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## Intra-guild spatial niche overlap among three small falcon species in an area of recent sympatry

A. BERLUSCONI <sup>1,2\*</sup>, D. PREATONI <sup>1</sup>, G. ASSANDRI <sup>3</sup>, F. BISI<sup>1</sup>, M. BRAMBILLA <sup>4</sup>,  
J. G. CECERE <sup>3</sup>, S. CIOCCARELLI <sup>4,5</sup>, N. GRATTINI<sup>6</sup>, M. GUSTIN<sup>7</sup>, A. MARTINOLI <sup>1</sup>,  
D. RUBOLINI <sup>2,4</sup>, A. SBRILLI<sup>2</sup>, A. ZANICHELLI<sup>7</sup>, A. MARTINOLI <sup>1</sup>, &  
M. MORGANTI <sup>2</sup>

<sup>1</sup>Environment Analysis and Management Unit - Guido Tosi Research Group - Department of Theoretical and Applied Sciences, Università degli Studi dell'Insubria, Varese, Italy, <sup>2</sup>CNR-IRSA National Research Council – Water Research Institute, Brugherio (MB) and Montelibretti (RM), Italy, <sup>3</sup>Area Avifauna Migratrice, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Ozzano dell'Emilia (BO), Italy, <sup>4</sup>Politiche Ambientali, Università degli Studi di Milano Dipartimento di Scienze e , Milan, Italy, <sup>5</sup>Ethology Unit, Department of Biology, University of Pisa, Pisa, Italy, <sup>6</sup>S.O.M., Stazione Ornitologica Modenese “Il Pettazzurro”, Modena, Italy, and <sup>7</sup>Conservation Department LIPU-Birdlife Italia, Parma, Italy

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### Abstract

Climate warming and land-use change are reshuffling the distribution of wild organisms on a global scale. Some species may expand their ranges and colonize new regions, which may greatly affect ecological interactions among pre-existing species and colonizers. In the last decades, such processes have originated a unique condition of sympatry among three Eurasian small *Falco* species (common kestrel *F. tinnunculus*, lesser kestrel *F. naumanni*, red-footed falcon *F. vespertinus*) in the intensively cultivated farmland habitats of the Po Plain (Northern Italy). This provides an excellent opportunity to investigate patterns of spatial niche overlap during the initial phases of the establishment of sympatry. To investigate spatial niche overlap of the three falcon species, we relied on Environmental Niche Models (ENMs) based on widespread breeding occurrence data obtained through field surveys and citizen science programs (during the 2018–2020 period). ENMs were based on bioclimatic and land-use variables in an ensemble modelling framework. We estimated species-specific relative contributions of each climatic and land-use variable and its response curves effect. Eventually, we generated spatial correlation maps of the potential species' distributions to derive spatially-explicit predictions of potential co-occurrence areas among the three species. Overall, eco-climatic determinants of the distribution of lesser kestrel and red-footed falcon were similar, resulting in a strong association with intensive arable lands and dry continental climate. Consistently, we found a high spatial correlation between the suitability maps of the two species, with highly suitable areas located in the Central-Eastern area of the Po Plain, corresponding to the core range of both species. Conversely, the common kestrel emerged as a habitat generalist and was widely distributed throughout the Po Plain. Our findings suggest that the recent sympatry between lesser kestrels and red-footed falcons in the Po Plain may promote ecological interactions and intra-guild competition.

**Keywords:** Agricultural landscapes, environmental niche models, falcons, interspecific competition, coexistence

### Introduction

Climate and land-use changes are among the main drivers of the reshuffling of animals distribution and abundance patterns at a global scale (Clavero et al.

2011; Barnagaud et al. 2012). Specifically, this is well identified by animal communities settled in heavily anthropized landscapes, where the effects of complex interactions of ecological and

\*Correspondence: A. Berlusconi, Environment Analysis and Management Unit - Guido Tosi Research Group - Department of Theoretical and Applied Sciences, Università degli Studi dell'Insubria, Via J. H. Dunant 3, 21100 Varese, Italy. Email: [aberlusconi@uninsubria.it](mailto:aberlusconi@uninsubria.it)

anthropogenic drivers have determined large-scale reassembling over different spatial scales (Oliver et al. 2017). This is the case of birds living in intensively cultivated agricultural habitats, where the conflict between nature conservation and economic needs is harsh (Donald et al. 2001; Brambilla 2019). For instance, the ban of some specific pesticides has caused the return of locally extinct species in many agroecosystems (Green 2005), while climate warming has favoured the northward expansion of several species towards new breeding areas, sometimes even for species declining at a global scale (Barbet-Massin et al. 2012; Bellard et al. 2012). Such “newcomers” (Beddall 1963; Holtmeier 2015) are those species that rapidly expanded into new areas naturally (thus excluding alien species), by often adapting to anthropogenic changes in the environment, and may interact together or with local species that share similar ecological needs, since they could represent new competitors or predators (Pigot et al. 2018).

Understanding how ecologically similar species can coexist and which dynamics emerge during the colonization process are central goals for evolutionary ecology (Barabás et al. 2016). Indeed, it is key to understand the mechanisms at the basis of the maintenance of diversity over evolutionary times (Chesson 2000), while also suggesting potential solutions to specific conservation issues. Identifying and quantifying the eco-climatic parameters defining the spatial niche of a species (or population) is essential to understand how it can thrive in a specific environment (Schoener 1974) and to understand patterns of coexistence among ecologically similar species (i.e. those belonging to the same guild). Coexistence among species is achieved by niche partitioning, whereby coexisting species exploit different portions of the niche space, eventually minimizing competition to narrow their own realised niche (Capula et al. 1993; Pande et al. 2018; Ye et al. 2021).

In this context, Ecological Niche Models (ENMs hereafter) represent an effective tool to define the eco-climatic variables that quantitatively describe the spatial niche of a given species (Soberon & Peterson 2005; Sutton & Puschendorf 2020). ENMs are based on the association between spatially explicit information on species occurrence with maps representing the variability of ecological, climatic or land-use factors to gather an ideal range of values in which the species is likely to occur, allowing to estimate habitat suitability also over areas that could not be directly censused (Guisan & Thuiller 2005). ENMs are routinely used into a broad variety of research disciplines, which include the study of the biological responses to climate

change (Graham et al. 2007; Sutton 2020), invasive species biology (Thuiller et al. 2005) as well as in ecological and evolutionary biology in general (Kozak & Wiens 2006). Moreover, these modelling techniques are highly suitable to compare the eco-climatic preferences among similar species and to investigate current and future patterns of co-occurrences and infer potential ecological interactions (e.g. Brambilla et al. 2020).

