Climate and land-use change drive habitat loss in a mountain bird species

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Mountain areas still feature remnants of traditional land use and consequently constitute a large proportion of the remaining species-rich habitats in Central Europe. However, their biodiversity is increasingly threatened by changes in climate and land use. The Alpine Ring Ouzel *Turdus torquatus alpestris* is a typical mountain bird that has recently declined in most of its breeding range. In this study we compared the historical (1986–1987) and recent (2017) distribution of breeding Ring Ouzels in 62 randomly selected 750 × 750 -m plots and analysed local colonization and extinction patterns in 558 subunits (= 'grid cells') in the southern Black Forest (south-western Germany). Our study revealed that habitat occupancy has decreased by about one-third, mainly at lower elevations and in depressed landforms, during the past three decades. Local colonization amounted to 25% and extinction to 66% of the previously vacant or occupied grid cells, respectively. Habitat occupancy and local colonization and extinction were driven by climate and habitat parameters. The Ring Ouzel preferred convex landscape formations such as mountain peaks and ridges with long snow-cover duration for breeding. Sites with high proportions of deciduous forest and abandoned pasture were avoided. Local colonization was higher at convex landscape formations and by high coniferous forest coverage and forest-edge length. Local extinction, on the other hand, was lower at convex landscape formations and high-elevation sites. Our results suggest that shorter persistence of snow fields caused by climate change and degradation of feeding grounds through land-use abandonment might severely deteriorate food availability for the species, which is likely to have contributed to the observed decline. For conservation of the Alpine Ring Ouzel, we recommend adopting measures to mitigate the negative effects of climate warming and improve habitat quality. The creation of small-scale mosaics of sparse conifer forests and regularly grazed pastures, especially on north- and east-facing slopes on the lee sides of hills, mountain peaks or ridges, should be supported.

Keywords: abandonment, Alpine Ring Ouzel, Black Forest, conservation management, global warming, grazing, *Turdus torquatus alpestris*.

The recent loss of biodiversity is among the most severe threats to life on Earth (Johnson *et al.* 2017). Current species extinction rates exceed the natural background rate by about a thousand times, and the trend is rising (Pimm *et al.* 1995, Vos *et al.* 2014). There is overwhelming evidence that the ongoing biodiversity crisis is mainly driven by human-induced global change, in particular changes in climate and land use (Foley *et al.* 2005, IPCC 2013).

The magnitude of climate change is particularly large in mountain areas, with the rate of warming being twice that of the global average (Brunetti *et al.* 2009). Additionally, mountain ranges harbour many cold-adapted species, which are likely to be extremely vulnerable to climate change (La Sorte & Jetz 2010, Streitberger *et al.* 2016).

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Altitudinal range shifts and habitat loss have been shown for a variety of species in montane environments in response to climate warming (e.g. Lehikoinen *et al.* 2014, MacLean & Beissinger 2017, Löffler *et al.* 2019, Fumy *et al.* 2020).

In Central Europe, traditional land-use practices have for centuries contributed to the development of semi-natural ecosystems harbouring outstanding species richness (Plieninger *et al.* 2006, Poschlod 2017). However, since the beginning of the industrial era, land-use change has led to a substantial loss of wild biota (Donald *et al.* 2006, Johnson *et al.* 2017). Remnants of traditional land use are mainly found in mountain areas which, consequently, host a large proportion of the remaining species-rich habitats in Central Europe (Plieninger *et al.* 2006).

Birds are excellent indicators of biodiversity in general (Gregory *et al.* 2008, Gregory & van Strien 2010, see also Sander & Chamberlain 2020). They respond sensitively to climate change (Crick 2004, Jenouvrier 2013, Lehikoinen *et al.* 2014) and habitat alteration (Fuller 2012), which is especially true for alpine species (e.g. Oswald *et al.* 2020). Due to their complex habitat requirements, they are also frequently used as umbrella species whose conservation is expected to secure the protection of a large number of naturally co-occurring species (Roberge & Angelstam 2004).
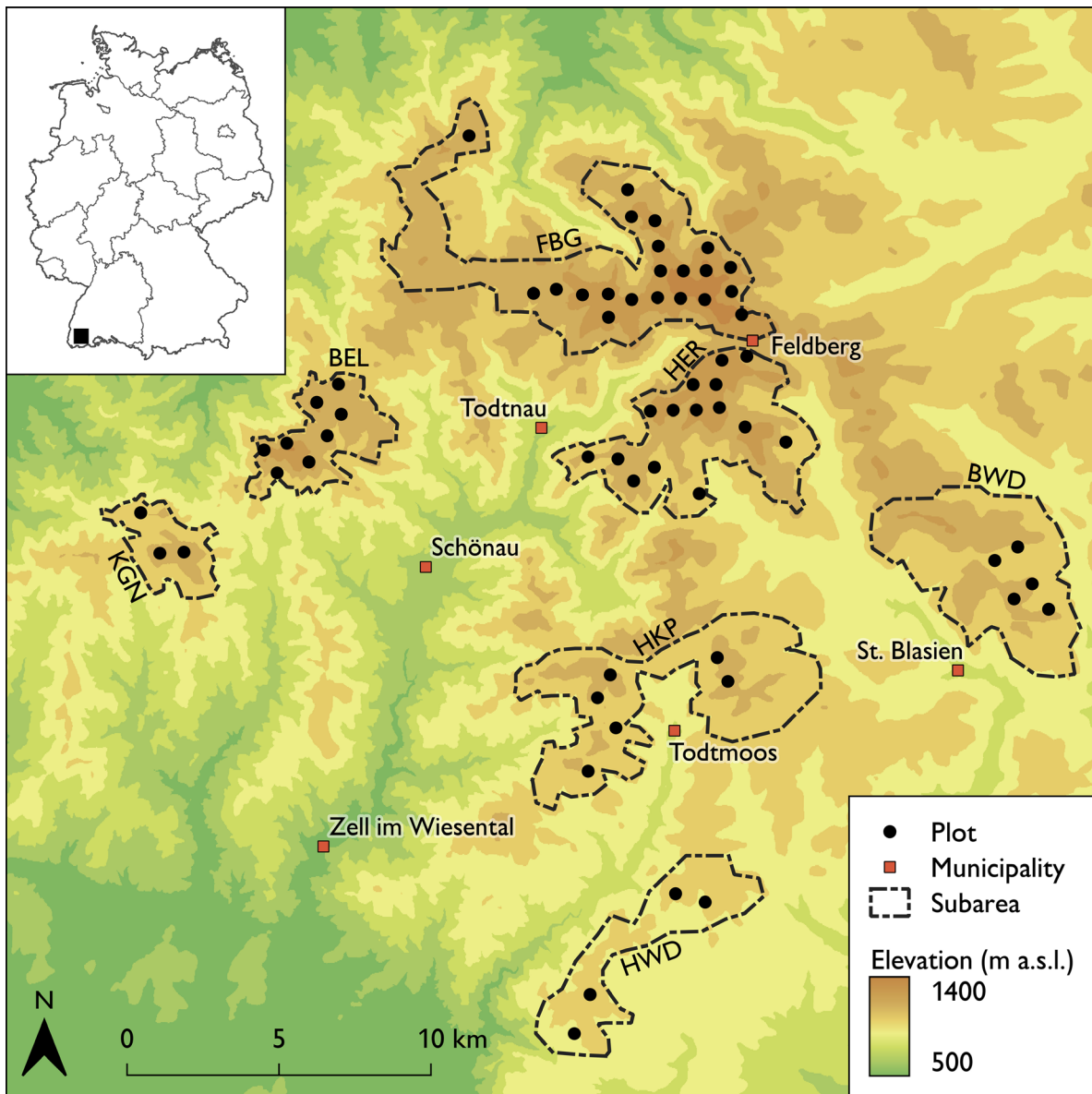
The Alpine Ring Ouzel *Turdus torquatus alpestris* (Brehm, CL, 1831) is a typical mountain bird, occurring in the Alps, Pyrenees, Balkans, Greece and Asia Minor (Glutz von Blotzheim & Bauer 1988). Smaller, potentially genetically differentiated populations occur in the low mountain ranges north of the Alps (Bacht *et al.* 2013). In Germany, the largest population outside the Alps is located in the southern Black Forest, Baden-Württemberg. It has recently been debated whether the current decline of the species in the Alps is driven by climate change or habitat alteration (dem Bussche *et al.* 2008, Knaus *et al.* 2018, Barras *et al.* 2019) and there is evidence that the population declines and range contractions of the subspecies *T. t. torquatus* (Linnaeus, 1758) are linked to climate change (Beale *et al.* 2006). In the northern Black Forest, Anger *et al.* (2020) observed a strong decline of the species and local extinctions at lower elevations. Similar range retractions have been assumed for the southern Black Forest (Bauer *et al.* 2013). However, population dynamics, distribution change and underlying mechanisms have not been studied so far in this region.

