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Article

Dynamic species distribution models reveal spatiotemporal habitat shifts in native range-expanding versus non-native invasive birds in an urban area

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Urbanisation as a major driver of changes leads to the extinction of some species while others increase in abundance, especially non-native species. Spatiotemporal distribution patterns of these successful species are likely to be shaped by their response and tolerance to urban features. This study assesses the anthropo-ecological requirements of two co-occurring bird species, the native range-shifting jackdaw *Corvus monedula* and the non-native invasive ring-necked parakeet *Psittacula krameri*. We built yearly models over an eight-year period using an ensemble modelling approach assessing response differences through time and between species. Predictors describing human-made structures, socio-ecological proxies and resources availability were extracted from temporally coincident databases. Dispersal and habitat constraints were implemented in final models to provide more realistic forecasts of species future distributions. Ensemble models evaluated with a random partition of the training dataset showed a higher accuracy than those evaluated with an independent dataset from another time period. Our results highlight temporal variations in the relative importance of predictors for both studied species. Single-season occurrence data may thus be insufficient to characterize species ecological requirements. The ring-necked parakeet and the jackdaw showed different responses to urban features. Jackdaws preferred the more urbanized part of the city while the distribution of parakeets was strongly positively associated with the density of exotic ornamental trees. We concluded that ring-necked parakeet range expansion is likely to be driven by its effective ability to exploit urban resources which native species do not or under exploit, suggesting an open window of foraging opportunities. However, the jackdaw may be misled by a high cavity availability and a large amount of low-quality anthropogenic food in the urban core. We suggest that dynamic SDMs are a critical tool not only to forecast the future expansion of invasive species but also for a better understanding of processes driving urban biodiversity persistence.

Keywords: *Psittacula krameri*, *Corvus monedula*, empty niche hypothesis, dispersal constraints, Mediterranean city, ensemble modelling, multi-season datasets



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Introduction

Cities are expanding geographically at a higher rate than human population growth, particularly in biodiversity hotspots (Seto et al. 2012) and the forecast of human population in urban areas is estimated to more than 60% in 2050 (United Nations 2014). Thus, a better understanding of urban features that promote or limit biodiversity is necessary for conservation issues and sustainable urban planning. Urbanization processes destroy natural habitats and drastically transforms landscapes by altering resource flows (Henry and Dicks 1987), increasing disturbance frequencies (Rebele 1994) and replacing natural vegetation by impervious surfaces and novel plant communities (McKinney 2002). The structure and form of urban areas are extremely diverse, depending among others on their extent, from small villages to megacities, on their geographical localization, and on cultures and histories of human populations (Chace and Walsh 2006, Clergeau 2007). Urban landscapes are composed of human-made features such as urban-industrial structures (buildings, roads), agricultural areas, ornamental parks and private gardens, and by patches of remnant vegetation and water surfaces. The response of bird species to these neo-habitats mainly depends on their ability to deal with the human-induced disturbances and to exploit the novel pool of resources present (Lowry et al. 2013). The heterogeneity of their response to urbanization induces changes in species occurrence and abundance, including the local extinction of some native species (commonly called urban avoiders) while few others increase in abundance and take advantages of the new opportunities cities offered (commonly called urban exploiters, Blair 1996, McKinney 2002, Chace and Walsh 2006, Croci et al. 2008). For the latter, urban areas can be viewed as places of opportunities such as, for example, the European swift *Apus apus* which nest in buildings (Kark et al. 2007), or the yellow-legged gull *Larus michahellis*, which nest on buildings' roofs (Soldatini et al. 2008), both species reaching peak densities in urban cores. Food resources may also be both higher and more predictable in urban areas compared to surrounding rural habitats, due to anthropogenic wastes and (bird) feeders supplies (Tryjanowski et al. 2015).

Among urban exploiters, non-native bird species are especially successful (Blair 1996, Kark et al. 2007). Independently of the nature of the ecosystem to which non-native birds are introduced, several intrinsic biological traits have been linked to the success of non-native invasive species, including aspects of morphology, behavior, and life-history. Invasive species are more likely to have broad environmental tolerances (Shea and Chesson 2002, Hellmann et al. 2008), a higher competitiveness which may allow them to displace native species from their niches ('competition hypothesis', Sol et al. 2012) and their ability to exploit resources that are no longer monopolized by other species or resources that other species are not able to exploit ('empty niche' and 'resource opportunity hypothesis', Tilman 2004, Sol et al. 2012). Non-native invasive birds often occupy human-dominated sites in which human activities may positively influence their establishment

('human-activity hypothesis', (Taylor and Irwin 2004, Leprieur et al. 2008) for example by providing nesting sites (e.g. buildings, nest-boxes) and supplementary food resources. In this study, we aim to determine the differences and/or the similarities in the response to urban environment between two co-occurring, expanding cavity-nesting bird species in the same Mediterranean city: a recently introduced non-native species, the ring-necked parakeet *Psittacula krameri*, and a native range-expanding species, the western jackdaw *Corvus monedula*. We examined the relationship between anthropo-ecological predictors and species' breeding distributions, and hypothesize that the drivers of species' breeding presence, and thus the response to urban features, will be different between the non-native and native species, with a broader tolerance to the human activities for the non-native ring-necked parakeet.

The ring-necked parakeet *Psittacula krameri* is a Psittacine species native from Asia and sub-Saharan Africa and is the most widely distributed parrot species in the world (Forshaw 2010). The total number of individuals in Europe has been estimated to number at least 85 000 with populations successfully established in ten countries (Pârâu et al. 2016). Popular as pet, introduction events of this species outside its native range result of accidental or deliberate releases. In France, the three principal breeding populations are located in the north (Paris and Lille) and on the Mediterranean coast in the south (Marseille). With more than five million of breeding pairs, the western jackdaw is a corvid species native to and commonly found in Europe. Jackdaws are usually found breeding in vertical structures like cliff faces but it has spread spatially and numerically in French cities since the middle 1990s (Frèze 2015). The RNP and the jackdaw share life-history traits that have been related to a higher probability of successful establishment in novel environments: they are sedentary (Veltman et al. 1996), have a relatively large brain (Sol and Lefebvre 2000), are sexually monochromatic (McLain et al. 1995) and have an opportunistic feeding regime (Jokimäki and Suhonen 1998). Both species are cavity nesters, semi-colonial and gather at night in communal roost sites. Their recent demographic increases in French cities raised concerns by urban planners regarding their potential impacts. The main introduction event of the ring-necked parakeet and the expansion of the jackdaw from natural to urban habitats in the city of Marseille have occurred at the same time, i.e. around 1990s which makes these populations good candidates to study factors that drive the success of urban species.

We used a set of detailed habitat variables implemented in an ensemble forecasting of species distribution models (SDMs). SDMs encompass a wide range of statistical approaches which quantify relationships between spatial distributions of species and the characteristics of their environment (Guisan and Zimmermann 2000, Franklin 2010). They have been widely used in ecology and evolution, including for informing conservation decisions (Guisan et al. 2013), and for predicting the potential distributions of invasive species or disease vectors (Peterson 2003, Purse and Golding 2015). Yet, SDMs have been criticized, not only because model predictions can strongly vary depending on the technique

used (Elith et al. 2006, Syphard and Franklin 2009), but also because SDMs are inherently static, correlative models relying on the assumption that species occurrences used for modelling are representative of species' true distributions and that observed species distributions are in equilibrium with limiting environmental factors (Guisan and Thuiller 2005). Therefore, here, to account for the variability of SDMs algorithms, we applied an ensemble modelling framework. Ensemble models combine input parameter settings and outputs of several different model algorithms (Araújo and New 2007, Marmion et al. 2009), and allow to derive the central tendency of individual SDM predictions, and of the factor underlying species' predicted distributions. To account for the fact that invasive and range-shifting species are, by definition, not in pseudo-equilibrium with their environment (Guisan and Theurillat 2000, Václavík and Meentemeyer 2012), we explicitly included estimates of species dispersal capacities in our modelling framework. The necessity of including dispersal limitations into SDMs has been stressed by several authors (Guisan and Thuiller 2005, Beale and Lennon 2012), but studies that account for this process are still rare. Indeed, considering that species have unlimited or no dispersal capacities are unrealistic scenarios which can respectively overestimate and underestimate the forecasted future distribution of species (Guisan et al. 2006, Engler and Guisan 2009). Lastly, we move beyond purely static distribution models by relying on a multi-season occurrence datasets and detailed covariates extracted from temporally consistent databases to account for possible fluctuations of resources through time.

