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RESEARCH ARTICLE

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Climate matching and anthropogenic factors contribute to the colonization and extinction of local populations during avian invasions

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Abstract

Aim: Concern about the impacts of biological invasions has generated a great deal of interest in understanding factors that determine invasion success. Most of our current knowledge comes from static approaches that use spatial patterns as a proxy of temporal processes. These approaches assume that species are present in areas where environmental conditions are the most favourable. However, this assumption is problematic when applied to dynamic processes such as species expansions when equilibrium has not been reached.

Location: Iberian Peninsula.

Taxon: Birds.

Methods: In our work, we analyse the roles played by human activities, climatic matching and spatial connectivity on the two main underlying processes shaping the spread of invasive species (i.e. colonization and extinction) using a dynamic modelling approach. We use a large data set that has recorded the occurrence of two invasive bird species—the ring-necked (*Psittacula krameri*) and the monk (*Myiopsitta monachus)* parakeets—in the Iberian Peninsula from 1991 to 2016.

Results: Human activities and climate matching play a role on species range dynamics. Human influence and urbanization were the most relevant factors explaining colonization. Additionally, an effect of climate matching was found. Persistence (the inverse of extinction) was mainly affected by human influence for the monk parakeet and by the extent of urban environments for the ring-necked parakeet.

Main conclusions: Human activities play a major role not only on colonization of new locations, but also on persistence during range expansion. Additionally, natural processes—notably climate matching—also affect new colonizations. These findings add to our understanding of the mechanisms that might allow alien species to expand their geographic range at new locations and might help to improve our capacity to assess invasion risks and impacts accurately.

KEYWORDS
biological invasions, birds, dispersal, environmental-matching, human alterations, occupancy models, spread

1 | INTRODUCTION

Human activities are accelerating the introduction and subsequent establishment of alien species in places far away from their native ranges (Seebens et al., 2018, 2021). Concern regarding the impacts of biological invasions and the need for their effective prevention and management have generated a great deal of interest in understanding the factors that determine invasion success to be able to predict invasion outcomes (e.g.Abellán et al., 2017; Redding et al., 2019). The chances of transiting throughout the different invasions stages [i.e. transport, introductions, establishment and spread; (Blackburn et al., 2011)] have a stochastic component that may make predictions difficult. The importance of stochasticity is reflected by the central role of propagule pressure (understood as a composite measure of the number of individuals released into a region in which they are not native) as one of the main factors explaining invasion success (Blackburn et al., 2009; Blackburn et al., 2015).

Propagule pressure is not the only determinant of invasion success. Species-specific traits, such as life-history or behavioural flexibility and variability, can allow certain species to deal with novel environments (Carrete & Tella, 2011; Sol & Maspons, 2016). Additionally, the suitability of the environment where a species is introduced can greatly enhance the probability of transition across different invasion stages (Abellán et al., 2017; Redding et al., 2019). Several not mutually exclusive hypotheses about the role of location-level variables have been proposed to understand the distribution and invasive dynamics of alien species, including the "human-activity" hypothesis and the "climate matching" hypothesis. The former hypothesis states that human activity make a new environment more invasible by altering native communities and reducing their biotic resistance or offering new niche opportunities such as supplementary feeding (Sax & Brown, 2000; Sol et al., 2017). Human activities may also increase the chance of repeated introductions and large propagule pressure in humanized environments (Blackburn et al., 2009; Gallardo & Aldridge, 2013) or favour environmental matching by increasing the likelihood that a species that relies on human-altered environments in its native area ends up established in such type of environments after being introduced (Cardador & Blackburn, 2019; González-Lagos et al., 2021; Sol et al., 2017).The climate matching hypothesis, in turn, states that alien species have a higher probability of success if they are introduced into regions with a climate similar to that found in their native area (Abellán et al., 2017; Redding et al., 2019), as species tend to conserve their native climatic niche (Cardador et al., 2016; Cardador & Blackburn, 2020; Petitpierre et al., 2012; Strubbe et al., 2013). However, this vision has been challenged by cumulative evidence that some species may also have notable success in areas climatically distinct from those occupied in their native ranges. For instance, among birds, colonization of alien areas where conditions were different from those occupied in their native ranges was apparent for nearly 30% of alien bird species established in Europe (Strubbe et al., 2013) and 34% at a global scale (Cardador & Blackburn, 2020). Niche shifts have been also observed in other taxonomic groups (e.g. Hill et al., 2017; Parravicini et al., 2015; Petitpierre et al., 2012).

Mismatches between environmental conditions occupied in native and alien distribution ranges are often interpreted as evidence of species adaptations in response to selection pressures imposed by the novel environment. This interpretation might be limited as species occurrences used to characterize species niches reflect the realized (i.e. the occupied), not the fundamental niche (Guisan et al., 2014). Also, most of our current understanding comes from static approaches that use spatial patterns as a proxy for temporal processes. These approaches implicitly assume that species are present in areas where environmental conditions are the most favourable (Araújo & Peterson, 2012). This assumption is problematic when applied to expanding species (i.e. when equilibrium has not been reached), as in the case of biological invasions (Václavík & Meentemeyer, 2012; Yackulic & Ginsberg, 2016; Zurell et al., 2009). Thus, current alien species distribution patterns could be largely the result of dispersal limitations from initial introduction sites, with some unfavourable colonized locations likely to disappear in the future (Yackulic et al., 2015). Thus, alien species distributions are highly dynamic and determined by two different underlying processes: colonization and extinction. Understanding the factors affecting these two different processes simultaneously holds promise of a better spatial and temporal understanding of invasions (Aagaard & Lockwood, 2016; Bled et al., 2011, 2013; Kéry et al., 2013; Yackulic et al., 2012, 2015).

In this study, we take advantage of a large data set recording the occurrence of two invasive bird species, the monk (*Myiopsitta monachus)* and ring-necked (*Psittacula krameri*) parakeets, in the Iberian Peninsula from 1991 to 2016 (Abellán et al., 2016, 2017) to determine the role of human activities, climatic matching, and spatial connectivity on range dynamics of alien species. We relax the assumption of equilibrium inherent to classical static approaches by explicitly modelling the colonization and extinction processes using multi-season occupancy models while controlling for imperfect detection based on repeated sampling in time and space (Louvrier et al., 2017). We hypothesize that colonization and extinction might be driven by different environmental factors. In particular, we expect colonization to be largely influenced by spatial connectivity related to the dispersal of individuals from previously occupied sites (i.e. diffusion) and by propagule pressure mediated by human activities. A role of habitat characteristics and climatic similarity on colonization is only expected if habitat matching choice occurs (i.e. individuals choose to settle in habitats that best fit their phenotype). Conversely, habitat characteristics and climatic similarity to native ranges are expected to have a major role in the probability of extinction, so that only individuals settled in areas that best fit their phenotype are expected to persist.

