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Predictive models of distribution and abundance of a threatened mountain species show that impacts of climate change overrule those of land use change

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Abstract

Aim: Climate is often the sole focus of global change research in mountain ecosystems although concomitant changes in land use might represent an equally important threat. As mountain species typically depend on fine-scale environmental characteristics, integrating land use change in predictive models is crucial to properly assess their vulnerability. Here, we present a modelling framework that aims at providing more comprehensive projections of both species' distribution and abundance under realistic scenarios of land use and climate change, and at disentangling their relative effects.

Location: Switzerland.

Methods: We used the ring ouzel (*Turdus torquatus*), a red-listed and declining mountain bird species, as a study model. Based on standardized monitoring data collected across the whole country, we fitted high-resolution ensemble species distribution models to predict current occurrence probability, while spatially explicit density estimates were obtained from N-mixture models. We then tested for the effects of realistic scenarios of land use (land abandonment versus farming intensification) and climate change on future species distribution and abundance.

Results: Occurrence probability was mostly explained by climatic conditions, so that climate change was predicted to have larger impacts on distribution and abundance than any scenarios of land use change. In the mid-term (2030–2050), predicted effects of environmental change show a high spatial heterogeneity due to regional differences in climate and dominant land use, with farming intensification identified as an important threat locally. In the long term (2080–2100), climate models forecast a marked upward range shift (up to +560 m) and further population decline (up to −35%).

Main conclusions: Our innovative approach highlights the spatio-temporal heterogeneity in the relative effects of different environmental drivers on species distribution and abundance. The proposed framework thus provides a useful tool not only for better assessing species' vulnerability in the face of global change, but also for identifying key areas for conservation interventions at a meaningful scale.

1 | INTRODUCTION

Mountain ecosystems are rapidly changing globally, under the influence of anthropogenic drivers (Huber et al., 2006). Human-induced climate change represents a particular challenge for high-elevation biodiversity (Lehikoinen et al., 2019), through increasing ambient temperatures, altered hydrological cycles and more frequent extreme weather events (Beniston, 2003); in effect, these phenomena are more acute in mountains than in the lowlands (CH2018, 2018; Pepin et al., 2015). Moreover, species living at high elevations are particularly vulnerable due to their fine-tuned adaptations to naturally harsh environmental conditions and short periods of reproduction (Martin & Wiebe, 2004), with a high risk of range contraction and fragmentation (Dirnböck et al., 2011) as well as phenological mismatches (Scridel et al., 2018). In parallel, changes in land use are increasingly impacting mountain ecosystems and are considered an equally, if not more important threat than climate change in European cultural landscapes (Chamberlain et al., 2016; Mollet et al., 2018). Nevertheless, extant research predicting future species distributions has mainly focused on the effect of increasing ambient temperatures, while neglecting the role of land use changes (Sirami et al., 2017; Titeux et al., 2016). Integrating land use into future scenarios is, however, crucial to properly assess species vulnerability in the face of global change (Howard et al., 2015; Maggini et al., 2014) and thus make meaningful conservation recommendations (Braunisch et al., 2014), especially in ecosystems that are already heavily modified by humans.

Subalpine forests in Europe have been exploited for centuries (Mollet et al., 2018). In particular, the upper transition zone between wooded and open landscapes, the so-called treeline ecotone, has been largely shaped by anthropogenic activities (Körner, 2012; Mollet et al., 2018). A long tradition of summer grazing by cattle and sheep has pushed the treeline to areas below the elevation threshold at which local environmental conditions naturally limit tree growth (Dirnböck et al., 2011; Gehrig-Fasel et al., 2007; Körner, 2012). In the Alps, as a result, the treeline belt consists of a complex mosaic of coniferous stands, patches of dwarf shrubs and grassland that can stretch over an elevational range of few hundred meters. This heterogeneous habitat harbours a rich biodiversity (Körner, 2012; Mollet et al., 2018), which is now threatened by a dichotomous trend of either agricultural abandonment or management intensification of traditional pastures and meadows (Tasser & Tappeiner, 2002). On the one hand, less accessible or unproductive grasslands are not grazed or mown anymore, which leads to progressive shrub and ultimately forest encroachment (Laiolo et al., 2004; MacDonald et al., 2000). On the other hand, the management of biodiversity-rich grasslands is intensified through an increase in direct nitrogen input to enhance fodder productivity (Andrey et al., 2014; Britschgi et al., 2006;

Humbert et al., 2016). Both drivers, in some places accompanied by atmospheric nitrogen deposition, lead to the homogenization of mountain ecosystems, threatening these rich ecological communities that rely on semi-open and open habitats (Bani et al., 2019; Chamberlain et al., 2016; García-Navas et al., 2020).

In order to quantify the relative impacts of climate versus land use changes on species occurring in mountain environments, we chose as a model the ring ouzel (*Turdus torquatus*), a thrush species that inhabits exclusively mountain and upland ecosystems across its range (Glutz von Blotzheim & Bauer, 1988). The subspecies *T. t. alpestris* is present in central Europe and typically breeds in semi-open subalpine forests. In Switzerland, its breeding population has been declining by more than one-third in the 30 last years, mostly at lower elevations, resulting in a mean upward distribution shift of +84 m (Knaus et al., 2018). This strongly suggests that climate change, with a linear mean increase in ambient temperature of 0.9°C over the same period (Meteoswiss, 2019), might be responsible for the decline (Barras et al., 2021; Beale et al., 2006). Nevertheless, this climatic trend has been paralleled by accelerating land abandonment, which is the main driver of forest cover increase and upward shift in the country (Gehrig-Fasel et al., 2007), with a 46,200 ha wooded area gain in the Swiss Alps from 1985 to 2009 (SFSO, 2013). For a species relying strongly on semi-open habitats, a progressive forest closure may both lessen habitat suitability and negatively affect its demography. Moreover, the fertilization of mountain grasslands has also drastically increased, through direct and indirect (i.e. atmospheric) nitrogen inputs, favouring fast-growing nutrient-tolerant plant species (Andrey et al., 2014; Britschgi et al., 2006; Tasser & Tappeiner, 2002). Since ring ouzel relies on patches of short and sparse ground vegetation to forage (Barras et al., 2020; Burfield, 2002), high-productivity grasslands are usually avoided (Buchanan et al., 2003; von dem Bussche et al., 2008). Therefore, it is unknown to which extent these other, parallel changes in land use could also contribute to species' fall, and by extension to the decline of other sympatric mountain species (Knaus et al., 2018; Lehikoinen et al., 2019).

Species distribution models (SDMs), which describe current relationships between species occurrence and environmental variables, offer the additional opportunity to predict the effect of different scenarios of environmental change on future habitat suitability, and consequently on species distribution and abundance (Guisan et al., 2017). With the increasing availability of databases on species occurrence and environmental variables (e.g. from remote sensing), it is now possible to build models over wide geographic areas at a biologically meaningful resolution, that is matching the scale at which species perceive habitat and respond to environmental circumstances. These more accurate, finer-grained models are crucial to avoid the caveat of overestimating the effect of large-scale forces

like climate and to better integrate local-driving forces such as functional species–habitat relationships into projections (Chamberlain et al., 2013; Jiménez-Alfaro et al., 2012; Maggini et al., 2014). In addition, predictions of abundance are generally much more informative than mere estimates of occurrence probability, especially when it comes to assess the drivers of species declines and plan conservation action (Howard et al., 2015; Johnston et al., 2015; Renwick et al., 2012; Virkkala & Lehikoinen, 2014). While the use of SDMs is on the increasing side in conservation research (Guisan et al., 2017), only few studies have simultaneously considered effects of land use and climate change on bird species abundance (Howard et al., 2015; Renwick et al., 2012), and we are not aware of any that did so for predicting future species density.

