Foraging ecology and wintering monitoring of the White-winged Snowfinch (*Montifringilla nivalis*) in the Swiss Alps.

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Abstract

Global change is massively impacting alpine ecosystems and their biodiversity, including avifauna. Understanding the breeding and foraging ecology of high-elevation birds is an absolute prerequisite to conservation guidance. We investigated the link between nestling diet, food abundance and foraging habitat composition in a breeding Snowfinch population in the Swiss Alps throughout the breeding season of 2018 (June to August). Chicks' diet was assessed by photographing adults delivering prey to their nestlings, while invertebrate food availability was assessed by a combination of visual observations, soil scratching and pitfall trapping at foraging grounds where habitat composition was mapped in parallel. Habitats exhibiting patches of snow, especially snow front, harboured a higher invertebrate abundance than habitats with more bare ground and rocks. Including many invertebrate larvae, chicks' diet was less diverse in the middle of the breeding season than at its onset, while towards the end of the season chicks' diet was getting more diverse and incorporated even fewer larvae. It seems that Snowfinch parents compensated for an overall lower invertebrate biomass availability by enlarging diet spectrum through hunting for prey becoming less profitable, this as the season progresses. The three invertebrate sampling methods provided different information, visual observations providing less reliable data. A combination of pitfall trapping and scratching appears thus more promising for accurately estimating invertebrate availability. Prey-habitat relationships showed that invertebrate larvae, which make the bulk of chicks' diet, were more abundant in habitats covered with new vegetation and at snow melting front, making them key food providers. Conservation action should focus in priority on the maintenance of such crucial habitats.

.**Key words**

Alpine ecosystems • Climate change • European Alps • Invertebrates • Larvae • Mountains • Nestling diet • Wintering dynamics

Introduction

Alpine ecosystems are facing several threats due to global change. Alpine regions have shown to be warming twice as high (Brunetti *et al.* 2009) than all the other ecosystems due to climate change. As a reaction to climate change, species interactions will change, because life-cycle events, which relay on environmental triggers, are leading to phenological mismatches (Hughes 2000; Green 2010; Cahill *et al.* 2013). Another expected and already experienced impact of climate change is a shift in the altitudinal and latitudinal distribution of species (Hughes 2000; Parmesan 2006) with tree lines moving up accordingly (Kullman 2002; Harsch *et al.* 2009). But a shift towards higher elevation is limited, because the higher species move, the less space there is due to the conical shape of mountains (Dirnbock, Essl & Rabitsch 2011). It was shown that alpine species will face the highest extinction risk due to range contractions (Parmesan & Yohe 2003; Parmesan 2006; Sekercioglu *et al.* 2008; Lehikoinen *et al.* 2014), with a highest decline in population for species which breed at highest elevation (Flousek *et al.* 2015). Additionally, human leisure activities in nature are increasing, such as in alpine regions where winter activities and ski resorts lead to a decline in habitat (Arlettaz *et al.* 2007; Braunisch, Patthey & Arlettaz 2011) and human leisure activities in summer were shown to have negative impacts on physiology, immediate behaviour, abundance and reproductive success in birds (Steven, Pickering & Castley 2011). Last but not least, agricultural practices change as alpine grasslands are more rarely used as pastures and increasingly abandoned leading to a change in habitat (Laiolo *et al.* 2004; Garcia *et al.* 2008) which will end in a loss of open habitat in the future (Dirnbock, Essl & Rabitsch 2011; Chamberlain *et al.* 2013).

Not only is the alpine region one of the most vulnerable biomes due to climate change (Gonzalez *et al.* 2010), but it is also a harsh environment with challenging abiotic factors such as high winds, prolonged snow cover, steep terrain, extremes of hot and cold temperature and intense ultraviolet radiation (Billings & Mooney 1968). Due to this extreme conditions, species breeding at higher elevation should cope with shorter breeding season and higher environmental stochasticity (Martin 2001). The strong seasonality is therefore an important characteristic of alpine ecosystems, with alpine species' traits having evolved accordingly. For example, in alpine ecosystems there is a strong temporal resource gradient in spring time associated with melting snow fields (Martin 2001). Due to different climates throughout the season, there is also a strong spatial resource gradient. This leads to high energetic costs for living and breeding species, as there is a smaller window of time of optimal conditions (Martin & Wiebe 2004) and the availability of resources differs considerably throughout the year (Martin 2001). As a consequence, species need to use different habitats during the year and have to adapt in their life-history

Alpine birds are at particular risk due to climate change as they appear in high elevation facing the above mentioned challenges (Sekercioglu *et al.* 2008; Gonzalez *et al.* 2010; Chamberlain *et al.* 2012; Lehikoinen *et al.* 2014). Their reproductive success is thought to be lower with increasing elevation, which makes them less plastic to react to perturbations (Lu *et al.* 2009; Boyle, Sandercock & Martin 2016). Additionally, several studies showed that bird communities do not shift upwards or they do it slower than projected by climate change (Archaux 2004; Popy, Bordignon & Prodon 2010; Maggini *et al.* 2011), which might even increase their vulnerability.