In this study, we compare the historical (1986–1987) and recent (2017) distribution of breeding Ring Ouzels in the southern Black Forest. To identify the drivers of habitat loss, we relate Ring Ouzel breeding territory occupancy as well as local colonization and extinction to climate and habitat parameters. Based on the results, we give recommendations for the conservation of the Ring Ouzel in times of global change.

METHODS

Study area

The study area comprises the submontane, montane and subalpine zones of the southern Black Forest in the federal state of Baden-Württemberg (SW Germany, 900–1493 m a.s.l.; Fig. 1). Compared with the average conditions of Central Europe, the climate is cool and wet, with a mean annual temperature of 3.8–5.5 °C and a mean annual precipitation of 1650–2200 mm (30-year period 1981–2010; Deutscher Wetterdienst: Climate Data Center, 2018). Due to the harsh climate, the nutrient-poor soils on acidic bedrock and the pronounced relief, the study area features a heterogeneous landscape with extensively managed semi-natural pastures, montane conifer forests, bogs and a huge variety of microclimatic conditions (Geis *et al.* 2013, Ministerium für Ländlichen Raum und Verbraucherschutz, 2016). Exceptionally for Central Europe, several of the pastures in the study area are common pastures, which have been under low-intensity grazing management by the local communities for centuries (Landesanstalt für Umweltschutz Baden-Württemberg 2004) and which are of high nature conservation value (Schwarz *et al.* 2018, Fumy *et al.* 2020). The conifer forests comprise a large gradient from dense and dark stands with closed canopy to sparse woodlands with a high degree of shrub cover, mainly *Vaccinium myrtillus* (Ludemann 2012, Wippel *et al.*, 2016). The landscape heterogeneity results in a high species richness. Consequently, the study area is part of the German biodiversity-hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann & Sachteleben 2012). Some of the mountain peaks are major tourist attractions, such as the Feldberg and Belchen (Landesanstalt für Umweltschutz Baden-Württemberg 2004, Geis *et al.*, 2013). Most of the more remote areas, in contrast, are rarely visited by tourists.

Figure 1. Location of the study area and plots in the southern Black Forest (SW Germany).

Study species

The Ring Ouzel *Turdus torquatus* is a passerine bird, with the subspecies *T. t. alpestris* being a typical inhabitant of the Central European mountain ranges. Its breeding range extends from the northern Iberian Peninsula and Central Europe to the Carpathians. Breeding is restricted to the sub-montane–alpine zone and the birds' wintering grounds are located in NW Africa, especially the High Atlas (Glutz von Blotzheim & Bauer 1988, Bacht *et al.* 2013).

Characteristic breeding habitats of the Ring Ouzel are mosaics of sparse montane conifer forests, and semi-open and open landscapes with a cool and humid microclimate (Schirutschke 2005, Bauer *et al.* 2013). The nests are usually built in the branch forks of evergreen conifers, mainly Norway Spruce *Picea abies* and European Silver Fir *Abies alba*. In contrast to leafless deciduous trees, evergreen conifers provide hidden places for nest-building at the beginning of the breeding season (Glutz von Blotzheim & Bauer 1988, Gatter & Mattes 2018). The Ring Ouzel forages on the ground (Glutz von Blotzheim & Bauer

1988). The staple food of the nestlings is earthworms (Glutz von Blotzheim & Bauer 1988). In the Black Forest, the species breeds at elevations above 900 m a.s.l. (Knoch 1970, Mann 1990).

Germany hosts 2600–5000 breeding pairs of the Ring Ouzel but numbers are decreasing (Gedeon *et al.* 2014). The largest populations in Germany occur in the Alps and the southern Black Forest. The population size in the Black Forest is estimated to range from 300–500 (Bauer *et al.* 2013) to 370–950 (Gedeon *et al.* 2014) breeding pairs. In Baden-Württemberg the species is now considered to be threatened with extinction (Bauer *et al.* 2013).

Sampling design

Bird surveys

In this study, we compared the historical (1986–1987; hereafter referred to as 1987) and recent (2017) distribution of breeding Ring Ouzels in the southern Black Forest. Data for the historical distribution were derived from Mann (1990), who conducted an area-covering survey of Ring Ouzel territories in the southern Black Forest. In 2017, we mapped territories (Bibby *et al.* 2000, Andretzke *et al.* 2005) at 62 plots of 750×750 m in seven sub-areas of the study area (Fig. 1). Random plot selection was based on a spatial grid that was superimposed on the area surveyed by Mann (1990) and stratified across the respective elevation gradient. Contiguous mountain ridges were defined as sub-areas which represent the entire elevation gradient occupied by the Ring Ouzel in the Black Forest. Survey methods were identical to those described by Mann (1990). Mapping of Ring Ouzel breeding territories took place from April to June 2017. Each plot was visited three times in good weather conditions with an interval of at least 10 days between each visit (Fischer *et al.* 2005). Mapping was conducted between 1 h before and 90 min after sunrise. All observations of territorial behaviour, such as singing, were recorded according to Bibby *et al.* (2000) on a map (scale 1 : 1500) by following a non-linear transect covering the entire plot. Based on the guidelines provided by Andretzke *et al.* (2005), establishment of a territory was assumed if a bird showed territorial behaviour at least twice within a span of 10 days between each survey and at least one of these observations was from mid-May onwards.

In contrast to our study, clustered breeding was not differentiated into single breeding territories by Mann (1990). Accordingly, his study does not provide information on population densities within the plots but instead presents fine-scaled data on the spatial distribution of clustered or single breeding territories. To compare these data with those of our study, we divided each plot into nine grid cells of 250×250 m and used the percentage of occupied grid cells per plot (= 'occupancy ratio') as a response variable in further analyses. Grid cells were considered 'occupied' when at least one territory centre was located inside the respective unit.

Habitat quality

To determine habitat quality, we gathered data on climate, elevation, topography and habitat composition in each plot. As the Ring Ouzel is a relatively long-lived passerine species with high breeding-site fidelity (Knoch 1970), and to account for possible interannual variation, we averaged climate data over 5 years with the survey year as the last year of each period (1983–1987 and 2013–2017, respectively). We considered spring (April–June) mean temperature and precipitation sum as well as snow-cover duration (days per year), which were provided by the German Meteorological Service (resolution: 1×1 km; Deutscher Wetterdienst: Climate Data Center, 2018).

Elevation data were provided by the U.S. Geological Survey and had a resolution of 75×75 m (USGS Earth Resources Observation & Science Center 2018). These data were also used to calculate the topographical position index (TPI) according to Weiss (2001), with a search radius of 975 m around the centre of each grid cell, using the 'spatialEco' package (Evans 2019). TPI values ranged from −48 to +148 m. Negative values indicate grid cells with an elevation lower than the surrounding landscape (e.g. valleys or depressions), and positive values indicate hills, mountain peaks or ridges surmounting the adjacent landscape. For further analysis, elevation and TPI data were averaged per plot.

In each plot we mapped the cover of the habitat types listed in Table 1 in the field according to Riecken (2014). The Shannon index of habitat types served as a measure of habitat diversity H' (Fartmann *et al.* 2018, Schwarz *et al.* 2018):

$$H' = -\sum_i p_i \cdot \ln p_i \cdot with \ p_i = \frac{n_i}{N}$$

where N is the number of habitat types per plot and n_i is the area of each habitat type in the plot. We mapped managed and private mountain huts with a

Table 1. Mean ($\pm$ se) of environmental parameters in the study plots. Climate parameters are averaged over 5-year periods (1983–87 and 2013–2017). Parameters included as coefficients in multivariate models (1987, 2017: occupancy ratio models; Col, Ext: colonization and extinction models) are indicated with the letter c (climate models), h (habitat type models) and s (synthesis models). Parameters included in the calculation of the habitat diversity index are indicated in column *H'*.

