

Past and future climate-driven shifts in the distribution of a warm-adapted bird species, the European Roller *Coracias garrulus*

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ABSTRACT

Capsule: The distribution range of the European Roller *Coracias garrulus* has undergone large changes over geological times, but although the species is warm-adapted, the human induced climate change is predicted to affect negatively the range of the currently large populations.

Aim: Information on species-specific vulnerability to climate change is crucial not only for designing interventions and setting conservation goals, but also to inform conservation decision-making. Our goal was to map climate suitability for the European Roller in the Western Palaearctic under current climate, and for past (last glacial maximum and mid-Holocene) and future (2050 and 2070) climate scenarios.

Methods: We used MaxEnt for species distribution modelling based on the reconstructed distribution map of the species.

Results: Our results suggest that during glacial periods Rollers persisted in small southern refugia, and then spread and colonized northern latitudes during the mid-Holocene. In the future, our models forecast a shift in climatically suitable range towards northern latitudes and an overall small range contraction (4.5–5.5%). Warmer temperatures will increase climate suitability in northern countries where the species is currently declining or became locally extinct. On the other hand, wide suitable areas under current climatic conditions are predicted to become unsuitable in the future (35–38% by 2050 and 2070, respectively), significantly impacting large populations such as those in Romania, Spain, Bulgaria and Hungary. French and Italian populations are identified to be future key populations for Roller conservation.

Conclusions: Our findings suggest that future climate changes will likely amplify the impacts of existing threats on the majority of large European Roller populations in Europe.

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Introduction

At geological time scales, geographic ranges of species have cyclically expanded and contracted in response to cold and warm periods associated with glacial and interglacial episodes (Graham & Grimm 1990, Hewitt 1996, Hewitt 2000). In the Quaternary, during the height of the Pleistocene glaciations, temperate-adapted species that are today widespread in Europe are thought to have survived in small and climatically

favourable refugia ('glacial refugia hypothesis') located in the southern peninsulas of Iberia, Italy and Balkans (Taberlet *et al.* 1998, Provan & Bennett 2008). Climate refugia offered opportunities for species to retreat, persist and following the last glacial maximum (LGM hereafter, 19,000–23,000 years ago), recolonize northern latitudes, as climate warming (reaching its maximum in the mid-Holocene) forced ice sheets to recede (Taberlet *et al.* 1998, Hewitt 2004).

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Understanding the effect of past climate changes on the composition of communities and its change over time and space is one of the major aims in ecology and paleoecology (Walther *et al.* 2002, Ovaskainen *et al.* 2013, Carotenuto *et al.* 2016) and a key challenge for forecasting species' susceptibility to future climate changes. Whilst climate change has gone on continuously throughout Earth's history, current human-driven climate changes apparently have no parallel in recent geological history (IPCC 2018). Since the nineteenth century, the global mean surface temperature has increased between 0.3°C and 0.6°C and warming is predicted to continue or even accelerate (Stocker *et al.* 2014) impacting species and ecosystems (Walther *et al.* 2002, Parmesan 2006, Walther 2010, Nolen *et al.* 2018).

Compelling evidence has been found for the impact of climate change on distribution, phenology, migratory behaviour, breeding biology and population dynamics of many bird species (Crick 2004, Both *et al.* 2006, Carey 2009, Gregory *et al.* 2009). Poleward shifts in species distributions have been documented for both breeding and wintering populations of birds, as well as upslope movements and range contractions or expansions (Thomas & Lennon 1999, Böhning-Gaese & Lemoine 2004, Maclean *et al.* 2008, Brommer *et al.* 2012, Reif & Flousek 2012). Robust predictions of potential distributions are needed to design and implement conservation strategies and to adjust existing effective networks of protected areas as a tool for biodiversity conservation in the face of climate change (Pressey *et al.* 2007, Araújo *et al.* 2011, Dawson *et al.* 2011).

Species distribution models (Austin 2002, Guisan & Thuiller 2005) have become an important tool used to model current patterns of species distributions and to predict changes in the distribution and abundance of species under environmental change (Gritti *et al.* 2006, Wiens *et al.* 2009, Pelletier *et al.* 2015, Morganti *et al.* 2017), however they have to be used with caution (Journé *et al.* 2019). Based on presence-absence or presence-only data, species distribution models combine observations of species occurrence or abundance with environmental descriptors (e.g. climate, soil, elevation, land use) and are increasingly proposed to support conservation decision making (Margules & Pressey 2000, Addison *et al.* 2013, Rodríguez-Ruiz *et al.* 2018). Nonetheless, climate-only envelope models are biased to predict accurate range shifts. Modelling frameworks and the modelled species can affect the model's ability to predict future distributions and models can be poor at predicting species range contractions (Rapacciuolo *et al.* 2012). Most of these

models do not account for dispersal limitations, however considering dispersal capacity is important to get better estimates of the future distribution (Hellmann *et al.* 2016) as well as biotic factors such as species interactions and habitat and/or land-use changes are usually missing from modelling procedures. Range-shift predictions assume that the climate variables used in the models are adequate surrogates of the species distribution range, but other factors such as species-specific traits or human land-use practices may drive distribution and therefore the results of species distribution models (Lehikoinen & Virkkala 2016).

Over the past century, there have been two major causes of changes in species' distribution range: land-use change and climate change. Anthropogenic climate change is expected to be the greatest long-term threat to global biodiversity (Cahill *et al.* 2017). Indeed, many bird populations have experienced a reduction in their historical breeding range because the former range may no longer be suitable due to intensified land use change. The distribution area of the European Roller *Coracias garrulus* (hereafter Roller) in Europe changed from 1960 to the end of 1980s as the species suffered marked population declines accompanied by local extinctions and overall range contraction due to land use changes (Kovács *et al.* 2008). These changes have justified the inclusion of the species into the Birds Directive (2009/147/CE) Annex I. The lack of nest-site and foraging habitats are probably two main factors for the observed declines of Roller populations (Kovács *et al.* 2008). Successful nest-box programs (Avilés *et al.* 1999, Václav *et al.* 2011, Kiss *et al.* 2014, Gameiro *et al.* 2020) indicate that nest-site availability is one of the most important limiting factors for European Rollers, driving past range contractions and possibly decreasing the realized breeding range in the future in the cases where appropriate nest-boxes provisioning is missing. Ongoing land use change is not only driven by climate change but also by agricultural policies (Audsley *et al.* 2006). In Europe, Common Agricultural Policy (CAP) had various effects on biodiversity, although some measures affected positively the targeted taxa, many of them were unfavourable (Kleijn *et al.* 2009, Kleijn *et al.* 2011, McMahon *et al.* 2010, Emmerson *et al.* 2016, Brambilla 2019). Besides, agricultural policies have higher dependence on political decisions and their long term effect on land use change is thus highly unpredictable.

