theory predicts that as population density increases and resources become limited, individuals become less selective in their habitat use to compensate for the limitation in the availability of the preferred resources (Avgar et al., 2020; Rosenzweig, 1991). In this case, when population size increases, the niche breadth of the population is expected to increase as individuals start using poorer-quality resources. Population density might also favour the rise of dispersal due to competition (density-dependent dispersal) (Matthysen, 2005), changing the availability of resources over time as the geographic area occupied by the population increases.

However, niche shifts over invasions might also occur as result of changes in habitat preferences over time for all (or part) of the individuals in the alien population, particularly in depauperate assemblages such as those from cities (niche expansion hypothesis) (Costa et al., 2008). This might increase the capacity of invasion of the species and the total fraction of habitat that could be invaded (Hernández-Brito et al., 2022). Thus, while much research has

focused upon the idea that habitat selection allows alien individuals to select those habitats or resources that better fit their phenotype when they arrive to a new location (Sol & Maspons, 2016); it is increasingly recognized that in new environments, individuals can initially prefer or avoid particular resources based on formerly used environmental cues that are not necessarily linked to the availability of key limiting resources in these new environments (Hale & Swearer, 2016), or might need time to learn how to use new resources effectively (Sol et al., 2002; Sol & Maspons, 2016).

In this study, we take advantage of a large dataset recording the occurrence of the invasive monk parakeet, *Myiopsitta monachus* (Psittacidae family) in the city of Barcelona, which has increased from six breeding pairs in 1981 (Batllori & Nos, 1985) to >2000 breeding pairs in 2015 (Senar et al., 2017), to investigate the spatiotemporal patterns of habitat use and selection during a biological invasion and the factors influencing it. Our analysis focus on changes in the selection of different tree substrates for nesting. In early stages of the invasion, the Barcelona's monk parakeet population showed a great preference for nesting in palm trees (Sol et al., 1997). Here, we investigated whether the patterns of nesting habitat use has been maintained over time or there has been an increase in the diversity of nesting substrates used over time, as expected based on habitat selection theory (Rosenzweig, 1991) and the niche expansion hypothesis (Costa et al., 2008). Since changes in nesting tree use were observed, we subsequently tested whether these changes were the result of changes in habitat availability over time or changes in habitat selection. Finally, since changes in nesting tree selection were observed, we tested where these changes were more likely in relation to conspecific presence. If changes in nesting resource selection is the result of optimal habitat selection, we predicted the use of new resources to occur preferentially in the more populated patches, where occupation of preferential resources might not be so beneficial because of density dependent effects and competence (Avgar et al., 2020). In this case, a reduction in population growth rates over time would be also expected, as the general quality of available patches decrease due to competence.

2 | METHODS

2.1 | Study area and species

The monk parakeet is one of the most widespread invasive bird species in the world (Calzada Preston & Pruett-Jones, 2021), with potential impacts on other species (e.g. spread of parasites, Ancillotto et al., 2018) and human commodities and infrastructures (e.g. damage to crops or electric poles) (Castro et al., 2022; Menchetti & Mori, 2014; Senar et al., 2016). The species is originally from South America (Del Hoyo et al., 1997). It breeds in colonies and is the only

psittaciform able to build its own nests (with sticks and branches, [Eberhard, 1998]) on different nesting substrates (different tree species and human infrastructures [Di Santo et al., 2017; Reed et al., 2014]). A single nest can contain different chambers each occupied by a different pair or kin groups (Eberhard, 1998). As with other psittaciformes (parrots) the origin of most of their established alien populations worldwide are related to the global pet trade (Cardador et al., 2017). In Spain, the monk parakeet is widely distributed and one of the most abundant alien species (Ascensáo et al., 2021; Cardador et al., 2022; Muñoz & Real, 2006). Its first documented breeding was in 1975 in Ciutadella Park, Barcelona (Batllori & Nos, 1985). During the past 50 years, the increase in the population in Barcelona has been accompanied by an increase in its geographic range (Figure 1).