Parameter	Mean $\pm$ se 1987	2017	Multivariable model 1987	2017	Col	Ext	*H'*
Topography							
Elevation (m a.s.l.)	1190 $\pm$ 15		.	.	c	cs	.
TPI (m)[a]	48.4 $\pm$ 5.4		c	cs	cs	cs	.
Climate							
Spring temperature (°C)	7.18 $\pm$ 0.1	8.46 $\pm$ 0.08	.	.	.	.	.
Spring precipitation (mm)	499 $\pm$ 3.8	471 $\pm$ 5.6	c	.	.	.	.
Snow-cover duration (days/year)	151 $\pm$ 1.8	114 $\pm$ 1.9	c	cs	.	.	.
Habitat characteristics							
Habitat type (%)							
Forest	.	66.6 $\pm$ 3.0	.	.	.	.	.
Coniferous forest	.	42.7 $\pm$ 2.9	.	.	hs	h	✓
Deciduous forest	.	20.6 $\pm$ 2.5	.	h	h	.	✓
Glade	.	3.31 $\pm$ 0.37	.	h	h	h	✓
Open land	.	32.6 $\pm$ 2.9	.	.	.	.	.
Nutrient-poor pasture	.	19.8 $\pm$ 2.3	.	h	.	.	✓
Abandoned pasture	.	8.74 $\pm$ 1.4	.	hs	h	.	✓
Improved grassland	.	2.82 $\pm$ 0.81	.	h	h	.	✓
Copse	.	1.29 $\pm$ 0.28	.	.	h	h	✓
Other habitats[b]	.	0.78 $\pm$ 0.18	.	.	h	h	.
Habitat diversity (*H'*)	.	0.6 $\pm$ 0.01	.	h	.	.	.
Forest-edge length (km)	.	2.16 $\pm$ 0.17	.	.	hs	hs	.
Highly frequented area (%)[c]	.	7.26 $\pm$ 1.2	.	hs	h	h	.

[a]Topographical position index (TPI) values ranged from –53 to 143 m. Negative values indicate study plots that are situated lower than the surrounding landscape (e.g. valleys or depressions) and positive values indicate hills, mountain peaks or ridges surmounting the adjacent landscape. [b]Built-up areas, roads and water bodies. [c]Buffer of 150 m around managed and 15 m around private mountain huts.

buffer of 150 and 15 m, respectively, as areas highly frequented by tourists. Additionally, we manually measured the forest-edge length from aerial imagery using straight line segments of 20 m length to represent the treeline. For spatial analysis we used the open source software R (R Core Team 2020) and QGIS (QGIS Development Team 2018).

Statistical analysis

Differences between historical and recent period
Differences in plot occupancy, occupancy ratio (= proportion of occupied grid cells per study plot) and climatic conditions between the historical and recent period were tested using the McNemar test (plot occupancy) and the Wilcoxon test (all other variables).

Habitat occupancy and environmental parameters
To determine the relationship between Ring Ouzel habitat occupancy and environmental parameters, we computed generalized linear mixed-effects models (GLMMs) with a proportional binomial error structure and random intercepts. Separate models were calculated for the historical (only topography and climate; data on historical habitat characteristics were not available) and recent period, using the respective occupancy ratio as a dependent variable ('lme4' package; Bates *et al.* 2015). Possible spatial autocorrelation was taken into account by adding sub-area as a random effect. At first, we conducted a GLMM for each environmental parameter separately (Appendices 1 and 2). *P*-values were obtained from likelihood ratio tests comparing model fits for each parameter to the intercept-only model. In the next step, we calculated multivariate models evaluating the following categories: climate in the historical period, and climate, habitat and synthesis in the recent period. The synthesis model was calculated using the significant predictor variables from the respective climate and habitat models.

To increase model robustness and identify the most important environmental parameters in the models, we conducted model averaging based on an information-theoretic approach (Burnham & Anderson 2010, Grueber *et al.* 2011). Proceeding from an all-coefficients full model, we evaluated all possible fixed-effect combinations for each category. From these, we subsequently calculated average models including the top-ranked models within delta Akaike information criterion (ΔAIC_C) < 3 (Grueber *et al.* 2011). Only significant variables of the climate and habitat model were integrated into the synthesis model. These analyses were carried out using the 'MuMIn' package (Bartón 2017). For all models, we computed Nakagawa's conditional and marginal pseudo-R^2 (Nakagawa *et al.* 2017).

Prior to these multivariate analyses, Spearman rank correlations (r_s) of all numerical variables listed in Table 1 were conducted to identify those with strong intercorrelations ($|r_s| \geq 0.5$; see Appendix 3 for the historical and Appendix 4 for the recent period) (Dormann *et al.* 2013). Intercorrelated variables were not allowed together in one model. For each category (climate, habitat and synthesis), we calculated preliminary models with all permissible maximum variable combinations. Final variable selection for the full models used in the actual analyses was based on the AIC of these preliminary models. Table 1 lists the full-model variable combinations of all categories.

Fine-scale changes in habitat occupancy
We examined changes in habitat occupancy between the two study periods. Therefore, we analysed 'local colonization' and 'local extinction' based on historical and recent grid-cell occupancy. Our data were split into two datasets according to their occupancy status in the historical period. Of all grid cells not occupied in the historical period (= dataset one), we defined those occupied in the recent period as 'local colonization' events. Conversely, of all grid cells occupied in the historical period (= dataset two), those not occupied in the recent period were considered 'local extinction' events.

The analyses followed a similar path to the habitat occupancy analyses: we conducted univariate and subsequently multivariate binomial GLMMs on local colonization and extinction using study plot nested in subarea as random factors and only environmental variables from the recent period as fixed effects in the models. The climate parameters were excluded from these analyses because they were at too course a scale relative to the other variables. Variable combination selection and model averaging followed the same procedures as described in the section 'Habitat occupancy and environmental parameters'. See Appendix 4 for variable intercorrelations and Table 1 for final variable selection for the multivariate analyses.

Preliminary models showed that across all modelling approaches, there were no quadratic effects of the considered environmental parameters on the target variables used. Hence, we did not consider quadratic terms in our models. We also included all possible combinations of interaction effects of non-intercorrelated variables in explorative models at all stages of multivariate analyses. As none of these improved our models, we decided not to include interaction terms in our final analyses.

We used R 3.6.1 for all statistical analyses (R Core Team 2020).

RESULTS

Environmental conditions

The mean elevation of the plots ranged from 928 to 1402 m a.s.l.; on average ($\pm$ se) the plots were situated at an elevation of 1194 ± 15 m (Table 1). A mean TPI of 48.4 ± 5.5 m indicates that most plots were clearly above the surrounding landscape. In 1987, the average values of spring precipitation, spring temperature and snow cover were 499.0 ± 3.8 mm, 7.2 ± 1.0 °C and 151 ± 1.8 days, respectively. From 1987 to 2017, climatic conditions in the plots had changed (Fig. 2). Mean spring temperatures increased by 1.28 ± 0.03 °C, mean spring precipitation decreased by 28.3 ± 4.4 mm and mean annual snow cover declined by 37.0 ± 0.5 days.

Forests covered two-thirds of the plots in 2017; the remaining third was occupied by open land. Two-thirds of the forests were coniferous and one-third was deciduous forest. Open land was composed of two-thirds nutrient-poor pasture and one-third abandoned pasture. Other habitat types covered only very small proportions of the plots. The mean habitat diversity was 0.49 ± 0.01 and forest edges had an average length of 3.2 ± 0.2 km per plot. Within the plots, $7.3 \pm 1.2\%$ of the areas were highly frequented by tourists (Table 1).

Habitat occupancy

In 1987, 56 (90%) of the 62 studied plots were inhabited by at least one breeding pair of Ring Ouzels. In 2017, we detected 219 territories on only 49 occupied plots (79%). However, this decrease in plot occupancy was not significant (Fig. 3). The occupancy ratio, on the other hand, declined significantly between the historical and recent study period: in 1987, 40 ± 0.3% of the grid cells were occupied per plot, whereas in 2017 this was only true for 28 ± 0.3% (Fig. 3). Of 221 grid cells occupied in the historical period, 146 became extinct, and of 337 historically vacant grid cells, 83 were colonized in the recent period.

Model results

The occupancy ratio was related to climate and habitat parameters. In the univariate models, the historical and recent occupancy ratio increased with spring precipitation, snow-cover duration, elevation and TPI, and decreased with spring temperature (Appendix 1). Habitat parameters were only analysed for the recent period. The occupancy ratio increased with the cover of conifer forests and glades, but decreased with deciduous forest, open-land, abandoned pasture and highly frequented area coverage (Appendix 2).