This study aimed at characterizing the eco-climatic factors affecting habitat suitability in a guild composed by three small falcons, and comparing the spatial niche derived from ENMs. We focused on the intensively cultivated Po Plain (Northern Italy) where recently lesser kestrel (*Falco naumanni*), red-footed falcon (*Falco vespertinus*) and common kestrel (*Falco tinnunculus*) are breeding in sympatry. Climate change has favoured the north-ernwise breeding expansion of the lesser kestrel in the area (Morganti et al. 2017), with the first breeding attempt in 2000; hypothetically due to climate and, most likely, land-use changes, the area was firstly colonised by red-footed falcon in 1995 (Ravasini 1995), with a recent expansion through the area; at the same time, from 1980s, Po Plain experienced an expansion and population increase of the common kestrel (Rete Rurale Nazionale & Lipu 2021), whose causes remain still uncertain. These three species are typically tied to open or semi-open landscapes and exploit similar ecological resources, thus can be defined as a guild (*sensu* Root 1967), potentially competing for spatial or trophic resources. On the other hand, they tend to differ in migratory patterns, degree of sociality, phenology, habitat selection (Palatitz et al. 2018; Sarà et al. 2019; Costantini & Dell’Omo 2020). Furthermore, while there are several areas in Eurasia where two of these three species coexist, the Po Plain is the only part of their global range where they are all breeding in sympatry, thus this unique circumstance could promote new competitive interactions in terms of interference and/or exploitation (see Remington 1985). Exploring the eco-climatic preferences of these three species and predicting their potential distributions in the Po Plain thus offer the unique opportunity to investigate the extent of spatial niche overlap at a regional scale (Elith et al. 2006; Graham et al. 2007), to study intra-guild competition at an early stage of sympatry.

Using breeding occurrence data, collected both directly on the field and obtained from a citizen-science database, we modelled potential species distributions. Then, we estimated the spatial niche overlap among species by comparing the responses to the various eco-climatic variables entered in the

models as predictors. Eventually, we produced spatially explicit correlation maps to estimate the degree of potential range overlap among the distributions of the species pairs. We then discuss how our findings improve the knowledge about the mechanisms of the intra-guild co-occurrence and suggested future research lines that should be investigated in the next future to shed light on the potential consequences of interspecific interactions at a population level.

## Materials and methods

### *Study area*

The study area was located in the Po Plain (Northern Italy, mean latitude 45°N, mean longitude 11°E) in an area extended ~46,000 km<sup>2</sup> (Figure 1). Yearly rainfall varies between 700 and 1,200 mm, with maximums during autumn and spring. The annual mean temperature is 12°C, with a marked temperature seasonality (Arpa -

Agenzia Regionale Prevenzione e Ambiente dell'Emilia-Romagna 2004). Starting from the 1960s, the whole area has been significantly affected by climate change, with an increase in average temperatures (the 2019 was 1.7°C higher than 1961–1990), extreme summer heatwaves and an increase in drought events (during 2019 the overall precipitation was 220 mm less than the reference climate 1961–1990) - the latter decrease mainly due to the lack of summer precipitation (Arpae 2020).

Land-use in the area has also changed in the last two decades. Specifically, in Emilia-Romagna, the Region that hosts most of the breeding occurrences of falcon guild, the enforcement of the Common Agricultural Policy (2003) has favoured the extension of alfalfa cultivation (+19.6%) and set-aside (+102.4%). These environmental-friendly crops replaced maize, which reduced in the same period by the 23.5%. Noteworthily, over the same period, the extent of urbanized areas has also strongly increased (+50%) at the expense of arable land (-40%) (Regione Emilia-Romagna 2009).

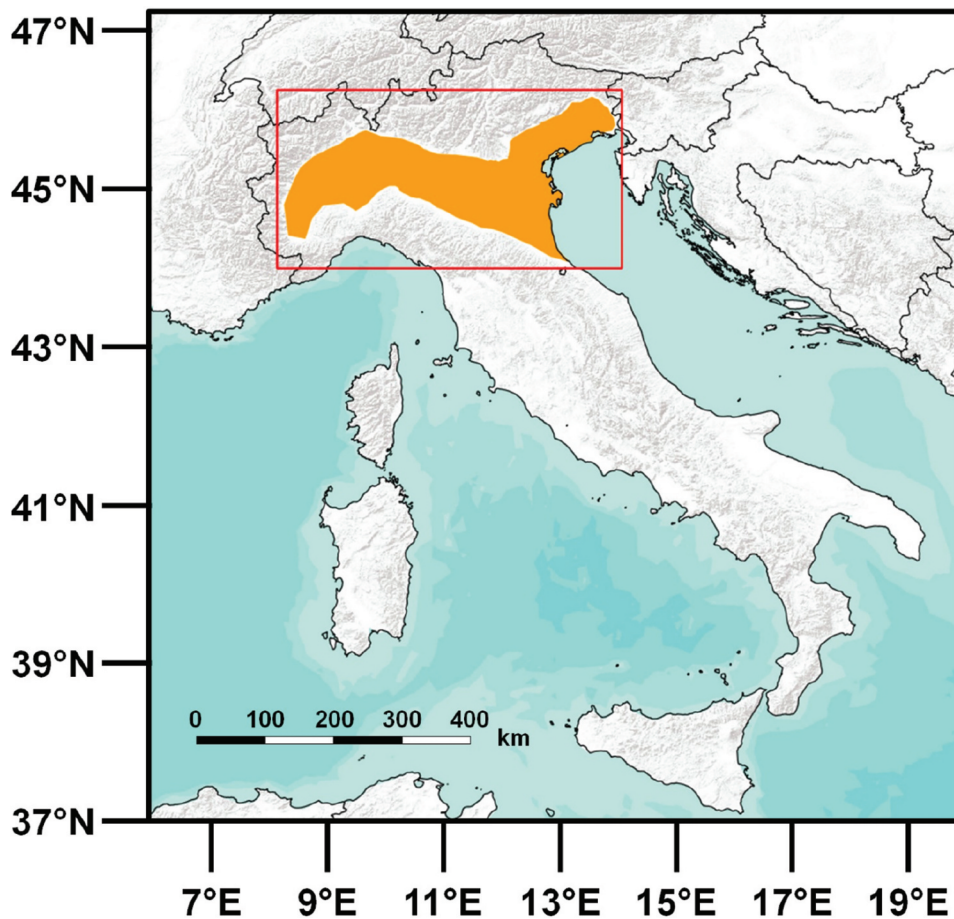


Figure 1. Map of Italian Peninsula and study area. Orange area represents Po Plain in its entirety. Red rectangle is the polygon extent of Po Plain with 10-km-buffer where Ecological Niche Models were performed.



We added 10-km-buffer-radius to the study area of Po Plain as a whole, then we generated a rectangular polygon extent whose limits are 41.00°N, 23.22°E and 46.06°N, 25.83°E (Figure 1). We considered this extent to perform Ecological Niche Models (see also Radosavljevic & Anderson 2014; Quillfeldt et al. 2017; Brambilla et al. 2019; Sutton & Puschendorf 2020).