In this study, we used species distribution models to predict changes in the climatically suitable range of the Roller during historical times across Europe and to derive spatially explicit predictions of climatic suitability for the species in the future. Rollers breed

throughout temperate and Mediterranean zones characterized by warm summer weather (BirdLife International 2017) and occupy semi-desert habitats and are resilient to heat (Catry *et al.* 2015). Overall predictions for potential distribution of European breeding birds have been performed by Huntley *et al.* (2007) which pointed out the potential adverse climatic effects upon the Roller's breeding range. In that work, distribution data were derived from the European Bird Census Council's Atlas of European Breeding Birds (Hagemeijer & Blair 1997) which contains presence and absence records in on a 50 × 50 km grid square resolution. Due to the collapse of Roller populations in several countries, the distribution of the species in the atlas do not cover the entire climatic range, therefore, here we aimed to use more precise distribution data including those areas where the species is currently absent due to agricultural and forestry intensification and to have better information on presences and absences of the species in the European breeding range. Moudrý & Šimová (2012) suggested the use of accurate species occurrence data and large sample sizes for conservation purposes, in this paper instead of using a single large grid database, we aimed to use a more precise dataset based on strong bibliographic research and by consulting experts in most important countries. Thus, the specific goals of this study were to reconstruct the historical climatically suitable range of the species to gain better knowledge on its climatic requirements and furthermore to understand how the European Roller is able to cope with the past and future climate changes. Specifically, we aimed to (i) predict the species' climatic refugia in southern Europe and (ii) reconstruct the colonization pattern and northwards range expansion from Ice Age refugia following the glacial maxima and throughout the warming mid-Holocene period (6000 years ago). Species distribution models of the current distribution were estimated based on occurrence data and were then projected onto the historical climatic layers to estimate the past (LGM and mid-Holocene) range of the Roller. Similarly, we used the predicted current potential distribution and climate models to (iii) forecast the future climatically suitable range of the species in 2050 and 2070. Finally, we aimed to (iv) compare the extension of current and future climatically suitable areas and quantify the overall range change, i.e. the proportion of current climatically suitable areas projected to become unsuitable in the future ('loss') and the proportion of future areas projected to become suitable in previously unsuitable areas ('gain') and (v) evaluate which populations will likely suffer range-

contraction in the near future. Overall, we aimed to assess the Roller's sensitivity to climate changes, to inform species-specific management planning through the identification of critical key areas for future conservation.

Methods

Study species

The Roller is an insectivore species associated with open landscapes, including mixed farmland, open forests with clearings, Mediterranean plains and steppes occurring below 400–600 m above sea level (Fry & Fry 1992, Cramp 1998). It is a long-distance migrant breeding between May and July (Cramp 1998). Rollers are obligatory secondary cavity breeders, using various nest-sites such as abandoned cavities of large woodpeckers or natural holes in sandbanks and cliffs (Fry *et al.* 2017). Alternatively, when natural cavities are scarce, they can rely on artificial nest-boxes (Avilés *et al.* 1999, Kiss *et al.* 2017). In Europe, breeding distribution of the Roller historically ranged across much of southern, central, and eastern Europe, extending north to southern Sweden and across the Baltic states (Fry *et al.* 2017). However, during the last century, the species underwent a long-term range contraction, with the species now extinct in Sweden, Denmark, Germany, the Czech Republic, and Slovenia (BirdLife International 2017). The main causes of the recent widespread decline include the loss of suitable habitat due to changes in agricultural and forestry practices (which affect foraging habitat quality and extent) and the loss of nest sites (Kovács *et al.* 2008, BirdLife International 2017).

Reconstruction of the breeding range

Spatial distribution data for birds are rarely available for the period before the beginning of national and European scale monitoring programs relying on citizen data such as the Pan-European Common Bird Monitoring Scheme (<https://www.ebcc.info/pan-european-common-bird-monitoring-scheme-pecbms/>). However, due to its relative scarcity and decreasing population trends in several countries, occurrence records of Rollers were collected and published before that period as well (online Table S1). We obtained occurrence data for breeding Rollers between 1850 (except one from Finland 1787) and 2016 from 25 countries covering the major part of the Western Palaearctic distribution of the species. Even under cooler climatic conditions the European

Roller used to breed from the Mediterranean region to the southern Sweden and Finland and it occurred regularly at higher elevations in the Carpathian basin than today (Kiss & Tokody 2017). The current distribution of the species does not, therefore, cover all of its climatic range as the population has undergone a widespread and large decline during the twentieth century, so distribution data from this long time period was required to predict the potential bioclimatic niche of the species, unbiased by modern land use changes. Historic land-use change might also affected the breeding range; however, birds of farmlands and grasslands have been abundant until the agricultural intensification in the twentieth century. Main sources included historical data from the Carpathian Basin (district centroids of data between 1892 and 1998), georeferenced map points (primary literature and internet sources) and georeferenced breeding locations from national monitoring programs, surveys and specific studies, which provide a representative coverage of all breeding areas in the studied region. Distribution range studies generally use databases covering several decades or less (Huntley *et al.* 2007), however, exceptions are also found such as those covering periods of 60–70 years (Telfer *et al.* 2002, Morán-Ordóñez *et al.* 2017). The recently colonized coastal area of Croatia was not included in the analysis because of the lack of related archive data, but the present prediction found that the area is suitable for the species under present climatic conditions (online Table S2). Overall, we used 6111 occurrence points (Table 1 and Figure 1), including records of exactly known breeding locations as well as potential breeding areas at the national grid level (2.5 km (Hungary) to 10 km grid (Spain, Baltic states)) and observations of the species during the breeding season. We consider a site as potential if Rollers were observed during the breeding season. As our data covered a long time period during which the climate had changed, we also modelled Rollers' distribution using (a) data without Finland and Denmark, the two countries from where the Rollers first became extinct, (b) data from the beginning of the twentieth century, and (c) without occurrence points dating before (1960) (online Tables S2–S4 and Figures S1–S3).

Climate data

We retrieved 19 bioclimatic predictors describing current climatic conditions (1960–2000) from the WorldClim database (<http://www.worldclim.org>, Hijmans *et al.* 2005) at a spatial resolution of 2.5

Table 1. Sources of occurrence points of the Roller (see also online Table S1).