In this study, we developed a framework to assess and predict the effects of climate and land use changes on the ring ouzel in the Swiss Alps and Jura mountains. We used an ensemble modelling approach (Araújo & New, 2007), based on precise species locations, to predict area-wide occurrence probability at a fine scale. We further fit N-mixture models (Royle, 2004) to translate occurrence probability into abundance estimates and total population size. In particular, we aimed (a) to assess the relative importance of climate, land use/cover and topography for characterizing species' habitat suitability; (b) to evaluate the impact of plausible scenarios of climate and land use changes, and combination thereof, on species distribution and abundance in different areas, especially in relation to elevation; and (c) to delineate key areas that will remain or may become climatically suitable for ring ouzel in the future, so as to designate them as focal areas for targeted conservation management.

2 | METHODS

2.1 | Study area

Four biogeographical regions of Switzerland were considered, namely the Jura mountains, the northern, central (i.e. inner) and southern Alps (Gonseth et al., 2001; Figure 1). The fifth region, the Plateau, was excluded since the ring ouzel does not breed and anyways very rarely occurs in the Swiss lowlands. These four regions vary in area (4,203; 11,486; 10,671; 3,671 km^2, respectively), mean elevation (816; 1,385; 2,144; 1,493 m above sea level (asl)) and also climate: the Jura and northern Alps are under the influence of an oceanic climate with regular precipitation all year round and low sunshine duration, the central Alps are under a continental (inner-Alpine) climate with very low precipitation, while the southern Alps are subject to the Insubrian climate (N Italy), characterized by intense precipitation events in spring and autumn, but also high sunshine duration (CH2018, 2018; Price et al., 2015). The study area
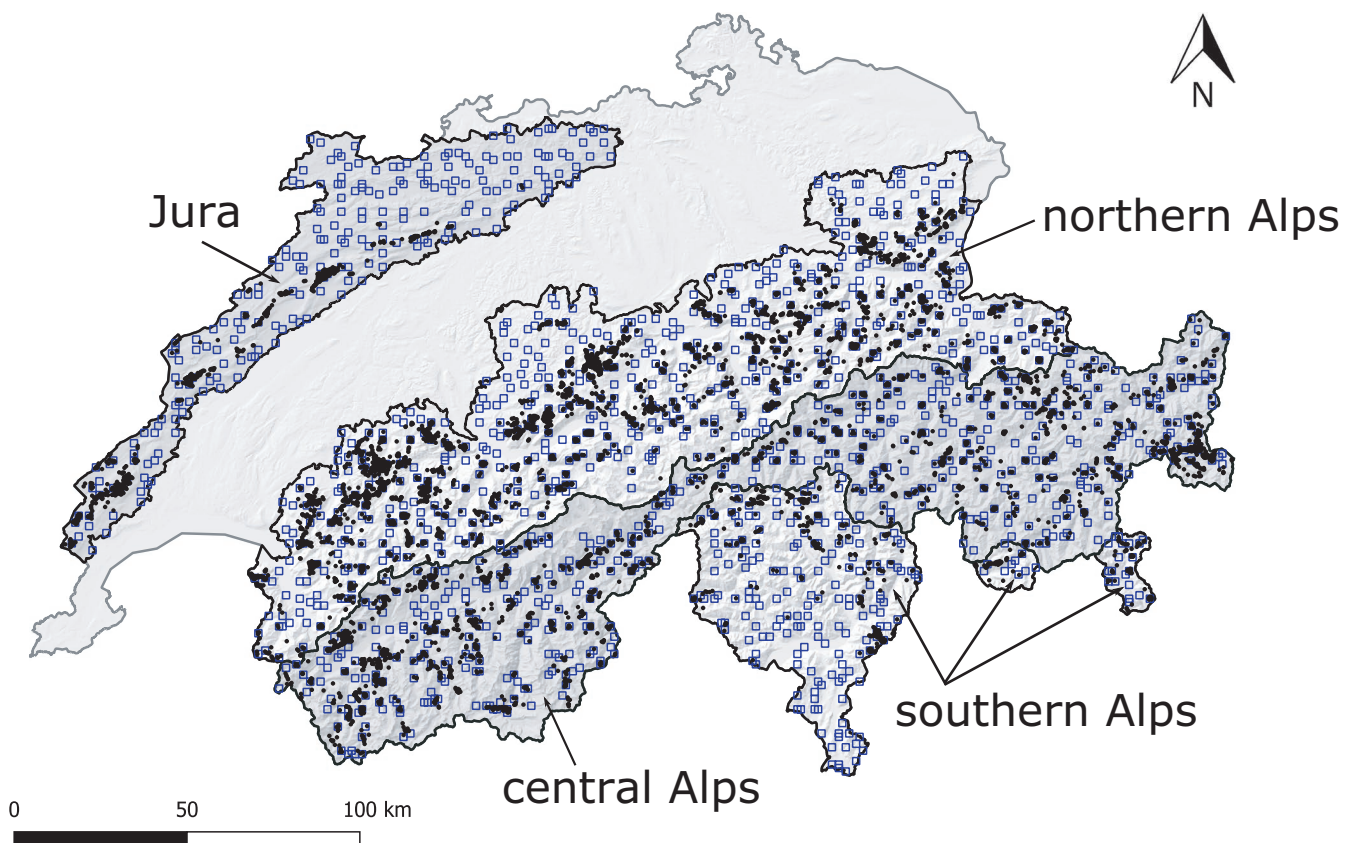

FIGURE 1 Map of Switzerland with depiction of the four study biogeographical regions. Black dots: locations of ring ouzel observations considered in the presence-only and presence–absence datasets. Empty blue squares: monitored 1-km^2 squares in which abundance data were available

encompasses most of the climatic conditions experienced by ring ouzels across their whole breeding range (Table S1) so that the risks of overestimating range shift or contraction in our predictions are deemed marginal. As a result of these contrasted circumstances, land use varies considerably between our study regions: forests predominate in the southern Alps (49.1%) and Jura (47.4%), agricultural areas (mostly grasslands) have a wide coverage in the Jura (43.4%) and northern Alps (37.5%), whereas the central Alps are mostly

TABLE 1 List of environmental variables included in the occurrence models, along with their possible ecological relevance for ring ouzel, as retrieved from the literature

Variables	Original resolution	Resampling method	Possible relationship	Source
Topography				
Elevation	25	Average	Clear elevational optimum across the breeding range[1,2,3,4]	DEM[a]
Slope	25		Influence of topography on important soil characteristics for foraging[4,5,6] and on the preferred vegetation structure at the territory scale,[1,2] for example through natural dynamic. Preference for nesting in steep slopes in the UK[3,4].	DEM[a]
Northness	25			DEM[a]
Eastness	25			DEM[a]
Topographic Position Index	25			DEM[a]
Climate				
Temperature Breeding Season (BS)	100	Nearest neighbour	Importance of climatic factors detected at various spatial scales[2,3,7]. Functional links to the breeding ecology[4,5,6,7,8], mostly through the impacts on food availability.	MeteoSwiss/WSL[b]
Solar radiation BS	100			MeteoSwiss/WSL[b]
Potential evapotranspiration BS	100			MeteoSwiss/WSL[b]
Precipitation BS	100			MeteoSwiss/WSL[b]
Precipitation seasonality BS	100			MeteoSwiss/WSL[b]
Precipitation winter	100			MeteoSwiss/WSL[b]
Forest structure				
Treeline length	—	—	Selection for low distance to forest edges,[1] or for open stands among mountain grasslands.[2] Avoidance of conifer plantations in the UK.[3]	TLM3D[c]
Treeline distance	50			TLM3D[c]
Number of solitary trees	—			TLM3D[c]
Land use/cover				
Low-productivity meadow cover	10	Sum	Important role of mountain grassland cover and management, with preferences for nutrient-poor over nutrient-rich grasslands at the territory scale.[2,3] Avoidance of dense and high grass swards for foraging.[4,5]	TLM3D[c]/AS[d]/GRID[e]
High-productivity meadow cover	10			TLM3D[c]/AS[d]/GRID[e]
Low-productivity pasture cover	10			TLM3D[c]/AS[d]/GRID[e]
High-productivity pasture cover	10			TLM3D[c]/AS[d]/GRID[e]
Unused grassland cover	10			TLM3D[c]/AS[d]
Rock and screes cover	10		Absence of soil and therefore belowground invertebrate prey.[9] Preference for intermediate rock cover for nesting sites in the UK.[3]	TLM3D[c]
Forest cover	10		Importance of intermediate forest cover[1,2]	TLM3D[c]

Note: For the data that were not directly available at 50 m resolution, the method of data aggregation/resampling is indicated.