2 | METHODS

2.1 | Study species

The monk parakeet and the ring-necked parakeet are two of the most widespread invasive bird species in the world (Calzada Preston & Pruett-Jones, 2021), with demonstrated impacts on native fauna (Hernández-Brito et al., 2014, 2018; Strubbe & Matthysen, 2009a), agriculture and infrastructure (Castro et al., 2022; Menchetti & Mori, 2014; Senar et al., 2016). The monk parakeet is native to South America (Edelaar et al., 2015) and the ring-necked parakeet to two large, geographically disjoint regions (sub-Saharan Africa and South-Asia, mostly the Indian subcontinent), although most of the European ring-necked parakeet alien populations appear to have an Asiatic origin (Cardador et al., 2016; Strubbe et al., 2015). Both species have been largely traded in Europe as wild-caught cage-birds, whose accidental escape or release resulted in several invasive populations (Pârâu et al., 2016; Strubbe & Matthysen, 2009b). The first European populations appeared in the 1960–1970s, but very few records existed until 1990, when the species started to spread (Domènech et al., 2003; Pârâu et al., 2016; Strubbe & Matthysen, 2009b). Today, monk and ring-necked parakeets are abundant, coexist as aliens and continue to spread in many areas of the Iberian Peninsula (e.g. [Hernández-Brito et al., 2022]). These species present different ecological traits that make them good complementary study models. For example, the monk parakeet breeds in colonies and is the only psittaciform able to build its own nests with sticks and branches, (Hernández-Brito, Carrete, et al., 2021), while the ring-necked parakeet is mostly considered an obligate cavity-nester (but see [Hernández-Brito, Tella, et al., 2021]). Thus, we hypothesize that colonization and extinction might be driven by different environmental factors in both species. In particular, the role of habitat characteristics, specifically the presence of urban environments, and climatic similarity is expected to be major for the ring-necked parakeet. As previously noted, this species is an obligated cavity-nester, with distributions limited by the presence of wholes and might thus benefit more from nesting opportunities (e.g. cavities in large trees from urban parks or holes in building walls) and lower competition from altered native communities in urban environments than the monk parakeet. In the case of climatic similarity, a higher effect on ring-necked parakeet persistence is also expected because this species roosts in trees in the open, while the monk parakeet roosts colonially and inside their nests, which may allow them to remain warm on cold nights and thus survive in colder environments (Caccamise & Weathers, 1977).

2.2 | Species occurrences

Temporal occurrence data for the monk and ring-necked parakeets were obtained from a comprehensive database of exotic birds in mainland Spain and Portugal, which compiled records of exotic species observed in the wild in both countries from 1912 to 2012 through a systematic review of scientific and grey literature and observations from local experts (Abellán et al., 2016, 2017). This data set was updated until 2016 using the same methodology and complemented with "human observation" data from the Global Biodiversity Information Facility (GBIF.org, 2020, for a complete list of GBIF occurrence downloads, see Supporting Information Table S1). Given that both species are highly conspicuous and differentiable from native and other exotic species, we considered all reported occurrences as true. The date of each record, necessary for analyses, were provided in the vast majority of cases (records with date: monk parakeet, 89% of all records, $N = 18,290$; ring-necked parakeet: 91% of all records, $N = 4680$). As in other European countries, very few occurrence data existed until the 1990s (Figure S1). Thus, 1991 was set as the initial year for analyses (Figure 1). Locations were incorporated to a Geographic Information System (GIS) using a cylindrical equal-area projection at 10 km resolution to fit the maximum daily distances covered by the species (Hyman & Pruett-Jones, 1995; Strubbe & Matthysen, 2011).

2.3 | Modelling

We followed a multi-season occupancy approach to model the dynamics of the invasion process while accounting for imperfect detection and site- and survey-specific covariates (Kéry et al., 2013; MacKenzie et al., 2003).

2.3.1 | Occupancy submodel

Under multi-season occupancy models, site occupancy dynamics are a function of colonization and local extinction. The probability of extinction ε is defined as the probability that an occupied site at time t becomes unoccupied at time $t+1$. The probability of colonization γ is defined as the probability that an unoccupied site at t becomes occupied at $t+1$. The probability that a site is occupied at time $t+1 (\Psi_{t+1})$ in its simplest form is then:

$$\Psi_{t+1} = \Psi_t \bullet (1-\varepsilon) + (1-\Psi_t) \bullet \gamma$$

All parameter estimates (ε, γ, ψ) can be expressed as a function of covariates using a logit-link function.

2.3.2 | Observation-process submodel

To account for imperfect detection, the observation-process submodel estimates the detection probability p provided that replicate