Country	Period	Number of occurrence points
Baltic states (Estonia, Latvia, Lithuania)	2000–2011	385
Belarus	1990s	40
Bulgaria	2007	508
Carpathian Basin (Hungary, Slovakia, Romania, Austria, Serbia)	1894–1983	534
Croatia	1894–1967	28
Cyprus	2016	3
Denmark	before 1900, 1900–1964	119
Finland	1787	1
France	1970–2011	2061
Germany	1962–1976	96
Greece	2010s	7
Hungary	1978–1985	230
Italy	2005–2014, 1970s, 2011 and 2013	84
Poland	1900–2005, 1960–1996	830
Portugal	1973–2004, 2009	91
Russia	NA	67
Slovenia	1894–1972, 1979–1986	12
Spain	1985–2002	777
Serbia	1894–1972	7
Sweden	mid 1800s–1967	87
Turkey	2008	41
Ukraine	1980–2015	93

arc-minutes, as this resolution corresponds roughly to home range sizes of Rollers (Cramp 1998). We generated future climatic projections for the mid (2050) and late (2070) twenty-first century using the downscaled global climate model (GCM) data from Coupled Model Intercomparison Project 5 (CMIP5, Stocker *et al.* 2014) provided by the WorldClim database. Data representing future conditions provide climatic projections of global climate models (GCMs) for four representative concentration pathways (RCP2.6, RCP4.5, RCP6.0 and RCP8.5), considered as the most recent GCM climate projections applied by the Fifth Assessment Intergovernmental Panel on Climate Change (IPCC) report (Stocker *et al.* 2014) out of which we decided to apply RCP4.5 which provides a widely accepted medium stabilization scenario. This approach assumes that global annual greenhouse gas emissions (measured in carbon dioxide equivalents) peak around 2040, with emissions declining substantially thereafter (Gent *et al.* 2011, Stocker *et al.* 2014). GCM output records were downscaled and corrected for bias applying WorldClim 1.4 as baseline 'current' climate. Besides applying RCP 4.5, known as the most conservative scenario, we repeated all analysis for all other scenarios (online Tables S4 and S5, Figures S4 and S5). Past climate conditions were

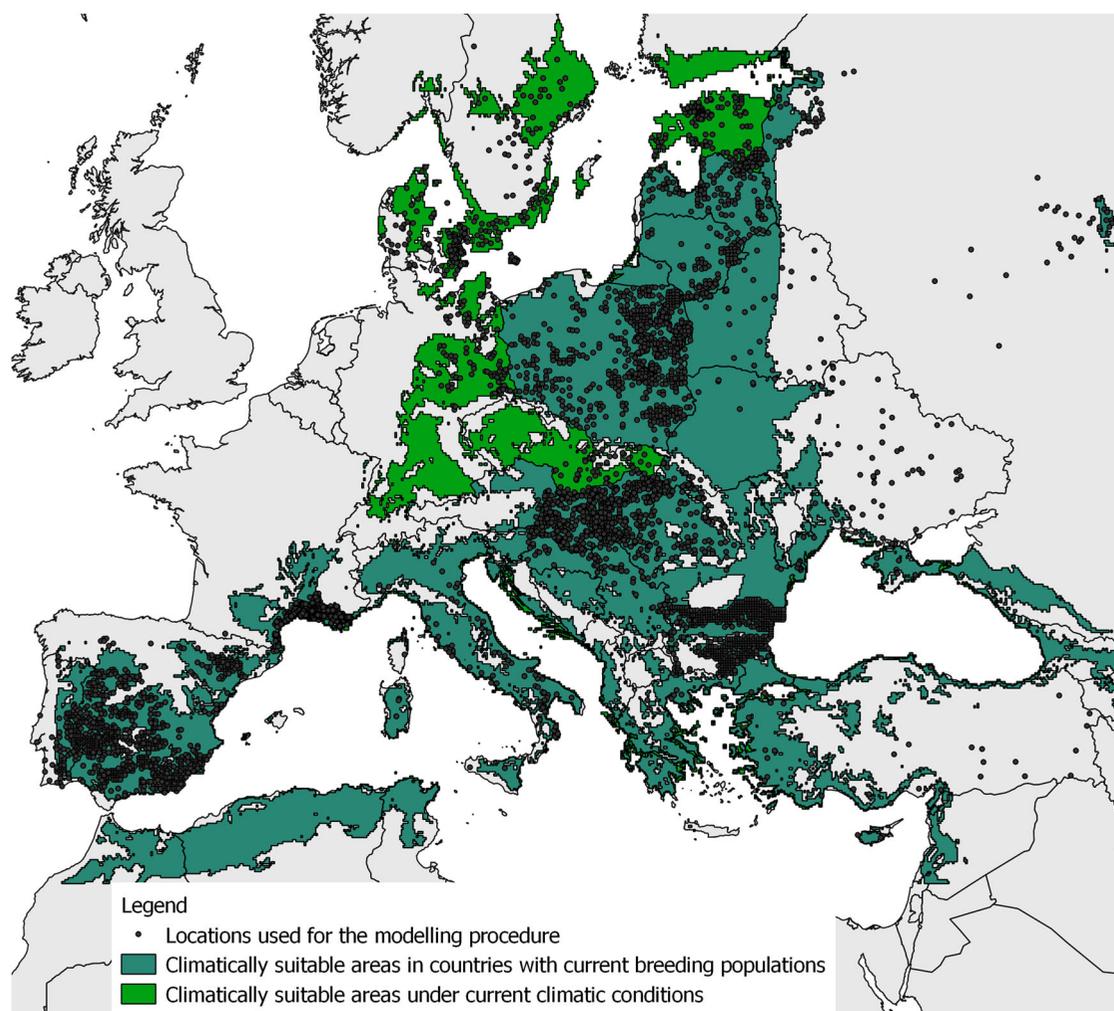


Figure 1. Distribution of climatically suitable areas for the Roller under current (1950–2000) climatic conditions modelled using MaxEnt.

obtained from the WorldClim database (Community Climate System Model 4), which used the data available by CMIP5 downscaled and calibrated using WorldClim 1.4 as a baseline ‘current’ climate, available both for mid-Holocene and LGM timescales (<http://www.worldclim.org>).

Population data

To assess relationships among population trends and climatic responsiveness, the population size was classified into three categories at the country level. According to the most recent European Union Red List assessments (BirdLife International 2015) populations consisting of more than 1000 breeding pairs were considered large, whereas medium was defined as those having between 100 and 1000 pairs and small indicating populations with less than 100 pairs (Table 3).