#### *Target species*

The common kestrel is a largely resident or short-migrant species (Morganti et al. 2021), which uses many different habitats, reaching the highest abundances in farmland areas, nesting in rural houses and abandoned corvid nests on trees (Costantini & Dell’Omo 2020). The common kestrel population has increased in the Po Plain between the 1980s and early 2000s, when the population reached a plateau (Brichetti & Fracasso 2020; Rete Rurale Nazionale & Lipu 2021). The European populations of lesser kestrel and red-footed falcon feature both long-distance migrant patterns, overwintering in the Sahelian belt (Sarà et al. 2019) and in equatorial and southern Africa (Palatitz et al. 2018), respectively. While the lesser kestrel is widely distributed in the Mediterranean region (mostly at latitudes below 40°N), the geographic limit of the red-footed falcon distribution is mostly longitudinal, since it is concentrated in the Carpathian Basin and Eastern Europe, being absent in western countries (BirdLife International 2017; Keller et al. 2020). These two species first reproduced in the Po Plain in 2000 and 1995, respectively (Ravasini 1995; Roscelli & Ravasini 2009). Since the early 2000s, both species have been expanding their breeding ranges, eventually overlapping into the Po Plain: the lesser kestrel breeds in colonies in abandoned rural farmhouses, while the red-footed falcon is a facultative colonial raptor occupying corvid nests on isolated trees and tree rows. Genetic evidence shows that the lesser kestrels of the Po Plain originated from the Southern Italian population (Bounas & Rubolini 2020). Re-sightings of colour-ringed birds suggest that red-footed falcons come from Hungary and eastern Europe (Berlusconi et al. 2019; Brichetti & Fracasso 2020).

#### *Data collection*

We gathered occurrence data of the three target species through field surveys and, for common kestrel only, by collecting data from the citizen-science database “Ornitho.it” (Italian Biologion platform).

To identify occurrence sites of the target species (i.e. breeding colonies of lesser kestrel and nesting sites of common kestrel and red-footed falcon) we defined as a nesting site any location where at least one active nest was observed (we defined “active nest” any nest containing eggs, nestlings, or incubating adults), or where one pair (or more) of adults performed any behaviour which is unequivocally related to reproduction (e.g. territorial behaviour, prey exchange among adults, food delivery to chicks) during at least one breeding season (April – July). Field data collection was carried out during three breeding seasons (2018–2020). Species-specific survey methodologies were applied for each of the three target species.

The distribution of lesser kestrel was poorly known until 2017 in the Po Plain, with a few exceptions. Scattered in small colonies, mostly of 2–4 pairs concentrated in abandoned rural buildings, where common kestrels are very abundant, most of the lesser kestrel colonies were likely to have been overlooked. To overcome this issue, from 2018 to 2020 we visited all those rural buildings (N = 821) that were likely to host lesser kestrels, in a buffer of ~20 km of radius from the known colony sites in the study area, since the distribution of lesser kestrel colonies is normally aggregated at a landscape scale (see Ursúa Sesma 2006). Preliminary identification of the buildings was performed through observation of satellite imagery. We conducted the survey through a standardized method, based on those proposed for lesser kestrel census by Ursúa Sesma (2006) and implemented within the framework of the LIFE FALKON project (LIFE17 NAT/IT/000586 – Actions A1; Morganti et al. 2020), which proved to be also efficient in detecting breeding pairs of common kestrels, that frequently breed in rural buildings as well. In 2019 and 2020, we also surveyed tree rows to identify new red-footed falcon nesting sites. Occasionally, also common kestrels were recorded to nest in trees, occupying abandoned corvid nests, similarly to red-footed falcons.

Eventually, we pooled the field data of the common kestrel with those entered and validated by local experts in “Ornitho.it”, a database of citizen-science observations about birds and biodiversity across Italy, with spatial accuracy equal to or higher than 1 km. Specifically, we retained only the data classified as “confirmed breeding” in the whole study area from 2010 to 2020.

Repeated occurrences within the same 1 × 1 km grid cell were removed to reduce spatial autocorrelation (see next paragraph). Thus, the final data set used for modelling included the following number of 1 × 1 km cells occupied by each species: 40 for lesser

kestrel, 91 for red-footed falcon and 1,192 for common kestrel.

#### *Selection of eco-climatic variables*

To reduce the number of variables to be used in the models, we relied on an expert-based approach (Guisan & Zimmermann, 2000) obtaining a set of bioclimatic and land-use variables potentially affecting the breeding distribution of the target species in our study area, based on the available literature (Palatitz et al. 2011; Morganti et al. 2017, 2021; Costantini & Dell’Omo 2020). We modelled the target species distribution with eco-climatic variables representing bioclimatic and land-use parameters. Bioclimatic variables ( $N = 19$ ) were obtained from the WorldClim2 database (Fick & Hijmans 2017), revised in 2020, while land-use data were obtained from the CORINE Land Cover database ( $N = 44$ ) (CLC v. 8, European Union, Copernicus Land Monitoring Service 2018). Although bioclimatic parameters from WorldClim2 are given for 1970–2000 timeframe, we wanted to refer to mean conditions and thus the mean values reported for this period are to date considered a “gold standard” for this kind of analysis (see Morganti et al. 2017; Sutton 2020). The original CLC variables were reclassified to seven variables, to allow robust result interpretation: urban areas and infrastructures, intensive crops, extensive crops, wetlands, grasslands, forest areas, and sterile areas (Table S1). Three out of seven variables were related to farmland habitats: we retained more details about farmland land-uses to highlight the differences in the continuous intensive lowland agricultural landscape, which may underpin crucial preferences (and relative differences) of (and among) the target species. Land use data were considered as the relative coverage within each  $1 \times 1$  km cell.

All variables were resampled at  $1 \times 1$  km resolution with bilinear interpolation. We chose this specific spatial resolution due to the behaviour ecology and mean home range size of the three species (Cecere et al. 2018; Palatitz et al. 2018; Costantini & Dell’Omo 2020).

Finally, we tested the collinearity among predictors through the variance inflation factor (VIF) using R “usdm” package (Naimi et al. 2014). The full set of predictors (including the reclassified land-uses) was thus reduced by excluding the variables with the highest VIF value and eventually reduced to a set of predictors with values below 4.00 (Zuur et al. 2010; Morganti et al. 2017). The original set of variables and their VIF values are given in Table

S2, while their cluster dendrogram is reported in Fig. S1. The final set of predictors included wetlands, extensive crops, intensive crops, grasslands, urban areas, annual mean temperature (BIO01), mean diurnal range (BIO02), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of the warmest quartile (BIO18). The final VIF scores of the variables included in the models are given in Table S3. A map of each predictor is reported in Fig. S2.