Thus, our data and dynamic 'hybrid' modelling framework allow not only to test whether introduced, invading and native, range-shifting species differ in their response to features of urban habitats, but also enables us to provide a more realistic forecast of the potentially colonisable habitats of our target species, representing the suitable areas that species will be able to colonise in the next 50 yr. Our study highlights how ecological knowledge and tools can provide landscape-scale ecological assessments allowing urban planners and conservation managers to make more informed decisions.

Methods

Study area

The study was carried out in the urbanized part of the city of Marseille. Geographically constraints by the availability of remote-sensed predictor variables, the total extent of the study area covers 97 km² (Fig. 1).

Marseille is a coastal city located in the Mediterranean southeast coast of France and is the second most populous city in the country with an estimated human population of 855 000. At the north, east and south, the city is surrounded by calcareous massifs. Unlike the majority of big Mediterranean cities, the rural fringe adjacent to the suburban area is absent in Marseille. This characteristic induces a particular spatial structure where the urban part of the city is directly

adjacent to natural areas. Since 2010, the southern part of the city is classified as National Park.

Species breeding occurrences

For the period 2009 to 2015, yearly breeding site locations of both jackdaws and ring-necked parakeets were compiled from the database of the regional antenna of the French Bird Protection League, a national network which compiles observations made by volunteers (Collectif, in <www.faune-paca.org>, subject to a convention and extracted on December 2015). When using volunteer observation networks, potential biases in the sampling effort and uncertainties in the spatial location of occurrence points may occur (Dickinson et al. 2010). To account for a possible uneven sampling effort, we included as bias predictors in the models the density of human population and the distance to small and main roads (Mair et al. 2017). In order to reduce possible localization errors, we verified that all breeding occurrences were located within a circular buffer of 5 m around a tree or a building (i.e. most representative locations for urban cavity-nesting birds) for both species. All the occurrences which did not fall into a buffer were removed from the dataset.

Breeding occurrences for the year 2016 were collected during an extensive field survey following a true-census sampling design. To ensure an equal sampling time of different parts of the city, the study area was divided into a regular grid with a spatial resolution of 1 km and each cell was visited once during a 30 min period from December 2015 to April 2016. If a nesting pair of jackdaw or RNP was found (i.e. observations of individuals inside cavities and/or a male feeding a female located within a cavity and/or in the case of the RNPs individuals with a damaged tail entering in a cavity), the exact coordinates of the nest were recorded. The exact location of every nest was then mapped and converted into a 50 m grid resolution raster. Considering that both species are conspicuous and frequent vocalists, we are confident our sampling accurately reflects their breeding distributions in the city. The final datasets were composed of a presence-only dataset for the period 2009–2015 and a Boolean dataset of presence–absence points for the year 2016, with a total of 1084 jackdaw breeding occurrences and 1830 RNP breeding occurrences.

Anthropo-ecological predictor variables

Based on the literature and on our ecological knowledge, we selected a set of 21 candidate predictor variables for the period 2009 to 2013, and 20 variables for the period 2014 to 2016 (summarized in Table 1).

No strongly correlated variables were included (verify using variance inflation factor < 5, R package 'usdm'). We used the density of built-up areas given that human-made structures may affect the urban species distribution at local scale (Evans et al. 2009). Anthropogenic food resources may affect the distribution and abundance of invasive species (Fuller et al. 2008, Galbraith et al. 2015).

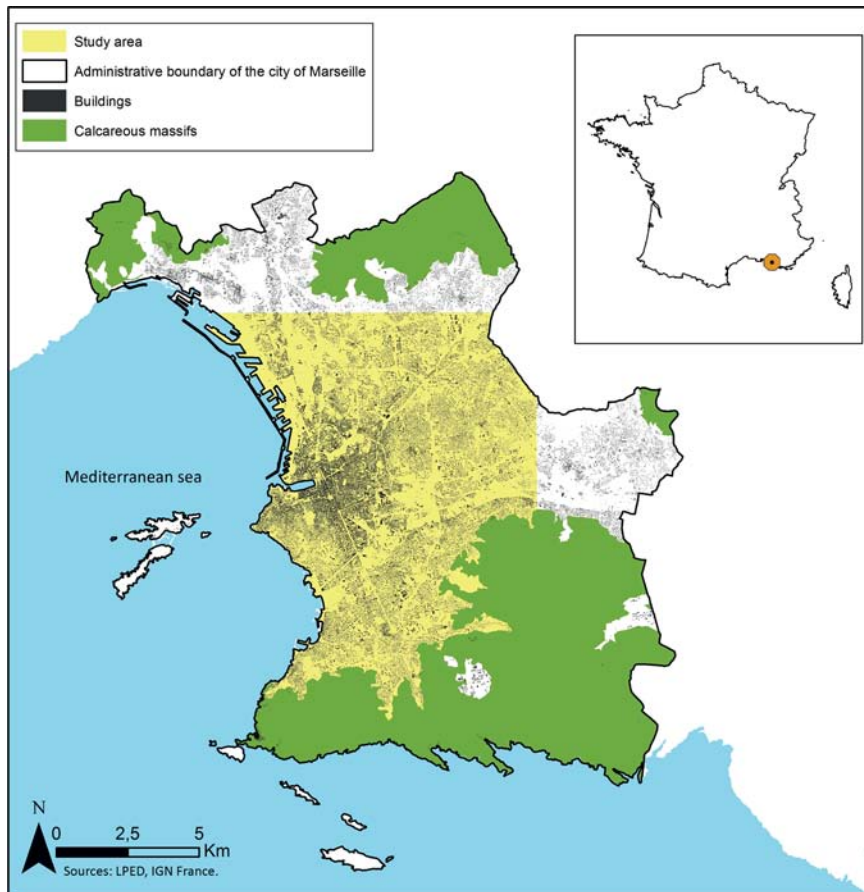


Figure 1. The geographical location of the study area in Marseille, France.

Given that a quantitative measure of bird feeders and direct feeding is difficult to obtain, the density of retired people (Davies et al. 2009), and the distance to healthcare establishments were used as proxies. The density and the presence/absence of *Platanus* sp. trees were also used as a predictor of cavities availability. Indeed, *Platanus* sp. is widely used by the RNP for breeding in its introduced range (Wegener 2007, Clergeau et al. 2009, Czajka et al. 2011, Hernández-Brito et al. 2014), especially in the study area (Le Louarn et al. 2017). Moreover, *Platanus* sp. is the most abundant broadleaf trees in Mediterranean cities and may display the highest number of available cavities (Ake et al. 1991). For the period 2009–2014, we extracted the spatial distribution of individual *Platanus* sp. from a geodatabase of the municipality. For the years 2015 and 2016, we used the GIS layer of the *Platanus* sp. trees coverage produced by a previous study (Le Louarn et al. 2017). To obtain the density of *Platanus* sp. trees for each grid cell, we divided the total coverage of the trees by the average leaf area of 50 trees calculated by visual interpretation on a spring Pléiade image ($n = 50$, $\mu = 43.95 \pm 31.64 \text{ m}^2$). Birds may prefer to nest on highest sites due to a lower predation risk (Nilsson 1984), thus the height of buildings was extracted from the National Inst. of Geographic Information (IGN) and included as predictor variables as well as natural potential food resources including herbaceous and agricultural areas, freshwater sur-

faces and the density of exotic plant species known to be consumed by the RNP (i.e. the total number of individual trees, detailed information can be found in Supplementary material Appendix 1 Table A1).