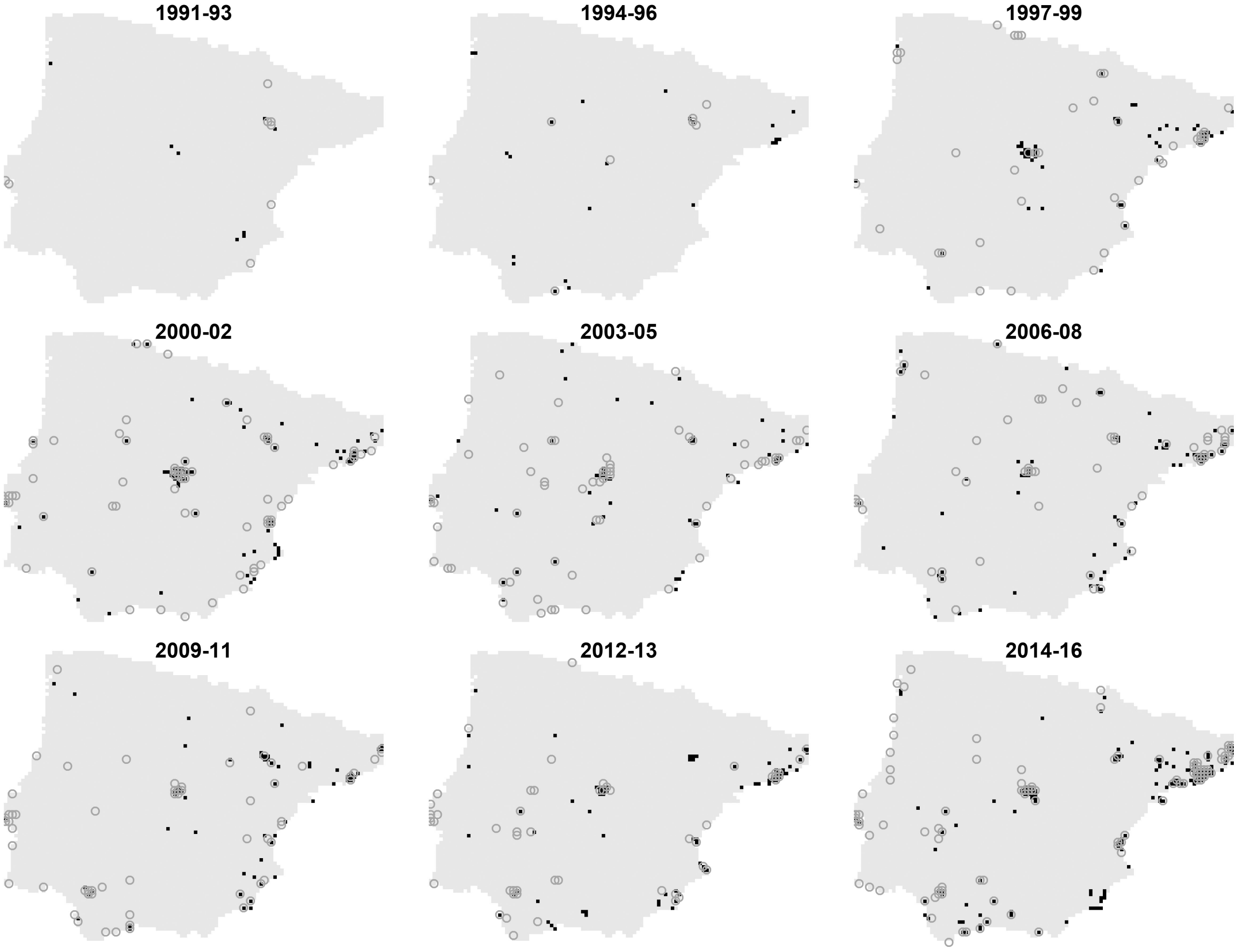

FIGURE 1 Temporal evolution of monk (black squares) and ring-necked (grey circles) parakeet detections at 10 km resolution in the Iberian Peninsula for the period 1991–2016

observations of "presence/absence" (more accurately "detection/non-detection") are available for the sampling sites within survey seasons, when the occurrence state of a site is assumed not to change (i.e. closure assumption). We used as sampling sites for analyses the 10-km grid cells in the Iberian Peninsula (see in section "Species occurrences"). The occurrence data in each sampling site were classified in surveys seasons and replicate observation periods within seasons using the date of the records. To account for potential variation related to the criteria used to classified the data, we considered three alternative sampling schemes: (1) survey seasons of one calendar year with two replicate observation periods (Jan-Jun and Jul-Dec), (2) survey seasons of two calendar years with two replicate observation periods (each of 1 calendar year) and (3) survey seasons of three calendar years with two replicate observation periods (each of 1.5 years). We did so, because for biological invasions, it is difficult to define a single sampling scheme using an ecological criterion, as invasion dynamics are not only dependent on the species biology but also on human activities. We considered a maximum value of 3 years for the duration of sampling periods because this is the number of years commonly used to evaluate bird presence in bird atlases (e.g. [Estrada et al., 2004]). To account for potential detection biases related to an uneven sampling effort across time and space, we included an estimate of sampling effort as a survey-specific covariate of detection probability in models (Cardador & Blackburn, 2019). This variable was computed as the cumulative value of observation records of both native and alien bird individuals retrieved from GBIF ("human observation" category, Table S1) in a particular sampling site and observation period considered. Occurrence data from species in the same taxonomic class are expected to suffer from the same sampling limitations, reducing the effect of sampling biases in observed distribution patterns. Additionally, sites with no bird records in a given observation period were considered as not surveyed as recommended in Louvrier et al. (2017) and thus omitted from analyses. We assumed that the large number of bird records in the Iberian Peninsula during the study period (>25 million records, GBIF.org, 2020) allowed us to consider as surveyed only the sites where one or more bird observations were reported in a given observation period.

2.3.3 | Predictors of colonization and extinction

To test the climatic matching hypothesis, we calculated the climatic similarity between each of the sites in the study area and the species native ranges (Figure S2a,b) using multivariate environmental similarity surfaces (MESS) (Elith et al., 2010) based on six climatic variables globally describing temperature and precipitation gradients (source: WorldClim v.1, [Hijmans et al., 2005]) and known to affect the distribution of the study species (e.g. Cardador et al., 2016, 2019): annual mean temperature, mean temperature of the warmest month, mean temperature of the coldest month, temperature seasonality, annual precipitation, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality. MESS values represent how similar a point is to a reference set of points regarding the set of predictor variables until a maximum value of 100, with negative values representing novel environments for the species (Elith et al., 2010). MESS values were used as predictors in occupancy models. Native occurrence data for MESS computations were compiled from GBIF (Table S1) and classified as pertaining to the species native breeding ranges according to BirdLife International and NatureServe (2014). For the ring-necked parakeet, considering data for the whole native distribution range or only the Asian distribution (from which most European alien individuals originated, Strubbe et al., 2015; Cardador et al., 2016)) for MESS calculations makes little difference (Pearson correlation coefficient, $r > .99$). Thus, for simplicity and consistency with analyses of the monk parakeet, we used MESS values based on the whole species native range.

Human activities are known to mediate propagule pressure and their characteristics can also affect the invasion process (Blackburn et al., 2009; Sax & Brown, 2000). To test these hypotheses, we considered three variables describing human-transformed environments as predictors in occupancy models: (i) the Global Human Influence Index, which provides a weighed composite map of anthropogenic impacts including urban extent, population density, land cover, night lights and distance to roads, railways, navigable rivers and coastlines (Sanderson et al., 2002) and two more specific descriptors of anthropogenic habitats known to affect invasions (Chytrý et al., 2009; Veran et al., 2016), the percentage of ii) urban environments (including urban and built-up areas) and iii) farmland in sampling sites (Figure S2c-e). These two land-use variables were derived from 0.5 km MODIS-based Global Land Cover Climatology (Broxton et al., 2014).

To account for the effect of spatial connectivity, we considered an autologistic covariate in models representing the mean occupancy probability in neighbouring sites in the previous season (Eaton et al., 2014; Veran et al., 2016; Yackulic et al., 2012). We considered different sizes of neighbourhood to test for the capacity of diffusion of the species. We kept for the following steps of model selection the neighbourhood size that fitted the data better according to an Akaike's information criterion (AIC, Table S2). The smallest neighbourhood considered included the first layer of surrounding cells, and thus a maximum diffusion distance of 20 km corresponding to the most distant points from two adjacent cells. The largest neighbourhood considered included a possible diffusion distance from up to four cells, which corresponds to a maximum diffusion distance of 50 km.