#### *Ecological niche modelling*

Ecological niche modelling was performed through an ensemble approach to reduce method-specific biases (see Hijmans et al. 2016; Quillfeldt et al. 2017, Thuiller *et al.* 2019; Hao et al. 2019). Specifically, we run 100 models for each of the six following methods we considered the most robust (see Brambilla et al. 2019): MaxEnt, generalized linear models (GLM), generalized boosted models (GBM), random forests (RF), artificial neural networks (ANN) and flexible determinant analysis (FDA). For the lesser kestrel and the red-footed falcon, we generated 10,000 random points as background locations within the study area (see Barbet-Massin et al. 2012). For these two species, the occurrence locations fed to the model are supposed to accurately represent the species distribution in the study area. Concerning common kestrel, we accounted for the unevenly distributed sampling effort (Kramer-Schadt et al. 2013), which was higher in those areas with many “Ornitho.it” observers (i.e. major cities). Thus, we created an ad-hoc background layer (Fourcade et al. 2014): specifically, we first calculated a bias map expressing the geographic density of presence points; successively, we generated 10,000 background points (Barbet-Massin et al. 2012) with the same density of presence points (see Morganti et al. 2017). This method allows to effectively control for the sampling effort, as recommended when treating with citizen-science data (Geldmann et al. 2016). Due to the high number of background points in relation to occurrences, models resulted zero-inflated, so we had to correct for this bias by forcing the total weights of the absences to equalling those of the presences as suggested by Barbet-Massin et al. (2012). We cross-validated the models to assess their performance (80/20 random partition train-to-validation ratio for each model). The predictive capacity of the model was estimated by calculating the area under the ROC curve (AUC) (see Chiffard et al. 2020; Hao et al. 2019). Eventually, we calculated an ensemble model, merging predictions of all

the single models that reached an AUC value of at least 0.70 (cf. Thuiller et al. 2013). We defined the relative importance of each model weight for the ensemble projections: the attributed weights are proportional to the evaluation scores given by the AUC value (Thuiller et al. 2013). Statistics of the fitted values obtained with the ensemble model for the prediction of suitability habitat for each species are reported in Table S4. Some descriptive statistics of the predicted suitability areas were shown (km<sup>2</sup> with suitability >0.5 and >0.8).

In the following step, we aimed to obtain a qualitative comparison of the effect of the eco-climatic variables on the three target species. We compared the mean contribution of each predictor to the ensemble model of each species. The variable contribution was expressed as a value ranging between 0 (no contribution) and 1 (maximum contribution) for each variable. Furthermore, we compared the slope of the response curves of each variable among species. This offered the possibility to view how, for each species, the effect of a single variable increased or decreased the estimated suitability value while easing a comparison of the eco-climatic predictor effects among species.

All the models were performed in the “biomod2” package for R (Thuiller et al. 2013). All statistical analyses, including modelling, were run in R 4.0.3 (R Core Team 2020).

#### *Spatial correlation among species*

We explored the spatial correlation of the distribution of the three species, by generating correlation maps using Pearson’s coefficient using the three suitability raster maps. Firstly, we reduced the geographical borders of suitability raster maps for each species, in order to consider only the areas included in the Po Plain. Thus, we filter out low-suitability areas from the suitability raster maps, considering a threshold value as 0.30 for lesser kestrel and red-footed falcon, and 0.20 for common kestrel, to exclude extreme low values. We used such different threshold values because threshold selection in the case of presence-background models is necessarily model-specific, and in this case reflected the different distribution patterns between common kestrel and the other two species: wide and with low mean suitability values in the former case, while concentrated and with high suitability values for the other two species (see Figure 2 for the complete maps). These threshold values were thus opportunistically selected to provide a reliable approximation of the real distribution of each model species. Using the same threshold for the three species would have

ended with non-representative maps for either common kestrel (if maintaining the same threshold of 0.30) or for the other two species (if maintaining the same threshold of 0.20) (see Pineda & Lobo 2009). We therefore obtained a realistic suitability map according to the empirically most reliable approximation of the current range of each species; notably, when using different thresholds to “cut” the map, results were not qualitatively affected (details not shown for brevity). We maintained continuous raster maps above the threshold suitability value.

Correlations were calculated with a neighbourhood cell size of 5 (i.e.: 5 × 5 cells moving mask centred on the focal cell), with the significance threshold set at  $p = 0.05$  (Wegmann et al. 2016). This method was applied for each combination of species. We then calculated the average values of Pearson’s coefficient and p-value for each pair of species and generated three different maps showing the areas of strong positive correlations (Pearson’s coefficient >0.70). Analyses were performed in R 4.0.3 (R Core Team 2020) and the “raster” package (Hijmans 2020).

## **Results**

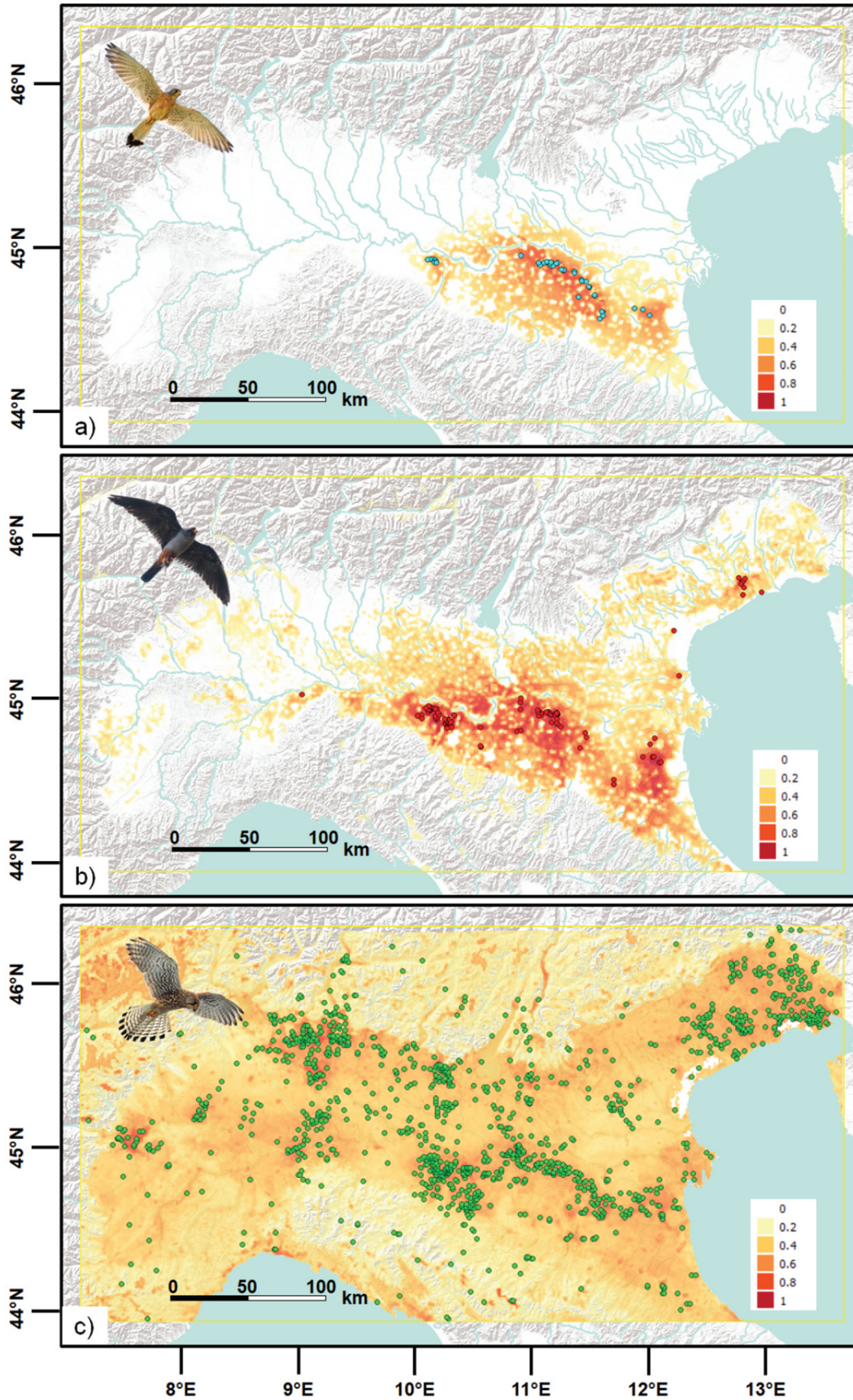
### *Occurrence data: results from field surveys and data collection*

