



# Spatio-temporal patterns of earthworm abundance suggest time-limited food availability for a subalpine bird species

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## ABSTRACT

Changes in food availability may act as a major mechanism by which global change impacts populations of birds, especially in seasonal environments at high elevations or latitudes. Systematic sampling of invertebrates, which constitute the diet of many bird species during the breeding season, is however largely missing in mountain ecosystems and is overall very rare for soil-dwelling species or stages. Here, we repeatedly sampled earthworms (Lumbricidae), the staple prey of the Ring Ouzel *Turdus torquatus*, over a whole breeding season in a study area in the Swiss Alps. Our main goal was to finely characterise spatio-temporal patterns of food availability for this declining bird species, in relation to elevation, habitat type and snowmelt stage. In 24 sampling plots, we extracted two soil cores every week for 6–10 weeks and hand-sorted soil invertebrates separately for two 5-cm soil layers. We then analysed the abundance of earthworms in those two layers in relation to various environmental parameters. We show that within our study area, edaphic and topographical parameters are poor predictors of the mean abundance of earthworms over the breeding season. Ground vegetation cover and soil moisture, however, are suitable predictors for the number of earthworms within the soil profile at each sampling time, i.e., of their availability for Ring Ouzels. Moreover, we provide evidence for a clear seasonal peak in earthworm availability, which was more pronounced in open grasslands compared to forested areas and happened later in the season where snow lingered. This study, by improving our understanding of the factors driving food availability for a mountain bird species, provides insights into how shifts in land-use and climate might lead to altered predator-prey interactions.

## 1. Introduction

Rapid environmental change is having profound impacts on mountain biodiversity worldwide (Huber et al., 2006) but the underlying mechanisms often remain poorly understood. A growing body of evidence indicates that altered species interactions may play a major role in driving community changes, although they are rarely taken into consideration (Brambilla et al., 2020; Descombes et al., 2020). In birds for instance, changes in prey availability may represent a key mechanism by which environmental change is leading to reduced productivity and/or survival, in turn affecting population trends (Benton et al., 2002; Pearce-Higgins et al., 2010; Sillett et al., 2000). This might particularly affect species living in highly seasonal environments, such as at high elevations and latitudes, given the challenge of matching reproduction

with a brief peak in food resources (Martin and Wiebe, 2004; Pearce-Higgins, 2010).

Evidence of such phenological mismatches exists (Møller et al., 2008; Visser et al., 2004) but is limited, partly due to the challenge of quantifying the abundance of invertebrates over time (Benton et al., 2002), especially in remote and harsh ecosystems. For arctic regions, several studies have highlighted that phenological shifts in invertebrate abundance could lead to a reduced breeding success in shorebird species (McKinnon et al., 2012; Saalfeld et al., 2019). Systematic sampling of invertebrate populations is however largely missing in mountain ecosystems (Pearce-Higgins, 2010) and is overall very rare for soil-dwelling species or stages (Eisenhauer et al., 2019; Steinwandter et al., 2018). This lack of knowledge clearly limits our understanding of the potential implications for taxa relying on invertebrates as main prey. It also raises

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concerns because soil invertebrates provide numerous other key functions in ecological systems, such as nutrient cycling, soil formation as well as erosion and flood control (Eisenhauer et al., 2019; Lavelle et al., 2006).

Among the soil macrofauna, earthworms account for most of the biomass (Lavelle and Spain, 2002), which generally holds true in sub-alpine and alpine grasslands (Cuendet, 1984; Steinwandter et al., 2017). Earthworms also provide the most ecologically important functions and are hence considered as typical “ecosystem engineers” (Blouin et al., 2013). Like other soil invertebrates, earthworms are under-recorded taxa (Carpenter et al., 2012) and this hampers predictions about their response to environmental change. Given their strong relationship with soil moisture and temperature (Edwards and Bohlen, 1996; Gerard, 1967), there are serious indications that earthworms communities will be particularly affected by climate shifts (Eggleton et al., 2009; Fourcade and Vercauteren, 2022; Pearce-Higgins, 2010).

Earthworms form a significant fraction of the diet of numerous bird and mammal species (Edwards and Bohlen, 1996), such as for thrush species in the Western Palearctic (Glutz von Blotzheim and Bauer, 1988). Among those, the Ring Ouzel *Turdus torquatus* is a mountain specialist relying almost exclusively on earthworms as a food source during the breeding season (Barras et al., 2021b; Burfield, 2002). The species is steadily declining in various parts of its range, especially at range margin (Barras et al., 2021a). It has been hypothesised that reduced food availability under a warmer and drier climate might be the underlying mechanism of these population trends (Beale et al., 2006). Despite indications of food limitation (Barras et al., 2021b; Sim et al., 2013), the direct empirical evidence is still missing, which calls for a monitoring of earthworm populations on the breeding grounds.

Here, we systematically and regularly sampled earthworms across a high-density breeding area for Ring Ouzels in the Swiss Alps, over a whole breeding season. Our primary goal was to identify main environmental factors driving earthworm distribution, both across the study area and within the soil profile. Moreover, we aimed to describe how earthworm availability fluctuates throughout Ring Ouzels’ reproduction period, and how it varies with elevation, habitat type and snowmelt stage.

## 2. Materials and methods

### 2.1. Study area and study species

The study area is located in the central, inner Swiss Alps, a region characterised by a continental climate with hot and dry summers and cold winters with rather large amounts of precipitation at high elevations (Gonseth et al., 2001). The study site (46.33 N, 7.43 E) covers ca. 200 ha and ranges between 1800 and 2200 m above sea level (m asl), comprising the full extent of the treeline ecotone; a dense forest dominated by Norway spruce (*Picea abies*) is present at lower elevations and gradually opens with an increasing occurrence of European larch (*Larix decidua*) up to 2100 m asl, above which the landscape is mostly open. The geological substrate is limestone and estimated soil depth is approximately 100 cm ([www.wsl.ch/soilmaps](http://www.wsl.ch/soilmaps)). Apart from a few dense forest patches, the entire area is used as a summer pasture for cattle from mid-June to mid-September, a common and widespread agricultural tradition in the Alps. This type of land use defines a mosaic of grassland interspersed with patches of coniferous forest or scattered trees, a particularly attractive habitat for breeding Ring Ouzels (Barras et al., 2021a; von dem Bussche et al., 2008), as well as for other elements of biodiversity (e.g. Patthey et al., 2012).