1. Ciach and Mrowiec (2013); 2. von dem Bussche et al. (2008); 3. Buchanan et al. (2003); 4. Burfield (2002); 5. Barras et al. (2020); 6. Sim et al. (2013); 7. Beale et al. (2006); 8. Barras et al. (2021); 9. Hagedorn et al. (2019).

[a]Digital Elevation Model (Swisstopo, 2005)

[b]Prepared by the research unit "Land Change Science" of the Federal research institute WSL from weather stations data from MeteoSwiss.

[c]Topographic Landscape Model of Switzerland (Swisstopo, 2018).

[d]Aerial Statistics (SFSO, 2013).

[e]NDVI data compiled from the Swiss Data Cube (Giuliani et al., 2017)

dominated by unproductive land (e.g. bare or sparsely vegetated areas, glaciers, lakes; 49.5%) (SFSO, 2013).

2.2 | Species data

Ring ouzel observations over the period 2013–2018 were gathered from various sources. We used observations from two standardized monitoring programmes, the Atlas of Swiss breeding birds (hereafter Atlas; Knaus et al., 2018) and the monitoring scheme of common breeding birds (hereafter MCBB; Schmid et al., 2004), as well as casual observations reported to the official national birding exchange platform www.ornitho.ch. For the Atlas and MCBB, experienced volunteers systematically visited pre-selected 1-km^2 squares regularly spaced across Switzerland (Figure 1). They recorded all bird observations on a map along a predefined walk transect (4–6 km) during three visits (only two for squares entirely above the treeline) between April–June in at least one year in the period 2013–2018. At the end of the season, the observations collected at each visit were aggregated into territories following a standardized protocol (for details, see Kéry, 2018; Schmid et al., 2004). As ring ouzels are essentially single-brooded in the Alps (Glutz von Blotzheim & Bauer, 1988), the estimated number of territories was unlikely to be inflated by potential relocations between a first and second brood. Concerning casual observations, we retained only precise enough (at least 50 m), confirmed records from May–June, discarding observations outside of the core reproductive period. We then grouped this information into three datasets: presence-only (PO), presence–absence (PA) and abundance (Figure 1). In the PO dataset, data from territory locations and casual observations were combined (n = 8,000). In the PA dataset, only territory centroids were retained as ascertained presence during breeding (n = 5,169), whereas a number of "absence points," equivalent to the number of territories, were generated and placed randomly in parts, or entire monitored 1-km^2 squares (throughout the study area) where no ring ouzel was observed. While we cannot totally exclude the selection of false absences which might impact predictions (Gu & Swihart, 2004), the risk was greatly reduced by selecting only squares covered by the standardized monitoring programmes described above. The abundance data consist of the number of territories with at least one bird detected per visit (e.g., $n_1 = 7$; $n_2 = 8$; $n_3 = 6$) in each Atlas or MCBB 1-km^2 squares (n = 1,460). As a potential sampling bias could occur in the casual observations from the PO dataset (Fourcade et al., 2014), we applied spatial filtering by randomly removing nearby observations closer than 113 m. This distance represents the mean radius of an estimated home range, assuming strict territoriality in ring ouzel pairs (i.e., half the mean distance between territory centroids obtained from the Atlas and MCBB surveys).

2.3 | Environmental data

We selected a set of environmental predictors referring to the literature on species–habitat relationships of the ring ouzel at various spatial scales (see Table 1), as well as on predictors that might be particularly important for mountain bird species in general. Predictors were classified into four categories, namely topography, climate, forest structure and land use/cover. For topography, all variables were derived from a 25 m resolution digital elevation model (DEM) (Swisstopo, 2005). Aspect (from which were derived eastness and northness), slope and the topographic position index (i.e. the position of a grid cell relative to the surrounding cells, indicating concavity or convexity of a landform) were all obtained using the raster analysis functions in the software QGIS 3.10 (QGIS Development Team, 2020). Climate variables were compiled for the period 1996–2016 by the Swiss Federal Research Institute WSL (research unit "Land Change Science"), using the software Daymet (Thornton et al., 1997). The latter performs a gridded interpolation of weather variables based on a DEM and daily-resolution data from weather stations, here precipitation and temperature measured at, on average and respectively, 120 and 400 stations belonging to the network of the Federal Office of Meteorology and Climatology (MeteoSwiss). We extracted mean ambient temperature, total precipitation, precipitation seasonality, solar radiation and potential evapotranspiration over the ring ouzel breeding period (April–July), as well as the total winter precipitation (December–March) as a proxy for snow cover upon arrival of the birds in spring. All three forest structure variables (number of solitary trees, treeline length and distance to treeline) were derived from the topographic landscape model (TLM^{3D}) of Switzerland (Swisstopo, 2018) as were the land cover variables "forest" and "rock & screes." For the grassland habitats, we combined information from the TLM^{3D} and the Swiss Land Use Statistics (SFSO, 2013), to classify grassland areas into meadows and pastures, that is mown and grazed grasslands, respectively. Additionally, we used the normalized difference vegetation index (NDVI) as a proxy of grassland productivity (Pettorelli et al., 2005) and hence of management intensity (Weber et al., 2018). NDVI data were compiled in the Swiss Data Cube (www.swissdatacube.org; Giuliani et al., 2017) from Landsat 5 & 7 satellite pictures. To get rid of the effect of snow cover and capture essential information about maximum local vegetation productivity, we considered the maximum NDVI over the entire breeding season, averaged over the period 2005–2009. Then, for any given grassland type, we used the median NDVI value as a cut-off between low- and high-productivity categories. This resulted in four layers, namely pastures and meadows with two levels of productivity each.

All variables available as raster data were prepared as raster maps of 50 m resolution, either by resampling or aggregation (Table 1), subsequently assigning to each cell the mean value within a circular moving window of 113 m radius (40,115 m^2) corresponding to the mean home-range size as described above. For vector data, namely treeline length and number of solitary trees, the total line length or point sum within a 113 m radius, respectively, was assigned to each 50 × 50 m cell.

2.4 | Modelling

Prior to model fitting, we checked for pairwise correlations between all environmental predictors to reduce collinearity, considering a slightly more restrictive rejection threshold (Spearman's $|r_s| > 0.6$) than the rule-of-thumb (>0.7; Dormann et al., 2013), given that several variable pairs showed correlations between 0.6–0.7 (Figure S1). At that step, five predictors were removed (see Figure S1, for details on the variable selection process). We further calculated variance inflation factors (VIF), which are based on R-squared values from the regression of each predictor on all others (Miles, 2014), and confirmed that there were no multicollinearity issues (all VIF < 10). The whole model fitting and selection process was performed in the software R 3.6.1 (R Development Core Team, 2019). A schematic summary of the model framework can be found in Figure 2, and the ODMAP protocol of the modelling process following Zurell et al. (2020) is provided as Table S2.