Until 2018, a total of 23 lesser kestrel breeding occurrences (grouped in 17 colonies) were known for the whole Po Plain. During the 2019 and 2020 surveys, we found 23 new buildings hosting breeding lesser kestrels, grouped into 16 new colonies. During 2019 and 2020, the red-footed falcon surveys led to a census of 91 nests. Field surveys led to the identification of 201 breeding pairs of common kestrels, while 991 further locations were obtained from “Ornitho.it”, totalling 1,192 breeding occurrences of the species. The spatial distribution of the breeding occurrences for each species is reported in Figure 2.

### *Environmental Niche Models: effects of the eco-climatic variables*

The mean relative contributions and the response curves of the eco-climatic variables entered in the models are summarized in Table I and Figure 3. Some of the eco-climatic variables had a considerable and positive effect on the suitability for all of the three species. This is the case for annual mean temperature and mean diurnal temperature range, although the relative contributions were different among species: 0.116 and 0.328 respectively





for lesser kestrel, 0.116 and 0.379 for red-footed falcon, 0.253 and 0.082 for common kestrel. The extension of intensive crops was by far the variable with the highest relative contribution in determining the suitability for lesser kestrel and red-footed falcon (0.448 and 0.556, respectively), entering into the model with a positive load. In the common kestrel model, this variable also had a positive effect but a much lower contribution (0.237). Annual cumulated precipitation entered in all the three models with a comparable importance among species (0.243 for lesser kestrel, 0.136 for red-footed falcon and 0.154 for common kestrel), but always with a negative load (Table I). The extension of urban areas exhibited a negative effect for both lesser kestrel (0.083) and red-footed falcon (0.041) models, though with small contributions, while it had a positive effect on the suitability for common kestrel (0.191) (Table I). Analogously, precipitation seasonality had a negative effect on suitability for red-footed falcon and lesser kestrel while it had a weak quadratic effect (i.e. with an optimal intermediate value) on common kestrel. Summer precipitation had a negative effect only for the lesser kestrel. Grasslands and extensive crops have a quadratic effect only for the common kestrel model. Wetland extent only had minor importance values on all species and was affecting the suitability for lesser kestrel (negatively) and common kestrel (positively) (Table I, Figure 3).

#### *Environmental Niche Models: suitability maps*

The potential distribution maps (Figure 2) identified areas of high suitability for both lesser kestrel and red-footed falcon along the Central-Eastern area of the Po Plain, corresponding to the core of the current species distributions. The overall suitable area (cells with suitability >0.5) for the lesser kestrel appeared to be small (1,556 km<sup>2</sup>) and confined to the South of the Po river and to the Central-Eastern sector of the plain, with a very limited portion of this resulting in a high degree of suitability (65 km<sup>2</sup> with suitability >0.8). The suitable area for the red-footed falcon was also tightly associated with the distribution of intensive landscapes, but resulted overall much higher than those of the lesser kestrel (5,389 km<sup>2</sup> with suitability >0.5) and expanded

towards East, to include Northern-East sectors of the Po Plain (Venice province). Wetlands, riparian vegetation and urbanized areas seemed to be negatively selected by the two species. Conversely, the suitability map for common kestrel included the whole Po Plain, extending also to mid and high elevations (Figure 2). Noteworthy, the distribution of common kestrel occurrences (but not of the other two species) show dense hotspots near to the major cities, possibly explained by the higher observation effort of the contributors of "Ornitho.it" in urban areas, even after controlling for this potential bias, as described in Methods section. This potential bias was taken into account for a proper interpretation of the results.

#### *Spatial correlation of environmental suitability between species*

The three maps reporting spatial correlation between the highly suitable areas for each pair of species are shown in Figure 4. It can be noted that almost the entire overlap area between lesser kestrel and red-footed falcon distributions is statistically and positively correlated. The correlation maps with the common kestrel have a few correlated areas, without an overall consistency and significance. We stress that a high correlation value in a group of neighbouring cells can occur when suitability is either high or low for both the considered species.

The spatial correlation between the lesser kestrel and red-footed falcon suitability maps was very high (median Pearson's  $r \pm SE$ :  $0.776 \pm 0.004$ ), leading to an overall significant correlation (median  $p < 0.001$ ). On the contrary, the spatial distribution of common kestrel suitability resulted less related to those of the two other species: lesser kestrel (median Pearson's  $r \pm SE$ :  $0.447 \pm 0.003$ ,  $p = 0.079$ ), red-footed falcon (median Pearson's  $r \pm SE$ :  $0.407 \pm 0.005$ ,  $p = 0.069$ ).

## **Discussion**

We obtained an exhaustive representation of the breeding occurrence of three *Falco* species of recent expansion in a wide portion of Northern Italy, centred over the Po Plain. The number of the new breeding occurrences doubled those known to the

←

Figure 2. Environmental and climatic suitability of the Po Plain (Northern Italy) for the three *Falco* species that recently expanded in the area. a) lesser kestrel, b) red-footed falcon, c) common kestrel. Colour intensity is proportional to the suitability, ranging from 0 (pale red) to 1 (dark red). Dots represent the certain breeding occurrences recorded for each species and used to run the models.