Ring ouzel breeds at a high density there and has been the focus of several autecological studies over the years (Barras et al., 2021b, 2020). The species forages on the ground, preferentially in areas with soft and moist soils within a short and sparse grass sward (Barras et al., 2020). It does so typically in open or semi-open habitats but can also be observed searching for food in rather dense forest stands (Glutz von Blotzheim and

Bauer, 1988). The nestling period of a brood, i.e., the time from hatching to fledging when the food requirements are particularly high, lasts 12–14 days and usually spans from the third decade of May to the third decade of June in our study area.

### 2.2. Earthworm sampling

Based on aerial pictures, we first divided the study area into three different habitat types: grassland, open forest and dense forest (Fig. 1). Dense forest was defined as tree-covered patches where the canopy is almost continuous and the ground layer not visible from above. Open forest represented habitat where trees are present but at low density and scattered, often with the grass layer visible underneath. Grassland patches were characterised by open patches with an extensive grass sward and without — or with only few isolated — trees. In addition, the area was separated into four elevational bands of 80 m span each (1820–1900; 1900–1980; 1980–2060; 2060–2140 m asl). Within each habitat type and elevational band, two squares of 10 × 10 m (100 m<sup>2</sup>) were selected, resulting in 12 pairs of sampling plots ( $n_{\text{tot}} = 24$ ; Fig. 1). One sampling plot of the pair was characterised by an early snowmelt (hereafter ‘ES plot’) and selected towards the end of April, when the first snow-free patches appeared across the study area. The other sampling plot was representative of a late snowmelt (hereafter ‘LS plot’) and defined empirically towards the end of May, where the last few snow patches remained. All plots were sampled on a regular basis in 2019, from May 1st to July 5th for ES plots (10 sampling sessions), and from May 30th to July 6th for LS plots (6 sessions). This period covered the whole breeding season of Ring Ouzel at that site, from incubation to post-fledging dispersal. We always sampled on days with no rainfall, and sessions were separated by about a week (5–7 days), except for the last two, which took place 10 days apart. All ES plots were sampled on a single day and all LS plots the next day. On one occasion (7th sampling session), however, the sampling of LS plots was postponed by 24 h due to bad weather conditions.

Within each sampling plot and for each session, two soil cores of 18 × 18 cm and 10 cm depth were extracted with a spade, 2 m apart from each other. To obtain a snapshot of the vertical distribution of earthworms in the soil profile, the extracted soil cores were immediately split horizontally into two 5-cm layers using a handsaw. Foraging Ring Ouzels are not probing the soil but capture earthworms by vigorously picking the surface, extracting them out of their burrows if necessary. Yet, because surfacing activity and vertical distribution of earthworms are both strongly and similarly influenced by environmental parameters, in particular by soil moisture (Onrust et al., 2019), we assumed that the number of earthworms in the upper soil layer was as suitable proxy for those accessible to foraging birds. Each layer was crumbled and sorted manually for 7.5 min on a white sheet, collecting all earthworms and storing them in tubes filled with 70% ethanol for later identification and weighing in the lab. Other soil invertebrates were also collected in addition. The extracted soil was subsequently returned to its original place to minimise disturbance. The location of a pair of soil cores in a sampling plot was randomly defined and changed for each sampling session, always ensuring that it was at least 1 m away from any previously extracted soil core.

### 2.3. Environmental variables

On each sampling occasion, a set of habitat variables (see Table 1) was measured in a 1-m radius area around each of the two extracted soil cores (further referred to as the ‘soil core scale’). We first estimated the ground cover percentage within this radius for seven categories: snow, mineral (gravel and rocks), dead wood (lying trunks and branches), litter (coniferous needle litter), bare ground, new grass (green herbaceous cover) and old grass (brown herbaceous cover from the previous year). We also measured the height (in cm) and patchiness (ordinal 1–3, from uniform to fragmented) of the grass sward. Regarding soil

