

**Foraging habitat selection by Ring Ouzels *Turdus torquatus* in alpine timberline ecosystems: building the evidence for species conservation management**

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# Foraging habitat selection by Ring Ouzels *Turdus torquatus* in alpine timberline ecosystems: building the evidence for species conservation management

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## SUMMARY

**1.** The wildlife of mountain ecosystems is considered as particularly vulnerable to climate change. In effect, the pace of warming is more pronounced at higher elevations than in the lowlands. It however remains unclear whether climate change is the main factor in the decline of several European mountain bird species, including the Ring Ouzel *Turdus torquatus*. Switzerland harbours 15% of the European breeding population of the Ring Ouzel, thus bearing international responsibility for its preservation. This also calls for management-oriented research that targets evidence-based action plans.

**2.** We aimed to identify key species-habitat associations in alpine timberline ecosystems, focusing on the demanding nestlings' provisioning period. We radiotracked 21 individuals, located their foraging whereabouts, mapped habitat characteristics at foraging sites and compared them with those mapped at randomly generated, pseudo-absence points. We analysed habitat selection at two scales, the micro-habitat scale (foraging site *per se*) and the meso-habitat scale (surroundings of the foraging site).

**3.** Among a set of variables, soil moisture and hardness, together with height of grass, were the best predictors of foraging occurrence. At both the micro- and meso-habitat scale, Ring Ouzels foraged preferentially in soft soils with intermediate moisture. Selection of short grass stalks was particularly clear at the meso-habitat scale. We did not find any strong relationship to snow cover, contrary to our prediction that Ring Ouzels favour the front of melting snow patches to forage.

**4. *Synthesis and applications.*** In the context of global warming, the characterisation of optimal habitat profiles for alpine and arctic wildlife is crucial

to decipher the ecological links to climatic conditions and apprehend whether adaptive habitat management can counterbalance the detrimental effects of climate change. As soil conditions depend to a large extent on snow cover while grass height is further influenced by grazing practices among alpine timberline ecosystems, Ring Ouzels appear especially vulnerable to both climate and land-use changes. Future research will have to appraise the complex interactions between these two drivers so as to propose realistic conservation measures.

326 words

## KEYWORDS

*Turdus torquatus* • habitat selection • radiotracking • mountain birds • timberline • soil conditions • adaptive management

## INTRODUCTION

In the last decades, conservation research conducted on European birds has mainly focused on farmland species. This is mainly attributable to the intensification of agricultural practices, which dramatically impacted biodiversity in lowland farmland landscapes (Donald, Green & Heath 2001). By contrast, bird species from higher altitudes, referred to further in the text as mountain birds, received less attention (Chamberlain *et al.* 2012; Lehikoinen *et al.* 2014). Reasons for this imbalance lie in the fact that land-use changes occurring in European mountain ecosystems are relatively recent (Tasser & Tappeiner 2002; Graf *et al.* 2014). Moreover, the logistical difficulty of monitoring populations breeding in remote regions also plays a role (Pearce-Higgins *et al.* 2009; Chamberlain *et al.* 2012). Our knowledge on high-altitude species is

consequently much more restricted than for lowland ones, as we often have little information on the ecology and dynamics of these populations (Laiolo *et al.* 2004; Chamberlain *et al.* 2012). This gap in knowledge has to some extent maintained the picture of stable mountain bird populations. Nonetheless, there is a growing body of evidence that several mountain species, even common ones, have recently been declining in Europe (e.g. Lehtikoinen *et al.* 2014; Flousek *et al.* 2015). Because these bird species have a short breeding season, are adapted to cold environments, and often confined to small elevational belts, they are expected to be highly susceptible to climate change, notably to warming ambient temperatures (Sekercioglu *et al.* 2008; Chamberlain & Pearce-Higgins 2013). On top of that, the rate of warming might be greater in mountainous regions, e.g. in the Alps, where it is twice the average (Brunetti *et al.* 2009), and is expected to further increase over the next century (Gobiet *et al.* 2014). Therefore, most predictions on the future distribution of mountain species predict upward shifts, with birds trying to track their climatic niche (Tingley *et al.* 2009; Chamberlain *et al.* 2013). Such uphill movements are already observed for some bird species in the Alps (e.g. Popy, Bordignon & Prodon 2010; Maggini *et al.* 2011). Following predictions, this phenomenon will ultimately lead to range contraction (Virkkala *et al.* 2008; Tingley *et al.* 2009), and thus to an increased extinction risk (Sekercioglu *et al.* 2008; La Sorte & Jetz 2010).

The Ring Ouzel *Turdus torquatus* is an emblematic mountain bird breeding mostly within Western Palearctic boundaries. The species has significantly decreased in parts of its range in recent decades; the most pronounced population decline has been noticed in the UK since the 1950s,

where the species is now listed as a species of high conservation concern (Wotton, Langston & Gregory 2002; Sim *et al.* 2010). Extensive research has aimed at understanding the causes of the UK population crash, but no obvious factor could be identified (Sim *et al.* 2010). However, these numerous studies uncovered essential aspects of Ring Ouzel's autoecology (e.g. Burfield 2002; Sim *et al.* 2013; Davies, Arthur & White 2014). In particular, the importance of an appropriate heather-grass mosaic was highlighted on several occasions (Burfield 2002; Buchanan *et al.* 2003; Sim *et al.* 2007) and first guidelines were provided for land managers (Sim *et al.* 2013). Additionally, Beale *et al.* (2006) highlighted the potential detrimental effects of warmer late-summer temperatures. In contrast to the British long-term decline, populations in most other parts of the distribution range appear fairly stable, but a lack of comprehensive monitoring might hide negative trends (Burfield 2002; Sim *et al.* 2010). Detailed monitoring data from Switzerland indicates a net decrease in the number of breeding pairs since the 1990s, mostly touching lower altitudes of the range (Schmid *et al.* 1998; von dem Bussche *et al.* 2008). This situation motivated a new status of “vulnerable” in the last revision of the Swiss Red List (Keller *et al.* 2010b). Moreover, Switzerland hosts 15% of the European breeding population of Ring Ouzels (Maumary, Valloton & Knaus 2007), thus having an international responsibility for this species. It is henceforth one of the 50 priority bird species for recovering programmes in the country (Keller *et al.* 2010a), calling for further research in the Alps.

The breeding habitat of the alpine subspecies *T. t. alpestris*, which occurs in mountain ranges of central and southern Europe, strongly differs from the one of *T. t. torquatus* that inhabits Scandinavia and the British uplands: in

the UK, the Ring Ouzel is associated with heather moorland, breeding in a totally open landscape (Sim *et al.* 2010); by contrast, the species can be found principally between 1200-2200 m above sea level (a.s.l.) in the European Alps, mostly in semi-open coniferous forests, with a core distribution at the timberline (Schmid *et al.* 1998; von dem Bussche *et al.* 2008). It is therefore difficult to draw direct parallels between the decline in the Alps and in the UK. Key ecological requirements should first be identified in both parts of the range, before framing more general hypotheses about the species decline. To the best of our knowledge, only two studies have investigated the patterns of habitat selection by *T. t. alpestris*, one in the Swiss Alps (von dem Bussche *et al.* 2008) and the other in the Western Carpathians (Ciach & Mrowiec 2013). Both highlighted the importance of a mosaic of coniferous forest stands exhibiting a sparse canopy and interspersed with open habitats such as clear-cuts or grasslands. von dem Bussche *et al.* (2008) also modelled the future distribution of the species across Switzerland based on the projected trends of several habitat predictors. Under a moderate climatic scenario, they predicted a 440 m upward shift of the species by the year 2070, which could explain the current retreat from lower altitudes. However, semi-open landscapes below the timberline mostly exist because they are used as farmland, regularly grazed or mowed. The current land-use changes taking place within this elevational range, such as abandonment of pastures (Tasser & Tappeiner 2002; Laiolo *et al.* 2004) or intensification of semi-natural grasslands (Tasser & Tappeiner 2002; Andrey *et al.* 2014; Graf *et al.* 2014), might impact the Ring Ouzel more strongly than direct climatic effects.