The White-winged Snowfinch *Montifringilla nivalis* (hereafter Snowfinch) is an alpine bird species well adapted (e.g. physiology, breeding biology, ecology) to the cold and harsh environmental conditions occurring in alpine ecosystems. Despite the species is not considered within the Swiss bird priority list, current studies suggest it may considerably suffer from climate change due to a remarkably loss of habitat suitability (Lu *et al.* 2009; Smith *et al.* 2013; Brambilla *et al.* 2017). It lives in alpine and subalpine elevations of temperate zones, where in summer the species occurs up to 4000m a.s.l. In wintertime, it moves down to high-situated valleys (Heiniger 1991b; Cramp & Perrins 1994). The species breeds inside rock crevices in cliffs, but also nest in human infrastructures such as buildings or ski pylons and, in some cases, nestboxes (Heiniger 1991a; Heiniger 1991b). Normally, nest-building is started in the first half of May and the chicks fledge between the end of June and mid-July. Foraging in the early summer season is focused on edges of melting snow patches (Brambilla *et al.* 2017; Resano-Mayor *et al.* 2019) where they find higher abundance and availability of invertebrates, particularly Tipulidae larvae (Heiniger 1991a; Resano-Mayor *et al.* 2019). Later in the season, foraging microhabitat selection is driven by heterogeneous vegetated patches with short grass height mediated by higher abundance of larger and more diverse sort of invertebrates (see also Arlettaz *et al.* 2012; Resano-Mayor *et al.* 2019). These fine-scaled habitat requirements suggest that the species could be particularly sensitive to climate warming (Brambilla *et al.* 2017). In wintertime, the species searches for seeds in scarp faces or in snow free patches. However, when weather conditions are very bad, they frequently take advantage of human implemented feeders (Heiniger 1991b).

At the Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, an alpine bird project was launched in 2015. Regarding the Snowfinch, the project has involved the monitoring of both wintering and breeding individuals. During the breeding seasons of 2015-17, the Snowfinch foraging microhabitat selection was studied at different breeding sites (Valais, Switzerland) and spatial scales (1 and 5m radius) by means of radio-tracking (2015-16) and visual observations (2017) (Resano-Mayor *et al.* 2019). However, the link between habitat selection and diet composition remained to be studied. Therefore, the main aim of this MSc thesis was to investigate the link between nestling food provisioning, habitat composition and food abundance and biomass in the foraging grounds of Snowfinch breeding sites. First, we assessed food abundance and biomass at the main foraging habitat types by comparing three different invertebrate sampling methods. Second, the main invertebrate groups in the nestling diet were determined throughout the season. Third, we investigated whether nestling diet depended on food availability. Finally, we analysed the habitat requirements of the most important invertebrate groups found in the diet.

An additional aim of the MSc thesis was to monitor a wintering Snowfinch population in Val Ferret (Valais, Switzerland) and to collect data in a standardized way for future survival analysis.

Material and methods

Breeding module

<u>Data collection</u>

Study area

Between June and August 2018, data collection was done below the Gornergrat in Zermatt, Valais (Switzerland), at an elevation between 2500 and 2950m a.s.l. The broods were found by checking nest sites from previous years and observing the whole area. Broods were normally found when the female was still incubating, and then it was checked frequently to find out when the nestling provisioning period started (i.e. adults bringing food to their chicks). In total, we monitored 7 broods, the earliest started provisioning the 30th May and the latest started the 20th July. Three out of the seven broods failed, one because of predation, one because of human disturbance and the last one probably because of sun radiation building up heat in the ski pylon. The monitoring of each brood was divided into three sessions of a week (Fig. 1) in order to cover the whole Snowfinch nestling period of about 21 days (Heiniger 1991a; Cramp & Perrins 1994).

