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at the home range and landscape scales

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ABSTRACT

Mountain ecosystems are facing various threats, notably rapid climate and land use changes. Knowledge about the ecology of species living at high-elevation is usually insufficient to properly predict their response to the new drivers impacting their habitat. This represents a serious impediment to develop effective, spatially-explicit conservation programmes. In particular, we lack a mechanistic understanding of species-habitat relationships at multiple spatial and temporal scales. We investigated the habitat selection of the Alpine Ring Ouzel, a declining and threatened bird species of timberline ecosystems. The main objective was to identify the factors driving both territory (home range) selection and variation in population density across space and time. A second, methodological aim was to compare the performance of field-collected vs remote-sensed data for developing appropriate predictive, mechanistic habitat suitability models. We mapped habitat characteristics (field surveys) in 47 landscape units of 1 km^2 (W Swiss Alps) for which data about presence, population density and demographic trend were available from nation-wide monitoring schemes. If field-collected data better predicted territory selection, population density was better predicted by either remote-sensed data alone, or a combination of both field and remote-sensed information. The main results were that: 1) Ring Ouzels selected areas characterised by short and sparse ground vegetation; 2) open and/or steep habitat offering wet and relatively nutrient-poor soil conditions supported higher population density; 3) the proportion of pasture and unproductive land positively influenced demographic trends. From a mechanistic viewpoint, many of these factors link to the previously evidenced foraging requirements of Alpine Ring Ouzel, notably in terms of prey availability (abundance mediated by accessibility). Important for informing conservation, these results attest that climate and land use changes both exert an impact on Ring Ouzel occurrence, density and population trend.

Key words : alpine ecosystem – climate – land use – multi-scale – conservation

INTRODUCTION

Mountainous regions host a rich and unique biodiversity across the world, but these habitats are highly threatened by diverse factors. The most commonly cited driver is climate change, with its known effects on range shrinkage, e.g. by impacting individual fitness or species interactions (La Sorte & Jetz 2010; Scridel *et al.* 2018). In temperate mountain ecosystems, land use change is also a threat, affecting habitat heterogeneity through the intensification of the most productive zones and the abandonment of the less accessible ones (Laiolo *et al.* 2004; Sirami *et al.* 2017; Lehikoinen *et al.* 2019). As well, the increase of year-round leisure activities throughout the year put these regions at risk (Arlettaz *et al.* 2007; Patthey *et al.* 2008). In Europe, the Alps represent a biodiversity hotspot, so that alpine countries share the responsibility to conserve and manage mountainous ecosystems appropriately. Within those habitats, the timberline ecotone is one of the most biodiversity rich, but one subject to rapid changes, primarily due to the strong increase in land abandonment leading to encroachment (Bolliger *et al.* 2007; Gehrig-Fasel, Guisan & Zimmermann 2007; Price *et al.* 2015) but also due to its predicted upward shift under rising temperatures (Carlson *et al.* 2017). Therefore, one can expect an evident reduction of the timberline ecotone surface at higher elevations due the mountains' pyramidal shape. Moreover, it is unlikely that whole communities will simply shift upwards since species-specific reactions to these drivers may differ in space and time (Reif & Flousek 2012; Scridel *et al.* 2018). Therefore, beyond predictions about broad-scale future species distributions according to climate and land use scenarios (Maggini *et al.* 2011; Geary *et al.* 2015), there is a need to understand the mechanisms of species-habitat interactions occurring at multiple scales. Such information is still largely lacking and it prevents to precisely define targeted management measures and their spatial priority (Arlettaz *et al.* 2012; Braunisch, Patthey & Arlettaz 2016).

The Ring Ouzel (*Turdus torquatus*) is part of these species inhabiting mountains and confronted with those threats. It is declining across some parts of its breeding range, such as the UK (Wotton, Langston & Gregory 2002) where several studies were undertaken (Beale *et al.* 2006; Sim *et al.* 2007), and Switzerland, where it is on the list for the development of a recovery programme with the highest level of priority (Keller *et al.* 2010). Indeed, Switzerland, where this species has faced an important decline since the 1990s, hosts 15% of the European breeding population (Knaus *et al.* 2018). This concerns the subspecies *T.t. alpestris,* that also occurs in other mountain ranges in central Europe, and inhabits open forests and the timberline ecotone as described by a few studies on its ecology (von dem Bussche *et al.* 2008; Ciach & Mrowiec 2013). Yet, no recovery programme has been formulated, so that it appears crucial to study more in depth the mechanisms driving its habitat selection at several scales.

Multi-scale studies help to understand the habitat selection processes of a species according to environmental factors occuring at one or several spatial or temporal scales, which is even more important for highly mobile species living in heterogenous habitats (Johnson *et al.* 2004), like Ring Ouzels do. Indeed, habitat selection is a hierarchical process that intervenes at multiple levels (Mayor *et al.* 2009; Apolloni *et al.* 2018; Fattebert *et al.* 2018). The smallest scales about foraging site and patches selection, respectively orders 3 and 4 following the definition of Johnson (1980), give information about mechanisms driving habitat selection and essential ecological needs (Brambilla *et al.* 2018). In a recent study on the Ring Ouzel, these small scales were investigated and revealed the high importance of prey availability driven by soil conditions, ground cover and vegetation structure, all showing marked seasonality patterns (Barras *et al.* 2019). Nevertheless, studies about its habitat selection at larger scales in central Europe are too rare to completely understand its ecology (but see von dem Bussche *et al.* 2008; and Ciach & Mrowiec 2013). At the home range scale (order 2), the individual or pair will try to find an habitat of the best quality for a succesful reproduction, taking into account various envionmental cues, such as predation pressure or food and nesting site availability (Coudrain, Arlettaz & Schaub 2010; Bosco *et al.* 2019). Understanding these functional species-habitat associations helps to define targeted habitat management for species conservation. Studying habitat selection at the largest scale (order 1) allows to know how a population settled across a landscape, which is useful to refine habitat management and particularly to prioritize it spatially (Braunisch, Patthey & Arlettaz 2016).

Moreover, when it comes to identifying habitat preferences of a species, it is crucial to choose the type of data that best fits the focus scale, either acquired from the field (FD) or from remote sensed methods (RSD) (Jähnig *et al.* 2018). Indeed, data collected in the field offers a better precision on environmental factors intervening at fine spatial and temporal scales and a good coverage of small areas but is hard to obtain on larger zones as it is time consuming to collect. Data extracted from remote sensed methods allows covering large areas, provides a better general view about landscape composition and can be used for predictions according to future scenarios or for spatial prioritization. However, there is a risk to miss some important fine-grained information. It is really valuable to compare FD and RSD performance at several scales to possibly identify remote sensed factors that can be used as good proxies for data collected in the field, and thus have easily accessible and area-wide data that is ecologically meaningful (Braunisch, Patthey & Arlettaz 2016).

The first aim of this study was to define the Ring Ouzel's breeding habitat preferences at the larger spatial scales. As a second aim, we wanted to compare the performance to predict habitat selection of both FD and RSD explanatory factors, as well as the combination of both. At the home range scale, we thus analysed the occurrence probability to investigate the best predictors of habitat selection with both FD and RSD. At the landscape scale, we studied Ring Ouzels population density with the two types of data as well. We also looked for predictors of population trend, this time only with RSD. In the western Swiss Alps, we selected squares (1 km^2) within the set of the national breeding birds surveys areas, from which we had species count data. In those, we collected habitat information in the field (FD) and extracted RSD from available environmental GIS layers. Finally, the general aim of the study was to shed some light on the reasons behind the species decline in order to define targeted management and spatial priority for its conservation.

MATERIAL & METHODS

Study Area

The study was conducted in the western Swiss Alps within the Ring Ouzel's altitudinal breeding range (1300-2200 m a.s.l.). This area is divided into two biogeographic regions: the northern Alps (including the Prealps) and the central Alps (Fig. 1). The northern Alps are under oceanic climatic influence with a mean temperature of -1.7°C in January and 14.2°C in July at Adelboden (1'327 m a.s.l.) (Federal Office of Meteorology and Climatology 2016) with more than 1'200 mm/year of precipitation at 1000 m a.s.l. (Ott *et al.* 1997). The dominant winds come from the north and west and the subalpine forest is dominated by spruce (*Picea abies*) that co-exists with fir (*Abies alba*) at lower elevations (Ott *et al.* 1997). The central Alps are mostly protected by the alpine massif which leads to a continental climate with a lower precipitation regime, between 600 and 900 mm/year at 1000 m a.s.l (Ott *et al.* 1997) and mean temperature of -1.6°C in January and 14.9°C in July at Montana (1'427 m a.s.l.) (Federal Office of Meteorology and Climatology 2016). There, spruce and larch (*Larix decidua*) dominate the subalpine region. They are replaced by Swiss stone pine (*Pinus cembra*) and mountain pine (*Pinus mugo*) at higher elevations, while lower down there are mostly forests with Scotch pine (*Pinus sylvestris*) (Ott *et al.* 1997).

Species data

The dataset on Ring Ouzel observations was collected within the Swiss breeding bird Atlas survey (Atlas) and the monitoring of the common breeding birds (MHB) by numerous volunteers, under the supervision of the Swiss Ornithological Institute (SOI). We also used precise sightings of the species submitted on the ornitho.ch platform.

The MHB is a national survey following standardized methods, on 267 squares of 1 km^2 systematically distributed over the country. The squares are visited three times per year (two for the high elevation ones) since 1999. At each visit, the observer follows a fixed transect, the same every year and crossing the different habitats covering the square and reports every observation (visual or auditive) of all bird species as a precise point on a map. After the three visits and for each species, the observer groups his observations (only the ones corresponding to criteria that ensure a breeding event) into territories according to his knowledge about the species, km^2 specificities and his observations details (like two males singing at the same time). Finally, the SOI controls and corrects the territory delimitation in a standardized manner. This simplified territory mapping protocol is described in detail in Kery, Royle & Schmid (2005),

The Atlas is also a monitoring scheme running systematically over the country every 20 years since 1973-76. During the last period (2013-2016), 2'318 km^2 (including the major part of the MHB squares) were visited. The same methods as for the MHB are used but the 3 visits per km^2 are done in only one year during an Atlas period of 4 years (Knaus *et al.* 2018).

For the home-range analysis, we thus used the precise observation points from both of these surveys and from submitted sightings on ornitho.ch for the 10 last years during the breeding peak from May to June (Appendix A.1). For the landscape scale analysis, we first used the estimated density of the period 2013-2016, i.e. the raw number of Ring Ouzels' territories assessed in a visited km^2 for the Atlas or MHB. We retained the mean density over this period for squares that were visited more than once. In addition, we also considered an estimate of the population trend over the last 20 years. For this, we used the difference between the modelled densities in the Atlas period 1993-96 and 2013-16 (Appendix A.2 and A.3), and not between estimated densities because those of the first period were truncated to a maximum of 10 territories. The density was modelled by the SOI using a binomial mixture model taking into account the species-specific detection probability, a set of environment variables and spatial autocorrelation, in order to maximise the predictive performance over Switzerland (see Guelat & Kery 2018; and Knaus *et al.* 2018). In summary, we worked with a binomial variable of presence/absence at the home range scale and retained the estimated density from standardized surveys along with the modelled population trend for the landscape scale analyses.

Km^2 selection

In order to define habitat suitability at both scales, we chose 47 km^2 visited within the Atlas or MHB surveys and widespread across the study area (Fig. 1). We stratified our selection according to the modelled density in 2013-16 (Appendix A.2), the population trend (Appendix A.3) and the elevation (Appendix B.1) in order to have a representative sample of the Ring Ouzel's habitat and distribution range. For the km^2 selection only, we used the modelled density instead of the estimated density. We first categorized squares into high and low density, with a threshold at the median (= 4) of all surveyed km2 with more than 2 territories/km^2 over Switzerland (Appendix B.2). Squares were further categorized into decreasing population trend (density difference < -1) or stable or increasing (≥ -1) (Appendix B.3). To select squares with a decline, we did not allow the 95% CI to cross zero, so that our selection was more robust. We thus ended up with four categories (low and stable density, low and decreasing, high and stable, high and decreasing) and with a similar altitudinal gradient for each of them. The last criteria were the accessibility and the distance for fieldwork feasibility. For the analysis on population trend, 105 additional km^2 were selected to increase our sample size so that 152 km^2 were considered in the analysis (Fig. 1).