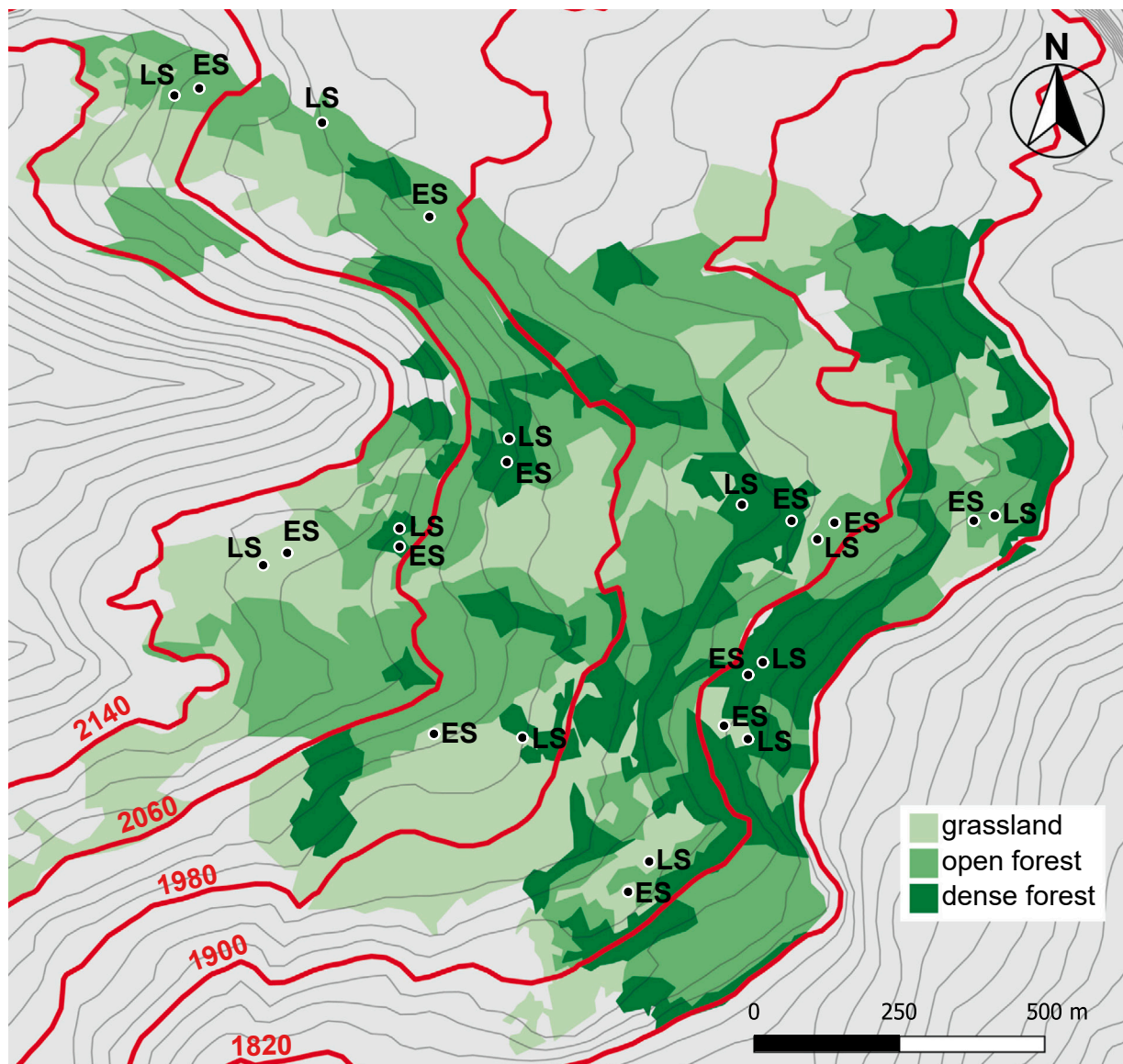


Fig. 1. Map of the study area symbolizing the cover of the three habitat types, four elevational bands and sampling plots ('ES': early snowmelt plots, 'LS': late snowmelt plots). Contour lines are shown at 20-m intervals.

conditions, we measured soil moisture as volumetric water content (VWC) in both layers (from 0 to 5 cm and from 5 to 10 cm) using a specific dual probe that measures conductivity with two 51-mm rods (SM150; Delta-T, Cambridge, UK). Soil surface penetrability was measured with a penetrometer (EL 29–3729; ELE International, Loveland, USA), indicating the force ( $\text{kg}/\text{cm}^2$ ) needed to insert a metal tip to a depth of 6.35 mm into the soil. In addition, for each  $10 \times 10$  m sampling plot (further referred to as the 'sampling plot scale'), we estimated the distance of the nearest snow patch with steps under 50 m, visually beyond that. Ground temperature was retrieved on an hourly basis using an iButton (DS1921G-F5, Thermochron, Baulkham Hills, Australia) placed 5 cm below-ground in the SW corner of every sampling plot. Lastly, air temperature and precipitation amount were not measured for each sampling plot but at a single location; air temperature was recorded on an hourly basis using an iButton placed in a constantly shaded place at 0.5 m above ground in the centre of the study area whereas precipitation information (as mm/hour) was obtained from the nearest automatic weather station (Anzère: 46.305 N, 7.408 E, 3.2 km distance; MeteoSwiss). We calculated precipitation sum in the 72 h (i.e., 3 days) preceding the sampling day, as we expected a small lag in the

earthworms' response to increased soil humidity.

In addition to these 'temporally-explicit' variables, we collected information on the soil composition and topography at each sampling plot on one occasion. A soil sample of 50 mL was collected at each plot at the time of first sampling. It was dried at  $50^\circ\text{C}$  for 48 h, sieved to  $< 2$  mm and processed in the lab to retrieve seven variables: the pH, the concentration of C, N and S, and the percentage of sand, silt and clay. Soil texture was measured with laser diffraction (Mastersizer 2000, Malvern Instrument GmbH, Herrenberg, Germany) according to Ryzak and Biganowski (2011). For the other measurements, samples were previously crushed 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  $\text{CaCl}_2$ ), whereas concentration of C, N and S, was determined by dry combustion and analysis of released gases with a CNS analyser (vario EL Cube, Elementar Analysensysteme, Langenselbold, Germany). As for topography variables, aspect (northness and eastness) and slope were measured with a compass.

**Table 1**

List of measured environmental variables, along with their mean and standard deviation. The ‘scale’ indicates at which scale the measurement took place: ‘SC’ for measurements on the soil core or around it (1-m radius), ‘SS’ for those at each sampling plot and ‘SA’ for single measurements for the whole study area.

Measurements	Unit	Scale	Mean ± sd
<i>Habitat variables</i>			
Snow cover	%	SC	5.13 ± 13.89
Mineral cover	%	SC	1.48 ± 2.72
Dead wood cover	%	SC	2.73 ± 3.61
Litter cover	%	SC	26.26 ± 25.64
Bare ground cover	%	SC	2.52 ± 4.57
New grass cover	%	SC	41.37 ± 33.27
Old grass cover	%	SC	20.50 ± 23.73
Ground vegetation height	cm	SC	5.79 ± 5.06
Ground vegetation patchiness	ordinal (1–3)	SC	2.01 ± 0.91
Soil moisture upper layer	VWC <sup>a</sup>	SC	37.00 ± 9.55
Soil moisture lower layer	VWC <sup>a</sup>	SC	37.21 ± 7.11
Soil penetrability	kg/cm <sup>2</sup>	SC	1.40 ± 0.57
<i>Weather variables</i>			
Distance to snow	m	SS	46.74 ± 49.55
Ground temperature	°C	SS	9.11 ± 4.12
Air temperature	°C	SA	10.52 ± 3.98
Precipitation (3-days sum)	mm	SA	10.73 ± 10.90
<i>Soil composition</i>			
pH	pH	SS	5.00 ± 0.68
C	%	SS	3.91 ± 0.99
N	%	SS	0.32 ± 0.07
S	%	SS	0.04 ± 0.01
Sand	%	SS	8.31 ± 2.51
Silt	%	SS	74.02 ± 2.57
Clay	%	SS	17.68 ± 1.80
<i>Topography</i>			
Slope	°	SS	18.96 ± 10.66
Northness	cos(aspect <sup>b</sup> )	SS	0.16 ± 0.48
Eastness	sin(aspect <sup>b</sup> )	SS	0.78 ± 0.39

<sup>a</sup> volumetric water content.