2.4.1 | Occurrence models

In order to model species' occurrence probability, we used an ensemble modelling approach, combining models fitted with different algorithms to account for the high variability among predictions (Araújo & New, 2007; Thuiller, 2004). Ensemble modelling is now routinely used in the field of species distribution modelling as it produces more robust predictions and allows to quantify uncertainties (Araújo & New, 2007; Guisan et al., 2017). Here we fitted SDMs based on five commonly used algorithms: generalized linear models (GLM), random forest (RF), boosted regression trees (BRT), artificial neural network (ANN) and maximum entropy (MaxEnt). The MaxEnt model was fitted on PO data

and 20,000 randomly generated background points, whereas all other four algorithms used PA data. Prior to model fitting, we partitioned each dataset into four spatially structured folds of equal size based on longitude and latitude, using the "ENMeval" package (Muscarella et al., 2014). We used this partitioned data to run a fourfold cross-validation for each model, that is to evaluate spatial transferability, and evaluated model's performance with the area under the receiver operating characteristics curve (AUC; Bradley, 1997) of the test folds. For fitting and selecting the different models, we used the package "SDMtune" (Vignali et al., 2020). For each algorithm except the GLM, we first identified the combination of hyperparameters resulting in the best performing model in terms of mean test AUC using the *optimizeModel* function. Then, in all models, we sequentially removed variables having a permutation importance of less than 1% until an optimum in test AUC was reached, using the function *reduceVar*. The performance of the so-obtained model was evaluated through mean AUC and true skills statistics (TSS; Allouche et al., 2006) on the test folds. Finally, we merged all four folds together to fit a final model from which variable importance and probability of occurrence over the whole study area were computed. Variable importance was estimated using ten permutations for each variable in each model. Concerning the occurrence probability, we further calculated the mean and standard deviation (SD) of the five model predictions. For MaxEnt models, we retained the "cloglog" output, which is equivalent to the occurrence probability predictions of the other SDM algorithms used here (Phillips et al., 2017).

2.4.2 | Abundance model

To model species abundance in our 1-km^2 squares, we applied a binomial N-mixture model to the territory counts, which accounts
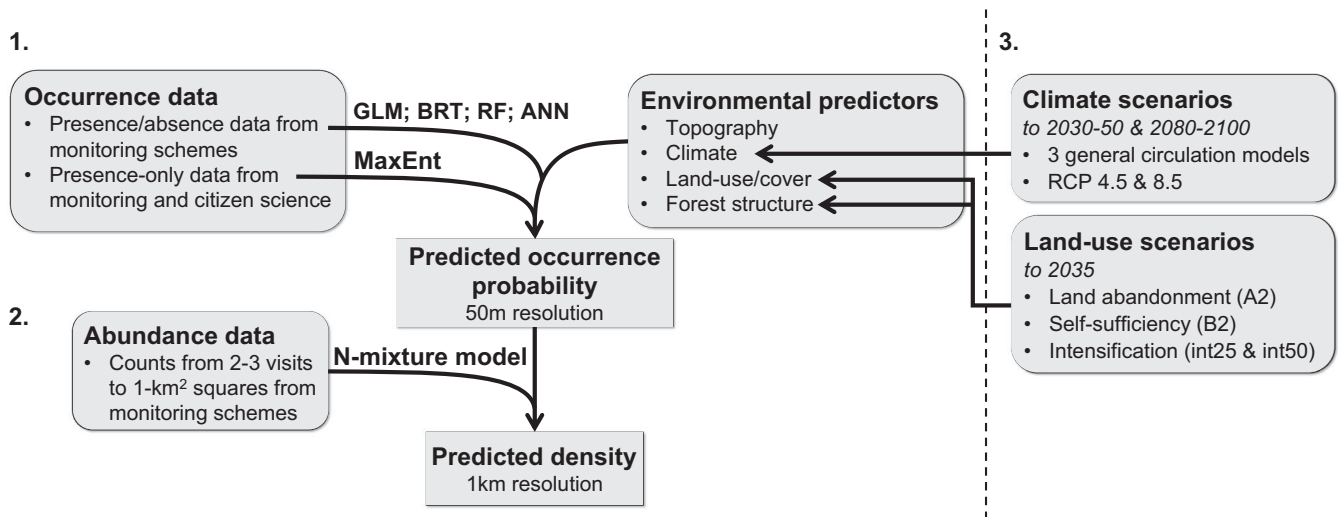

FIGURE 2 Modelling framework used in the present study. In a first step (1), occurrence probability was modelled at a 50 m resolution with a set of environmental predictors and two different datasets as inputs (presence-only & presence/absence), using five different algorithms (MaxEnt: maximum entropy, GLM: generalized linear model, BRT: boosted regression trees, RF: random forest and ANN: artificial neural network). In a second step (2), abundance per surveyed 1-km^2 square was modelled as a function of mean occurrence probability using an N-mixture model accounting for imperfect detection. In the final step (3), we used the fitted models to predict future occurrence probability and population density under different realistic scenarios of climate and land use change

for imperfect detection and therefore produces more reliable estimates of abundance (Kéry & Royle, 2016; Royle, 2004). Following the recommendations by Kéry (2018), we based our selection of the abundance mixture distribution on Akaike's information criterion but checked for potential identifiability problems, establishing that the zero-inflated Poisson distribution was the best option for our data. We fitted the model using the package "unmarked" (Fiske & Chandler, 2011) with covariates in the detection part being the survey date and session (1–3). For the abundance part of the model, we used as a covariate the mean occurrence probability in each 1-km^2 square, obtained from aggregating the results of the occurrence ensemble model to this resolution. Goodness of fit of the model was assessed by calculating the c-hat based on parametric bootstrapping with 1,000 simulations (Kéry & Royle, 2016), as well as by the root-mean-square error (RMSE) and the mean absolute error (MAE). We then produced an estimate of regional and total population sizes in Switzerland by rounding the number of breeding pairs per km^2 to integer values and summing up the abundance predictions for the area of interest. Finally, we also retrieved the density-weighted mean elevation (total and regional) of the species distribution, that is the average elevation of occupied squares with abundance estimates as weights.

2.5 | Climate change scenarios

Future climate was modelled for two 20-year periods, in the mid-term (2030–2050) and long term (2080–2100), using data from the European branch of the coordinated regional climate downscaling experiment, EURO-CORDEX (www.euro-cordex.net; 0.11 degree resolution). Two representative concentration pathways (RCPs), RCP 4.5 and 8.5, were considered. RCPs represent possible scenarios of greenhouse gas emissions as described in the IPCC (2014), with RCP 4.5 being a moderate scenario assuming a decrease in emissions from 2050 onward, while RCP 8.5 represents an extreme scenario with a continuous increase up to 2,100. Data were downscaled using the same regional climate model CLMcom-CCLM4-8-1, for three general circulation models (GCMs): CNRM-CERFACS-CNRM-CM5, ICHEC-EC-EARTH and MPI-M-MPI-ESM-LR, resulting in six climate scenarios for each period. Those GCMs were selected as their projections covered a broad range of possible future climate conditions, although the first two GCMs are considered rather similar (Knutti et al., 2013). The resulting data were further downscaled using the delta change method (Anandhi et al., 2011). Using this method, the coarse-scale maps of future climate from EURO-CORDEX are expressed as anomalies relative to the baseline period 1996–2016. These anomalies are then interpolated bilinearly to 100 m and combined with the equivalent baseline fine-scale maps (from Section 2.3) to obtain absolute values, thus assuming that relative fine-scale differences in current climate will remain the same. All data were provided by the Federal Research Institute WSL.

