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Snow cover phenology is the main driver of foraging habitat selection for a high-alpine passerine during breeding: implications for species persistence in the face of climate change

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Abstract

High-alpine ecosystems are strongly seasonal and adverse environments. In these ecosystems, the brevity of optimal breeding conditions means species must efficiently track spatiotemporal variations in resources in order to synchronise their reproductive effort with peaks in food availability. Understanding the details of prey-habitat associations and their seasonality in such ecosystems is thus key for deciphering species' ecological niches and developing sound conservation action. However, the ecological requirements of high-alpine avifauna remain poorly documented. Furthermore, mountain ranges in the Old World are affected not only by profound alterations of climate, but also by changes in land-use, the interaction of which hampers both proper forecasting of species' resilience to environmental change and delivery of evidence-based conservation guidance. Here, we investigate the prey-habitat associations of a high-alpine passerine, the White-winged Snowfinch (*Montifringilla nivalis*), by radio-tracking breeding adults in the Swiss Alps. In late spring and early summer, Snowfinches foraged preferentially next to invertebrate-rich, melting snow patches where Tipulidae larvae abound. Later, in mid-summer, they favoured flower-rich alpine meadows. When foraging, they always preferred short ground vegetation while avoiding rock and scree. Their pattern of foraging habitat selection reflects trade-offs between food abundance and accessibility, i.e. prey availability. The reliance of this passerine on a habitat mosaic where snow plays a major role questions its ability to cope with climate change due to future habitat loss and potential phenological mismatches. Targeted grazing could possibly help in habitat management by aiming at maintaining invertebrate-rich meadows with short vegetation. Yet, it remains an open question whether habitat management would suffice to compensate for the potentially detrimental effects of the progressive retreat of snow fields to higher elevations.

Keywords Alpine ecosystems · Climate change · European Alps · Invertebrates · Mountains · Seasonality

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Introduction

The use an animal makes of its environment is a fundamental issue in ecology (Johnson 1980; Morris 2003). Habitat selection describes the process whereby individuals preferentially use a non-random set of available habitats and resources (Johnson 1980; Manly et al. 2002). The spatial and temporal scales at which habitat selection occurs are multiple, from wide-scale distributions (e.g. species geographic ranges) to local microhabitat selection (e.g. foraging or nesting sites). The study of those sites specifically selected for functional processes, such as foraging grounds, can deliver information about species' ecological requirements such as preferred habitat types and associated food resources (Eierman and Connor 2014; Harwood et al. 2003). That information is key to the forecasting of distribution ranges under various scenarios of environmental change.

It is vital for any animal species to efficiently acquire food (White 2008). Optimal foraging theory posits that animal feeding strategies result from a maximization of net energy (ratio of energy gain from acquired food, to the cost induced by its acquisition) that aims at increasing fitness parameters such as reproduction and survival (Emlen 1966; Pyke et al. 1977; Schoener 1971). In this regard, food availability (i.e. food abundance mediated by its accessibility) is known to be a main driver of foraging site selection in a myriad of taxa and environments (e.g. Arlettaz 1999; Gehr et al. 2017; Machin et al. 2017; Tufto et al. 1996). From an adaptive and evolutionary point of view, it is essential for animals to synchronize their breeding phenology (usually, the most energy demanding period during the yearly life cycle) with peaks in food quality and availability (McKinnon et al. 2012; Visser and Both 2005). This is because food supply determines fecundity, offspring growth rate, breeding success, and survival (Arlettaz et al. 2017; Naef-Daenzer et al. 2000; Pearce-Higgins and Yalden 2004). In strongly seasonal environments, however, it is a challenge for individuals to track the marked spatiotemporal change in food availability for optimizing both foraging and the timing of life history activities (Stephens and Krebs 1986).

This challenge is exacerbated in mountain ecosystems, where climate change is more acute than in the lowlands (Beniston 2003; Pepin et al. 2015), and where the temporal window of resource availability is particularly short (Miller-Rushing et al. 2010). As a result, disruptions of trophic interactions can be particularly marked at higher elevation, with phenological mismatches negatively impacting the fitness, population trends, and spatial distribution of a number of taxa (Aldridge et al. 2011; García-González et al. 2016; Pearce-Higgins et al. 2005). The double constraint generated by a short breeding season and a faster pace of ambient temperature warming thus exerts an immense pressure on high mountain animals; many have evolved such specific behavioural, physiological, and life-history adaptations that they may have little room for further phenological adjustments (Bastianelli et al. 2017; Bears et al. 2009; Laiolo and Obeso 2017; Martin 2001). Their fine-tuned adaptations respond in particular to environmental circumstances that result from the interplay between ambient temperature, snow cover, and vegetation growth that commonly drive resource selection patterns in mountainous regions (Rehnus et al. 2016; Zweifel-Schielly et al. 2009).

In this respect, snow-related parameters have been shown to directly and indirectly affect the breeding phenology and reproductive performance of alpine birds. For instance, the timing of snowmelt affects the reproductive success of the Pyrenean rock ptarmigan (*Lagopus muta pyrenaica*) by influencing diet quality: in years with late snowmelt hens are in poorer body condition at the onset of reproduction because the peak of food quality has already passed (García-González et al. 2016). Thus, local snow conditions—mainly ruled

by precipitation regime, elevation, and slope aspect—appear fundamental for determining the availability of key resources (Edwards et al. 2007; García-González et al. 2016; Giersch et al. 2017; Rosvold 2016; Wipf and Rixen 2010), and may hence operate as an important driver of alpine biodiversity.

