1 **Projected dynamics of breeding habitat suitability for a steppe-land bird**

2 **warrant anticipatory conservation actions**

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21 Short title: Breeding suitability for a steppe-land bird

22

1 ABSTRACT

2 Understanding spatial and temporal variations of habitat suitability is fundamental for
 3 species' conservation under global change. Steppic species are particularly sensitive to
 4 anthropogenic change and have undergone large declines in the last decades. We aimed to
 5 describe current and future breeding habitat suitability for the Eurasian stone-curlew
 6 *Burhinus oedicnemus*, a steppic species of conservation concern, and to identify critical areas
 7 for its conservation. We collected 1628 presence records covering the period 1992-2016. We
 8 developed a species distribution model using a dynamic Maxent algorithm and a set of
 9 pseudo-absences with a spatial density weighted on a fixed kernel density estimated on the
 10 presences, to mitigate the potential sampling bias. We projected this model under a set of
 11 carbon emission, socioeconomic and land-use/land-cover scenarios for the years 2030, 2050,
 12 2070 and 2090. Finally, we described the cell-wise and mean change of breeding habitat
 13 suitability through consecutive time intervals and identified the areas critical for the species'
 14 conservation.

15 All scenarios predicted a short-term northward shift of suitable areas, followed by a period of
 16 stability. We found no consistent trends in the mean change of breeding habitat suitability,
 17 and similar extents of suitable areas under current and future scenarios. Critical areas for the
 18 conservation of the species are mainly located in Northern Europe, Israel and parts of North
 19 Africa, the Iberian Peninsula and Italy. According to our results, the Eurasian stone-curlew
 20 has the potential to maintain viable populations in the Western Palearctic, but dispersal
 21 limitations might hinder the colonization of shifted suitable areas. Targeted conservation
 22 interventions in the critical areas are therefore recommended to secure the future of the
 23 species under global change.

24 **Keywords:** Eurasian stone-curlew, *Burhinus oedicnemus*, species distribution models, habitat
 25 suitability, steppe-land, environmental change.

26

1 INTRODUCTION

2

3 Human-driven environmental change has relevant impacts on the distribution and life-history
 4 of organisms (Parmesan, 2006; Chen *et al.*, 2011) and their likelihood of extinction (Román-
 5 Palacios & Wiens, 2020). Several studies reported distributional shifts in animal species
 6 according to climate change (Vanderwal *et al.*, 2013), physiological constraints (Root *et al.*,
 7 2003) and in response to land-use and land-cover modifications (LULC; Sala *et al.*, 2000). In
 8 birds, habitat suitability is affected by both climate and LULC change (Barbet-Massin,
 9 Thuiller, & Jiguet, 2011), and its variation has been linked to population trends (Green *et al.*,
 10 2008).

11 Steppe-land birds are particularly sensitive to environmental change, and large declines in
 12 steppe-land birds' populations have been reported during the last decades, primarily as a
 13 consequence of agricultural intensification and afforestation following land abandonment
 14 (Burfield, 2005; Onrubia & Andrés, 2005). The Eurasian stone-curlew *Burhinus oedicephalus*
 15 (Linnaeus, 1758; hereafter stone-curlew) is a wide-ranging steppe-land species occurring in
 16 pseudo-steppes and farmlands in the Palearctic (Vaughan & Vaughan-Jennings, 2005). The
 17 species suffered a severe population decline (>30%) in the second half of the 20th century,
 18 mainly due to agricultural intensification (BirdLife International, 2018). It is now classified
 19 as Least Concern by the IUCN (BirdLife International, 2021), but information on the status of
 20 its populations is limited and positive trends might be due to the increased monitoring effort
 21 (Gaget *et al.*, 2019). Indeed, the species is still considered of European conservation concern
 22 (SPEC3; BirdLife International 2017), and ongoing declines are reported for many regions of
 23 its range (BirdLife International, 2017; Gaget *et al.*, 2019). Moreover, the stone-curlew is
 24 considered both an umbrella and flagship species (Caro, 2010; Hunter *et al.*, 2016), and its
 25 conservation can therefore benefit steppe-land ecosystems (Hawkes *et al.*, 2019).

1 To establish effective conservation practices, state-of-the-art habitat suitability scenarios for
 2 the focal species are required (Miller-Rushing, Primack, & Sekercioglu, 2010; Mcshea,
 3 2014), and rigorous analyses of suitability dynamics are essential to reveal the sensitivity of
 4 species to global change and to guide conservation efforts (Stiels *et al.*, 2021). Moreover,
 5 recent studies are increasingly evidencing the importance of distinguishing between the
 6 effects of long-term vs. short-term environmental change (Reside *et al.*, 2010; Milanese, Della
 7 Rocca, & Robinson, 2020). Previous studies using species distribution models (SDM, Guisan
 8 & Zimmermann 2000) to model habitat suitability for steppe-land birds reported northern
 9 range shifts and the persistence of large suitable areas according to global change scenarios
 10 (Estrada *et al.*, 2016; Kiss *et al.*, 2020). Huntley *et al.* (2007) used SDMs to forecast the
 11 future distribution of the stone-curlew under climate change scenarios, highlighting a
 12 northward shift of suitable areas.