In the multivariate climate models for both study periods, the TPI had a positive effect on the occupancy ratio (Table 2). In the recent period, occupancy also increased with snow-cover duration. In the multivariate habitat model for the recent period, a negative effect of deciduous forests, abandoned pastures and highly frequented areas on occupancy was observed. The multivariate synthesis model identified positive effects of snow-cover duration and negative effects of proportion of abandoned pasture on recent Ring Ouzel occurrence (Table 2, Fig. 4). Marginal pseudo-R^2 for the multivariate models of occupancy ratio ranged between 0.15 and 0.21, and conditional pseudo-R^2 ranged between 0.19 and 0.27 (Table 2). In the univariate models, local colonization was related positively to elevation, TPI, coniferous forest cover and forest-edge length, but negatively to deciduous forest cover and highly frequented area proportion (Appendices 1 and 2). Local extinction was related negatively to elevation, TPI and forest-edge length. In the
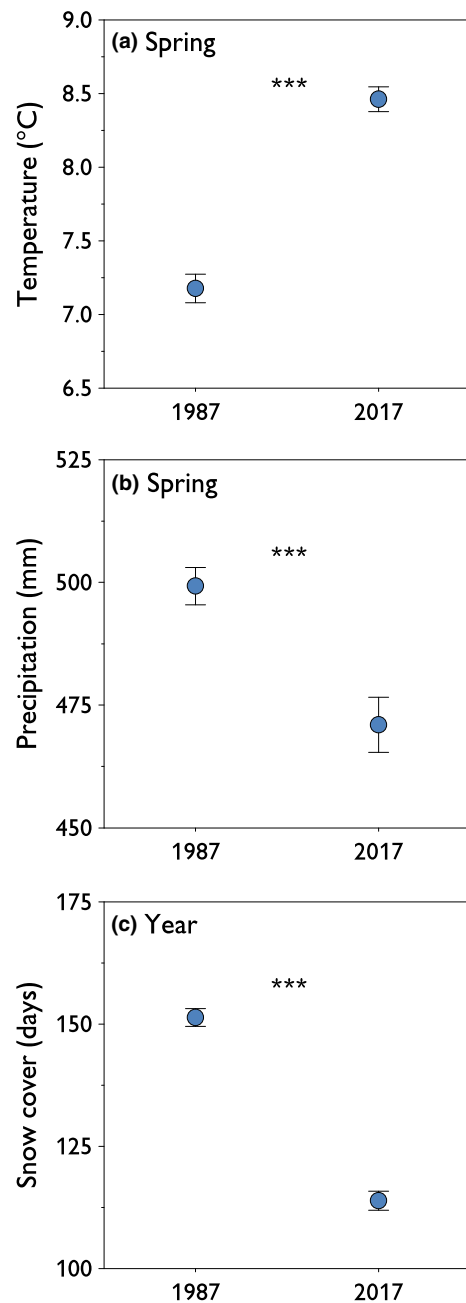
Figure 2. Mean (± se) values of climate parameters: spring temperature (a), spring precipitation (b) and annual snow cover (in days) (c). n_{plots} = 62. Differences between historical and recent climatic conditions were tested using the paired Wilcoxon test: (a) V = 1812, ***P < 0.001; (b) V = 1745, ***P < 0.001; (c) V = 1953, ***P < 0.001.

multivariate models, local colonization was positively related to TPI (climate and synthesis model), coniferous forest cover and forest-edge length
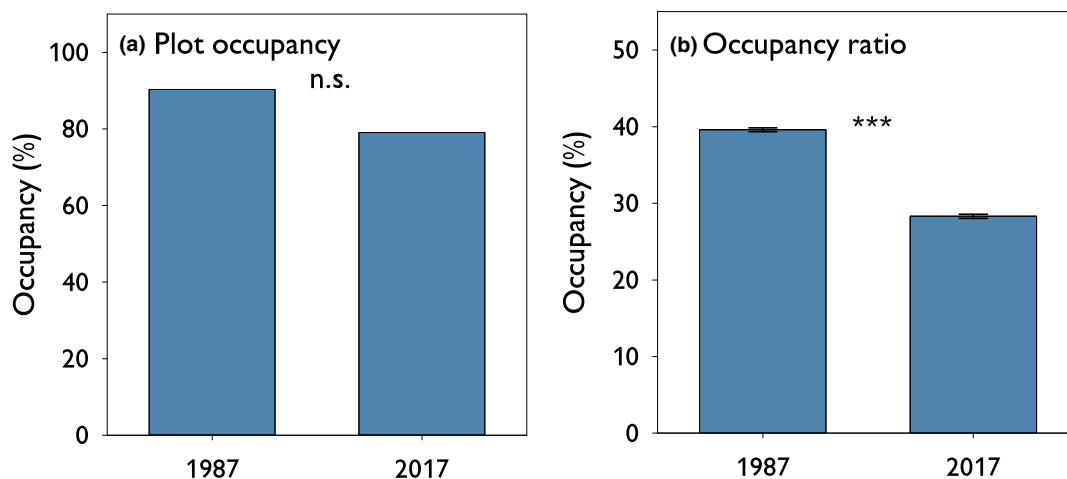
Figure 3. Habitat occupancy. (a) Plot occupancy and (b) occupancy ratio $\pm$ se of breeding Ring Ouzels in 1987 and 2017. $n_{plots} = 62$. Differences in plot occupancy and occupancy ratio were tested by McNemar test and paired Wilcoxon test, respectively: (a) McNemar's $\chi^2 = 2.77$, df $= 1$, ns (not significant) $P > 0.05$; (b) $V = 988$, ***$P < 0.001$.

(habitat and synthesis model; Table 2, Fig. 5). Local extinction was related negatively to TPI and elevation (climate and synthesis model) as well as forest-edge length (habitat model). For the colonization and extinction models, respectively, marginal pseudo-R^2 ranged from 0.11 to 0.31 and from 0.07 to 0.13, and conditional pseudo-R^2 from 0.36 to 0.48 and from 0.08 to 0.16.

DISCUSSION

Our study revealed that over the past three decades, habitat occupancy by the Ring Ouzel has decreased by about one-third in the southern Black Forest, mainly at lower elevations and in depressed landforms. Local habitat occupancy changes were relatively frequent: 66% of the historically occupied grid cells were not occupied in the recent survey, whereas local colonization occurred in 25% of the historically vacant grid cells. Both the occupancy ratio and local changes in habitat occupancy were driven by climate and habitat parameters: the Ring Ouzel preferred convex landscape formations (high TPI values), such as mountain peaks and ridges, that were characterized by long periods of snow cover for breeding. In contrast, sites with high cover of deciduous forests and abandoned pastures were avoided as breeding habitats in the recent period. Local colonization was more likely at convex landscape formations with long snow-cover duration as well as at sites with high coniferous forest cover and long forest-edge length. Local

extinction, on the other hand, was more likely at depressed sites (low TPI values) with short snow-cover duration and at sites with short forest-edge length.

As a result of climate change, spring temperatures had increased from 1987 to 2017 in the study plots, whereas spring precipitation and snow-cover duration had decreased. All three parameters were a function of elevation (except precipitation in the historical period). Disentangling the effects of the different climate parameters on Ring Ouzel habitat use was therefore not straightforward. However, models with the variable 'snow-cover duration' performed slightly better than those with the other climate parameters.