2.6 | Land use change scenarios

As future land use, we used the model predictions of Price et al. (2015) covering the whole of Switzerland. Using socio-economical and biogeographical variables, these authors predicted land use by 2035 (i.e. matching the mid-term climate scenarios described above), along various storylines of climate change as described in the Special Report on Emission Scenarios IPCC (2000). Here, we retained the two different scenarios B2 and A2, which correspond to the RCPs 4.5 & 8.5, respectively, as defined in the newest IPCC assessments (Rogelj et al., 2012). Under the A2 scenario (hereafter land abandonment), high economic and population growth with low support for conservation and agricultural subsidies is assumed; Price et al. (2015) predict that over 46,000 ha of pastures will be abandoned and encroached in the Alps and Jura, while another 28,000 ha of overgrown areas will become forest. Nevertheless, 19,000 ha of overgrown areas will be reconverted into pastures. Under the B2 scenario (hereafter self-sufficiency), population growth will be moderate and there will be high support for biodiversity conservation, as well as for maintaining extensive agriculture in remote areas; no pastures would be abandoned and transformed into forest, while 46,000 ha of overgrown areas will be converted back into grasslands. In both scenarios, no loss of forest was allowed.

Since the categories of land use from Price et al. (2015) (hereafter LU categories) were not identical to the variables used as predictors in our models, we translated the scenario predictions into our land use/cover and forest structure variables. For this, we identified raster cells where the LU category was predicted to shift according to Price et al. (2015) and changed the values of each of the retained predictors accordingly (see details in Figure S2). For areas whose cover shifted towards grasslands under future scenarios, type (pasture or meadow) and productivity (low or high) were assigned according to the characteristics of the nearest grassland patch in the current landscape. Finally, we also simulated a farming intensification process of the managed grasslands up to two elevation thresholds (1635 and 2010 m asl), by changing the productivity of all meadows and pastures below the respective elevation-limit to "high productivity." Elevation thresholds were defined as the 0.25 and 0.5 elevation quantiles of low-productivity pastures, so that scenarios would reflect an intensification of respectively 25% and 50% of the lower-elevation pastures (hereafter int25 & int50 scenarios). The same thresholds were then also applied to meadows. Land use scenarios were calculated assuming constant climate and in combination with climate change scenarios for the mid-term period only.

3 | RESULTS

All SDMs of the ensemble individually show excellent (>0.9) to good (>0.8) predictive accuracy for the cross-validated mean test AUC (MaxEnt = 0.88, GLM = 0.91, BRT = 0.91, RF = 0.91, ANN = 0.91) and good (>0.4) accuracy for TSS (MaxEnt = 0.62, GLM = 0.68,

BRT = 0.67, RF = 0.66, ANN = 0.67) according to classification thresholds summarized in Guisan et al. (2017). The most important variable for explaining species occurrence was mean ambient temperature during the breeding season, with a clear optimum detected in all models at 5–10°C (see response curves in Figure S3). Solar radiation was ranked second, followed by habitat variables like cover of forest and low-productivity pastures as well as the number of solitary trees present in the home range (Table 2), all showing curvilinear relationships but that differed between algorithms (Figure S3), so that it was difficult to define clear optimal ranges. Eleven other variables were retained in at least one of the five models, but all had relatively low permutation importance (Table 2).

The fit of the abundance (N-mixture) model was good as well as assessed by RMSE = 1.91 and MAE = 0.96 (see Table S3, for parameter estimates). Calculation of the over-dispersion parameter (c-hat = 1.5) suggested slight over-dispersion in the zero-inflated Poisson model, which was taken into account by multiplying the variance-covariance prediction matrix by the c-hat value (following Kéry & Royle, 2016).

We estimated a current population size of 60,218 breeding pairs (95% CI: 53,070–67,349) in Switzerland, at a mean elevation of 1,803 m asl. Abundance maps, in contrast to mere occurrence probability maps, identified clear population density hotspots in the landscape, with 68 1-km² squares harbouring more than 20 breeding pairs each, 88% in the northern Alps and the rest in the central Alps (Figure 3b). Concerning mid-term predictions, land use scenarios had limited effects on the species range and population size (from +1.6% for A2 to −4.8% for int50), resulting in only small changes in mean elevation (from −1 m for B2 to +16 m for int25; Figure 4). For the same time horizon, both climate scenarios delivered similar predictions with little changes in population size (on average −1.2% and −3.7% for RCP 4.5 & 8.5, respectively) but a clear upward elevational shift (on average +85.7 m and +144.7 m for RCP 4.5 & 8.5, respectively) which was consistent across the three different general circulation models used (Figure 4). Effects of climate change scenarios were much more pronounced for the end of the century (2080–2100) than in the mid-term, especially for the RCP 8.5 with a mean 30.5% (range 25.2%–35.2%) decrease in population size and a +512 m (484–560 m) elevational shift (Figure 3). When combining land use change with the mid-term climate change scenarios, population size estimates were indicating additive rather than interactive effects of both drivers (Figure 4).

Looking at the biogeographical regions independently, our models predicted divergent responses of the different breeding populations. At this scale, the magnitude of change caused by climate change appeared much more pronounced than the different scenarios of land use in the mid-term. The size of the populations occurring at lower