Species distribution models

We used the MaxEnt bioclimatic modelling software (Phillips & Dudík 2008) to model the suitability of future (2050 and 2070) and past (LGM and mid-Holocene) climate for breeding Rollers by projecting the optimized current bioclimatic model to past and future climatic maps (Elith *et al.* 2011). The spatial extent of the projections was determined by dataset points on the eastern and western edges, the Arctic circle was used as the northern boundary and Tunisia as southern boundary. MaxEnt applies a machine-learning algorithm based on the maximum entropy approach to predict the potential range of species calculating presence-only data and environmental parameters and considered as the leading statistical approach to species distribution modelling (Phillips *et al.* 2006). To estimate the importance of predictors (as the parameter estimates cannot be retrieved from complex machine-learning algorithms), we used the jackknife test as a built-in functionality of MaxEnt,

formulating models with each bioclimatic proxy alternatively excluded. This procedure generates models entering each proxy in isolation to compute variable importance (Shcheglovitova & Anderson 2013). To control for the sampling effort, we generated a sampling bias grid, that is, a weighting surface based on the species records weighted by a Gaussian kernel with a standard deviation (Elith *et al.* 2011), by applying the topic-specific functions of the ‘raster’ and ‘MASS’ packages of the R statistical programming environment. To provide a different independent estimate of the importance of environmental parameters, we calculated permutation importance, obtained from the final MaxEnt model disregarding the path of model development. The contribution of each parameter is calculated by randomly permuting predictor values among birds’ presences and background training points and then estimating the resulting decrease in training area under the curve (AUC), this is the single model evaluation metric available in MaxEnt, that is capable of capturing the overall accuracy independent of a particular threshold (Deleo 1993). Large decreases in this measurement indicate that the model depends on the specific variable (Phillips & Elith 2010). The discrimination performance of all bioclimatic models was assessed by AUC, in order to distinguish reliably between the presences and the background points. AUC ranges between 0.0 and 1.0, where 1.0 is considered perfect prediction, while values lower than 0.5 indicate predictions that are not better than random (Fielding & Bell 1997). During variable selection, we considered the results of the jackknife test and biological information on the studied species, as follows. First, we analysed the results of the jackknife test of the full set of bioclimatic variables (AUC = 0.785) which showed the importance of bio1 (annual mean temperature), bio4 (variance of temperature seasonality), bio6 (Min Temperature of Coldest Month), bio7 (Temperature Annual Range), bio9 (Mean Temperature of Driest Quarter), bio10 (Mean Temperature of Warmest Quarter) and bio11 (Mean Temperature of Coldest Quarter) with training gains (TG) > 1.00 (online Figure S6). Out of this set of supported proxies, we chose to use only those which are expected to have a substantial impact on the distribution of the European Roller. Specifically, the annual mean temperature is a reliable predictor of the breeding habitat, as the species prefers the warm summer climates and avoids oceanic influence (Cramp 1998, Fry *et al.* 2017) and increased precipitation may have an impact on its distribution range (Durango 1946, Kalela 1949). As all of these are considered as potentially supported predictors of the

distribution area of the Roller, we choose to apply all these proxies for generating MaxEnt models. MaxEnt model results generate logarithmically scaled calculations of the presence probability estimated by the 10-percentile training presence threshold (Radosavljevic & Anderson 2014). By using this threshold, suitable habitats are identified which include 90% of the data included in the model formulation. Thus, raster grids with presence probabilities larger than the 10-percentile training presence threshold will be considered as predicted presence points. We used exclusively bioclimatic variables rather than other physical environmental or vegetation habitat variables to predict Roller distribution (Porfirio *et al.* 2014, Morganti *et al.* 2017). In Europe, many Roller pairs currently rely on the presence of artificial nest boxes which are replacing one of the most important habitat factors, the nesting site. Therefore, by using locations of pairs breeding in nest boxes we may fail to include the crucial habitat for breeding. The provision and maintenance of artificial nest-sites are highly dependent on the local financial support for conservation measures, therefore using it for generating predictions at continent scales may add significant uncertainty to the results. Moreover, the presence of natural cavities is highly dependent on (i) the presence of cavity maker species (in the case of Rollers: Black Woodpeckers *Dryocopus martius*, Green Woodpeckers *Picus viridis* and European Bee-eaters *Merops apiaster*) and the presence of old softwood patches, treelines or even isolated trees. The available continent-level habitat or land-cover databases e.g. Corinne Land Cover do not provide information about the age structure of woody vegetation.

All bioclimatic modelling was carried out in the statistical framework provided by the MaxEnt programming environment, applying the ‘dismo’ package of the R statistical programming environment (R Development Core Team 2019). All other data management and analyses were conducted applying the R environment, by employing its topic-specific ‘shapefiles’ (Stabler 2013), ‘maptools’ (Lewin-Koh *et al.* 2011), ‘spatstat’ (Baddeley & Turner 2005), ‘raster’ (Hijmans & Van Etten 2014), ‘rgdal’ (Bivand *et al.* 2014), and ‘rJava’ packages (Urbanek 2013).

Current and future climatic suitable areas

We quantified the change between current and future climatic suitability for Rollers by comparing the number of 2.5 arc-minute resolution grid cells with suitable climatic conditions between current and future (2050 and 2070) scenarios. We classified the results of

future predictions into four values for each cell: (i) high impact areas, where a species potentially occurs under present conditions but will not be suitable in the future; (ii) areas outside of the realized niche, which are neither suitable under current nor future conditions; (iii) low impact areas, where the species can potentially occur under both present and future climates; and (iv) new suitable areas, where a species could potentially occur in the future, but not under current conditions (Scheldeman & Zonneveld 2010). Finally, we calculated overall range change, the proportion of currently suitable areas projected to become unsuitable ('loss') and the proportion of future suitable areas projected to occur in currently unsuitable areas ('gain'). The extent of the area of overlap between its present distribution and its future potential climatically suitable range provides an indication of the effects of future climatic change: species with limited or no overlap are expected to be much more vulnerable than are species with extensive overlap because a large overlap provides a species with an effective buffer against problems that may arise.

Results

Evaluation of MaxEnt models and importance of bioclimatic predictors

MaxEnt modelling of the breeding distribution under current climatic conditions was robust and performed substantially better than random sampling (model AUC = 0.788), showing that the mean temperature of warmest quarter (bio10) and annual temperature range (bio7) were the most important predictors of Roller occurrence (Table 2). Among these predictors, bio7 was represented by the highest value of variable support (Training Gain, TG = 0.34), calculated as training gain of models including each variable separately (Table 2). Interestingly, no other bioclimatic parameter emerged as a variable of key importance, as the performance of models including these proxies in isolation was similar ($0.21 \leq TG \leq 0.251$; Table 2). Distribution of climatically suitable areas for breeding Rollers under current climatic conditions is shown in Figure 1. There was an overall agreement between our predictions of suitable climatically areas and occurrence points of Rollers. Except for Turkey, projected distribution in central and southern Europe consistently matched the geographic occurrences (Figure 1). At northern latitudes, deficiencies include failure to predict scattered locations at range margins (Sweden, Ukraine, and Russia) (Figure 1). Finally, whilst there were no occurrence points of breeding

Table 2. Statistical properties of MaxEnt model performance fitted on the occurrence points of the European Roller.

