Factors ruling prey availability for Alpine Ring Ouzel throughout the breeding season: a possible phenological mismatch?

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vorgelegt von:

Ivan Federico Mario Candolfi

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Leiter der Arbeit:

Prof. Dr. Raphaël Arlettaz

Abstract

Biodiversity inhabiting high altitude ecosystems is predicted to be particularly vulnerable to climate and land-use changes. Besides the direct effects that those drivers have on mountain species, there is increasing evidence and awareness that negative impacts might arise through altered species interactions. For alpine bird populations, changing patterns of prey availability might represent a major threat, with a high risk of phenological mismatch impacting reproduction and consequently population dynamics. This study investigates the abundance and accessibility of belowground invertebrates in one study area in the Swiss Alps. In particular, it focuses on earthworms, the staple food source of the Alpine Ring Ouzel (Turdus torquatus alpestris). Our aim was to identify important habitat characteristics and climatic variables that influence spatio-temporal patterns in prey availability during the breeding season. We also compared those patterns to the breeding phenology of Ring Ouzels in order to detect possible phenological mismatches. At the microhabitat scale, we show that soil moisture and organic matter (old grass, litter, dead wood) drive the abundance of earthworms as well as their vertical distribution in the soil. On a broader scale, we document a clear seasonal peak in the availability of earthworms, that is also influenced by precipitation, snowmelt stage, elevation and habitat type. Additionally, we show that, in 2019, the peak in breeding effort occurred after the peak in earthworm availability, which indicates a potential phenological mismatch in terms of efficient reproductive effort. Altogether, our results underline the vulnerability of alpine species in a changing climate, especially through effects that an advanced snowmelt and increasing extreme weather events might have on prey availability. Nevertheless, we stress that a mosaic of grassland and coniferous stands would offer sufficient foraging opportunities for the Ring Ouzel and should thus be maintained through active habitat management, notably via extensive grazing.

Keywords

Alpine birds • Earthworm • Climate change • Land-use change • Habitat selection • Phenology

1. Introduction

Climate change has become a major threat to global biodiversity nowadays (Chamberlain & Pearce-Higgins 2013; Parmesan et al. 2006), and because of the quicker increase in ambient temperatures at higher elevations (Brunetti et al. 2009), species of mountain ecosystems are particularly at risk (Braunisch et al. 2014). Moreover, changes in land-use are also particularly pronounced in mountain regions (Schulz et al. 2018; MacDonald et al. 2000) and concomitantly impact alpine species and limit their distribution (Laiolo et al. 2004). Of major concern are both the abandonment and intensification of mountain grasslands (Laiolo et al. 2004; MacDonald et al. 2000; Spiegelberger et al. 2006). The cessation of agricultural extensive management of grasslands leads to a rapid encroachment by shrubs and forest (Laiolo et al. 2004; MacDonald et al. 2000), resulting in the loss of key habitats for alpine organisms depending on open and semi-open elements (Spiegelberger et al. 2006; Braunisch et al. 2014). On the other hand, still managed areas are increasingly intensified, with detrimental consequences on species composition and ecosystem functioning (Andrey et al. 2014; Spiegelberger et al. 2006). On top of that, the increase in ambient temperatures and altered precipitation regimes induced by climate change (Brunetti et al. 2009) are having large impacts on mountain ecosystems. In the Alps, documented effects such as an advanced snowmelt (Klein et al. 2016) and treeline shifts to higher elevations (Gehring-Fasel et al. 2007) are already impacting species composition and distribution (McCarty 2001; Chamberlain & Pearce-Higgins 2013). In addition, phenology, i.e. the timing of seasonal activities (e.g. breeding, flowering, migration, diapause), is shifting for many organisms under the influence of a changing climate (Walther et al. 2002). The magnitude of this shift often varies between species as it depends on their response to different environmental factors such as temperature or daylength (Visser & Both 2005). This can potentially have detrimental effects on organisms which depend on the relationship and timing with others (Visser & Both 2005).

Due to the extreme environmental conditions in which boreo-alpine birds live (Martin & Wiebe 2004), their breeding season is a very short and sensitive period. Indeed, favourable climatic conditions only last for a given period, and define a brief peak in food availability, through effects on prey abundance and/or accessibility (McKinnon *et al.* 2012; Pearce-Higgins 2010). The challenge is

therefore to reproduce during the time window when the resources are abundant and accessible, making them especially prone to phenological mismatches with their prey (Chamberlain & Pearce-Higgins 2013; Scridel et al. 2018). The latter can have detrimental effects on bird population size and viability (Miller-Rushing et al. 2010; McKinnon et al. 2012) as the high energy demand during breeding period cannot be met (Martin 1987). While effects of global change are increasingly documented for mountain birds, those on invertebrates are often overlooked (Steinwandter et al. 2017; Steinwandter et al. 2018; Martay & Pearce-Higgins 2018), although they provide key functions in ecological systems such as nutrient cycling, soil formation, primary production and herbivory (Lavelle et al. 1997; Lavelle et al. 2006). Importantly, invertebrates represent the main food source for many vertebrate species, therefore playing a major role during the reproduction period (Pearce-Higgins 2010; Niffenegger 2019; Brambilla et al. 2017) since food availability at that time is crucial for reproduction success (Siikamäki 1998) and population viability (Siikamäki 1996; Scridel et al. 2018). Nevertheless, we still know little about the ecology of invertebrates in alpine ecosystems (Steinwandter et al. 2017; Steinwandter et al. 2018; Pearce-Higgins 2010), in particular those having belowground stages. Special attention should be given to their distribution, phenology and weatherrelated responses, as well as to factors affecting their abundance and accessibility. Investigating these little-studied aspects might represent a prerequisite to fully decipher the mechanistic impact of rapid ongoing climate and land-use changes on populations of boreo-alpine bird species.

Soil macrofauna in mountain ecosystems is known to respond to land-use changes, as significant changes in abundance, biomass and composition were found in alpine pastures and meadows after cessation of exploitation (Seeber *et al.* 2005; Steinwandter *et al.* 2017). Concerning intensification, examples come mostly from the lowlands, where negative effects on belowground invertebrate abundance and accessibility through quicker topsoil layer desiccation and compaction were evidenced (Onrust *et al.* 2019). In montane and subalpine grasslands, intensification has large impacts on aboveground community composition (Andrey *et al.* 2014), but studies on belowground communities remain scarce (Steinwandter *et al.* 2018). Climate change, through higher ambient temperatures and an increased frequency of droughts, can as well strongly affect populations of mountain soil invertebrates (Pearce-Higgins 2010). Precipitation regimes and soil humidity are

known to dictate vertical movements of earthworms in the soil (Onrust *et al.* 2019; Edwards & Bohlen 1996), which are hence no more accessible to birds in dry and hot conditions. Therefore, climate and land-use changes may affect populations of boreo-alpine birds through their impacts on prey availability: on one side, land-use change is altering mostly the abundance and composition of important soil macrofaunal organisms (Andrey *et al.* 2014; Seeber *et al.* 2005; Steinwandter *et al.* 2017), while on the other side, temperature and precipitation changes may affect their abundance and accessibility, and phenology thereof (Pearce-Higgins 2010; Edwards & Bohlen 1996).

In this study, we focused on the relationship of the Alpine Ring Ouzel (Turdus torquatus alpestris) with its staple food source, earthworms (Lumbricidae). This thrush species breeds in semiopen coniferous forest in mountain ranges of southern and central Europe, especially at the timberline between 1200-2200 m a.s.l (Schmid et al. 1998; Ciach & Morwiec 2013), therefore experiencing all changes and threats mentioned before. Recent declines of the species in central Europe (e.g. -36% since 1990 in Switzerland; Swiss Ornithological Institute 2019) suggest that it could be responding to climate change. As a consequence, the Ring Ouzel is now red-listed in Switzerland and within the seven bird species with the highest priority for conservation (Keller et al. 2010a; Keller et al. 2010b), urging further research on its ecology to understand factors of the decrease. Previous studies in the Alps exist and have focused mostly on the selection of the foraging habitat (Barras 2016; Barras et al. 2020; Ettlin 2016; Berclaz 2017; Marti 2018). The importance of short vegetation, soft and moist soils was evidenced, highlighting the constraint of a very brief time window with ideal foraging conditions. Furthermore, factors driving nest site selection (Candolfi 2018) and nestling diet (Hunziker 2019; Niffenegger 2019) have been investigated. Yet, studies focusing on the ecological requirements, availability and phenology of Ring Ouzel's prey are missing. A better understanding of those aspects might be pivotal to assess the vulnerability of the Ring Ouzel to global change, as several authors suggested that low prey availability in hot and dry years might be an important constraint (Barras et al. 2020; Pearce-Higgins 2010; Sim et al. 2015).