<sup>b</sup> measured in radians

## 2.4. Statistical analyses

All analyses were performed using the software R 4.0.4 (R Development Core Team 2021). Variables of cover percentage were ‘arcsine-square-root’-transformed and all continuous variables were standardised (mean = 0 and sd = 1) prior to the analyses. Abundance and biomass of earthworms over all soil cores were strongly correlated (Spearman’s  $r_s = 0.86$ ,  $P < 0.001$ ). Model fits, as visually assessed with QQ-plots and scatter plots of the residuals, were better for abundance data, so that all analyses were performed with those as a response variable.

In a first step, we analysed if edaphic and topographical parameters could explain the abundance of earthworms at a sampling plot. For this, we summed earthworms in both layers and both soil cores for each session and plot, and considered the average over all sessions as a response variable, referred to further in the text as “mean total abundance of earthworms”. Since several soil composition variables were highly correlated (Spearman’s  $|r_s| > 0.7$ ), we first performed a principal component analysis (PCA) including the seven measured variables and the C/N ratio. Following the Kaiser rule (Kaiser, 1958), we then retained only the principal components (PC) showing eigenvalues  $> 1$ , and integrated the latter along with northness, eastness and slope as explanatory variables of mean total abundance of earthworms in a single linear model with a Gaussian error distribution. To identify the best fitting models, we ranked models with all possible combinations of variables from the full to the null model based on the Akaike information criterion (AIC) and retained those within  $\Delta AIC < 2$  from the first-ranked one, using the function *dredge* from the package ‘MuMIn’ (Bartoń, 2020).

In a second step, we assessed how local environmental conditions influence the vertical distribution of earthworms in the soil. For this, we performed two separate analyses at the soil core scale with different

response variables: the first was the number of earthworms in the upper 5-cm layer, and the second was the number of earthworms in the lower layer. Models were fitted as generalised linear mixed-effects models (GLMM) with a Poisson error distribution using the *glmer* function in the package ‘lme4’ (Bates et al., 2015), including crossed random effects ‘session’ and ‘sampling plot identity’. These Poisson GLMMs showed no signs of overdispersion (all dispersion factors  $< 1.4$ ), as assessed using the *dispersion.glmer* function in the package ‘blmeco’ (Korner-Nievergelt et al., 2015). We first performed a pre-selection of explanatory factors by fitting univariate models for each variable measured at the soil core scale (see Table 1). For variables for which we hypothesised a hump-shaped relationship (soil moisture and cover of litter, bare ground, and new grass), we tested both linear and quadratic terms. We retained only variables (or terms) whose coefficient estimates were different from zero on a 90% confidence level (i.e.,  $P < 0.1$ ). Once this pre-selection was operated, we checked that no pair of correlated variables was included ( $|r_s| > 0.7$ ), removing the one in a pair with the lowest confidence level (i.e., highest  $P$ ) if necessary. We then integrated all retained variables in a single GLMM and ranked models with all possible combinations of variables from the full to the null model based on AIC.

In a third step, we looked at the effect of weather variables (see Table 1) and day of year on the abundance of accessible earthworms, separately for ES and LS plots. As a response variable, we summed earthworm abundance in the upper layer of both soil cores of a sampling plot for each session, and fitted models were again GLMMs, with only the ‘sampling plot identity’ included as a random effect. Using a Poisson error distribution led to overdispersion issues (dispersion factor  $> 1.4$ ), so that negative binomial GLMMs were fitted instead, using the *glmer.nb* function in the ‘lme4’ package (Bates et al., 2015). We followed the same model selection approach as described above to identify the best fitting model, including both linear and quadratic terms of day of year in the full model. Once the best-fitting model was identified, we also added individually *i*) the habitat type categorical factor (and interaction thereof with day of year) *ii*) the elevational band categorical factor (and interaction thereof with day of year), to explore their respective effect on the seasonal pattern of earthworm abundance.

If not specified otherwise, response curves of earthworm abundance against a specific variable were produced based on the coefficient estimates from the first-ranked model. 95 % credible intervals around the regression line represent the 2.5 % and 97.5 % quantiles of the posterior distribution as obtained with 10,000 simulations using the R-package *arm* (Gelman and Su, 2021), following the procedure described in Korner-Nievergelt et al. (2015).

## 3. Results

In total, 384 soil cores were collected from the 24 sampling plots, 240 from the ES plots and 144 from the LS plots. Most of the collected invertebrates (82.4%) were Lumbricidae: 2205 individual earthworms were extracted from the soil cores, 1317 from the upper layer and 888 from the lower layer. This corresponds to an average density of 180.3 ind/m<sup>2</sup> per plot and sampling session (range: 0–509.3). Eight different species (*Allolobophora chlorotica*, *Aporrectodea caliginosa*, *A. icterica*, *A. longa*, *A. rosea*, *Octolasion cyaneum*, *O. lacteum*, *Dendrobaena octaedra*) were identified, and some individuals only to the genus level (*Lumbricus* sp.) (Supplementary Materials, Table S1). However, most earthworms (77 %) had no clitellum, indicating immature individuals that were either very difficult or impossible to visually identify at species level. Therefore, all earthworms were treated together in the statistical analyses. In the remainder of sampled invertebrates, we found individuals from various taxonomic groups: adults and larvae of Diptera, adults and larvae of Coleoptera, Lepidoptera larvae, Hymenoptera larvae, Chilopoda and Diplopoda. However, all groups were present in much smaller numbers than earthworms, from a minimum of one Diptera adult to a maximum of 174 Coleoptera larvae, for a total of 471 identified

individuals (Supplementary Materials, Table S1). Given the low sample size and the marginal importance of those other taxa as food source during the breeding season of Ring Ouzels (Barras et al., 2021b), they were not considered in further statistical analyses.