Evaluation metric	Value			
Number of training samples	3017			
Regularized training gain	0.5252			
Number of iterations	500			
Training Area Under the Curve (AUC)	0.7883			
Variables	Variable contribution	Training gain with variable in separation		
bio1 (Annual Mean Temperature)	97126	0.2259		
bio4 (SD of Temperature Seasonality)	47815	0.2508		
bio6 (Min Temperature of Coldest Month)	23149	0.2123		
bio7 (Temperature Annual Range)	497631	0.3430		
bio9 (Mean Temperature of Driest Quarter)	63364	0.2327		
bio10 (Mean Temperature of Warmest Quarter)	151649	0.2292		
bio11 (Mean Temperature of Coldest Quarter)	66945	0.2097		
10% logistic threshold of training presence	0.3814			
Model AUC	RCP 46	RCP 26	RCP 60	RCP 85
<i>Present</i>	0.8677			
<i>Mid-Holocene</i>	0.7468			
<i>LGM</i>	0.6208			
<i>2050</i>	0.7865	0.8110	0.7327	0.7252
<i>2070</i>	0.7631	0.8038	0.6562	0.6588

Rollers in North Africa, this region was systematically included in all models.

Projections of climate change-driven shifts in the distribution of Rollers

The comparison of present and past range projections shows that during the last glacial maximum (LGM) the distribution of Rollers was confined to the Balkans, Turkey, South Iberia and North Africa, and the size of the occupied area amounted only to 12.6% of the range projected under current climatic conditions (Figure 2 (a)). When comparing the mid-Holocene and current projected distributions, 70.14% of the mid-Holocene distribution overlapped with the current while 48.9% of current distribution overlapped with the mid-Holocene (Figure 2(b)).

The geographic extent of currently climatically suitable areas indicates a slight decline by 2050 (5.5%). By 2070, the overall decrease will be 4.5% compared to the current potential distribution range due to the increase at the northern edge of the breeding range (Figure 3(a,b)). Besides the predicted climatically suitable range shrinkage, future area projections for both 2050 and 2070 indicate a northward expansion from current northern distribution edge 61° to 63° and 65° latitude by 2050 and 2070, respectively (Figure 3(a,

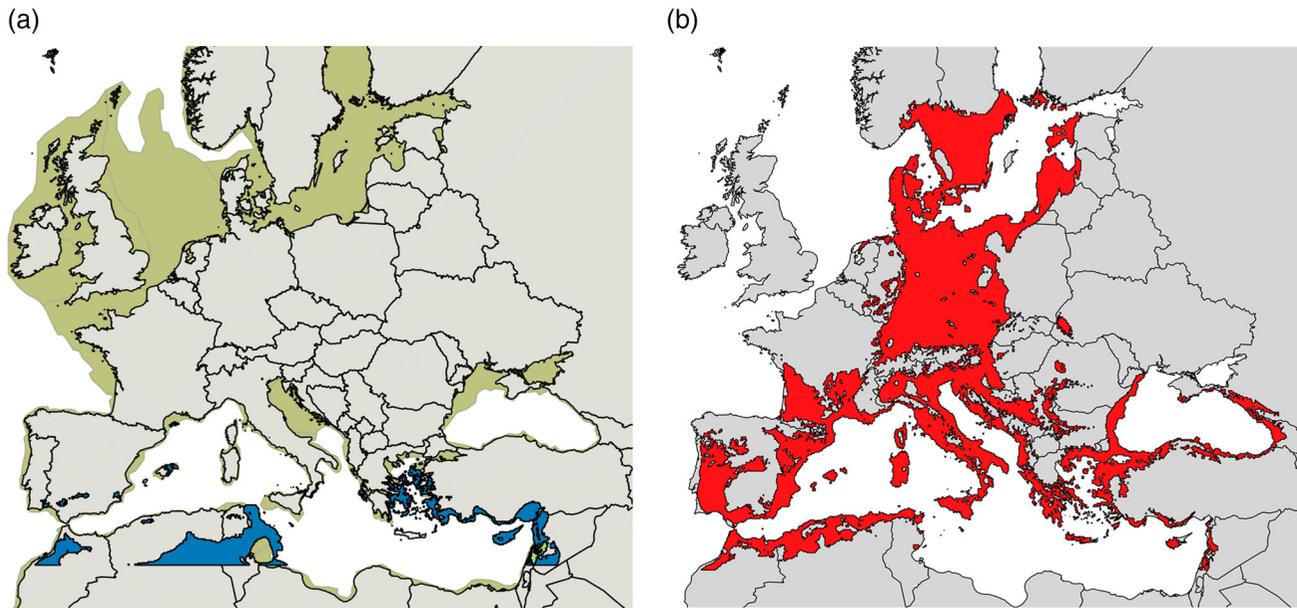


Figure 2. Projections of the geographical distribution of the Roller (a) during the Last Glacial Maximum (LGM, 19,000–23,000 years ago) (extended coastlines are indicated according to Ray & Adams (2001)) and (b) mid-Holocene (6000 years ago).

b)). Under future projected climate, 34.8% and 38.2% of the current range is predicted to become unsuitable (lost) for the species by 2050 and 2070 (Figure 4). However, currently unsuitable areas may become climatically suitable for the species (gain). In future, 35.7% of the distribution area is predicted to be newly suitable by 2050 and 31% by 2070 which is equivalent to 29.3% and 33.7% ‘gain’ by 2050 and 2070, respectively (Figure 4).

Moreover, countries holding most important populations (large and medium) such as Cyprus, Spain, Romania, Bulgaria and Hungary are predicted to suffer from the major declines of 9.18–64% by 2070 in suitable areas (Table 3, Figure 5). The exceptions are France and Italy, countries with large populations and increasing trends that are predicted to maintain or increase their suitability for Rollers. Projected unsuitable areas that are predicted to become suitable under future scenarios (‘gain’) correspond mainly to countries with small and declining or extinct populations (Figure 5, Table 3).

The repetition of all analyses for all RCPs yielded qualitatively similar results (pairwise Pearson correlation, $P < 0.001$ for all cases; online Table S5)

Discussion

Understanding how species have responded to climate changes throughout geological times is known to be critical to unveil evolutionary processes such as adaptation, speciation and extinction, but also to

forecast future impacts of current climate warming. Here, we showed that the natural distribution of the warm-adapted Roller under future climatic suitability may pull breeders outside their current breeding ranges.