Habitat coverage

As an estimate of the main habitat types around breeding sites, we built a 300m radius plot around the nest and visually mapped the habitat in the area for each session (once per week). The habitat mapping was always done from the same point, usually a high elevated point with a good view over the whole area. Then, to have a more detailed picture, we additionally mapped within the 300m radius the five main habitats: snow, snow front, grassland, bare ground and minerals. For each brood we chose randomly one site for each habitat and mapped it within a 5m radius. We mapped the ground coverage and took severable other measurements such as northing, slope, vegetation height and temperature (Table 1). In session two and three, the snow front had to be tracked as the snow melted, which means that with each session a new snow front plot had to be set. The old snow front plots were kept in the pitfall plots (not in scratching), which resulted in two more habitats, namely snow front after one and after two weeks.

Invertebrate sampling

The invertebrate sampling was carried out by three different methods: scratching, pitfalls and visual observation. All these methods were applied on each of the five main habitat types described above for each session and brood.

Scratching was carried out at a different site than the pitfalls, which was chosen randomly with 25 to 50m apart from the pitfall plots. Scratching was carried out the same day as the pitfalls were closed. Scratching was done at 1m radius plots. First, flying and crawling invertebrates were collected by hand, and then with the use of a rake the ground surface was scratched to find the larvae at the upper soil layer. All collected invertebrates were stored in Ethanol 70%.

The second method consisted in systematically placing three pitfalls within a 5m radius plot that was randomly selected. In the analysis, always the mean invertebrate number and biomass of the three pitfalls was used. A cover was used to protect the pitfalls from rainfall. The pitfalls were kept open for five days and closed for two days per session. Propylenglykol with water was used as a liquid to capture the invertebrates. Lastly, all collected invertebrates were stored in Ethanol 70%.

The third method used was visual observation, which consisted on carefully watching a plot of 1m radius for two minutes. The plot was within the 5m radius plot selected for the pitfalls. For the first minute, all invertebrates that crawled on the ground were noted, and for the second minute, all flying invertebrates. This was carried out twice per session, when the pitfalls were opened and four days later when they were closed.

Diet assessment

To assess the invertebrates brought to the nestlings, we monitored each brood once per session by taking pictures. This was done by a field technician who stayed in the vicinity of the nest and took pictures of all feeding events with the help of a camera (NIKON D5, objective NIKON 800MM, f/5.6 with a multiplier of 1.25 which corresponds with a focal length of 1000mm), for at least two hours in the morning and two hours in the afternoon. The diet assessment was only held in non-rainy weather conditions.

<u>Invertebrate identification</u>

Invertebrates sampling

All the collected invertebrates from scratching and pitfalls were identified in the lab afterwards with the use of a binocular microscope (MSA Wild Heerbrugg, Switzerland). Each invertebrate item was identified to family, suborder or order level (Table 2). Biomass was not measured directly but measurements from previous years of a similar study (Resano-Mayor *et al.* 2019) were taken as a reference (Appendix A).

Diet assessment

The diet was assessed based on the pictures taken from the adults provisioning the chicks. First, each time they brought food, time and sex was noted and then the beak load was assessed visually, where the beak itself is used to measure the size of the beak load. We defined five load categories: no items, a third of the beak with items, two thirds of the beak with items, one full beak with items and more than a beak with items. Then, we noted how many items were in the beak (minimum amount of invertebrates) and identified them if possible, either on family, suborder or order level (Table 2). The number of identified invertebrates also served as a measure for diversity (diversity of identified invertebrates). Biomass was assessed the same way as it was done with the invertebrate sampling.

<u>Statistical analysis</u>

Habitat coverage

The change of the habitat in the home-range was graphically plotted by using the package "arm" (Gelman & Su 2018) for R.

Method comparison

Invertebrate sampling methods were compared visually with a histogram in Excel by using relative abundance of the main invertebrate groups. The main invertebrate groups were chosen by relative abundance and by relative biomass, the invertebrate groups which showed smaller relative abundance or biomass than 2% were excluded from the dataset and not considered in all the following analysis. As pitfalls provided the most numerous and consistent dataset, further statistical analyses other than descriptive were performed only with pitfall data.

Invertebrate abundance and biomass

Proportion variables, namely habitat coverages, were arcsin square root transformed, all explanatory variables were scaled, and response variables were log- or sqrt-transformed. To get an overview of the seasonal change of total invertebrate abundance and biomass, univariate linear mixed models with the package "lme4" (Bates *et al.* 2015) were built with brood (n=7) as random factor and date as explanatory variable for pitfall and scratching data.