2.2 | Data compilation and management

2.2.1 | Abundance and occurrence data

The breeding population of the monk parakeets in the city of Barcelona has been monitored from 1975 (Batllori & Nos, 1985; Domènech et al., 2003), with information on location and substrate of breeding sites systematically compiled later by censuses conducted by the Zoology Museum of Barcelona and Museum of Natural Sciences of Barcelona (MNSB) in 3 years (2001, 2010 and 2015) (Domènech et al., 2003; Molina et al., 2016; Rodríguez-Pastor et al., 2012). We focused the analyses on nesting habitat selection in these three censuses (2001, 2010, 2015), which consisted in systematical inspection of all areas in the city of Barcelona where monk parakeets might potentially build nests between December and February, including all parks, gardens and squares, as well as streets with trees (Domènech et al., 2003; Rodríguez-Pastor et al., 2012). The location of occupied nesting sites and substrate was incorporated to a Geographic Information System (QGIS 3.22.1. program) using a UTM 31N projection (Datum ETRS89) (Figure 1). All occupied nesting sites ($n = 2258$) were used for variable compilation, and thus thinned to a 20-m resolution for analyses to avoid pseudoreplication (i.e. only one nesting site among duplicated nesting sites within 20-m circular radius were randomly retained). A total of 1269 nesting sites at the 20-m resolution were available for habitat use and selection analyses.

2.2.2 | Environmental layers

We compiled information on habitat variables likely to affect nesting habitat selection of the species (Rodríguez-Pastor et al., 2012;
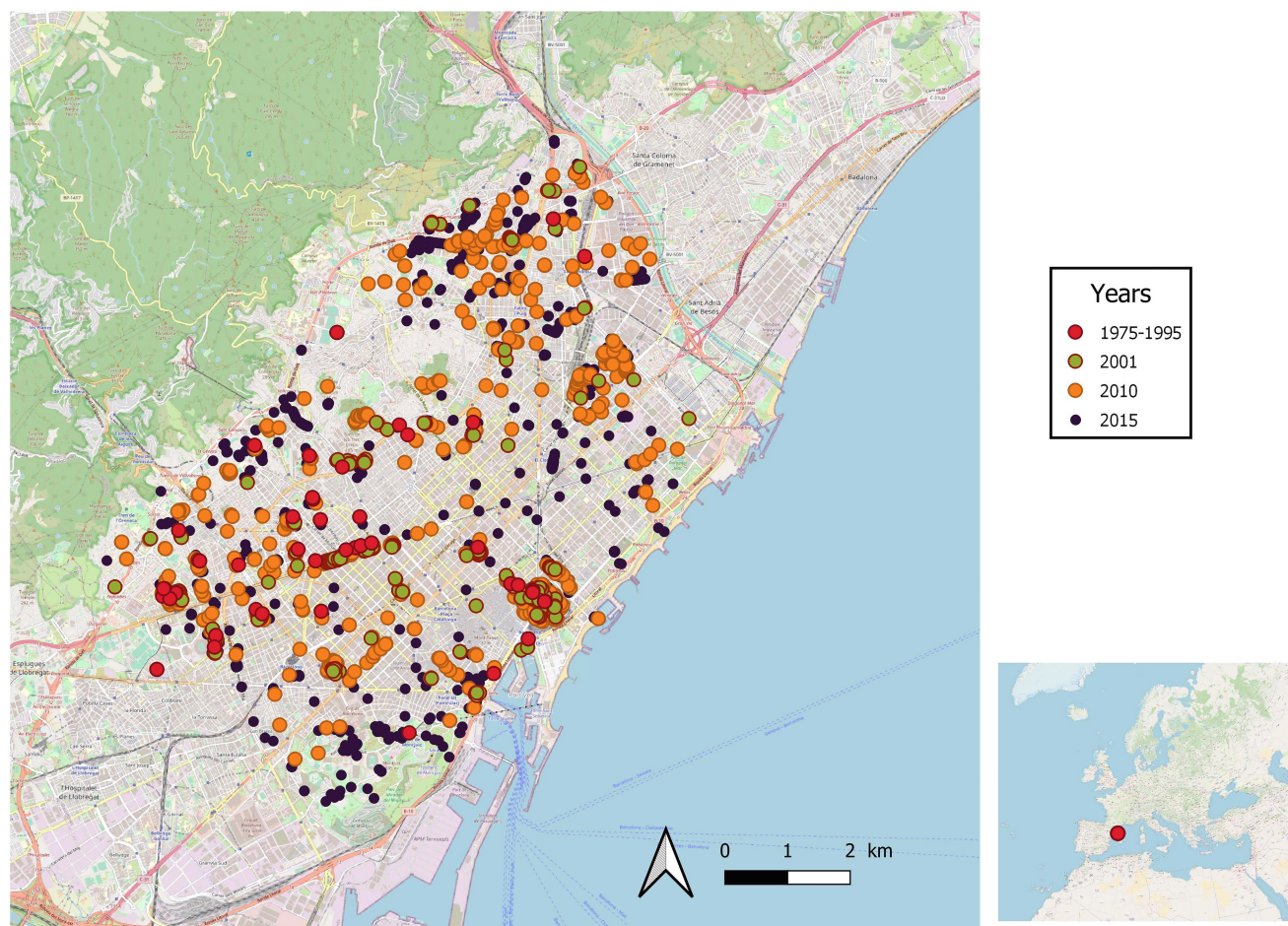