Our main aim was hence to gain deeper insights into the key role of prey availability during the breeding season. We used regular and simultaneous soil sampling and bird population monitoring to identify (1) which habitat factors drive both the abundance and accessibility of

belowground invertebrates (2) how their availability varies across the breeding season and (3) how well it matches with the breeding phenology of Ring Ouzels. We further discuss those results in the light of known foraging habitat preferences of the species and discuss implications in the context of current climate and land-use changes in alpine timberline ecosystems.

2. Material and Methods

2.1 Study area

The study was conducted in the central Swiss Alps in the canton of Valais, which are characterised by a continental climate with hot and dry summers and cold and partially wet winters. The study area was located in the community of Ayent (46°19'50" N, 7°25'40" E) and covers 205 ha ranging from 1800 to 2200 meters above sea level (m asl), broadly representing the timberline zone. Dominated by Norway Spruce (*Picea abies*) and rather dense at lower altitudes, the forest gradually opens and extends until an elevation of around 2100 m asl, with an increasing occurrence of European Larch (*Larix decidua*). The zone is used as a summer pasture from mid-June to mid-September, a common and widespread tradition in the Swiss Alps (Schulz *et al.* 2018) that results in a habitat mosaic of grasslands interspersed with patches of coniferous forest or isolated trees. These characteristics represent a particularly attractive zone for breeding Ring Ouzels (von dem Bussche *et al.* 2008) which are present there at a high density.

2.2 Data collection

The study area was first divided into three different habitat types (grassland, open forest and dense forest) by visual classification based on aerial pictures. Four elevation bands of 80 m span each (1820-1900; 1900-1980; 1980-2060; 2060-2140 m asl) were also defined. Within each habitat type in each elevation band, two sampling sites of 100 m² (squares of 10x10 m) were selected, resulting in 24 sampling sites (Fig. 1). One of the two sampling sites per habitat patch was characterised by

an early snowmelt (hereafter "ES site") and selected towards the end of April, when the first snowfree patches appeared across the study area. The other sampling site was representative of a late snowmelt (hereafter "LS site") and defined towards the end of May, when much fewer snow patches remained. The ES and LS sites of a pair were always located in closest vicinity in order to minimize variability (e.g. in soil conditions or ground vegetation) apart from their snowmelt stage and the phenological stage of the vegetation. This resulted in 12 ES sites sampled on a weekly basis from May 1st to July 5th (10 sampling sessions) and 12 LS sites sampled on a weekly basis from May 30th to July 6th (6 sampling sessions). This period covered the whole breeding season, from incubation to post-fledging dispersal. During each sampling session and at each sampling site, two soil cores of 18x18 cm and 10 cm depth were extracted with a spade two meters apart from each other. The extracted soil cores were subsequently horizontally divided at a depth of 5 cm to separate prey items in the upper and lower layers. This was done in order to differentiate between temporary accessible (upper layer) and inaccessible (lower layer) prey items for the Ring Ouzel (Onrust 2017). Finally, by merging prey items from the two layers together, we obtained the representative total earthworm abundance of the given soil core. Each soil core was sorted on the field for a maximum of 7.5 minutes per layer, crumbling it on a white sheet and collecting all invertebrates. The extracted soil was subsequently returned to its original place in order to minimize disturbance, and invertebrates were kept and stored in plastic tubes filled with 70% ethanol until identification and counting in the lab. The location of the pair of soil cores in each sampling site was randomly defined and changed for each sampling session. It was always at least 1 m apart from any previously extracted soil core. All ES sites were always sampled on a single day and LS sites on the following day, except once (7th sampling session), when the sampling of the latter was postponed by one day due to bad weather conditions. Sampling sessions were always separated by 5-7 days, except for the last sampling session that occurred 10 days after the previous one in order to investigate earthworm availability later in the season and extend the sampling period.

Furthermore, during each sampling session, a set of habitat variables (listed in Table 1) were measured in the whole 10x10 m sampling site (further referred as the sampling site scale) and in a 1m radius area around each of the two extracted soil cores (further referred as the soil core scale).

Sampled habitat variables were classified into six main categories: ground cover, vegetation and soil conditions (measured at the soil core scale) and topography, climatic and soil composition (measured either at the sampling site or at the study area scale; Table 1). Ground cover variables consisted of seven classes: snow, mineral (gravel and rock), dead wood (lying trunk and branches), litter (coniferous needle litter), bare ground, new grass (new green annual living plants) and old grass (old brownish dead lying plants from the previous year) which were assessed as cover percentage. Vegetation variables were grass height and patchiness (ordinal 1-3 depending on how patchy was ground vegetation in the plot). Regarding soil conditions, we measured soil moisture as the conductivity in milliVolts (mV) in both layers (upper 5 and lower 5 cm of the soil core) using a specific dual probe with two 51-mm rods (SM150; Delta-T, Cambridge, UK). Soil penetrability was measured with a penetrometer (EL 29-3729; ELE International, Loveland, CO, USA) that indicated the force (kg/cm²) needed to insert a metal tip to a depth of 6.35 mm into the soil surface. Concerning variables measured at the sampling site scale, 50 ml of soil were collected once for each sampling site, dried at 50°C for 48h, sieved to < 2 mm and processed in the lab in order to retrieve seven soil composition variables: C, N, S, sand, silt and clay concentration and pH. Soil texture was measured with laser diffraction (Mastersizer 2000, Malvern Instrument GmbH, Herrenberg, Germany) according to Ryzak & Bieganowski (2011). For soil pH and C, N and S concentration, measurements samples were previously milled with a ball mill (PM 200, Retsch, Haan, Germany). Soil pH was measured with a pH electrode (soil:solution ratio 1:2.5 in 0.01 M CaCl₂), whereas C, N and S concentration were determined by dry combustion and analysis of released gases with a CNS analyser (vario EL Cube, Elementar Analysensysteme, Langenselblod, Germany). Regarding topography variables, aspect (northness and eastness) and slope were measured with a compass, elevation with a GPS and distance to snow was counted with steps under 50 m, roughly estimated beyond that. For what concerns climatic variables, ground temperature was retrieved on an hourly basis through two iButtons placed 5 cm belowground in every sampling site corner, whereas air temperature was retrieved from two iButtons placed at the centre of the study area in a permanently shaded location 0.5 m aboveground. Precipitation (mm/hour) was retrieved from the nearest meteorological station located in Anzère (46°30'52" N, 7°40'76" E; 1614 m asl; 3.2 km from the study area).

Concerning Ring Ouzel breeding phenology, four walk transects (one per elevation band; see Figure 1) were visited on a weekly basis from May 23rd to July 13th for a total of eight sessions, between 6-10 am. During each visit, all Ring Ouzel sightings were pin-pointed on a map along with their associated atlas code, i.e. an international coding system to describe main behaviour and level of breeding evidence (possible, probable or certain; see Appendix S1).

2.3 Statistical analyses

We first fitted models of prey abundance at the soil core scale with habitat variables measured at the same resolution as explanatory variables (see Table 1), using generalised linear mixed-effects model (GLMM) with a Poisson error distribution in the R-package *Ime4* (Bates *et al.* 2015). Habitat variables were included as fixed effects, whereas non-independence of the data coming from the same sampling site was accounted for with a random effect. Models were always fitted with, as response variable, prey abundance in both (hereafter total) or in a single soil layer, either the upper or the lower one. Regarding soil moisture, as it was retrieved for both layers, values of this explanatory variable refers to the corresponding analysed layer if not specified differently. For the analysis of total abundance, we considered the mean soil moisture over the two layers.