TABLE 2 Permutation importance of retained environmental variables in each of the five models fitted for species occurrence (MaxEnt: maximum entropy, GLM: generalized linear model, BRT: boosted regression trees, RF: random forest and ANN: artificial neural network), as well as averaged across models
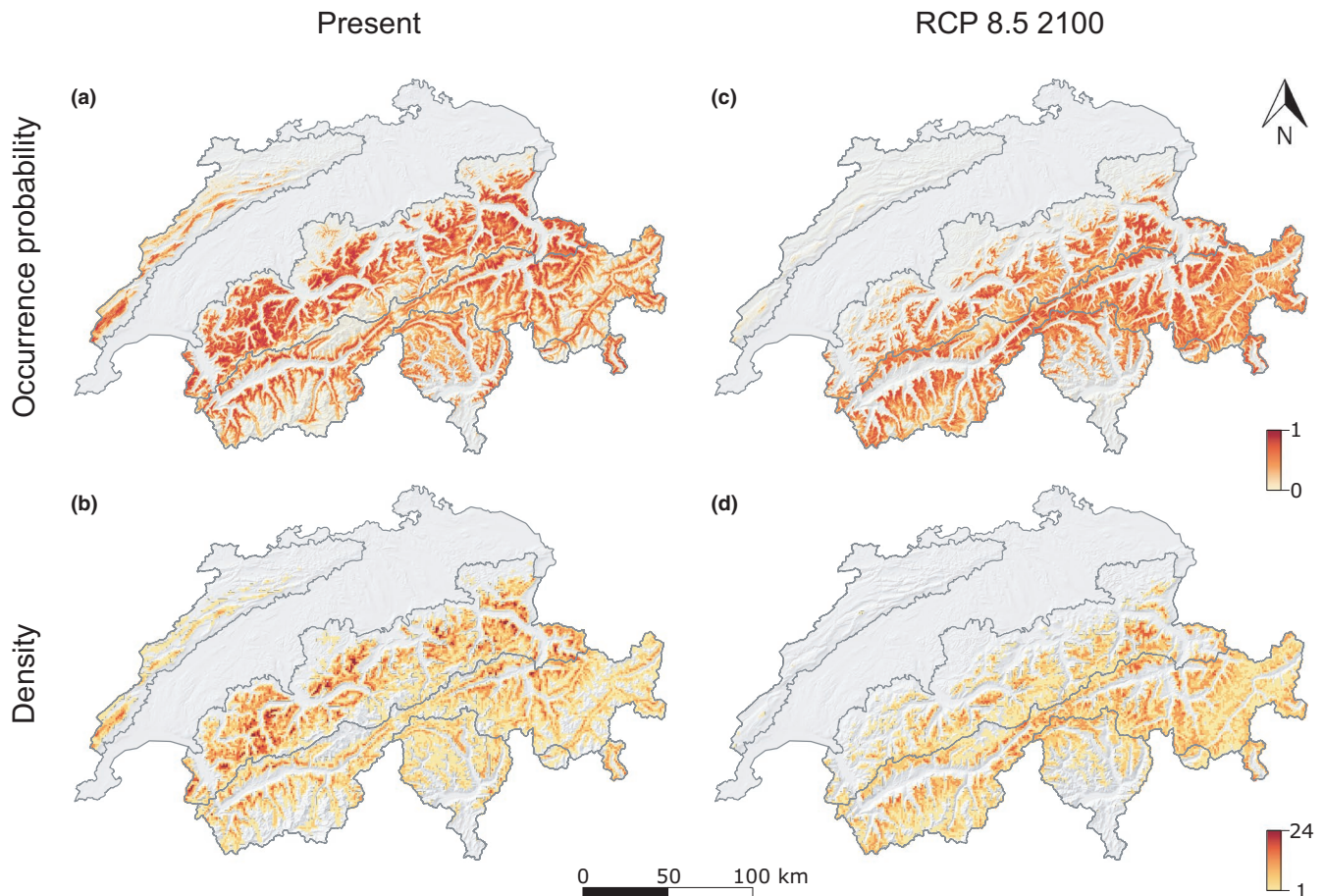
Variables	Permutation importance (%)					
	MaxEnt	GLM	BRT	RF	ANN	Average
Temperature BS	81.4	72.6	68.3	79.5	56.9	71.74
Solar radiation BS	7.1	9.2	12	7	9	8.86
Forest cover	2.3	4.5	4.3	1.9	8.9	4.38
Low-productivity pasture cover	1.1	2.9	1	0.8	9.3	3.02
Number of solitary trees	1.8	2	4.5	2.3	3.4	2.8
Slope	4.2	2.1	2.2	1.6	1	2.22
Precipitation BS	0	1.6	3.7	3.9	1.7	2.18
High-productivity pasture cover	0	2.3	0	0.2	5.6	1.62
Northness	0	1.4	1.6	0.6	1.7	1.06
Precipitation seasonality BS	0	0.7	1.6	1.9	0.4	0.92
Rock and screes cover	2.2	0.1	0	0.1	0	0.48
Unused grassland cover	0	0.6	0	0	1.3	0.38
Low-productivity meadow cover	0	0	0.7	0	0.5	0.24
Eastness	0	0.1	0	0.2	0	0.06
High-productivity meadow cover	0	0	0	0	0.3	0.06
Topographic Position Index	0	0	0	0.1	0	0.02

Note: The importance of variables was set to zero in models in which there were not retained.

Present

RCP 8.5 2100

FIGURE 3 Spatial predictions of occurrence probability and population density of ring ouzels (number of breeding pairs per km^2) in Switzerland at present (a, b) and under the most extreme climate change scenario (RCP 8.5) for the period 2080–2100, considering the CNRM-CM5 general circulation model (c, d)

elevations would clearly decrease (up to −100.0% and −69.2% in the Jura and northern Alps, respectively), whereas it would increase in the high-elevation regions (up to +33.9% and +29.6% in the central and southern Alps, respectively; Figure 5). Especially under the most extreme climate change scenario (RCP 8.5) towards the end of the century, we expect that the ring ouzel would become extinct in the Jura mountains and its Alpine population strongholds would shift from the northern to the central Alps (Figure 5). Nevertheless, land use change scenarios had also noticeable effects in some regions, such as a predicted decrease (−10.4%) in the northern Alps under a regime of farming intensification (here int50) and a slight increase (+5.5%) in the central Alps under land abandonment. The self-sufficiency scenario had no clear effects in any of the four regions (from −0.8% to +0.1%). Predictions of all scenarios per time periods and regions are summarized in Table S4.

4 | DISCUSSION

Taking as an example the ring ouzel, a threatened mountain bird species, this study presents an innovative approach for both modelling current species distribution and abundance and projecting them into

the future under realistic scenarios of changes in climate and land use. By not only focusing on distribution ranges but also integrating actual population size estimates, our analytical framework provides more realistic assessments of species' vulnerability to environmental change, while at the same time yielding key spatial information for targeted conservation planning.

4.1 | Current occurrence and abundance predictions

Habitat suitability was modelled here over a wide geographic range but choosing a scale (home range) at which fine-grained, ecologically functional species–habitat relationships were integrated (Chamberlain et al., 2013; Jiménez-Alfaro et al., 2012). All species distribution models within our ensemble had good predictive accuracy and emphasized that ring ouzel occurrence is mostly driven by climate, namely the mean ambient temperature, here integrated over the breeding season. Although it is generally recognized that climate is a weaker predictor of bird occurrence than habitat circumstances at finer scales (Brambilla et al., 2019; Howard et al., 2015; Thuiller, 2004), there are several examples of alpine species for which ambient temperature remains a crucial predictor at
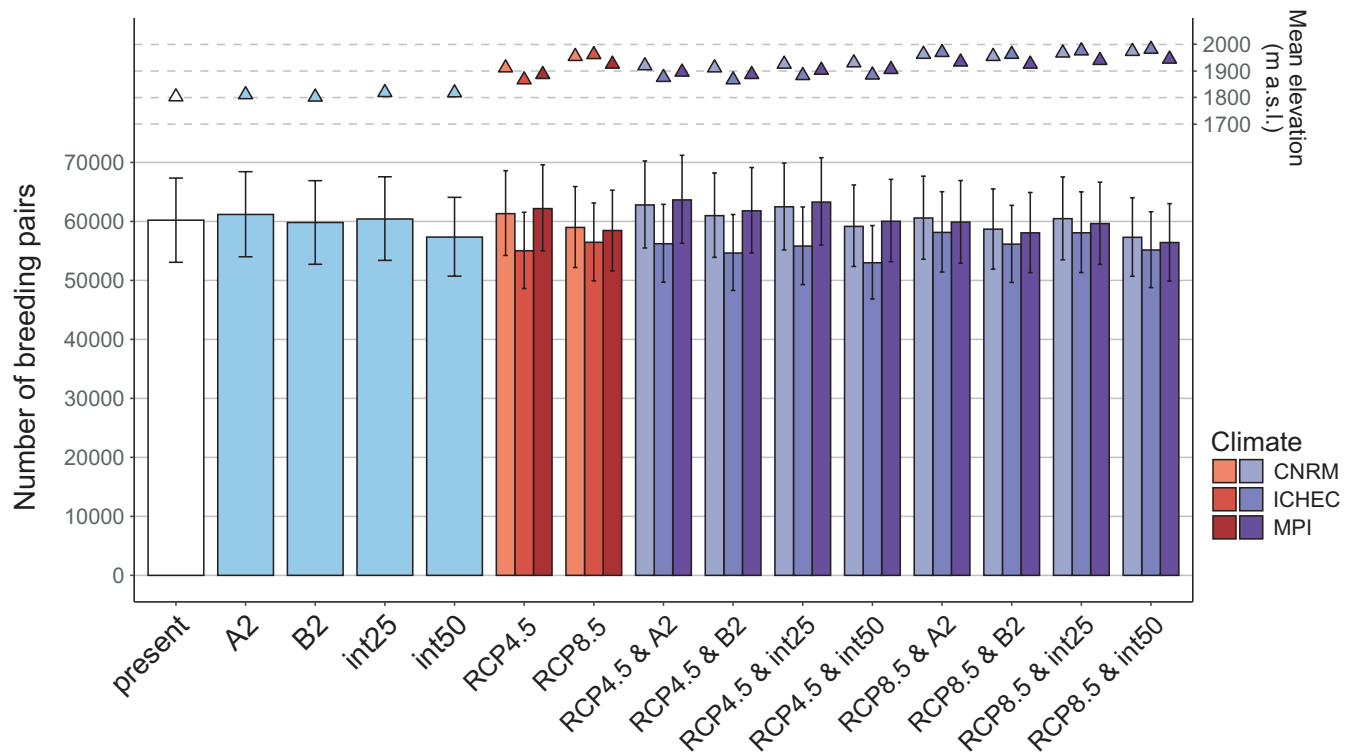
FIGURE 4 Present (very left) and mid-term (2030–2050) projected total population size (histogram) and density-weighted mean elevation (triangles) of the ring ouzel in Switzerland under various scenarios of land use (A2, B2, int25, int50; blue bars) and climate change (RCP 4.5 & 8.5, red bars), either tested individually or in combination (purple bars). Colour intensity in triple bars depicts CNRM, ICHEC and MPI, that is different general circulation models (CNRM-CERFACS-CNRM-CM5, ICHEC-EC-EARTH and MPI-M-MPI-ESM-LR, respectively; see Material and Methods for more details). Error bars show 95% confidence intervals