Table I. Contributions of each of the eco-climatic variables in the final ensemble models for each *Falco* species (different columns). The symbols in the brackets indicate the direction of the effect as derived by the observation of the loess (see Figure 2) expressing the relation between each variable and the suitability for the species: positive (+), negative (-), quadratic ( $\pm$ ); i.e. with an optimum value;), very weak effect (0).

Eco-climatic variables	Lesser kestrel	Red-footed falcon	Common kestrel
Annual mean temperature (BIO01)	0.116 (+)	0.116 (+)	0.253 (+)
Annual precipitation (BIO12)	0.243 (-)	0.136 (-)	0.154 (-)
Precipitation seasonality (BIO15)	0.382 (-)	0.152 (-)	0.068 ( $\pm$ )
Precipitation of the warmest quartile (BIO18)	0.312 (-)	0.202 (+)	0.254 (+)
Mean diurnal temperature range (BIO02)	0.328 (+)	0.379 (+)	0.082 (+)
Urban areas	0.083 (-)	0.041 (-)	0.191 (+)
Intensive crops	0.448 (+)	0.556 (+)	0.237 (+)
Wetlands	0.020 (-)	0.054 (0)	0.075 (+)
Extensive crops	0.028 (0)	0.026 (0)	0.034 ( $\pm$ )
Grasslands	0.008 (0)	0.004 (0)	0.055 ( $\pm$ )

date in the case of lesser kestrel and those of red-footed falcon increased more than five times. The expanded database of breeding occurrences supported the realisation of ENMs.

Environmental Niche Models allowed us to investigate which factors drive the current distribution of the target species at a wide regional spatial scale, providing useful information on the environmental factors limiting the species' range. The eco-climatic suitability for the lesser kestrel and the red-footed falcon is primarily associated with intensive crops, while common kestrel is much less related to this kind of habitat. The two former species also had similar loads regarding other eco-climatic predictors and thus – not surprisingly – the distributions of their suitability resulted strictly spatially correlated. Common kestrel suitability is primarily determined by a positive association with annual mean temperature and it results ubiquitous in the area. Therefore, the common kestrel suitability is not significantly spatially related to any of the two former species.

#### *The similarities between lesser kestrel and red-footed falcon*

The strong positive relation that we found between the distribution of the two more threatened species of our study (lesser kestrel and red-footed falcon) and the distribution of intensive crops may seem counterintuitive. Indeed, agricultural intensification is one of the main threats to biodiversity, indirectly causing the steep decline observed for farmland bird populations in the last decades (Donald et al. 2001; Boatman et al. 2004; Rosenberg et al. 2019) and this holds true for the Po Plain too. This is particularly true for lesser kestrels in other breeding areas: several foraging habitat selection studies reported that lesser kestrel selects grassland fields, legumes,

artichokes, cereal while avoiding permanent and intensive crops (Donazar et al. 1993; Catry et al. 2012; Di Maggio 2018; Morganti et al. 2021; Assandri et al. 2022). In these works, populations in semi-natural environments have always been studied, and it was clear the negative selection of intensive arable land. Until now, no one in Italy has ever studied lesser kestrel populations ecology in exclusively intensive agroecosystems. However, the importance of intensive crops for lesser kestrel and red-footed falcon revealed by ENMs needs to be critically considered. The category “intensive crops” indeed included non-irrigated arable lands and permanently irrigated arable lands (CLC classes 211 and 212), thus comprehending all the irriguous (such as maize) and non-irriguous (such as alfalfa or cereals) land-uses (see Table S1). Merging these two categories was unavoidable because the non-irrigated arable land reported only a few huge patches of forage crops into the CLC map for the Po Plain, so that the category is under-represented at this regional scale level (Kosztra et al. 2017). This could be related to crop rotation and/or misclassification; in fact, the distinction in the CLC between categories non-irrigated and permanently irrigated arable lands is unlikely to be fully reliable for our study area. Deserves a critical consideration, literature data and field-evidence agree in suggesting that only non-irrigated crops are elective foraging sites for (at least) the lesser kestrel (Assandri et al. 2022) and the red-footed falcon (Palatitz et al. 2018). Lesser kestrels in the Po Plain area forage over harvested cereals, natural grasslands and alfalfa crops and avoid maize crops (Cioccarelli 2020; Assandri et al. 2022). Furthermore, these cultivations are prey-rich farmland habitats (Johst et al. 2001; Scaravelli & Gustin 2020). An increase in cultivated crops subject to repeated mowing during the spring,