To take into account a possible spatial-scale dependent process in the habitat selection, the density and the height of buildings, the density of agricultural areas, exotic tree species, *Platanus* sp. trees, freshwater surfaces and herbaceous areas were calculated using three circular buffers (50, 500 and 1000 m) using ArcGis Spatial Analyst (ESRI 2014). To ensure temporal coherence between predictors and response variables, raster layers were extracted from temporally coincident databases for each year of the study time window (Table 1). The spatial resolution of all predictors was 50 m except for human population and retired people densities which were only available at the IRIS neighborhood resolution, the smallest unit of French demographic statistics defined by Insee (National Inst. of Statistics and Economic Studies <www.insee.fr>). These two predictor variables were thus resampled to a 50 m resolution.

We used the global Moran's indice (Moran 1950) to assess the spatial autocorrelation of each predictor and each occurrence datasets. The GMI was transformed into a Z-score calculated at different distances (corresponding to the three buffer distances used) for significance test and no spatial autocorrelation was found.

Table 1. Details of the variables used in the species distribution models. The spatial resolution was 50 m for all the predictors except for 'Density of human population' and 'Density of retired people' for which the spatial resolution was the IRIS neighborhood.

Abbreviation	Variable description	Source/reference	Date of datasets
Dist_MRoad	Distance to main roads (highways, national roads, departmental roads)	National Inst. of Geographic and Forestry Information (IGN)/Mair et al. (2017)	2011; 2014; 2016
Dist_SRoad	Distance to small roads	IGN/Mair et al. (2017)	2011; 2014; 2016
Densi_pop	Density of human population (number of human individuals per IRIS neighborhood)	National Inst. of Statistics and Economic Studies (INSEE)/Strubbe and Matthysen (2009b), Mair et al. (2017)	2009; 2010; 2011; 2012; 2013
Densi_retired	Density of retired people (number of retired individuals per IRIS neighborhood)	INSEE/Davies et al. (2009)	2009; 2010; 2011; 2012; 2013
Dist_health	Distance to healthcare establishments	IGN	2011; 2014; 2016
Densi_agri_50; Densi_agri_1000	Density of agricultural areas calculated in buffers of 50 m and 1000 m	Urban atlas (EEA 2014), Urban Community of Marseille Provence Métropole (MPM)/Strubbe and Matthysen (2009a)	2009
Densi_exo_50; Densi_exo_500; Densi_exo_1000	Density of exotic tree species on which <i>Psittacula krameri</i> and <i>Corvus monedula</i> are known to feed and calculated in buffers of 50 m, 500 m and 1000 m (Supplementary material Appendix 1 Table A1)	Marseille municipality; Supplementary material Appendix 1, 2	2009
PA_exo	Presence-absence of exotic tree species on which <i>Psittacula krameri</i> and <i>Corvus monedula</i> are known to feed (binary variable encoded 0 for absence and 1 for presence)	Marseille municipality; Supplementary material Appendix 1, 2	2009
Densi_Plat_50; Densi_Plat_500; Densi_Plat_1000 PA_Plat	Density of <i>Platanus</i> sp. trees calculated in buffers of 50 m, 500 m, and 1000 m Presence-absence of <i>Platanus</i> sp. trees (binary variable encoded 0 for absence and 1 for presence)	Remote-sensed predictors based on Le Louarn et al. (2017) and Marseille municipality database Remote-sensed predictors based on Le Louarn et al. (2017) and Marseille Municipality database	2009; 2015 2009; 2015
Densi_wat_50; Densi_wat_500; Densi_wat_1000 Dist_wat	Density of freshwater surface calculated in buffers of 50 m, 500 m and 1000 m Distance to freshwater surfaces	IGN/Strubbe and Matthysen (2009a) IGN/Strubbe and Matthysen (2009a)	2011; 2014; 2016 2011; 2014; 2016
Densi_herb_50	Density of herbaceous areas calculated in a buffer of 50 m	Remote-sensed predictors based on Strubbe and Matthysen (2007)/Le Louarn et al. (2017)	2015
Height_buil_50; Height_buil_1000 Densi_buil_50	Height of buildings calculated in buffers of 50 m and 1000 m Density of built-up areas calculated in a buffer of 50 m	IGN/Pellissier et al. (2012) IGN, Remote-sensed predictors based on Strubbe and Matthysen (2009b)/Le Louarn et al. (2017)	2011; 2014; 2016 2011; 2014; 2015; 2016

Modelling procedure

We built our ensemble model using four machine learning algorithms: Random Forests (RF, Breiman 2001), Maximum Entropy (MAXENT, Phillips et al. 2006), Gradient Boosting Model (GBM, Friedman 2001) and Artificial Neural Networks (ANN, Ripley 1996). Unlike parametric approaches, machine learning methods allow to model non-linear relationships and these methods are among the best performing techniques currently available (Elith et al. 2006, Olden et al. 2008).

For each species and for each year of the period 2009 to 2015, the four SDMs were trained and evaluated using 1) a 10-fold cross-validation procedure randomly sampling 80% of the occurrences for calibration and 20% of the remaining data for evaluation, 2) 100% of the occurrences for calibration and the presence-absence dataset of the considered species in the year 2016 as an independent evaluation dataset. Models for the year 2016 itself were evaluated using 10-fold cross-validation procedure whereby 80% of the occurrences were used to calibrate the models and the remaining 20% to evaluate the models. For each

yearly species models, we constructed the ensemble model by combining all SDMs with an AUC value > 0.7 using the weighted mean probability of occurrence (Araújo and New 2007, Marmion et al. 2009). Some of the algorithms we used required absence data to be fitted. As only jackdaw and RNP presence data were available for the period 2009–2015, we randomly generated 10 datasets of pseudo-absences for each species and for each year following the recommendations of Barbet-Massin et al. (2012). To assess the model accuracy, we used a threshold-independent evaluation statistic, the area under the receiver operating characteristic curve (AUC, Fielding and Bell 1997, Elith et al. 2006). The predictions of models with an AUC value above 0.7 were considered as good and reliable (Thuiller et al. 2009). For each year and each species, the variable importance score in the ensemble model was calculated using 10-times randomization. We calculated the mean importance value of all the predictors and defined the most important predictors as those with an importance score above this mean value. The predictor importance scores were then standardized as a percentage of the sum of all variable importance scores. SDMs and the ensemble modelling were run using the 'BIOMOD2' package (Thuiller et al. 2009) in R software (R Development Core Team). Other modelling parameters are detailed in Supplementary material Appendix 2. To account for possible interactions among predictors, we used the method proposed by Capinha and Anastácio (2011) to plot the variation of the habitat suitability along the gradient of the most important predictors for each species through the study period. To achieve this, we first reclassified each predictor variable raster into constant-interval classes (e.g. the values of the density of built-up areas were grouped using class amplitudes of 5%) and for each class, the corresponding median predicted habitat suitability value was extracted. Response curves were then obtained by plotting incremental predictor variables classes (x-axis) against their corresponding median habitat suitability (y-axis).

Dispersal-and-habitat-constrained final model

To account for dispersal limitation, we used MigClim (Engler and Guisan 2009), a cellular-automaton method which allows to take into account of the dispersal capacity and constraints of a species to obtain its likely future distribution. MigClim calculates the probability that a grid cell will become colonized based on dispersal distances, barriers to dispersal and habitat suitability (derived from niche models). As input data, we used the most recent breeding distribution of jackdaws and parakeets (i.e. the year 2016) as the species initial distribution. A TSS-maximising threshold was applied to reclassify the 2016 ensemble model predictive map of suitable habitat of considered species into presence-absence predictions, and used in MigClim as habitat suitability maps.