There is still missing knowledge on fine-scale species-habitat associations for many alpine species (Chamberlain *et al.* 2012), the Ring Ouzel being no exception. Fine-grained studies would help to sharpen the picture of optimal habitat profiles, with the aim to provide clear guidelines for management strategies (Arlettaz *et al.* 2012; Braunisch *et al.* 2014). Moreover, such high-resolution studies are more likely to make us understand the underpinning ecological mechanism of an observed decline (Morris *et al.* 2001). For example, identifying which environmental variables are crucial in the selection process of a ground-foraging bird can inform us about which parameters of prey availability – notably accessibility vs abundance - most influence species' foraging behaviour (Morris *et al.* 2001; Schaub *et al.* 2010; Arlettaz *et al.* 2012). Finally, such information would help refining our understanding of how climate and land-use changes could reduce habitat suitability, and therefore if appropriate adaptive habitat management might compensate adverse climatic effects (Braunisch *et al.* 2014).

In the present study, we investigated the foraging habitat selection of the Ring Ouzel during the period of nestlings' provisioning, using radiotracking. This method allows taking into account individual variability and guarantees less bias in detection than visual observations, which would result in drawing incomplete habitat profiles. Our main aim was to assess in what realised foraging locations differ from random ones in their habitat structure, in order to identify key associations between the Ring Ouzel and its breeding habitat at the alpine timberline. Our main research questions were the following: (1) Which habitat variables best predict the foraging occurrence of the Ring Ouzel? (2) In particular, how crucial is the vicinity of melting snow patches? (3) Does the

selection pattern vary between the micro-habitat scale (foraging site) and meso-habitat scale (surroundings of foraging sites)? (4) Which aspect of prey availability – which is abundance modified by accessibility - may best explain identified preferences? Responses to these questions will set the first steps towards conservation management guidance.

## **MATERIAL & METHODS**

### **Study area**

The study took place during the 2015 breeding season in Serin (46°19'50"N, 7°25'40"E), a wooded summer pasture (1.9 km<sup>2</sup>) located in the inner Alps, canton of Valais, SW Switzerland. The study area ranges from 1700 to 2200 m a.s.l., where most Ring Ouzels pairs are breeding. It covers the whole timberline zone, from a dense picea *Picea abies* forest at the lower altitudes, which gradually opens upwards with a growing occurrence of larches *Larix decidua*, up to a fully open area at around 2100 m a.s.l.. The substrate is calcareous, defining a karstic landscape with few surface waters, and no permanent stream.

### **Captures and radiotracking**

To perform this habitat selection study, we captured birds with mist nets between mid-April and early May. Capture sessions usually lasted the whole day, from dawn to dusk, and location of the mist nets was changed every 3-4 days. Nets were mostly placed along snow patches and forest edges. 60 birds were captured during this period and 20 of them equipped with a radio-tag (PD-

2P, 3.7g, lifespan of 4 months, Holohil Systems Ltd., Canada). As one individual was predated and its radio-tag retrieved, we equipped a 21<sup>st</sup> breeding individual later in the season (capture the 10<sup>th</sup> of June). All birds were ringed with one metallic ring on the right leg (ring size H, SEMPACH HELVETIA) and an individual combination of 3 colour rings (one on the right, two on the left leg). Radio-tags were placed on the synsacrum, and attached with a leg-loop harness, following the method of Rappole and Tipton (1991). Harnesses were made out of stretch-nylon tubes of 0.6 mm diameter. This material was selected so as to hold for a limited period, with the idea that the bird would be freed of it before the postnuptial migration. The loop-span was of approximately 76.5 mm, as calculated following the formula in Naef-Daenzer (2007) and assuming a mean Ring Ouzel body mass of 100 g (Jenni 1994).

We radiotracked these individuals from the very first day of tagging, in order to find their nest and assess breeding status. Birds were located by the "homing-in on the animal" technique, using a Titley Australis 26k<sup>TM</sup> receiver coupled with a three-element hand-held antenna. Recording of foraging locations started as soon as we suspected hatched broods in the study area and continued as long as birds could be observed foraging (ranging from 7<sup>th</sup> May to 18<sup>th</sup> June). Once a bird was located by its radio-signal, we ensured its identity by looking at the colour rings. Observations were performed with 10x42 binoculars. Staying at good distance, we noted the exact spot of the first observed successful food item picking event, i.e. the first actual prey capture, referred to further in the text as the foraging point. We restricted our foraging points to captures of earthworms (Oligochaeta: Lumbricidae) and big invertebrate larvae, as they constitute the main diet of nestlings (Glutz von

Blotzheim & Bauer 1988; Burfield 2002) and because actual capture was more easily assessed. As soon as the bird had left the foraging site, the exact foraging point was marked with a labelled flag. To avoid spatial autocorrelation, a time span of at least 30 min between two subsequent foraging records was kept, making sure not to further track the same bird during this period. In addition, not more than three points per bird and day were recorded.

### **Sampling design**

With the aim of comparing the habitat characteristics of the so-obtained foraging points with those in the neighbouring available habitat not visited at the same time, we randomly generated 4 pseudo-absence points in the surroundings of each foraging point. An azimuth for placing these pseudo-absence points was first selected at random ( $\alpha$ : 0 - 359°). The four pseudo-absence points were then aligned along this azimuth axis, two on each side of the actual foraging point, and at two different distance ranges: at a random distance between 5 and 14 m, and between 15 and 50 m (Fig. 1). The span of the first range (5 - 14 m) was chosen in order to investigate foraging micro-habitat selection: at this scale, all points are potentially easily accessible by a hopping bird, typically as observed in a single foraging bout (according to Burfield 2002). The second range (15 – 50 m) is assumed to express foraging selection at the meso-habitat scale: here conditions of a foraging point are compared with those at random points located in the wider surrounding area, which would usually not be accessed by hopping but by flying, though such sites would still be included within an individual home range. These random points were generated instantly after an actual foraging observation, so as to promptly

map habitat characteristics. Environmental conditions encountered by the bird could thus be accurately described. This sampling design was crucial as habitat variables can quickly change at these altitudes due to the rapid spring snowmelt. The mapping was therefore always performed as soon as possible after the recording of a foraging point, i.e. mainly within the same half-day, and included a whole stratum, i.e. a set consisting of the actual foraging point and its four paired pseudo-absence points.

### **Habitat mapping**

Habitat mapping was performed in the same way for presence and pseudo-absence points. Within a 1 m radius circle around each point, referred to as the foraging or random plot, we first described the percentage of ground cover for 11 habitat variables (Table 1). From field experience, it appeared meaningful to aggregate the variables bare soil and leaf/needle litter cover, creating a new variable that was described as accessible ground (AG). In addition to these 11 habitat variables, we measured the mean height of the old and new grass layer, respectively referred to as height of brown and green vegetation. Moreover, slope and aspect were measured with a compass. As aspect is a circular variable, it was partitioned between northing (cosine of aspect) and easting (sine of aspect). Distance to the nearest snow patch was determined as well, if snow was present in a radius of 50 m. Eventually, two soil properties were measured: (a) soil hardness was determined with a penetrometer (EL 29-3729, ELE International, Loveland, USA): this device measures the force needed to insert a tip of 4.5 mm diameter into the soil to a depth of 6.35 mm, at a 0.05kg/cm<sup>2</sup> resolution; (b) soil moisture was measured at a 1 mV resolution ( $\pm$

7.5 mV accuracy) with a specific probe (SM150, Delta-T, Cambridge, UK) by fully inserting its two 51 mm rods perpendicularly into the soil. For both soil properties, 3 measurements were taken each time near every foraging or random point, and their mean was considered in the analyses. We ended up with a set of 19 habitat variables, summarized in Table 1.