FIGURE 1 Map showing the location and distribution of the monk parakeet population in the city of Barcelona from 1975 to 2015.

Sol et al., 1997) for each occupied and available nesting site. We considered as available nesting sites all the trees present in the city of Barcelona. Compiled habitat variables included (i) nesting substrate (i.e. the tree type) and two variables describing the availability of foraging habitat around each nesting site, namely (ii) minimum Euclidean distance to a green area (dgreen) and (iii) the percentage of green areas in a 200-m radius around the nesting site (green200). This radius (*r*) was calculated on the basis of the formula $r = (A/\pi)^{1/2}$, where the area (A) is the mean kernel home-range size of the species, 12.4 Ha (Senar et al., 2021). The data on available trees were obtained from the official website of the Barcelona City Council updated in 2022 (datasets: 'Arbrat dels parcs de la ciutat de Barcelona', 'Arbrat de zona de la ciutat de Barcelona' and 'Arbrat viari de la ciutat de Barcelona' available at https://opendata-ajuntament.barcelona.cat/data/ca/dataset). We defined the nesting substrate according to 4 main categories representing the 3 most commonly used tree types used by the species (that is, palms [*Phoenix* species], pine trees [*Pinus* species] and plane trees [*Platanus* species] as well as a category 'others' including all other tree types not so frequently used [Table S1, each representing ≤5% of total records]). Human infrastructures were only scantily used by the species in the study area (1.9% of total records) and were not considered in habitat selection analyses due to the difficulty in estimating their availability. Data on green areas were obtained from land use maps provided by 'Servei de Parcs i Jardins de l'Ajuntament de Barcelona' (categories 'Verd privat' and 'Parcs i Jardins Urbans').

To assess the effect of conspecific presence on habitat use and selection patterns, we estimated the minimum Euclidean distance from each nesting site to the nearest occupied nesting site in the previous census period (NND) and an aggregation index (aggregation) describing the relative position of a given nesting site within the spatial distribution of the breeding population in the previous census period in a 200-m radius. Aggregation was obtained using the formula $\Sigma\exp(-d_{ij})$ with ($i \neq j$), with *d* representing the distance of a nesting site *i* with respect to a previously occupied nesting site *j*. To calculate these variables in our first study year (2001), we considered as previously occupied sites, the pool of nesting trees recorded in the period 1975–1995. We used this criterion because occupied trees in the population are commonly maintained over time. Information on the number of nests and chambers per tree was not available for all the study periods and, as shown, was thus not taken into account to estimate conspecific aggregation. However, preliminary analyses based on available data for years 2010 and 2015 showed that accounting for the total number of chambers in a previously occupied site *j* (A_j) in calculations ($\Sigma\exp(-d_{ij})\cdot A_j$ with ($i \neq j$)) provided highly correlated results (Pearson correlation coefficient, $r = 0.90$, $n = 1852$).

Prior to analyses, continuous variables were standardized. A correlation matrix among variables was created. The correlation coefficients were lower than 0.55 for all variables and thus all of them were considered for analyses. All spatial and statistical analysis were conducted using the program R Studio 4.2.1 version.