Persistence of snow fields was reflected by three variables: 'snow-cover duration' and the intercorrelated 'elevation' as well as 'topographical position index' (TPI). High TPI values indicated long persistence of snow fields at a finer spatial scale than the relatively coarse-grained data of days with snow cover (resolution 1 × 1 km, cf. Habitat quality). In most high-elevation mountain ranges, snow accumulation is mainly driven by avalanches leading to long-lasting snow beds in small valley bottoms. The study area, however, is characterized by a smoother relief so that the lee-sides of convex landscape formations such as hills, mountain peaks or ridges (= high TPI values) were usually characterized by thick snow cornices in spring (F. Fumy pers. obs.; Geiger *et al.* 1995). All three parameters, especially

Table 2. Results of model-averaged GLMMs: relationship of climate parameters with historical (1987) and recent (2017) occupancy ratio of the 62 study plots, local colonization ($n_{grid\ cells}$ = 337) and local extinction ($n_{grid\ cells}$ = 221).
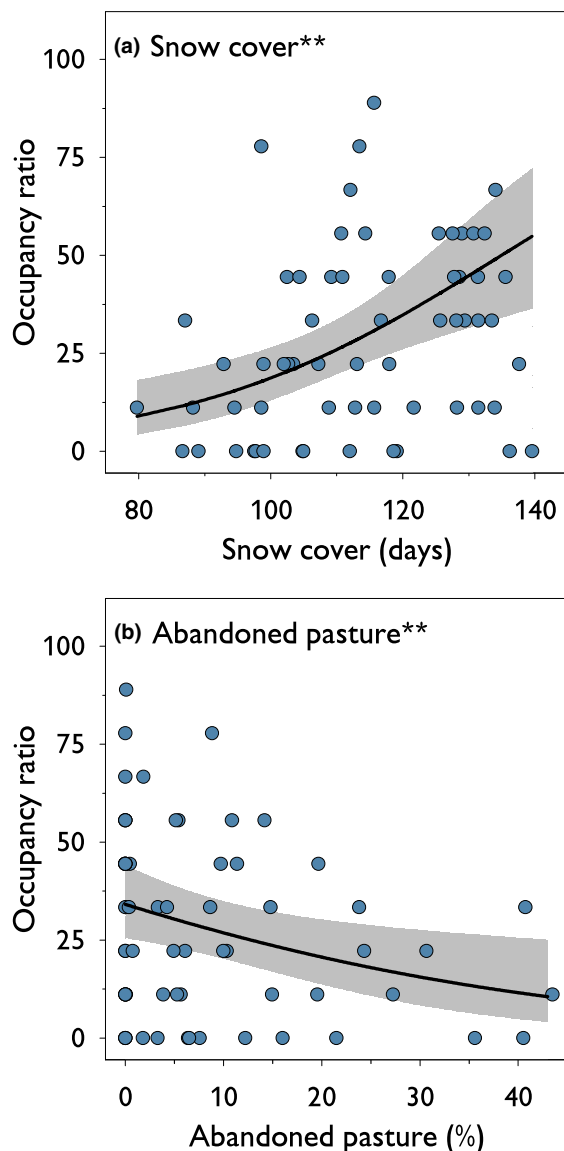
Parameter	1987 Est. ± se	P	2017 Est. ± se	P	Colonization Est. ± se	P	Extinction Est. ± se	P
(a) Climate model	R^2_c = 0.19, R^2_m = 0.17		R^2_c = 0.21, R^2_m = 0.18		R^2_c = 0.48, R^2_m = 0.23		R^2_c = 0.15, R^2_m = 0.12	
Intercept	−0.40 ± 0.16	*	−0.88 ± 0.18	***	−1.43 ± 0.25	***	0.97 ± 0.21	***
TPI	0.41 ± 0.11	***	0.32 ± 0.13	**	1.04 ± 0.23	***	−0.5 ± 0.2	*
Elevation	.	.	.	.	.	.	−0.42 ± 0.18	*
Snow-cover duration	.	.	0.47 ± 0.16	**	.	.	.	.
(b) Habitat model	.	.	R^2_c = 0.23, R^2_m = 0.15		R^2_c = 0.4, R^2_m = 0.11		R^2_c = 0.08, R^2_m = 0.07	
Intercept	.	.	−0.98 ± 0.24	***	−1.41 ± 0.38	***	0.79 ± 0.19	***
Coniferous forest	.	.	.	.	0.63 ± 0.19	**	.	.
Deciduous forest	.	.	−0.33 ± 0.14	*	.	.	.	.
Abandoned pasture	.	.	−0.34 ± 0.15	*	.	.	.	.
Forest-edge length	.	.	.	.	0.37 ± 0.18	*	−0.47 ± 0.18	**
Highly frequented area	.	.	−0.37 ± 0.16	*	.	.	.	.
(c) Synthesis model	.	.	R^2_c = 0.27, R^2_m = 0.21		R^2_c = 0.36, R^2_m = 0.31		R^2_c = 0.16, R^2_m = 0.13	
Intercept	.	.	−0.94 ± 0.2	***	−1.4 ± 0.24	***	0.93 ± 0.21	***
TPI	.	.	.	.	1.01 ± 0.22	***	−0.43 ± 0.22	*
Elevation	.	.	.	.	.	.	−0.5 ± 0.19	*
Snow-cover duration	.	.	0.66 ± 0.19	***	.	.	.	.
Coniferous forest	.	.	.	.	0.53 ± 0.19	**	.	.
Abandoned pasture	.	.	−0.42 ± 0.16	**	.	.	.	.
Forest-edge length	.	.	.	.	0.39 ± 0.18	*	.	.

Model-averaged coefficients (full average) derived from the top-ranked models (ΔAIC_C < 3). Occupancy ratio was analysed via a GLMM with proportional binomial error structure, with number of occupied grid cells per plot as response variable and sub-area (n = 7) as a random factor. Colonization and extinction models were analysed via a GLMM with binomial error structure, occupancy status of grid cells as response variable and plot (n = 62) nested in sub-area (n = 7) as random factors. All fixed effects were standardized prior to the analyses. For each average model, Nakagawa's conditional (R^2_c) and marginal (R^2_m) pseudo-R^2 of the respective best single model is presented. *P < 0.05. **P < 0.01. ***P < 0.001.

TPI, were among the most important environmental variables in all multivariate models of our study and indicated a positive effect of long-persisting snow on the Ring Ouzel.

The Ring Ouzel is a cold-adapted species restricted to mountain ranges. Like other mountain species, it is potentially highly vulnerable to climate warming, which might have caused the observed range retraction through uphill shifts at the lower distribution boundary (e.g. Stuhldreher & Fartmann 2018, Ewing *et al.* 2020). The mechanisms driving such range shifts and retractions can differ strongly across different taxa. Whereas poikilothermic species, such as invertebrates, might be affected by climate change immediately, e.g. through accelerated metabolism (e.g. Stuhldreher *et al.* 2014, Stuhldreher & Fartmann 2018), homoiothermic species should rather be affected by changes in the complex ecological networks of which they are part.

In spring, we often observed Ring Ouzels feeding in moist microhabitats with short vegetation that had only recently become free of snow. Especially during the breeding season, Ring Ouzels mainly feed on earthworms and other below-ground invertebrates (Glutz von Blotzheim & Bauer 1988). For hunting Ring Ouzels, a key property of soils is thus their penetrability, which depends largely on their moisture content (Barras *et al.* 2019). Slowly melting snowfields imbue subjacent and surrounding soils at a fairly constant rate, rendering them suitable hunting grounds. Due to the fast runoff and the mostly shallow soils, the continuous water supply is of particular interest in mountainous areas: the soil penetrability is probably driven to a much greater extent by the snowpack than by precipitation. Additionally, it has been shown that invertebrate activity and density is particularly high shortly after thaw (Harry *et al.* 2019). A strong dependence of foraging Ring