Based on patterns of genetic variation and climatic reconstructions, many temperate species are believed to have become restricted to southern Europe during the height of the Pleistocene glaciations, surviving in small and climatically favourable glacial refugia (Hewitt 2000, Stewart *et al.* 2010). Our results support this hypothesis: widely distributed in temperate regions, the Roller likely survived the Pleistocene glaciations (and specifically the last glacial maximum, LGM) in small southern European (Spain, Greece, Turkey and the Balkans) and North African refugia. Isolation in Mediterranean and North African areas have been described for other bird species such as the Red Kite *Milvus milvus*, Green Woodpecker *Picus viridis*, Tawny Owl *Strix aluco*, Little Owl *Athene noctua*, Common Chaffinch *Fringilla coelebs* or the Coal Tit *Periparus ater* (Griswold & Baker 2002, Brito 2005, Roques & Negro 2005, Pentzold *et al.* 2013, Pellegrino *et al.* 2014, Perktas *et al.* 2015). Following the LGM, rapid post-glacial wide-range expansion and recolonization of northern latitudes is thought to have occurred as suggested by the projected distribution range of the Roller for the mid-Holocene. Warm climates during the mid-Holocene (warmer than present days) likely provided suitable conditions for the species to spread and cover large areas in northern latitudes, showing an overall agreement with the northward shift projected

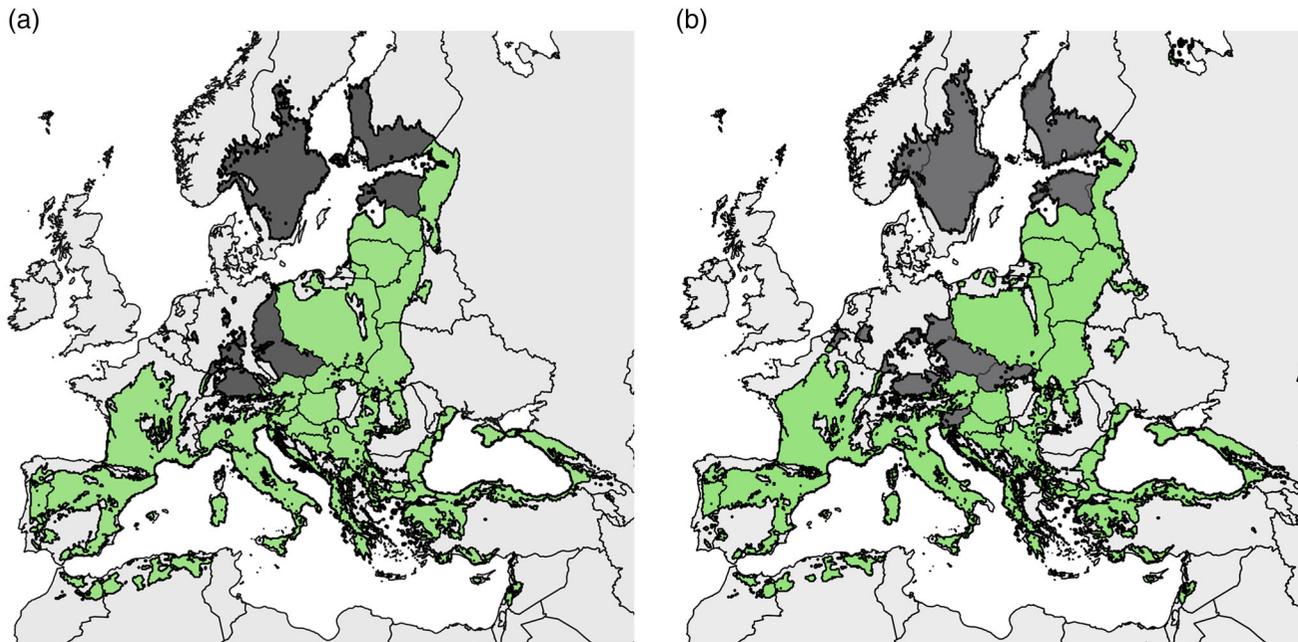


Figure 3. Projections of future geographical distribution of the Roller by 2050 (a) and 2070 (b) modelled using MaxEnt Climate data was obtained from global climate layers (RCP 4.5, WorldClim). Light green indicates distribution area in countries with current breeding population of the European Roller.

under future climate warming. Nonetheless, future predictions show that some regions of Germany and Denmark likely occupied in the mid-Holocene are not expected to be recolonized again. This could be explained by variations in insolation due to changes in the Earth's orbital parameter which resulted in different climate of those areas in the future. Ganopolski *et al.* (1998) found warming over the

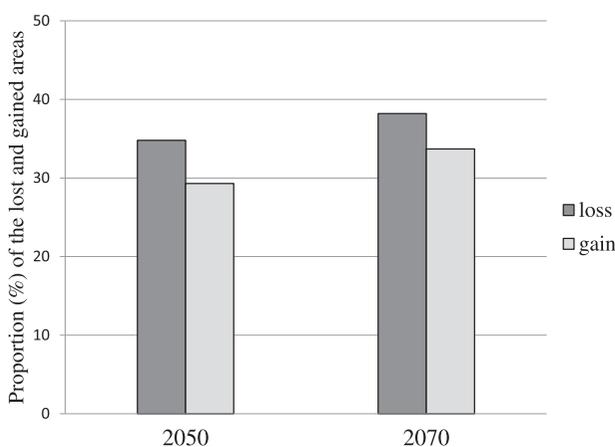


Figure 4. Projected changes in climatically suitable areas for the European Roller under future climatic projections of global climate models (GCMs; RCP 4.5), relative to the current period 'loss' refers to the proportion of current climatically suitable areas projected to become unsuitable in the future, while 'gain' refers to the proportion of future areas projected to become suitable in previously unsuitable areas.

continents of the northern hemisphere in summer but cooling in winter and spring during the mid-Holocene. Moreover, global annual increase of precipitation at mid-Holocene was mainly caused by the intensification of northern hemisphere summer monsoon in North Africa, South Asia and East Asia. However, since the end of nineteenth century in Denmark, both average annual precipitation and frequency of extreme rainfall events have continuously increased (Gregersen *et al.* 2015) probably make this area unsuitable for Rollers. In the future, phylogeographical studies could confirm the existence of important glacial refugia as well as reconstruct colonization patterns and identify post-glacial expansion routes during the Pleistocene.

Under future climate conditions, most species are predicted to shift their distributions poleward and range contractions are expected as the southern ranges become climatically unsuitable (Huntley *et al.* 2006, Pearce-Higgins & Green 2014). Agreeing with Huntley *et al.* (2007), our model predictions forecast a small contraction and a northward shift of the Roller's breeding range. Although the overall range contraction is predicted to be small (5.5% by 2050 and 4.5% by 2070, RCP 4.5), 35% and 38% of the current distribution will be confined outside the climatically suitable areas by 2050 and 2070, respectively. The projected lost area includes important regions in countries considered as part of the species stronghold

Table 3. Population size (BirdLife International 2015) of the Roller by country and predicted changes between current and future climate scenarios (for 2050 and 2070, RCP 4.5) (+) range expansion and (–) range contraction for the distribution area are shown along with the proportion of future areas projected to become suitable in previously unsuitable areas (gain) and the proportion of current climatically suitable areas projected to become unsuitable in the future (loss).