We ran a similar analysis at the sampling site scale, this time summing up prey abundance in the two soil cores, but still fitting independent models for total or single-layer prey abundance. At this scale, we also investigated the phenology, therefore including Julian date (linear and quadratic terms) as well as climatic variables as explanatory variables, using again a Poisson GLMM with sampling site ID as a random effect. To test for the effect of soil composition and topographical variables, we first averaged response variables over all sampling sessions, as those explanatory variables were measured only once and should not vary over such a short timeframe. Overdispersion in GLMM models was checked for with function *dispersion_glmer* from the R-package *blmeco* (Korner-Nievergelt *et al.* 2015).

Preceding model selection, all ground cover variables were arcsin-square-root transformed to give higher importance to small proportion values, and subsequently standardized (mean = 0,

standard deviation = 1) as all other explanatory variables. For litter and soil moisture, as we hypothesised that those variables could have a hump-shaped relationship to invertebrate abundance, both linear and squared terms were tested. Then, we fitted univariate models for each variable corresponding to each analysis (see above): soil core scale, sampling site scale for climate variables and sampling site scale for topographical and soil composition variables. In order to avoid collinearity in multivariate models, the variables resulting significant at the univariate level were tested for collinearity with Spearman's correlation coefficient, retaining only variables with $|\mathbf{r}| < 0.7$ and showing P < 0.1 in univariate models for the next step, i.e. multivariate models selection.

With the resulting variables from the selection described above, a list of all possible candidate models was generated and ranked by AICc (Akaike Information Criterion) using the *dredge* function from the R-package *MuMln* (Bartoń 2015). Best models were defined as those within Δ AICc < 2 from the first-ranked model after excluding models with uninformative parameters, i.e. models that contained additional parameters compared with better ranked models but with a higher AICc value (Arnold 2010). Best model performance was evaluated by calculating the R-squared with the function *r.squaredGLMM* from the R-package *MuMln*. Estimates reported afterward for the different multivariate analysis always refer to the best model as it always showed consistent coefficient estimates with all other retained models of the same analysis.

In addition to that, we also tested if prey abundance phenology in the upper layer (i.e. accessibility) would vary across elevation, habitat type and snowmelt stage (ES or LS sites). For this, we fitted an individual Poisson GLMM for each of the three categorical variables, including Julian date (linear and quadratic terms) and interaction with the latter as explanatory variables, with again plot ID as a random effect.

For the analysis of the Ring Ouzel breeding phenology, we kept only observations with atlas code 8 (e.g. alarming adults) and atlas code 13 (e.g. fledglings). The number of alarming adults should give an indication of nests with nestlings or where fledging already occurred and should hence peak when most adults are provisioning chicks. The number of fledglings is a precise indication of when fledging occurs, so that it should peak a bit later. For our analysis we assumed that both cases reflect the fledging date. It means that parents had already provisioned their chicks

for 12-14 days (we assumed 14) before the observation and will continue to do so for another two or three weeks (Cramp 1988; we assumed again 14 days) after the observation. For this reason for each session and over all four transects, we summed observations of alarming adults (atlas code 8) and those of fledglings (atlas code 13) and transformed that number, extended for the 14 days before and after the observation, into the percentage of total observations over the whole season for a given atlas code. Finally, to compare Ring Ouzel breeding phenology with earthworm phenology, we fitted three different models: 1. a Poisson GLMM of total prey abundance at the sampling site scale against Julian date (linear and quadratic terms) with plot ID as random effect 2. a linear model of the percentage of alarming adults against Julian date (linear and quadratic terms). All three fitted curves were displayed on a single plot to visually assess the overlap or mismatch.

All analyses were performed using the software R 3.6.1 (R Development Core Team 2019). Plots of prey abundance against a given variable were produced based on model-averaged coefficients (from models within Δ AlCc < 2), or best model coefficients if only one model was retained. 95% credible intervals around the regression line were obtained from the 2.5% and 97.5% quantiles of the posterior distribution obtained with 1'000 simulations using the R-package *arm* (Gelman and Su 2015), following Korner-Nievergelt *et al.* (2015).

3. Results

In total 384 soil cores were collected from the 24 sampling sites, 240 from the ES sites and 144 from the LS sites. A total of 2205 individual earthworms were extracted from the soil cores, 1317 from the upper layer and 888 from the lower layer. Nine different species (*Lumbricus ssp., Aporrectodea caliginosa, A. chlorotica, A. rosea, A. longa, Octalasium cyaneum, O. lacteum, Dendrobaena octaedra* and *Allolobophora icretrica*) were identified, although the majority of earthworms (77%) had no clitellum, indicating immature individuals that could not be visually identified to species level (see Appendix S2). Therefore, all earthworm species were considered together in further statistical analyses. Regarding the other sampled invertebrates, we found individuals from various taxonomic

groups: *Diptera* adults and larvae, *Coleoptera* adults and larvae, *Lepidoptera* larvae, *Hymenoptera* larvae, *Chilopoda* and *Diplopoda*. However, all groups were present in much smaller numbers: from a minimum of one *Diptera* adult to a maximum of 174 *Coleoptera* larvae, for a total of 471 items identified (see Appendix S3). Given low sample size and the marginal importance of those other taxa as food source during the breeding season (Hunziker 2019; Niffenegger 2019), those were not considered in further statistical analyses.

3.1 Earthworm abundance at the soil core scale

Looking at total earthworm abundance, nine variables showed P < 0.1 (soil penetrability, soil moisture, soil moisture², grass height, patchiness, dead wood, old grass, litter and litter²) in univariate models. Grass height was preferred over new grass cover with which it was correlated (r = 0.85), in order to enable the comparison with the known habitat preference identified by Barras *et al.* (2020). In the multivariate model selection, a final set of five models within Δ AICc < 2 was obtained. The best model explained a relatively low amount of variation: $R^2 = 0.11$. All variables retained in the five models (soil moisture, soil moisture², litter, dead wood, grass height and old grass) showed consistent coefficient estimates, so that the best-ranked model was representative of their effects (Table 2). All variables had a positive effect on earthworm abundance: litter ($\beta \pm se = 0.11 \pm 0.04$, P = 0.009), dead wood ($\beta \pm se = 0.06 \pm 0.03$, P = 0.059), grass height ($\beta \pm se = 0.10 \pm 0.04$, P = 0.016), old grass ($\beta \pm se = 0.07 \pm 0.04$, P = 0.059) and soil moisture ($\beta \pm se = 0.22 \pm 0.03$, P < 0.001), except soil moisture² ($\beta \pm se = -0.03 \pm 0.02$, P = 0.098) suggesting a hump-shaped relationship with an optimum around 800mV, although not significant (Fig. 2).

Regarding earthworm abundance in the upper layer, the exact same variables as for the total abundance were retained for the multivariate model analysis. A final set of four models within Δ AlCc < 2 was obtained, and the best model explained intermediate amount of variation (R² = 0.25). In this case as well, all variables retained in the four best models (soil moisture, soil moisture², litter, litter², dead wood, grass height and old grass) showed consistent coefficient estimates, so that the best-ranked model was again representative (Table 2). All variables had a positive effect on earthworm

abundance: litter ($\beta \pm se = 0.23 \pm 0.07$, P < 0.001), dead wood ($\beta \pm se = 0.07 \pm 0.04$, P = 0.105), grass height ($\beta \pm se = 0.17 \pm 0.05$, P = 0.002), old grass ($\beta \pm se = 0.13 \pm 0.05$, P = 0.005) and soil moisture ($\beta \pm se = 0.38 \pm 0.04$, P < 0.001), except soil moisture² ($\beta \pm se = -0.09 \pm 0.02$, P < 0.001) and litter² ($\beta \pm se = -0.08 \pm 0.04$, P = 0.041) suggesting hump-shaped relationships with an optimum around 800 mV moisture and 60% litter cover (Fig. 3).