Invertebrates versus habitat coverage

To analyse the influences of environmental features (Table 1) on total invertebrate abundance and biomass from pitfall data, univariate linear mixed models with the package "lme4" (Bates *et al.* 2015) were built with brood (n=7) nested with habitat as random factor. All variables with a p-value smaller than 0.1 were put in a multivariate model, which was dredged with the package "MuMIn" (Barton 2018). This process provided the top models from which the best models within an AIC smaller than two were kept and averaged, leading to the final model. Always the full-average model was considered. To visualise these models, the data was simulated by using the package "arm" (Gelman & Su 2018).

Diet assessment

Only six broods could be used to analyse the diet, as one of the observed seven broods had only one day of picture monitoring with only the female feeding the nestlings. As not all larvae could be identified to order level, they were grouped in two ways. First, an overall category "all larvae" was built with all identified and unidentified larvae in it. Then, categories on order level, such as Lepidoptera, Coleoptera and Tipulidae, were built with the identified larvae, which were already included in the “all larvae” category. Univariate linear mixed models were built with the package “lme4” (Bates *et al.* 2015) with brood (n=6) as random factor to explain how environmental features (Table 1) were influencing minimum amount of invertebrate abundance and biomass, diet diversity and beak load. Additionally, an analysis of Lepidoptera larvae and all larvae together as response variable and the above-mentioned environmental features as explanatory variables was performed as well.

Diet versus invertebrate availability

To compare the diet with the collected invertebrates, the two data sets had to be combined which left a relatively small data set. As invertebrate identification was not as much into detail in the diet assessment as it was in pitfalls, the invertebrate groups from the pitfalls had to be grouped so that they matched the identification level of the diet. Each session with a diet estimate, abundance of the main invertebrate groups, was compared to the invertebrate sampling estimate, also abundance of the main invertebrate groups.

To get the composition of the invertebrates in the diet compared to pitfalls and scratching, a multinomial model was built with the help of the packages “rstan” (Stan Development Team 2018) and “shinystan” (Gabry 2018) by using abundance. The analysis showed the mean abundance with its confidence interval of 2.5% and 97.5% of each invertebrate group per sampling method. Larvae could only be analysed as one category, because in diet estimates many larvae could not be identified to order level.

Main invertebrate groups in the diet versus pitfall data

The invertebrate groups being more or equally abundant in the diet as in the pitfalls and scratching from the multinomial analysis were then analysed by using pitfall data to explain the habitat requirements of these groups. The multinomial analysis could only be performed on all the larvae groups together, but for this analysis, the separate larvae groups were analysed additionally. The analysis was performed the same way as for the "Invertebrate abundance and biomass". Only biomass data was used as for biological reasons, biomass is a better estimate of the requirements of Snowfinches.

All the statistical analyses were done with R (R Core Team 2018).

Wintering module

<u>Data collection</u>

Study area

The monitoring of the wintering population was conducted in Val Ferret (Valais, Switzerland) at two mountain villages, La Fouly (1,600m a.s.l) and Branche d'en Haut (1,400m a.s.l), ca. 4km apart one from each other, where people provide food in winter at feeding sites. The feeding sites were already existing bird feeders at private places. It was assumed that the same population visited both feeders as several birds were observed at both feeders, also in previous years. The monitoring of the wintering population in Val Ferret already started in the winter of 2015 by capturing Snowfinches attending the feeders and marking them with metal rings. In 2016, however, it was decided to continue the marking program with colour rings in order to facilitate re-sighting events. During the winters of 2016-2017, a total of 100 individuals were colour banded and so far about 70 recaptures or re-sightings could opportunistically be obtained. To continue and elaborate this monitoring, data was collected between November 2017 and April 2018 with two different methods: capturing and video recording.

Capturing and ringing

In total, we conducted seven capturing events throughout the whole season (November 2017 to April 2018): four in November and December and three in January and February. This capturing effort was similar to previous years. Three capturing events were done in La Fouly and four in Branche d'en Haut. Birds were captured by using mist nets, which were set up around the feeder early in the morning at sunrise. The capturing was always done during bad weather conditions (previous snowfall or currently snowing). Unringed birds were marked with a conventional metal ring on one tarsus, and a colour (red) alphanumeric (white digits) ring on the other. Biometrics (wing, third primary and tarsus length), weight and muscle score were recorded for all birds.