territory scale (Brambilla et al., 2019; Chamberlain et al., 2013; Jähnig et al., 2020). The second most important variable was solar radiation during the breeding season, with an optimum towards higher values. Yet, as solar radiation increases with elevation ($r_S = 0.44$; see Figure S1), its effect probably underpins the species association with high elevations rather than with sun-exposed areas. Despite their lower relative importance, habitat variables were also high-ranked, corroborating former findings regarding species' preferences for a forest-grassland mosaic (Barras et al., 2020; Ciach & Mrowiec, 2013; von dem Bussche et al., 2008). The most important grassland type was the fraction of low-productivity pastures in the home range, a proxy for extensively-managed pastures characterized by low nutrient inputs (Weber et al., 2018). This is in accord with the known preferences of ring ouzels for nutrient-poor grasslands (Buchanan et al., 2003; von dem Bussche et al., 2008) and foraging sites with short and sparse grass swards (Barras et al., 2020; Burfield, 2002).

Our modelling framework also delivered spatially explicit predictions about ring ouzel population abundance. Those mirrors the spatial distribution of habitat quality more accurately than maps of occurrence probability (Howard et al., 2015; Johnston et al., 2015; Renwick et al., 2012) and enabled the delineation of high density hotspots. Furthermore, our abundance estimates allowed delimiting species' distribution range, this without relying on the arbitrary thresholds that are conventionally used for

converting occurrence probability into presence–absence data (Guisan et al., 2017) and can strongly affect the extent of forecast range shifts (Thuiller, 2004; von dem Bussche et al., 2008). Finally, the density-weighted mean elevation of breeding birds, in other words the "centre of gravity" of the entire Swiss population, could be calculated. The latter is crucial to highlight elevational or latitudinal shifts that might be invisible when looking only at mere distribution maps (Virkkala & Lehikoinen, 2014). Yet, using mean occurrence probability to predict abundance relies on the assumption that abundance and occurrence depend on the same factors (Brown, 1984), which might not hold true in some cases (e.g., Johnston et al., 2015) although it was used successfully in others (e.g., Hill et al., 2017). Our approach resulted in a good fit, apparently delivering a reliable estimate of total population size (95% CI: 53,070–67,349 breeding pairs) when compared to quantitative appraisals by the last national Atlas (50,000–75,000; see Knaus et al., 2018).

4.2 | Effects of climate and land use scenarios

According to our models, the magnitude of predicted changes in population size and mean elevation was overall much larger for climate change scenarios than for any land use scenario, especially
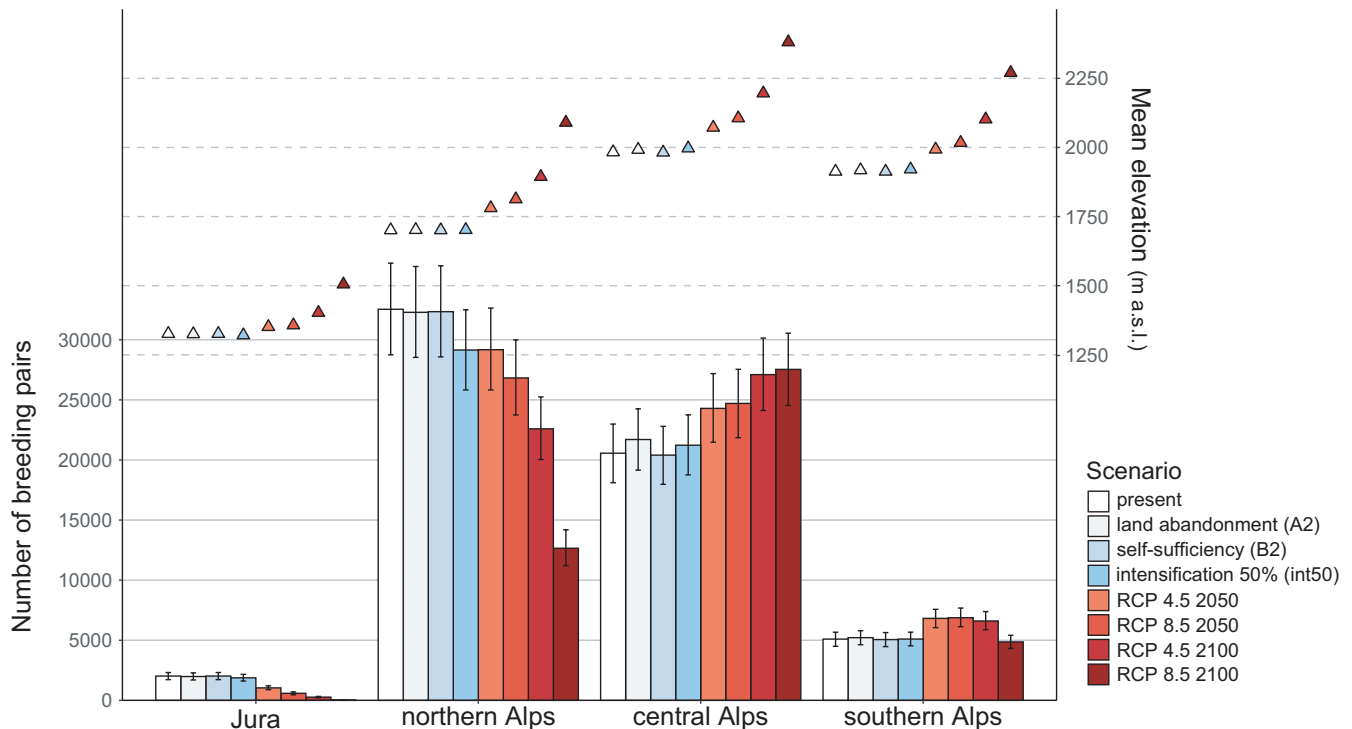
FIGURE 5 Present and projected population size (histogram) and density-weighted mean elevation (triangles) of the ring ouzel in each of the four Swiss biogeographical regions considered, under various scenarios of land use (blue bars) and climate change (red bars). Land use scenarios refer to 2035, whereas climate change scenarios are for two periods (2030–2050 and 2080–2100), considering the CNRM-CM5 general circulation model. Error bars show 95% confidence intervals

at the regional level (Figure 5). A noticeable exception to that general pattern was the scenario of increased grassland productivity in the northern Alps, whose detrimental effect on population size was equivalent to the moderate scenario of climate change. This highlights that further intensification of grassland management (or steady increase in nitrogen atmospheric deposition) could have additional negative effects regionally. In contrast, grassland abandonment resulted only in minor changes in population size, contradicting our hypothesis that forest encroachment would be detrimental to ring ouzels (see Bani et al., 2019). As a matter of fact, the foreseen increased habitat suitability in newly forested areas above the current treeline simply compensated for any habitat loss through vegetation encroachment at lower elevations. This is in line with findings from Chamberlain et al. (2013), who predicted positive effects of forest upward expansion for other treeline passerines in the European Alps, but not with observations of a net range loss reported for those species in Bani et al. (2019), suggesting complex responses of the bird community in treeline ecotones.