13 Their analysis was limited to a coarse scale (ca. 50 km), Europe, one future period (end of the
 14 21st century) and a single climate scenario. An in-depth analysis integrating LULC and a
 15 range of climatic scenarios might validate their conclusions and provide time-varying
 16 predictions for conservation practitioners.

17 Therefore, in this study we aimed to: (i) test whether the stone-curlew's distribution is driven
 18 by long-term or short-term environmental conditions, (ii) describe the current availability of
 19 suitable breeding habitats for stone-curlew, (iii) provide a range of future breeding habitat
 20 suitability scenarios considering both climate and LULC changes, (iv) test the hypothesis of a
 21 Northern shift for the stone-curlew, at higher spatial resolution than Huntley *et al.* (2007) and
 22 on multiple time-steps, and (v) identify the critical areas for its conservation. We predicted
 23 that (1) our models would highlight a northern shift of suitable breeding areas for the stone-
 24 curlew, (2) large areas of the Western Palearctic would be suitable for the species under
 25 future scenarios. As the stone-curlew is a species of warm temperate areas, it is unlikely that

1 mean breeding habitat suitability will drop rapidly with global warming, as this is fastest at
2 northern latitudes (IPCC, 2013). Therefore, we also predicted a stable or increasing mean
3 breeding habitat suitability for the species under future conditions.

4

5 **MATERIALS AND METHODS**

6

7 *Spatial scale*

8 To reduce the spatial extent while retaining sufficient environmental variation, we limited our
9 analysis to the Western Palearctic (*sensu* Snow & Perrins, 1998). We thus excluded *B. o.*
10 *harterti* for poor data availability, and the two Macaronesian subspecies (*B. o. distinctus*, *B. o.*
11 *insularum*), as these show distinctive responses to the environment, being genetically
12 different (Mori *et al.*, 2017), and have a distribution restricted to small oceanic islands
13 (Vaughan & Vaughan-Jennings, 2005).

14 As spatial resolution, we considered as appropriate the finest grain available based on future
15 LULC scenarios (i.e. ~ 5.5x5.5 km grid cells; Chen *et al.*, 2020) as this cell size approximates
16 the breeding home-range of the species (Caccamo *et al.*, 2011; Hawkes *et al.*, 2021), thereby
17 representing a biologically meaningful scale.

18

19 *Species occurrences*

20 We used occurrences for the breeding season (May-July; Vaughan & Vaughan-Jennings,
21 2005) for the period 1992-2016 retrieving data from eBird, Global Biodiversity Information
22 Facility (GBIF), ornitho.it, ornitho.cat and xeno-canto.org as in previous SDM studies
23 (Avalos & Hernández, 2015; Coxen *et al.*, 2017; Engelhardt, Neuschulz, & Hof, 2020;
24 Ramellini *et al.*, 2020). We also included survey data from the British Trust for Ornithology
25 (in agreement with BTO's data policy), data for Greece from the Ornithotopos database and

the second European Breeding Bird Atlas (hereafter EBBA) and 2x2 km surveys in Greece (in formal agreement with the Hellenic Ornithological Society), data for the Deux-Sèvres department from the Nature79 database provided by Alexis Martineau. For Northern Italy, the dataset was integrated with nest points opportunistically collected by Dimitri Giunchi in the period 2012-2018.

We used data with a maximum positional uncertainty of 5.5 km to fit the resolution of predictors (Guisan, Thuiller, & Zimmermann, 2017), retaining the first occurrence in chronological order (i.e. the one reported in the first year available for the cell) when more than one point occurred in the same cell. We cut observations on the species' range to exclude vagrant individuals in non-breeding areas, developing a range shapefile (see Fig. 1) based on the BirdLife species distribution dataset (<http://datazone.birdlife.org/species/requestdis>), the EBBA1 (Hagemeijer & Blair, 1997) and the EBBA2 (Keller *et al.*, 2020). We then applied a spatial filtering of the data to reduce spatial autocorrelation (Kramer-Schadt *et al.*, 2013), using the R package 'spThin' (v. 0.2.0; Aiello-Lammens *et al.*, 2015) with a minimum distance of 5.5 km between points. The final dataset comprised 1628 presences (Fig. 1).

Species distribution models

Contrasting results on the performance of different SDM algorithms have been reported (e.g. Qiao *et al.*, 2015; Norberg *et al.*, 2019). Therefore, we carried out preliminary tests to compare single-algorithm approaches and ensemble forecasting (i.e. a set of SDM algorithms combined to account for inter-model variability; Araújo & New, 2007). We then compared standard SDMs (hereafter static SDMs; Milanesi *et al.*, 2020a) to dynamic SDMs. The first relate temporally dynamic occurrences to static predictor variables (e.g. 30-year climate averages), yielding potentially biased estimations of species-environment relationships

(Milanesi *et al.*, 2020a), whereas the latter combine occurrences with time-specific raster values (Reside *et al.*, 2010; Milanesi *et al.*, 2020a). We therefore tested whether the stone-curlew's distribution is driven by long-term or short-term environmental conditions comparing static and dynamic SDMs. In summary, we developed and compared four classes of models:

- (i) single static SDMs: seven algorithms were developed (see Table S1 for a list of the employed techniques), using static variables (see *Environmental variables*);
- (ii) ensemble SDMs: the single static SDMs were combined according to the mean and the weighted average (Marmion *et al.*, 2009). In the weighted average method, the AUCtest (see *Evaluation methods*) was used to weight model contribution to the final prediction. Static variables were employed;
- (iii) single dynamic SDMs: seven algorithms (Table S1) were employed, using dynamic variables (see *Environmental variables*);
- (iv) ensemble dynamic SDMs: the single dynamic SDMs were combined according to the mean and the weighted average, using dynamic variables.