### 3.1. Soil composition analysis

Following the PCA, the first three PCs were retained and explained 50.4 %, 22.4 % and 15.6 % of the variance, respectively. On a bidimensional graph with PC1 and PC2 as axes, sampling plots in dense forest clustered apart from those within grassland and open forest, which were more similar (Fig. 2). Plots in the dense forest appeared to have a higher C/N ratio and lower N and S concentrations than those in the other habitat types. The best-ranked model on the mean total abundance of earthworms was the null model (Supplementary Materials, Table S2), indicating that edaphic and topographical factors did not explain this variation, although slope and northness showed positive trends in competitive models (Supplementary Materials, Table S2).

### 3.2. Soil core scale

Two variables were retained in the single most competitive model on earthworm abundance in the upper 5-cm layer (Table 2a), namely cover of new grass and soil moisture in the lower layer. Both were showing a unimodal effect (Fig. 3a & 3b), the latter being much more pronounced. In the analysis of earthworm abundance in the lower 5-cm layer, new grass cover and soil moisture in the upper layer were retained (Table 2b). If the first variable showed a linear negative relationship (Fig. 3c), visually similar to the effect on earthworm abundance in the upper layer (Fig. 3a), the effect of soil moisture was the opposite, showing a bimodal relationship with higher earthworm abundance under low as well as under high moisture values at the soil surface (Fig. 3d).

### 3.3. Seasonal patterns of abundance

For the analysis on ES plots, none of the weather variables were pre-selected (see Supplementary Materials, Table S3) and a single best model came out of the selection approach (Table 3a), showing a hump-shaped relationship of earthworm abundance in the upper layer in relation to day of year, i.e., to season advancement (Fig. 4a). When adding habitat type as a categorical factor, it became obvious that this peak was mostly marked in open forest plots, whereas abundance was much more constant in forest and grassland plots, being overall lower in the latter (Fig. 4b). Regarding elevation, we could not show obvious

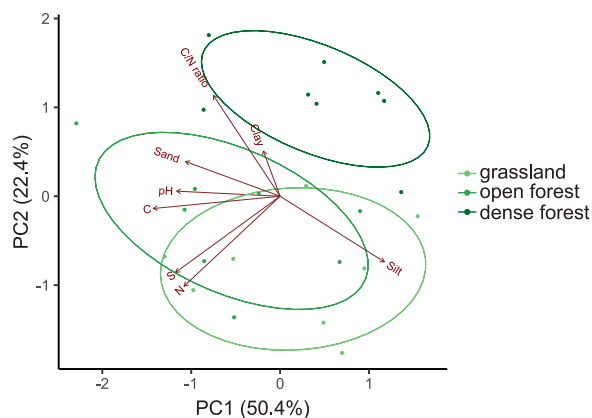


Fig. 2. Biplot of the principal component analysis (PCA) on soil composition variables in the 24 sampling plots, with the two first principal components selected as the x- and y-axis. Circles depict the normal data ellipses for each habitat type and arrows are loadings of the 8 variables used in the PCA.

differences between the four different bands (Supplementary Materials, Fig. S1).

For the analysis on LS plots, several variables were pre-selected (see Supplementary Materials, Table S3). A single best model came out of the selection approach, including again the linear and quadratic terms of day of year (Fig. 4a), but also the total precipitation amount in the 3 days before sampling, which had a significant positive effect (Table 3b). Regarding the effects of habitat type and elevation on the seasonal pattern of earthworm abundance, no clear differences were highlighted for plots with a late snowmelt, except that the amplitude of the peak appeared slightly larger in grassland plots (Fig. 4c), but with a large uncertainty around the response curves.

## 4. Discussion

Food availability is a major determinant of breeding season length and breeding success in birds living in highly seasonal environments, such as temperate mountain ecosystems (Martin et al., 2017; Pearce-Higgins, 2010). Nevertheless, the factors underpinning the spatio-temporal variability in food resources are poorly known, especially for soil invertebrate prey (Eggleton et al., 2009; Eisenhauer et al., 2019; Martay and Pearce-Higgins, 2018). In this study, we investigated these aspects for earthworms, which represent the staple food source of a declining mountain bird species, the Ring Ouzel. We show that within our study area, soil composition and topography perform poorly to explain the mean abundance of earthworms over the breeding season of the Ring Ouzel. Ground vegetation cover and soil moisture are, however, good predictors of the distribution of earthworms within the soil profile, and hence of their accessibility for ground-foraging birds. In addition, we provide evidence for a seasonal peak in earthworm availability, which differs depending on the snowmelt stage and habitat type.

### 4.1. Spatio-temporal patterns of earthworm abundance

The abundance of earthworms in both layers was affected negatively by the cover of new grass, that is, by the growing herbaceous sward. A potential explanation is that this correlated negatively in our plots with the cover of litter and old grass, which are particularly important food sources for many species of earthworms that forage almost exclusively at the soil surface (i.e., epigeic and anecic species *sensu* Bouché, 1977). The other major factor related to earthworm abundance in our sampling plots was soil moisture. For earthworms close to the soil surface, there was a clear optimum around 45–50% of volumetric water content (Fig. 3b). Soil moisture has been repeatedly identified as the most important driver of earthworm activity (Curry, 2004; Edwards and Bohlen, 1996), and thus of their distribution within the soil profile (Gerard, 1967; Onrust et al., 2019). Some species (i.e., endogeic and anecic *sensu* Bouché, 1977) have the possibility to retreat deeper in the soil to avoid unsuitable conditions (Edwards and Bohlen, 1996), and thus probably underpin the short-term fluctuations that we observed in the top 5 cm of the soil. The opposite pattern in the lower layer, i.e., higher abundance under dry or wet conditions at the soil surface, indeed corroborated these vertical movements. Yet, although most species are described as highly sedentary and rarely move more than a few meters (Lavelle, 1988), the mobility of earthworms might be underestimated (Mathieu et al., 2010). Horizontal movements to track optimal moisture conditions, typically along the snowmelt gradient, could therefore also contribute to the distribution we observed.