We simulated parakeet and jackdaw spread over a period of 50 yr, from 2017 to 2066. Given that parakeets and

jackdaws are strong fliers that regularly cover large distances, we assumed no strong barriers to dispersal across the city of Marseille. As our simulations were made without future environmental change scenarios, the environmental change steps parameter was setting with a value of one. For both species, initial maturity age was set to two years to reflect that the species need time to reach their full reproductive potential. We used a negative exponential dispersal kernel to approximate the probability of a propagule dispersing to pixels until the maximum dispersal distance of the species is reached. For the ring-necked parakeet, the maximum regular dispersal distance was set to 400 m, which corresponds to the mean dispersal distance found by Butler (2003) across London, UK. The possible range of long-distance dispersal events was set to a minimum of 450 m and a maximum of 15 000 m (longest recorded distance between a breeding site and the roost, MLL unpubl.) with a probability of 0.01 per dispersal step.

As no information is available about dispersal distances of western jackdaws, we set the maximum regular dispersal distance to 600 m, corresponding to the natal dispersal of the closely related American crow *Corvus brachyrhynchos* in urban habitats (Withey et al. 2005). Distance range of long-distance dispersal events was set to a minimum of 650 m and a maximum of 22 000 m (longest distance between a breeding site and the roost in our study area, pers. obs. MLL), again with a probability of 0.01 per dispersal step.

The output of MigClim is a raster which displays the species' dispersal-constrained predicted distribution at the end of the time-period chosen. The use of variable buffers and distances may result in a 'spread out' habitat suitability pattern that needs to be restricted to actual suitable breeding sites. Thus, we extracted from the habitat suitability map only pixels where trees and buildings were to obtain a more realistic map of the potential future distribution.

Results

Ensemble models tested with the 2016 independent dataset showed a lower but still good accuracy than models tested with cross-validation technique (Table 2). AUC values when randomly partitioning training dataset ranged between 0.98 and 0.95 while AUC values ranged between 0.89 and 0.76 when using an independent evaluation dataset, which indicates in all cases a good to excellent model accuracy.

Our results show that while factors underlying parakeet and jackdaw breeding distribution differed between years (Fig. 2), our non-native invasive and range-shifting native species exhibit both differences and similarities in their tolerance to urban features (Fig. 3 and Fig. 4, Supplementary material Appendix 1 Fig. A3 and Fig. A4).

A striking difference is that for all breeding seasons considered, the probability of parakeet presence decreased with

Table 2. Area under the receiver operational characteristic curve (AUC) values for ensemble models for *Psittacula krameri* and *Corvus monedula* for each modeled year according to the evaluation procedure (evaluation with a random partition of the training dataset or with an independent dataset).

Ensemble models Year	Cross-validation AUC		'Independent' AUC	
	<i>Psittacula krameri</i>	<i>Corvus monedula</i>	<i>Psittacula krameri</i>	<i>Corvus monedula</i>
2009	0.96	0.97	0.76	0.78
2010	0.99	0.97	0.78	0.76
2011	0.99	0.98	0.81	0.80
2012	0.96	0.96	0.85	0.87
2013	0.95	0.96	0.84	0.83
2014	0.95	0.97	0.86	0.82
2015	0.96	0.98	0.86	0.89
2016	0.95	0.98	NA	NA

increasing density of built-up areas (Fig. 3) while the opposite is true for jackdaws (Fig. 4). A similar pattern was observed for the density of exotic tree species, which consistently had a strong positive effect on parakeet presence but was negatively correlated to jackdaw breeding presence. Parakeets and jackdaws responded in a similar way the availability of freshwater and the height of city buildings. Both species preferred to breeding in areas close to or with an ample supply of freshwater and preferred habitats characterized by intermediate values for buildings heights, although these relationships were more constant and pronounced for parakeets than for jackdaws (Fig. 2). At least in some years, jackdaws were less likely to nest in parts of the city where more agricultural lands were present (Fig. 4). Contrary to our expectations, the density of *Platanus* sp. trees was not a consistent driver of ring-necked parakeet breeding occurrences (Fig. 3), and even in the years where it has a non-negligible influence, parakeets were less, not more, likely to breed in or close to *Platanus* trees.

When forecasting the future geographical spread of both species based on their most recent breeding distribution (i.e. the year 2016), our results indicate areas highly suitable for ring-necked parakeets are mostly found in the south-western part of the city while smaller kernels of suitability are dispersed across intra-urban parts in the east and north (Fig. 5a). Optimal jackdaw habitats are mainly grouped in the city center in the west and dispersed in small kernels in the south-west, south, and north (Fig. 5b). After thresholding our predictions of habitat suitability to binary projections, we find that in total 5.21% ($n = 2022$ cells, 5.05 km^2) of the total extent of Marseille are suitable for parakeets (Fig. 5c) and 25% ($n = 8498$ cells, 21.24 km^2) for jackdaws (Fig. 5d). The spatial overlap of suitable pixels between the two species represents 69.32% of the total suitable area for the parakeet and 17.27% for the jackdaw.

During the MigClim simulation, the jackdaw colonized the areas adjacent to known breeding occurrences on the first steps then new areas closed to calcareous massifs to the south, east and north followed by colonization of more intra-urban areas (Fig. 6b). The dispersal process of the ring-necked parakeet was restricted to areas adjacent to the known breeding occurrences mainly in the south of the city (Fig. 6a). All the suitable pixels were colonized by the parakeet during the

first steps of the dispersal process and around the year 2050, almost all the parakeets' suitable habitats were colonized (Fig. 7). Although the colonization of all suitable habitats ended around the same time, the jackdaw displays a greater colonization potential.

Discussion

In this study, we assess how two co-occurring, expanding bird species, the native western jackdaw and the non-native ring-necked parakeet, respond to different features of urban environments in the same Mediterranean city. Urban areas are often characterized as more stable and constant compared to more natural systems (Anderies et al. 2007), yet we find that even in these areas, single-season occurrence data may be insufficient to adequately characterize species' habitat requirements, as the relative importance of different predictor variables varied strongly through time. Using single-season datasets may only represent a temporal snapshot of the ecological requirements of species and our results highlight the advantage of using multi-season datasets to better understand species' ecological requirements. Our results support previous findings (Araújo et al. 2005, Hijmans 2012, Eskildsen et al. 2013) that model validation with a partition of the training dataset (non-independent evaluation dataset) shows higher predictive accuracy in comparison with model validation based on an independent dataset from a further time period.

We expected that native range-expanding jackdaws would be more strongly associated with habitat variables reminiscent of their original rural habitats while non-native invasive parakeets should be more closely associated with urban land cover. Building on an occurrence dataset spanning eight years, we find that this expectation is however only partially met. Ring-necked parakeets are indeed more likely to breed in areas characterized by urban features such a high density of exotic tree species, but avoid breeding in the immediate vicinity of buildings. In contrast to the parakeets, jackdaws preferred breeding close to urban structures, but contrary to expectations, there was no evidence they selected breeding sites close to agricultural lands, their main rural foraging habitat. This suggests that the apparently similar colonization