Environmental data collection

Each of the selected 47 km^2 was split into 16 quadrats of 200x200m (4 ha) after the exclusion of a 100m width internal buffer (Fig. 2). Field data (FD) was collected in 8 of those quadrats arranged in a checkerboard pattern, and two of them were retained for the home range analysis, one as a presence and one as a pseudo-absence. This selection was based on the distribution of observations of potential breeding birds from the past 10 years, with the presence containing the highest density of observation points and the pseudo-absence no observation at all (Fig. 2). The area of the quadrat approximates well the size of a home range in the Alps (Barras, unpublished data), but to be conservative, we did not allow a presence and a pseudo-absence to be contiguous. Remote-sensed data (RSD) was prepared at two resolutions: 200m for the home range analysis and 1km for landscape scale models.

<u>Occurrence probability at the home range scale</u>

To obtain the FD at the home range scale, we mapped the habitat at the presence and pseudo-absence quadrats (Fig. 2) of each selected km^2 according to a predefined set of environmental variables (Table 1). Before the mapping, we played a tape luring of the fledgling's distress call to make a supplementary control of occurrence and to ensure that the pseudo-absence quadrat was not occupied. We also played this tape in the 6 other quadrats to assess presence, so that we could find a replacement pseudo-absence when the first one turned out to be a false absence. Then, we measured the environmental variables over different reference areas on the quadrat to best describe the habitat (Table 1): in a 50m radius and in two 20x20m plots (one centred and one at 50m distance with a random bearing), in which some variables were also measured on two 10x10m diagonal subplots (Fig. 2). For the analysis, we used the mean between the two 20x20m plots within one quadrat. We measured variables linked to the vegetation layers' composition and structure, like the forest, bush or grassland cover. We also mapped the ground cover, particularly the variables influencing the ground accessibility, like bare ground/ litter or grass/forbs covers and ground vegetation patchiness or height. The land use state was also considered, through the grazing intensity or the cover of shrub, re-generation and bushes, because in abandoned lands, woody plants and trees grow again and their covers increase. Moreover, as the soil conditions appeared to be im-portant for the foraging habitat selection (Barras *et al.* 2019), we investigated the soil wetness and nutrient content. These two variables were qualitative and related to the Landolt's values of some predefined widespread plant species (Appendix C.3). In addi-tion, only at this scale, we measured the soil moisture and penetrability in the 2 diagonal subplots. (following Barras *et al.* 2019). In the analysis, we also tested the addition of a quadratic term of some variables for which we hypothesized a unimodal response: soil moisture and hardness, accessible ground cover, ground vegetation cover and canopy cover.

In addition to FD, we prepared a set of RSD with three categories: climate, topography and land cover (Table 2). Precipitation and temperature data was obtained from World-Clim (www.worldclim.org) with a resolution of 1km. All topography data was extracted from a digital elevation model (DEM) of 25m resolution (from the Swiss Federal Office of Topography, SwissTopo). The land cover data came from the Swiss Map Vector 25 BETA (rasterized to 25x25m; SwissTopo), but the cover of meadow, pasture and unpro-ductive land was calculated with land use data of the Swiss Federal Statistical Office at 100m resolution and masked with the cover of other soils from the Vector 25 to increase the precision. We aggregated all these layers as raster maps of 200m resolution taking the mean values (Appendix C.2).

For the analysis, the variables with more than 70% of zero values were set as binary, presence/absence factors (1/0), and we removed the marginal ones (> 90% zero values) (Appendix C.1 and C.2). The variables indicating a cover were arcsine-square-root trans-formed and we standardized the whole set of explanatory variables.

Estimated population density at the landscape scale

For the FD at the landscape scale, we also mapped the 6 other 200x200m quadrats of each km^2 with the same methods as for the home range scale, but only the middle 20x20m plot per quadrat was mapped (Fig. 2) and without measuring soil moisture and penetrability (Table 1). For the statistics, we used the common habitat variables meas-ured in all 8 quadrats (including the presence/pseudo-absence ones) and we took the median values of each factor per km^2 (Appendix C.1). Here, the median value seemed more representative as there was often a high heterogeneity within a km^2. Moreover, as we expected that the heterogeneity of the habitat could play an important role, we also calculated the median absolute deviation (MAD) for some variables like the vegetation cover or the grazing intensity, which composed one additional category in this dataset (Table 1).

We used the same set of RSD as for the home range scale and added a mineral category with the cover of limestone bedrock, scree, rock and anthropogenic area (Table 2) Here, all the RSD were aggregated to a resolution of 1km considering the mean (Appendix C.2), and for the same reason as above, we also calculated the standard deviation for some variables about vegetation covers, composing another category in this dataset too (Table 2). The variable transformation followed the one explained for the home range scale.

Population trend at the landscape scale

Since the modelled population trends partially depended on RSD, the comparison between the predictive ability of FD and RSD was not meaningful in this case. For this model, we therefore used only RSD - the same as in the analysis on estimated density (Table 2) - that we also prepared for the 105 additional km^2 (Appendix C.2), increasing our sample size to 152 km^2.

Statistical analysis

Occurrence probability at the home range scale

To investigate home range selection, we compared the habitat factors (FD and RSD) between the presence and the pseudo-absence quadrats (Fig. 3), so at a 200m resolution. With this binomial response variable, we used a hierarchical logistic regression for the habitat selection model; we thus performed a generalized linear mixed effect model (GLMM) with a binomial error distribution and a logit link function (Arlettaz *et al.* 2012). We used the function *glmer* from the lme4 R-package (Bates *et al.* 2015) to run this analysis. The habitat characteristics were our explanatory variables and we set the km^2 identity as random effect to avoid non-independence of the data from a quadrat pair.

Estimated population density at the landscape scale

We aimed to investigate which environmental characteristics drive the Ring Ouzel's population density at the landscape scale, at 1km resolution. Therefore, we carried out modelling processes with the estimated density according to our FD and RSD as explanatory sets, on the 47 km^2 selected (Fig. 3). We used generalized linear models with a normal distribution (GLMM) and not Poisson, since averaged densities over several years were sometimes non-integer values. The response variable was thus log-transformed to fit a normal distribution. The models were performed with the *glm* function from the stats R-package (R Core Team 2017).

Population trend at the landscape scale

To better understand the reasons behind the Ring Ouzel's decline, we performed a model on the population trend according to RSD from the 152km^2 (Fig. 3). The population trend response variable was continuous and followed a left-skewed negative distribution; to make it correspond to a normal distribution, we applied the following transformation: $\sqrt{(maximum\ trend\ value + 0.001) - trend}$. Furthermore, we had a higher amount of squares, some close to each other and we suspected that spatial autocorrelation could be a problem. The calculation of the Moran's I factor on the full generalized linear model showed a strong spatial autocorrelation (p-value < 2.2 e^{-16}), so that we opted for a linear model using generalized least squares (*gls* function) from the nlme package (Pinheiro & Bates 2019) taking into account this autocorrelation. To find the appropriate correlation structure class, we built a full model without correlation structure and 5 others with the available classes (gaussian, spherical, exponential, linear and rational). Then, we compared them with *anova* function from the stats package (R Core Team 2017) and we opted for the gaussian class as it had the lowest AICc.

Model selection process

For both presence/absence and estimated density as response variables, we went through two first model selection processes: one with the FD and one with the RSD as explanatory factors. For the population trend model, we ran the selection only with RSD only (Fig. 3). The model selection was the same for each dataset type. Due to the large number of explanatory variables, each set was further divided into categories to ease the selection process (Table 1 & 2). Per category, we removed variables with a high Spearman correlation coefficient ($|r_s|$> 0.65), keeping the factor with the lowest p-value in the univariate models. In each model fitted with variables of one category, we checked for variance inflation factor (VIF) <3, removing the variable with the highest VIF until all VIFs went under this threshold. Thereafter, on each of those models, we used the *dredge* function from the MuMIn package (Bartoń 2018) which computed a list of all candidate models ranked by their AICc (Akaike Information Criterion with correction for small samples). We selected the best ranked models, keeping only those with ΔAICc < 2 from the best one, and removing those with uninformative parameters (Arnold 2010). As a last step, we ran a model with all variables retained in the best-models set of each category and once again, we performed the same selection process with the *dredge* function. Finally, we used the function *model.avg* from the MuMIn package (Bartoń 2018) to obtain the conditional averaged model from this last candidate models sets (from the ΔAICc < 2). After this selection, we obtained two final models (one with FD and one with RSD) for both the occurrence probability and the estimated density, and only one (with RSD) for the population trend. For the two former analyses, we computed a third selection for the combined models, i.e. containing all the explanatory factors retained in the first selection step of both FD and RSD models (Fig. 3). We used the same process as before, checking the correlation coefficient and the VIF, then ran the *dredge* process and averaged the candidate models set. To assess the performance of the various models obtained (FD, RSD and combined models) for occurrence probability and estimated density, we calculated the adjusted R-squared (adj R^2) using the function *r.squaredGLMM* from the MuMIn package (Bartoń 2018) and the AICc value for models within the ΔAICc < 2 sets. At the end, we plotted each response variable according to the significant explanatory factors. For the occurrence probability and the estimated density, we drew the joint posterior distribution with the arm package (Gelman & Su 2018) and 10'000 simulations (*sim* function) using the conditional averaged models predictions. This method (following Burnham & Anderson 2002), taking into account the quantity of samples per model and model weights, computes the model-averaged posterior distribution with the 95% credible interval of the variable of interest while the others are set to their mean. For the population trend, we used the *predict* function of the stats package (R Core Team 2017) that draws the 95% confidence intervals from the averaged model too. We used the software R 3.3.3 (R Development Core Team 2018) for all the analysis.

RESULTS

We visited 47 km^2 between 1'312 and 2'121 m a.s.l and collected the habitat variables in the field between the end of May and mid-July. Within them, we mapped 45 presence and 42 pseudo-absences quadrats. On those km^2, we also extracted the RSD at the home range (200m) and landscape scales (1km). Moreover, we prepared RSD on the 105 additional km^2 for the population trend analysis on the 152 km^2. The distribution of the km^2 can be found in Figure 1.

Occurrence probability at the home range scale

Using FD, the ΔAICc < 2 set contained 3 models (Table 3.1.A) with 4 explanatory variables: the cover of bushes, edge presence, ground vegetation patchiness and height. The best model explained a relatively low proportion of variance (adj R^2 = 0.24) and its AICc was 112. From the averaged model (Table 4.1.A), the ground vegetation patchiness (average estimate $\pm$ SD; 0.60 $\pm$ 0.27 and P = 0.027) and height (- 0.66 $\pm$ 0.27 and P = 0.015) were the two most important variables (importance value = 1 for both), showing the Ring Ouzel's preference for shorter and patchy ground vegetation (Fig. 4). The bush cover had a marginal but positive effect (0.46 $\pm$ 0.25 and P = 0.075).

Regarding the model with RSD, 3 models were in the ΔAICc < 2 too but with only 2 variables (Table 3.1.B). Here, the best model had a very low performance according to the adj R^2 = 0.06 and the AICc value was substantially higher than the best FD model (122). Moreover, in the averaged model, the elevation (0.40 $\pm$ 0.23 and P = 0.084) and the presence of meadows (- 1.11 $\pm$ 0.64 and P = 0.09) had only a marginal impact on the occurrence probability (Table 4.1.B). At this scale, the RSD had a very low prediction ability unlike FD.

Finally, the combined model with FD and RSD had 9 candidate models in its ΔAICc < 2 set with the 2 same predictors as the RSD model and the 4 from the FD one (Table 3.1.C). The best model explained a similar proportion of variance than the FD model (adj R^2 = 0.26) and the AICc value was also close (111). In the averaged model, the presence of an edge (0.95 ± 0.54 and P = 0.082) influenced marginally the Ring Ouzel's presence, but the ground vegetation height and patchiness were still the most important variables (1 and 0.88) (Table 4.1.C). As the candidate models of the combined model were quite numerous with an output similar to the model with only FD and that the model with RSD had a very low performance, the FD was the best predictor of occurrence at the home range scale.

Estimated population density at the landscape scale

With FD, 3 models remained in the ΔAICc < 2 set with 4 variables and the best model had a low performance regarding the adj R^2 = 0.19 (Table 3.2.A). The AICc value of the best candidate model was 101. At this scale, the grazing heterogeneity (MAD) (estimate ± SD; 0.17 ± 0.10 and P = 0.11) and vegetation height (- 0.17 ± 0.10 and P = 0.09) were both retained, but showed no significant effect in the averaged model. The soil wetness and nutrient content were the most important predictors (importance value = 1 for both) (Table 4.2.A).

Only one model was retained in the ΔAICc < 2 set with the RSD and contained 3 factors (Table 3.2.B). This model predicted better the estimated population density than with FD (adj R^2= 0.27, AICc = 96). The mean precipitation during the breeding season showed a strong positive impact (0.30 ± 0.10 and P = 0.003). It appeared that the cover of open forest (0.20 ± 0.09 and P = 0.036) and the slope steepness (0.24 ± 0.10 and P = 0.014) had a positive influence too. (Table 4.2.B and Fig. 5). Moreover, at this scale, RSD performed better than at the home range scale.