Country	Population size	2050			2070		
		range	gain	loss	range	gain	loss
Czech Rep	extinct	23.5	31.8	8.3	22.1	33.4	11.3
Denmark	extinct	–99.9	0.0	99.9	–100.0	0.0	100.0
Estonia	extinct	0.1	0.1	0.0	–0.1	0.1	0.2
Finland	extinct	421.5	429.8	8.4	524.7	546.3	21.6
Germany	extinct	–12.6	26.8	39.3	–34.7	23.8	58.5
Slovakia	extinct	19.1	24.6	5.6	10.8	24.5	13.7
Slovenia	extinct	11.0	23.8	12.8	23.0	26.0	3.0
Sweden	extinct	146.6	180.2	33.6	163.1	202.2	39.1
Switzerland	extinct	–41.8	45.9	87.7	–24.3	51.0	75.3
Bulgaria	large	–34.3	15.0	49.4	–40.0	17.4	57.5
Cyprus	large	–53.4	0.0	53.4	–64.0	0.0	64.0
France	large	310.9	324.5	13.6	379.0	387.5	8.4
Hungary	large	–33.7	0.0	33.7	–40.4	0.0	40.4
Italy	large	15.5	21.4	5.9	10.9	22.1	11.2
Romania	large	–51.1	10.8	61.9	–58.6	7.6	66.2
Russia	large	–9.3	33.4	51.0	–9.2	36.6	53.8
Spain	large	–15.0	28.5	43.6	–19.9	31.1	51.0
Turkey	large	2.6	41.5	38.8	1.7	44.8	43.1
Ukraine	large	–41.3	7.1	48.5	–25.9	10.4	36.3
Greece	medium	–27.2	17.3	44.5	–40.2	16.3	56.5
Macedonia	medium	–3.0	92.6	95.5	–25.2	74.2	99.4
Serbia	medium	–3.1	5.7	8.8	–11.0	5.4	16.4
Albania	small	49.0	50.7	1.7	47.3	57.7	10.4
Austria	small	48.8	55.5	6.8	57.3	65.4	8.1
Belarus	small	–25.6	3.4	29.0	28.7	33.9	5.1
Croatia	small	10.4	14.1	3.6	11.7	16.7	4.9
Latvia	small	1.3	2.9	1.6	2.9	2.9	0.0
Lithuania	small	1.9	1.9	0.0	1.8	1.9	0.1
Poland	small	–10.3	3.1	13.4	–13.7	2.7	16.4
Portugal	small	5.3	34.4	29.0	–9.3	35.7	45.0

in Europe such as Cyprus, Spain, Romania, Bulgaria and Hungary. Range contractions in the Mediterranean Basin agree with global projections for the region, as the region is a climate change hotspot (Giorgi 2006), where biodiversity losses are predicted to be the greatest (Sala *et al.* 2000). Such range reduction could eventually lead to critical population declines if Rollers are unable to achieve climate adaptation by shifting their breeding ranges to more suitable areas. In fact, if the species could colonize future areas projected to become suitable in previously unsuitable areas in forecasted proportion (34.8% and 38.2% by 2050 and 2070, respectively), it could halt its range reduction. However, the occupancy of the predicted distribution area for 2050 and 2070 is questionable and presents only a best-case situation allowed by climatic niches. Climatic conditions are predicted to be improving in the northern part of the distribution range where Rollers have recently become extinct (Sweden, Finland, Estonia and Germany) or have small populations with steep declining trends (Poland, Latvia, Lithuania and Belarus) suggesting that, besides climate, other constraints, can shape realized distribution of Rollers. Large population declines and extinction in northern

ranges are mainly associated with historical changes in land use (agricultural intensification) and forestry practices, leading to the inevitable loss of nesting sites and degradation of foraging conditions. Therefore, the capacity of Rollers to recolonize new climatically suitable areas is doubtful, due to habitat unsuitability. Targeted nest-box provisioning programmes could be able to facilitate the colonization and/or recolonization of new areas neighbouring with large populations with increasing trend (Kiss & Tokody 2017, Ruzic *et al.* 2017, Barisic *et al.* 2018, Gameiro *et al.* 2020), but the large recent increase of the Hungarian population was not able to prevent either the extinction of the Slovakian population or the current critical decrease in the number of breeding pairs in Austria. Our results highlight that warm-adapted species like the Roller have been able to successfully tackle climate change on geological time scales, but recent climate change could present a significant threat, not even considering unpredictable changes in land use. Our results suggest that although the climatic conditions are expected to become suitable for the species at higher latitudes the northward shift in the distribution of Rollers can be stopped by dispersal constraints and the lack of

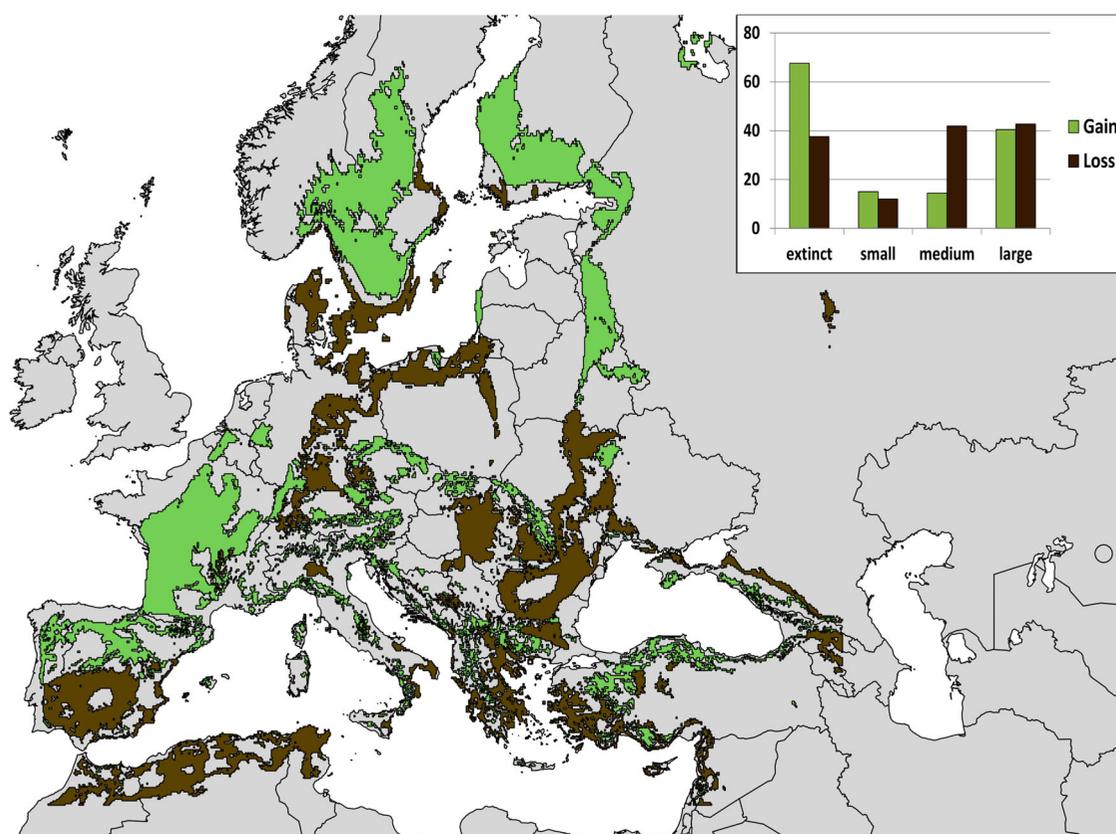


Figure 5. Projections of future climatically suitable areas for the European Roller under future (2070) climatic projections of global climate models (GCMs; RCP 4.5), relative to the current period. Range ‘loss’ (dark brown) represents current climatically suitable areas projected to become unsuitable whereas ‘gain’ (light green) refers to areas projected to become climatically suitable in previously unsuitable areas. Columns show the percentage of losses and gains amongst the large, medium, small and extinct populations by 2070.