All models were developed in the 'biomod2' (v. 3.3-7) R package (Thuiller *et al.*, 2016).

Pseudo-absence selection

We generated a set of pseudo-absence points (i.e. surrogates of true absences; Barbet-Massin *et al.*, 2012), also using them as background points for Maxent. Pseudo-absences are often drawn at random in the study area, whereas occurrences typically show a spatial bias. Therefore, models could discriminate between the environmental features of sampled and unsampled areas, rather than between those of suitable and unsuitable areas (Phillips *et al.*, 2009). To avoid this problem, Phillips *et al.* (2009) proposed the 'target-group' method, where pseudo-absences consist of other species' data collected with the same methods used

1 for the focal species. We used an approach similar to the observer-oriented one (Milanesi,
2 Mori, & Menchetti, 2020). We considered as our pseudo-absences GBIF data of other bird
3 species recorded by the same observers of the presence data, assuming they were collected
4 with the same sampling bias. However, this approach could only be implemented on the
5 GBIF data, and some biases might still arise. Therefore, we developed an alternative
6 approach and refer to it as the ‘Kernel density approach’. We generated a large number of
7 pseudo-absences, weighting their spatial distribution according to a fixed kernel density
8 estimated on all the presence points, by means of the ‘adehabitatHR’ (v. 0.4.18) R package
9 (Calenge, 2006). We used the *ad hoc* method for the estimation of the smoothing parameter
10 (Worton, 1989). The procedure was independently repeated on the occurrences separated by
11 year for the period 1992-2016. For both pseudo-absence selection methods, if a cell contained
12 more than one record, the chronologically oldest was retained in the dataset. Finally, we
13 removed pseudo-absences outside the study area and randomly sampled them to obtain a 0.1
14 prevalence (i.e. the ratio between presences and pseudo-absences ensuring an optimal
15 performance; Barbet-Massin *et al.*, 2012). To identify the best pseudo-absence method, we
16 developed and evaluated a set of Maxent models for each method, using static variables (see
17 *Environmental variables*). We expected the kernel density approach to outperform the target-
18 group method, as the former might be more effective at cancelling out the potential spatial
19 bias in the presence dataset.

20

21 ***Environmental variables***

22 We followed a two-step variable selection procedure, involving first an expert-based pre-
23 selection and then a reduction of multicollinearity. In the first step, we used an expert-based
24 approach (Santini *et al.*, 2021) to derive 17 biologically meaningful environmental predictors
25 (Table 1). We describe the biological rationale supporting expert-based variable choice and

1 the process of variable preparation in the Appendix S1. For static SDMs, we averaged
 2 variables between the years 1973-2013 (climatic and ‘prey suitability’ variables) and 1992-
 3 2016 (LULC variables). Collectively, we refer to these variables as static variables. For
 4 dynamic SDMs, we associated occurrence/pseudo-absence pixels with year-specific values
 5 for a given variable (Milanesi *et al.*, 2020a). We refer to these variables as dynamic variables.
 6 In the second step, we calculated the Variance Inflation Factor (VIF) to address
 7 multicollinearity between predictors. We used the *vifstep* function in the ‘usdm’ R package
 8 (v. 1.1-18; Naimi, 2013), using a threshold of three (Zuur, Ieno, & Elphick, 2010). We
 9 reported the initial and final VIF values for static and dynamic variables in Table 1.
 10 According to this analysis, the precipitation of the warmest quarter was only retained in the
 11 dynamic variable set and the temperature of the warmest quarter only in the static variable
 12 set. We excluded precipitation of the warmest quarter, retaining temperature of the warmest
 13 quarter for both static and dynamic variable sets. In the end, 13 variables were used in the
 14 models (Table 1).

15

16 *Future variables*

17 Future projections of bioclimatic conditions were obtained from four Intergovernmental
 18 Panel on Climate Change (IPCC) General Circulation Models (GCMs) that gained the
 19 minimum score in interdependence (Sanderson, Knutti, & Caldwell, 2015): ACCESS1-3,
 20 CESM1-BGC, CMCC-CM and MIROC5. We considered two emission scenarios
 21 corresponding to the IPCC’s Representative Concentration Pathways 4.5 and 8.5 (RCP 4.5
 22 and RCP 8.5) for the years 2030, 2050, 2070 and 2090. Bioclimatic variables for every
 23 GCMxRCP combination and time interval were produced from the climatic variables
 24 available in the CHELSA CMIP-5 timeseries (Karger *et al.*, 2017). Future LULC scenarios
 25 were retrieved from Chen *et al.*, 2020. To create a LULC dataset consistent with bioclimatic

1 scenarios, we selected LULC projections for the MIROC general circulation model (the
2 remaining GCMs used for bioclimatic variables were not available), under RCP 4.5 and 8.5
3 and the Shared Socioeconomic Pathway 5, for 2030, 2050, 2070 and 2090. In future LULC
4 scenarios, urban cover was kept at its 2016 value, due to the extremely low correspondence
5 between the two LULC datasets.