2.3 | Statistical analyses

2.3.1 | Changes in nesting substrate use

We tested for potential temporal changes in the frequency and probability of use of different tree types using a Chi-squared test and a multinomial model with year as covariate using the *multinom* function in R (nnet package). We used palms as the reference category for multinomial models. As not only the type of tree but also the availability of green areas in their surrounding might affect habitat use (Rodríguez-Pastor et al., 2012; Sol et al., 1997), the multinomial model was conducted including the distance and percentage of surrounding green areas as covariates. Model coefficients were considered significant when its 95% confidence interval did not include zero. To describe the diversity of nesting substrates used over time, we used the Shannon's diversity index on the four tree categories considered (pine, palm, plane and 'other' trees).

2.3.2 | The role of habitat selection on changes in nesting substrate use

To assess whether changes in nesting substrate use over time were the result of a change in habitat selection, we conducted logistic generalized linear models (GLM) with a binomial error distribution and a logit-link function. We used random samples of non-occupied available sites of the same sample size as occupied sites in each year to estimate the habitat available for the species. We fitted the nesting substrate, year and their interaction as target predictors in GLMs and occupancy (occupied vs non-occupied) as the dependent variable. Distance and percentage of surrounding green areas were also included as control. According to the resolution of analyses (~20-m), only trees further than 20-m from an occupied tree were considered as available and not occupied. We considered tree availability year-specific, so that trees occupied at time *t* were not considered as available at time *t* + 1. Likewise, we considered as occupied trees at time *t* only the newly occupied trees. To take into account potential effects of non-occupied sites considered, we conducted 100 models—each considering a random sample of non-occupied trees from the total pool of 19,320 ± 271 (mean ± SD) available per year at the 20-m resolution—and averaged model results.

2.3.3 | Conspecific presence and temporal changes in habitat selection

To assess whether temporal changes in nesting substrate selection varied in relation to the presence of conspecifics, we repeated our logistic models while also considering the potential effect of the two variables describing conspecific presence (NND and aggregation) and its interaction with nesting substrate and year (two-fold

and three-fold interactions). Since effects of several variables can be masked or confounded when included together in models, analyses were conducted using a multimodel selection approach (MuMIn package) based on Akaike information criterion (AIC), where all potential combinations of the variables were tested. As with analyses of changes in nesting substrate selection, we repeated the procedure 100 times. For each replicate, we retained all equally probable models (ΔAIC $\leq$ 2) to average results.

We checked for spatial autocorrelation in model residuals using Moran's I tests with 100 permutations using the function 'moran. mc' from package 'spdep' in R. Preliminary analyses showed spatial autocorrelation in model residuals. Thus, we computed a spatial variable to be included in all logistic models using spatial regression with eigenvector spatial filters (spherical model) using the functions 'meigen' and 'esf' from the 'spmoran' package in R. We used the residuals of the saturated logistic model as the vector of explained variables in the computation of the spatial variable.

2.3.4 | Population trends

All available yearly estimates of the number of individuals in the population from 1975 to 2015 were used for analyses on population trends. Estimates for years 2001, 2010 and 2015 were based on the total number of nests and chambers identified in the city of Barcelona in each year, and the mean number of birds estimated to roost per chamber (Domènech et al., 2003; Molina et al., 2016; Rodríguez-Pastor et al., 2012). Data on the numbers of parakeets present during previous years were derived from data reviewed in Domènech et al. (2003). To look for signs of saturation in the Barcelona monk parakeet population we considered four functions to fit the time series', namely: (1) a linear [$y = a + bx$], (2) an exponential [$y = ae^{bx}$] and (3) an asymptotic [$y = a + (b-a)$ $(1 - e^{-x/c})$] increase in individual numbers y with time x, where a, b and c are constants; and (4) a Weibull distribution to take into account a potential decline in recent years. Models were fitted using the 'nls' function from the package 'stats' in R. Models were ranked using the AIC.

3 | RESULTS

3.1 | Habitat use patterns

Significant changes in the frequency of use of different nesting substrates were observed throughout the 3 years of the study ($\chi^2 = 33.05$, df $= 6$, $p < .001$) (Figure 2a). Palm trees were the most frequently used nesting substrate in all years, but its use declined over time in comparison to other substrates (Figure 2a). According to fitted values of multinomial models (controlling for the distance and availability of green areas around trees), the probability of use of palms decreased by approximately 15% over the study period (Figure 2b). The probability of use almost duplicated for the type 'others' (165%) and triplicated for plane trees (323%) (Figure 2b). Accordingly, the diversity of nesting trees used (Shannon's diversity index) increased in subsequent years (from 0.43 in 2001, to 0.79 in 2010 and 0.88 in 2015) as expected based on both habitat selection and niche expansion hypothesis.