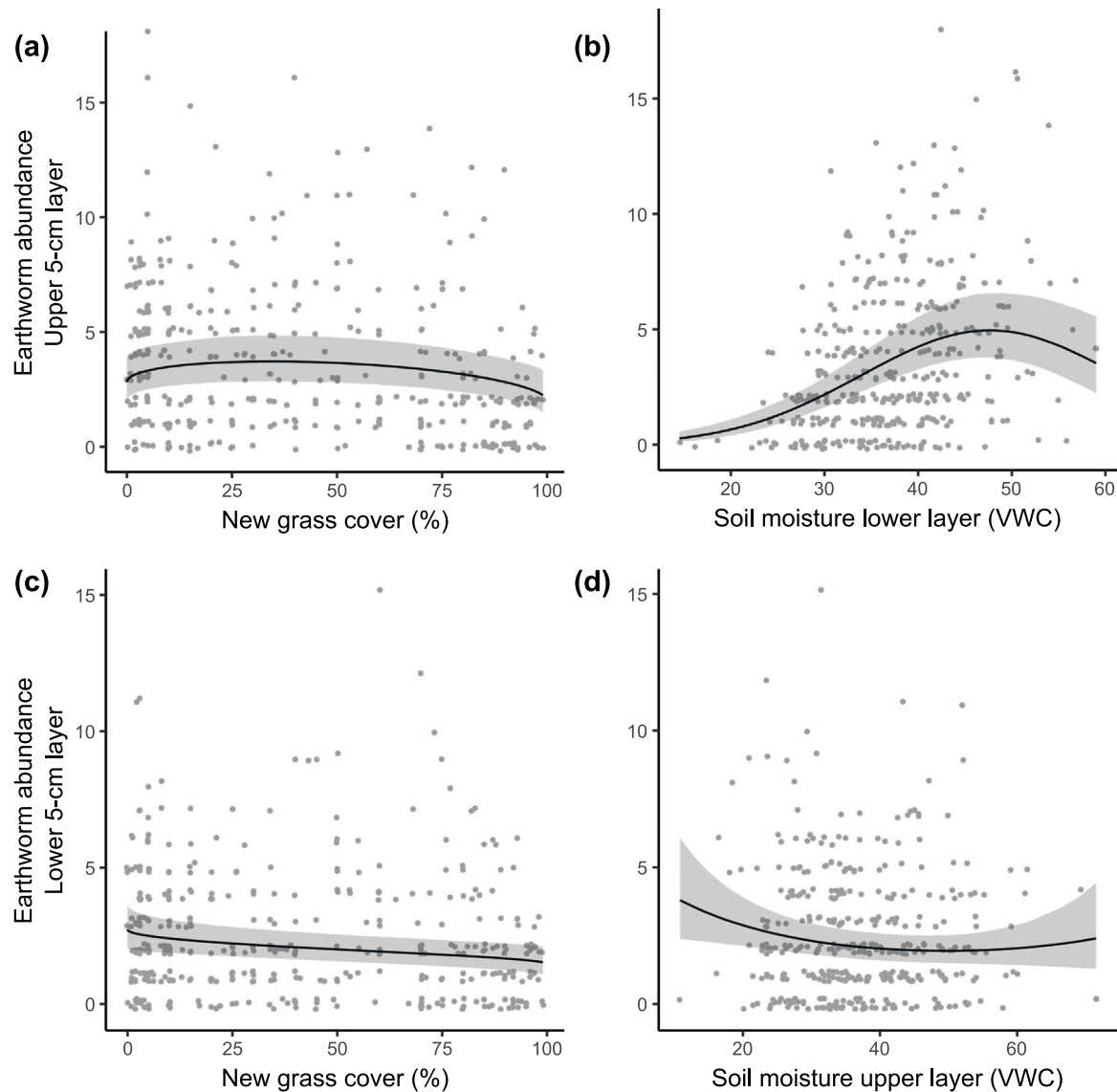
In mountain environments in spring, water availability, and hence soil moisture, are largely determined by the melt of the seasonal snowpack (Beniston, 2003; Slatyer et al., 2022). This is most likely the ecological reason for the phenological differences in earthworm availability between plots with an early snowmelt and those with a late snowmelt. The abundance of earthworms in the top layer appeared rather stable in plots characterised by an early snowmelt, with an optimum of small magnitude around the 3rd of June. As the soil moisture

**Table 2**

List of best-ranked models (within  $\Delta AIC < 2$ ) from the soil core scale analysis on the number of earthworms in (a) the upper 5-cm layer (b) the lower 5-cm layer, respectively. Numbers indicate coefficient estimates and symbols the P-value (\*\*\*)  $< 0.001$ , \*\*  $< 0.01$ , \*  $< 0.05$ ,  $< 0.1$ ). Horizontal bars stand for variables that were not retained in a specific model.

					df	AIC	$\Delta AIC$	$w_i$
A. Upper 5-cm layer								
#	New grass cover	New grass cover <sup>2</sup>	Soil moisture lower layer	Soil moisture lower layer <sup>2</sup>	7	1721.36	0	1
1	-0.03	-0.12 **	0.40 ***	-0.13 ***				
B. Lower 5-cm layer								
#	New grass cover		Soil moisture upper layer	Soil moisture upper layer <sup>2</sup>	6	1563.04	0	0.62
1	-0.16 *	-	-0.11 *	0.04	5	1563.98	0.94	0.38
2	-0.17 **	-	-0.10 *	-				

df: degrees of freedom, AIC: Akaike Information Criterion,  $w_i$ : model weight



**Fig. 3.** Relationships between earthworm abundance (a,b) in the upper 5 cm-layer or (c,d) in the lower 5-cm layer of the soil core and the environmental variables in the respective best-ranked model (Poisson GLMM). Fitted curves and shaded areas (which depict the 95% credible intervals) are drawn from this model.