Figure 4. Relationship between occupancy ratio and the significant parameters of the averaged synthesis model. n_{plots} = 62. The regression slopes were fitted using multivariable predictor GLMMs with proportional binomial error structure (see Table 2). **$P < 0.01$.
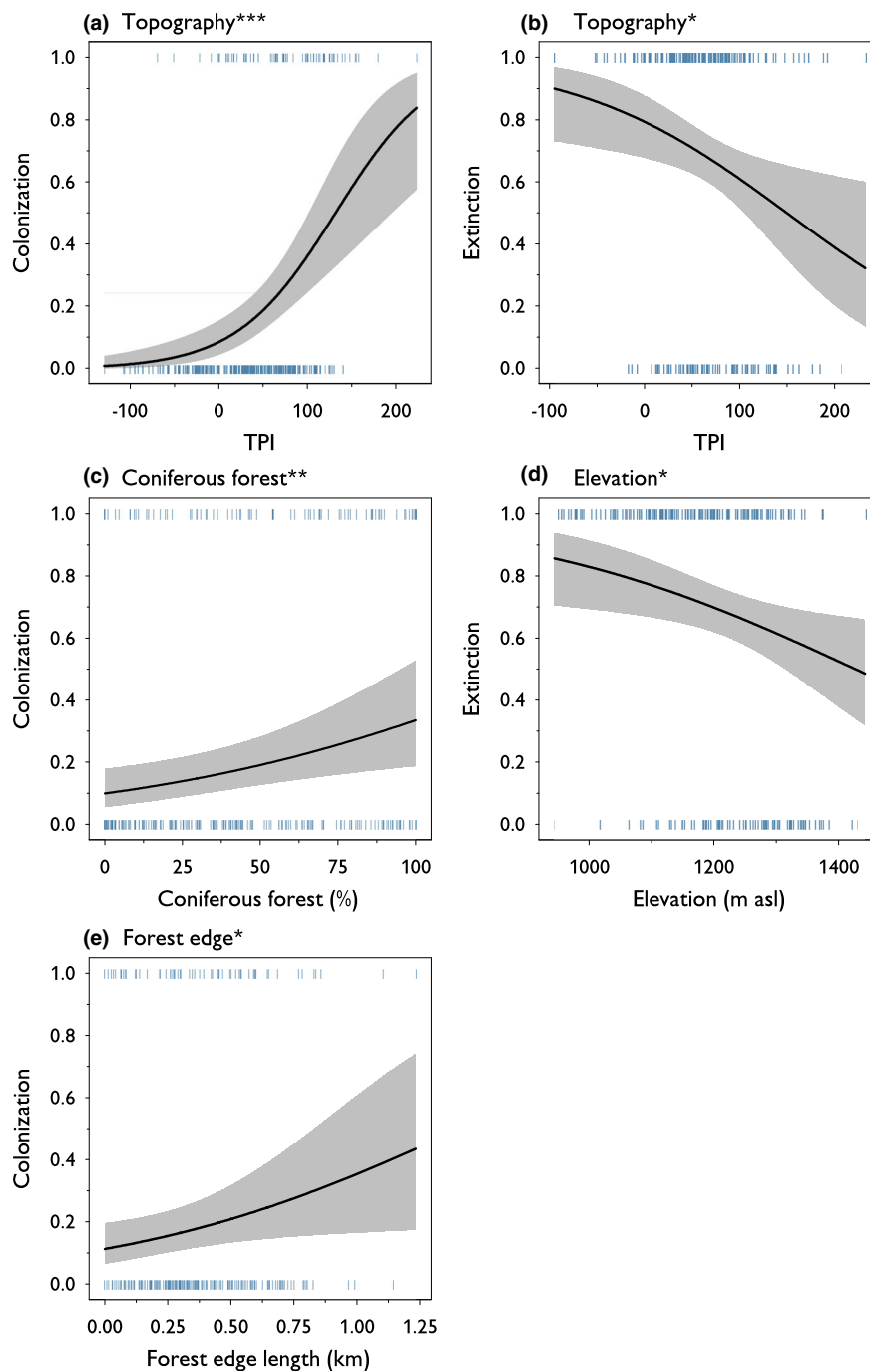
developments have great potential to affect the breeding success of the species negatively. We conclude that the ever-earlier thaw of snow fields is probably one of the main reasons for the observed decline of the species at lower elevations and in depressed landforms.

Snow is an important, yet perhaps underestimated environmental factor (but compare e.g. Stuhldreher *et al.* 2014). Among the species adapted to cold environments, the Ring Ouzel is thus probably not an exception with respect to its dependency on long snow-cover duration. In the study area, other endangered cold-adapted species such as the Moorland Clouded Yellow *Colias palaeno* or the Citril Finch *Carduelis citronella* may also depend on long periods of snow cover. Further examples of possible snow cover–areal relationships include the Eurasian Dotterel *Charadrius morinellus* (Ewing *et al.* 2020) and the Woodland Ringlet *Erebia medusa* (Stuhldreher *et al.* 2014, Stuhldreher & Fartmann 2018). Future research should thus focus more on the impact of advanced thawing.

The Ring Ouzel is known to be a characteristic breeding bird of mosaics of sparse montane conifer forests with semi-open and open habitats (Schirutschke 2005, Bauer *et al.* 2013). In agreement with this, the occupancy ratio was positively related to conifer forests and glades, whereas deciduous forests and abandoned pastures were avoided. Among these four predictors, the cover of abandoned pastures was the only significant variable in the synthesis model. The fine-scale models on local colonization and extinction indicated that the forest-edge length is another decisive habitat factor for territory establishment, underpinning the specialization of the species on ecotones.

Alpine Ring Ouzels build their nests in coniferous trees. Feeding, however, mainly takes place in open habitats (Glutz von Blotzheim & Bauer 1988, Ciach and Mrowiec, 2013, Barras *et al.* 2019). We frequently observed hunting Ring Ouzels in grasslands with short-growing, sparse vegetation; high-growing grasslands were avoided. These observations are in line with the findings from the Carpathians (Ciach & Mrowiec, 2013) and Alps (Barras *et al.* 2019). Similar feeding behaviour has also been reported for the subspecies *T. t. torquatus* in Scotland (Burfield 2002). Low-growing, sparsely vegetated grasslands are characteristic of traditional grassland

Ouzels on patches with short swards and moist soils, which appear in the vicinity of snow beds after snow melt, has also been reported for the Swiss Alps (Barras *et al.* 2019). In the face of climate change, snow fields with their important foraging habitats disappear earlier in spring. Additionally, reduced precipitation rates generally lead to drier, less penetrable soils. These

Figure 5. Relationship between recent grid-cell occupancy of historically vacant grid cells (colonization models; a, c and e) and historically occupied grid cells (extinction models; b and d) with the significant parameters of the averaged synthesis model. n_{colo} = 337, n_{exti} = 221. The regression slopes were fitted using multivariable predictor GLMMs with binomial error structure (see Table 2). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

management, which has increasingly been abandoned in European mountain areas (Caraveli 2000, MacDonald *et al.* 2000), including the Black Forest (Landesanstalt für Umweltschutz Baden-Württemberg 2004, Geis *et al.* 2013, Ministerium für Ländlichen Raum und

Verbraucherschutz 2016). The abandoned pastures, and also those which are grazed only sporadically, in the study area were characterized by dense and tall swards and partly encroached by shrubs (F. Fumy & T. Fartmann pers. obs.). These grasslands are thus probably of low importance for feeding Ring Ouzels. The abandonment of traditional grazing similarly threatens several other bird species which also require short-growing, sparsely vegetated feeding grounds, such as the Common Wheatear *Oenanthe oenanthe*, the Meadow Pipit *Anthus pratensis*, the Rock Bunting *Emberiza cia*, the Tree Pipit *Anthus trivialis*, the Water Pipit *Anthus spinoletta* and the Woodlark *Lullula arborea* (Ebenhöh 2003, Landesanstalt für Umweltschutz Baden-Württemberg 2004, Bauer *et al.* 2013). In contrast, land-use intensification played a minor role in our study area and seems mainly to impact lower-elevation sites in the Black Forest (Fumy *et al.* 2020).

Close vicinity of feeding grounds (short-growing grasslands) with coniferous trees which serve as song posts and nest-sites probably facilitates successful breeding. This assumption is supported by the importance of forest-edge length in our analyses for local habitat colonization and extinction. Long forest-edge length (up to 1.2 km in a plot of 250 × 250 m) indicates a strong interconnection of forest and open land. As a consequence of landscape homogenization in the course of land-use change, the extent of such ecotones has been greatly reduced in Central Europe (Poschlod 2017). Not as much is known about the effects of ecotone loss on biodiversity in general. However, it seems obvious that the numerous species specialized on these complex habitats – such as the Ring Ouzel – could be affected negatively.

Besides the effects of climate change and habitat alteration by land-use abandonment, disturbance by humans can also affect bird species (Monz *et al.* 2013, Coppes *et al.* 2017). We observed a negative relationship between occupancy ratio and areas that were highly frequented by tourists. Hence, the ever-increasing touristic activity (e.g. e-Mountainbiking and 'premium mountain huts') indeed may be an additional driver of the species' decline. This assumption is supported by Anger *et al.* (2020), who linked the abandonment of the most important, traditional breeding sites of Ring Ouzels in the northern Black Forest to the installation of touristic attractions.

To sum up, we have strong indications that both climate and land-use change were responsible for the habitat loss of the Ring Ouzel in the study area. We consider long-persisting snow fields as key requisites for foraging during spring and early summer, and hence for the breeding success of the species. Due to climate change, snow-cover duration decreased substantially between 1987 and 2017. As a consequence, the species retreated to higher elevations and to the most exposed sites with plentiful snow. At the same time, the abandonment of grazing reduced the extent of short-growing, sparsely vegetated grasslands, which are the main feeding grounds of the species. The presence of touristic infrastructure further limited the availability of breeding habitats.