3.2 | Habitat selection

According to logistic models, the temporal variation in habitat use was consistent with a change in habitat selection for the category 'others'. A significant interaction between nesting substrate (type 'others') and year was observed (estimate $\pm$ SE $= 0.26 \pm 0.09$, $p < .005$, Table S2). Results were obtained while accounting for the percentage of and distance to green areas and space. Occupation probability increased significantly in relation to the percentage of green areas (estimate $\pm$ SE $= 0.40 \pm 0.10$, $p < .0001$, Table S2).

3.3 | Effect of conspecific presence

According to more complex models, changes in habitat selection patterns throughout time was not significantly affected by spatial distribution of conspecifics (no support for three-way interactions *habitat type*year*conspecific metrics*, AIC weights <0.01, Table S3).
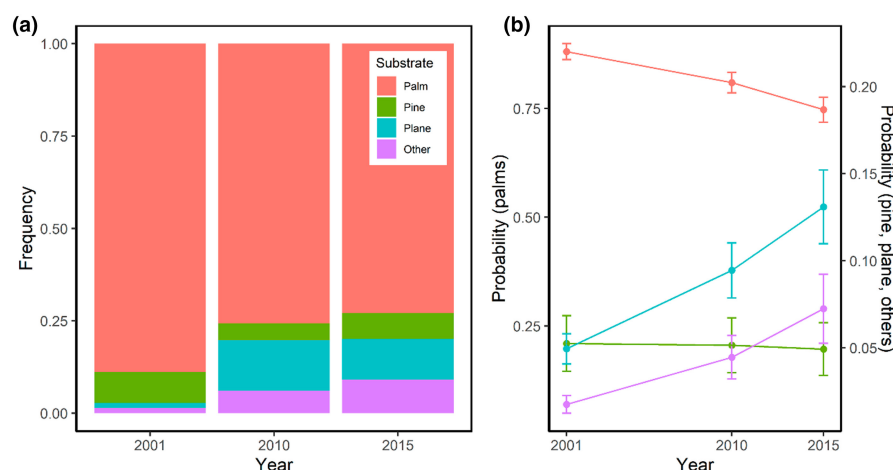

FIGURE 2 Temporal variation in the frequency (a) and modelled probability of use (b) of different nesting substrates by the monk parakeet in the city of Barcelona over the study years. Substrate is the type of tree used for nesting. Colours used for different tree categories in (b) are the same as in (a).