Lastly, the output of the combined model's selection contained only one model too, with 1 variable from RSD and 2 from FD (Table 3.2.C). Its performance was similar to the model with RSD only (adj R^2= 0.28, AICc = 95). Here, the two factors linked to the soil condition (wetness and nutrient content) came up again with the same effects: negative for the nutrient content (- 0.34 ± 0.11 and P = 0.004) and positive for the wetness (0.29 ± 0.11and P = 0.012). The population density was significantly higher where the soil conditions were moderately wet and nutrient poor (Fig. 6.1 and 6.2). A predictor that was not retained in the RSD model, the cover of limestone bedrock, showed a strong positive relationship (0.27 ± 0.09 and P = 0.007) with the population density (Table 4.2.C and Fig. 6.3). As the model with RSD and the combined one were the most performant, we consider both of them as equivalent for the prediction of population density at this scale. However, the model with FD only performed rather badly so that RSD appears as the best predictor at this scale.

Population trend at the landscape scale

For the model on population trend, 2 models stayed in the $\triangle$AICc < 2 set with 3 environmental factors (Table 3.3). From the averaged model, the cover of open forest had a marginal negative effect (average estimate $\pm$ SD; - 0.03 $\pm$ 0.02 and $P = 0.087$). The 2 other factors were linked to the land use and impacted positively the population trend (Fig. 7): the proportion of pasture (0.05 $\pm$ 0.02 and $P = 0.008$) and unproductive land (0.06 $\pm$ 0.02 and $P = 0.004$) (Table 4.3).

DISCUSSION

In this study, we used a multi-scale approach to characterize the breeding habitat selection of Ring Ouzels in the western Swiss Alps. In particular, we investigated which environmental factors best describe occurrence probability at the home range scale, as well as population density and trend at the landscape scale. Moreover, we highlighted that field collected data performed better at the smaller scale while remote sensed variables or a combination of both were better predictors of patterns at the larger scale. Within the home range, the ground vegetation structure, through patchiness and height, was the most important factor. Concerning the landscape scale, the soil conditions and the habitat heterogeneity through forest openness and slope steepness appeared crucial to support higher population densities. Finally, a high proportion of pasture and unproductive land seemingly influence positively the population trends.

In our study, we used presence/absence data, raw density estimates and modelled densities taking into account spatial autocorrelation and imperfect detectability. We have to recall that the raw population estimated densities can be easily underestimated due to the discrete behaviour of the species (Kery, Royle & Schmid 2005), but we didn’t expect detectability to change a lot between the squares, so that relative differences would be equivalent. Moreover, as the aim was to understand the ecological reasons behind density differences across the landscape, and not to make realistic projections of density over Switzerland, the use of this data was appropriate in this form. Concerning modelled densities, those represented the only way to get an estimate of population trend, as Atlas data from the previous period was collected in a slightly different manner. Since those densities predictions were modelled using environmental variables present in our RSD, comparison between FD and RSD performance was not possible in this case. It was also hard to completely take into account the spatial autocorrelation for this model. Furthermore, population trend does not seem independent from density, since decline occurs mostly in the regions with high densities. We thus have to be careful when interpreting the results about population trend.

This study underlines the importance of choosing the appropriate type of data (RSD or FD), i.e. the one that best fits the focus scale, to identify habitat preferences (Jähnig *et al.* 2018). Actually, field mapping produces more precise data, but is time consuming, especially in harsh environment like mountains. On the other hand, remote sensed variables are quite easy to collect and allow covering large regions, but they often offer incomplete information about precise features. The most efficient technique would be to identify RSD that can be used as reliable proxies (i.e. substitute variables) for FD. From this study, it appeared that FD predicted better the Ring Ouzel's presence at the home range scale, whereas the population density at the landscape scale was better explained either by RSD or a combination with FD. This confirms the difficulty to predict precise features at a small scale with remote sensed methods. We could identify a potential proxy at the landscape scale: the precipitation amount during the breeding season had a similar effect on the estimated density as the soil wetness assessed in the field and both were positively correlated ($r_s = 0.49$). However, at the home range scale, the RSD had a very low predictive ability overall and no predictors appeared as a reliable proxy of important FD variables. Looking across scales, it is possible that the slope steepness revealed at the landscape scale reflects the higher availability of patchy and short ground vegetation identified as important at the home range scale.

Several factors linked to the soil characteristics appeared as crucial for Ring Ouzels' habitat selection. These particularities have been shown to be relevant habitat features for several other bird species foraging on the ground (Patthey *et al.* 2012; Brambilla *et al.* 2017; Salek, Zeman & Vaclav 2019). One underlying mechanism could be the soil accessibility, through the relationships with ground vegetation patchiness and height at the home range scale, which confirms findings at the foraging scale on Ring Ouzels populations from the UK (Burfield 2002), the Carpathians (Ciach & Mrowiec 2013) and the Alps (Barras *et al.* 2019). Indeed, the grassy patches act as a reservoir where soil invertebrates are more abundant while they are easier to catch on bare areas (Arlettaz *et al.* 2012; Leal *et al.* 2019). In addition, soil accessibility is as well increased in the selected short grass swards, as already highlighted for other alpine species (Brambilla *et al.* 2018). It is likely that the ground vegetation structure, and therefore soil accessibility, act as an environmental cue when choosing the home range, as a signal of food availability. The fact that this species-habitat relationship is still detected at larger scales may indicates that it is particularly crucial for Ring Ouzels habitat selection.

The soil conditions through the wetness and the nutrient content at the landscape scale were also identified as crucial predictors. The soil moisture importance was already highlighted at the foraging scale (Barras *et al.* 2019) and for other thrush species like the song thrush *Turdus philomelos* (Peach, Robinson & Murray 2004). Actually, earthworms constitute the major part of the regime of the Ring Ouzel and several other thrush species (Burfield 2002; Maumary, Valloton & Knaus 2007), and their preference for moist soils is well known. As a consequence, they move deeper in the soil during dry periods and reach the surface in wetter soil or after rainfalls (Onrust *et al.* 2019). They are thus more accessible for the birds when the soil is more humid. The positive influence of the amount of precipitation during the breeding season (still at the landscape scale) also reflects this preference for wetter conditions. Interestingly, the relationship with soil humidity that we detected at the landscape scale was linear, while it was hump-shaped at the foraging site scale (Barras *et al.* 2019). This can be an illustration of the hierarchical habitat selection process, with the bird selecting first regions containing essentials habitat features and then foraging sites with a precise optimum (see Bosco 2014). Concerning the nutrient content in the soil, Ring Ouzels prefer relatively poor soil which supports the population preference to establish in extensively pastured landscape with nutrient poor grassland, assessed in the Alps (see von dem Bussche *et al.* 2008). However, earthworm abundance has been shown to correlate positively with rich soils in alpine grasslands (Steinwandter *et al.* 2019). Although the Ring Ouzel's prey may be more abundant in nutrient-rich soils, the grass layer will also grow denser and higher (Humbert *et al.* 2016), and it is also known that the inputs of organic matters dries out the soil surface (Onrust *et al.* 2019). Both effects may therefore decrease ground invertebrate availability. The influence of these soil conditions on the population density reveals probably the prey availability importance for Ring Ouzels' breeding and thus highlights this essential species-habitat relationship at the landscape scale too.

Ring Ouzels density seemed higher where limestone bedrock was present. The parental substrate influences soil conditions through physical properties, the pH, the availability of essential component (phosphate, nitrogen and potassium) among others (Gobat, Aragno & Matthey 2013). These characteristics drive the vegetation community and thus the next trophic levels. The biological activity is often also stronger on limestone due to the specificities of this bedrock type (Gobat, Aragno & Matthey 2013) which results in the formation of more organic matter and could reflect an abundance of earthworms (Curry 2004). Moreover, some woody plants like blueberry (*Vaccinium myrtillus*) or rhododendron (*Rhododendron ferrugineum*) that often form a dense layer and reduce soil accessibility are not abundant on lime substrate (Ellenberg 1992). However, within the study area, this bedrock type is situated mostly in the northern Alps where precipitation amount is also higher and where the highest population densities occur. Therefore, it is difficult to disentangle the individual effects of these factors, but it is well possible that both play a role.

It has been shown that Ring Ouzels select open and heterogeneous habitat across their breeding range (Sim *et al.* 2007; Ciach & Mrowiec 2013). In the Alps, it typically breeds at the timberline ecotone, where the forest is interspersed with open grasslands (von dem Bussche *et al.* 2008). At the landscape scale, this preference was confirmed by the positive influence of the open forest cover on the estimated density. Nevertheless, it did not appear at the home range scale, maybe because the species does not rely on a particular forest structure within its home range as long as it is within the subalpine belt. Still at the landscape scale, bird abundance was higher in steeper slopes. Those habitats are often not used for pasture or agriculture, but are characterized by a strong natural dynamic driven by the steepness (Salek, Zeman & Vaclav 2019). Indeed, they are often corridors where avalanches prevail in winter or where erosion is strong and the soil layer generally thinner. These parameters prevent upper vegetation layers from developing too high and dense, naturally creating a heterogeneous and open habitat. Ground vegetation is patchier and shorter for the same reasons and this also promotes prey availability. Finally, in the context of land use change, with the decreasing heterogeneity in human modelled areas, the steep slopes offer a less degraded and still heterogeneous habitat.

Looking at the factors influencing the population trend, both pasture and unproductive land covers are linked to land use. Where their proportions were higher, the population seemed more stable. The pasture areas in the Alps are extensively grazed during the summer months, with a clear impact on the ground vegetation and the shrub layers. It artificially maintains the heterogeneity and openness of the habitat (Laiolo *et al.* 2004; Snell, Peringer & Bugmann 2017) like on the steep slopes or at the natural timberline, which is very rare in the Swiss Alps. The areas classified as unproductive are often composed of rocky and less fertile soils, hence harbouring a high heterogeneity, and are less valuable for agriculture although they can be regularly grazed too (e.g. sheep). These areas are however mostly present at high elevations (with a correlation coefficient of r_s= 0.64 between these factors), which makes this relationship more difficult to interpret. Furthermore, the apparent negative effect of the open forest cover on population trend was in contradiction with the positive relationship with the estimated density. The reason could be that the regions supporting the highest densities are also facing the strongest decline.

We could highlight that the Ring Ouzel's breeding ecology in the Alps is closely linked to climate and land use characteristics, in particular through soil characteristics and habitat heterogeneity. Therefore, it is most likely that predicted changes of climate and land use will have an impact on its populations (von dem Bussche *et al.* 2008; Barras *et al.* 2019). Firstly, as the precipitation regime is predicted to increase in winter in the mountains, but more as rain than snow, and to decrease in summer, drier conditions during the breeding season are to be expected (CH2018 2018). Secondly, the increasing land abandonment in the less productive zones associated with intensification at the lower elevations of the range is leading to the homogenization of the habitat (Price *et al.* 2015; OFAG 2017). Indeed, in abandoned pastures, the ground is almost no longer accessible due to the densification of the bush layer. In the intensified zones, the grass layer is densified to increase yield (Humbert *et al.* 2016) which similarly reduces soil accessibility and can increase the soil surface desiccation, that impacts prey availability too.

Since our study represents a basis to a better assessment of the vulnerability of the species in regard to environmental changes and that those are predicted to be amplified in the future (Reif & Flousek 2012), we propose specific management measures to conserve Ring Ouzel's optimal habitat under changing conditions. We therefore suggest focusing Ring Ouzels recovery programme on habitat heterogeneity and in this purpose, to re-adapt the land use practices which could also to some extent buffer the detrimental effects of climate change. Moreover, priority should be put on the less accessible and less productive zones where land abandonment occurs and is predicted to increase (Price *et al.* 2015). A come back to the traditional extensive pasture would favour earthworm abundance providing a bit more soil nutrient than abandoned areas (Steinwandter *et al.* 2019) but less than intensive ones. Cattle will also maintain the ground vegetation patchy and low (Leal *et al.* 2019). This management will slow down forest ingrowth and soil dewatering due to climate change, by keeping habitat open and diversified. Regarding these important factors, it would be complementary to address further studies on relationships between the Ring Ouzel and its staple prey, as well as on predictions according to diverse scenarios of climate and land use changes to better assess the vulnerability and spatially prioritize habitat management. Furthermore, the restoration of habitat heterogeneity within the subalpine belt would potentially profit to a number of other bird species (Patthey *et al.* 2012; Braunisch, Patthey & Arlettaz 2016; Jähnig *et al.* 2018).