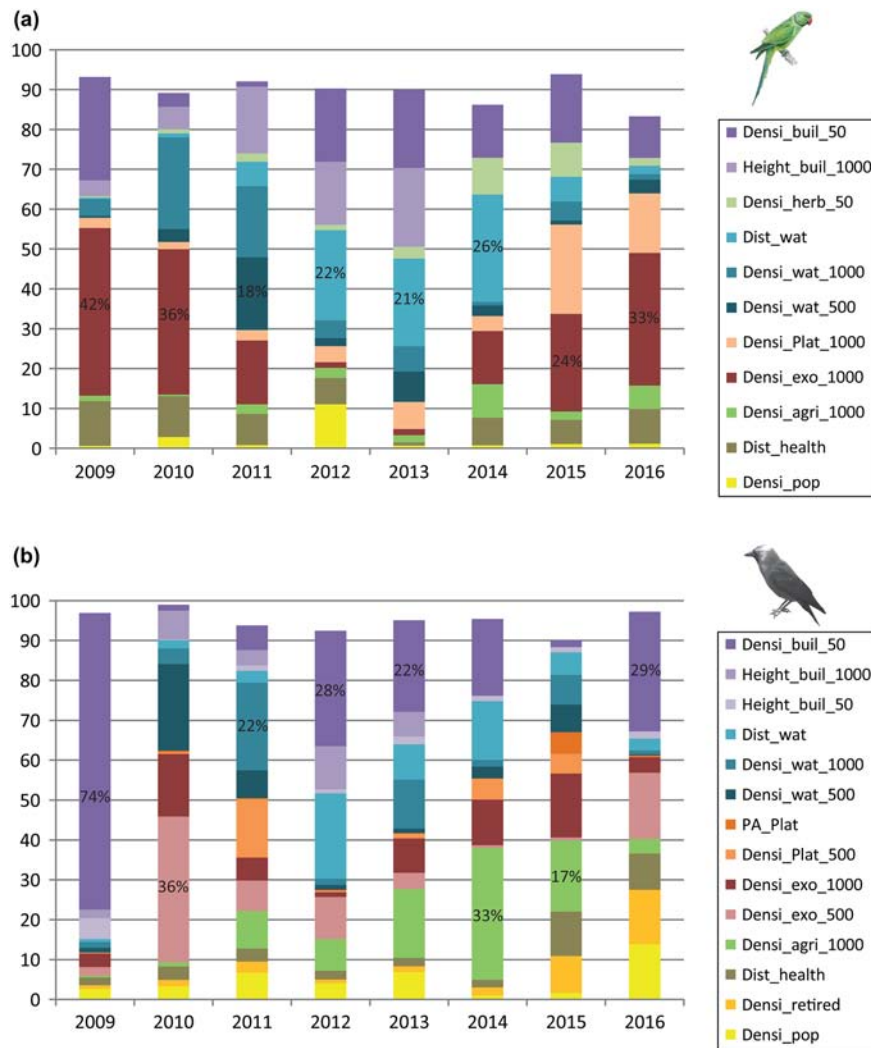


Figure 2. Yearly relative importance of the predictors as a percentage for ensemble models used to predict the distributions of (a) *Psittacula krameri* and (b) *Corvus monedula*. Each variable score, measured by randomization technique, was standardized into a percentage of the sum of all variable importance scores. The mean importance value of all predictors was calculated and only the predictors with an importance score above the mean value were kept. The relative contribution of the most important predictor per year is indicated. Abbrev.: Densi_buil_50 (density of built-up areas in a 50 m buffer), Height_buil_1000 and Height_buil_50 (respectively height of buildings in a 1 km buffer and in a 50 m buffer), Densi_herb_50 (density of herbaceous areas in a 50 m buffer), Dist_wat (distance to freshwater surface), Densi_wat_1000 and Densi_wat_500 (respectively density of fresh surface water in a 1 km buffer and in a 500 m buffer), Densi_Plant_1000 and Densi_Plant_500 (respectively density of *Platanus* sp. in a 1 km buffer and in a 500 m buffer), PA_Plant (presence-absence of *Platanus* sp.), Densi_exo_1000 and Densi_exo_500 (respectively density of exotic tree species in a 1 km buffer and in a 500 m buffer), Densi_agri_1000 (density of agricultural areas in a 1 km buffer), Dist_health (distance to healthcare establishments), Densi_retired (density of retired people), Densi_pop (density of human population).

process of urban areas by both species may be driven by different underlying mechanisms. To our knowledge, only one study has compared the ecological space occupied by co-occurring expanding native and non-native species using SDMs (Pouteau et al. 2015) and none in urban areas specifically. Although the tolerance of species to different types of habitat and resources could be a key determinant for colonization and dominance in new environments (Sax and Brown 2000), Pouteau et al. (2015) found no evidence that non-native plant species have broader environmental tolerances

than natives that might facilitate invasion success into a wide range of habitats.

Despite between-year variability, the density of built-up areas in the immediate vicinity (i.e. within 50 m) consistently ranked among the most important predictors of jackdaw breeding distribution. In non-urban habitats, jackdaws typically prefer to breed in wide, open natural tree cavities (Johnsson et al. 1993, Balen et al. 2002), but a recent review by Meyrier et al. (2017) concluded that these birds may be attracted to cities because buildings provide ample cavities,

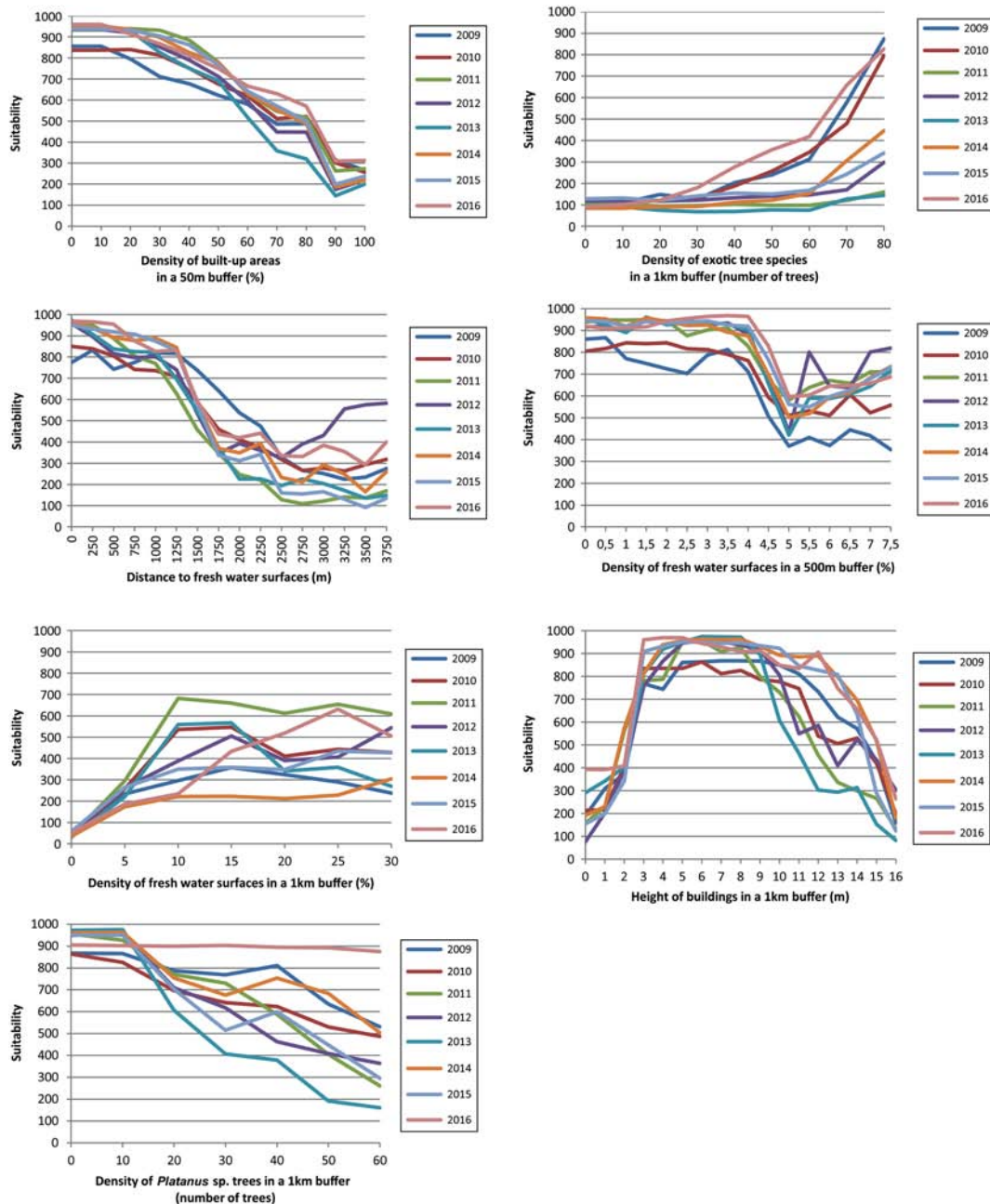


Figure 3. Suitability curves along the gradients of the most important predictors for *Psittacula krameri* for an eight-year period (from 2009 to 2016).

crevices, and elevated platforms, which may serve as roosting or breeding sites. Several studies have found a higher density of jackdaws in the urban core of Finnish (Jokimäki and Suhonen 1998) and Israeli cities (Kark et al. 2007), compared to adjacent non-urban areas. Yet, increasing evidence suggests that cities may act as an ecological trap for jackdaws. They may be attracted to urban areas by the availability of nesting sites, but the reduced availability of natural food sources combined with the generally poor nutritional quality of anthropogenic foods (Pierotti and Annett 2001) typically leads to low breeding success (Harrison et al. 2010, Plummer et al.