continuously decreased throughout the season (Supplementary Materials, Fig. S2), we hypothesise that cold ambient temperatures causing frost of the soil surface force most earthworms to stay deeper in the soil early in the season (Holmstrup, 2003). Soil freezing no longer occurs by the time LS plots are freed of snow, so that numbers of earthworms peak almost instantly or shortly after snowmelt, to then decrease rapidly as the season advances. Of course, precipitations contribute increasingly to

the water supply as the snowpack melts, and the availability of earthworms is known to increase very rapidly in relation to rainfall (Edwards and Bohlen, 1996; Martay and Pearce-Higgins, 2018). We could document such short-term increases in LS plots, as the amount of precipitation 3 days prior to sampling had a clear positive effect, but not for ES plots. This again suggests other limiting factors, such as frost early in the season as mentioned above. The seasonal pattern in earthworm

**Table 3**

Coefficient estimates ( $\pm$  se), Z- and P-values of variables retained in the single best-ranked model (negative binomial GLMM) on the number of earthworms in the top layer in (a) early snowmelt plots and (b) late snowmelt plots, respectively.

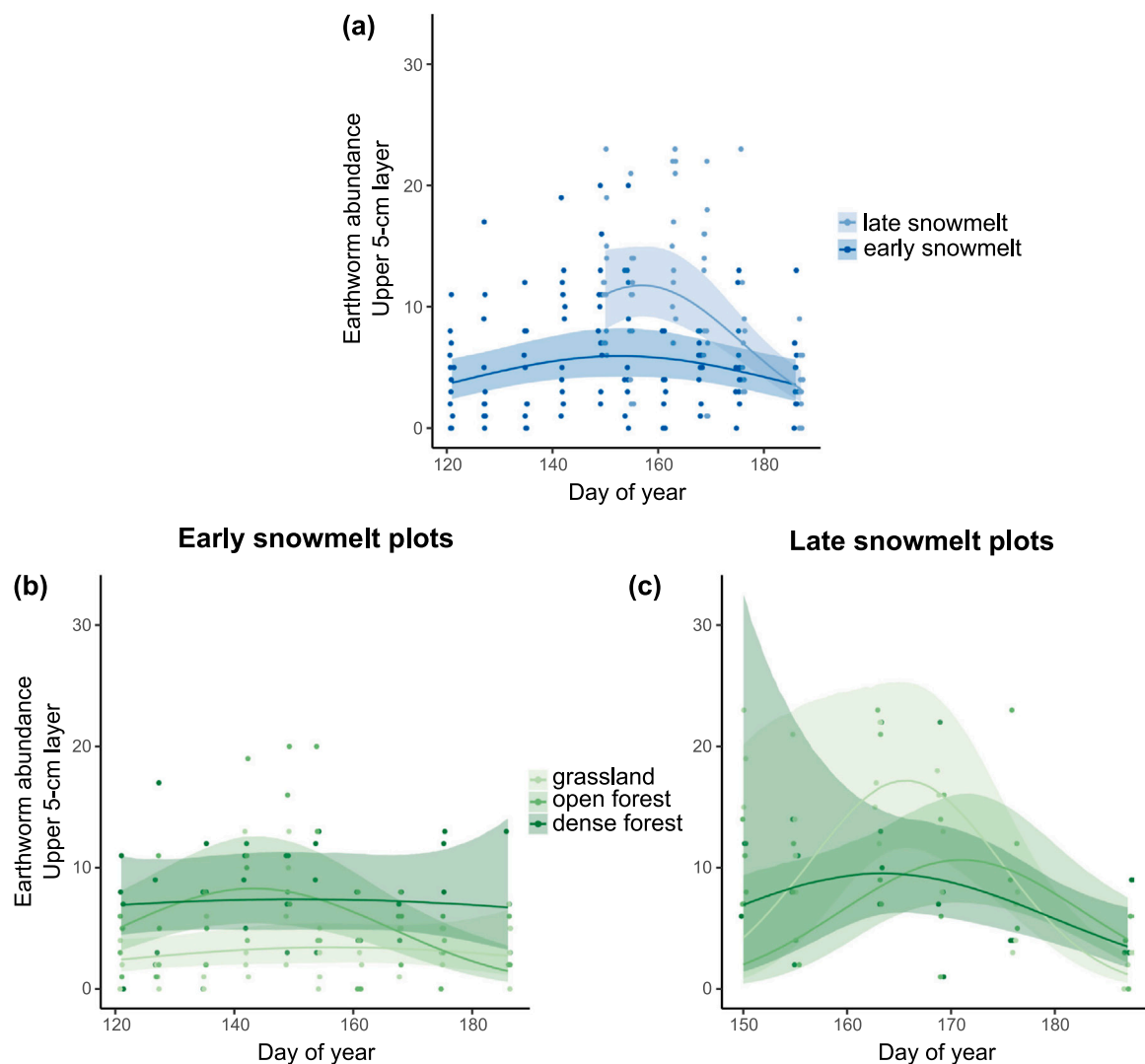
Variable	Estimate $\pm$ se	Z-value	P-value
<b>A. Early snowmelt plots</b>			
Day of year	-0.08 $\pm$ 0.07	-1.12	0.261
Day of year <sup>2</sup>	-0.17 $\pm$ 0.06	-2.60	0.009
<b>B. Late snowmelt plots</b>			
Day of year	-0.02 $\pm$ 0.18	-0.13	0.894
Day of year <sup>2</sup>	-0.52 $\pm$ 0.16	-3.28	0.001
3-days precipitation	0.11 $\pm$ 0.05	2.20	0.028

availability also differed across habitat types, especially for ES plots. For the latter, the availability of earthworms was consistently high throughout the season within dense forest plots, while there was a clear mid-seasonal peak in open forest plots. We suspect that the observed discrepancies in the temporal pattern of earthworms close to the soil surface in different habitats depend on distinct environmental conditions, notably soil moisture (see Fig. S2), which in turn determines the community composition. Indeed, a shift in ecological categories of earthworms has been documented with advancing forest succession (Grossi and Brun, 1997; Steinwandter et al., 2017). Among other factors,

the canopy and associated litter which limit direct solar radiation, and hence buffer variations in soil temperature and moisture (James et al., 2003), could favour epigeic species. Yet, it remains unclear if the same applies to coniferous, mixed and deciduous forests (Grossi and Brun, 1997).