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Tables

Table 1 Field predictors (FD) distributed into the categories used for model selection. Factors in italic were measured only in the presence/absence quadrats.

Variables **per category**	Description	Unit	Reference area
Ground cover			
SNOW	Percent of snow	%	10x10m
MOSS	Percent of moss	%	10x10m
REGEN10	Percent of regeneration	%	10x10m
WP10	Percent of woody plants	%	10x10m
STEMS	Percent of stems	%	10x10m
MIN	Percent of rocks and stones	%	10x10m
DW	Percent of deadwood	%	10x10m
OTHER	Percent of other cover	%	10x10m
AG	Percent of accessible ground (bare ground and litter)	%	10x10m
GV	Percent of ground vegetation (grass and forbs)	%	10x10m
Structure < 1.3 m			
GRASS *	Percent of grassland	%	50m radius
REGEN20 *	Percent of regeneration (trees < 1.3m)	%	20x20m
WP20 *	Percent of juniperus, berry bushes and rhododendron	%	20x20m
VEGH	Ground vegetation height	cm	10x10m
PATCH	Ground vegetation pattern: 1 = homogeneous, 2 = clumped, 3 = patchy	1-3	10x10m
Structure > 1.3 m			
EDGE	Edge presence	Yes/No	50m radius
FOR *	Percent of forest	%	50m radius
COMPT	Proportion of coniferous and deciduous tree: 1= only deciduous, 2 = mostly deciduous, 3 = mix, 4 = mostly coniferous, 5 = only coniferous	1-5	50m radius
BUSH *	Percent of bush	%	50m radius
CANOP *	Percent of canopy (>5m)	%	20x20m
SHRUB *	Percent of shrub (1.3m < x <5m)	%	20x20m
Condition			
WET50 *	Soil wetness assessment from 1 = dry to 4 = muddy soil	1-4	50m radius
GRAZ *	Pasture intensity from 1 = no pasture to 5 = intense grazing	1-5	50m radius
NSOIL *	Soil nutrient content index from 1 = very poor to 5 = very fertile soil	1-5	20x20m
WET20 *	Soil wetness index from 1 = dry to 4 = moist soil	1-4	20x20m
MOIST	Soil volumetric water content (moisture)	VWC	10x10m
HARD	Soil penetrability (hardness)	kg/cm^2	10x10m

* Variables for which we also calculated the median absolute deviation to compose the category "heterogeneity" for the model selection at the landscape scale.

Table 2 Remote sensed variables (RSD) distributed into the categories used for model selection. The “mineral” category was used only in the landscape scale models.

Variable **per category**	Description	Unit	Source
Climate + Topography			
PREC57	Mean summer precipitation (May-July)	mm	Worldclim
PREC122	Mean summer precipitation (December-February)	mm	Worldclim
TAVE57	Average summer temperature (May-July)	°C	Worldclim
TAVE122	Average winter temperature (December-February)	°C	Worldclim
ALT	Elevation	m a.s.l	DEM
SLOPE	Slope	degree	DEM
NORTH	Northness (cosine of aspect)		DEM
SOLRAD36	Solar radiation (March-June)	$W*h/m^2$	DEM
Structure < 1.3 m			
MEAD *	Percent of meadow	%	Swiss land use statistics
PAST *	Percent of pasture	%	Swiss land use statistics
UNPROD *	Percent of unproductive land	%	Swiss land use statistics
GRASS	Percent of grassland (sum of MEAD, PAST and UNPROD)	%	Swiss land use statistics
Structure > 1.3 m			
BUSH	Percent of bushes	%	Vector 25
OPEN *	Percent of open forest	%	Vector 25
DENS *	Percent of dense forest	%	Vector 25
FOR *	Percent of forest (sum of OPEN and DENS)	%	Vector 25
LTREE	Treeline length	%	Vector 25
DLTREE	Distance to the treeline	%	Vector 25
NBTREE	Number of solitary trees	n	Vector 25
Mineral			
LIME	Percent of limestone bedrock	%	Vector 25
SCREE	Percent of scree	%	Vector 25
ROCK	Percent of rock	%	Vector 25
ANTHRO	Percent of anthropogenic infrastructures	%	Vector 25

* Variables for which we also calculated the standard deviation to compose the category “heterogeneity” for the model selection at the landscape scale.

Table 3 Candidate models retained in the △AICc < 2 set. For the variable description see Tables 1 and 2. If "01" is added to a name, the variable was set as a binary factor at this scale.

3.1 Models set for the home range scale about occurrence probability with FD, RSD and both.

Rank	**Models on occurrence probability**	K	Deviance	AICc	△AICc	Weight	adj R^2
	A. Field data						
1	BUSH + EDGE + PATCH + VEGH	6	99.26	112.32	0	0.436	0.263
2	BUSH + PATCH + VEGH	5	102.02	112.75	0.44	0.35	0.234
3	PATCH + VEGH	4	105.24	113.74	1.42	0.214	0.194
	B. Remote sensed data						
1	ALT + MEAD01	4	113.9	122.39	0	0.421	0.079
2	MEAD01	3	116.84	123.13	0.74	0.291	0.044
3	ALT	3	116.86	123.15	0.75	0.288	0.0425
	C. Combined model						
1	ALT + EDGE + MEAD01 + PATCH + VEGH	7	95.84	111.26	0	0.186	0.311
2	ALT + EDGE + PATCH + VEGH	6	99.04	112.09	0.83	0.123	0.256
3	ALT + EDGE + MEAD01 + VEGH	6	99.06	112.12	0.86	0.121	0.266
4	EDGE + PATCH + VEGH + BUSH	6	99.26	112.32	1.06	0.11	0.211
5	ALT + MEAD01 + PATCH + VEGH	6	99.34	112.38	1.13	0.106	0.282
6	EDGE + MEAD01 + PATCH + VEGH	6	99.56	112.61	1.35	0.095	0.271
7	ALT + PATCH + VEGH	5	101.9	112.64	1.38	0.093	0.233
8	PATCH + VEGH + BUSH	5	102.02	112.75	1.5	0.088	0.234
9	MEAD01 + PATCH + VEGH	5	102.26	113	1.74	0.078	0.246

3.2. Models set for the landscape scale about the density with FD, RSD or both.

Rank	**Models on estimated density**	K	deviance	AICc	△AICc	weight	adj R^2
	A. Field data						
1	NSOIL + WET20 + VEGH	5	89.38	100.85	0	0.384	0.201
2	NSOIL + WET20 + GRAZ	5	89.66	101.12	0.27	0.336	0197
3	NSOIL + WET20	4	92.52	101.48	0.63	0.281	0.152
	B. Remote sensed data						
1	OPFOR + PREC57 + SLOPE	5	84.96	96.43	0	1	0.269
	C. Combined model						
1	LIME + NSOIL + WET20	5	84.44	95.91	0	1	0.277

3.3 Models set at the landscape scale about the population trend and only with RSD variables.

Rank	**Models on population trend**	K	deviance	AICc	△AICc	weight	adj R^2
	Remote sensed data						
1	OPEN + PAST + UNPROD	7	36.89	51.67	0	0.602	0.899
2	PAST + UNPROD	6	39.92	52.5	0.82	0.398	0.890

Table 4 Regression coefficient, standard error, P value and importance of the variables in the conditional averaged models from the ΔAICc < 2 set.

4.1. Values for the occurrence probability models at the home range scale according to FD, RSD or both

Averaged model: occurrence probability

Response variable	Coefficient	Standard error	P	variable importance
A. Field data				
(Intercept)	-0.183	0.423	0.668	
Bush	0.459	0.254	0.075	0.79
Forest edge (1)	0.85	0.517	0.106	0.44
Patchiness	0.603	0.268	0.027	1
Vegetation height	-0.664	0.268	0.015	1
B. Remote sensed data				
(Intercept)	0.193	0.245	0.437	
Elevation	0.401	0.229	0.084	0.71
Meadow (1)	-1.106	0.644	0.09	0.71
C. Combined model				
(Intercept)	-0.218	0.46	0.639	
Elevation	0.479	0.258	0.067	0.63
Forest edge (1)	0.949	0.537	0.082	0.63
Meadow (1)	-1,286	0.734	0.084	0.59
Patchiness	0.556	0.278	0.049	0.88
Vegetation height	-0.693	0.277	0.014	1
Bush	0.459	0.254	0.075	0.2

4.2 Results for the models about estimated density at the landscape scale with FD, RSD or both.

Averaged model: estimated density

Response variable	Coefficient	Standard error	P	variable importance
A. Field data				
(Intercept)	1.9	0.096	< 0.001	
Soil nutrient content	-0.27	0.122	0.032	1
Soil wetness 20	0.318	0.119	0.01	1
Vegetation height	-0.168	0.098	0.094	0.38
MAD grazing intensity	0.169	0.103	0.11	0.34
B. Remote sensed data				
(Intercept)	1.9	0.091	< 0.001	
Open forest	0.201	0.093	0.036	1
Precipitation (5-7)	0.304	0.096	0.003	1
Slope	0.243	0.095	0.014	1
C. Combined model				
(Intercept)	1.9	0.09	< 0.001	
Limestone	0.267	0.094	0.007	1
Soil nutrient content	-0.342	0.113	0.004	1
Soil wetness 20	0.293	0.112	0.012	1

4.3 Values for the model at the landscape scale about population trend with RSD.

Averaged model: population trend

Response variable	Coefficient	Standard error	P	variable importance
(Intercept)	2,065	0.096	< 0.001	
open forest	-0.033	0.019	0.087	0.64
pasture	0.053	0.02	0.008	1
unproductive land	0.057	0.02	0.004	1

Figure legends

Fig.1 Map of the study area showing: the selected 47km^2 and their respective classification regarding modelled density and trend, the 105 additional km^2 used population trend models and the 2 biogeographic regions considered.

Fig. 2 Schema explaining the field data sampling on a km^2. The 8 200x200m blue quadrats are the mapped ones. The 2 circled are the ones used for the home range analysis: in green the presence and in red the pseudo-absence, which were chosen according to the Ring Ouzels observations (yellow dots). The zoom on a quadrat shows the different reference areas used for habitat mapping: 50m radius in green; in orange, the 20x20m plot in which ground cover variables were sampled in two diagonal subplots of 10x10m, the central plot (A) was mapped in the 8 quadrats while the offset one (B) was only sampled on the 2 presence/absence quadrats.

Fig. 3 Schematic representation of the different fitted models according to the scales, the responses variables and the sets of the environmental factors. In green, the 7 types of models built in this study.

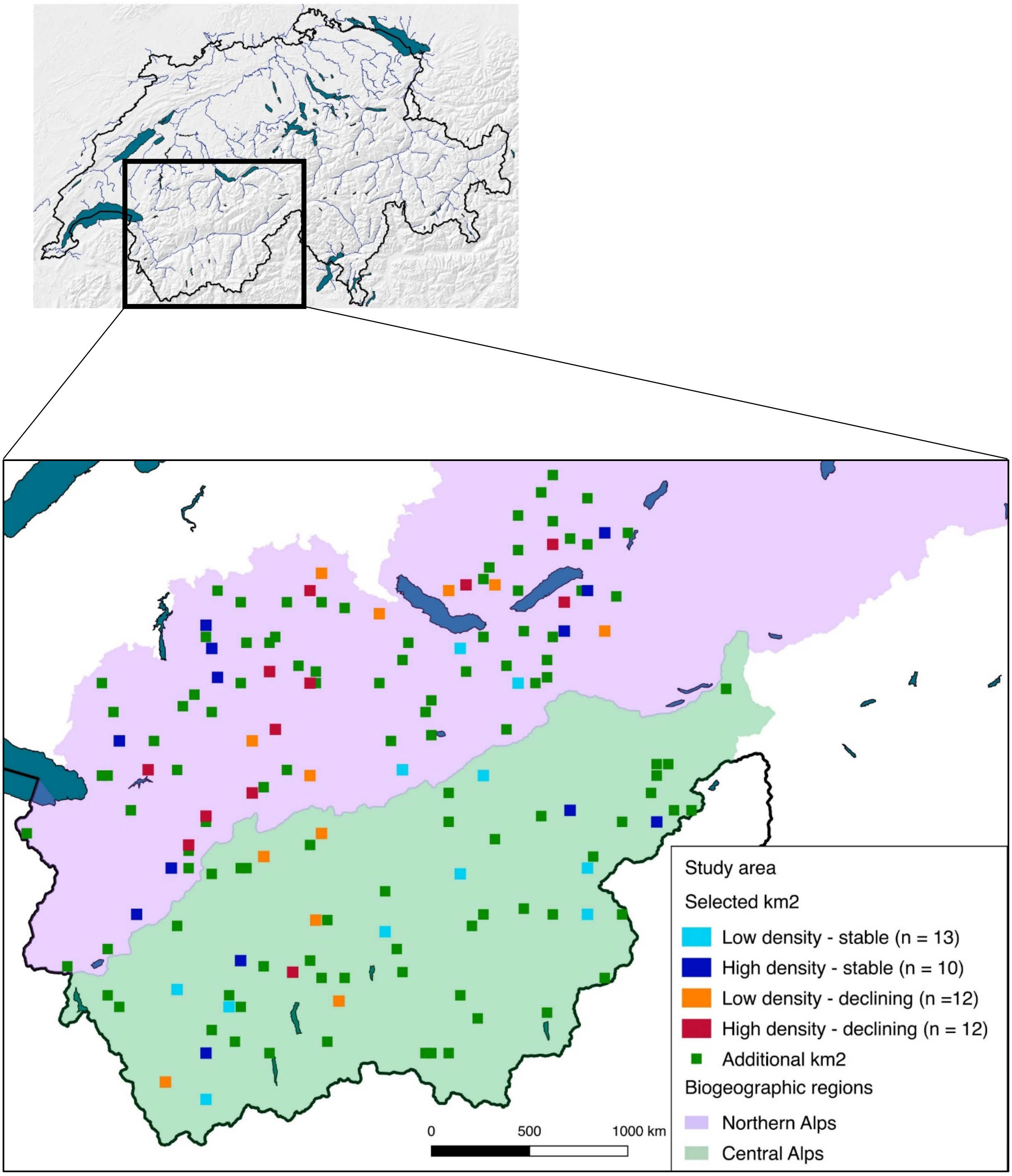
Fig.4 Plots of estimates from the conditional averaged model with FD for the two variables with a significant effect according to occurrence probability, at the home range scale. The 95% credible intervals are in grey around the regression line and the red dashed lines correspond to the neutral selection: above the selection is positive and negative below.
4.1 Shows the relation with the ground vegetation height in cm and **4.2** with the ground vegetation patchiness from 1(homogeneous) to 3 (patchy).