7 ***Model evaluation***

8 We evaluated models based on the block cross-validation procedure implemented in the
9 ‘ENMeval’ (v. 0.3.1) R package (Muscarella *et al.*, 2014). In this procedure, data are
10 partitioned into four geographically independent bins; four models are then produced, with
11 three bins used for training and the remaining one used for testing. We used as performance
12 statistics the area under the curve (AUC; Fielding & Bell, 1997) of the receiver operating
13 characteristic plot, and the Continuous Boyce Index (CBI; Boyce *et al.*, 2002). The AUC
14 metric was computed with the R package ‘biomod2’ (v. 3.3-7, Thuiller *et al.*, 2016); the CBI
15 with the ‘ecospat’ (v. 3.1) R package (Di Cola *et al.*, 2017). To detect overfitting in our
16 models, we computed the difference between AUCtest and AUCtrain (AUCdiff;
17 Radosavljevic & Anderson, 2014). In case of contrasting indications between AUCtest and
18 CBI, we gave priority to the latter, as the usefulness of AUC in SDM has been questioned
19 (Lobo, Jiménez-Valverde, & Real, 2008).

20 We evaluated variable importance using a model-independent approach (Thuiller *et al.*, 2009)
21 and expressed it as percentage. We then produced the response curves for each model using
22 the evaluation strip method (Elith *et al.*, 2005). To check the ecological validity of the
23 models, we used an expert-based evaluation (Perennes *et al.*, 2021). We defined two
24 subjective scores: (i) Quality of Spatial Prediction (QSP) and (ii) Plausibility of Response
25 Curve (PRC). The QSP was evaluated comparing qualitatively the spatial output of each

1 model with the species' distribution in the EBBA1 and EBBA 2 (Hagemeijer & Blair, 1997;
2 Keller *et al.*, 2020) and with the modelled distribution in the EBBA 2 (Keller *et al.*, 2020).
3 The PRC was evaluated based on the agreement between current knowledge on the species'
4 ecological preferences and the model's response curves for the four variables with the highest
5 percentage contribution. Both scores had three possible values (zero, one, two), with higher
6 values indicating a better performance. Values were jointly discussed and assigned by Andrea
7 Simoncini and Samuele Ramellini.

8

9 ***Projections***

10 The models developed during the model-selection phase were either projected on the static
11 variables (static SDMs) or on variables representing the year 2016 (dynamic SDMs). The
12 year 2016 was selected to describe current conditions as it was the closest year to the present
13 time represented in our climatic dataset. The selected model was then projected to future
14 conditions. We initially used a static LULC (i.e. the 2016 LULC variables) in future
15 predictions to constrain climatic outputs (Pang, De Alban, & Webb, 2021). We then
16 performed an additional analysis projecting models calibrated with the same historical LULC
17 database on scenarios from the future dynamic LULC database (Chen *et al.*, 2020). However,
18 the difference between LULC databases did not allow quantitative interpretations of mean
19 breeding suitability change.

20 In static LULC projections, for each RCP scenario and time interval we developed four
21 projections (one per each GCM) averaging them in a final projection representing breeding
22 habitat suitability for the species. We also computed the standard deviation between the four
23 projections to account for the uncertainty arising from different climatic scenarios
24 (Beaumont, Hughes, & Pitman, 2008; Porfirio *et al.*, 2014). In dynamic LULC projections,
25 we developed a single projection for each RCP and time interval, under the Shared

1 Socioeconomic Pathway (SSP) 5 and the MIROC circulation model (other GCMs were not
2 available).

3 When projected to new time periods, SDMs might encounter environmental conditions that
4 are not found in the calibration area (Elith, Kearney, & Phillips, 2010; Zurell, Elith, &
5 Schröder, 2012), producing spurious predictions (Owens *et al.*, 2013). This occurs when: (i) a
6 variable is outside the range found when training (i.e. strict extrapolation; Elith *et al.*, 2010),
7 or (ii) each variable is within the calibration range, but the combination of predictors is new
8 (i.e. combinational extrapolation; Zurell *et al.*, 2012). We thus used the environmental
9 overlap mask (Zurell *et al.*, 2012) to identify the areas where extrapolation occurs. We used
10 the ‘mecofun’ (v. 0.1.0.9000) R package, with one bin per variable for strict extrapolation
11 and five bins per variable to include combinational extrapolation (Zurell *et al.*, 2012).

12

13 ***Cell-wise change of habitat suitability***

14 To describe the dynamics of breeding habitat suitability for the stone-curlew, we computed
15 the difference of breeding suitability between consecutive time periods for each cell.
16 Therefore, we obtained a set of rasters describing the magnitude of breeding habitat
17 suitability change through consecutive time intervals, accounting for different RCPs and
18 LULC scenarios.