Mountain birds play an important role as bioindicators and environmental sentinels (Becker 2003; Chamberlain et al. 2012; Lehikoinen et al. 2014; Lindenmayer and Likens 2011). Whilst the general decline in lowland European bird populations is well documented, resulting mainly from land use changes (Flousek et al. 2015; Lehikoinen et al. 2014), mountain avifauna has received comparatively little attention (Lehikoinen et al. 2014) due to challenging research logistics (Chamberlain et al. 2012). Even basic information on birds' ecological requirements such as diet is still lacking, which hampers drawing sound mechanistic projections about their future response to environmental change. In this study, we investigated habitat selection and foraging conditions in one of the most specialized high-elevation passerines of Europe, the White-winged Snowfinch (*Montifringilla nivalis*, hereafter, Snowfinch).

The Snowfinch represents in effect an archetype of wildlife adapted to the contrasted, often harsh and rapidly fluctuating conditions typically encountered in barren habitat at very high elevations next to the nival belt (Cramp and Perrins 1994). It roosts and builds well insulated nests in deep, wind protected crevices (Heiniger 1991) or in human infrastructures such as ski-lift pylons (Del Hoyo et al. 2009), and forages upon invertebrates in snowfields and short grassy patches (Antor 1995; Brambilla et al. 2017). Heiniger (1991) has pointed out in particular that leatherjackets (Tipulidae larvae) that develop at the front of the melting snow pack may constitute a staple food source for chick provisioning, but quantitative information is missing. The specific objectives of this study were to describe the foraging microhabitat selection by Snowfinches and related habitat-specific invertebrate availability, and variation thereof during the breeding season. This information will be key to understanding the resilience potential of high-alpine bird species to climate change, i.e. to more accurately predict the possible responses of high-elevation vertebrate taxa to various scenarios of environmental change.

Materials and methods

Study area

In May–July 2015 and 2016, we radio-tracked 14 breeding Snowfinches at five different sites in the Swiss Alps (Canton of Valais, SW Switzerland; 46°17′N, 7°32′E; Fig. 1). The study sites were all situated above the tree line, between 2200 and 2700 m a.s.l. The habitat consisted of barren rocky zones interspersed with cliffs, alpine grasslands, snowfields and small watercourses, often not far from human infrastructure such as roads, buildings and ski-lifts (as we selected easily accessible study sites).

Study design and data collection

The study of foraging microhabitat selection was designed to compare habitat features, invertebrate communities and abundances at plots where Snowfinches collected food for chick provisioning with randomly located pseudo-absence plots in the direct surroundings, i.e. locations nearby where birds were not observed foraging during the radio-tracking
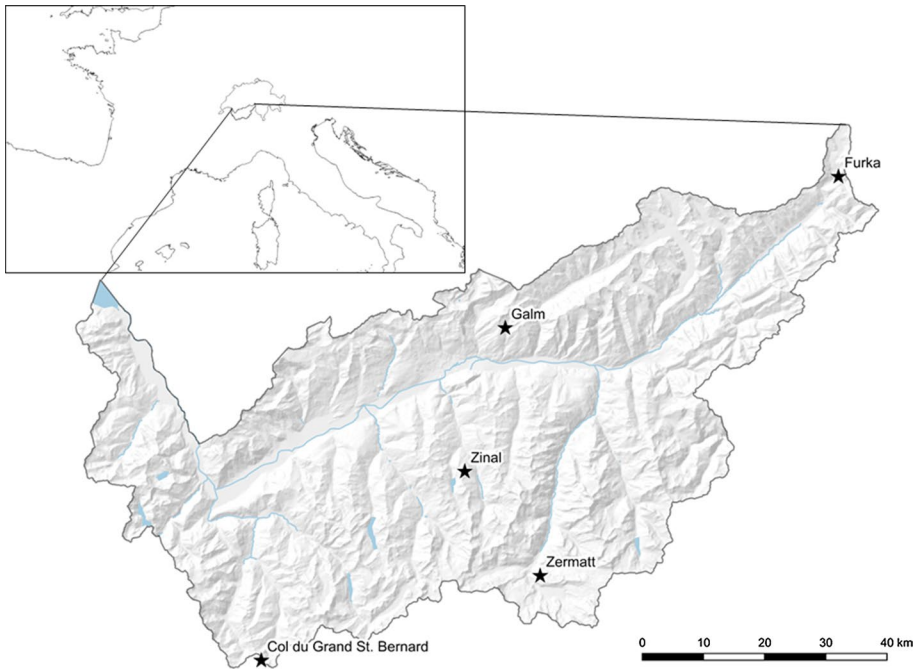
Fig. 1 Location of the study area with the five study sites (Valais, SW Switzerland) within Switzerland (insert)

sessions (hereafter, "foraging" and "pseudo-absence" plots, respectively, with "pseudo-absence" plots considered as sort of suboptimal because apparently avoided).