For what concerns earthworm abundance in the lower layer, only the quadratic term of soil moisture of the upper layer had P < 0.1 and was kept for multivariate model selection, along with its linear term. A final set of two models with $\Delta AICc < 2$ was obtained: the best model, containing soil moisture and soil moisture² and explained a very low amount of variation ($R^2 = 0.01$), and the null model (Table 2). In detail, soil moisture of the upper layer had a negative non-significant effect ($\beta \pm$ se = -0.06 ± 0.04, P = 0.126) whereas soil moisture² ($\beta \pm$ se = 0.05 ± 0.02, P = 0.041) had a positive effect, suggesting an opposite pattern as in the upper layer, with minimal earthworm abundance at an intermediate soil moisture.

3.2 Earthworm phenology at the sampling site scale

Concerning the phenological analysis of total earthworm abundance, only four variables had a P < 0.1: Julian date, Julian date², ground temperature and precipitations, i.e. the sum of precipitations over three days before the sampling session. Ground temperature was excluded from the multivariate model selection as it was correlated with Julian date (r = 0.78) and the latter better explained earthworm's phenology over time. Only one model within $\Delta AICc < 2$ was obtained after multivariate model selection, with all variables retained (Table 3), although explaining a relatively low amount of variation ($R^2 = 0.10$). Precipitation showed a positive effect on earthworm abundance ($\beta \pm se = 0.13 \pm 0.02$, P < 0.001) whereas Julian date ($\beta \pm se = -0.15 \pm 0.03$, P < 0.001) and Julian date² ($\beta \pm se = -0.14 \pm 0.02$, P < 0.001) showed a negative effect, meaning a hump-shaped relationship with the higher earthworm abundance at the end of May/beginning of June (Fig. 4).

For earthworm abundance in the upper layer, the same three variables as for total earthworm abundance were retained for multivariate model selection, where a single best model was obtained and explained a moderate amount of variance ($R^2 = 0.19$). All three variables were retained in the best model with Julian date ($\beta \pm se = -0.23 \pm 0.04$, P < 0.001) and Julian date² ($\beta \pm se = -0.25 \pm 0.03$, P < 0.001) having a negative effect and showing again an optimum around the end of May/beginning of June, meaning a higher earthworm accessibility during this period. Precipitations ($\beta \pm se = 0.14 \pm 0.02$, P < 0.001) had a positive effect (Table 3; Fig. 5).

Finally, concerning abundance in the lower layer, only precipitation at the univariate level showed a significant relationship and it was the only model retained in the set of best models within Δ AICc < 2, but explained a low amount of variance (R² = 0.01). Precipitation had a positive significant effect (ß ± se = 0.07 ± 0.03, *P* < 0.026) on earthworm abundance (Table 3).

For the analysis of soil composition and topographical variables influence on earthworm abundance, no significant relationship was evidenced at the univariate level. Therefore, we did not run any model selection process.

When looking at the influence of the categorical variables such as elevation band, snowmelt stage and habitat type on the phenology of earthworm accessibility (upper layer), we detected significant effects, while the curvilinear relationship with Julian date was clear (Table 4). In addition, several interaction terms were significant. This means that the temporal patterns of accessible earthworms differed across habitat types, snowmelt stage and elevation band (Fig. 6). We first showed that there was a clear earthworm abundance optimum in grasslands (June 4th) and open forests (May 30th), whereas earthworm abundance was much more constant over time in dense forests, with a small non-significant decline over time (Fig. 6A). Earthworm abundance also showed a quadratic negative relationship over time within all elevation bands (Table 4). However, the abundance peak seemed to slightly differ between them, with higher elevations showing an optimum later in the season compared to lower elevation bands (Fig. 6B). Regarding snowmelt stage, both LS and ES sites had and optimum in earthworm abundance around June 9th, although the peak was much more pronounced in the LS sites (Fig. 6C).

3.3 Ring Ouzel breeding phenology

The peak in the provisioning effort, as assessed from alarming adults, was around June 17th, while the peak in the number of fledglings was a bit later, toward June 24th. Hence, both peaks happened after the peak in earthworm total abundance (May 30th; see Fig. 7). Counting 14 days for the nestling period, this also means that the estimated hatching peak (June 10th) occurred later than maximum earthworm abundance.

4. Discussion

In this study, we provide new insights into the availability of the main food source of a threatened alpine bird species during the breeding season. We show how both fine- and coarse-grained habitat and climatic factors affect spatio-temporal patterns of prey abundance. Our findings are crucial to better understand how land-use and climate may influence belowground invertebrates, here earthworms, hence allowing a mechanistic appraisal of species-prey interactions under global change when combined with known species' preferences of the foraging habitat. In particular, we document a marked seasonal pattern in the availability of earthworms, that is influenced by precipitations, snowmelt stage, elevation and habitat type. At the microhabitat scale, we also highlight important habitat characteristics like the amount of soil moisture and organic matter (grass, litter, dead wood) that drive the abundance of earthworms as well as their vertical distribution in the soil. Additionally, investigating both earthworm and Ring Ouzel phenology during the whole breeding season of the latter, we detected the presence of a potential phenological mismatch, in the sense that the peak in breeding effort during spring 2019 happened after the abundance peak in the staple food source.

When looking at earthworm habitat selection, it seems clear that the availability of food resources plays an important role. At the soil core scale, this is shown by the choice of zones which provide high amounts of organic matter in the form of dead wood, needle litter or old ground vegetation, as already shown in other studies (Onrust *et al.* 2019; Curry & Schmidt 2007; Curry 2004). This means that all three different habitat types (dense forest, open forest and grassland) can potentially provide enough food sources for earthworms and we could not evidence a clear effect

of habitat type on their mean abundance. The effect-size of organic matter on earthworm abundance was larger for the upper layer than for the lower layer and both layers. This suggests that earthworms in the first five centimetres of soil are more influenced by soil surface characteristics than those in the lower one, where conditions are probably spatially more uniform.

Moreover, we evidence the high importance of soil moisture, which is known to strongly influence earthworm abundance and activity (Edwards & Bohlen 1996). Interestingly, soil moisture of the top layer influenced abundance of earthworms in both layers, but in opposite ways: the humpshaped relationship in the upper layer indicated a preference for intermediate soil moisture while this curve was U-shaped in the lower layer. This shows that when moisture conditions are favourable in the soil, earthworm move from the lower to the upper layer, hence becoming accessible to birds. This trend is probably mostly driven by anecic earthworms (Onrust 2017), which undertake verticals movement, whereas epigeic live at the surface and endogeic mainly move horizontally (Bouché 1977). Hence, the accessibility of anecic earthworms might vary a lot, highlighting the importance of a diverse community with species that are available in other soil conditions (e.g. epigeic) and therefore during other times of the year. Results at the sampling site scale suggest that precipitations mainly drive those movements, as we show a higher abundance and accessibility of earthworms in days following rainfall. This is consistent with other studies that reported higher earthworm abundance and activity after rainfall (Martay & Pearce-Higgins 2018). In mountain habitats however, the melt of the snowpack has a big influence on soil moisture too (Resano-Mayor et al. 2019). Indeed, we found both a higher earthworm abundance and accessibility in sites characterised by a late snowmelt.

Those findings highlight the importance of precipitations for earthworm availability. In the form of rain during late-spring and summer, precipitations enable short term increases in earthworm activity. In the form of snow during the winter, precipitations build a snowpack whose melt will result in constant and high soil moisture for a limited period in the spring, in turn boosting earthworm availability during the Ring Ouzel breeding period. As a matter of fact, previous research has shown that prolonged drought periods with high temperatures are particularly detrimental for birds relying on climate-sensitive food sources (Pearce-Higgins *et al.* 2010), as they translate into reduced prey

accessibility but also reduced overall abundance (Pearce-Higgins 2010). Nevertheless, habitat characteristics may buffer such effects to some extent: we showed that earthworm abundance in the top soil layer was much more constant over time in dense forest compared to open forest and grassland. This is most probably due to both the canopy and litter cover, which limit soil desiccation, while higher solar radiation in semi-open and open habitats leads to fast and marked variations in soil moisture (James *et al.* 2003). At the same time, the peak in earthworm accessibility seemed delayed at higher elevations, probably reflecting a later snowmelt phenology. This might represent the proximal mechanism of upward shifts observed for the Ring Ouzel in Switzerland (Knaus *et al.* 2018), as well as for other alpine species in response to climate change (Chamberlain & Pearce Higgins 2013). There is however an upper limit, where soils are not sufficiently developed to harbour belowground invertebrates and where soil formation will probably not keep pace with the rapid increase in temperatures (Kaufmann 2001).