Video recording

During the whole winter season, we had 19 video recording sessions. These sessions were divided into good (n=9) and bad (n=10) weather conditions. Good weather conditions served as a control, because from previous experience it was known that Snowfinches only use the feeders during bad weather (snowy) conditions. Video recording was done at both sites at the same day and did not overlap with capturing days. In order to gain re-sighting data during the whole day, video cameras (Sony DCR-SR200E) were set up early in the morning (before sunrise) next to the feeder and were operating the whole day (approximately 10 hours). Feeders were always full of food, also on non-filming days. Other known bird feeders in the surrounding were either covered up while the video cameras were operating, or people were asked to not put food.

Video analysis

Each video of a re-sighting session was watched with a speed of 6.00x. Each time one or more Snowfinches came to the feeder, the alphanumeric ring-code was identified (only in few cases it was not possible), and the time spent at the feeder was noted. As not all Snowfinches were ringed, the total number of Snowfinches attending to the feeder was noted as well. Additionally, all other species attending the feeder were noted but not counted.

Statistical analysis

Statistical analyses were not performed on the wintering module, due to time contraints. Descriptive analysis was performed with Excel to display the total re-sighting events by building a histogram with the number of re-sightings per individual. Also, the individual re-sighting history over the whole monitoring period was visualised.

Results

Breeding module

Habitat coverage

The habitat within the 300m radius plot around the nest changed over the season. Especially, there was a change from snow cover early in the season to new vegetation later on. Water cover stayed the same over the season, whereas old vegetation decreased slightly over the season and bare ground and mineral increased slightly over the season (Fig. 2).

Method comparison

The relative abundance and biomass of the most represented invertebrate groups collected by pitfalls was similar to that obtained by scratching. However, less represented invertebrate groups differed by method in the rank for abundance and biomass. The invertebrate composition estimated by visual observations differed considerably with the other two methods regarding the main invertebrate groups (Appendix B).

Invertebrate abundance and biomass

Scratching

A total of 714 items were collected with a total biomass of 8,428mg. The most abundant groups were Coleoptera adults (n=149), Lepidoptera larvae (n=144), Coleoptera larvae (n=82), Homoptera (n=50), Formicidae (n=46), Lepidoptera adults (n=44), Araneae (n=37) and Brachycera (n=31). When considering biomass, the picture changed slightly with the larvae being the most represented: Coleoptera larvae (n=4,314mg), Lepidoperta larvae (n=2,105mg), Orthoptera (n=586mg), Coleoptera adults (n=475mg), Araneae (n=236mg), Tipulidae larvae (n=140mg) and Lepidoptera adults (n=93mg).

Snow, snow front and grassland provided more invertebrates than bare ground and rocks. When considering biomass, snow front and grassland harboured more invertebrate biomass than any other habitats (Appendix C).

Pitfalls

A total of 5,533 items were collected summing up to a biomass of 46,940mg. In general, the most abundant groups were Coleoptera adults (n=1,740), Brachycera (n=903), Coleoptera larvae (n=553), Araneae (n=384), Lepidoptera larvae (n=339), Opiliones (n=301) and Lepidoptera adults (n=262). But when considering biomass, the results changed slightly, as the groups with highest biomass were Coleoptera larvae (n=29,085mg) and adults (n=5,551mg), Lepidoptera larvae (n=4,961mg), Araneae (n=2,455mg), Brachycera (n=1,778mg), Opiliones (n=632mg), Lepidoptera adults (n=556mg) and Tipulidae larvae (n=421mg).

For all the habitats, except full snow cover, the invertebrate abundance reached its maximum at the end of July. Full snow cover was the habitat type with the lowest overall invertebrate abundance, whereas snow front after two weeks had the highest total abundance (Fig. 3a). However, the total invertebrate abundance at the snow front, grassland, bare ground and rocks did not significantly differ.

For all the habitats, except full snow cover, there was a maximum invertebrate biomass at the beginning of July. Full snow cover had the lowest total biomass and snow front after two weeks had the highest, followed by grassland (Fig. 3b). Snow front, bare ground, rocks and snow front after one week did not significantly differ from each other.

Invertebrates versus habitat coverage

Invertebrate abundance was explained by several habitat variables, whith new vegetation showing a negative quadratic relationship (-0.57±0.16, z=13.67, $p<0.001$) while moss showed a significant positive linear relationship (0.77±0.22, z=3.55, $p<0.001$), and date having a significant negative quadratic relationship (-0.44±0.11, z=3.78, $p<0.001$) (Fig. 4). Invertebrate biomass showed a significant negative quadratic relationship with snow cover (-0.48±0.08, z=-6.37, $p<0.001$), while it was significant and positively related with new vegetation (0.39±0.09, z=4.34, $p<0.001$)and date showing a significant negative quadratic relationship (-0.47±0.07, z=-6.94, $p<0.001$) (Fig. 5).