Fig. 5 Plots of estimates from the conditional averaged model with RSD for the three variables with a significant effect according to estimated population density, at the landscape scale. The 95% credible intervals are in grey around the regression line.
5.1 Shows the relation with the precipitation amount during the breeding season in mm, **5.2** with the proportion of open forest cover in % and **5.3.** with the slope steepness in degrees.

Fig. 6 Plots of estimates from the conditional averaged model with RSD and FD (combined) for the three variables with a significant effect according to the estimated population density, at the landscape scale. The 95% credible intervals are in grey around the regression line.
6.1 Shows the relation with the soil nutrient content from 1 (very poor soil) to 5 (very fertile soil), **6.2** with the soil wetness form 1 (dry soil) to 4 (very moist soil) and **6.3.** with the proportion of limestone bedrock in %.

Fig. 7 Plots of estimates from the conditional averaged model for the two variables with a significant effect according to the population trend, at the landscape scale. The 95% confidence intervals are in grey around the regression line.
7.1 Shows the relation with the proportion of pasture in % and **7.2** unproductive land in %.

Fig.1



Study area
Selected km2
Low density - stable (n = 13)
High density - stable (n = 10)
Low density - declining (n =12)
High density - declining (n = 12)
Additional km2
Biogeographic regions
Northern Alps
Central Alps
0
500
1000 km

Fig. 2

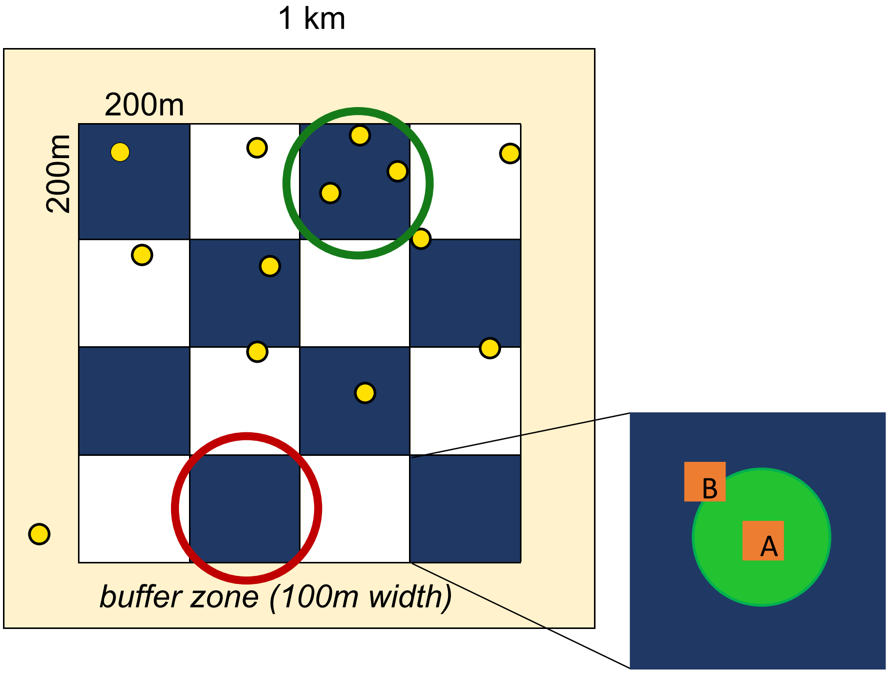


Fig.3

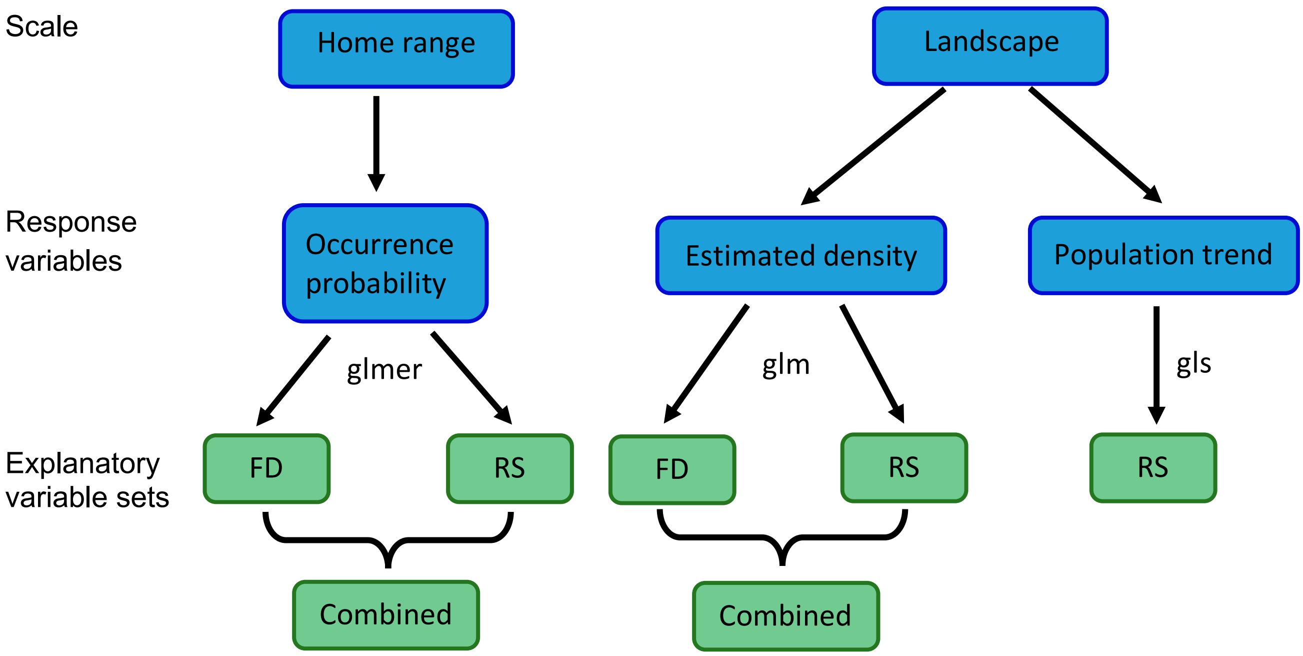
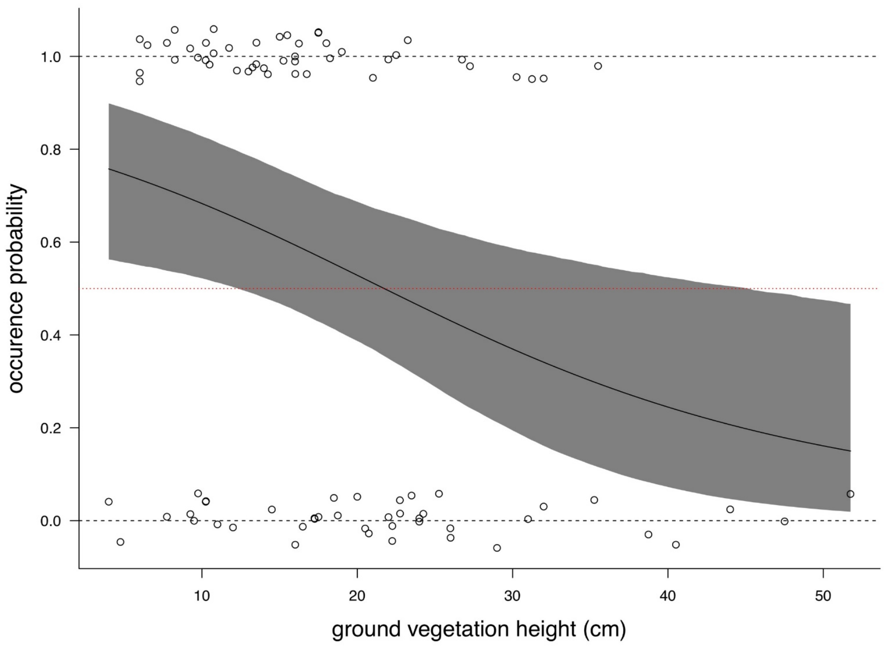

Scale
Home range
Landscape
Response variables
Occurrence probability
Estimated density
Population trend
glmer
glm
gls
Explanatory variable sets
FD
RS
FD
RS
RS
Combined
Combined

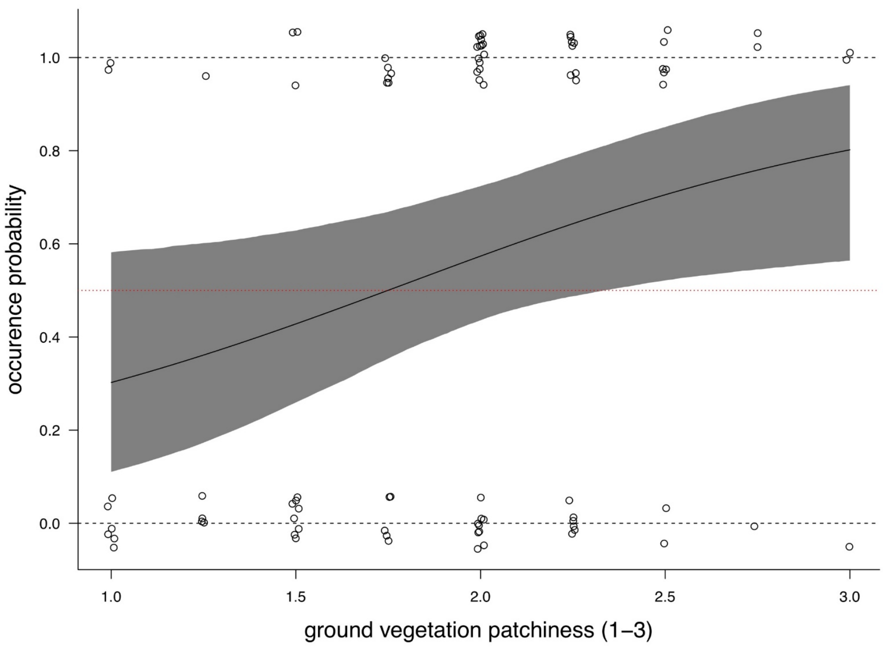
Fig. 4

4.1



1.0
0.8
0.6
0.4
0.2
0.0
occurence probability
10
20
30
40
50
ground vegetation height (cm)