From 25th May till 18th June, i.e. during territory establishment, nest building or incubation, five males and nine females were captured using mist nets and tape luring. Each captured individual was ringed and equipped with a radio-transmitter (Holohil Systems Ldt., model BD-2, weight: 1.4 g—corresponding to 3.4–4.1% of the birds' body mass, life span: 9 weeks), which was fitted on the birds by using a leg-loop harness (Naef-Daenzer 2007; Rappole and Tipton 1991) made up of thin elastic nylon cord. Studies of the effects of small radio-transmitters on passerines show no relevant negative impact on physiology, behaviour and survival (Naef-Daenzer et al. 2001; Neudorf and Pitcher 1997). Radio-tracking of breeding individuals started after hatching, which corresponds to the onset of the nestling period (18–22 days) when food demand peaks during the year life cycle because of the need to sustain rapid chick growth (Del Hoyo et al. 2009). In 2015, radio-tracking started 16 days earlier (6th of June) than in 2016 (22nd of June) due to an earlier snowmelt and hence onset of breeding. Radio-tagged birds were approached relying on the homing-in of the animal location technique and precisely located with the aid of a hand-held three-element folding Yagi antenna attached to a radio-receiver (Australis 26 k, Lawnton, Australia). Once spotted with the aid of binoculars, the foraging bird was followed until it captured a prey, with this first prey capture defining a unique foraging location per foraging session. The exact foraging location was land-marked with a pole after the bird had left the area. Then, within a 1-m radius around the foraging location—the resulting circle forming our foraging plot—habitat variables were mapped in situ (Table 1), while all invertebrates retrieved after ground surface scratching with a rake (2–3 cm

Table 1 Habitat and invertebrate variables recorded within 1-m radius plots at foraging sites and at nearby randomly generated, pseudo-absence locations

Habitat	Description
Snow (%)	Cover of snow
Old grass (%)	Cover of previous year grass
New grass (%)	Cover of new grass (e.g. Poaceae, Cyperaceae)
Herbaceous green vegetation (%)	Cover of other herbaceous green vegetation (herbs)
Flowers (%)	Cover of flowers
Mosses and lichens (%)	Cover of all types of mosses and lichens
Bare ground (%)	Cover of bare soil
Rock and scree (%)	Cover of all type of rocks, from emerging rocks to scree
Water (%)	Cover of lakes, ponds, watercourses
Cow dung (%)	Cover of dung from previous year
Bushes (%)	Cover of woody field layer (e.g. *Rhododendron*, *Juniperus*)
Other (%)	Cover of any other ground cover categories
Old grass height (cm)	Mean of 3 measurements of height of old grass vegetation
New grass height (cm)	Mean of 3 measurement of height of new grass vegetation
Soil moisture (mVolts)	Mean of 3 measurements of soil moisture. Measured with SM150T Soil Moisture Sensor (Delta-T device)
Slope steepness (angle, °)	Measured with the GPS Status app for Android
Exposition (aspect, 0°–359°) transformed into N versus S	Measured with a hand compass
Habitat diversity	Number of main habitat cover variables present (range 0–8, from lowest to highest diversity)

Invertebrate	Description
Tipulidae adults	Abundance and biomass of adult crane flies
Tipulidae larvae	Abundance and biomass of crane fly larvae (leatherjackets)
Brachycera	Abundance and biomass of Brachycera flies
Formicidae	Abundance and biomass of ants
Araneae	Abundance and biomass of spiders
Opiliones	Abundance and biomass of harvestmen
Coleoptera	Abundance and biomass of beetles
Orthoptera	Abundance and biomass of grasshoppers
Lepidoptera larvae	Abundance and biomass of caterpillars
Shannon index (H′)	Shannon–Weaver index of all invertebrate categories in a plot
Total invertebrate abundance	Sum of all invertebrate items in a plot
Total invertebrate biomass	Sum of all invertebrate biomass in a plot
Mean invertebrate body size	Weighted mean body size of all invertebrates in a plot
Invertebrate profitability	Total biomass divided by the total number of items

Retained invertebrate categories were those summing >5% of total abundance and/or biomass (see Table S1)

upper soil layer) within the same circle were stored in ethanol (70%) until being processed in the laboratory. For each foraging plot, two random, so called "pseudo-absence" locations were generated by selecting a random angle (0°–359°) and walking in that direction a random distance varying between 5–25 m (short-distance pseudo-absence plot) and 26–100 m

(long-distance pseudo-absence plot). This allowed us to compare used with surrounding non-used pseudo-absence plots that were not visited by the radio-tracked birds. However, they were not true absence points as we cannot discard that foraging birds, especially untracked individuals, may have been there in a few unobserved cases. At each pseudo-absence plot, habitat description and invertebrate collection were performed in the same way as at the foraging plots. Once in the laboratory, invertebrates were identified to the order or family level (Chinery 1993), and their body length was measured (mm) by using a binocular microscope (Leica MZ95). All invertebrates were dried at 80 °C for 72 h to constant weight in order to measure dry biomass to the nearest 0.1 mg with a Mettler-Toledo AB54-S precision balance.

Statistical analyses

Habitat mapping considered the following ground cover proportion variables: snow, old vegetation (brown grass), new vegetation (green grass), herbaceous green vegetation (herbs), flowers, mosses and lichens, bare ground, rock and scree, and others. The latter category included all marginal ground cover variables for which 0 values made up more than 90% of the entire sample. In addition, as regards to non-cover habitat variables, we measured the height of old and new grass vegetation, soil moisture, slope steepness, slope aspect, and habitat diversity (i.e. total number of main habitat cover variables present at a given plot) (Table 1).