Diet assessment

A total of 1,753 items were counted, of which 1,041 could be identified. The most abundant invertebrate groups were all larvae together (n=585), Lepidoptera larvae (n=306), Tipulidae adults (n=132), Lepidoptera adults (n=90), Coleoptera adults (n=82), Arachnida (n=74), Orthoptera (n=51), Tipulidae larvae (n=41) and Coleoptera larvae (n=24). A total of 371 larvae could be identified to order level, whereas 215 more items could only be classified as unknown larvae. Overall, the invertebrate biomass was estimated as 15,228mg with larvae becoming the most important groups: all larvae (n=12,550mg), Lepidoptera larvae (n=4,489mg), Orthoptera (n=1,290mg), Coleoptera larvae (n=1,270mg), Tipulidae larvae (n=731mg), Tipulidae adults (n=567mg), Arachnida (n=312mg), Coleoptera adults (n=250mg) and Lepidoptera adults (n=180mg).

In the third week, the adults were provisioning significantly more items to their nestlings than in the first week (0.19±0.053, t=3.55, $p<0.001$). Moreover, the later the season, the more invertebrates were brought to the nestlings with a significant positive quadratic relationship (0.07± 0.03, t=2.36, $p<0.05$) (Fig. 6a). The same was found for the beak load, with bigger beak load the third week (0.53±0.12,t=4.44, $p<0.001$) and later in the season (0.40±0.10, t=4.06, $p<0.001$) (Fig. 6c). Total biomass was significant and positively correlated with cloud cover (0.32±0.13, t=2.35, $p<0.05$) but not correlated with date. Finally, diet diversity was significant and positively influenced by cloud cover (0.03±0.01, t=2.09, $p<0.05$) and showed a significant negative quadratic relationship with date (0.06±0.02, t=2.68, $p<0.01$) (Fig. 6b). Date had an effect on the two most abundant groups from the diet assessment (all larvae together and Lepidoptera larvae separately), where the peak of all larvae biomass was earlier in the season than the peak of Lepidoptera larvae biomass (Fig. 7).

Diet versus invertebrate availability

When comparing the diet composition with invertebrate availability based on pitfalls, the multinomial analysis showed differences between consumed and available invertebrate groups (Table 3a, Fig. 8a). All larvae together made 64.3% of the total invertebrate items in the diet, but only 18.7% of the invertebrates collected in the pitfalls. Similarly, Lepidoptera and Tipulidae adults showed high numbers in the diet, which was not the case in pitfalls. On the other hand, Coleoptera adults, Diptera, Hemiptera and Hymenoptera were less abundant in the diet but in pitfalls they showed higher importance than other groups. Arachnida and Orthoptera were similarly represented in both the diet and pitfalls.

When performing the same analysis with invertebrate estimates from scratching, the results were slightly different (Table 3b, Fig. 8b). Not in regards all larvae, which were again very important in the diet (67.3%), whereas in scratching they were less abundant (21.2%). Also, Tipulidae adults were important in the diet, which was not the case in scratching. The opposite was found for Coleoptera adults, Diptera, Hemiptera and Hymenoptera. Finally, a similar importance in the two measurements was found for Lepidoptera adults, Orthoptera and Arachnida.

Main invertebrate groups in the diet versus pitfall data

The seven most abundant invertebrate groups in the diet were not the same as in the pitfalls. Some important groups from the diet, such as Orthoptera, Tipulidae larvae and adults, were barely found in the pitfalls. When comparing within the season with pitfall data, there was a peak of larvae biomass in mid-July, whereas for Lepidoptera larvae, Arachnida and Coleoptera larvae the biomass peak was slightly earlier (Fig. 9).

All larvae

Grassland, rocks, snow front after one week and after two weeks provided the highest larvae biomass. When looking closer at the habitat variables, snow cover had a significant negative quadratic relationship with larvae biomass (-0.39 ± 0.13, $z=-3.05$, $p<0.01$). New vegetation was significant and positively correlated with larvae biomass (0.52 ± 0.16, $z=3.32$, $p<0.01$). Date showed a significant negative quadratic relationship with larvae biomass (-0.63 ± 0.12, $z=-5.26$, $p<0.001$), with an optimum at the beginning of July (Fig. 10).