### **Statistical analyses**

We assessed foraging habitat selection by comparing habitat variables at presence (actual foraging) vs pseudo-absence (actual random) plots. Our response variable being binary (presence = 1, pseudo-absence = 0), we modelled habitat selection through hierarchical logistic regression, which corresponds to a generalised linear mixed-effects model (GLMM) with a binomial error distribution and a logit link function (following Arlettaz *et al.* 2012). The habitat variables were included as fixed effects. Non-independence of the data coming from a same stratum, or a same individual, was accounted for with random effects (Gillies *et al.* 2006). This is necessary to avoid pseudoreplication, independence being an assumption of logistic regression (Hosmer & Lemeshow 2000; Gillies *et al.* 2006). Moreover, the random effect stratum was nested within individual in our models, as several foraging points per individual had been recorded. All models were fitted using *lmer* function in the R-package *lme4* (Bates *et al.* 2015).

Each of the ground cover variables was arcsine-square-root transformed, as they constitute proportional data summing up altogether to 100%. Marginal ground cover variables (>90% of zero values) were removed from the analysis, and those with more than 70% of zero values were transformed to binary

presence/absence (1/0) variables. Even if there is no assumption on the distribution of explanatory variables in a logistic regression, right-skewed variables were log-transformed as it may improve model fit (Kay & Little 1987). Moreover, all variables were standardised to visualise the effect size directly from coefficient estimates in a model. Finally, we checked for correlation between the variables with Spearman correlation coefficient  $r_s$ . If  $|r_s| > 0.7$ , we excluded the variable being the least significant at fitting occurrence in a univariate model, so as to avoid the problem of collinearity (Hosmer & Lemeshow 2000).

In order to detect differences in the selection process between micro- and meso-habitat scales, we ran two sets of analyses. We first compared every foraging plot against the 2 random plots within the closer range (5 - 14m) and, in a second step, against the 2 random plots in the wider range (15 - 50m). The model selection process was identical for the two analyses; for each habitat variable, we fitted a univariate GLMM predicting the occurrence probability as a function of this variable. For further modelling, we kept only variables that showed a  $P < 0.1$  in their univariate model. At this step, we also tested the addition of squared terms to variables for which we hypothesised a curvilinear relationship in relation to occurrence probability: soil moisture, soil hardness, AG and green vegetation cover. We kept only squared terms if they showed a significant coefficient estimate ( $P < 0.05$ ). Interaction terms were also investigated between soil moisture and hardness, and between AG and height of green vegetation, as this relation was shown to be important in previous habitat selection studies on ground-foraging birds (e.g. Weisshaupt *et al.* 2011; Tagmann-loset *et al.* 2012).

With all the retained variables, we generated a list of candidate models from all possible combinations, and ranked them by AICc (Akaike Information Criterion with correction for small samples), using the *dredge* command in the R-package *MuMIn* (Bartoń 2015). In this way, the drawbacks of a stepwise selection process were avoided, as every possible combination was tested to ensure detection of the most parsimonious model. We defined the set of best-supported models as the one including all models within  $\Delta\text{AICc} < 2$  from the first-ranked one. The respective AICc weights ( $w_i$ ) of these different models were calculated in order to obtain information about the probability of each one to be the best among the set (Burnham & Anderson 2002). We also performed model averaging on this set of models, and the resulting model was used when plotting occurrence probability against a given habitat variable, all other retained variables being then set to their mean. 95% credible intervals around the regression line were drawn from the 2.5% and 97.5% quantiles of the posterior distribution, obtained with 10,000 simulations with R-package *arm* (Gelman & Su 2015). All statistical analyses were performed with R statistical software, version 3.2.1 (R Development Core Team 2015).

## RESULTS

11 males and 10 females were captured and equipped with radio-tags. Out of these 21 individuals, 19 could be successfully tracked over 44 days in May and June 2015. In total, we recorded 145 foraging locations, on average ( $\pm$  SD)  $7.63 \pm 3.89$  locations per bird (range: 1 - 12). Of these 19 birds, 18 attempted to breed, resulting in 14 broods, as we had 4 pairs with both members radio-

tagged. 3 broods failed, whereas the 11 others proved successful, with at least one fledgling. Of these 14 nests, at least 3 were replacement broods, but surprisingly no second brood was observed.

Out of the 19 habitat variables, only AG and green vegetation cover were strongly correlated ( $r_s = -0.71$ ). Green vegetation cover was removed from the analysis, as it was less significant (estimate  $\pm$  SE,  $-0.23 \pm 0.09$ ,  $z = -2.52$ ,  $p = 0.012$ ) than AG ( $0.4 \pm 0.09$ ,  $z = 4.36$ ,  $p = 1.28 \cdot 10^{-5}$ ) at fitting occurrence probability in a univariate GLMM. Moreover, as all ground cover variables sum up to 100 % at every plot, the fact that one variable is described by all the others could have led to multicollinearity. Removing the variable yielding highest values solved this issue, which in our case was green vegetation cover, with, on average ( $\pm$  SD),  $51.2 \pm 30.86\%$  per point.

In the analysis at the micro-scale (5 – 14 m), we ended up with 285 pseudo-absence for 145 presence plots, following the removal of plots with missing values. At the end of the selection process, our best-supported model according to AICc included the following habitat variables: height of green vegetation, soil hardness, soil moisture and its quadratic term, as well as the interaction between soil moisture and hardness. This first-ranked model received moderate support ( $w_i = 0.395$ ), with 3 other models completing the set within  $\Delta AICc < 2$  (Table 2A). However, the additional variables northing and AG in the second- and third-ranked models can be considered as uninformative, from the minor reduction in deviance they induce (Burnham & Anderson 2002; Arnold 2010). Moreover, their effect size was very low according to coefficient estimates from the averaged model (Table 3A). Most important predictors were

indeed soil moisture, followed by soil hardness and height of green vegetation (Table 3A).

In the analysis considering the meso-scale (15 - 50m), the ratio after removal of missing values was of 283 pseudo-absences for 145 presences. The first-ranked model contained the same predictor variables as the one from the micro-scale analysis, plus the northing. It received substantial support ( $w_i = 0.523$ ), with only 2 other models within 2 units of  $\Delta AICc$  (Table 2B). In this case, the small  $w_i$  and the higher deviance of the model without northing (3<sup>rd</sup> rank) suggest that this variable has some explanatory ability. However, AG along with its quadratic effect seemed uninformative. This is supported by the low relative importance given by coefficient estimates in the averaged model (Table 3B). Most important predictors were again soil moisture, followed by height of green vegetation, soil hardness and northing.

At both scales, the birds selected a restricted range of soil moisture for foraging, between 650-900 mV, with a peak at 780 mV (Fig. 2). In terms of volumetric water content (VWC), accounting for calibration for a mineral soil (equation in Appendix 1), this is equivalent to an optimal range of 45-62%, peaking at 53%. The selection for soft soils occurred at both scales too, as hard soils above 0.8 kg/cm<sup>2</sup> were avoided (Fig. 3). Height of green vegetation also played an important role, plots with a grass layer shorter than 5 cm being more visited (Fig. 4). This was particularly pronounced in the selection at the meso-scale, whereas it appeared less clear at the finer one. Similarly, the interaction between soil hardness and moisture was much stronger at the wider scale (Fig. 5). Finally, north exposed plots appeared to be selected at the meso-scale, but

this was only a tendency, as the coefficient estimate remained non-significant (Table 3B).