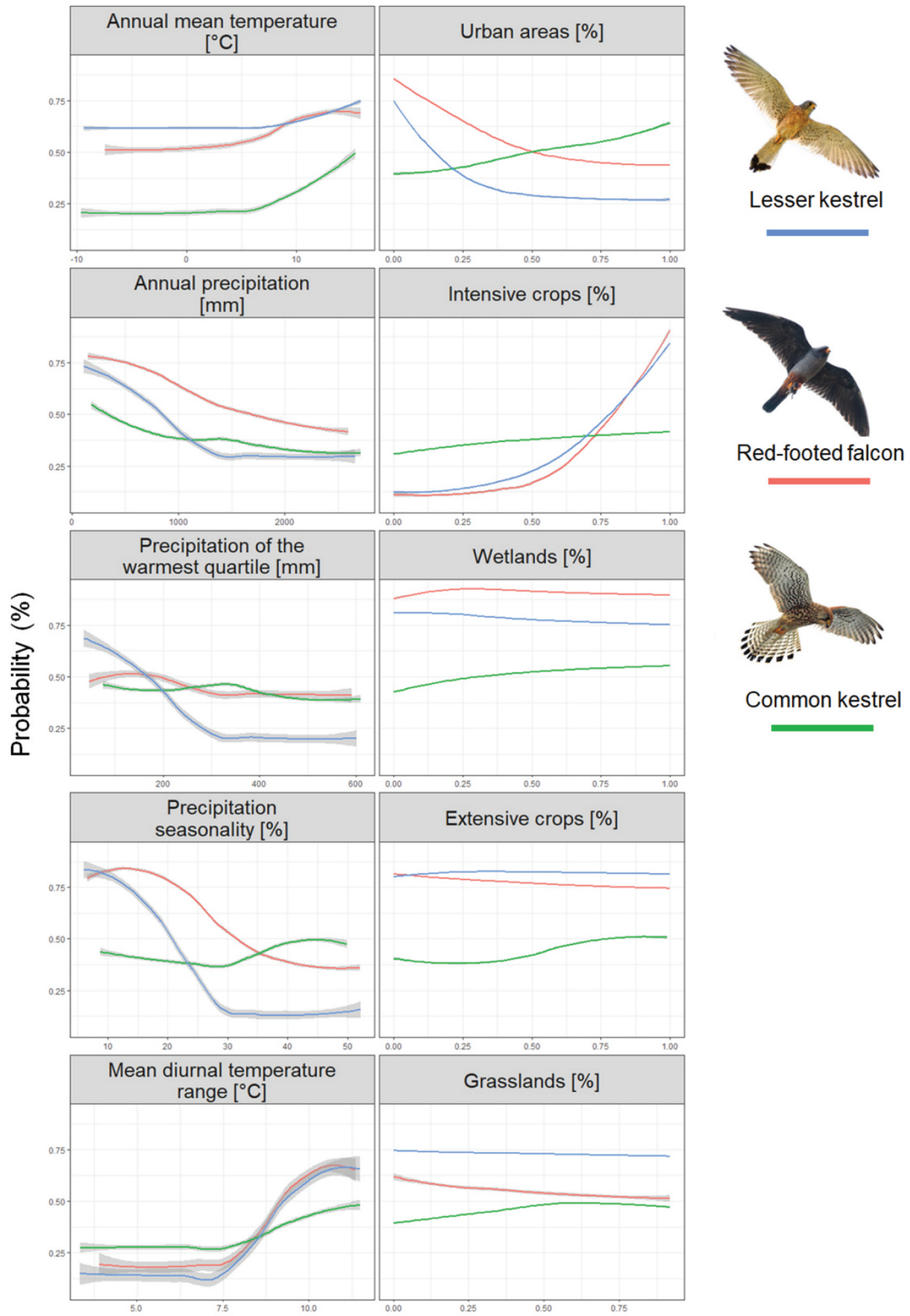


Figure 3. Response curves showing the average probability value of the ensemble model for each explanatory variable, for lesser kestrel (blue line), red-footed falcon (red line) and common kestrel (green line). The shades represent standard error bounds calculated with a t-based approximation.

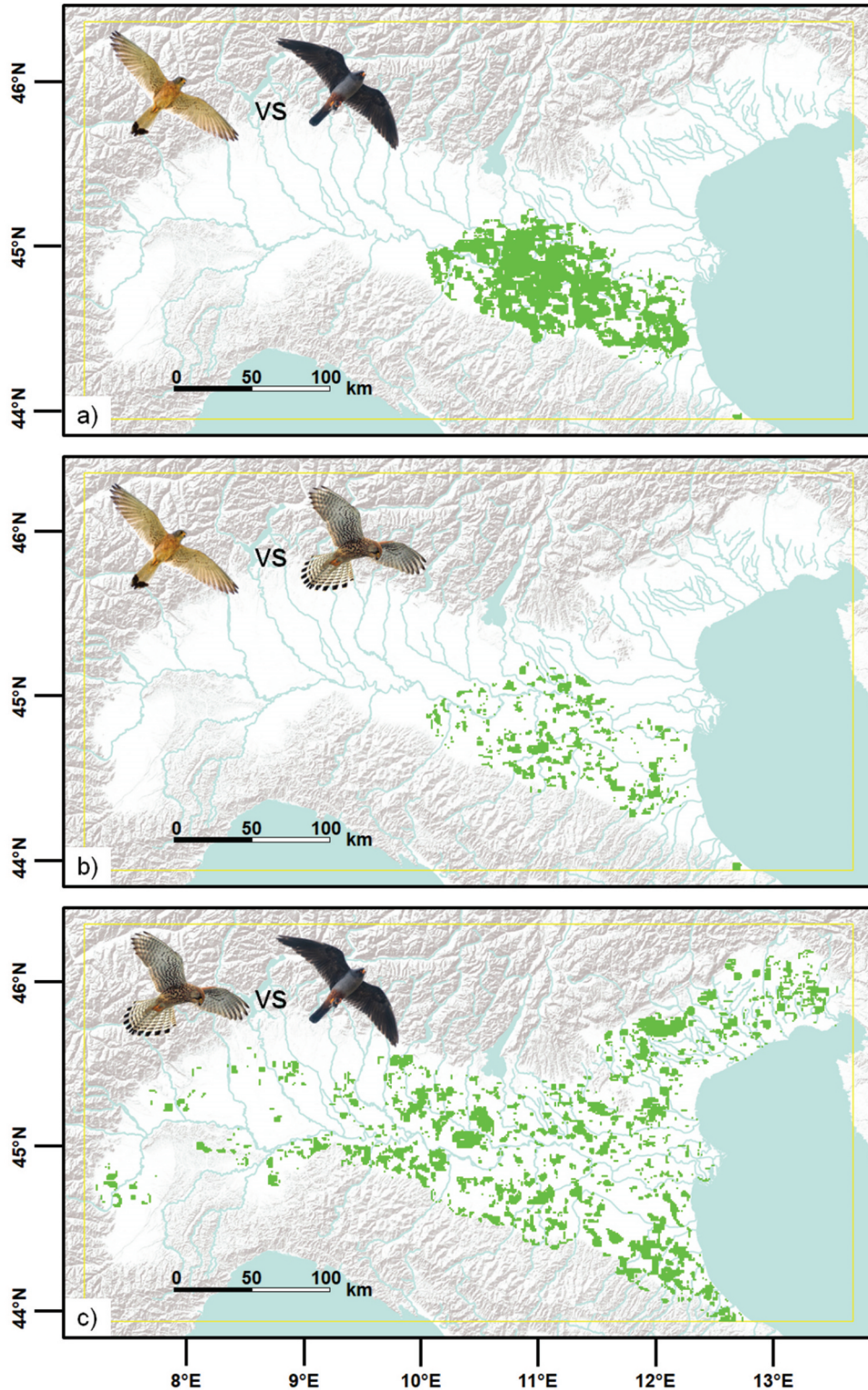


Figure 4. Correlation maps between species suitability: a) lesser kestrel vs red-footed falcon, b) common kestrel vs lesser kestrel, c) red-footed falcon vs common kestrel. Each map shows the statistically significant positive correlations areas (Pearson's coefficient > 0.70).

such as alfalfa and cereal crops, has probably favoured the expansion of the three-falcon guild in the Po Plain (Cioccarelli 2020). As birds of prey at

the top of the food chain, the species investigated select the best habitats, those in which intensive agricultural management is probably more



favourable to biodiversity in general, similarly to what happens in other parts of their range (Fehérvári et al. 2009; Morganti et al. 2021). Since these cultivation types fall into the “intensive crops”, it is not surprising to find a strict association to this specific category at a regional scale.

A serious threat that could affect the range expansion of two particularly endangered species in the future is represented by the increase of the extent of urban areas (Cioccarelli 2020). In particular, this feature seems to be in contrast with the well-studied life history of the lesser kestrel: in most of its breeding range its biggest colonies are typically located in towns and cities (La Gioia et al. 2017). However, in Northern Italy, cities and urban areas are very different from those where the species is adapted to breed: high population density, fewer old historic buildings, more urban and not immediately surrounded by farmland habitats.