19

20 ***Change of mean habitat suitability***

21 We evaluated the variation of breeding habitat suitability calculating the mean breeding
22 habitat suitability (among all raster cells) for each future projection and considered its
23 percentage change between two consecutive time periods, according to: each GCM under
24 RCP 4.5 and RCP 8.5, and each RCP using the mean of all GCMs. This analysis was carried
25 out for the static LULC projections only.

1

2 ***Critical areas for conservation***

3 Areas predicted as suitable under both current and future conditions are fundamental to plan
4 *in situ* conservation actions (Estrada *et al.*, 2016; Thuiller *et al.*, 2019). We binarized each
5 habitat suitability map according to the threshold that maximizes the sum of specificity and
6 sensitivity (Liu, Newell, & White, 2016). Then, we summed all binarized projections and
7 attributed a score of one if the cell was suitable in all the projections and a score of zero to all
8 other cells. Additionally, we calculated the percentage of currently suitable cells representing
9 critical areas.

10

11 Further details on the modelling procedure and workflow are reported in the Overview, Data,
12 Model, Assessment and Prediction (ODMAP) protocol (Zurell *et al.*, 2020; Appendix S1).

13

14 **RESULTS**

15

16 ***Pseudo-absence methods***

17 The mean AUCtest, AUCdiff and CBI did not show marked differences between the two
18 pseudo-absence methods (Table 2). However, except for the fourth run, the CBI was
19 consistently higher for the kernel density approach, which also provided higher quality spatial
20 predictions (Table 2, Fig. S1.2). Therefore, we decided to use the kernel density approach for
21 subsequent analyses. We selected the first run due to the particularly high CBI, a fair
22 AUCtest and a high-quality spatial prediction (Table 2).

23 Dynamic models gained consistently higher CBI and generally higher QSP and PRC than
24 static models (Table 3). Ensemble SDMs showed high AUCtest, but not significantly higher
25 than the best-performing single methods (i.e. Random Forest, Maxent, GLM), and a discrete

1 overfitting (Table 3). The CBI and PRC showed the same general pattern, with higher
 2 estimates for dynamic ensemble models (Table 3). Spatial predictions did not differ
 3 significantly between static and dynamic models, except for the ANN algorithm (Fig. S1.3-
 4 S1.4). However, static models identified suitable areas at the southern edge of the study area
 5 in the African continent where the species is absent (Keller *et al.*, 2020). Instead, we found a
 6 higher agreement in these areas between dynamic models' projections and the actual species'
 7 range (Fig. S1.3-S1.4). Ensemble models gained good quality spatial outputs but tended to
 8 over-predict habitat suitability at high latitudes (e.g. in Arctic Russia, where the species is not
 9 found) and under-predict at lower latitudes (e.g. in France and the Iberian Peninsula, where
 10 the species is widespread). Instead, GAM and Maxent provided excellent projections in these
 11 areas (Fig. S1.3-S1.4). Therefore, we retained the best performing single dynamic model (i.e.
 12 Maxent; Fig. 2), that showed a good AUC (0.803), an excellent CBI (0.999) and maximum
 13 QSP and PRC values (Table 3).

14

15 ***Future projections***

16 Projections of future breeding habitat suitability for the species differed between static and
 17 dynamic LULC scenarios, but not between RCPs and time periods (Fig. S1.5). Dynamic
 18 LULC projections described a similar spatial distribution of suitable areas for the species
 19 compared to static LULC projections, but with higher suitability estimates (Fig. S1.5). The
 20 agreement between GCMs for static LULC projections was mostly high (Fig. S1.7). Strict
 21 extrapolation was generally low (Fig. S1.8-S1.9, Fig. S1.12), although it occurred
 22 consistently in some regions at the margins of our study area (e.g. Northern Russia) and it
 23 was generally higher under RCP 8.5. Combinational extrapolation was far more extensive
 24 and showed increasing values with latitude and under RCP 8.5 (Fig. S1.10-S1.12).

25

Cell-wise change of habitat suitability

The cell-wise change of habitat suitability was particularly evident in the first time interval (i.e. 2016-2030), while quite small in the subsequent ones (Fig. 3). Suitable areas for the species are expected to shift northwards. Broad areas in the central-southern part of the range are predicted to be lost, most of them in the time interval 2016-2030. Differences between static and dynamic LULC are marked, with the suitability of the latter predicted to undergo a higher change (Fig. 3).

Change of mean habitat suitability

The mean breeding habitat suitability considering a static LULC is predicted to remain stable in all time intervals and for most GCMs (Fig. S1.6A and S1.6B). However, when comparing the predictions for different GCMs, the differences were quite marked. The RCP had also a significant effect, as the percentages under RCP 8.5 were remarkably higher (Fig. S1.6C).

Critical areas for conservation

France, South-Eastern UK, Northern Italy and Israel were the regions with the highest proportion of conservation critical areas (Fig. 4). The percentage of currently suitable areas predicted to remain suitable was relatively low (27.47 %).

DISCUSSION

Relying on 1628 occurrences of the stone-curlew, we developed a robust species distribution modelling framework for the species, based on a Maxent model built with year-specific variables and calibrated using a kernel density approach for the pseudo-absences. Our model predicted significant short-term changes in the spatial distribution of suitable areas for the

1 species and allowed the identification of areas critical for its conservation under global
2 change. Furthermore, our results suggested that the distribution of the stone-curlew might be
3 affected by short-term conditions, rather than long-term ones, and confirmed that broad areas
4 of the Western Palearctic are likely to be suitable for the species in the future.