For each invertebrate category, we calculated the total number of items and their overall relative abundance, total and relative biomass. Mean invertebrate size was estimated per plot and category, and the weighted arithmetic mean over all the plots was calculated for descriptive purposes. Invertebrate profitability was estimated per category as the total biomass divided by the total number of items, and invertebrate diversity was measured with the Shannon–Wiener index (H′) (Shannon and Weaver 1949) by considering all the identified categories. Marginal invertebrate categories ($<5\%$ of total abundance and/or biomass) were excluded from further analyses (see Tables 1 and S1 for more details).

Our habitat selection analyses consisted of a comparison of habitat and invertebrate community composition at foraging versus pseudo-absence plots. We first modelled habitat composition dependent on the plot type, year, and date. Then, we calculated preference indices for each habitat type based on the estimated proportional cover in the foraging and pseudo-absence plots. To model habitat composition, we fitted cubic regression lines over the date for each variable, including interaction terms between date and plot type (foraging *vs* pseudo-absence), and between date and year. We used cubic regression lines because we expected gradual changes with changes in slopes (S-shaped curves) for habitat cover with the seasonal progression. Stratum (i.e. the association between one foraging plot and its related pseudo-absence plots) and bird individual identity were included as random factors in our models to account for dependence between observations from the same individual. Linear mixed models were fitted by using the function *lmer* from the package *lme4* (Bates et al. 2015). In order to assure full plot coverage, the fitted values from the eight models (one per main habitat ground cover variable) were scaled so that their sum equalled one for each date, year, and plot type. Subsequently, we calculated the Jacob's preference index (Jacobs 1974) for each habitat cover per date and year by comparing their proportional occurrence in the foraging (u_i) and pseudo-absence plots (a_i):

$$J_i = \left(u_i - a_i\right) \big/ \left(u_i + a_i - 2u_i a_i\right)$$

The joint posterior distribution of the model parameters was obtained by assuming improper flat prior distributions ($\beta \sim 1$) via Monte Carlo simulations as implemented in the

function *sim* from the package *arm* (Gelman and Hill 2007). By transforming each of the 5000 simulated sets of parameter values into fitted values, and subsequently into Jacob's indices, we obtained a sample of random values from the posterior distribution of the Jacob's indices of which we used the 2.5% and 97.5% quantiles as lower and upper limits of the so called 95% credible interval.

We used generalized additive mixed models (GAMMs) with stratum and individual identity included as random factors and date as predictor in order to further characterise the seasonal changes, as well as the between-year differences, and the differences between the foraging and pseudo-absence plots for non-cover variables. We also used invertebrate biomass and diversity as response variables. GAMMs were fitted by using Markov chain Monte Carlo simulations as implemented in the package *bamlss* (Umlauf et al. 2017). We used regularised thin plate regression splines where the degree of smoothing is defined by the prior variance. The prior variance is derived from the parameter k that can be set by the user. We varied k from −1 (default value) to 6 in order to measure the sensitivity of the results in relation to this parameter. Some models with higher values for k failed to converge. Results for k values between −1 and 6 all looked essentially similar. The results presented are from the models fitted with the default value.

Finally, to assess the relationship between invertebrate biomass and all habitat variables, we used linear mixed models with a log response variable. Explanatory variables included the main habitat ground cover proportion variables that were all arcsin, square-root transformed, and standardized. Those variables were: snow (including linear and quadratic term); old and new vegetation; herbs; flowers; mosses and lichens; bare ground; and rock and scree. Further explanatory variables were: height of old and new grass; soil moisture; slope steepness; aspect; habitat diversity; date; year and plot type (foraging *vs* pseudo-absence). Stratum and individual were again included as random factors. Model assumptions were assessed from underlying standard residual plots that showed: a constant mean of zero along the fitted values and along each predictor variable; normal distribution; homogeneity of variance; and no overly influential observation. As before, uncertainty intervals were calculated as the 95% symmetric credible intervals defined by the 2.5% and 97.5% quantiles of the posterior distribution.

Statistical analyses were all conducted in R version 3.4.2 (R Core Team 2015).

Results

Habitat selection

The 14 radio-tracked breeding Snowfinches yielded 174 foraging plots and 548 randomly located pseudo-absence plots. Overall, the main types of ground cover were new grass (26.7% of the total coverage); rock and scree (14.3%); old grass (13.9%); bare ground (13.4%); herbaceous green vegetation (11.6%); mosses and lichens (10.7%); snow (5.0%); and flowers (1.8%). The remaining (2.6%) habitat types included water, cow dung, bushes and "others". Average snow cover at the pseudo-absence plots during the first week of radio-tracking was around 20%, both in 2015 and in 2016, decreasing to zero within 3–4 weeks, with a more rapid snow cover decrease at pseudo-absence than at foraging plots (Figs. 2a, S1). As the breeding season progressed, the cover of new grass quickly increased, progressively replacing snow and old grass, while flowers mainly appeared later on in the season. The Jacob's preference index revealed that Snowfinches preferred foraging near

Fig. 2 Patterns of micro-habitat selection in foraging White-winged Snowfinches with respect to habitat ▶ type. **a** Seasonal change in habitat cover variables (%), each depicted by a different colour (right panel legend), at foraging and pseudo-absence plots in 2015 and 2016. Note in particular the prolonged reliance on snow fields at foraging compared to pseudo-absence plots. **b** Habitat selection pattern throughout the season (denoted by the lines) in 2015 and 2016, drawn from Jacob's index, which ranges from − 1 (highly avoided) through 0 (used in proportion to availability) to + 1 (highly selected); note the over-selection operated for snow cover (both years) and flowers (2016). **c** Seasonal trends and 95% confidence intervals for the two key retained variables snow and flowers coverage. (Color figure online)

snow early in the season, while later on they showed a preference for plots with flowering plants. In contrast, they always seemed to avoid rock and scree (Fig. 2b, c).