All of the 3 key habitats predictor variables retained in our best-supported models were highly seasonal, as they varied both in time and elevation in the study area. We plotted values of each of these variables against time, distinguishing measurements from foraging and random plots. The difference between the two fitted curves informs about the time of the season when habitat selection mostly took place. From the measurements of soil moisture, a seasonal drying-out of the soil surface could be highlighted in all plots. This decline of moisture was however less pronounced in foraging plots, inducing a clear divergence with random plots by early June (Fig. 6A). Similarly, soils in the available habitat became less penetrable with time, whereas foraging plots showed no clear increase in hardness (Fig. 6B). Finally, height of green vegetation increased in both random and presence plots, but foraging grounds always showed shorter grass measurements at any time (Fig. 6C).

### **The snow-only analysis**

As only 34.5% (50/145) of the foraging points were distant by less than 50 m from snow, we could not include distance to snow as an habitat predictor in the main analysis, due to missing data. A separate analysis was therefore performed on this subset of the data, in order to test the hypothesis that birds are foraging next to snow patches, when snow still covers parts of their home range. Random points from both distance ranges were considered together in this analysis, resulting in the comparison of 50 presences against 190 pseudo-absences in the logistic regression. The univariate model fitting occurrence

probability in relation to snow distance revealed a negative but non-significant coefficient estimate ( $-0.2 \pm 0.15$ ,  $z = -1.36$ ,  $P = 0.174$ ). However, the squared term was significant at a 5% level, when included in the model ( $-0.44 \pm 0.19$ ,  $z = -2.27$ ,  $P = 0.023$ ). It appeared that birds foraged next to snow patches, in particular between 28-409 cm from the snow front (Fig. 7). Nevertheless, this was only the outcome of a univariate model. Following the same model selection process as in previous analyses, we ended up with 9 different models within  $\Delta AICc < 2$ , and distance to snow was retained in only 3 of them. Moreover, effect size of the latter variable was very small and non-significant in the averaged model (Appendix 2).

## DISCUSSION

Our findings provide insights into the foraging habitat selection pattern of alpine Ring Ouzels *T. t. alpestris*. At two different scales, we highlighted that three key habitat variables best characterise optimal foraging habitat profiles: soil moisture, soil hardness and height of green vegetation. This emphasises the importance of soil conditions in the habitat selection of a ground-foraging bird, a parameter that is often neglected (Gilroy *et al.* 2008).

We primarily identified an optimal range of soil moisture for foraging birds (45-62% VWC), with a clear avoidance of the driest and most saturated soils. Water content is known to strongly influence the biomass and activity of some invertebrates at the soil surface, notably earthworms that go deeper when the soil dries out (Gerard 1967; Curry 2004; Peach *et al.* 2004). As earthworms seem to constitute the main prey of chick provisioning Ring Ouzels (Glutz von

Blotzheim & Bauer 1988; Burfield 2002), we expected maximal abundance within the preferred moisture range above. However, from earthworm sampling in the same study area in 2014, highest abundance and biomass were observed at 35-45% moisture levels (Savioz unpublished). The other measured edaphic parameter, soil hardness, well predicted foraging occurrence, as birds definitely preferred soft soils. Although the relationship of prey, notably earthworms, to soil hardness was not investigated on the study area by Savioz (unpublished), there is an apparent mismatch between earthworm spatial abundance and habitat exploitation by Ring Ouzels from moisture measurements. The reason may first lie in prey availability, which is described as abundance modified by accessibility. Ring Ouzels forage both by picking up prey items from soil surface and beak drilling from the superficial layers of the soil, the latter notably for earthworms. The best foraging conditions might thus result from a trade-off between good food supply, i.e. high abundance and biomass of both underground and ground-dwelling arthropods, and prey accessibility, in this case constrained by soil hardness. It is all well known that soil compaction, i.e. hardness, can also negatively impact invertebrate abundance, in particular those having soil-dependent life stages (Gilroy *et al.* 2008). A second reason may be that earthworms are not the staple food of chick provisioning parents, meaning that the whole food supply arthropod community drives habitat preferences. Leatherjacket larvae (Diptera: Tipulidae), for instance, are often preyed upon by Ring Ouzels (Korodi Gál 1970; Glutz von Blotzheim & Bauer 1988; Burfield 2002), and they mainly occur in fairly swamped soils (Carroll *et al.* 2011). Information about local Ring Ouzel diet is necessary to get a better picture.

Soil moisture and hardness were retained among the best predictors of foraging occurrence in both the micro- and meso-habitat scale analyses. The negative interaction observed between these two habitat variables further emphasises the crucial role played by soil conditions in the foraging habitat selection process. Soil moisture depends on several site-specific parameters such as very local microtopography and vegetation circumstances (Janowicz, Gray & Pomeroy 2003). We suggest that these fine-grained habitat features might be more important than the general landscape configuration: they could notably explain why there was a weak selection for north-exposed topography at the meso-scale. Altogether it seems that habitat heterogeneity within individual home ranges, because it guarantees the retention of moist and soft soil patches in the last stages of the breeding season, is a capital requirement of breeding Ring Ouzels. This quest for mosaic habitats, such as alpine timberline ecotones, has already been demonstrated for alpine Ring Ouzels at the landscape scale (von dem Bussche *et al.* 2008; Ciach & Mrowiec 2013).

In addition to these edaphic factors, we could show that short grass swards were clearly preferred by Ring Ouzels, in accordance with several studies on this species (e.g. Burfield 2002; Sim *et al.* 2013) and other ground-foraging farmland insectivorous birds (e.g. Arlettaz *et al.* 2012; Tagmann-Loiset *et al.* 2012). In line with the food abundance vs food accessibility interpretation above, this preference is likely to result from a better prey accessibility for a ground-foraging predator, but here enhanced prey detectability may well play an additional role (Schaub *et al.* 2010; Arlettaz *et al.* 2012). The fact that AG (bare ground and/or leaf/needle litter) remained secondary as a habitat predictor might be simply due to a generally high accessibility in foraging

surfaces with fairly short grass cover. As earthworm biomass positively correlates with grass sward density (Curry 2004), prey accessibility seems to be more decisive than total abundance for foraging habitat selection. This is in line with previous research, showing that earthworm abundance is a poor predictor of Ring Ouzel foraging occurrence in Scottish breeding grounds (Burfield 2002). In the present study, the importance of grass height was particularly pronounced at the meso-habitat scale, suggesting that birds selected areas with predominantly short grass in a first step. This also explains the tiny variation between vegetation height at foraging vs random points at the micro-scale despite selection of shorter grass stalks was still evidenced. Altogether, these results suggest that prey accessibility plays a prominent role in meso-habitat selection, whereas soil conditions determine micro-habitat selection.