Lepidoptera larvae

Snow provided the smallest biomass of Lepidoptera larvae followed by snow front. All the other habitats shared a similar amount of Lepidoptera larvae biomass. New vegetation was significant and positively correlated with Lepidoptera larvae biomass (0.69 ± 0.19, $z=3.57$, $p<0.001$), and vegetation height showed an optimum around 7cm (-0.40 ± 0.13, $z=3.07$, $p<0.01$). There was a significant negative relationship between Lepidoptera larvae biomass and north exposition (-0.41 ± 0.14, $z=2.84$, $p<0.01$) (Fig. 11).

Tipulidae larvae

Data of Tipulidae larvae was very scarce in the pitfalls, therefore the potential effect of environmental variables could not be statistically analysed. However, data suggested that grassland, bare ground and snow front after one and two weeks provided more Tipulidae larvae biomass than the other habitats.

Coleoptera larvae

Coleoptera larvae biomass was significant and negatively correlated with snow (-1.32 ± 0.22, $z=6.07$, $p<0.001$) and negatively quadratic correlated with date (-0.83 ± 0.17, $z=4.78$, $p<0.001$), showing an optimum at the beginning of July (Fig. 12).

Tipulidae adults

Data of Tipulidae adults was very scarce in the pitfalls, therefore the effect of environmental variables could not be statistically analysed. However, our data suggested that Tipulidae adult biomass was highest in grassland, bare ground and rocks.

Orthoptera

Data of Orthoptera adults was very scarce in pitfalls, therefore the effect of environmental variables could not be statistically analysed. However, snow front after two weeks provided the highest biomass of Orthoptera, followed by grassland and rocks.

Arachnida

Arachnida were abundant in all the habitats except in snow. When checking the potential effects of environmental variables, Arachnida biomass had a significant negative quadratic relationship with snow (-0.42 ± 0.15, $z=2.82$, $p<0.01$), with an optimum around 30%. Date had a significant negative quadratic effect (-0.27 ± 0.07, $z=3.86$, $p<0.001$), with an optimum at the beginning of July (Fig. 13).

Wintering module

A total of 739 re-sighting events were obtained in winter 2017/2018 by video recording. During the video recording, 19 different species were recorded over the whole season. 67 different Snowfinch individuals could be identified by the colour ring code. Some individuals were re-sighted up to 44 times during several days, whereas other individuals were only sighted once (Fig. 14). In average, individuals were re-sighted 11.2 times. Additionally, some individuals were re-sighted over the whole winter, while others only one or two times before they disappeared. Several individuals showed up for the first time at the end of the season (Fig. 15).

Discussion

Recent studies have investigated the main foraging habitat types selected by the Snowfinch during the chick rearing period in the Alps, pointing out the importance of invertebrate-rich, melting snow patches early in the season and flower-rich, alpine meadows later on (Brambilla et al. 2017, 2018; Resano-Mayor et al. 2019). However, the link between habitat selection, food availability and nestling diet composition remained largely unknown. This study provides a deeper insight into the foraging ecology of the Snowfinch by analyzing the diet composition of the nestlings in relation with the main habitat types and the invertebrate availability at the nest surroundings. Overall, invertebrate larvae were the most important prey in the nestlings' diet, with a peak in biomass at the beginning of July. In particular, Lepidoptera larvae were found numerously in the diet, with the highest numbers at the beginning of July. Other larvae, however, were more difficult to identify to the Order level. Snow front and new vegetation harboured the highest larvae abundance, therefore playing a crucial role as preferred foraging habitats for the Snowfinch as already identified in previous studies (Brambilla et al. 2017, 2018; Resano-Mayor et al. 2019).