Implications for conservation

For the conservation of the Ring Ouzel, we recommend measures to mitigate the negative effects of climate change and to improve the quality of the habitats. In the Black Forest and many other low mountain ranges, the Ring Ouzel already occupies the highest elevations (Knoch 1970, Mann 1990, Knaus *et al.* 2018) and further uphill shifts in response to climate change are impossible. Accordingly, the creation or maintenance of suitable habitat should be supported, especially on north- and east-facing slopes on the lee sides of hills, mountain peaks or ridges (Streitberger *et al.* 2016, Stuhldreher & Fartmann 2018). In general, we recommend the maintenance and creation of small-scale mosaics of conifer forests and pastures. Within the forests, sparse stands should be established. Grassland management must include the re-introduction of regular livestock grazing without the application of fertilizers, preferably with traditional local breeds (e.g. 'Hinterwälder'). Areas with appropriate habitat configuration and long-lasting snow-cover should be protected from excessive visitor numbers in spring and early summer. Such measures should foster not only the Ring Ouzel but also a large set of other mountain taxa (Braunisch *et al.* 2014, Knaus *et al.* 2018, Barras *et al.* 2019, Fumy *et al.* 2020).

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AUTHOR CONTRIBUTION

Florian Fumy: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (equal); Software (lead); Validation (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (equal). **Thomas Fartmann:** Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Project administration (equal); Supervision (lead); Validation (equal); Visualization (supporting); Writing-review & editing (equal).

Data Availability Statement

The data collected in this study are available on request from the authors.

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Appendix 1. Climate and occupancy patterns. Significant relationships of climate parameters with historical (1987) and recent (2017) occupancy ratio of the 62 study plots, local colonization (n_{grid} cells = 337) and local extinction (n_{grid} cells = 221). Occupancy ratio was analysed via univariate GLMMs with proportional binomial error structure, number of occupied grid cells per plot as response variable and sub-area ($n = 7$) as a random factor. Colonization and extinction models were analysed via univariate GLMMs with binomial error structure, occupancy status of grid cells as response variable and plot ($n = 62$) nested in sub-area ($n = 7$) as random factors. All fixed effects were standardized prior to the analyses. *P*-values were obtained from likelihood ratio tests comparing model fits for each parameter with the intercepts-only model via analysis of variance (ANOVA).

Parameter	1987				2017			
	Est. ± se	*P*	R^2_c	R^2_m	Est. ± se	*P*	R^2_c	R^2_m
Spring temperature	−0.31 ± 0.15	*	0.09	0.03	−0.57 ± 0.15	***	0.14	0.09
Spring precipitation	0.38 ± 0.12	**	0.06	0.04	0.63 ± 0.12	***	0.13	0.12
Snow-cover duration	0.36 ± 0.14	*	0.12	0.08	0.59 ± 0.18	***	0.19	0.12
Elevation	0.5 ± 0.16	**	0.12	0.07	0.62 ± 0.17	***	0.17	0.13
TPI[a]	0.43 ± 0.11	***	0.11	0.05	0.36 ± 0.12	**	0.1	0.03

[a]Topographical position index (TPI) values ranged from −48 to 148 m. Negative values indicate grid-cells that are situated lower than the surrounding landscape (e.g. valleys or depressions). Positive values indicate hills, mountain peaks or ridges surmounting the adjacent landscape. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
Nakagawa's conditional (R^2_c) and marginal (R^2_m) pseudo-R^2 are presented.

Appendix 2. Habitat characteristics and occupancy patterns. Relationship of habitat parameters with recent occupancy ratio (n_{plots} = 62), local colonization (n_{grid} cells = 337) and local extinction (n_{grid} cells = 221). Occupancy ratio was analysed via univariate GLMMs with proportional binomial error structure, number of occupied grid cells per plot as response variable and sub-area (n = 7) as a random factor. Colonization and extinction models were analysed via univariate GLMMs with binomial error structure, occupancy status of grid cells as response variable and plot (n = 62) nested in sub-area (n = 7) as random factors. All fixed effects were standardized prior to the analyses. *P*-values were obtained from likelihood ratio tests comparing model fits for each parameter to the intercepts-only model via ANOVA.

Parameter	Occupancy ratio				Colonization				Extinction			
	Est. ± se	*P*	R^2_c	R^2_m	Est. ± se	*P*	R^2_c	R^2_m	Est. ± se	*P*	R^2_c	R^2_m
Habitat type												
Forest	0.22 ± 0.13	0.09	0.16	0.01	0.3 ± 0.14	0.09	0.28	0.03	0.15 ± 0.18	0.41	0.01	0
Coniferous forest	0.37 ± 0.11	***	0.2	0.04	0.55 ± 0.17	***	0.31	0.14	−0.14 ± 0.16	0.38	0.01	0
Deciduous forest	−0.38 ± 0.14	**	0.22	0.04	−0.39 ± 0.17	*	0.32	0.09	0.29 ± 0.16	0.06	0.04	0.03
Glade	0.3 ± 0.1	**	0.16	0.03	0.07 ± 0.21	0.73	0.27	0	−0.05 ± 0.11	0.64	0.01	0
Open land	−0.28 ± 0.13	*	0.17	0.02	−0.3 ± 0.14	0.08	0.29	0.03	−0.14 ± 0.18	0.44	0.01	0
Nutrient-poor pasture	−0.09 ± 0.13	0.49	0.16	0	−0.28 ± 0.14	0.11	0.29	0.02	−0.24 ± 0.19	0.2	0.02	0.01
Abandoned pasture	−0.34 ± 0.14	*	0.15	0.07	−0.05 ± 0.13	0.79	0.27	0.01	0.11 ± 0.21	0.61	0.02	0
Improved grassland	−0.22 ± 0.16	0.14	0.15	0.01	−0.1 ± 0.14	0.57	0.27	0	0.03 ± 0.6	0.96	0.01	0
Copse	0.13 ± 0.11	0.24	0.16	0	0.1 ± 0.15	0.5	0.28	0	0.06 ± 0.17	0.71	0.01	0
Other habitats[a]	−0.18 ± 0.16	0.23	0.16	0.05	−0.22 ± 0.18	0.24	0.29	0.02	0.46 ± 0.5	0.31	0.02	0.01
Habitat diversity (*H'*)	0.08 ± 0.11	0.51	0.16	0	−0.11 ± 0.13	0.77	0.28	0	0.01 ± 0.16	0.95	0.01	0
Forest-edge length	−0.14 ± 0.12	0.23	0.17	0	0.23 ± 0.13	*	0.27	0.08	−0.29 ± 0.15	*	0.1	0.09
Highly frequented area[b]	−0.39 ± 0.13	**	0.13	0.04	−0.44 ± 0.21	*	0.29	0.08	0.23 ± 0.21	0.25	0.02	0.01

[a]Built-up areas, roads and water bodies. [b]Buffer of 150 m around managed and 15 m around private mountain huts; *P < 0.05.; **P < 0.01; ***P < 0.001.
Nakagawa's conditional (R^2_c) and marginal (R^2_m) pseudo-R^2 are presented.

Appendix 3. Results of Spearman rank correlations (r_s) among climate parameters in the historical period. Variables with strong intercorrelations ($|r_s| \geq 0.5$) are in bold type. For further information, see Statistical analysis.

Variable	TPI	Precipitation	Temperature	Snow cover
Elevation	0.38[ns]	0.24[ns]	**−0.90[***]**	**0.89[***]**
TPI	/	0.16[ns]	−0.13[ns]	0.20[ns]
Precipitation	.	/	−0.36[ns]	−0.42[ns]
Temperature	.	.	/	**−0.96[***]**

TPI, topographical position index; ns, not significant *P > 0.05*; ***P < 0.001.

Appendix 4. Results of Spearman rank correlations (r_s) among environmental parameters in the recent period. Variables with strong intercorrelations ($|r_s| \geq 0.5$) are in bold type. For further information, see Statistical analysis.