#### 4.2. Predator-prey relationship in a changing environment

Our results clearly demonstrate that the availability of earthworms fluctuates considerably in space and time. This has certainly large implications for species relying on them as a main food source, such as Ring Ouzels on their breeding grounds. In a previous work, Barras et al. (2020) have shown that Ring Ouzels forage preferentially in areas with rather moist (40–65% VWC) and penetrable soils, with intermediate amounts of litter and bare ground cover (ca. 50 %). Here, we show that these conditions coincide, at least to some extent, with high availability of earthworms. This link between food availability and habitat selection has been reported for many bird species, including at larger scales, such as for thrushes in the UK (Martay and Pearce-Higgins, 2020). Moreover, Barras et al. (2020) demonstrated how the suitability of foraging grounds decreases rapidly as the breeding season progresses, which is corroborated here by the reduction in earthworm availability, especially drastic in LS plots. Monitoring of the provisioning activity at Ring



**Fig. 4.** Seasonal pattern of earthworm abundance in the top 5 cm of the soil in relation (a) to snowmelt stage, (b) to habitat type for early snowmelt plots, and (c) to habitat type for late snowmelt plots. Fitted curves and shaded areas (which depict the 95% credible intervals) are drawn from a negative binomial GLMM.

Ouzels' nests also suggests that the observed reduction in earthworm availability has a direct influence on the nestling diet, as the proportion and biomass of earthworms both decrease toward the end of the breeding season (Barras et al., 2021b). Taken together, these results indicate that the brevity of Ring Ouzel's breeding season is mainly constrained by the availability of their main prey, highlighting the potential risk of phenological mismatch and thus of food shortage. Because these results are limited to one sampling year (in 2019) and therefore do not reflect the variability of a per se complex ecosystem, their interpretation and generalisation require caution.

Knowing some of the factors that drive the availability of the staple prey of Ring Ouzels, we can discuss how rapid environmental shifts at these elevations might alter this predator-prey relationship in the future. With climate change, on the one hand, we can expect reduced soil water content to cause a change in the distribution of earthworms, with ultimately a shift from epigeic to endogeic species (Eggleton et al., 2009; Fourcade and Vercauteren, 2022). Indeed, drought events can lead to short-term population collapses in epigeic species (Eggleton et al., 2009; Gerard, 1967), which might be exacerbated by an advancing snowmelt and associated reduced water availability. Altogether, earthworms might find themselves increasingly out of reach of ground-foraging bird species. In addition, an earlier melt of the insulating snow layer could increase the frequency of soil freeze-thaw cycles in early spring, and potentially also have negative effects on earthworm populations (Makoto et al., 2019), as it does for other species of soil invertebrates (Slatyer et al., 2017). Concerning the management of alpine pastures, on the other hand, the ongoing abandonment of remotest areas, followed by forest succession, also has documented effects on the abundance, biomass and community composition of earthworms (Bueno and Jiménez, 2014; Grossi and Brun, 1997; Steinwandter et al., 2017). Changes in management intensity in the most accessible areas might likewise have large implications for the abundance and distribution of earthworms (Bacher et al., 2018; Bueno and Jiménez, 2014; Edwards and Bohlen, 1996). In the case of Alpine grasslands, the widespread tradition of summer pasturing by livestock is beneficial for soil macro-invertebrates (Steinwandter et al., 2018), but it remains unclear if the aforementioned changes may reduce their availability for predators. Overall, as the peak in prey availability may not only occur earlier, but also be reduced in dimension and duration, food shortage might become an issue for some bird populations. Direct management measures to boost invertebrates' availability exist, yet they are very context-specific — e.g. in the UK, liming for earthworms (McCallum et al., 2016) or drain blocking for Tipulidae (Carroll et al., 2011) — and hence challenging to apply on a large scale. It appears that in this context, extensive summer pasturing by cattle is the key to maintain a mosaic of different habitats (Pittarello et al., 2016) and hence to secure numerous and constant foraging opportunities.

## 5. Conclusions

Detrimental effects of reduced prey availability on population demography certainly represent a key mechanism by which drivers of global change might impact bird species (Benton et al., 2002), especially for those breeding in highly seasonal environments (Pearce-Higgins, 2010). Here, we show how numbers of earthworms vary chiefly across the soil profile in a subalpine study area as the spring season advances and we discuss implications for the Ring Ouzel, a declining mountain bird species that relies mostly on earthworms to feed its nestlings. While the current study focuses on a single bird species and its staple food source, we believe that our findings are of relevance for the numerous species of mountain birds or mammals feeding principally on earthworms or other climate-sensitive soil invertebrates (Bueno and Jiménez, 2014; Pearce-Higgins, 2010; Resano-Mayor et al., 2019). Our work

underlines the crucial need to extend and develop the monitoring of both above- and below-ground invertebrate populations in mountain environments, to further our understanding of the impacts of global change on these vulnerable ecosystems.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data Availability

Data that support the findings of this study have been deposited at doi: 10.6084/m9.figshare.20430708.

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## Author contribution

A. G. Barras and I. Candolfi designed the study, collected and analysed the data. I. Candolfi performed lab work and species identification. A. G. Barras wrote the first draft. R. Arlettaz launched and supervised the research and participated to the final editing of the manuscript.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.pedobi.2022.150826.

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