5 The northern shift of suitable areas predicted by our model is consistent with our hypothesis,
6 with the projection for the species (Huntley *et al.*, 2007), and with projections for other
7 pseudo-steppic species (e.g. the Great Bustard *Otis tarda* and Little Bustard *Tetrax tetrax* in
8 Estrada *et al.*, 2016 and the European Roller *Coracias garrulus* in Kiss *et al.*, 2020). The loss
9 of suitable areas in the Mediterranean region is not surprising as the Mediterranean
10 biogeographical region represents a hotspot of global change, and extensive biodiversity
11 losses have been predicted (Sala *et al.*, 2000).

12 Even if strong variations between GCMs and RCPs in the expected trajectories of mean
13 breeding habitat suitability for the stone-curlew may hinder sound conclusions, the predicted
14 gains and losses of mean habitat suitability were balanced, suggesting a stable mean habitat
15 suitability for the species through time. This agrees with our expectation that mean habitat
16 suitability for the species would remain stable or increase, as global warming is milder in
17 warm temperate areas (IPCC, 2013) and might therefore have a limited impact on mean
18 habitat suitability. Dispersal ability, biotic interactions and the carrying capacity of suitable
19 habitats might determine whether a stable mean habitat suitability translates into a stable
20 population size (Bateman *et al.*, 2013; Holloway, Miller, & Gillings, 2016).

21 Habitat suitability has been linked to population size and trends in birds (Green *et al.*, 2008;
22 Stiels *et al.*, 2021). We showed that large areas of the study region are predicted as suitable in
23 the future, and that a stable mean habitat suitability is likely. Hence, according to our
24 forecasts, the species may be able to maintain viable populations in the Western Palearctic.
25 However, given the relatively low percentage of areas suitable under both current and future

1 conditions and the predicted shift of suitable areas, the species might need to track its niche in
2 the future. Evidence of the ability of animals to track their niche is contrasting (Devictor *et*
3 *al.*, 2008; Chen *et al.*, 2011) and many terrestrial organisms have been shown to shift their
4 distribution at a sufficient pace to track recent temperature changes (Chen *et al.*, 2011).
5 Species affected by global change may also persist under unfavourable conditions being
6 phenotypically plastic and becoming locally adapted (Valladares *et al.*, 2014). Moreover,
7 biological interactions and movement/dispersal constraints might prevent them from
8 colonizing newly suitable areas (Bateman *et al.*, 2013; Holloway, Miller, & Gillings, 2016).
9 Our results point toward a critical use of the target-group pseudo-absence method, and we
10 recommend its explicit testing especially when using multi-source citizen science datasets.
11 Our results did not evidence a better performance for ensemble methods, contrary to other
12 studies (e.g. Marmion *et al.*, 2009), and support a tailor-made choice of the modelling
13 method. Dynamic models performed better than static ones (Table 3) as expected, supporting
14 previous works explicitly testing the two approaches (e.g. Reside *et al.*, 2010; Milanesi *et al.*,
15 2020a). Due to its minimal contribution to the final model, the ‘prey suitability’ variable (Fig.
16 S1.1) probably failed to describe the real patterns of habitat suitability for the stone-curlew’s
17 preys (Table 1). This might depend on the exclusion of relevant prey items, as the species
18 exploits a wide spectrum of food items (Vaughan & Vaughan-Jennings, 2005) that is difficult
19 to model through SDMs. We nevertheless highlight the importance of considering biotic
20 predictors though suggest including the entire trophic web of a species.
21 Correlative species distribution models assume an equilibrium condition between the species
22 and the environment (Araújo & Pearson, 2005). Areas that have been abandoned by the
23 stone-curlew during the last decades of the past century can be recolonized, as happened in
24 the UK following the targeted conservation efforts of the LIFE11INF/UK000418 ‘Securing
25 the future of the stone-curlew throughout its range in the UK’. This suggests that suitable

1 climate and LULC conditions at the relatively coarse scale of our study exist in those areas.
 2 Therefore, the SDMs' equilibrium assumption for this species might be violated and future
 3 studies could explicitly account for non-equilibrium conditions (Václavík & Meentemeyer,
 4 2012). SDMs also assume the evolutionary conservatism of the species' ecological niche
 5 through time (Peterson, Soberón, & Sanchez-Cordero, 1999; Barbet-Massin *et al.*, 2011), a
 6 condition that is difficult to prove and deserves specific attention. Thanks to constant
 7 improvements in climate and LULC scenarios, in the future our workflow could be applied to
 8 a wider spectrum of scenarios, to better represent all the components of uncertainty (Thuiller
 9 *et al.*, 2019). However, the two RCPs employed in our study can provide valuable insights on
 10 the effect of global change on habitat suitability, as demonstrated by their extensive use (e.g.
 11 Kiss *et al.*, 2020; Stiels *et al.*, 2021). We also limited our study to the breeding period:
 12 understanding the drivers and changes of habitat suitability for the stone-curlew across
 13 migratory and wintering grounds might provide further insights for its conservation.