Finally, only seven sites were occupied by monk parakeets and three by ring-necked parakeets in 1991, the first year of analyses. These sample sizes were too low to assess the effects of covariates on initial occupancy probability. Thus, we considered this parameter as constant in models.

2.3.4 | Model fitting, selection and validation

Multi-season occupancy models were conducted using the R-package “RPresence” and the software PRESENCE (https://www.mbr-pwrc.usgs.gov/software/presence.html) for autologistic models. To assess the best combinations of predictors affecting the colonization-extinction processess, we used a multimodel inference approach and used AIC for model selection. Due to the large number of possible parameter combinations to consider for a model set, we used a secondary candidate set strategy for model selection (Morin et al., 2020). We began our analysis by developing a set of simple models to establish which predictors were best supported by model selection for detection, colonization and extinction parameters independently (Tables S3–S7). We used sampling effort as potential predictor for the detection submodel (Table S3) and all potential combinations of predictors described above for colonization (Tables S4 and S5) and extinction submodels (Tables S6 and S7). Structure of non-target parameters in different submodels was held constant (Morin et al., 2020). We used a relaxed AIC threshold (ΔAIC <10) for model selection at this step to avoid excluding submodel structures with potential strong support in more complex models (Morin et al., 2020). In a second step, we combined the top set of submodels for model selection (Tables S8 and S9). We report linear-logistic β coefficient estimates for each well-supported model (i.e. ΔAIC ≤2) and computed averaged values of model predictions for model validation and plotting. We assessed the relative contribution of each predictor to total variation in occupancy patterns explained by models using a likelihood ratio test (LRT), comparing the deviance between a model containing all the predictors retained in the set of well-supported models (saturated model) and the saturated model without one factor at a time. The different LRT values obtained were then transformed to sum 1 and used as a measure of relative contribution (Veran et al., 2016). All variables were standardized before modelling. We used observation data from 1991 to 2013 (or 2014 in the case of survey seasons of 3 years) for model training, selection and parametrization. The remaining data were used to assess model performance using the following approach: starting from the forward conditional estimates of occupancy for each site in the final year of fitted data, we projected the probability of presence in each cell for one extra survey season (of 1, 2, or 3 years, according to the different sampling classifications considered; see above). We calculated the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS) using the R package "Proc." For TSS calculations, we set the threshold that maximized the sensitivity plus specificity. Because a high selectivity for human-altered environments, particularly for urban environments, might lead to an overestimation of model performance, we repeated model testing by restricting analyses to sites where urban environments is present (562 sites from a total of 5852 sites).

3 | RESULTS

3.1 | Model validation

Between 3 and 6 models were well supported (ΔAIC <2) for the monk parakeet according to different sampling classifications considered (13 models in total, Table S8) and between 2 and 3 for the ring-necked parakeet (8 models in total, Table S9). Estimates of β coefficients were overall consistent among models and sampling classifications considered, with main differences related to the inclusion or not of non-significant predictors (Tables S10 and S11). Model-averaged predictions across well-supported models for each species and sampling classification showed a high agreement with occurrences in the Iberian Peninsula (mean ± SD across sampling classifications, $n = 3$, monk parakeet: AUC = 0.93 ± 0.01, TSS = 0.80 ± 0.03; ring-necked parakeet: AUC = 0.95 ± 0.004, TSS = 0.82 ± 0.01; Figure 2 and Figures S3 and S4). Model performance was lower but still high when the testing region was restricted to sites with presence of urban environments (monk parakeet: AUC = 0.83 ± 0.02, TSS = 0.57 ± 0.06; ring-necked parakeet: AUC = 0.86 ± 0.01, TSS = 0.54 ± 0.04).

3.2 | Sampling effort and detectability

The model best supported by the data had detection as a function of sampling effort in all the sampling survey classifications considered for both parakeets (Tables 1 and 2, see also Tables S10 and S11 for coefficients of all well-supported models). The contribution of this variable to occupancy models ranged from 1% to 18% for the monk parakeet according to the different sampling schemes considered and from 23% to 28% for the ring-necked parakeet (Figure 3). Response curves of model-averaged predictions showed a similar pattern for both species, the probability of detection increasing with increments in sampling effort, until reaching a value of around 6000 records when the curve flattened around 1 (Figures 4 and 5).

3.3 | Predictors of occupancy dynamics

3.3.1 | Initial occupancy probability

As expected, predicted initial occupancy probabilities were low for both the monk and the ring-necked parakeet as few sites were detected as occupied at the beginning of the 90s. Model estimates for initial occupancy probabilities ranged from 0.003 to 0.008 for the monk parakeet and from 0.006 to 0.009 for the ring-necked parakeet according to the different sampling schemes considered and different well-supported models (Tables S10 and S11).

3.3.2 | Colonization probability

Human activities were good predictors of colonization probability (Tables 1 and 2). A significant positive effect of both urban environments and GHII was found for both species in all well-supported models (Tables S10 and S11). In particular, the contribution of urban environments to models ranged from 31% to 83% for the monk parakeet depending on the sampling scheme considered and from 11% to 22% for the ring-necked parakeet (Figure 3). The probability of colonization was close to zero in cells covered by <20% of urban environments (Figures 4 and 5). The contribution of GHII ranged from 12% to 40% for the monk parakeet and from 25% to 35% for the ring-necked parakeet, but its effect on probability values was lower (Figures 4 and 5). Additionally, a positive effect of the climatic similarity between the native and invasive ranges on colonization was also supported for the ring-necked parakeet by all well-supported models (Figure 5 and Table S11). Its contribution ranged from 7 to 9%. A significant positive effect of climate matching was also suported for the monk parakeet by 9 of 13 well-supported models (Figure 4 and Table S10), although its contribution was lower (Figure 3).

3.3.3 | Extinction probability

In the case of the extinction probability, we mainly found support for a significant negative effect of the GHII for the monk parakeet (Figure 4 and Table 1) and the percentage of urban environments for the ring-necked parakeet (Figure 5 and Table 2). The effect of percentage of urban environments for the monk parakeet was also retained in all best supported models but was only significant according to models for one of three sampling schemes considered (Table S10). The effect of GHII for the ring-necked parakeet was also retained in the best supported models but was only significant according to models of one of three sampling schemes considered (Table S11). For both species, the probability that a site became extinct was around 0.8–0.9 for cells with nonhuman or nonurban environments (Figures 4 and 5). Support for a significant negative effect of spatial connectivity and climate matching was very low for both species (significant results only for a small proportion of well-supported models, Figure 3 and Tables S10 and S11).