Interpreting our findings in the light of those from Barras *et al.* (2020), we have a clearer picture of the constraints on Ring Ouzel foraging ecology. Barras *et al.* (2020) showed that the species select preferentially foraging sites with intermediate soil moisture and high soil penetrability, within a short grass layer interspersed with patches of accessible ground (either bare or litter covered). We show that some of those habitat characteristics correspond to higher abundance and accessibility of earthworms (Table 2). This is in accordance with findings of Martay & Pearce-Higgins (2020), that showed that the abundance of foraging thrushes was correlated with earthworm abundance in the UK. However, some other habitat characteristics such as low grass height corresponded to lower earthworm abundance. This highlights that foraging habitat selection is probably a trade-off between prey abundance and accessibility/detectability, as already evidenced for several farmland species (Schaub *et al.* 2010). Interestingly, our results, in combination with those of Barras *et al.* (2020), indicate that both prey abundance and accessibility are limited in time, so that they are strong temporal limitations for breeding.

When comparing the breeding phenology with the phenology of prey availability, we detected some indications of a mismatch (Fig. 7), although this was based on data from a single year, which give no indications on the trend over time. The main challenge was to find a representative

phenological indicator, as we could not systematically monitor many nests. Although not perfect, and dependent on detection probability, we chose the weekly percentage of alarming adults and fledglings as two different breeding phenology indicators. Both indicated that the estimated peak in provisioning effort occurred after the peak in prey abundance. This was first surprising, as the year of data collection was colder than the average, with recurring snowfall precipitations until mid-May. In fact, we have indications that most of the early breeding attempts have failed due to cold weather conditions (pers. obs.), leading to many replacement broods and hence delaying the main breeding effort. This is a likely cause of the detected mismatch, which might not be representative of a normal breeding season. Nevertheless, extreme weather events are predicted to increase due to climate change, in particular at higher elevations (Easterling *et al.* 2000). Both drought events and cold storms are challenging for breeding alpine birds (Martin & Wiebe 2004). Although they are adapted to severe environments, the increase in stochastic extreme weather events might represent the biggest threat, more than the linear increase in ambient temperatures. This additional factor, by affecting reproductive success and nestling survival, can really put at stake the long-term viability of some alpine birds' populations (Martin & Wiebe 2004).

Interpreting our findings in the light of the predicted development of the timberline ecotone due to ongoing land-use and climate change gives us some interesting discussion points. In the lowlands, land-use intensification seems to be a major threat for belowground invertebrates as it favours soil desiccation and compaction (Onrust *et al.* 2019), which is probably the case also at higher elevation as low grass height increase sward temperature (Gardiner & Hassall 2009). On the other hand, land-use abandonment is as well impacting composition and abundance of invertebrate communities (Seeber *et al.* 2005; Steinwandter *et al.* 2017) as well as alpine birds (Laiolo *et al.* 2004). Earthworms have been reported to decrease in abundance in meadows and pastures in the second decade after management abandonment in mountain grasslands, but effects vary a lot across taxonomic groups (Seeber *et al.* 2005; Steinwandter *et al.* 2017) and may change on longer term, i.e. when mature forest establish. Climate change can concomitantly accelerate soil desiccation through higher ambient temperatures, but as well through changes in precipitations regimes (Miralles *el al.* 2014). In particular, winter snowfalls and spring temperatures play a major

role in defining snowpack thickness at the start of the breeding season. The melt of this snowpack, in turn, provide soil moisture in the upper layer and enhance accessibility of important prey invertebrates (Resano-Mayor *et al.* 2019). This water supply is much more constant over time in comparison to stochastic rain events, making food resources more predictable for mountain birds. We also show that earthworm availability is more constant over time in closed forests compared to grasslands, suggesting that they may work as refuge foraging areas in hot and dry conditions (James *et al.* 2003). Overall, it appears that a mosaic of grassland and dense to open forest patches might represent the best management option for the Ring Ouzel (von dem Bussche *et al.* 2008) and associated treeline bird species (Patthey *et al.* 2012; Jähnig *et al.* 2018).

Given the sensibility of mountain bird populations to variations in prey abundance and accessibility (Pearce-Higgins 2010; Pearce-Higgins et al. 2010), it is pivotal to assess the impacts of climate and land-use change upon prey populations. In this study, we focused on a single bird species and its staple food source, but our findings can be relevant for other mountain species foraging principally on earthworms or other climate-sensitive prey such as Tipulidae (Pearce-Higgins 2010; Resano-Mayor et al. 2019). It is now central to integrate this knowledge in order to develop active management actions to buffer negative effects that climate and land-use changes are having on invertebrate prey, and hence secure sufficient food sources during the breeding season. As mentioned before, a mosaic of grasslands and coniferous patches should be beneficial by providing more numerous and constant foraging opportunities. In this respect, traditional farming with extensive grazing helps maintaining this mosaic of different habitats (Laiolo et al. 2004; Schulz et al. 2018) and provides higher prey abundance and accessibility compared to encroached areas (Seeber et al. 2005; Schaub et al. 2010; Steinwandter et al. 2017). Concerning negative effects of climate change, their mitigation through active management is more challenging, although above-mentioned measures might be beneficial. In addition to habitat management, long-term studies focusing on predator-prey associations, in particular on phenological aspects, appear important to readily assess the impact of ongoing global change. One crucial aspect is to understand if phenological mismatches are widespread and increasing in frequency, and the role of extreme weather events in long-term population viability.