14
 15 The stone-curlew is philopatric in the breeding areas (Green, 1990) and this might delay
 16 habitat-tracking under environmental change. Considering this latter scenario, critical areas
 17 might act as a stronghold for the species, and anticipatory conservation efforts should
 18 primarily focus on these areas (Thuiller *et al.*, 2019). Furthermore, ensuring high connectivity
 19 conditions for the species in areas predicted to become unsuitable might contribute to
 20 maintain viable populations and facilitate niche tracking (Heller & Zavaleta, 2009). Indeed,
 21 habitat fragmentation contributed to the species' decline in the '90s (Tucker & Evans, 1997).
 22 Finally, enhanced monitoring efforts in areas predicted to become suitable might increase
 23 early-detection probability and mitigate the negative effects of biotic interactions. Our model
 24 evidenced the importance of two LULC classes that are heavily affected by farming and
 25 harvesting activities (i.e. non-irrigated agricultural areas and grasslands). Precisely, the most

1 critical areas and the areas predicted to become suitable for the stone-curlew are in
2 intensively cultivated areas, corresponding to the ‘core of EU continental agriculture’
3 (D’Amico *et al.*, 2013), England and the Po Plain. Furthermore, in France, the country
4 hosting the largest portion of critical areas, over 60% of breeding pairs are found in the
5 Central/Western region within arable crops (Malvaud, 1996; Issa & Muller, 2015). In these
6 ecosystems, *ad hoc* management interventions on a local scale can be effectively used to
7 favour stone-curlew’s presence (Hawkes *et al.*, 2021).

8 In conclusion, our study refines current knowledge on the effects of global change for the
9 stone-curlew, providing predictions of breeding habitat suitability for the species at high
10 temporal and spatial resolutions, and conservation planners might benefit from our results by
11 incorporating indications on the most relevant conservation areas in the development of
12 action plans for the species.

13

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2

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6

1 DATA ACCESSIBILITY STATEMENT

2

3 Presence data used to develop species distribution models for the Eurasian stone-curlew are
4 available at: <https://doi.org/10.6084/m9.figshare.16727296.v1>

5 Longitude, latitude and year are reported for each observation. Data from the British Trust for
6 Ornithology are omitted in agreement with the data access policy. Data from ornitho.it are
7 accompanied by a citation, in compliance with the site's rules.

8

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18

- 1 **Table 1** Candidate environmental variables to calibrate SDMs for the Eurasian stone-curlew.
- 2 To describe the correlation among variables, we report the VIF (Variance Inflation Factor)
- 3 for the initial and final sets of static and dynamic variables. Variables included in the
- 4 dynamic Maxent model used for future projections are shown in bold, and their percentage
- 5 contribution is reported.

Variable	Static		Dynamic		Contribution (%)
	VIF _{in}	VIF _{fin}	VIF _{in}	VIF _{fin}	
Percentage cover of agricultural areas (non-irrigated)	3.432	1.407	5.007	2.319	27.6 %
Temperature of the warmest quarter	810.809	2.206	171.087	-	23.9 %
Temperature seasonality	69.530	1.773	20.111	1.207	17.4 %
Percentage cover of grass	1.736	1.274	2.541	1.684	10.8 %
Percentage cover of agricultural areas (irrigated)	1.135	1.022	1.339	1.088	10.1 %
Slope	1.463	1.229	1.977	1.684	9.0 %
Percentage cover of trees	3.948	1.955	3.532	2.318	8.7 %
Karst area	1.072	1.041	1.082	1.057	6.9 %
Distance from water	2.002	1.831	1.767	1.557	4.8 %
Percentage cover of urban areas	1.158	1.114	1.232	1.152	4.5 %
Precipitation seasonality	1.747	1.607	1.823	1.722	3.6 %
Percentage cover of shrubs	1.428	1.216	2.039	1.345	3.0 %
Prey suitability	1.667	1.557	1.358	1.323	0.5 %

Annual temperature	1000.396	-	142.475	-	-
Annual precipitation	6.717	-	3.686	-	-
Precipitation of the warmest quarter	7.323	-	3.754	2.198	-
Percentage cover of bare areas	9.983	-	6.365	-	-

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Table 2 Evaluation metrics of the static Maxent models for the Eurasian stone-curlew calibrated with two pseudo-absence approaches (target-group and kernel density), for four cross-validation runs. We report Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) of the training and test datasets and their difference; Continuous Boyce Index (CBI); Quality of Spatial Prediction (QSP) and Plausibility of Response Curve (PRC). Quality of Spatial Prediction (QSP) and Plausibility of Response Curve (PRC) are qualitative subjective scores (value of zero, one or two) describing the ecological validity of a model. Mean and standard error are reported for each approach.