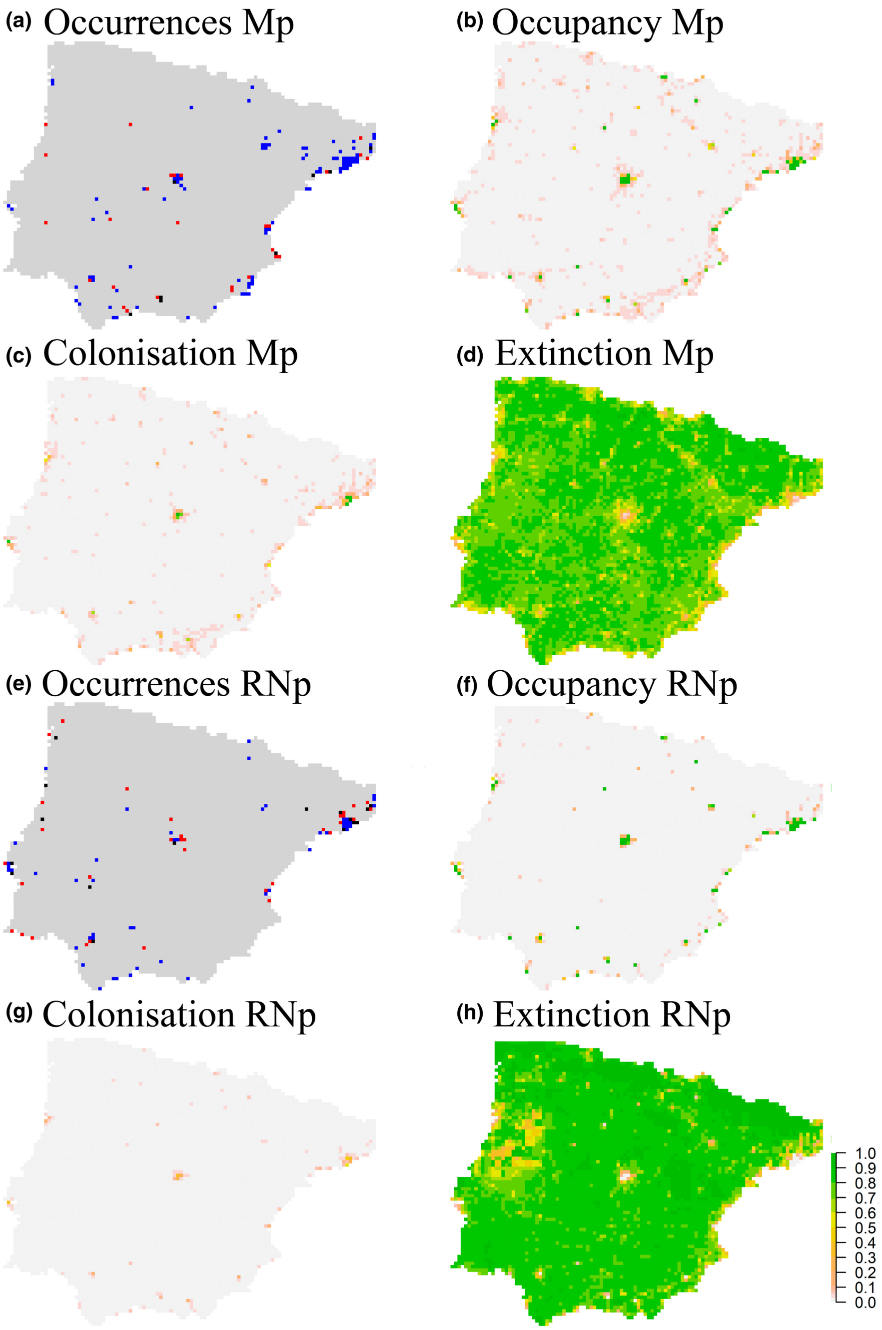

FIGURE 2 Observed distribution of monk (Mp) and ring-necked (RNp) parakeet occurrences in 2014–2015 (a and e) and estimated probabilities of occupancy (b and f), colonization (c and g) and extinction (d and h) in the Iberian Peninsula in the same period according to dynamic models trained in 1991–2013 based on survey seasons of 2 years with two observation periods. For the observed distribution, persistent locations (black), extinct locations (red) and new colonized locations (blue) with respect to the previous survey season (2012–2013) are shown

4 | DISCUSSION

Although prevention is widely accepted as the most environmentally desirable strategy to avoid the introduction of alien species, thousands of exotic species are continuously moved far from their native ranges worldwide, several of which go unnoticed until they successfully establish viable populations in novel areas. From then on, the most urgent question is to be able to predict whether and where they can spread. Our models, applied to two of the most widespread invasive birds of the world, highlight that both human activities and the climate matching between the native and invasive areas play a relevant role on their range dynamics by modulating the two underlying processes leading to their successful spread, namely colonization and extinction.

According to our initial expectations, we found support for a relevant role of human activities on the colonization probability of both parakeets. The positive relationships with human predictors could be partially explained by the increased chance of repeated introductions and large propagule pressure in humanized environments (Gallardo & Aldridge, 2013), particularly taking into account that, as with other recent bird introductions (Abellán et al., 2016), these species have been largely traded to Europe as pets, with most introductions resulting from the accidental escape or release of individuals (Cardador et al., 2016; Strubbe & Matthysen, 2009b). However,

TABLE 1 Estimates of coefficients for the monk parakeet for the model including the best combination of environmental predictors and best-fitted neighbourhood size for the autologistic term

	Estimates (SE)						
Survey season	**Intercept**	**Urban**	**Farmland**	**GHII**	**Clim match**	**Autologistic**[a]	**S. Effort**
1 year (2 observation periods)							
Initial	**−5.70 (070)**						
Colonization	**−5.40 (0.12)**	**0.13 (0.02)**	-	**0.69 (0.06)**	**0.39 (0.12)**	-	
Extinction	**1.05 (0.32)**	**−0.28 (0.09)**	-	**−0.37 (0.16)**	-	-	
Detection	**−0.61 (0.10)**						**0.09 (0.03)**
2 years (2 observation periods)							
Initial	**−5.05 (0.42)**						
Colonization	**−5.10 (0.14)**	**0.34 (0.08)**	-	**0.70 (0.09)**	**0.34 (0.14)**	-	
Extinction	**1.27 (0.31)**	−0.14 (0.12)	0.25 (0.17)	**−0.47 (0.19)**	-	−0.004 (0.005)[b]	
Detection	**−0.77 (0.22)**						**0.18 (0.05)**
3 years (2 observation periods)							
Initial	**−4.83 (0.36)**						
Colonization	**−4.82 (0.15)**	**0.47 (0.10)**	-	**0.69 (0.09)**	-	-	
Extinction	**1.52 (0.35)**	−0.16 (0.12)	0.27 (0.17)	**−0.48 (0.19)**	**−0.84 (0.36)**	−0.006 (0.004)[c]	
Detection	**−0.75 (0.15)**						**0.21 (0.05)**

Note: The probabilities of colonization and extinction are modelled as a function of the percentage of farmland and urban environments, the global human influence index (GHII), the climatic match and an autologistic term. Predictors not retained in the best model are indicated with a dash. Detection probability is modelled as a function of sampling effort. Bold numbers indicate estimates with $p < .05$. Results for models considering different sampled schemes are shown.