2013a, b). Urban jackdaws may have undertaken long and energetically costly foraging trips to reach high-quality food outside urban areas, or settle for low-quality human-provided foods, which contains two to three times less protein than invertebrates (Heiss et al. 2009). Worryingly, we found no evidence that jackdaw breeding was more likely in urban areas closer to agricultural lands, nor was there any indication that jackdaws use of alternative, ‘novel’, high-quality foods sources offered by the diverse community of exotic tree species present in the city of Marseille. In France, the jackdaw was listed as a protected species in 1989, and their populations have

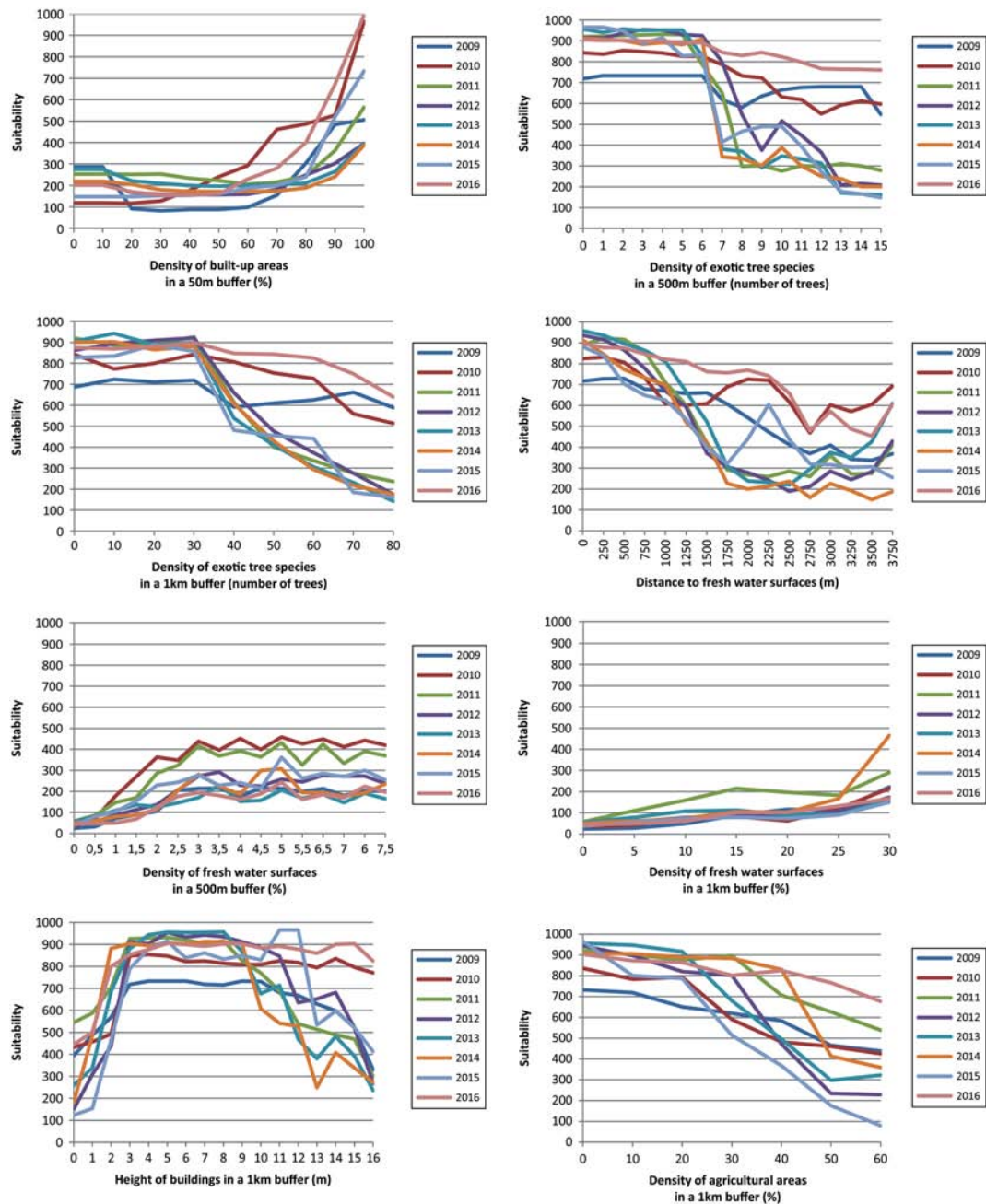


Figure 4. Suitability curves along the gradients of the most important predictors for *Corvus monedula* for an eight-year period (from 2009 to 2016).

since strongly increased in size and range (Jiguet 2016). Our results from Marseille suggest that increasing rural population densities and/or changing ‘landscape of fear’ after the species became legally protected drive jackdaws into urban areas, where they are attracted by a high cavity availability and abundant, yet likely substandard, food resources. We suggest that further research aimed to evaluate jackdaw breeding success and population dynamics, especially regarding its urban diet. Indeed, previous studies have highlighted that the more urbanized individuals of starlings *Sturnus vulgaris* have a lower reproductive success (Mennechez and Clergeau 2006),

and despite a higher density of individuals in urban core, the nutritional state of the American crow *Corvus brachyrhynchos*, and the nestling development and survival of sparrows *Passer domesticus* are lower than in suburban and rural habitats (Peach et al. 2008, Heiss et al. 2009).

This is in stark contrast to the situation of the ring-necked parakeet. This non-native, invasive species was first noticed in Marseille in the middle of the 1990s (Barthélemy 2015), but its population has rapidly grown to almost 2000 individuals in the year 2016 (MLL unpubl.), corresponding to the rapid spread commonly observed in