The height of old vegetation remained fairly constant while the height of new vegetation increased over the season, with a consistently lower sward height at foraging compared to pseudo-absence plots (Fig. 3a, b). This indicates that Snowfinches actively selected foraging plots with shorter ground vegetation. Soil moisture decreased over the season in both years, but foraging plots exhibited, on average, higher soil moisture compared to pseudo-absence plots (Fig. 3c). In contrast, there was no preference whatsoever for slope steepness (Fig. 3d) and aspect (Fig. 3e). The habitat diversity index increased over the season, with foraging plots showing slightly greater habitat diversity than pseudo-absence plots, especially later in the season after total snowmelt (Fig. 3f).

Invertebrate abundance and biomass

Overall, 3,051 invertebrate items (total dry biomass: 17.2 g) were identified and classified into 26 categories (see Table S1 for details). The most abundant invertebrate categories were: Formicidae (21.3%); Tipulidae adults (12.3%); Coleoptera (11.8%); Araneae (11.2%); Opiliones (8.9%); Brachycera (7.5%); and Orthoptera (6.7%) (Fig. S2a). In terms of biomass, the categories with the highest contributions were: Orthoptera (30.4%); Coleoptera (13.2%); Araneae (12.6%); Tipulidae adults (9.7%); Lepidoptera larvae (9%); and Tipulidae larvae (8.4%) (Fig. S2b).

Invertebrate abundance and biomass started to increase earlier in the season in 2015 than in 2016. This was a result of an earlier snow melting process (see above; Fig. 4). In 2015, Tipulidae larvae and adults together with Coleoptera contributed the greatest biomass early in the season, whereas later on, Brachycera, Araneae and Opiliones dominated for a while, prior to grasshoppers eventually taking over (Fig. 4). In contrast, in 2016, Araneae and Formicidae were dominant during the whole season. Early in the season, Coleoptera were also frequent, whereas later on, Opiliones, Lepidoptera larvae, and Orthoptera became more abundant. Overall, in both years, foraging plots had generally higher invertebrate biomass and diversity than pseudo-absence plots, with Tipulidae (first larvae, later adults), Brachycera, Formicidae, Coleoptera and Orthoptera being overrepresented at foraging plots (Figs. 4 and 5).

Invertebrate biomass versus habitat selection

The biomass of the main invertebrate categories was differently affected by habitat features, with some marked interannual and seasonal variation (Fig. 5). The most striking effect was a strong correlation between the biomass of Tipulidae larvae and snow cover, with 72 out of 82 (88%) of these larvae having been found within one meter from the snow
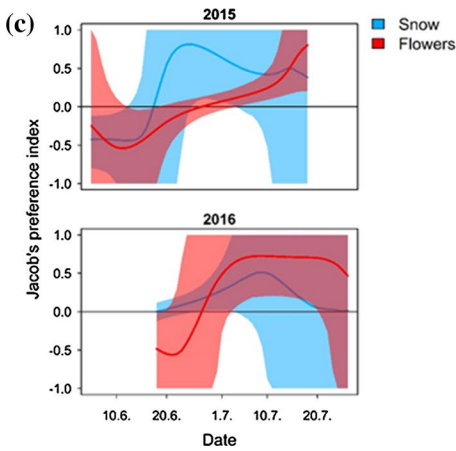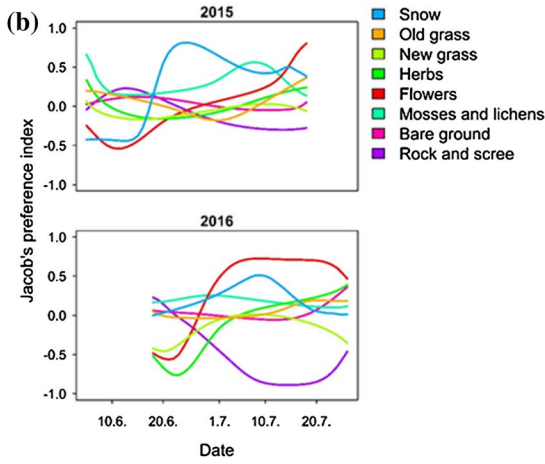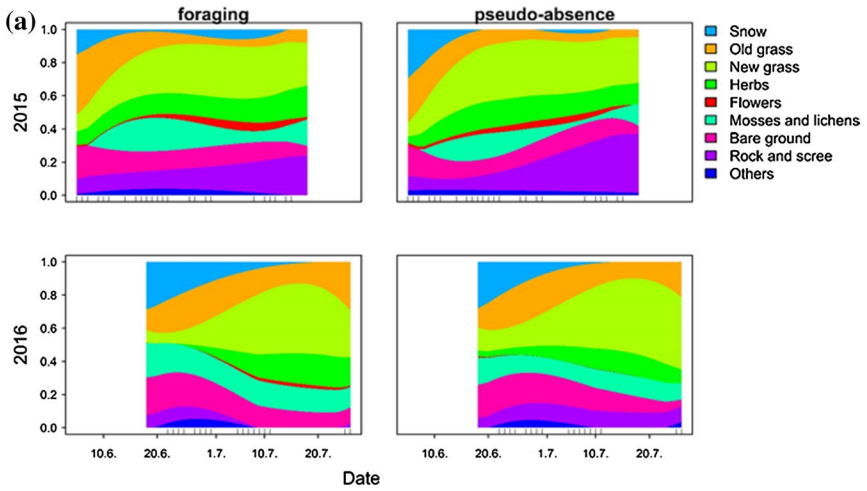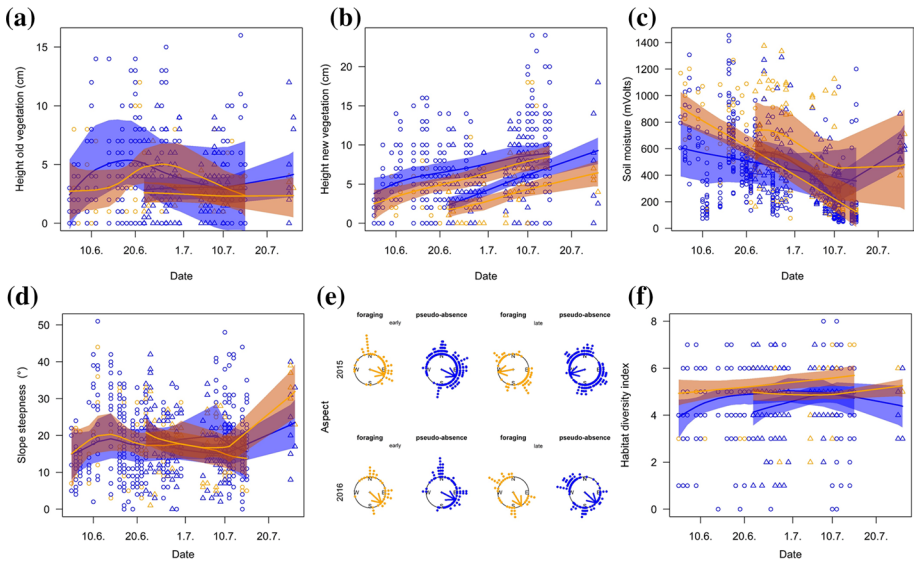
Fig. 3 Patterns of micro-habitat selection in foraging White-winged Snowfinches with respect to vegetation and soil charateristics, topographic context and habitat diversity. Seasonal changes in the height of **a** old and **b** new ground vegetation, **c** soil moisture, **d** slope steepness, **e** aspect, and **f** habitat diversity in 2015 (earlier start of the breeding season, dots) and 2016 (later start, triangles) at both foraging plots (orange) and pseudo-absence plots (blue). (Color figure online)