All three top habitat predictors showed seasonal variation, in direct relation to the snow-melting pattern. Snow cover is one major climatic factor affecting alpine ecosystems (Beniston 2003; Beniston 2012). Firstly, the melting of the snowpack provides water in spring, which determines soil conditions later in the season. The pattern was very distinct in our study area, with a progressive decrease in soil moisture and penetrability during the course of the reproduction period. This also means that patches with adequate soil conditions for foraging become increasingly scarce as the season progresses. Secondly, snowmelt advancement defines the onset of the annual vegetation cycle (Beniston 2012), dictating the phenology of the alpine fauna too. In our study, vegetation height increased quite fast: as short grass cover is a clear Ring Ouzel's breeding requisite, the time window available for reproduction is short. On the other hand, we could not evidence a clear direct foraging association

with the snow melting front, contrary to our prediction. However, the snowmelt was relatively early in 2015 and most snow was gone by the time the first pairs had started feeding their nestlings, meaning that our sample size was rather small for a proper analysis of that relationship. Nonetheless, our univariate model reveals that some relationship must exist, which is corroborated by field observations: early in the season, the first radiotracked individuals definitely exploited the vicinity of melting snow patches situated close to their nests. Additional years of sampling would be necessary to clear up this dependency upon the snow melting front.

### **Conservation implications**

A future goal of conservation research on the Ring Ouzel will be to disentangle the effects of climate and land-use change on the species' foraging ecology and population dynamics, though these two factors could act either singly or synergistically.

Climate warming is more acute at high elevation in the Alps than in the nearby lowlands (Beniston 2012; Gobiet *et al.* 2014). The spring snowmelt will hence be advanced and accelerated, while precipitation in the form of rain can only exacerbate the whole process (Beniston 2003; Beniston 2012). A vertical seasonal shift in the snowpack will ultimately lead to an altitudinal shift in suitable soil conditions for the Ring Ouzel. This risks creating some mismatch between species' trophic and breeding site requirements. In effect, alpine Ring Ouzels nest mostly in trees, which at a point might no longer be present where suitable soil conditions occur for efficient foraging. To which extent these birds can adapt to such drastic alterations of environmental conditions remains

unknown. The obstacle to foraging represented by a much denser grass sward resulting from anticipated vegetation phenology will further complicate Ring Ouzels' life cycle accomplishment. Last but not least, more weather variation is predicted by future climate projections, with more frequent droughts and floods (Beniston 2003), which would dramatically increase spatiotemporal fluctuations in soil conditions. However, it should be recalled that climate model projections, even if they have gained in precision, are still coarse (Beniston 2012). In the end, landscapes with complex terrain, which provide particularly heterogeneous habitat conditions, may offer some buffer for coping with environmental changes (e.g. Visinoni *et al.* 2015). A possibly less concerning issue relates to the migratory behaviour of the Ring Ouzel. The main wintering grounds are seemingly in the Atlas mountain range and possibly also in Spain (Burfield 2002). Swiss Ring Ouzels tend to depart late from their breeding grounds (September-October), while they return quite early (March-April), with a few individuals even attempting to overwinter in the Alps when weather is not too adverse (Maumary, Valloton & Knaus 2007). Given that they are short-distance migrants, we speculate that Ring Ouzels may be able to adjust migration phenology to overall environmental change contrary to what is observed in long-distance migrants (Both *et al.* 2010).

Concerning land-use changes, the trends are contrasted. On the one hand, one observes abandonment of traditional grazing practices in many alpine areas, which leads to rapid encroachment by woody vegetation succession (Tasser & Tappeiner 2002; Laiolo *et al.* 2004) and ultimately to a loss of the habitat mosaic typical of timberline ecosystems (Patthey *et al.* 2012). On the other hand, agricultural intensification, which dramatically alters

vegetation structure as well as plant and arthropod communities (Andrey *et al.* 2014), is more and more spreading to accessible areas at higher elevations (Tasser & Tappeiner 2002; Graf *et al.* 2014). Both aspects represent another potential threat for the Ring Ouzel. To which extent the sprawl of outdoor leisure infrastructure (implying e.g. soil compaction) and activities represent an additional threat ought to be considered (Laiolo & Rolando 2005; Arlettaz *et al.* 2007, 2015).

This study provides first hints about the challenge faced by Ring Ouzels in their alpine environment. However, we believe that before providing concrete guidance for habitat management, it will be necessary to disentangle the effects of climate and land-use change, an adaptation of the latter potentially offering some potential for combatting the detrimental effects of the former, as demonstrated in other ecosystems (Braunisch *et al.* 2014).

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## TABLES

**Table 1:** List of the 19 habitat variables mapped at each foraging and random plot

Habitat predictors	Median $\pm$ median absolute deviation (0:1 counts)		
	Foraging plots (n = 145)	Random plots (n = 580)	
<b>Ground cover variables (%)</b>			
1	Brown (old) vegetation	$8 \pm 6$	$6 \pm 4$
2	Green (new) vegetation	$47 \pm 27$	$60 \pm 25$
3	Accessible ground (bare ground + litter)	$28 \pm 20$	$10 \pm 9$
4	Mineral (rock, stones)	$1 \pm 1$	$1 \pm 1$
5	Woody plants*	$0 \pm 0$ (110:35)	$0 \pm 0$ (450:130)
6	Dead lying wood	$1 \pm 1$	$1 \pm 1$
7	Moss*	$0 \pm 0$ (107:38)	$0 \pm 0$ (440:140)
8	Lichens/dry moss**	$0 \pm 0$	$0 \pm 0$
9	Cow dung*	$0 \pm 0$ (129:16)	$0 \pm 0$ (493:87)
10	Trees/stumps**	$0 \pm 0$	$0 \pm 0$
11	Snow cover**	$0 \pm 0$	$0 \pm 0$
<b>Microhabitat/topography variables</b>			
12	Distance from snow (cm)***	$585 \pm 560.5$	$1225 \pm 1045$
13	Slope (angle°) Exposition (aspect, 0 - 359°)	$16 \pm 6$	$15 \pm 6$
14	- Northing: cosine of aspect	$0.022 \pm 0.738$	$-0.009 \pm 0.697$
15	- Easting: sine of aspect	$0.150 \pm 0.656$	$0.018 \pm 0.703$
<b>Vegetation height variables</b>			
16	Brown (old) vegetation height (cm)	$2 \pm 1$	$2.5 \pm 1$
17	Green (new) vegetation height (cm)	$4.5 \pm 1.5$	$7 \pm 3$
<b>Soil conditions (mean value of 3 measurements)</b>			
18	Soil hardness (kg/cm <sup>2</sup> )	$0.78 \pm 0.32$	$1.07 \pm 0.42$
19	Soil moisture (mVolts)	$750.3 \pm 108.3$	$564.8 \pm 199.3$

\* Variables transformed to a binary variable, because of >70% of 0 values

\*\* Marginal variables (>90% of 0 values), which were removed from the analysis

\*\*\* Only if snow present within a radius <50 m; n<sub>foraging</sub> = 50 and n<sub>random</sub> = 190

**Table 2:** Ranking of the GLMMs within 2 units of  $\Delta\text{AICc}$  from the first-ranked model. All models include individual and stratum as random effects. Fixed effects: HNV, height of green vegetation; MOIST, soil moisture;  $\text{MOIST}^2$ , quadratic term of soil moisture; HRD, soil hardness; AG, accessible ground cover;  $\text{AG}^2$ , quadratic term of accessible ground cover; NRTH, northing of the aspect