suitable habitats in countries with currently extinct or decreasing populations.

Conservation implications of anthropogenic climate change

Conservation and management strategies could mitigate the negative effects that climate change may have on species. Increasing connectivity to allow species to move significant distances or directly assisting in poleward migrations, protecting current habitats, promoting climate change resilience, and identifying potential refugia have been referred as the most favourable options to face climate change (McLachlan *et al.* 2007, Heller & Zavaleta 2009, Morecroft *et al.* 2012).

Shifts in bird ranges due to climate change have been demonstrated many times, although the capability of species to tackle recent changes fast enough is questionable (Devictor *et al.* 2008). The ability of Rollers to adapt to future climate changes will also depend on the life-history traits and the conservation status of its populations. In birds, generalist species

with high annual fecundity, which live longer than expected based on body size, have the greatest potential to shift their ranges (Estrada *et al.* 2018), but as long distance migrant with one brood per year, the Roller does not meet these requirements. Ralston *et al.* (2017) found that species with increasing trends are better able to colonize new sites compared to declining ones, which exhibited lags relative to the change in climate. In the case of Rollers, whereas northern populations are unlikely to track climate change given their current declining trends, southern and central European populations with increasing trends could serve as sources for colonization, but further dispersal and habitat connectivity studies are needed for developing future effective conservation planning (Mazaris *et al.* 2013). Our results showed that large future expansion of the range is expected in France and Italy, suggesting these countries as future key areas for Roller conservation. Consistently with this prediction, northern and western expansion of the French population range has been observed in the past two decades (Tron *et al.* 2008, Aleman & Laurens 2013), although current lack of suitable nest sites may

jeopardize the successful expansion of the species in the near future (Aleman & Laurens 2013, Finch *et al.* 2019).

For declining populations, which include a significant proportion of the Roller range in Europe, promoting persistence in currently occupied habitats and identifying climate refugia not requiring dispersal may provide the most benefits (Ralston *et al.* 2017). As land use changes and habitat fragmentation may exacerbate future impacts of climate change (Opdam & Wascher 2004, Barbet-Massin *et al.* 2012, Brambilla 2014), traditional conservation practices, such as habitat restoration and management within protected areas may support function and resilience by allowing existing systems to absorb the amplifying effects of climate change (Dickinson *et al.* 2015). Conservation measures targeted at the Roller could include the promotion of foraging and nesting habitats through the implementation of agri-environmental schemes (Catry *et al.* 2017) and nest box supplementation (Kiss *et al.* 2017). The effectiveness of such measures is supported by recent studies considering climate and agricultural change scenarios in France which found that the adaptive management of landscape such as promoting extensive agricultural practices may mitigate negative impacts of climate change on farmland birds (Princé *et al.* 2013, Princé *et al.* 2015).

Model limitations and uncertainty

Although the climate is often considered ultimately responsible for determining the geographical distribution of species, other constraints can shape species distributions, and climate-only models could benefit from the inclusion of other environmental variables such as land use or topography (Márquez *et al.* 2011). Birds of farmland and grassland have been declining since the middle of the last century (Donald *et al.* 2001, 2006), both in the western (Fuller *et al.* 1995, Chamberlain *et al.* 2000) and the eastern parts of Europe (Reif *et al.* 2008, Szép *et al.* 2012), especially long-distance migrants (Sanderson *et al.* 2006) and insectivorous species (Bowler *et al.* 2019). As part of this threatened group of birds, the distribution range of Rollers had already decreased by the end of twentieth century. Many populations in Europe are still decreasing because of the lack of food availability (Hebda *et al.* 2019) or genetic depletion (Nebel *et al.* 2018), therefore they were unable to track the habitat changes and to recolonize habitats if they are still or newly available. Although intensified agricultural practices can have negative effect on Roller populations (Avilés & Parejo 2004) and limiting factors can vary across the species' range (Finch *et al.* 2019), some

populations have been able to increase both in population size and distribution range (Kiss & Tokody 2017, Ruzic *et al.* 2017) following nest-box provisioning. Several studies already address to include of both climatic and land-use variables to gain more precise prediction about future distributions (Princé *et al.* 2013, 2015, Mateo-Tomás & Olea 2015). Despite the limitations, bioclimatic models can play a significant role in improving our understanding of the potential future effects of climate change, although more complex process-based models have been built to project climate induced shifts in vegetation types and biomes, these models also have limitations and large associate uncertainties (Lawler *et al.* 2009). In this study, we only aimed to predict the potential climatically suitable areas for Rollers because however well our dataset represents the European distribution, it has a constraint for land-use modelling. It covers a large timeframe when significant land-use changes happened all over Europe. Moreover, nowadays many Roller populations are maintained by constant provision of artificial nesting sites ensuring the missing key habitat elements from the landscape, therefore they may not indicate currently suitable habitats properly which can result in uncertainty when trying to detect important land-use variables at a European scale. As the dataset covered an unusually long period, we performed two further models which led to qualitatively similar final conclusion (online Tables S2–S4, Figures S1–S3, S6).

Conclusions

Our findings show that the distribution range of breeding Rollers is predicted to suffer significant changes under future climate change. These changes will negatively affect mostly the currently stable or even increasing populations which have successfully coped with current major threats, such as habitat loss. Assessing the vulnerability of the Roller to past, present and future climate changes allows for prioritization of climate adaptation efforts and development of species-specific strategies that promote its conservation.

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Data accessibility statement

The European Rollers' occurrence data were provided by Groupe de Travail Rollier (France), CORACIAS (Gruppo italiano Ghiandaia marina)(<http://coraciasblogspothu/>) and Bulgarian Society for the Protection of Birds / BirdLife Bulgaria (Bulgarian Breeding Bird Atlas) in cooperation with MME/ BirdLife Hungary. Sources of used data are enlisted in online Table S1.

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