The climate change in recent years seems to have favoured the expansion of lesser kestrel (Morganti et al. 2017) and likely that of the red-footed falcon too in the Po Plain. Specifically, the progressive increase in temperature and the reduction in rainfall is modifying the Po Plain climate towards a more intense degree of continentality (Arpaè 2020), thus favouring steppe species. The ENMs developed here are coherent with these hypotheses and describe for the first time an association between the occurrence of the two species and the continental-dry climate, defined by high temperatures, marked diurnal temperature range and scarce precipitation.

*The spatial correlation between lesser kestrel and red-footed falcon: suggestion for possible competition*

Lesser kestrel and red-footed falcon models show an overall similarity in the variables' importance and in the response curves, and consequently their suitability maps are remarkably similar. These two species are shown to breed in sympatry for the first time in Europe, selecting the same breeding occurrences, often nesting at close distances (less than 1 km). Coexisting bird species are supposed to differ in resource use to avoid overlap fitness stress. Habitat preferences of sympatric bird species could be critical to ensure coexistence and avoid competitive exclusion (Martin 1998). The sympatry of two newcomer's species in the study area offers the opportunity to observe the first stages of intraguild competition phenomena in terms of interference and/or exploitation (Rolando & Giachello 1992). Exploitative competition refers to indirect negative interactions resulting from species using the same,

limited resources, as often happens in situations between native and alien species (Gurnell et al. 2004; Pintor & Sih 2009; Damas-Moreira et al. 2020). This process could occur during this establishing phase in the Po Plain, while the species are expanding their breeding range in the area, thus finding a coexistence by niche partitioning (Malanson et al. 1992; Capula et al. 1993). However, the use of specific space resources by one species, more aggressive and competitive, may exclude partially or definitively their use by another (Sarà et al. 2005; Brambilla 2019). At a regional scale, species distributions and coexistence are determined by both biogeographical and ecological factors, including even competition (Pigot et al. 2018).

*Common kestrel as the most divergent species*

Models unravelled how the common kestrel differs from the other two falcons. This generalist openland predator is widespread throughout the whole study area, so that there is no high spatial correlation with lesser kestrel or red-footed falcon, which show a much more restricted range (either realised and potential ones). We observed that the common kestrel is not specifically associated with continental-dry climate type, both for the variable curve slopes and low importance effect values, though it is the species whose current distribution is mostly positively linked to the mean annual temperature and summer precipitation. In fact, the species is widely adaptable, generalist and widespread throughout the Old World, able to cope with a wide range of climates, however it reaches the high population density in pseudo-steppe habitats (Costantini & Dell'omo 2020). Grasslands (including high altitude ones) have a positive effect on the common kestrel suitability, while no effect is evident for lesser kestrel and red-footed falcon. This is probably due to grasslands being very scarce in lowlands, while they represent the only type of open high-altitude habitat where common kestrel breeds, especially at mid-latitudes (Carrillo & González-Dávila 2009). As previously suggested, the positive selection of urban areas may partly reflect an observation effort biased towards cities, hard to be completely removed from the database (but see Geldmann et al. 2016). In our specific case, we compensate for the uneven distribution of the observations at the modelling stage, distributing the background points with a density proportional to the observation density. However, there may be a genuine preference for common kestrel for cities. The species is commonly breeding

in cities (e.g. Graham et al. 2007; Fraissinet & Fuglione 2008; Grattini 2009), and it has undergone a marked density increase in cities during the last few decades. Hence, our data may reflect a genuine preference for common kestrel for urban habitats, which substantially raised in recent times. Indeed, our results confirm that rural farmland habitats seem to remain the most suitable environments for common kestrel, where its population reaches the highest densities (Casagrande et al. 2008; Costantini & Dell’Omo 2020), also proved by the predictor importance values.

## Conclusions

Our results revealed a high spatial correlation and overlap between lesser kestrel and red-footed falcon, with consequent frequent co-occurrence. The widespread sympatry, which may be favoured by recent colonisations, may eventually lead to fitness consequences that could become visible at the population level over time. By focusing on an earlier stage of the co-occurrence dynamics, our study was not affected by the potential impact of competitive exclusion, allowing an easier assessment of the link between species distribution and eco-climatic variables. So far, our results should not be interpreted as the real ecological niche (Soberon & Peterson 2005).

Given the recent establishment of this co-occurrence is hard to hypothesize whether one of the two species will eventually outcompete the other. Indeed, taxonomic affinity may be a good proxy for competition, since closely related species are more likely to have similar niche requirements (Powell *et al.*, 2021). The presence of “newcomers” into ecosystems pose a particular problem because niche differentiation needs long time to stabilize. In this case, both lesser kestrel and red-footed are “newcomers”. The outcome of competition may depend on differences in the respective abilities of the species to use habitat and trophic resources. Frequently, the occurrence of competitive interactions shapes the distribution patterns of related species possibly more than eco-climatic variables themselves (Pigot et al. 2018; Brambilla et al. 2020). Alternatively, populations that appear to be sympatric in their geographical distributions may diverge ecologically, achieving effective allopatric distribution at a local scale (Lovette & Hochachka 2006; Demaya et al. 2020). This ecological segregation can minimize the strength of competitive interference or exploitation. In the lesser kestrel vs red-footed falcon system, coexistence in the same macro-habitats may be achieved either by segregation at a micro-scale of both foraging and breeding

habitats, as well as on diet differentiation. Phenological segregation may also support the coexistence of these two species since the reproductive cycle in the lesser kestrel tends to be earlier. Regarding the potential competition of these two species with common kestrel, its broader ecological requirements will likely limit competitive interactions and will eventually determine the maintenance of the wide distribution currently observed.

Future research efforts should be devoted to shed light on these interactions, deepening the current knowledge on resources overlap, fine-scale habitat use, diet, behavioural interactions and unravel competition mechanisms, eventually exploring ultimate fitness consequences.

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## ORCID

A. Berlusconi  <http://orcid.org/0000-0001-7491-8971>  
 D. Preatoni  <http://orcid.org/0000-0001-8760-1316>  
 G. Assandri  <http://orcid.org/0000-0001-5161-5353>



M. Brambilla  <http://orcid.org/0000-0002-7643-4652>  
 J. G. Cecere  <http://orcid.org/0000-0002-4925-2730>  
 S. Cioccarelli  <http://orcid.org/0000-0002-5912-1937>  
 A. Martinoli  <http://orcid.org/0000-0001-7192-5033>  
 D. Rubolini  <http://orcid.org/0000-0003-2703-5783>  
 A. Martinoli  <http://orcid.org/0000-0003-0298-0869>  
 M. Morganti  <http://orcid.org/0000-0002-8047-0429>

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