front (i.e. melting snow patches) (Fig. S3). The proportion of herbaceous green vegetation cover, which increased throughout the season, led to an augmentation of the biomass of Opiliones. The biomass of Lepidoptera larvae and Orthoptera was negatively correlated to old grass height, while Orthoptera biomass correlated positively to new grass height. Higher Araneae and Coleoptera biomass was associated with high soil moisture. The biomass of Opiliones and Orthoptera was negatively correlated with slope steepness, with south-exposed aspects furthermore hosting greater biomass of Formicidae and Orthoptera but lower biomass of Lepidoptera larvae. Biomass of all invertebrate categories clearly differed between the years. In 2015, there was an overall higher biomass of Tipulidae larvae and adult, Brachycera, Opiliones, and Orthoptera. But in 2016, there was a higher biomass of Formicidae, Araneae, Coleoptera, and Lepidoptera larvae. Formicidae biomass was high early in the season and decreased towards the end of the season, while the biomass of Brachycera, Opiliones and Orthoptera increased during the course of the season (Fig. 5, Table S2).

Discussion

This study demontrates that the foraging microhabitat selection of the Snowfinch, an emblematic bird of high-alpine ecosystems, is governed by the strong seasonality of vegetation phenology. That strong seasonality is induced principally by the snow melting process that creates variegated prey-habitat associations. Parents provisioning their chicks track those associations. This strong link to snow conditions has implications for a species'
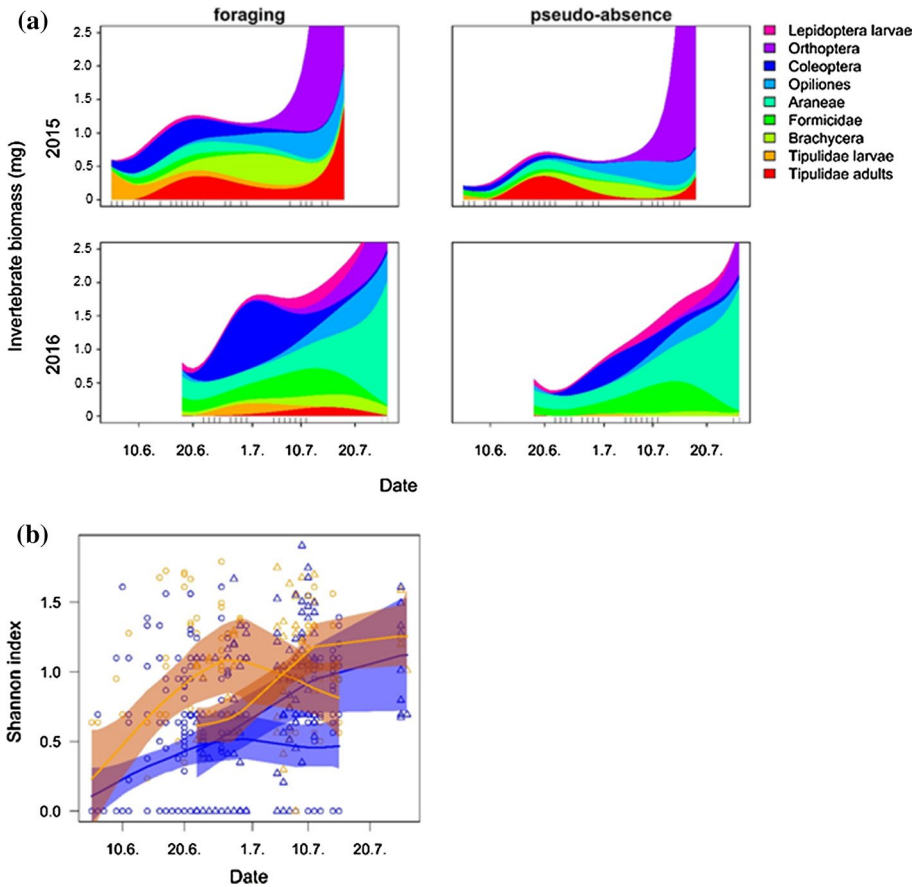
Fig. 4 Seasonal changes in invertebrate biomass and diversity at foraging and pseudo-absence plots. Change in **a** total biomass per invertebrate category (see panel legend) and **b** invertebrate diversity (Shannon index) in 2015 (earlier start of the breeding season, dots) and 2016 (later start, triangles) at both foraging plots (orange) and pseudo-absence plots (blue). (Color figure online)