[a] For the autologistic term, we considered the size of neighbourhood with the lowest AIC.

[b] The neighbourhood selected included the first layers of surrounding cells (maximum diffusion distance of about 20 km).

[c] The neighbourhood selected included the two first layers of surrounding cells (maximum diffusion distance of about 30 km).

TABLE 2 Estimates of coefficients for the ring-necked parakeet including the best combination of environmental predictors and best-fitted neighbourhood size for the autologistic term

	Estimates (SE)						
Survey season	**Intercept**	**Urban**	**Farmland**	**GHII**	**Clim match**	**Autologistic**[a]	**S. Effort**
1 year (2 observation periods)							
Initial	**−5.09 (0.63)**						
Colonization	**−5.37 (0.21)**	**0.11 (0.03)**	-	**0.59 (0.08)**	**0.60 (0.19)**	-	
Extinction	**1.37 (0.46)**	**−0.43 (0.11)**	-	−0.19 (0.14)	−0.33 (0.43)	**−0.07 (0.003)**[b]	
Detection	**−1.15 (0.14)**						**0.27 (0.05)**
2 years (2 observation periods)							
Initial	**−4.72 (0.39)**						
Colonization	**−5.08 (0.16)**	**0.21 (0.05)**	0.14 (0.08)	**0.62 (0.08)**	**0.59 (0.18)**	-	
Extinction	**1.75 (0.49)**	**−0.57 (0.15)**	-	−0.25 (0.16)	−0.86 (0.51)	−0.003 (0.003)[c]	
Detection	**−1.11 (0.12)**						**0.21 (0.04)**
3 years (2 observation periods)							
Initial	**−4.69 (0.37)**						
Colonization	**−4.77 (0.16)**	**0.28 (0.05)**	0.15 (0.08)	**0.60 (0.18)**	**0.59 (0.17)**	-	
Extinction	**2.49 (0.62)**	**−0.62 (0.18)**	-	−0.44 (0.19)	**−1.23 (0.61)**	−0.003 (0.003)[b]	
Detection	**−1.04 (0.12)**						**0.29 (0.05)**

Note: The probabilities of colonization and extinction are modelled as a function of the percentage of farmland and urban environments, the global human influence index (GHII), the climatic match and an autologistic term. Predictors not retained for autologistic models are indicated with a dash. Detection probability is modelled as a function of sampling effort. Bold numbers indicate estimates with $p < .05$. Results for models considering different sampled schemes are shown.

[a] For the autologistic term, we considered the size of neighbourhood with the lowest AIC.

[b] The neighbourhood selected included the first layers of surrounding cells (maximum diffusion distance of about 20 km).

[c] The neighbourhood selected included the two first layers of surrounding cells (maximum diffusion distance of about 30 km).

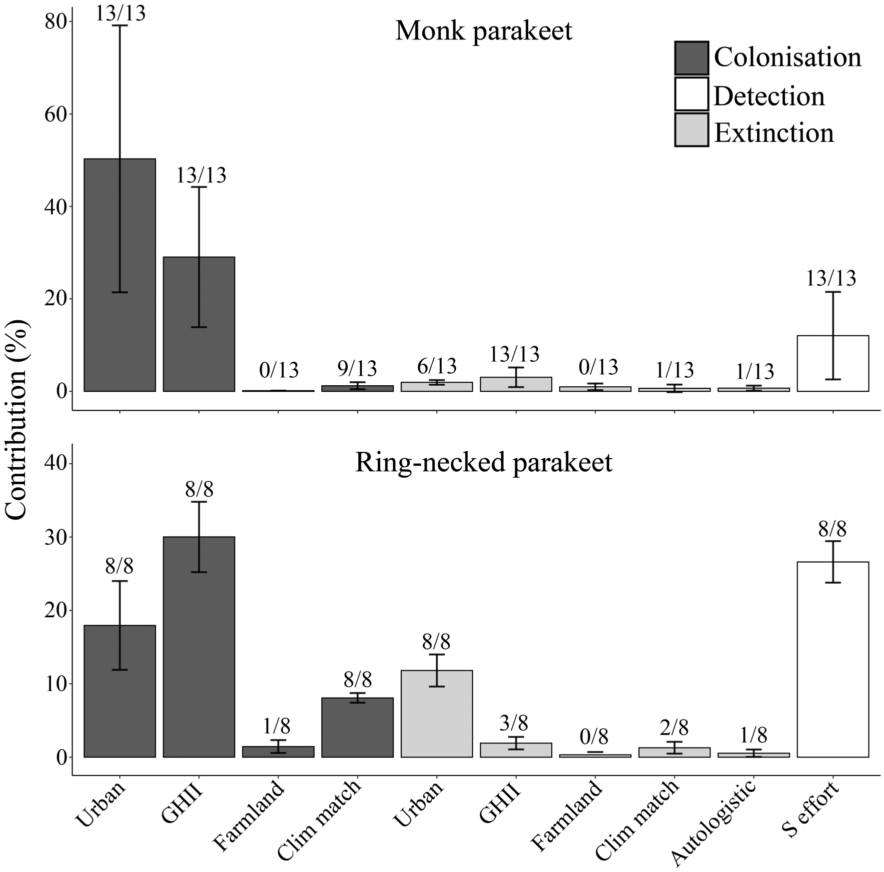

FIGURE 3 Relative contribution to total deviance explained by occupancy models of the different covariates considered for colonization, extinction, and detection probability of monk (a) and ring-necked (b) parakeets in the Iberian Peninsula. Mean and standard variation according to the three sampling schemes considered for each species are shown. The ratio between the number of well-supported models were a predictor is retained as significant ($p < .05$) and the total number of well-supported models ($\Delta AIC < 2$) for all sampling schemes is shown

it is important to note that the importation of wild bird species was prohibited in Europe after 2005 (Cardador et al., 2017) when a reduction of new species introductions was observed (Cardador et al., 2019). Even so, post-hoc analyses restricting the data to the period after 2005 also showed a positive role of human predictors on colonization (Tables S12 and S13), suggesting that, beyond new introductions, human habitats may have also favoured colonizations in other ways.