Parameter	TPI	Preci	Temp	Snow	Forest	ConFo	DecFo	Glade	OpenL	NpPas	APas	lGras	Copse	OHab	H'	FoLeng	HfArea
Study plots																	
Elevation	0.38ns	0.69***	−0.91***	0.92***	−0.14ns	0.21ns	−0.48ns	0.14ns	0.17ns	0.22ns	0.35ns	−0.53***	0.03ns	−0.10ns	0.11ns	0.13ns	−0.07ns
TPI	/	0.27ns	−0.20ns	0.19ns	0.27ns	0.29ns	−0.14ns	0.07ns	−0.25ns	−0.17ns	−0.07ns	−0.36ns	−0.17ns	−0.30ns	0.06ns	−0.25ns	−0.31ns
Precipitation	.	/	−0.75***	0.71***	−0.04ns	0.15ns	−0.30ns	0.32ns	0.07ns	0.20ns	0.16ns	−0.45ns	0.00ns	−0.28ns	0.17ns	0.13ns	−0.16ns
Temperature	.	.	/	−0.97***	0.21ns	−0.15ns	0.45ns	−0.18ns	−0.24ns	−0.29ns	−0.38ns	0.43ns	−0.07ns	0.09ns	−0.11ns	−0.17ns	0.03ns
Snow-cover duration	.	.	.	/	−0.27ns	0.12ns	−0.50***	0.14ns	0.29ns	0.37ns	0.33ns	−0.47ns	0.16ns	−0.09ns	0.14ns	0.21ns	−0.01ns
Forest	.	.	.	.	/	0.63***	0.34ns	0.39ns	−0.99***	−0.85***	−0.54***	0.31ns	−0.53***	−0.28ns	−0.16ns	−0.69***	−0.52***
Coniferous forest	.	.	.	.	.	/	−0.44ns	0.41ns	−0.64***	−0.55***	−0.29ns	−0.29ns	−0.30ns	−0.19ns	−0.25ns	−0.46ns	−0.36ns
Deciduous forest	.	.	.	.	.	.	/	−0.14ns	−0.35ns	−0.29ns	−0.27ns.	0.09n.s	−0.23ns	0.02ns.	0.17n.s	−0.16ns	−0.11ns
Glade	.	.	.	.	.	.	.	/	−0.38ns	−0.27ns	−0.16ns	−0.32ns	−0.25ns	−0.30ns	0.09ns	−0.21ns	−0.23ns
Open land	.	.	.	.	.	.	.	.	/	0.87***	0.53***	0.29ns	0.53***	0.22ns	0.16ns	0.68***	0.48***
Nutrient-poor pasture	.	.	.	.	.	.	.	.	.	/	0.22ns	0.09ns	0.58***	0.02ns	0.29ns	0.64***	0.32ns
Abandoned pasture	.	.	.	.	.	.	.	.	.	.	/	0.05ns	0.07ns	0.25ns	0.20ns	0.39ns	0.37ns
Improved grassland	.	.	.	.	.	.	.	.	.	.	.	/	0.14ns	0.26ns	−0.21ns	0.23ns	0.28ns
Copse	.	.	.	.	.	.	.	.	.	.	.	.	/	0.14ns	0.34***	0.52***	0.34ns
Other habitats	.	.	.	.	.	.	.	.	.	.	.	.	.	/	−0.12ns	0.20ns	0.65***
Habitat diversity (H')	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.43n.s	0.08n.s
Forest-edge length	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.42n.s
Grid cells: colonization																	
Elevation	0.46***	.	.	.	−0.11*	0.11*	−0.36***	−0.01ns	0.14*	0.11*	0.26***	−0.41***	−0.03ns	−0.1ns	−0.31***	0.03ns	−0.13*
TPI	/	.	.	.	0.16**	0.21***	−0.14*	0ns	−0.12*	−0.15**	0.05ns	−0.28***	−0.12*	−0.2***	−0.31***	−0.14*	−0.24***
Forest	.	.	.	.	/	0.63***	0.47***	0.33***	−0.96***	−0.77***	−0.48***	−0.31***	−0.41***	−0.28***	−0.26***	−0.43***	−0.4***
Coniferous forest	.	.	.	.	.	/	−0.25***	0.37***	−0.63***	−0.54***	−0.21**	−0.18**	−0.22**	−0.17**	−0.24***	−0.16*	−0.23***
Deciduous forest	.	.	.	.	.	.	/	0.13*	−0.45***	−0.32***	−0.32***	−0.07ns	−0.26***	−0.09ns	0.3***	−0.12*	−0.18**
Glade	.	.	.	.	.	.	.	/	−0.47***	−0.38***	−0.19***	−0.15*	−0.17*	−0.16**	0.15**	−0.11*	−0.22***
Open land	.	.	.	.	.	.	.	.	/	0.81***	0.5***	0.31***	0.34***	0.23***	0.21***	0.47***	0.37***
Nutrient-poor pasture	.	.	.	.	.	.	.	.	.	/	0.11*	0.06ns	0.34***	0.12*	0.23***	0.42***	0.26
Abandoned pasture	.	.	.	.	.	.	.	.	.	.	/	0.11*	0.11	0.19***	0.14**	0.37***	0.22**

(continued)

Appendix 4.   (continued)

Parameter	TPI	Preci	Temp	Snow	Forest	ConFo	DecFo	Glade	OpenL	NpPas	APas	IGras	Copse	OHab	H'	FoLeng	HfArea
Improved grassland	.	.	.	.	.	.	.	.	.	.	.	/	0.07^{ns}	0.33^{***}	0.44^{**}	0.17^{**}	0.37^{***}
Copse	.	.	.	.	.	.	.	.	.	.	.	.	/	0.11^{*}	0.27^{***}	0.39^{***}	0.08^{ns}
Other habitats	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.16^{*}	0.13^{*}	0.64^{***}
Habitat diversity (H')	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.54^{***}	0.15^{**}
Forest-edge length	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.18^{***}
Grid cells: extinction																	
Elevation	0.21^{**}	.	.	.	-0.4^{***}	0.05^{ns}	-0.46^{***}	0.03^{ns}	0.39^{***}	0.31^{***}	0.43^{***}	-0.25^{***}	0.09^{ns}	0.08^{ns}	-0.06^{ns}	0.36^{***}	0.17^{*}
TPI	/	.	.	.	-0.11^{ns}	-0.04^{ns}	-0.03^{ns}	0.07^{ns}	0.05^{ns}	0.04^{ns}	0.05^{ns}	-0.18^{**}	0.03^{ns}	-0.1^{ns}	0.04^{ns}	0^{ns}	-0.13^{ns}
Forest	.	.	.	.	/	0.53^{***}	0.29^{***}	-0.04^{ns}	-0.81^{***}	-0.73^{***}	-0.54^{***}	-0.1/	-0.34^{***}	-0.24^{***}	-0.49^{***}	-0.67^{***}	-0.25^{***}
Coniferous forest	.	.	.	.	.	/	-0.53^{***}	0.16^{*}	-0.46^{***}	-0.45^{***}	-0.29^{***}	-0.07^{ns}	-0.24^{***}	-0.12^{ns}	-0.66^{***}	-0.33^{***}	-0.17^{*}
Deciduous forest	.	.	.	.	.	.	/	-0.06^{ns}	-0.25^{***}	-0.2^{*}	-0.24^{***}	0.02^{ns}	-0.09^{ns}	-0.08^{ns}	0.48^{***}	-0.15^{*}	-0.06^{ns}
Glade	.	.	.	.	.	.	.	/	-0.4^{***}	-0.36^{***}	-0.23^{***}	-0.17^{**}	-0.03^{ns}	$-0.$/	0.12^{ns}	-0.34^{***}	-0.06^{ns}
Open land	.	.	.	.	.	.	.	.	/	0.89^{***}	0.65^{***}	0.2^{**}	0.25^{***}	0.22^{**}	0.33^{***}	0.87^{***}	0.2^{**}
Nutrient-poor pasture	.	.	.	.	.	.	.	.	.	/	0.35^{***}	0.15^{*}	0.27^{***}	0.21^{**}	0.36^{***}	0.75^{***}	0.16^{*}
Abandoned pasture	.	.	.	.	.	.	.	.	.	.	/	0^{ns}	0.15^{*}	0.17^{**}	0.17^{*}	0.57^{***}	0.26^{***}
Improved grassland	.	.	.	.	.	.	.	.	.	.	.	/	$-0.$/	0.0/	0.16^{*}	0.21^{**}	-0.02^{ns}
Copse	.	.	.	.	.	.	.	.	.	.	.	.	/	0.3^{***}	0.31^{***}	0.26^{***}	0.21^{**}
Other habitats	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.19^{**}	0.26^{***}	0.62^{***}
Habitat diversity (H')	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.38^{***}	0.17^{*}
Forest-edge length	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	/	0.24^{***}

APas, abandoned pasture; ConFo, coniferous forest; DecFo, deciduous forest; Elev, elevation; FoLeng, forest length; HfArea, area highly frequented by tourists; IGras, improved grassland; NpPas, nutrient-poor pasture; OHab, open habitat; OpenL, open land; Preci, precipitation; Snow, duration of snow cover; Temp, temperature; TPI, topographical position index. ns, (not significant); *$P<0.05$; **$P < 0.01$; ***$P<0.001$