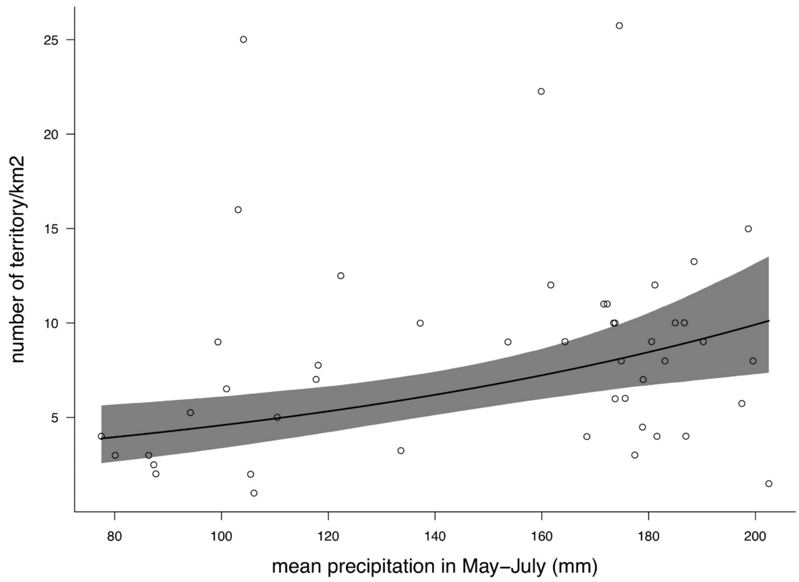
4.2



1.0
0.8
0.6
0.4
0.2
0.0
occurence probability
1.0
1.5
2.0
2.5
3.0
ground vegetation patchiness (1–3)

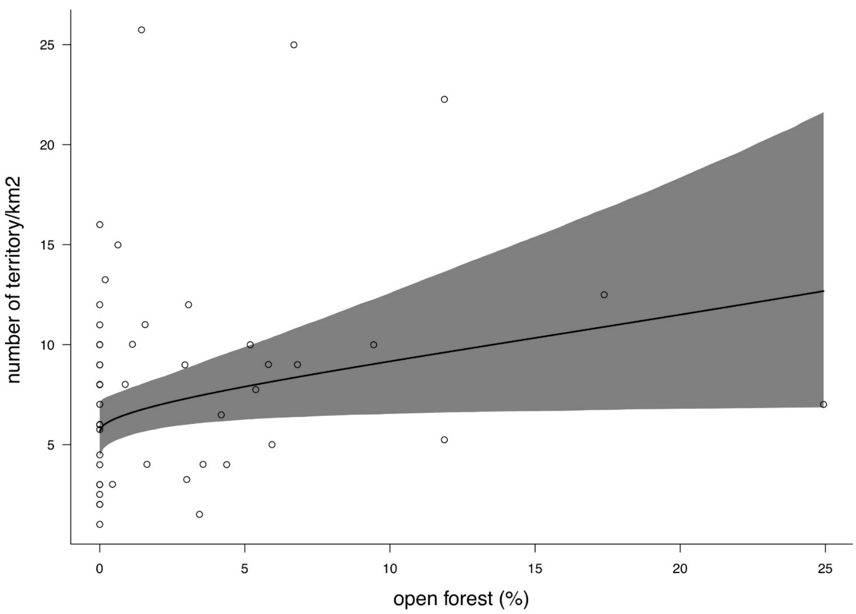
Fig. 5

5.1



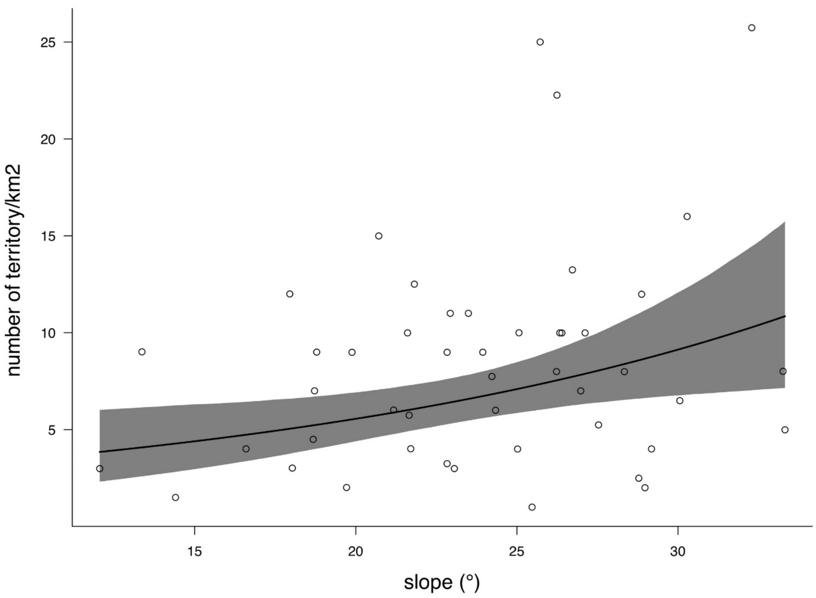
number of territory/km2
5
10
15
20
25
80
100
120
140
160
180
200
mean precipitation in May–July (mm)

5.2



number of territory/km2
5
10
15
20
25
0
5
10
15
20
25
open forest (%)

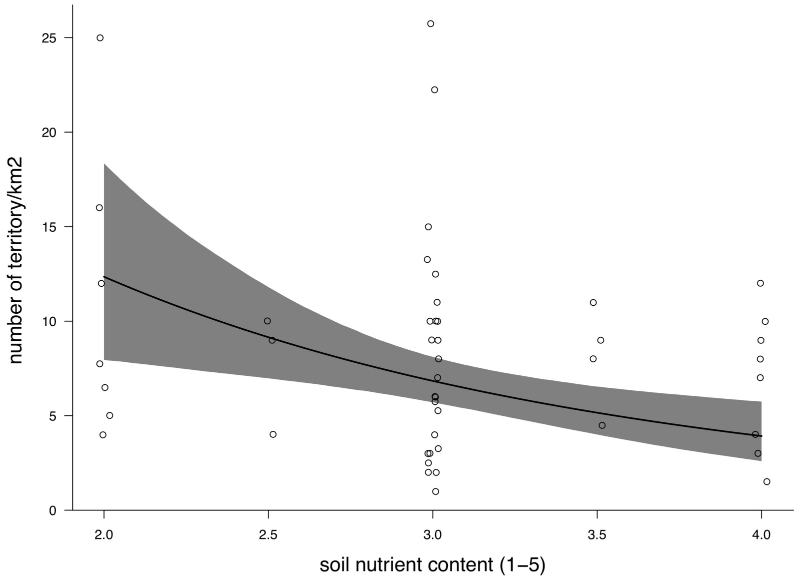
5.3



number of territory/km2
5
10
15
20
25
15
20
25
30
slope (°)

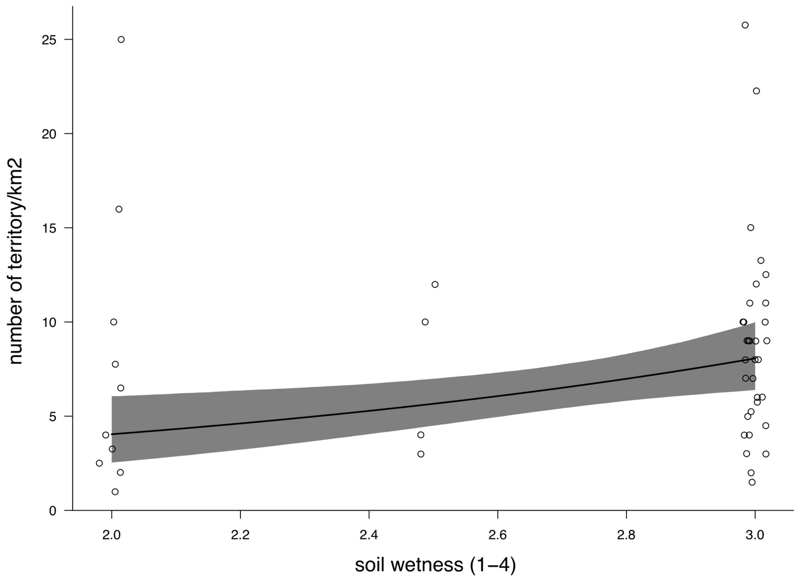
Fig. 6

6.1



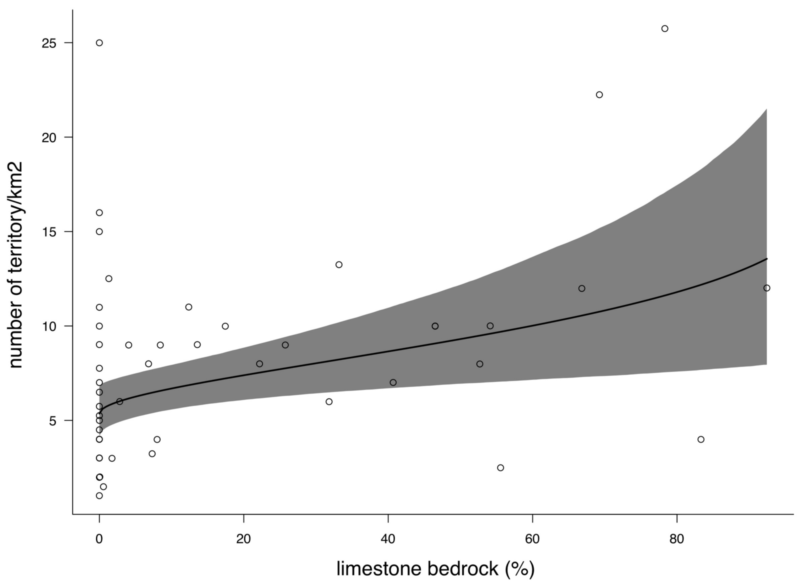
number of territory/km2
25
20
15
10
5
0
2.0
2.5
3.0
3.5
4.0
soil nutrient content (1–5)

6.2



number of territory/km2
25
20
15
10
5
0
2.0
2.2
2.4
2.6
2.8
3.0
soil wetness (1–4)

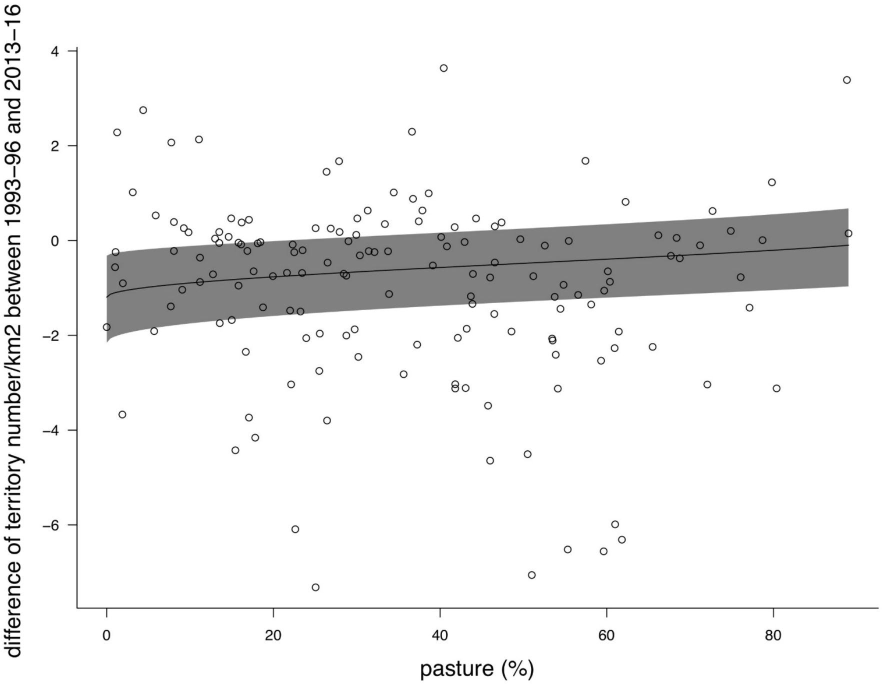
6.3



number of territory/km2
25
20
15
10
5
0
20
40
60
80
limestone bedrock (%)