FIGURE 3 Contour plots showing the temporal variation in the occupation probability of different tree types in relation to aggregation to previously occupied sites. Fitted values of occupation probabilities based on model averaged results of logistic regressions are shown. Warmer colours indicate higher probabilities of occupation. Standardized aggregation values are shown.
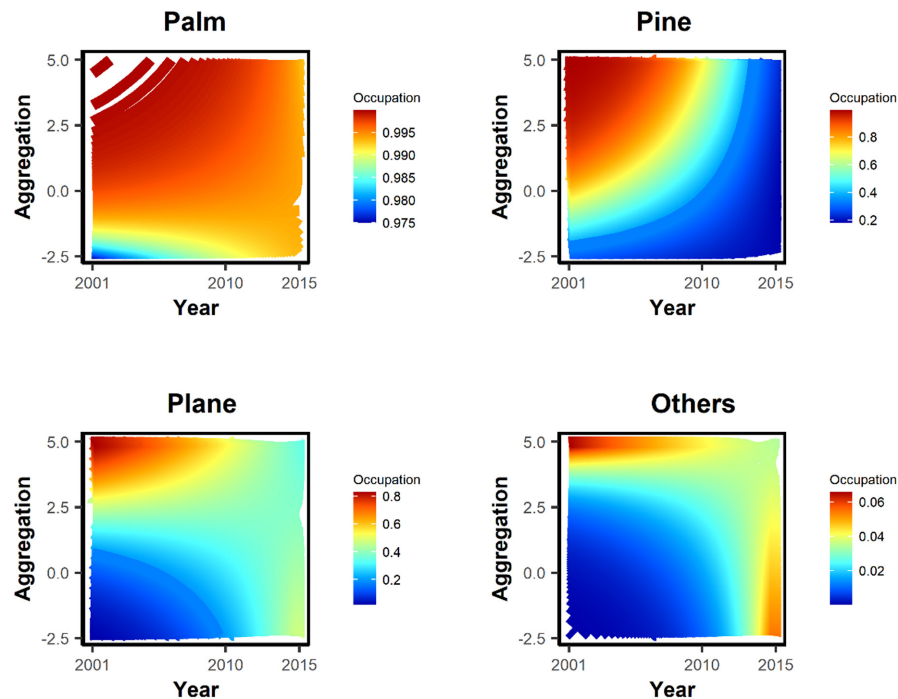
Rather, an additive effect of aggregation on occupation probability, independent of tree type, was observed (estimate $\pm$ SE $= 118 \pm 49$, $p = .02$, Table S3). The probability of new tree occupations increased with aggregation at the beginning of the study period, but this effect was reduced over time (significant interaction *year*aggregation*, estimate $\pm$ SE $= -0.06 \pm 0.02$, $p = .02$, Table S3; Figure 3). The shift in the relationship between aggregation and occupation probability throughout time was more evident for tree types increasingly selected over the study period (type 'others', significant interaction *others*year*, estimate $\pm$ SE $= 0.29 \pm 0.12$, $p = .01$, Table S3; Figure 3). Minimum distance to previously occupied sites only received scant support in models (AIC weight < 0.01) (Table S3).

3.4 | Population trends

The temporal trend of individual numbers between 1975 and 2015 was fitted well by an exponential model (Pearson correlation coefficient between raw and fitted values, $r = 0.99$; Figure 4). The linear (ΔAIC $= 32$), asymptotic (ΔAIC $= 56$) and Weibull (ΔAIC $= 6$) functions fitted the data worst.

4 | DISCUSSION

Understanding the patterns of habitat use and selection over the course of a biological invasion is very relevant from a theoretical and applied point of view. Our analyses, applied to one of the most widespread invasive bird species of the world, highlight that changes in nesting habitat preferences over invasions occur in relation to both the nesting habitat type and social environment of available patches. While palm species have been the most commonly used
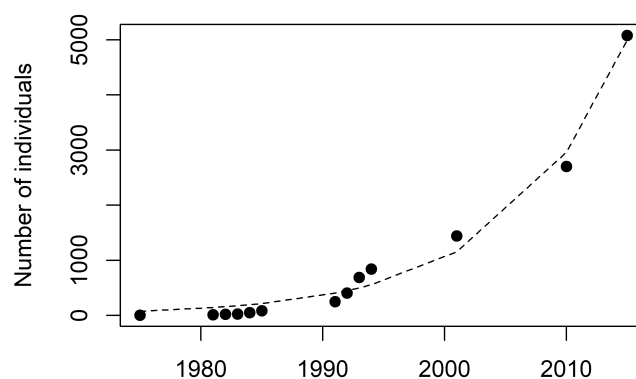

FIGURE 4 Temporal evolution of population numbers. Number of individuals based on raw data (dots) and fitted values according to an exponential model (line) are shown.

nesting substrate since the beginning of the invasion (Rodríguez-Pastor et al., 2012; Sol et al., 1997), the diversity and frequency of use of other nesting substrates has increased over time as expected based on both habitat selection and niche expansion hypotheses. Observed changes are consistent with a change in habitat preferences, which mostly involved increases in the occupation of the less-frequently used resources. Although a general role of conspecific aggregation on occupation patterns was observed, increases in occupation of the less-frequently used resources did not structure in relation to conspecific distribution, suggesting that other time-dependent processes, such as innovation and learning, are involved in the observed niche expansions.