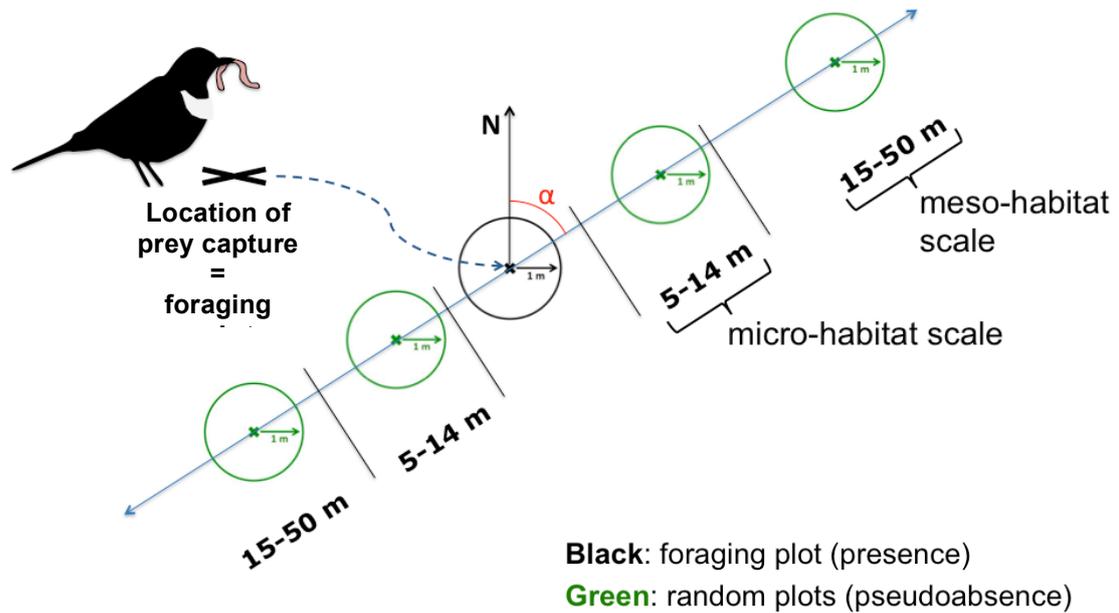
Rank	Model	Deviance	K	$\Delta\text{AICc}$	$w_i$
<b>A. Micro-scale analysis (5 -14 meters)</b>					
1	HNV + MOIST x HRD + $\text{MOIST}^2$ x HRD	475.36	7	0.00	0.39
2	HNV + AG + MOIST x HRD + $\text{MOIST}^2$ x HRD	474.55	8	1.29	0.21
3	HNV + NRTH + MOIST x HRD + $\text{MOIST}^2$ x HRD	474.61	8	1.35	0.20
4	HNV + MOIST + $\text{MOIST}^2$ + HRD	480.90	5	1.38	0.20
<b>B. Meso-scale analysis (15 -50 meters)</b>					
1	HNV + NRTH + MOIST x HRD + $\text{MOIST}^2$ x HRD	412.22	8	0.00	0.52
2	HNV + NRTH + AG + $\text{AG}^2$ + MOIST x HRD + $\text{MOIST}^2$ x HRD	409.38	10	1.39	0.26
3	HNV + MOIST x HRD + $\text{MOIST}^2$ x HRD	416.09	7	1.77	0.22

For each model, the respective deviance, the number of estimated parameters (K), the difference of AICc between that model and the best one ( $\Delta\text{AICc}$ ), and the Akaike weight ( $w_i$ ) are shown.

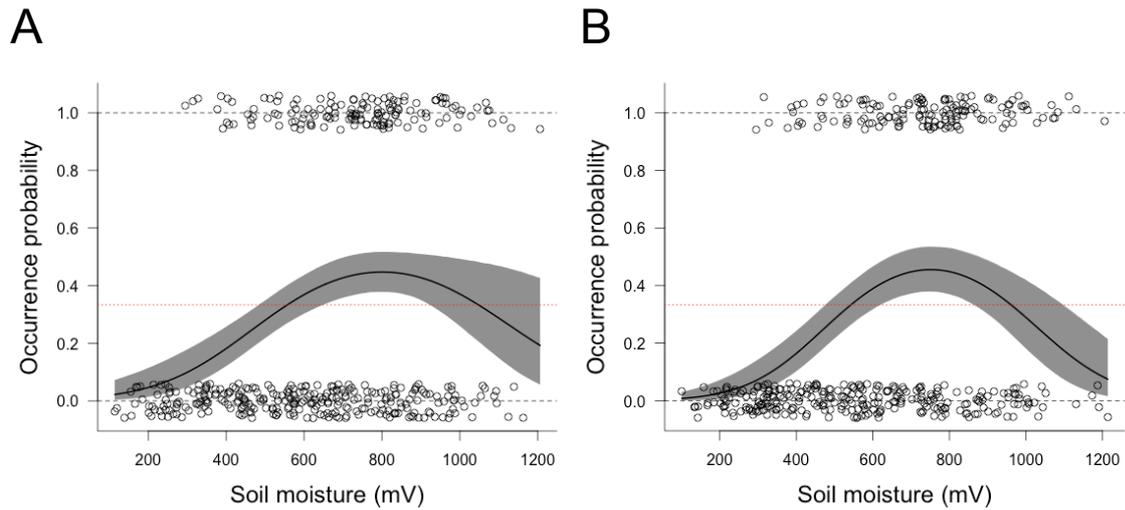
**Table 3:** Regression coefficients, standard error and *P* values of the conditional averaged model on the set of models within  $\Delta AIC_c < 2$

	Coefficient	Standard error	<i>P</i>
<b>A. Micro-scale analysis (5 - 14 m from foraging point)</b>			
Intercept	-0.875	0.127	<0.001
Soil moisture	0.661	0.158	<0.001
Soil moisture (quadratic term)	-0.517	0.149	<0.001
Soil hardness	-0.366	0.131	0.005
Height of green vegetation	-0.267	0.131	0.042
Accessible ground cover	0.113	0.126	0.370
Northing	0.101	0.118	0.390
Soil moisture: soil hardness	-0.226	0.139	0.103
Soil moisture (quadratic term): soil hardness	0.292	0.142	0.040
<b>B. Meso-scale analysis (15 - 50 m from foraging point)</b>			
Intercept	-1.107	0.155	<0.001
Soil moisture	0.737	0.185	<0.001
Soil moisture (quadratic term)	-0.785	0.166	<0.001
Soil hardness	-0.433	0.150	0.004
Height of green vegetation	-0.658	0.155	<0.001
Accessible ground cover	-0.009	0.148	0.950
Accessible ground cover (quadratic term)	-0.211	0.127	0.097
Northing	0.259	0.132	0.050
Soil moisture: soil hardness	-0.580	0.183	0.002
Soil moisture (quadratic term): soil hardness	0.341	0.143	0.017