adaptive potential to environmental change, notably climate warming, and will be instrumental for developing sound mechanistic predictive models and providing conservation management guidance.

In the two study years, parents started food provisioning for nestlings when snow cover in nest surroundings amounted to ca 20%, with a 2-week delay in 2016 compared to 2015 due to year-specific snowmelt phenology. This pattern of synchronising nesting with the snow melting phenology has been reported in previous studies of Snowfinches and other bird species that inhabit high-alpine and arctic ecosystems (Brambilla et al. 2018; Dickey et al. 2008; Liebezeit et al. 2014; Scridel et al. 2018; Wilson and Martin 2010). In our study area, the entire snow melting process lasted 3–4 weeks. In this brief time window it generated a complex habitat mosaic of snow fields and habitat patches recently freed by snow, offering variegated foraging opportunities for the Snowfinch, notably concentrated food resources that are easily accessible for a ground forager. Breeding Snowfinches track this spatiotemporal dynamic in resource availability in order to maximize chick provisioning.
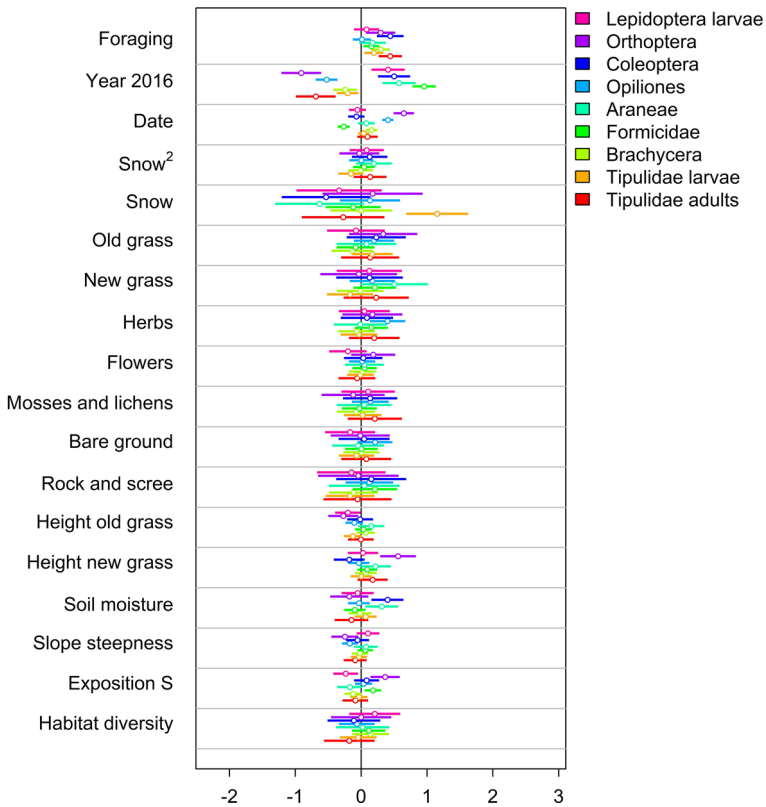
Fig. 5 Partial effect sizes of habitat variables on the biomass (log-transformed) of the main invertebrate categories (panel legend). The mean estimates (circles) stem from partial correlation coefficients, with 95% credible intervals (horizontal bars). All numeric predictors were centered and scaled by using 2 standard deviations (SD) so that the estimated effects correspond to a change in the biomass as a result of an increase in the explanatory variable by 2 SD. Note in particular the outstanding effect size for Tipulidae larvae and snow cover (on its linear tem). (Color figure online)