Target group						
Run	<i>AUC_{train}</i>	<i>AUC_{test}</i>	<i>AUC_{diff}</i>	<i>CBI</i>	<i>QSP</i>	<i>PRC</i>
1	0.891	0.679	0.212	0.852	1	2
2	0.878	0.746	0.132	0.977	0	2
3	0.854	0.824	0.030	0.842	1	2
4	0.850	0.832	0.018	0.654	1	2
Summary						
<i>Mean (SE)</i>	0.868 (0.010)	0.770 (0.036)	0.098 (0.046)	0.831 (0.067)	0.75 (0.25)	2 (0)
Kernel density						
Run	<i>AUC_{train}</i>	<i>AUC_{test}</i>	<i>AUC_{diff}</i>	<i>CBI</i>	<i>QSP</i>	<i>PRC</i>
1	0.888	0.783	0.105	0.999	2	1
2	0.884	0.871	0.013	0.985	1	1
3	0.885	0.727	0.158	0.887	2	2
4	0.892	0.799	0.093	0.333	2	2
Summary						
<i>Mean (SE)</i>	0.887 (0.002)	0.795 (0.030)	0.092 (0.030)	0.801 (0.158)	1.75 (0.25)	1.5 (0.29)

Table 3 Evaluation metrics of four species distribution modelling strategies for the Eurasian stone-curlew: single static, ensemble static, single dynamic and ensemble dynamic. The following single algorithms have been used: Artificial Neural Networks (ANN), Classification Tree Analysis (CTA), Generalized Additive Models (GAM), Generalized Boosting Models (GBM), Generalized Linear Models (GLM), Maximum entropy (Maxent), Random Forest (RF). The following metrics are reported: Area Under the ROC (Receiver Operating Characteristic) Curve (AUC) of the training and test datasets and their difference; Continuous Boyce Index (CBI). Quality of Spatial Prediction (QSP) and Plausibility of Response Curve (PRC) are subjective scores (value of zero, one or two) describing the ecological validity of a model. The model used for future projections is highlighted in bold.

Single static SDM						
Algorithm	<i>AUC_{train}</i>	<i>AUC_{test}</i>	<i>AUC_{diff}</i>	<i>CBI</i>	<i>QSP</i>	<i>PRC</i>
ANN	0.608	0.595	0.013	0.160	0	0
CTA	0.832	0.669	0.163	0.437	0	0
GAM	0.871	0.779	0.092	0.296	2	2
GBM	0.896	0.785	0.111	0.517	1	1
GLM	0.865	0.802	0.063	0.440	0	1
Maxent	0.889	0.784	0.105	0.994	2	1
RF	0.999	0.814	0.185	-0.147	0	1
Ensemble static SDM						
Algorithm	<i>AUC_{train}</i>	<i>AUC_{test}</i>	<i>AUC_{diff}</i>	<i>CBI</i>	<i>QSP</i>	<i>PRC</i>
Mean	0.952	0.815	0.137	0.321	1	1
Weighted average	0.954	0.815	0.138	0.360	1	1
Single dynamic SDM						

Algorithm	<i>AUC_{train}</i>	<i>AUC_{test}</i>	<i>AUC_{diff}</i>	<i>CBI</i>	<i>QSP</i>	<i>PRC</i>
ANN	0.713	0.687	0.026	0.533	0	0
CTA	0.758	0.634	0.123	0.675	1	0
GAM	0.858	0.794	0.064	0.837	2	2
GBM	0.882	0.784	0.098	0.726	2	1
GLM	0.851	0.793	0.058	0.471	0	2
Maxent	0.885	0.803	0.082	0.999	2	2
RF	0.999	0.809	0.190	0.660	0	1

Ensemble dynamic SDM

Algorithm	<i>AUC_{train}</i>	<i>AUC_{test}</i>	<i>AUC_{diff}</i>	<i>CBI</i>	<i>QSP</i>	<i>PRC</i>
Mean	0.944	0.808	0.136	0.847	1	2
Weighted average	0.946	0.810	0.136	0.870	1	2

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1 Figure 1.

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1 Figure 2.

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1 Figure 3.

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1 Figure 4.

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Figure 1 Occurrence and pseudo-absence points used to model breeding habitat suitability for the Eurasian stone-curlew. Target-group pseudo-absences are observations of other bird species recorded by the same observers of the presence data in the Global Biodiversity Information Facility (GBIF). Kernel density pseudo-absences are points with a spatial density weighted according to a fixed kernel density estimated from the presence points. For target-group and kernel density pseudo-absences, 500 randomly sampled points from the datasets are shown to improve image clarity. The grey area represents the species' range in the Western Palearctic, with the exclusion of the Macaronesian archipelago. Photo by Saverio Gatto.

Figure 2 (a) Current breeding habitat suitability map according to the dynamic Maxent model selected to project breeding habitat suitability for the Eurasian stone-curlew under global change scenarios, and (b) response curves for the four environmental variables with the highest percentage contribution in the same model.

Figure 3 Cell-wise change of breeding habitat suitability for the Eurasian stone-curlew under four time intervals (2016-2030, 2030-2050, 2050-2070, 2070-2090) and two Representative Concentration Pathways (RCP 4.5, RCP 8.5). S-LULC = Static Land-Use/Land-Cover; D-LULC = Dynamic Land-Use/Land-Cover.

Figure 4 Critical areas for the conservation of the Eurasian stone-curlew. Currently suitable areas predicted to remain suitable under all scenarios of breeding habitat suitability for the species are highlighted in red. Shaded areas represent the species' range in the Western Palearctic, with the exclusion of the Macaronesian archipelago.

1 **List of Appendices:**

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3 **Appendix S1. Overview, Data, Model, Assessment and Prediction (ODMAP) protocol**

4 **(Zurell *et al.* 2020).**

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