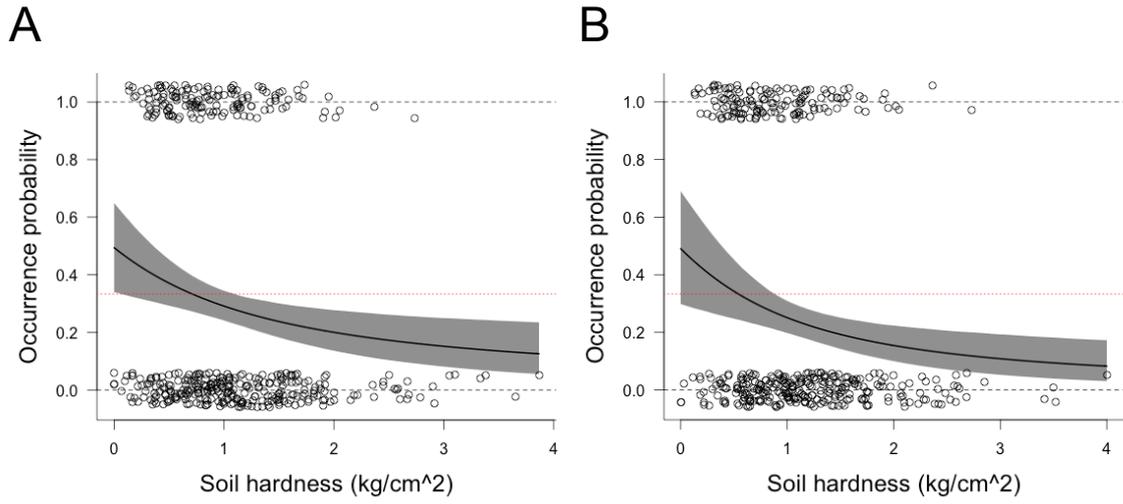
## FIGURES



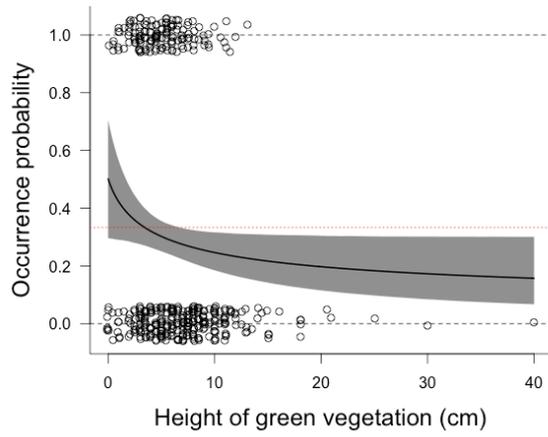
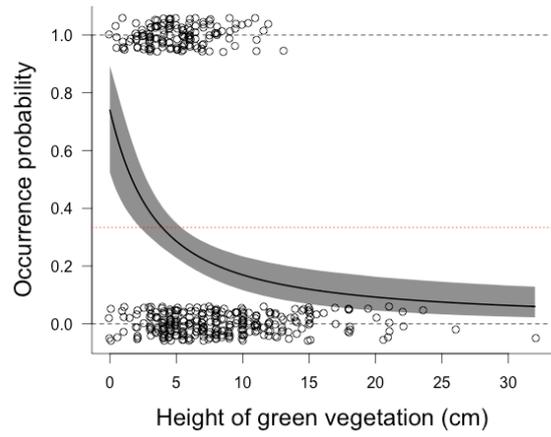
**Fig. 1:** Schematic graph of the sampling design of foraging and random points. The exact location of a prey capture defined a foraging point. From there, at a random angle from north ( $\alpha$ ), 2 pseudo-absence points were randomly generated within 2 distance ranges (5-14 m & 15-50 m). The same was done in the opposite direction ( $+180^\circ$ ), resulting in 4 pseudo-absences for every presence. Around each point, a 1 m radius circle defined the plot where habitat was mapped.



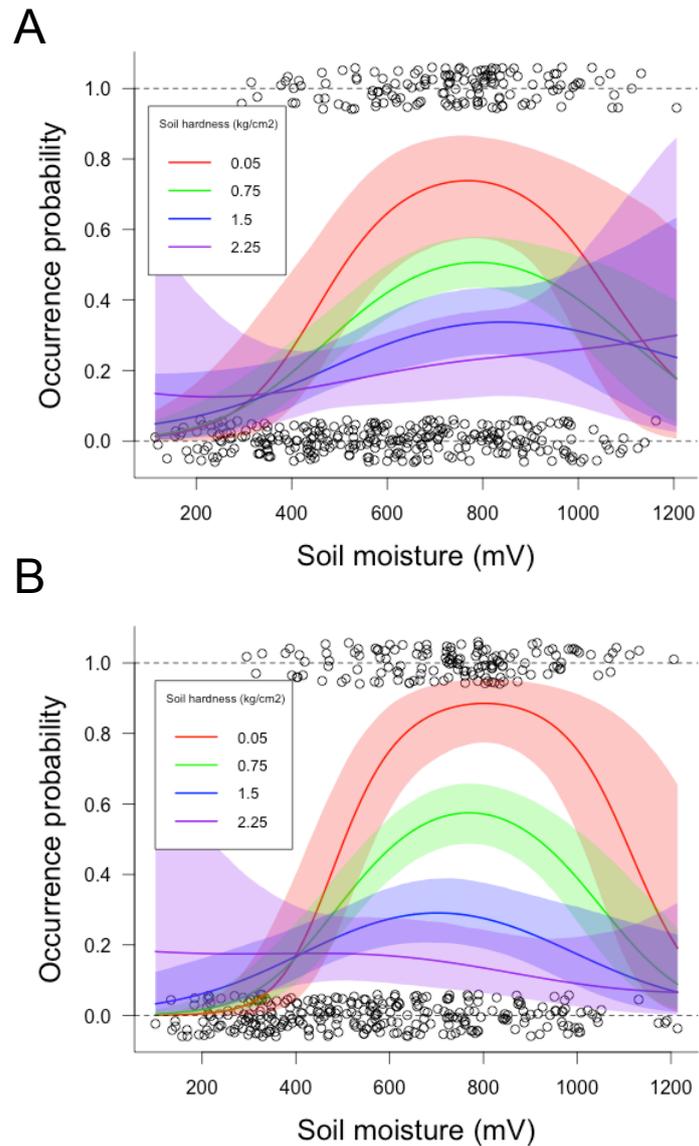
**Fig. 2:** Plots of marginal occurrence probability in relation to soil moisture (mV), based on the averaged model with other variables fixed at their mean, for A) the micro-scale analysis, and B) the meso-scale analysis. The dashed line ( $h = 0.33$ ) depicts the line of neutral selection (above it, the selection is positive, denoting a preference; below it, it is negative, denoting an avoidance). 95% credible intervals are drawn from simulations ( $n = 10'000$ ).