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7. References

- Andrey, A., Humbert, J.Y., Pernollet, C. & Arlettaz, R. (2014) Experimental evidence for the immediate impact of fertilization and irrigation upon the plant and invertebrate communities of mountain grassland. *Ecology and Evolution*, 4, 2610-2623.
- Arnold, T.W. (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management*, **74**, 1175–1178.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using Ime4. *Journal of Statistical Softwer*, **67**, 1–48.
- Barras A.G. (2016) Foraging habitat selection by Ring Ouzel *Turdus torquatus* in alpine Timberline ecosystems: building the evidence for species conservation management. MSc Thesis, University of Bern.
- Barras, A.G., Marti, S., Ettlin, S., Vignali, S., Resano-Mayor, J., Braunisch, V. & Arlettaz, R. (2020) The importance of seasonal environmental factors in the foraging habitat selection of Alpine Ring Ouzels *Turdus torquatus alpestris. Ibis,* **162**, 505-519.
- Bartoń, K. (2015) MuMIn: Multi-model inference. R package version 1.43.15. Available at: <u>http://CRAN.R-project.org/package=MuMIn</u> (accessed 01 August 2019).
- Berclaz, C. (2017) Foraging habitat selection by the ring ouzel (*Turdus torquatus alpestris*) in the Swiss Alps. MSc Thesis, University of Lausanne.
- Bouché, M.B. (1977) Strategies Lombricienne. Ecological Bulletins, 25, 122-132.
- Brambilla, M., Cortesi, M., Capelli, F., Chamberlain, D., Pedrini, P. & Rubolini, D. (2017) Foraging habitat selection by Alpine White-winged Snowfinches Montifringilla nivalis during the nestling rearing period. *Journal of Ornithology*, **158**, 277–286.
- Braunisch, V., Coppes, J., Arlettaz, A., Suchant, R., Zellweger, F. & Bollmann K. (2014) Temperate Mountain Forest Biodiversity under Climate Change: Compensating Negative Effects by Increasing Structural Complexity. *PLoS ONE*, **9**, e97718 (97716 p.).
- Brunetti, M., Lentini, G., Maugeri, M., Nanni, T., Auer, I., Böhm, R. & Schöner, W. (2009) Climate variability and change in the Greater Alpine Region over the last two centuries based on multi-variable analysis. *International Journal of Climatology*, **29**, 2197-2225.
- Candolfi, I. (2018) Nest site selection by the Ring Ouzel at the timberline zone in the Swiss Alps. BSc Thesis, University of Bern.
- Chamberlain, D. & Pearce-Higgins, J. (2013) Impacts of climate change on upland birds: complex interactions, compensatory mechanisms ant the need for long-term data. *Ibis*, **155**, 451-455.
- Ciach, M. & Mrowiec, W. (2013) Habitat selection of the Ring Ouzel *Turdus torquatus* in the Western Carpathians: the role of the landscape mosaic. *Bird Study*, **60**, 22-34.
- Cramp, S. ed. (1988) The birds of the western Palearctic. Vol. V. Tyrant flycatchers to thrushes. Oxford: Oxford University Press.
- Curry, J.P. (2004) Factors Affecting the Abundance of Earthworms in Soils. In: C. Edwards (Ed.), Earthworm Ecology (second ed.), *CRC Press*, pp 263-286.
- Curry, J.P. & Schmidt, O. (2007) The feeding ecology of earthworms A review. *Pedobiologia*, **50**, 463-477.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate Extremes: Observations, Modelling, and Impacts. *Science*, **289**, 2068-2074.
- Edwards, C.A. & Bohlen, P.J. (1996) Biology and Ecology of Earthworms. London: Chapman & Hall.
- Ettlin, S. (2016) Foraging habitat selection during the breeding season by the ring ouzel (*Turdus torquatus alpestris*) in the Swiss Alps. BSc Thesis, University of Bern.
- Gardiner, T. & Hassall, M. (2009) Does microclimate affect grasshopper populations after cutting of hay in improved grassland? *Journal of Insect Conservation*, **13**, 97-102.
- Gehring-Fasel, J., Guisan, A. & Zimmermann, N.E. (2007) Tree line shift in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science*, **18**, 571-582.
- Gelman, A. & Su, Y.–S. (2015) arm: Data analysis using regression and multilevel/hierarchical models. R package version 1.10-1. Available at: <u>http://CRAN.R-project.org/package=arm</u> (accessed 01 August 2019).
- Hunziker, Y. (2019) Quantifying the nestling diet of Ring Ouzels in the Swiss Alps. BSc Thesis, University of Bern.
- James, S.E., Pärtel, M., Wilson, S.D. & Peltzer, D.A. (2003) Temporal heterogeneity of soil moisture in grassland and forest. *Journal of Ecology*, **91**, 234-239.
- Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A. & Chamberlain, D. 2018. The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. *Journal of Ornithology*, **159**, 747–759.
- Kaufmann, R. (2001) Invertebrate succession on an alpine glacier foreland. Ecology, 82, 2261-2278.

Keller, V., Ayé, R., Müller, W., Spaar, R. & Zbinden, N. (2010a) Die prioritären Vogelarte der Schweiz: Revision 2010. *Der Ornithologische Beobachter*, **107**, 265-285.

Keller, V., Gerber, A., Schmid, H., Volet, B. & Zbinden, N. (2010b) Liste Rouge Oiseaux nicheurs. Espèces menacées en Suisse, état 2010., pp. 53. Office fédéral de l'environnement, Berne. Station ornithologique Suisse, Sempach.

Klein, G., Vitasse, Y., Rixen, C., Marty, C. & Rebetez, M. (2016) Shorter snow cover duration since 1970 in the Swiss Alps due to earlier snow melt more than later snow onset. *Climatic Change*, **193**, 637-649.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guélat, J., Almasi, B. & Korner-Nievergelt, P. (2015) Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS and Stan. *Elsevier*, 1. edition.

- Knaus, P., Antoniazza, S., Wechsler, S., Guélat, J., Kéry, M., Strebel, N. & Sattler, T. (2018) Swiss Breeding Bird Atlas 2013–2016. Distribution and Population Trends of Birds in Switzerland and Liechtenstein. Sempach: Swiss Ornithological Institute.
- Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A. (2004) Consequence of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology*, **41**, 294-304.
- Lavelle, P., Bignell, D., Lepage, M., Wolters, V., Roger, P., Ineson, P., Heal, O.W. & Dhillion, S. (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology*, **33**, 159–193.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P. & Rossi, J.P. (2006) Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, **42**, S3–S15.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J. & Gibon, A. (2000) Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *Journal of Environmental management*, **59**, 47-69.
- Martay, B. & Pearce-Higgins, J.W. (2018) Using data from schools to model variation in soil invertebrates across the UK: The importance of weather, climate, season and habitat. *Pedobiologia*, **67**, 1-9.
- Martay, B. & Pearce-Higgins, J.W. (2020) Opening a can of worms: Can the availability of soil invertebrates be indicated by birds? *Ecologycal Indicators*, **113**, 106222.
- Marti, S. (2018) Foraging habitat selection of Ring Ouzel *Turdus torquatus* in alpine timberline Ecosystem: assessing model transferability across temporal and spatial scales. MSc Thesis, University of Bern.
- Martin, K. & Wiebe, K.L. (2004) Coping Mechanism of Alpine and Arctic Breeding Birds: Extreme Weather and Limitations to Reproductive Resilience. *Integrative and Comparative Biology*, **44**, 177-185.
- Martin, T.E. (1987) Food as a limit for breeding birds: a life history perspective. *Annual review of Ecology and Systematics*, **18**, 453-487.
- McCarty, J.P. (2001) Ecological Consequences of Recent Climate Change. *Conservation Biology*, **15**, 320-331.
- McKinnon, L., Picotin, M., Bolduc, E., Julliet, C. & Bêty, J. (2012) Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology*, **90**, 961-971.
- Miller-Rushing, A.J., Høye, T.T., Inouye, D.W. & Post, E. (2010) The effects of phenological mismatches on demography. *Philosophical transactions of the Royal Society*, **365**, 3177-3187.
- Miralles, D.G., Teuling, A.J., van Heerwaarden, C.C. & Vilà-Guerau de Arellano, J. (2014) Mega-heatwave due to combined soil desiccation and atmospheric heat accumulation. *Nature Geoscience*, **7**, 345-349.
- Niffenegger, C. (2019) The effects of weather conditions on the nestling diet and provisioning rates of the alpine Ring Ouzel *Turdus torquatus alpestris*. BCs Thesis, University of Bern.
- Onrust, J. (2017) Earth, worm & birds. Groningen: Rijksuniversiteit Groningen. 146 p.
- Onrust, J., Wymenga, E., Piersma, T. & Olff, H. (2019) Earthworm activity and availability for meadow birds is restricted in intensively managed meadows. *Journal of Applied Ecology*, **1**, 1-10.
- Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology, Evolution and Systematics, **37**, 637-669.
- Patthey, P., Signorell, L., Rotteli, L. & Arlettaz, R. (2012) Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. *European Journal of Wildlife Research*, **58**, 59-70.
- Pearce-Higgins, J.W. (2010) Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research*, **45**, 119-130.
- Pearce-Higgins, J.W., Dennis, P., Whittingham, M.J. & Yalden, D.W. (2010) Impacts of climate on prey abundance account for fluctuation in a population of a northern wader at the southern edge of its range. *Global Change Biology.* **16**, 12-23.
- R Development Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <u>http://www.r-project.org/</u>.
- Resano-Mayor, J., Korner-Nievergelt, F., Vignali, S., Horrenberger, N., Barras, A.G., Braunisch, V., Pernollet, C.A. & Arlettaz, R. (2019) Snow cover phenology is the main driver of foraging habitat selection for a high-alpine passerine during breeding: implication of species persistence in the face

of climate change. Biodiversity and Conservation, 28, 2669-2685.