On the one hand, human infrastructures connecting urban environments and other human-transformed environments might have indirectly favoured the movement of individuals between humanized environments (Ascensão et al., 2020; Gallardo & Aldridge, 2013). There, human-related alterations may also make the environment easier to colonize by reducing biotic resistance and offering new niche opportunities, such as new feeding resources (Sol et al., 2017). The importance of predation release as a constraint in new colonizations of monk parakeets has been recently shown in Madrid (Spain), where the appearance of a behavioural innovation such as the use of white stork (*Ciconia ciconia*) nests resulted in a protective nesting association that counteracts the biotic resistance of the native community and allow the spread of the species into rural habitats (Hernández-Brito et al., 2020). On the contrary, it is also possible that individuals dispersing from previously occupied sites actively select to settle in these habitats, taking into account that this provides higher prospects of success (i.e. lower extinction rates) than less altered environments according to our results. In fact, contrary than expected, we did not found support for a relevant effect of spatial connectivity in colonization probability of new locations, suggesting that human-mediated dispersal and habitat sorting play a more relevant role on species range dynamics at the spatial scales considered.

Apart from the effect on colonization, we also found a positive effect of human habitats (and specifically, urban environments in the case of the ring-necked parakeet) on persistence probability. This result supports the expected role of habitat characteristics on extinction probability and can be related to different processes. Monk and ring-necked parakeets show tolerance to human-altered habitats in their native ranges. Prior adaptation to human-modified environments may have thus enhanced their persistence in human-modified lands (Cardador & Blackburn, 2019, 2020); with the differences in the relative importance of human influence in general or urban environments in particular between the two parakeets probably related to their different nesting behaviours. As with colonizations, human-related alterations may also favour persistence by reducing biotic resistance and offering new niche opportunities (Sol et al., 2017). Predation, which has been described as a key factor affecting population dynamics, is reduced in human-transformed environments, particularly urban environments (Rebolo-Ifrán et al., 2017), and may facilitate the survival of established individuals and, therefore, the persistence of alien populations. All of these factors, together with the higher propagule numbers typical of human environments, may have allowed populations to reach higher numbers rapidly, helping

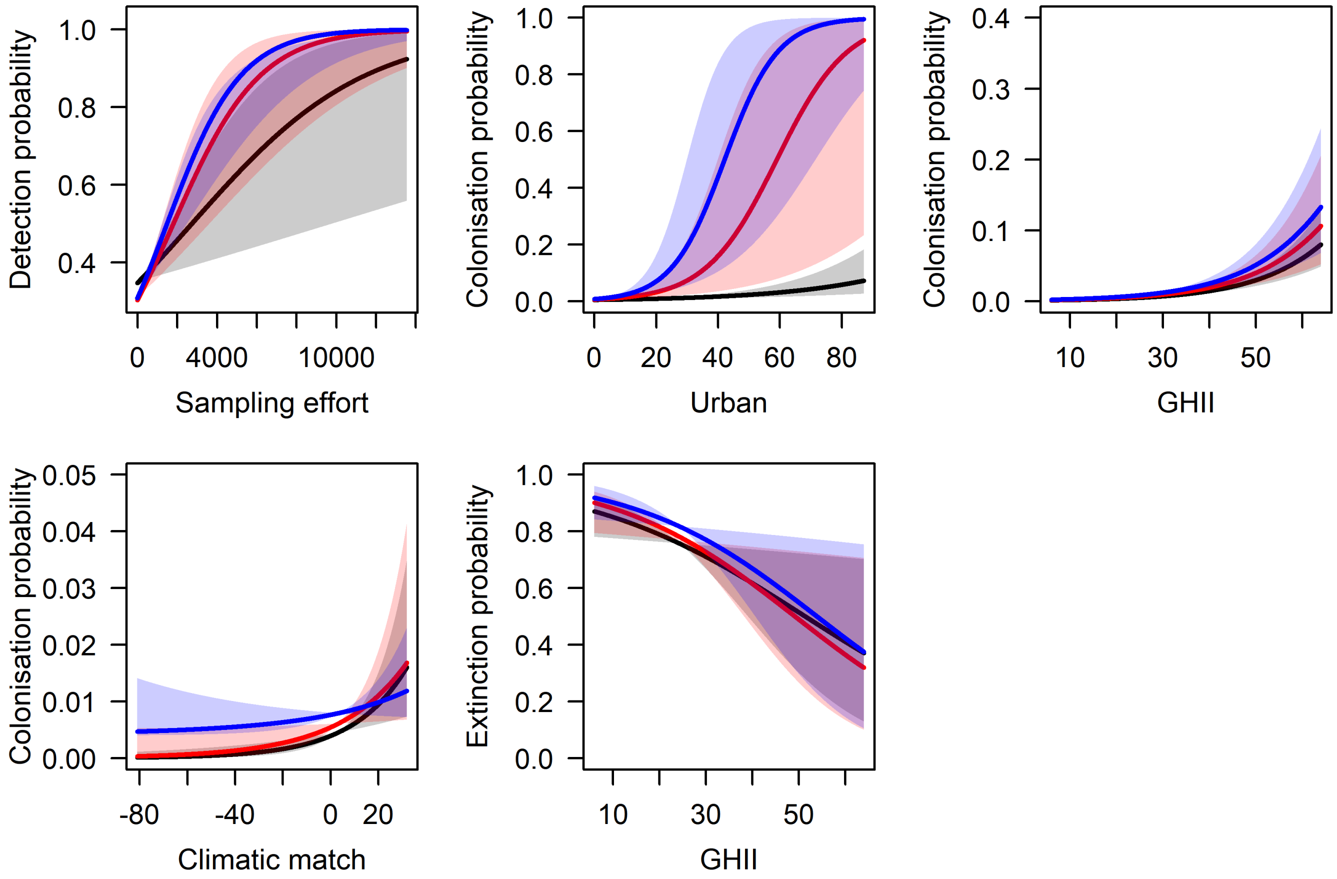

FIGURE 4 Partial response curves for the probability of detection, colonization and extinction of monk parakeets for predictors receiving high support in models (i.e. significant estimates in most well-supported models). Averaged mean values (lines) and 95% confidence intervals (shadow areas) across models within different sampling schemes are shown (black: One year with two observation periods; red: Two years with two observation periods; blue: Three years with two observation periods)

them to avoid stochasticity and population demographic processes (Blackburn et al., 2015), and thus reducing extinction risks.