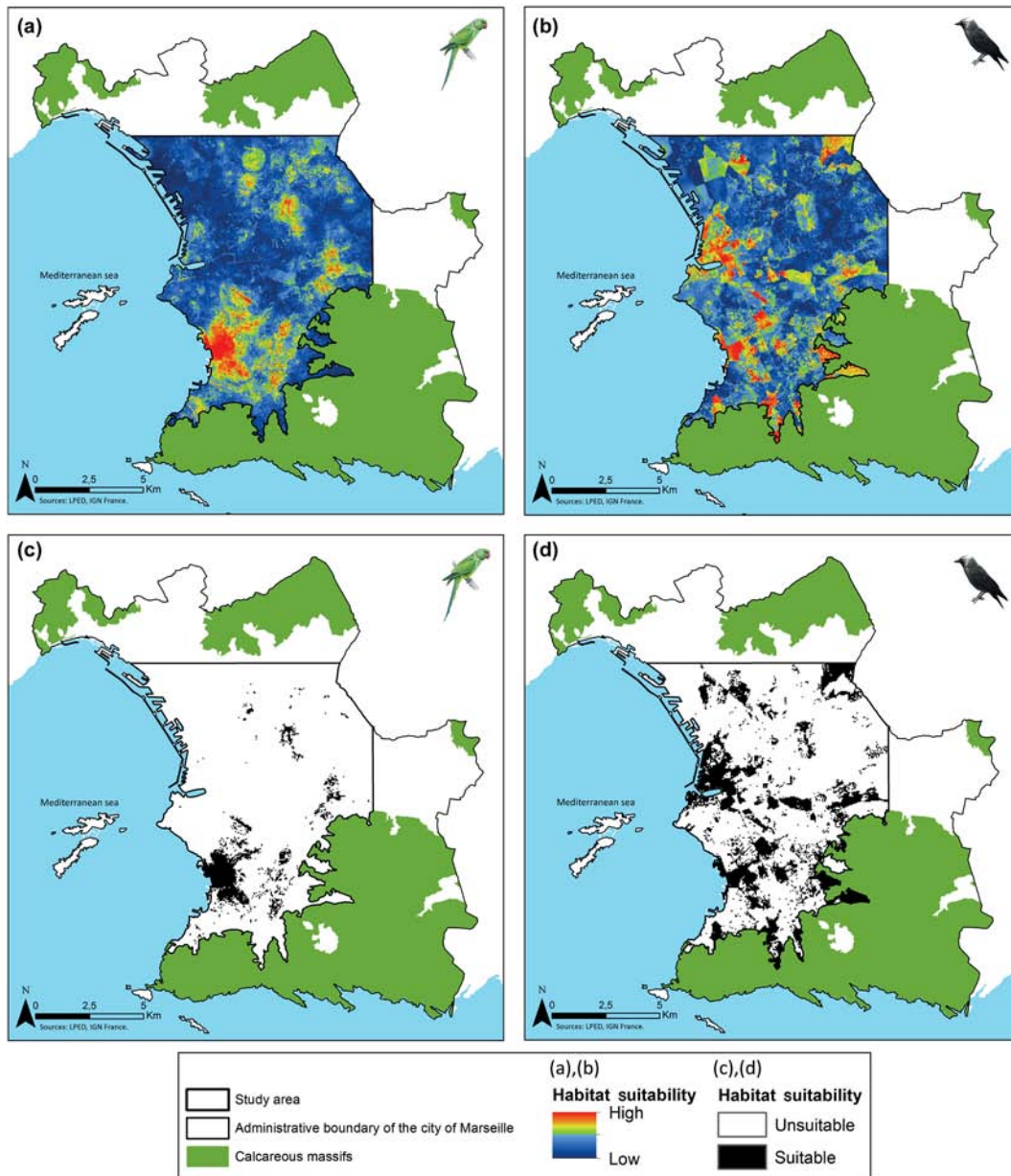


Figure 5. Habitat suitability maps for (a, c) *Psittacula krameri* and (b, d) *Corvus monedula*. Each map was built using ensemble modelling procedure in BIOMOD2 package, a set of environmental predictors and breeding occurrences of the year 2016 (maps (a) and (b)). A TSS-maximising species-specific threshold was applied to produce binary maps (maps (c) and (d)).

invasive species (Mack et al. 2000). There are no other, large parakeet populations nearby and the growth of the Marseille population, which is the second largest population in France, thus cannot be attributed to immigration from other areas. Our results suggest parakeet invasion success is attributable to the parakeets exploiting an ‘empty niche’ (Tilman 2004, Sol et al. 2012) in urban areas, as evidenced by the strong relation between their breeding occurrence and the density of exotic tree species. Very few studies on bird foraging behavior have taken into account the origin of plants but Mills et al. (1989) reported that in urban areas, native bird species richness is primarily driven by the availability of

(remnants of) native vegetation, and Gray and van Heezik (2016) found that non-native trees were almost always visited by native bird species only for invertebrates. Their findings may suggest an ‘open-windows’ of foraging opportunities for species that are spatially and temporally able to exploit seeds and fruits produced by exotic vegetation. Several studies have suggested that such an abundant food availability is a major factor underlying the ring-necked parakeet invasion success in European cities (Strubbe and Matthysen 2009a, 2011, Clergeau and Vergnes 2011), and have applied a range of proxies to try to quantify urban food availability. For example, in Brussels, Belgium, ring-necked parakeets were

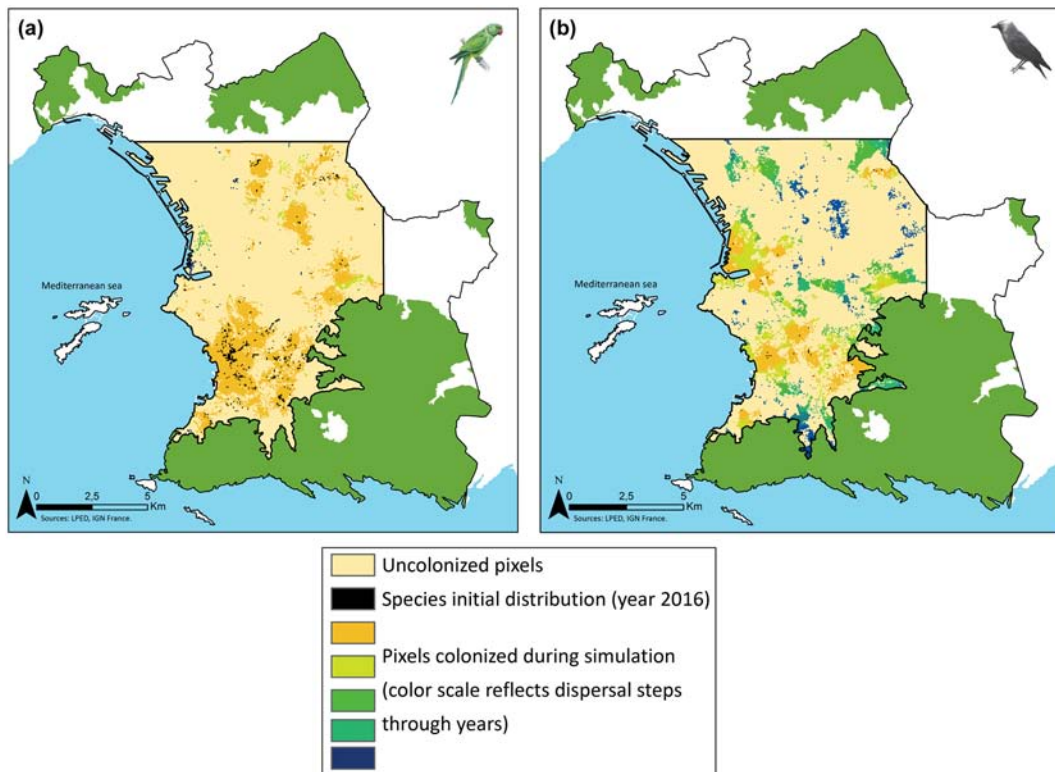


Figure 6. Habitat colonisability maps for (a) *Psittacula krameri* and (b) *Corvus monedula*. Each map was built from the habitat suitability map produced by BIOMOD2 ensemble models for each species implemented in MigClim package to account for dispersal constraints and in ArcGis to account for habitat constraints. Projections were made over 50 yr from 2016 and the color scale reflects every 10 yr' dispersal steps.

more likely to occupy habitats with a high density of built-up areas (Strubbe and Matthysen 2007, 2009b), and accounting for human modification of natural habitats strongly increased the accuracy of native-ranged based predictions of parakeet invasion risk across Europe (Strubbe and Matthysen 2009b). Across London, parakeet densities were found to be higher in areas where more retired people live (Pithon 1998), as they

are more likely to engage in bird feeding (Davies et al. 2009). Telemetry (Clergeau and Vergnes 2011) and video-recording (Le Louarn et al. 2016) based parakeet foraging behavior studies in northern France confirm that parakeets make ample use of backyard bird feeders while radio-tracking in Brussels, Belgium found that parakeets often forage on exotic tree and shrub species in urban park and gardens (Strubbe