- Ryżak, M. & Bieganowski, A. (2011) Methodological aspects of determining particle-size distribution using the laser diffraction method. *Journal of Plant Nutrition and Soil Science*, **174**, 624-633.
- Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F. Zbinden, N., Jenni, L. & Arlettaz, R. (2010) Patches of Bare Ground as a Staple Commodity for Declining Ground-Foraging Insectivorous Farmland Birds. *PLoS ONE* 5(10): e13115. doi:10.1371/journal.pone.0013115.
- Schmid, H., Luder, R., Naef-Daener, B., Graf, R. & Zbinden, N. (1998) Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und in Fürstentum Lichtenstein 1993-1996. Schweizerische Vogelwarte. Sempach.
- Schulz, T., Lauber, S. & Herzog, F. (2018) Summer Farms in Switzerland: Profitability and Public Financial Support. *Mountain Research and Development*, **38**, 14-23.
- Scridel, D., Brambilla, M., Martin, K., Lehikoinen, A., Iemma, A., Matteo, A., Jähnig, S., Caprio, E., Bogliani, G., Pedrini, P., Rolando, A., Arlettaz, R. & Chamberlain D. (2018) A review and meta-analysis of the effect of climate change on Holarctic mountain and upland bird populations. *Ibis*, **160**, 489-515.
- Seeber, J., Seeber, G.U.H., Kössler, W., Langel, R., Scheu, S. & Meyer, E. (2005) Abundance and trophic structure of macro-decomposer in alpine pastureland (Central Alps, Tyrol): effects of abandonment of pasturing. *Pedobiologia*, **49**, 221-228.
- Siikamaki, P. (1996) Nestling growth and mortality of Pied Flycatchers *Ficedula hypoleuca* in relation to weather and breeding effort. Ibis **138**, 471-478.
- Siikamäki, P. (1998) Limitation of Reproductive Success by Food Availability and Breeding Time in Pied Flycatcher. *Ecology*, **79**, 1789- 1796.
- Sim, I.M.W., Wilkinson, N.I., Scridel, D., Anderson, D. & Roos, S. (2015) Food supplementation does not increase demographic rates in a passerine species of conservation concern. *Nature Conservation*, **10**, 25-43.
- Spiegelberger, T., Matthies, D., Müller-Schärer, H. & Schaffner, U. (2006) Scale-dependant effects of land use on plant species richness of mountain grassland in the European Alps. *Ecography*, **29**, 541-548.
- Steinwandter, M., Rief, A., Scheu, S., Traugott, M. & Seeber, J. (2018) Structural and functional characteristics of high alpine soil macro-invertebrate communities. *European Journal of Soil Biology*, **86**, 72-80.
- Steinwandter, M., Schilck-Steiner, B.C., Seeber, G.H.U., Steiner, F.M. & Seeber, J. (2017) Effects of Alpine land-use changes: Soil macrofauna community revisited. *Ecology and Evolution*, 7, 5389-5399.
 Swiss Ornithological Institute 2019. Breeding population indices. Available at:
- https://www.vogelwarte.ch/en/birds/bird s-of-switzerland/ring-ouzel/maps-and-charts (accessed 31 August 2019).
- Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need of a yardstick. *Proceedings of the Royal Society*, **272**, 2561-2569.
- von dem Bussche, J., Spaar, R., Schmid, H. & Schröder, B. (2008) Modelling the recent and potential future spatial distribution of the Ring Ouzel (*Turdus torquatus*) and Blackbird (*T.merula*) in Switzerland. *Journal of Ornithology*, **149**, 529-544.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389-395.

8. Tables and Figures

Table 1 List of variables measured at the scale of the soil core, sampling site and study area, respectively. Mean values ± standard deviation are displayed for each continuous variable. The patchiness was measured as a categorical variable and counts per level are provided instead.

	Habitat variables	Unit	Mean ± sd
Soil c	ore scale measured variable	e (1m radius)	
Groun	d cover		
1	Snow	%	51+139
2.	Mineral	%	1.6 ± 2.7
3.	Dead wood	%	2.7 ± 3.6
4.	Litter	%	26.3 ± 25.6
5.	Bare ground	%	2.5 ± 4.6
6.	New grass	%	41.4 ± 33.3
7.	Old grass	%	20.5 ± 23.7
Vegeta	ation		
8.	Grass height	cm	5.8 ± 5.1
9.	Patchiness	ordinal (1-3)	155/70/159
Soil co	onditions		
10	. Soil moisture	mV ^a	523.1 ± 128.3
11	. Soil penetrability	kg/cm ²	1.4 ± 0.6
_			
Samp	ling site scale measured va	riables (10x10	lm)
Topog	raphy	•	
1.	Slope	· .	19.6 ± 10.6
2.	Elevation	m asl	1977.1 ± 86.6
3.	Northness	cos(aspect ^o)	0.1 ± 0.5
4.	Eastness	sin(aspect ^o)	0.8 ± 0.4
D. Climat		m	44.8 ± 50
Climat	IC Cround tomporature	° Coloiuo	01.11
U. Soil co		Celsius	9.1 ± 4.1
7	nH	nН	5 + 0 7
7. 8	C (carbon)	рп %	3 0 + 1
9. 9	N (nitrogen)	/0 %	0.3 ± 0.1
10	S (sulphur)	%	0.3 ± 0.1
11	Sand	%	83+25
12	Silt	%	74 + 2 6
13	. Clav	%	17.7 ± 1.8
.0		, .	
Study	area scale		
Climat	ic		
1.	Air temperature	° Celsius	10.1 ± 4.9
2.	Precipitations (3 days' sum)	mm	10.7 ± 10.9
	· · · · ,		

^amilliVolts. ^bexpressed in radians.

Table 2. Environmental variables retained in the set of best models within $\triangle AICc < 2$ in the analysis at the soil core scale for the analysis on (1) earthworm abundance in both layers of the soil core sample (2) in the upper layer and (3) in the lower layer. Coefficient estimates, and Z- and P-values are from the best-ranked model in each analysis, whereas importance of the variable (from 0 to 1) is the sum of Akaike weights from the models where it appears out of all model combinations.

Verieble Estimate Lod Z Dyclus Importance					
variable	Estimate ± so	Z	P-value	Importance	
Total					
Dead wood	0.06 ± 0.03	1.89	0.059	0.86	
Grass height	0.10 ± 0.04	2.41	0.016	0.77	
Litter	0.11 ± 0.04	2.62	0.009	0.88	
Old grass	0.07 ± 0.04	1.89	0.059	0.63	
Soil moisture	0.22 ± 0.03	6.91	<0.001	1.00	
Soil moisture ²	-0.03 ± 0.02	-1.65	0.098	0.79	
Umman					
upper	0.07 . 0.04	4.00	0.405	0.50	
Dead wood	0.07 ± 0.04	1.62	0.105	0.56	
Grass height	0.17 ± 0.05	3.08	0.002	1.00	
Litter	0.23 ± 0.07	3.39	<0.001	1.00	
Litter ²	-0.08 ± 0.04	-2.05	0.041	1.00	
Old grass	0.13 ± 0.05	2.81	0.005	1.00	
Soil moisture up	0.38 ± 0.04	8.65	<0.001	1.00	
Soil moisture up ²	-0.09 ± 0.02	-3.69	<0.001	1.00	
Lower					
Soil moisture up	-0.06 ± 0.04	-1.53	0.128	1.00	
Soil moisture up ²	0.05 ± 0.02	2.04	0.041	1.00	

² quadratic term

Table 3. Variables retained in the set of best models within $\triangle AICc < 2$ in the analysis at the sampling site scale for the analysis on (1) earthworm abundance in both layers of the soil core sample (2) in the upper layer and (3) in the lower layer. Coefficient estimates, and Z- and P-values are from the best-ranked model in each analysis, whereas importance of the variable (from 0 to 1) is the sum of Akaike weights from the models where it appears out of all model combinations.

Variable	Estimate ± sd	Z	<i>P</i> -value	Importance	
Total					
Julian date	-0.15 ± 0.03	-5.52	<0.001	1.00	
Julian date ²	-0.14 ± 0.02	-6.38	<0.001	1.00	
Precipitations	0.13 ± 0.02	6.15	<0.001	1.00	
Upper					
Julian date	-0.23 ± 0.04	-6.38	<0.001	1.00	
Julian date ²	-0.25 ± 0.03	-8.06	<0.001	1.00	
Precipitations	0.14 ± 0.02	5.71	<0.001	1.00	
Northness	0.18 ± 0.11	1.70	0.088	0.43	
Lower					
Precipitations	0.07 ± 0.03	2.23	0.026	1.00	

² quadratic term

Table 4. Effect difference between elevation bands (1st elevation fixed as intercept), habitat type (grassland fixed as intercept), snowmelt stage (early snowmelt fixed as intercept) and Julian date (linear and quadratic term), and interaction thereof, on earthworm abundance in the upper layer. Coefficient estimates, standard error, Z- and P-values are from individual poisson GLMM models for each of the 3 categorical variables.