Our results also provide support to the climate matching hypothesis, with colonizations positively influenced by the climatic similarity between the native and invasive ranges in both species. Notably, the relevance of climate matching on colonization was more relevant for the ring-necked parakeet, as expected attending to their different roosting behaviour. The importance of climate matching on spread partially agree with previous findings based on inter-specific comparisons, which showed that the spread rate of alien species positively relates to climate matching (Abellán et al., 2017). However, contrary to our expectations, we find very low support for an effect of climate matching on persistence. This could be due to the fact that most colonizations in our study area occur in humanized environments where microclimatic and microhabitat conditions can buffer against broader climatic effects (Pickett et al., 2001). It is also worth mentioning that the low variability in climatic conditions across the study area (Figure S2a,b), particularly across colonized sites, may also be precluding the detection of any important, significant effect in our study model. Climatic effects on the persistence of these species might be more relevant in colder regions and might be worth studying in the future.

Understanding the patterns and drivers of alien species distribution is relevant to predicting the fate of introduced species. Dynamic occupancy models can provide useful insights into the different factors underlying invasion range-dynamics. According to our study, human activities—probably linked to human-mediated dispersal and habitat filtering—play a major role not only on colonization of new locations, but also on persistence probability during range expansion. Additionally, alien species range dynamics is not just a function of human activities but also shows the signal of natural processes. Notably, we find a consistent positive association between colonization probability and climate matching to species native ranges. These findings help to fill the current gap in our understanding of the mechanisms that might allow alien species to expand their geographic range at new locations and might help to improve our capacity to assess invasion risks and impacts accurately. We hope our study will pave the way for future applications of dynamic models for a more acurate understanding of alien species range dynamics and its potential for management.

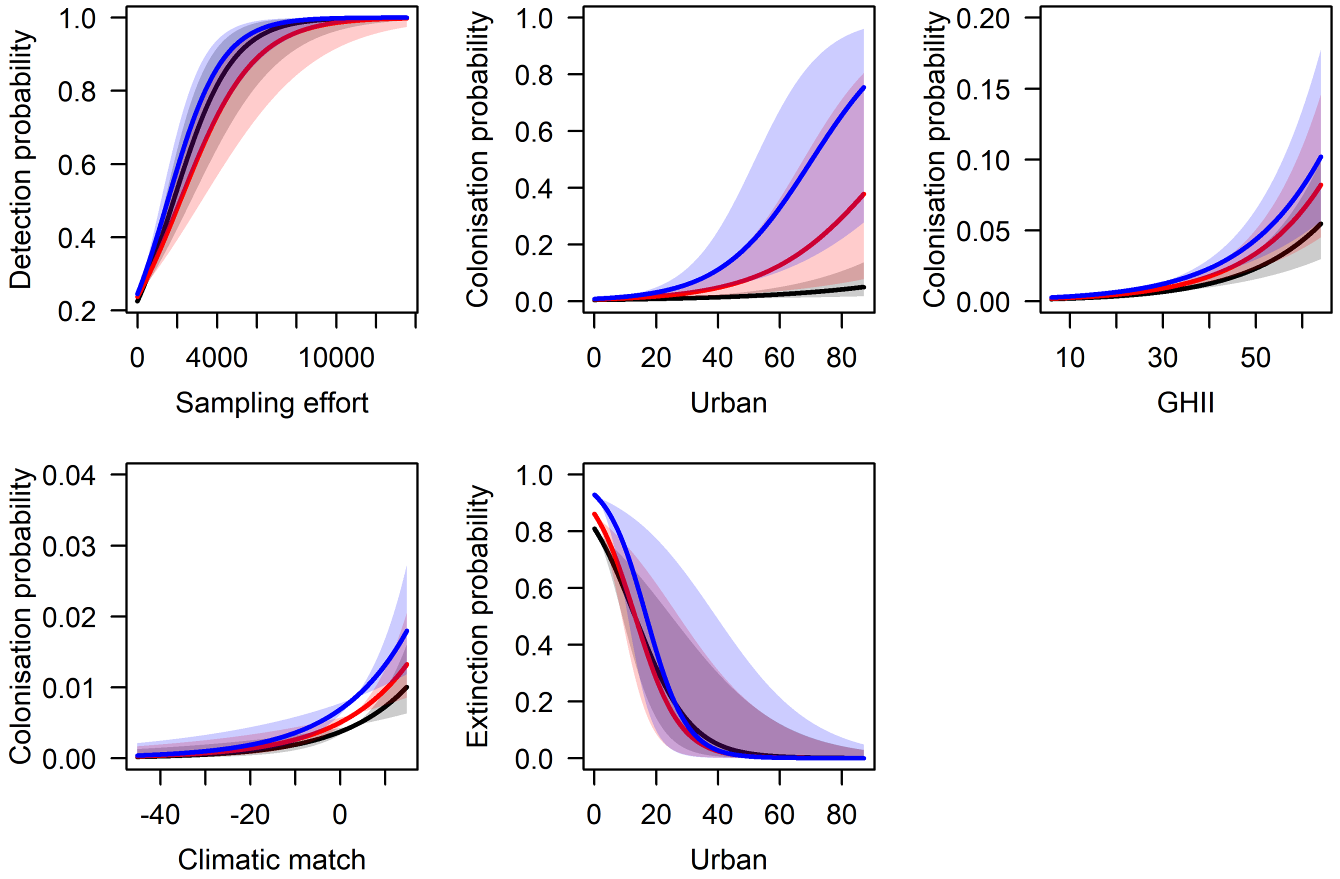

FIGURE 5 Partial response curves for the probability of detection, colonization and extinction of ring-necked parakeets for predictors receiving high support in models (i.e. significant estimates in all well-supported models of a given sampling scheme). Averaged mean values (lines) and 95% confidence intervals (shadow areas) for models using different sampling schemes are shown (black: One year with two observation periods; red: Two years with two observation periods; blue: Three years with two observation periods)

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

All data used in this manuscript and relevant scripts can be accessible via Dryad https://doi.org/10.5061/dryad.q573n5tm1.

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BIOSKETCH

The research team was brought together by a shared interest in understanding the ecological factors affecting the spatial distribution of species, and particularly those that contribute to the invasion success of alien species. All authors focus at least part of their research on biological invasions.

Author contributions: L.C. and M.C. conceived the original ideas; L.C., J.L.T., J.D.A., P.A. and M.C. compiled the data; L.C. analysed the data with inputs from J.L.; L.C., J.L.T., J.L., J.D.A, P.A. and M.C. discussed results, contributed critically to the drafts and gave final approval for publication; L.C. led the writing of the manuscript.

SUPPORTING INFORMATION

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

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