Concerning climate change scenarios, ring ouzel populations are likely to react differently with respect to the study region. Populations occurring at low elevations (Jura & northern Alps) are projected to decline further into the future, while populations located closer to the main axis of the Alpine chain (here central—or inner—and southern Alps) are predicted to increase, a pattern confirmed by recent estimates of regional population trends (Knaus et al., 2018). At the national level and in the mid-term, this would result in an elevational upward range shift by circa 100 m but with an

apparent demographic stability under both climate change scenarios. By the end of this century, however, the most extreme climate change scenario predicts a further loss of one-third of the total Swiss population and a particularly marked upward range shift of almost 500 m. This would cause the extinction of the species from the Swiss Jura (Figures 3d and 5) and a halving of the number of breeding pairs in the current species stronghold (northern Alps). Note that all these scenarios assume a high dispersal ability of the species, that is an immediate colonization of suitable habitat, which is a reasonable assumption for a short-distance migrant bird.

4.3 | Model implications and limitations

Our results suggest that the recent decline observed in ring ouzel populations inhabiting lower mountain ranges in Switzerland and neighbouring countries like France and Germany (Anger et al., 2020; Knaus et al., 2018) is mainly due to climate change. The intensification of grassland management in ring ouzel breeding habitat might have played an additional role, especially at lower elevations, analogous to the severe impact it exerted upon other grassland passerines (e.g., Britschgi et al., 2006). In contrast, it is unlikely that land abandonment has and will contribute much to the decline of the species in Switzerland. Indeed, the high intervention scenario in which forest encroachment is extensively combated (e.g., via targeted forestry measures or grazing) had no discernible effects on the Swiss population size although local

changes in habitat suitability were obvious. In this context, implementing the above habitat management measures to buffer the negative effects of climate change at lower elevations (see Braunisch et al., 2014) would make little sense. Instead, given that new suitable breeding habitat will appear through natural afforestation above the actual treeline, habitat management measures implemented at the advancing range-margin may represent a more promising adaptive strategy (Pearce-Higgins et al., 2011).

We decided not to account for changes in vegetation in our climatic scenarios, in contrast to land use scenarios. First, it is unclear whether factors that increasingly impact low-elevation forests, for example wildfires or insect outbreaks, will represent important drivers in subalpine forests in the future (Schumacher & Bugmann, 2006). Second, uncertainties about the pace of upward shifts in vegetation and soil development are high (Dirnböck et al., 2011; Hagedorn et al., 2019). In effect, treelines are predicted to lag behind climate change for 50–100 years due to the slow growth of trees at high elevation (Körner, 2012). In addition, grazing and browsing by livestock, and more and more, by growing and expanding populations of wild ungulates, especially red deer *Cervus elaphus*, will hamper spontaneous afforestation (Didion et al., 2011; Schumacher & Bugmann, 2006). Still, the question remains to which extent wild ungulates can compensate for the decrease in domestic livestock, that is whether their effectiveness in keeping open and semi-open habitats in the long run is comparable (San Miguel-Ayanz et al., 2010). Under these circumstances, one can expect an amplifying spatial mismatch between the optimal climatic niche and suitable habitat configuration for all treeline species whose occurrence largely depends on climatic factors (Bani et al., 2019; Chamberlain et al., 2013). This is obvious in our projections predicting above all an absolute decrease in population density rather than upward shifts in ring ouzel hotspots (Figure 3b,d). Nevertheless, pasture abandonment can lead to more rapid upward shifts of the treeline (Gehrig-Fasel et al., 2007; Körner, 2012), such that the accuracy of our predictions towards the end of the century may be contingent upon long-term modifications in land use. Those are, however, excessively challenging to predict (Verburg et al., 2013), which motivated our choice of relatively short-term projections (to 2035; Price et al., 2015). Even within that timeframe, the evolution of the national socio-political and economical contexts remains difficult to predict, which might limit the general applicability of our framework.

4.4 | Recommendations for species conservation

The innovative approach used here allowed us to identify current hotspot areas for the ring ouzel as well as sites that will remain or become suitable in the future. With that information, we could designate areas in the landscape where conservation efforts should be deployed in priority for maintaining habitat quality in the long run. As main management measures, we recommend to avoid further grassland intensification in the northern Alps and Jura mountains,

especially in recognized hotspots with high ring ouzel density, and to carefully monitor and manage shifting treelines in the central and southern Alps (Mollet et al., 2018). Regarding the latter, it remains contentious whether habitat should be managed in a way that assists tree migration to higher elevations or whether it should be slowed down (Bani et al., 2019; Chamberlain et al., 2013; García-Navas et al., 2020). In the Alps, upward shifts in treelines have already been documented, being mainly ascribed to woody vegetation encroachment following pastoral abandonment (Dirnböck et al., 2011; Gehrig-Fasel et al., 2007). At a first glance, this temporary habitat gain may provide a short-term window of opportunity for several treeline species (Laiolo et al., 2004). However, treeline upward shifts are also considered as a major threat (Bani et al., 2019; García-Navas et al., 2020), since open Alpine grasslands, which harbour a very rich biodiversity, would decrease in area as a result (Chamberlain et al., 2013; Dirnböck et al., 2011). This is, first, because of the pyramid shape of mountains, and second, because grasslands risk to get squeezed between a moving treeline and rocky substrates where soil development is especially slow (Hagedorn et al., 2019). An elegant solution to solve this apparent conservation dilemma would be to maintain extensive pasturing in mountain ecosystems, via financial incentives to farmers, as it probably represents the best management trade-off in the long term (Bani et al., 2019; Laiolo et al., 2004). This would allow keeping both biodiversity-rich open Alpine grasslands and semi-open wooded pastures whose habitat heterogeneity is key for ring ouzel and a number of associated treeline species of birds and mammals (Braunisch et al., 2016; Mollet et al., 2018; Rehnus et al., 2018).

5 | CONCLUSIONS

By modelling and projecting species occurrence and abundance at a fine scale under realistic scenarios of changes in climate and land use, the original framework deployed in this study represents a valuable tool not only for assessing species' vulnerability to environmental change and disentangling between different drivers, but also for delivering spatially explicit information for planning conservation interventions. Indeed, forward-looking approaches such as the present one would be the crux to properly identify and rank threats to biodiversity while delineating areas where adaptive and targeted conservation action should be prioritized. A wider use of this framework would allow to better predict abundance and distribution changes of species in the face of global change, accounting for regional specificities (Lehikoinen et al., 2019). The growing availability of both species and environmental data at unprecedented spatial resolutions offers new avenues for such an exemplary modelling of other threatened mountain species, providing that basic knowledge on their ecological requirements exists.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13247.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study were provided by the Swiss Ornithological Institute (www.vogelwarte.ch), the Federal Research Institute WSL (www.wsl.ch), the Swiss Data Cube (www.swissdatacube.org), the Federal Statistical Office (www.bfs.admin.ch), the Federal Office of Topography swisstopo (www.swisstopo.admin.ch) and the Federal Office of Meteorology and Climatology MeteoSwiss (www.meteoswiss.admin.ch). Restrictions apply to the availability of these data, which were used under licence for the current study and are thus not publicly accessible. Data are however available from the authors upon reasonable request and with permission of third parties listed above.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.