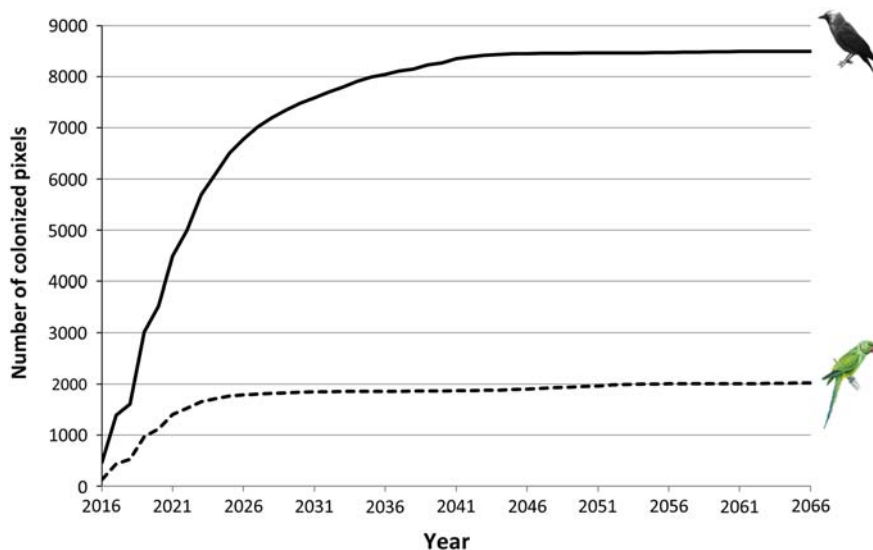


Figure 7. Colonization dynamics in the MigClim simulations for *Psittacula krameri* (dotted line) and *Corvus monedula* (solid line) over 50 yr.

and Matthysen 2011). While spatially explicit studies often have to rely on crude proxies of food availability, we were able to directly model the density of exotic tree species across our study area and found that this was indeed the most important predictor of parakeet breeding presence. Urban plant communities are characterized by a higher density and greater abundance of exotic species (Luck and Smallbone 2010), and positive relationship between non-native bird abundance and the density of exotic vegetation have been reported before (Mills et al. (1989)). Exotic horticultural species are planted for aesthetic purposes and their diversity may provide food resources all over the year for urban birds (Chace and Walsh 2006). Indeed, multiple exotic tree species planted across Marseille grow fruits during winter as well (e.g. *Diospyros* sp.), and the parakeets' powerful beaks allow them to exploit food items such as *Aesculus hippocastanum* fruits, which are difficult to access for most if not all native birds.

Interestingly, the often-used proxy, the density of retired people, and the first-used proxy, the distance to healthcare establishments, of supplementary feeding by humans did not have a strong positive effect on jackdaw and parakeet breeding habitat selection across Marseille, and the density of built-up areas even negatively influenced parakeet habitat suitability. A likely explanation is that in Mediterranean region where winter is rather mild, the necessity for birds to use bird feeders is lower and more natural (and likely healthier) resources, such as those offered by exotic vegetation, can sustain their populations. The geographical area of our study may also explain the importance of water resource related variables which can be attributed to frequent summer droughts and heat waves that affect the Mediterranean. This hypothesis may be supported by the fact that, in Belgium, predictor variables related to water availability were not important to explain the distribution of the ring-necked parakeet (Strubbe and Matthysen 2009b). In the near future, global changes could induce a scarcity of water resources, especially in Mediterranean areas and even in cities (Grimm et al. 2008).

Parakeet presence and abundance are generally higher in more urban areas (Strubbe and Matthysen 2009a, Hart and Downs 2014). The fact that we found an opposite relationship is likely due to the fact that we assessed urbanization in the immediate vicinity of the nest (i.e. within 50 m), rather than landscape-level scale. Breeding parakeets are known to usually forage within a few hundred meters from their nests (Strubbe and Matthysen 2011), and our metric of urbanization is thus likely not a proxy of food availability but of other habitat features. Parakeets nest loosely colonial, allowing them to protect their eggs and chicks against predators by effective communal mobbing behavior. Sites with a high degree of urbanization at the 50 m level likely harbor less nesting trees and thus breeding opportunities, suggesting that parakeet prefer to breed in areas with more nesting opportunities. That cavity availability (represented by the density of *Platanus* sp. trees) was not an important predictor of parakeet presence supports this interpretation: as nesting cavities are (at least currently) not a limiting factor, parakeets can choose to nest in areas where sufficient cavities are available

for their loose colonies. Despite the fact that it is commonly assumed that the availability of cavities is a limiting factor in urban areas, most studies have been conducted in forested areas. A similar proportion of excavated cavities between forests and urban parks has been found in the Chicago area (LaMontagne et al. 2015) and the *Platanus* trees preponderance in many European cities may increase cavity availability. This is likely to change however as the spatial expansion of *Ceratocystis platani*, a fungus responsible for the *Platanus*-specific lethal canker stain disease, forces urban green space managers to remove dying trees. These are then replaced by cavity-poor younger trees, such as the honeyberry tree *Celtis australis*, potentially leading to stronger competition between cavity-nesting species in the near future.

When applying our findings on parakeet and jackdaw habitat selection in Marseille to obtain spatially-explicit predictions of habitat suitability, we find more suitable habitats for jackdaws compared to parakeets. Ring-necked parakeets are likely to expand only into greener areas with a high amount of exotic trees, and parakeet range dynamics may be influenced by the urbanization history of the city of Marseille. As a legacy from the 14th century's bastides (small castles), Marseille's landscapes have a particular signature due to the presence of large gardens that belong to ancient bastide's estates and are mainly planted with ornamental exotic trees (Arrif and Hayot 1995, Roncayolo 1997). These areas offer parakeet both favorable nesting and foraging opportunities, fuelling their population increase and range expansion. Jackdaws, on the other hand, may be likely to colonize a larger part of the city because of their tolerance of, even preference for, strongly urbanized areas. While such habitats are in ample supply, it is not clear whether jackdaws will be able to obtain sufficient high-quality food for successful breeding and their colonization of Marseille may depend strongly on continued immigration from outside the city. Nonetheless, because of their higher dispersal capacities, jackdaws are predicted to spread more than the parakeets, highlighting areas where competition for breeding cavities between parakeets, jackdaws, and other cavity nesters is most likely to occur. Importantly, in the near future, the southern part of the city will be extensively colonized by both species. This area represents an important conservation spot because of its proximity to natural, biodiverse area such as the National Park of the Calanques (Lizée 2015), and we recommend conservation managers to prioritize this area either for preventing or slowing down of parakeet range expansion towards the area or by taking mitigation actions, such as ensuring an adequate supply of nesting cavities for vulnerable species.

Both target species in our study have small regular dispersal distances (less than 1000 m). Taking into account their dispersal capacities allows, therefore, to provide a more realistic forecast of their future distribution compared to projections based on unlimited dispersal scenarios. When addressing the issue of invasive species at local scale, dispersal can be a key factor that needs to be taken into account, especially in applied studies planning management strategies (Jeschke and Strayer 2008). The dynamic 'hybrid' modelling framework

proposed in our study should be used to investigate potential differences in the spatiotemporal patterns of both target species in other cities under different climates, but also to compare patterns of other species of successful urban birds.

Cities offer a unique environment in which a small number of species find new opportunities to establish and spread while others fail to maintain viable populations. Whether for conservation or management issues, it is therefore important to better understand the differential responses of species to this neo-ecosystem. Species distribution models are a widely used and an important tool to determine ecological requirements and forecast future distribution of urban invasive species. We hope that possible temporal variations and dispersal abilities will be more taken into account in these models in the future.

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Supplementary material (Appendix JAV-01527 at <www.avianbiology.org/appendix/jav-01527>). Appendix 1–2.