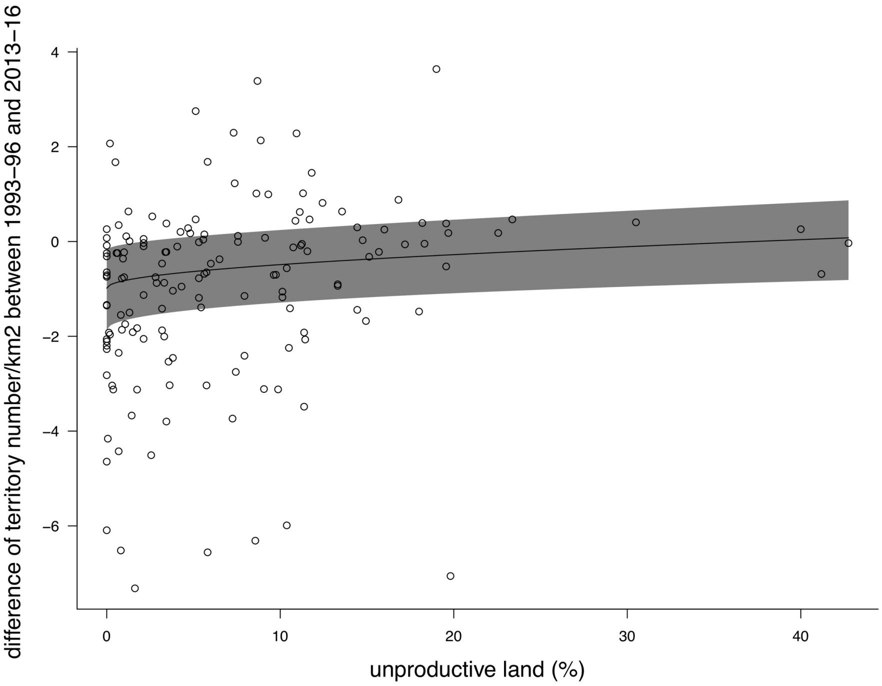
Fig. 7

7.1



difference of territory number/km2 between 1993–96 and 2013–16
4
2
0
−2
−4
−6
0
20
40
60
80
pasture (%)

7.2.



difference of territory number/km2 between 1993–96 and 2013–16
4
2
0
−2
−4
−6
0
10
20
30
40
unproductive land (%)

Additional Supporting Information

Appendix A. Maps with the observation points, the modelled density and the population trend obtained from the Swiss Ornithological Institute (SOI)

Appendix B. Histograms of the 3 variables taken in account to stratify and select the 47 km^2 within the Atlas and MHB sets

Appendix C. Descriptive statistics of the explanatory factors and list of the indicator plants

Appendix A Maps with the observation points, the modelled density and the population trend obtained from the Swiss Ornithological Institute (SOI)

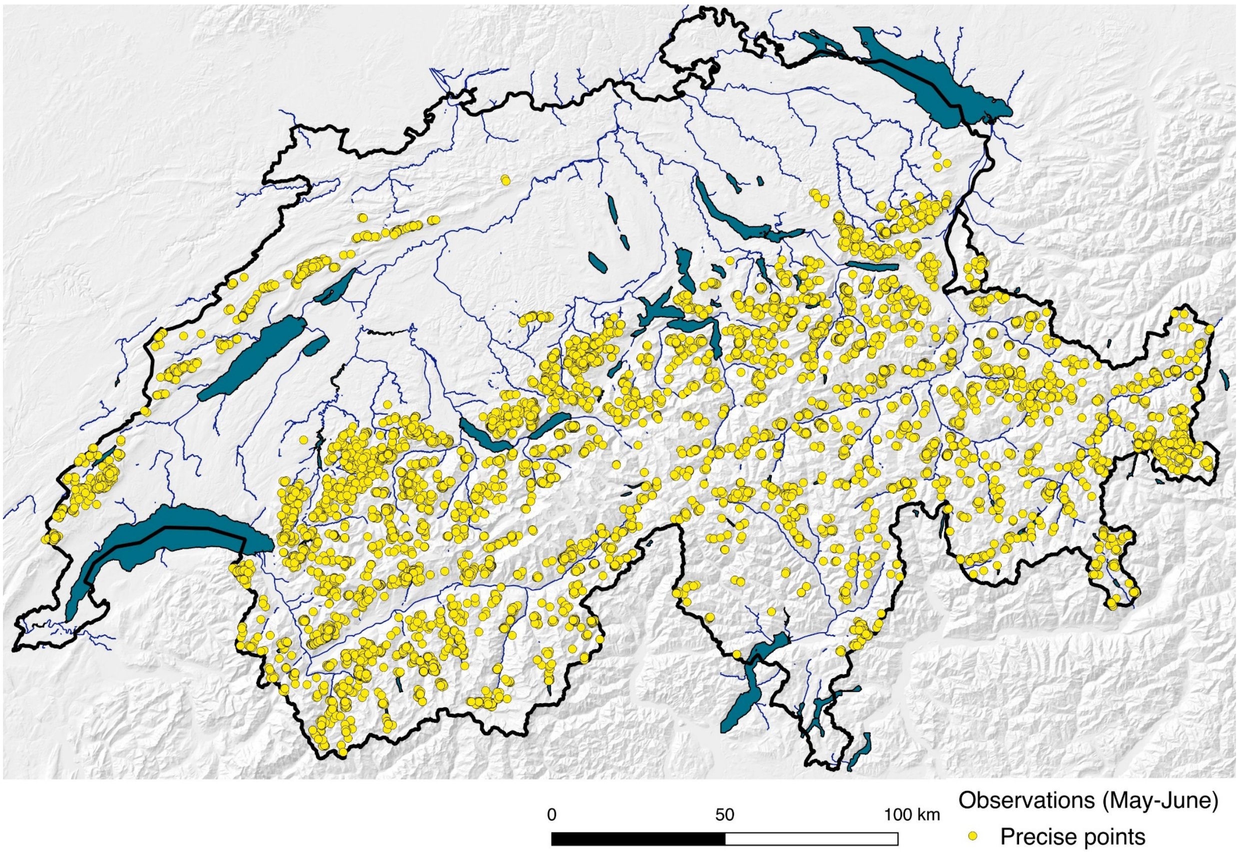


Fig. A.1 Precise observation points of Ring Ouzels for the period 2008-2017 and during the breeding season (May-June). This data come from the national surveys (Atlas and MHB) and from observations submitted on the ornitho.ch platform.

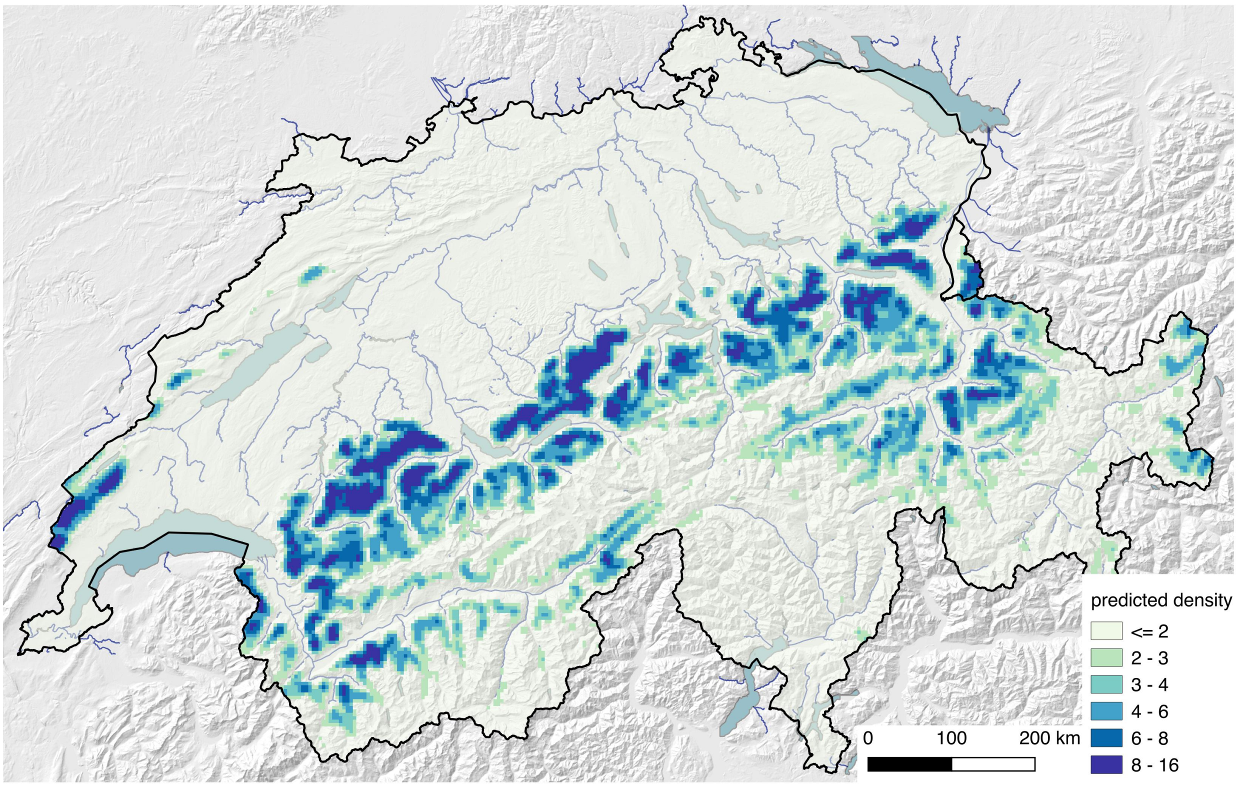


Fig. A.2 Modelled density (number of territory/km^2) for the period 2013-16 (from Knaus *et al.* 2018). Models are based on the estimated density from Atlas surveys, but corrected for detection probability and spatial autocorrelation, using land cover as predictors (see Guelat & Kery 2018).

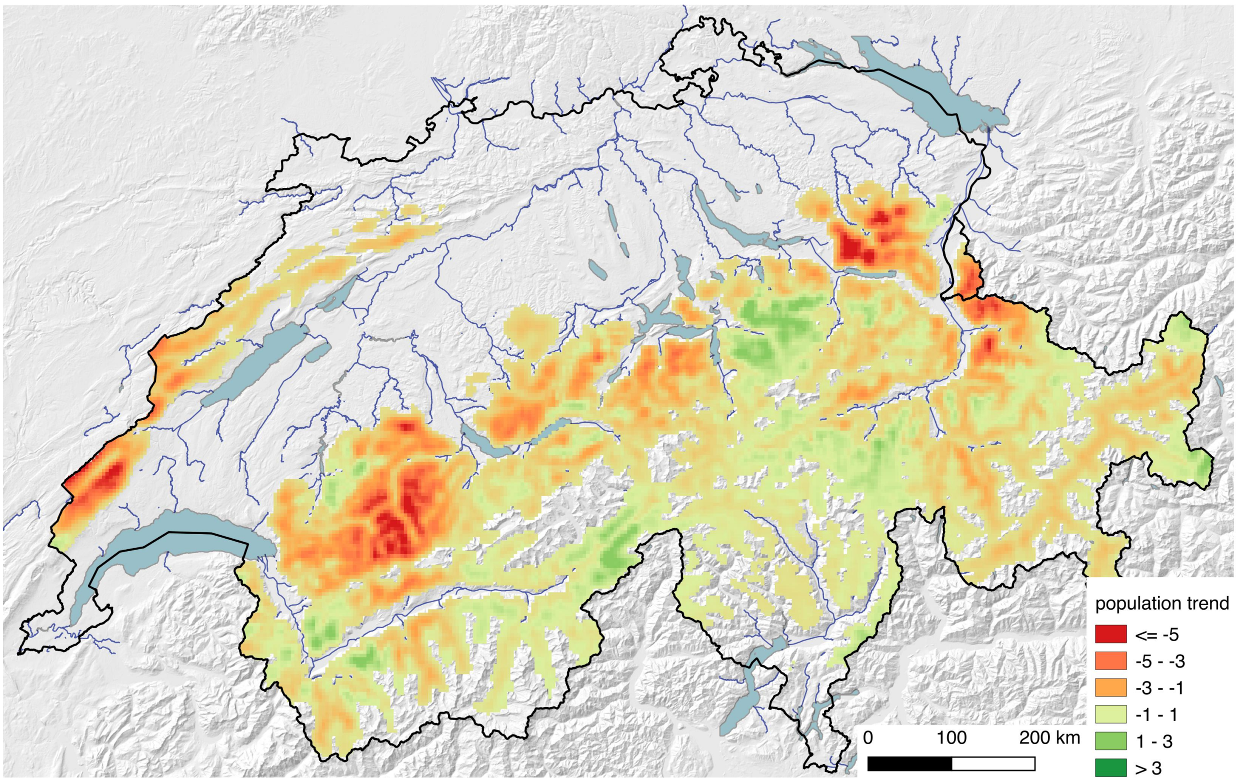


Fig. A.3 Ring Ouzels' population trend according to the difference between the modelled densities for the Atlas periods 1993-96 and 2013-16.