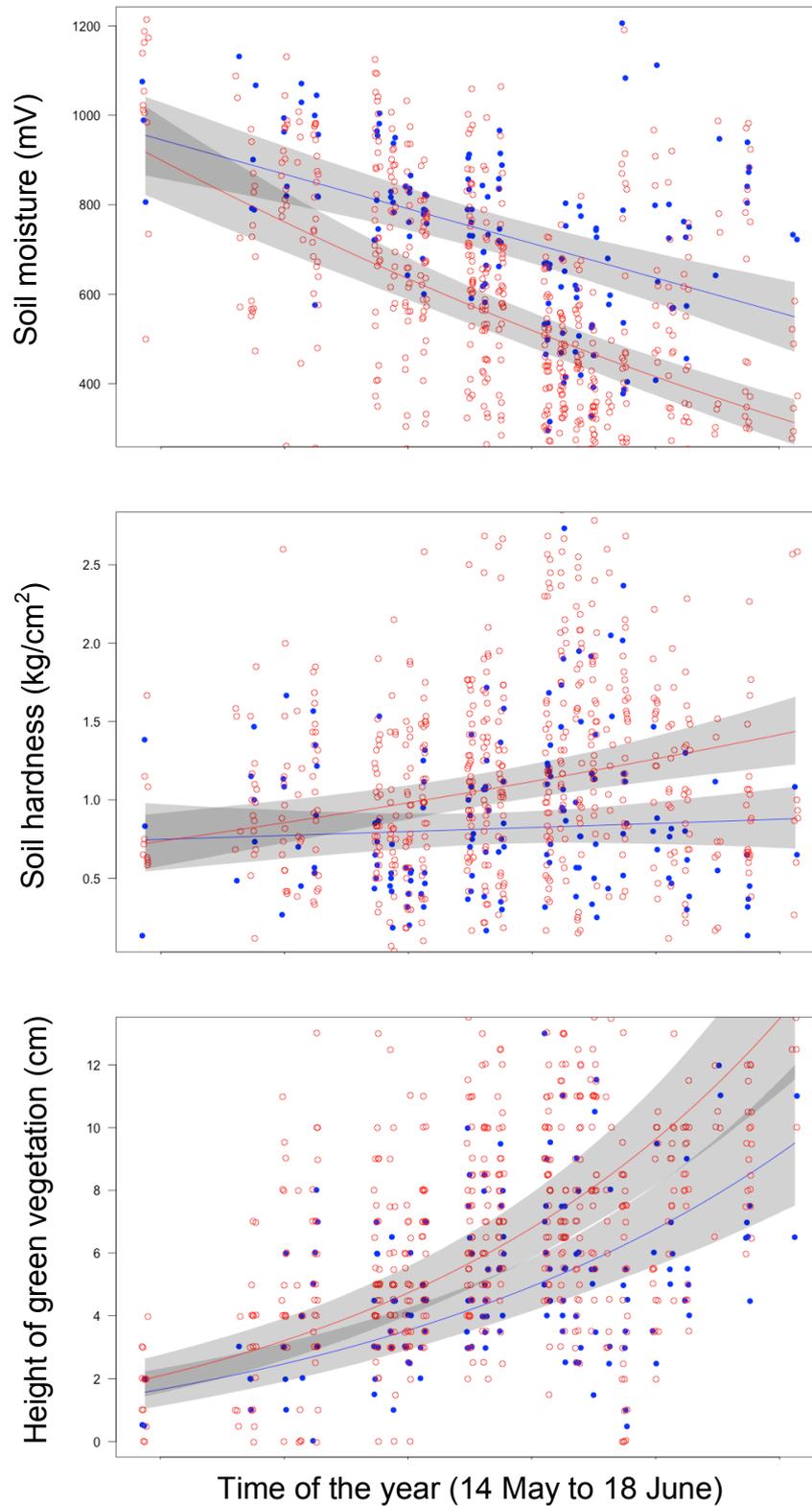
**Fig. 3:** Plots of marginal occurrence probability in relation to soil hardness (kg/cm<sup>2</sup>), based on the averaged model with other variables fixed at their mean, for A) the micro-scale analysis, and B) the meso-scale analysis. Further details, see legend of Fig. 2.

**A****B**

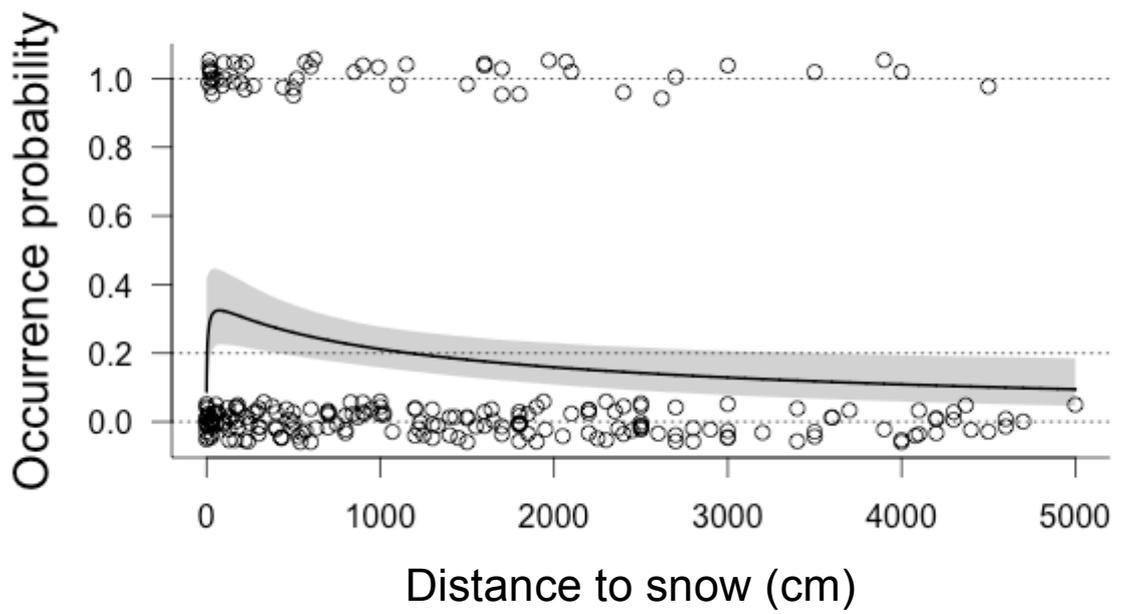
**Fig. 4:** Plots of marginal occurrence probability in relation to height of green (new) vegetation (cm), based on the averaged model with other variables fixed at their mean, for A) the micro-scale analysis, and B) meso-scale analysis. Further details, see legend of Fig. 2.



**Fig. 5:** Plots of marginal occurrence probability showing the negative interaction between soil moisture and soil hardness. Fitted curves are based on the averaged model with soil hardness fixed at different values (colors) and other variables fixed at their mean, for A) the micro-scale analysis, and B) the meso-scale analysis. 95% credible intervals are drawn from simulation ( $n = 10'000$  iterations).



**Fig. 6:** Plots showing the seasonal trends for the 3 key habitat predictors, in foraging plots (blue) and random plots (red). Fitted lines are drawn from univariate mixed linear models, with the variable of interest having been normal-transformed. 95% credible intervals are drawn from simulation (n = 10'000 iterations).



**Fig. 7:** Plot of occurrence probability in relation to distance to snow, based on a univariate model. The dashed line ( $h = 0.2$ ) symbolises the line of neutral selection. Further details, see legend of Fig. 2.

## APPENDICES

### Appendix 1

#### Calibration for a mineral soil

$$a_0 = 1.6$$

$$a_1 = 8.4$$

#### Conversion equation from volts to volumetric water content

$V = \text{volts}$

$\theta = \text{volumetric water content}$

$$\sqrt{\varepsilon} = 1 + 14.4396V - 31.2587V^2 + 49.0575V^3 - 36.5575V^4 + 10.7117V^5$$
$$\theta = (\sqrt{\varepsilon} - a_0)/a_1$$

### Appendix 2

**Table A1:** Regression coefficients, standard error and  $P$  values of the conditional averaged model on the set of models within  $\Delta\text{AICc} < 2$ , on the subset of the data with information on distance to snow ( $n_{\text{foraging}} = 50$ )

	Coefficient	Standard error	$P$
Intercept	-1.566	0.201	<0.001
Soil moisture	0.543	0.245	0.028
Soil moisture (quadratic term)	-0.328	0.236	0.167
Soil hardness	-0.127	0.202	0.532
Height of green vegetation	-0.353	0.205	0.086
Accessible ground cover	0.420	0.189	0.027
Distance to snow	0.195	0.221	0.380
Distance to snow (quadratic term)	-0.309	0.201	0.126
Soil moisture: soil hardness	-0.368	0.229	0.109
Soil moisture (quadratic term): soil hardness	0.364	0.197	0.066

## Declaration of consent

on the basis of Article 28 para. 2 of the RSL05 phil.-nat.

Name/First Name: Barras Arnaud Gian

Matriculation Number: 11-509-684

Study program: Master of Science in Ecology and Evolution

Bachelor  Master  Dissertation

Title of the thesis: Foraging habitat selection by Ring Ouzels *Turdus torquatus* in alpine timberline ecosystems: building the evidence for species conservation management

Supervisor: Prof. Dr. Raphaël Arlettaz

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 para. 1 lit. r of the University Act of 5 September, 1996 is authorised to revoke the title awarded on the basis of this thesis. I allow herewith inspection in this thesis.

Bern, den 30. Mai 2016

Place/Date

Signature