One of the most salient findings of this study was that the biomass of Tipulidae larvae heavily depends on the presence of a nearby snow patch (largest effect size of any prey-habitat relationships, Fig. 5). Meanwhile, the main driver of Snowfinch habitat selection early in the reproductive season is the presence of snow cover, although birds forage more often on the snow-freed sectors rather than directly on the snow pack (personal field observations). Our fined-grained foraging habitat selection analysis would thus corroborate the key role played by Tipulidae larvae in the diet of early Snowfinch nestlings [60% of prey volume from 218 neck collar samples yielded by four broods in Heiniger (1991)]. This observation furthermore highlights the general importance of Tipulidae larvae in the diet of Alpine avifauna (Cramp and Perrins 1994; Rolando and Laiolo 1997). Tipulidae larvae (e.g. *Tipula carolae*, *T. strobliana* and *T. truncorum*) typically live under thaw-freeze conditions in small water holes at ground level, being freed, sometimes in great numbers, when snow is melting (Heiniger 1991). With their fairly large body size, mean item biomass and energy content (17.6 mg/item, this study; 22.0 kJ/g dry mass, (Heiniger 1991)), Tipulidae larvae additionally represent the second most profitable main prey category in

this study, in terms of biomass by item, just after Orthoptera (25.5 mg/item) (Table S1). Orthoptera occur relatively late in the vegetation period due to their successive instars and are thus of secondary relevance for breeding Snowfinches. Moreover, given that Orthoptera have a very chitinous exoskeleton, Tipulidae larvae, which have relatively soft skins, represent an ideal staple food resource for Snowfinch nestlings.

Soil moisture was another important factor in Snowfinch foraging habitat selection. It is clearly related to the snow melting process, dramatically decreasing as the season advances (Fig. 3c), which again confirms the association of Snowfinches to a heterogeneous habitat mosaic containing snow fields. Coleoptera (represented mainly by Carabidae and Staphylinidae) and Araneae were also positively influenced by soil moisture, and they were likely collected by foraging Snowfinches although dietary evidence is lacking. Yet, our model yielded no significant effect size for soil moisture and Tipulidae larvae, which might be due to lack of statistical power because this taxon was relatively rare in our sample. On the one hand, other prey-habitat associations that we found were that Orthoptera and Formicidae preferred sun-exposed slopes, with Orthoptera also selecting non-steep slopes with tall new vegetation. On the other hand, Lepidoptera larvae chose preferentially north-exposed slopes, while Opilions were associated with non-steep slopes with higher coverage of herbs.

A third factor playing a key role in foraging habitat selection was the presence of short vegetation swards throughout the breeding season. The grounds freed by the retreat of the snowpack are covered by the flattened dead vegetation stalks of the previous year, which are progressively replaced by the new growing vegetation. During that initial phase, foraging habitat is optimal for Snowfinches, offering high accessibility to ground-dwelling prey. Later on, when ground vegetation cover has become denser, Snowfinches still show a preference for foraging grounds with a short vegetation sward, but they then select flowering alpine meadows that are likely to provide richer prey supplies. In summary, these seasonal changes in prey-habitat associations are well reflected in the locations of the radio-tracked parent Snowfinches when they search for prey. In this respect, we predict that if Tipulidae larvae and Coleoptera dominate the diet of Snowfinch chicks early in the season, their diet must become more diverse later on. However, no dietary studies have yet investigated the prey provisioned by parents throughout the chick rearing period (Heiniger 1991).

Our data show that prey supply and food biomass are potentially greater in mid-summer than in late spring and early summer (Fig. 4). The question that arises then is why Snowfinches are not breeding later in the season than observed. This could be explained by prey availability, whose abundance is modulated by accessibility. In effect, from the perspective of a typical ground-forager that needs a walkable substrate for hunting, feeding conditions are clearly more optimal in late spring and early summer (absence of fresh vegetation or short vegetation layer) than later in this season. Thus, Snowfinch foraging habitat selection would result from a trade-off between prey abundance and accessibility, as evidenced for several passerines (Douglas et al. 2008; Evans et al. 2015; Vickery and Arlettaz 2012; Vickery et al. 2001).

Prey-habitat associations above the tree line are naturally extremely dynamic (Arthur et al. 1996; Martin 2001). Accelerating environmental change, notably climate warming, exposes high-elevation wildlife to the growing and delicate challenge of synchronizing breeding phenology to peaks in resource availability (McKinnon et al. 2012). For instance, those years with late snowmelt the Pyrenean rock ptarmigan can miss the peak of food quality, with negative effects on its reproductive success (García-González et al. 2016). The dependence of the Snowfinch on snow and ground vegetation circumstances similarly suggests that climate warming, along with abandonment or change of farming activities, might markedly impact this highly specialized passerine (Brambilla et al. 2016; Maggini

et al. 2014). Snow depths and snow cover duration are clearly decreasing in the European Alps (Klein et al. 2016; Laternser and Schneebeli 2003), which might augment the risk of phenological mismatches between breeding effort and seasonal resource availability (see McKinnon et al. 2012). If elevational range-shifts towards mountain summits could partially compensate for the loss of suitable habitats at lower elevations, this would inevitably exacerbate range contraction given the reduction of habitat area with elevation (see Elsen and Tingley 2015; La Sorte and Jetz 2010; Maggini et al. 2011; Pernollet et al. 2015; Rehnus et al. 2018). This will first have dramatic consequences for populations of high-alpine species that presently occur in low-elevation and peripheral mountain ranges, where the nival belt is already minute. Snow conditions will depend on global climate remediation strategies, whilst ground vegetation circumstances can be modulated by farming practices, i.e. livestock grazing (see Brambilla et al. 2018). Whether and to what extent targeted grazing could help mitigate against the detrimental effects of climate warming remains to be investigated.

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