Variable	Estimate ± sd	Z	<i>P</i> -value	
Habitat type				
Julian date	-0.22 ± 0.08	-2.922	<0.001	
Julian date ²	-0.44 ± 0.07	-6.499	<0.001	
Open forest	0.09 ± 0.28	0.333	0.739	
Dense forest	0.01 ± 0.28	0.028	0.978	
Julian date*Open forest	0.06 ± 0.10	0.620	0.535	
Julian date*Dense forest	0.11 ± 0.09	1.185	0.236	
Julian date ² *Open forest	0.15 ± 0.09	1.750	0.080	
Julian date ² *Dense forest	0.33 ± 0.08	4.028	<0.001	
Elevation band				
Julian date	-0.14 ± 0.07	-2.040	0.041	
Julian date ²	-0.36 ± 0.06	-5.910	<0.001	
2 nd elevation	-0.58 ± 0.31	-1.845	0.065	
3 rd elevation	-0.19 ± 0.31	-0.623	0.533	
4 th elevation	-0.15 ± 0.31	-0.471	0.638	
Julian date*2 nd elevation	-0.34 ± 0.11	-3.069	0.002	
Julian date*3 rd elevation	0.04 ± 0.10	0.457	0.647	
Julian date*4 th elevation	0.08 ± 0.10	0.842	0.400	
Julian date ² *2 nd elevation	0.06 ± 0.09	0.691	0.489	
Julian date ² *3 rd elevation	0.14 ± 0.08	1.666	0.096	
Julian date ² *4 th elevation	0.16 ± 0.08	1.893	0.058	
Snowmelt stage				
Julian date	-0.11 ± 0.05	-2.501	0.012	
Julian date ²	-0.17 ± 0.04	-4.333	< 0.001	
Late snowmelt	0.71 ± 0.20	3.538	< 0.001	
Julian date*Late snowmelt	0.28 ± 0.13	2.134	0.033	
Julian date ² *Late snowmel	t -0.51 ± 0.12	-4.188	<0.001	

² quadratic term

Figure legends

Fig. 1. Map of the study area that symbolizes the cover of the three habitat types (dense forest in blue, open forest in pink and grassland in green), the four elevation bands (with limits in dark blue) and four monitoring transects (in black). The 24 sampling sites are symbolized as letters, with A-L being early snowmelt sites and M-Z late snowmelt sites.

Fig. 2. Relationships between earthworm total abundance at the soil core scale and the five variables retained in the set of best-ranked models (within Δ AICc < 2). Regression lines are based on the conditional averaged model with values for all other variables set to their respective mean. The 95% credible intervals around the regression line were obtained from the 2.5% and 97.5% quantiles of posterior distribution obtained with 1'000 simulations.

Fig. 3. Relationships between earthworm abundance in the upper layer (i.e. accessible) at the soil core scale and the five variables retained in the set of best-ranked models (within Δ AlCc < 2). Regression lines are based on the conditional averaged model with values for all other variables set to their respective mean. The 95% credible intervals around the regression line were obtained from the 2.5% and 97.5% quantiles of posterior distribution obtained with 1'000 simulations.

Fig. 4. Relationships between earthworm total abundance at the sampling site scale and the two variables retained in the set of best-ranked models (within \triangle AICc < 2). Regression lines are based on the conditional averaged model with values for all other variables set to their respective mean. The 95% credible intervals around the regression line were obtained from the 2.5% and 97.5% quantiles of posterior distribution obtained with 1'000 simulations. Julian date 120 = April 30th; Julian date 180 = June 29th.

Fig. 5. Relationship between earthworm abundance in the upper layer at the sampling site scale and the three variables retained in the two best multivariate models within \triangle AlCc < 2. Regression lines are based on the conditional averaged model with values for all other variables set to their respective mean. The 95% credible intervals around the regression line were obtained from the 2.5% and 97.5% quantiles of posterior distribution obtained with 1'000 simulations. Julian date 120 = April 30th; Julian date 180 = June 29th.

Fig. 6. Earthworm total abundance in relation to Julian date and (A) four different elevational bands (in green 1st, red 2nd, blue 3rd and black 4th elevation band), (B) three habitat type (in green dense forest, blue open forest and red grassland) and (C) plot phenology (in green ES site and blue LS site). The regression line and the 95% credible intervals around the regression line were obtained from the 2.5% and 97.5% quantiles of posterior distribution obtained with 1'000 simulations. Julian date 120 = April 30th; Julian date 180 = June 29th.

Fig. 7. Comparison of the phenology of earthworm total abundance (in black) with the breeding phenology of Ring Ouzels, based either on the percentage of total observations from alarming adults (in red) or from young birds that have just fledged (in blue). Julian date 120 = April 30th; Julian date 200 = July 19th.

Fig. 1















Appendix

Table S1: Description of atlas codes, according to the international coding system used to describe main behaviour and level of breeding evidence (possible, probable or confirmed)

Possible breeding	
1	Species heard or observed within safe dates, but not in suitable breeding habitat.
2	Species heard or observed within safe dates, and in suitable breeding habitat
3	Territorial behavior, including counter singing males, territorial singing (repeatedly singing from same locations within an area), drumming in woodpeckers, or aggressive interactions between same-sex individuals of same species
Probable breeding	
4	Pair (male and female) within safe dates, and in suitable breeding habitat
5	Pair (male and female) present at the same location 2 or more days apart
б	Courtship behavior (aerial displays, courtship feeding) or copulation
7	Visiting probable nest site
8	Agitated behavior and/or anxiety calls from an adult, suggesting presence of nearby nest or young
9	Brood patch (Note: code only applies to birds observed in hand and is reserved for experienced birder only)
10	Nest building observed at nest site (Note: for nest building by wrens, woodpeckers, kingfisher)
Confirmed breeding	
11	Distraction display (especially injury feigning, such as broken wing display) or attacking/dive- bombing humans in defense of unobserved nest or young
12	Used nest (occupied within period of survey); includes inactive nests
13	Recently fledged young that are incapable of sustained flight
14	Occupied nest, but contents not observed; adults entering and remaining for a period of time, then leaving or exchanging duties
15	Adult carrying a fecal sac
16	Adult carrying food for young
17	Eggshells found below nest
18	Nest with adult incubating
19	Nest with nestlings or eggs

Table S2: Number of earthworms found per species and per layer and their classification in ecological categories according to Bouché (1977).

Species	Upper layer	Lower layer	tot	Classification
Lumbricidae ssp	72.5	42	114.5	Epigeic/anecic
Allolobophora chlorotica	0	1.5	1.5	Endogeic
Allolobophora icterica	66	86	152	Endogeic
Apporectodea caliginosa	6	2.5	8.5	Endogeic
Apporectodea rosea	64.5	36.5	101	Endogeic
Apporectodea longa	3	0	3	Anecic
Octalasium cyaneum	14	8	22	Endogeic
Octalasium lacteum	28.5	12	40.5	Endogeic
Dendrobaena octaedra	4.5	6.5	11	Epigeic
Immature	1040	665.5	1705.5	
Unidentified	18	27.5	45.5	
Total earthworms	1317	888	2205	

Species	Upper layer	Lower layer	Total
Diptera adult	1	0	1
Diptera larvae	108	27	135
Tipulidae larvae	14	0	14
Coleoptera adult	37	4	41
Coleoptera larvae	125	49	174
Lepidoptera larvae	7	6	13
Chilopoda	8	8	16
Diplopoda	58	17	75
Hymenoptera larvae	2	0	2
Other invertebrates	56	28	84
Total	416	139	555

 Table S3: Number of invertebrates found per species and per layer.