There is indeed increasing evidence that there is a great capacity for innovation and learning in alien species, as well as to rapidly modulate behaviours by innate responses to external stimuli (Sol et al., 2002; Sol & Maspons, 2016). The observed increase in different nesting substrates used throughout time thus

aligns with the adaptive behaviour flexibility hypothesis. This hypothesis proposes that the expression of behavioural flexibility in alien populations decrease from introduction to establishment as result of social learning of successful behavioural variants and increase again during spreading (Wright et al., 2010). New successful variants might in turn be fixed socially, maybe increasing the invasion capacity of the population (Bucher & Aramburú, 2014). In the case of parakeets, for example, it is thus known that chicks born in a given substrate tend to breed in the same substrate when adults (Dawson Pell et al., 2023). Furthermore, according to available data focusing on pine and palm trees, breeding performance of monk parakeet in nesting substrates different to palm trees (the preferred nesting resource) are not significantly lower (Dawson Pell et al., 2023). This suggests that the appeal of a site for nesting might not be necessarily related to habitat quality. Behavioural mechanisms rather than selection pressures might explain the initial avoidance of particular nesting substrates at the beginning of the invasion. In this sense, greater neophilia and exploratory capacity have been described in spreading populations (Chuang & Peterson, 2016; Liebl & Martin, 2014), which might facilitate the occupation of suitable but initially avoided resources.

Temporal processes linked to innovation and learning rather than optimal habitat selection per se thus seem to explain observed expansion of used nesting resources. Nevertheless, a general effect of conspecific aggregation on selection patterns was found, suggesting that density-dependence processes were also relevant. When selecting a site at which to settle, individuals must simultaneously consider the quality of available sites in terms of their environmental conditions and conspecifics. Given that conspecifics are competitors, the addition of every new individual to a patch may decrease its suitability or even prevent its occupation by other individuals (Morris, 2011; Pietrek & González-Roglich, 2015; Platt & Bever, 2009). However, conspecifics can also provide advantages for settlers such as transmission of information relevant to improve foraging ability, predator detection or nest building (Donaldson-Matasci et al., 2013). In our study population, there was a positive influence of conspecific presence on nesting habitat selection at the beginning of the study period, so that the presence of individuals in the patch, attracted other individuals, but this effect diminished over years for all types of nesting trees. The fact that in later years, new occupations were negatively related to conspecific aggregation, and hence was done in unoccupied "new" areas, might be interpreted as a sign of saturation of the most crowded patches. However, our results point out that this did not prevent the population from continuously growing. An alternative explanation for the observed pattern might be that the benefits of breeding in highly populated patches (protection, knowledge transfer), decrease over time as the population become more familiar with the recipient environment.

Prevention is widely recognized as the most favourable approach to prevent the introduction of non-native species. However, once these species become established, the immediate concern for effective management is to determine their future spread. Our findings demonstrate that shifts in resource selection by individuals in a population can occur during the expansion stage, probably related to innovation and learning. These shifts can be accompanied by changes in density-dependent processes, which can favour the occupation of more isolated and previously unoccupied patches. Changes in habitat selection patterns present a significant challenge for forecasting and management efforts, as they increase the ultimate fractions of the landscape that might susceptible to invasion. However, our research indicates that niche expansions do not happen rapidly over time. After 40 years since their introduction, the monk parakeets in our study population continue to prioritize palm species for nesting. This indicates that there may be a considerable opportunity window for management before significant shifts in nesting preferences occur. However, our work also emphasizes that shifts occur and they persist, and therefore, applying the precautionary principle, the best strategy is to act as soon as possible.

CONFLICT OF INTEREST STATEMENT

None.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13761.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://datadryad.org/stash/share/2A4Y2YWx3f0y-tRgk1icYqgDwxq_xwLPx8UwQ3uYusA.

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BIOSKETCH

The research team was brought together by a shared interest in understanding the ecological factors affecting the invasion success of alien species. They combine knowledge on population dynamics, urban ecology, spatial ecology and niche shift dynamics.

Author contributions: Laura Cardador, Juan Carlos Senar and Zulema Núñez-Tobajas conceptualized the study and designed the methodology; Juan Carlos Senar was involved in the organization and funding acquisition of censuses; Juan Carlos Senar, José G. Carrillo-Ortiz, Zulema Núñez-Tobajas and Ruth Rodríguez-Pastor collected the data and performed data curation; Laura Cardador and Zulema Núñez-Tobajas analysed the data with inputs from Juan Carlos Senar; Laura Cardador and Zulema Núñez-Tobajas led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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