Appendix B Histograms of the 3 variables taken in account to stratify and select the 47 km^2 within the Atlas and MHB sets

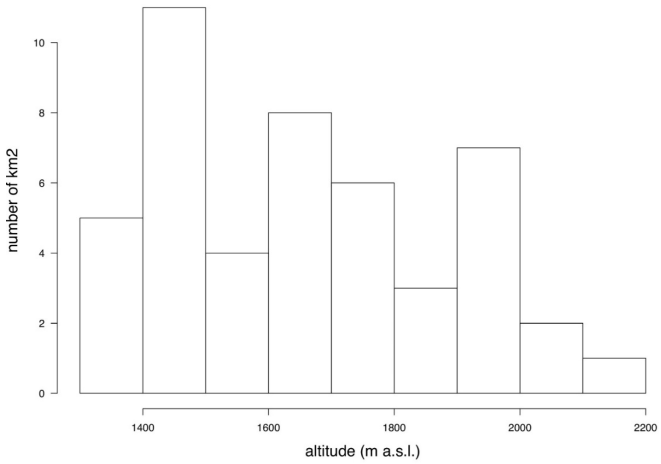


Fig. B.1 Frequency of km^2 according to their mean elevation

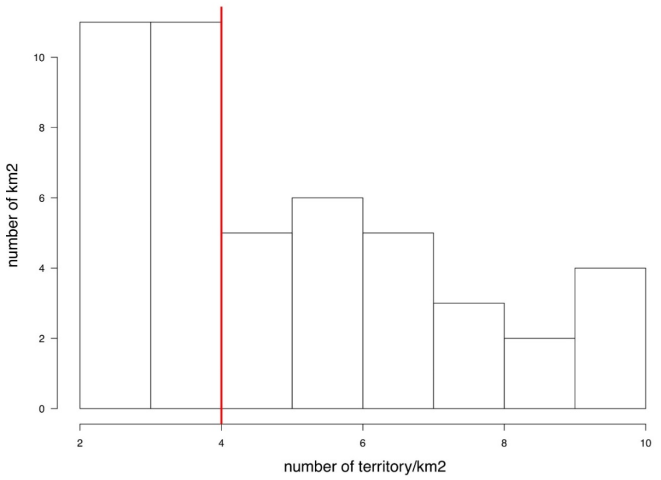


Fig. B.2 Frequency of km^2 according to the modelled density value. The vertical red line symbolizes the threshold value (median = 4) used to define the two strata: low and high density. Squares with density <2 were not considered

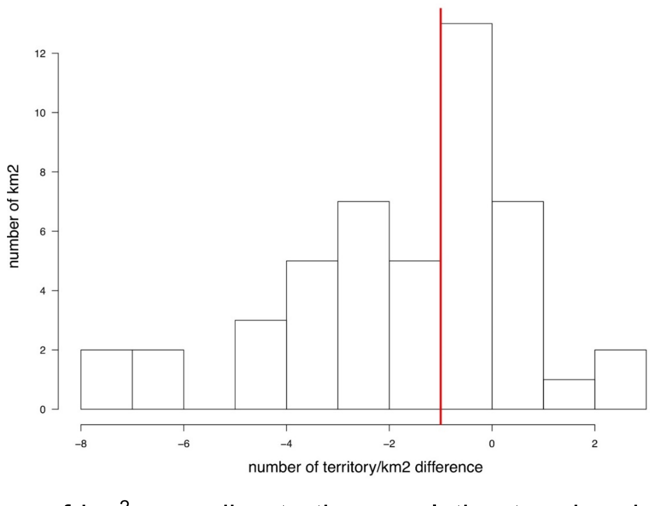


Fig. B.3 Frequency of km^2 according to the population trend and in red the threshold value (-1) used to define the two strata : declining and stable/increasing population.

Appendix C Descriptive statistics of the explanatory factors and list of the indicator plants

Table C.1 Habitat variables sampled in each km^2, distributed into categories used for model selection. For the home range analysis, the mean ± SD value are calculated, except for the edge presence/absence considered as a factor. For the landscape scale, the median ± MAD are computed. Marginal variables (>90% of 0 values) are in italics. The number 10, 20 or 50 after some variable corresponds to the reference area.

Habitat predictors **per Category**	Mean ± standard deviation (0:1 counts)		Median ± median absolute deviation
	Presence plots	Absence plots	km^2
	n = 45	n = 42	n = 47
Ground cover			
snow	0 ± 0	0 ± 0	0 ± 0
moss	3.2 ± 4.5	4 ± 5.8	0 ± 0
regeneration 10	1.4 ± 1.4	1.6 ± 2.5	0.8 ± 1.1
woody plants 10	8.1 ± 14.1	4.9 ± 9.6	1.2 ± 1.9
stems	1 ± 0.9	0.9 ± 0.9	0.8 ± 1.1
mineral	3.2 ± 2.7	3.3 ± 5.5	1.5 ± 2.2
dead wood	3.3 ± 3.4	3.2 ± 3	1.2 ± 1.9
other	0 ± 1	0 ± 1	0 ± 0
AG	17.6 ± 14.9	14.5 ± 14.3	9 ± 3.3
GV	62 ± 22.3	67.4 ± 24.8	68.5 ± 20.8
Structure < 1.3 m			
grassland cover	49.8 ± 28.6	53.7 ± 31	60 ± 29.7
regeneration cover 20	2.8 ± 3.6	3.1 ± 4.7	1 ± 1.5
woody plants cover 20	12.4 ± 20.8	6.6 ± 11.7	1.5 ± 2.2
vegetation height	15.9 ± 7.3	21.9 ± 11.2	19.8 ± 6.7
patchiness	2.1 ± 0.4	1.8 ± 0.5	2.2 ± 0.7
Structure > 1.3 m			
edge	(12:33)	(20:22)	1 ± 0
forest cover	41 ± 24.8	39.9 ± 31.1	27.5 ± 22.2
bush cover	12.5 ± 18.4	6.4 ± 8.4	5 ± 7.4
canopy cover	21.2 ± 19.4	23 ± 24.8	8.5 ± 12.6
shrub cover	5.4 ± 8.5	7.7 ± 11.6	0 ± 0
Tree composition	-	-	4.5 ± 0.7
Condition	2.8 ± 0.5	2.7 ± 0.5	
soil wetness 50	2.7 ± 1.1	2.6 ± 1.2	3 ± 0
grazing intensity	3 ± 0.6	3 ± 0.6	3 ± 1.5
soil nutrient content	2.8 ± 0.6	2.8 ± 0.6	3 ± 0
soil wetness 20	514.4 ± 326.9	524.4 ± 306.2	3 ± 0
soil moisture	0.7 ± 0.4	0.7 ± 0.3	-
soil hardness	0 ± 0	0 ± 0	-

Table C.2 Environmental factors extracted from remote sensed data for each presence/absence quadrat and km² and displayed according to the categories used for the model selection. For the statistics, the mean ± SD is calculated for each variable on both scales. Variable with (0:1 counts) were transformed as binary in the analysis concerned.

Habitat predictors **per Category**	Mean ± standard deviation (0:1 counts)		Mean ± standard deviation (0:1 counts)	
	presence plots	absence plots	km²	
	n = 45	n = 42	n = 47	n = 152
Topography + Climate				
precipitation (5-7)	150.7 ± 39.4	148.8 ± 40.2	150.4 ± 39.5	153.6 ± 41.2
precipitation (12-2)	104.1 ± 22.5	101.1 ± 23.6	103.3 ± 22.9	104.7 ± 25.2
temperature (5-7)	8.5 ± 1.3	9 ± 1.3	8.8 ± 1.4	80.7 ± 17.6
temperature (12-2)	-4.3 ± 0.9	-3.9 ± 0.9	-4 ± 0.9	-45.5 ± 12.4
elevation	1712.3 ± 211.3	1624.3 ± 217.9	1660.2 ± 223.3	1781.9 ± 303.9
slope	23.4 ± 6.5	21.8 ± 7.1	23.9 ± 5	25.1 ± 6.5
northness	0 ± 0.6	0.1 ± 0.6	0 ± 0.4	0 ± 0.4
solar radiation (3-6)	559049.6 ± 69786.8	545504.4 ± 69454	552286.8 ± 50797.1	547681.8 ± 59200.9
Structure < 1.3 m				
meadow	0 ± 0.1 (41:4)	0.1 ± 0.1 (32:10)	0.1 ± 0.1	0 ± 0.1
pasture	0.3 ± 0.3	0.3 ± 0.3	0.4 ± 0.2	0.4 ± 0.2
unproductive land	0.1 ± 0.1 (34:11)	0 ± 0.1 (35:7)	0 ± 0	0.1 ± 0.1
grassland	0.4 ± 0.3	0.4 ± 0.3	0.4 ± 0.2	0.5 ± 0.2
Structure > 1.3 m				
bush	0 ± 0.1 (37:8)	0 ± 0 (36:6)	0 ± 0	0 ± 0.1
dense forest	0.3 ± 0.3	0.4 ± 0.3	0.3 ± 0.2	0.2 ± 0.2
open forest	0.1 ± 0.2 (34:11)	0.1 ± 0.2 (35:7)	0 ± 0.1	0 ± 0.1
forest	0.4 ± 0.3	0.4 ± 0.3	0.3 ± 0.2	0.3 ± 0.2
treeline length	272.5 ± 206.6	311.2 ± 233.1	6497.9 ± 3472.1	-
distance to the treeline	107.6 ± 188.5	101.9 ± 167.9	125 ± 147.2	307.1 ± 469.8
number of solitary trees	4.2 ± 4.9	3.3 ± 3.9	80.6 ± 41.7	-
Mineral				
lime bedrock	-	-	0.2 ± 0.3	0.2 ± 0.3
scree	-	-	0 ± 0	0.1 ± 0.1
rock	-	-	0 ± 0	0.1 ± 0.1
anthropogenic area	-	-	0 ± 0 (33:14)	0 ± 0 (116:37)

Table C.3 List of the indicator plants used to determine the soil wetness (Landolt's H) and nutrient content (Landolt's N)

Species	Subalpine	Alpine	Month flowering	Type	Landolt's H	Landolt's N
Achillea millefolium	x	(x)	6-9	dry	2	3
Anthericum liliago	(x)		5-6	dry	1+	2
Arctostaphylos uva-ursi	x	x	4-7	dry	2	2
Aster alpinus	x	x	6-8	dry	2	2
Avenalla flexuosa	x	(x)	6-8	dry	2+w	2
Campanula rotundifolia	x	(x)	5-9	dry	2	2
Dianthus sylvestris	x	(x)	6-7	dry	1	2
Echium vulgare	x		5-10	dry	2	3
Erica carnea	x	(x)	3-6	dry	2	2
Euphorbia cyparissias	x	x	4-6	dry	2	2
Globularia cordifolia	x	x	5-7	dry	2w+	2
Juniperus communis	x	x	5-8	dry	2(w)	2
Oxytropis campestris	(x)	x	7-8	dry	2	2
Plantago lanceolata	x	(x)	4-9	dry	2w+	3
Plantago media	(x)		5-7	dry	2	3
Rumex sculatus	x		6-7	dry	2	2
Sedum album	x	(x)	6-9	dry	1w	2
Sempervivum montanum	x	x	7-8	dry	2	2
Sesleria caerulea	x	x	3-8	dry	2w	2
Silene nutens	x	(x)	6-7	dry	2	2
Sorbus aria	x		5	dry	2w	2
Trifolium montanum	x	(x)	5-7	dry	2w	2
Veronica fruticans	x	x	6-7	dry	2	2
Abies alba	(x)		5	humid	4w	3
Aconitum napellus	x	x	6-8	humid	4w+	5
Alnus incana/viridis	x	(x)	2-6	humid	4w+	4
Bartsia alpina	x	x	6-8	humid	4w+	3
Cirsium oleraceum	(x)		6-9	humid	4w	4
Filipendula ulmaria	x		6-8	humid	4w+	4
Parnassia palustris	x	x	7-9	humid	4w+	2
Petasites albus/hybridus	x		3-5	humid	4w+	4
Petasites paradoxus	x	x	4-5	humid	4w	3
Phleum alpinum	x	x	7-8	humid	4w	2
Pinguicula alpina/vulgaris	x	x	5-7	humid	4w+	2
Polygonum bistorta	x		5-7	humid	4w	4
Rumex acetosa	x		5-8	humid	3w	4
Rumex alpestris	x	(x)	7-8	humid	3+w	4
Rumex alpinus	x	(x)	7-8	humid	3+w	5
Soldanella alpina	x	x	5-7	humid	4w	3
Thalictrum aquilegiifolium	x	(x)	5-7	humid	4w+	3
Trollius europaeus	x	(x)	5-6	humid	4w+	3
Urtica dioica	x	(x)	6-9	humid	3+w+	5
Viola biflora	x	x	5-8	humid	4w	4

Declaration of consent

on the basis of Article 30 of the RSL Phil.-nat. 18

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Study program: Master of Science in Ecology and Evolution

Bachelor ☐ Master ☑ Dissertation ☐

Title of the thesis: Habitat selection of the Ring Ouzel Turdus torquatus alpestris at the home range and landscape scales

Supervisor: Raphaël Arlettaz, Veronika Braunisch and Arnaud G. Barras

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