The use of three different invertebrate sampling methods (pitfalls, scratching and visual observations) provided good data to assess invertebrate availability at the main different habitat types in a weekly basis. Nevertheless, the use of pitfalls was the only method encompassing invertebrate sampling during several days, while the scratching and visual observations were just a short snapshot of the invertebrate availability. Thus, for many analyses we just focused on data collected from pitfall sampling and, whenever possible, compared it with results from the scratching sampling. Whilst pitfall data was chosen for analysis mostly, this method also showed some drawbacks. Despite its huge dataset, due to the collections over several days and the detailed and secure identification of the invertebrates in the lab, the data collection was time and material consuming. But a more important drawback was that pitfalls were not a good option to collect some invertebrate groups, which has been proven before, namely Orthoptera (Schirmel, Buchholz & Fartmann 2010) and Diptera (Thomson, Neville & Hoffmann 2004). Additionally, pitfall collection in the snow did not work, as the snow melted around the pitfall, so that it was standing out of the snow and no invertebrates could crawl into it. Scratching, on the other hand, allowed a detailed identification of the invertebrates and was less time and material intense than pitfalls. Additionally, in snow habitat, it was a better method than pitfalls, as dead invertebrates could be collected as well, which the Snowfinches also make use of (Heiniger 1991a; Antor 1995). On the other hand, flying invertebrates could often not be collected. Unfortunately, scratching did not provide a big dataset because of the short sampling periods, but if the sampling effort would be increased towards several collections in the same habitat over several days, it might be an invertebrate sampling method as good as the pitfalls. Visual observation was not a good method in this study, as it did not allow a deep or trustful identification of the invertebrates. Additionally, the dataset was very small. But if the sampling effort would be increased with several invertebrate counts per day and identification does not need to go deeper than order level, it could be a good method to gather a general overview of the invertebrates in the habitat. All in all, for future studies about the foraging ecology of the Snowfinch a combination of pitfalls and scratching would be the most recommended invertebrate sampling method if we aim to harbour the most reliable dataset. However, the method should be chosen according to the research questions and the sampling effort associated to each method should be consider.

Assessing the diet by taking pictures was a non-invasive method, which gave a good overview but also showed some drawbacks. Despite having high-resolution pictures, not all items in the diet could be identified. Either the items were too small, the beak was too full, or the larvae could not be identified to the Order level. Some previous studies providing a more detailed dietary assessment used the invasive method of placing neck collars to the nestlings (Heiniger 1991a; Mellott & Woods 1993). On the other hand, alternative dietary assessment methods such as stable isotope analysis of C and N would probably not provide good resolution of the main ingested food items, while faecal analysis would be hardly possible (unless handling chicks in nest-boxes is an option), because the faecal sacs are dragged far away from the nest by the parental birds.

A main finding of this study was that the peak of invertebrate availability in abundance and biomass was different over the season. A peak of invertebrate abundance in most habitats was found late in July, whereas the peak of invertebrate biomass for nearly all habitats was found in early July. This pattern can be explained by the phenology of the invertebrates, as they provide more biomass in larvae stages, which was occurring in early July, whereas more invertebrates, but in later stages and therefore lower available biomass, were around in late July. This pattern was also found in the diet, as more invertebrates were brought to the nestlings at the end of July. Thus, the adult birds brought more invertebrates later during the breeding season probably in order to compensate for the lower invertebrate biomass. Moreover, the diet diversity was lower in early July when the highest number of larvae was brought to the nest, which was already suggested in a previous Snowfinch foraging habitat selection study conducted in the same region (Resano-Mayor *et al.* 2019). This suggests that foraging on larvae could be their optimal prey according to the optimal foraging theory (Stephens & Krebs 1986), suggesting that larvae provide the highest amount of energy while needing a low amount of energy to forage for it. However, the Snowfinches normally start to breed end of May (Heiniger 1991b; Cramp & Perrins 1994) and the chicks hatch before this peak of larvae abundance. The reason why they do not adapt to this peak of larvae could be explained by accessibility, as with later season the vegetation is higher, and invertebrates are less accessible (Vickery *et al.* 2001; Douglas, Evans & Redpath 2008; Vickery & Arlettaz 2012). Therefore, the Snowfinches could not make use of the peak of larvae abundance and must breed earlier.

Additionally, overall in the diet, larvae were the most numerous in abundance and biomass, followed by Arachnida and Orthoptera, which again showed how important larvae were. A rather surprising finding was that in the diet there were barely any Coleoptera larvae whereas in the pitfalls, they made a huge part of all the larvae. This might be a hint towards misidentification in the diet assessment or that Snowfinches did not feed them to their nestlings. An earlier study supports this suggestion, as it was shown that Snowfinches mainly fed on larvae of Diptera and Lepidoptera and barely any Coleoptera larvae (Heiniger 1991a). Not only were larvae the most abundant in the diet, but also when the diet was compared to availability, larvae were highly overrepresented in the diet, which showed again that Snowfinches positively selected them most probably because of their high biomass (Resano-Mayor *et al.* 2019). Another interesting finding was that the peak of Lepidoptera larvae biomass was earlier in the diet than in the pitfalls. This showed that Snowfinches positively selected Lepidoptera larvae early in the season, and when its biomass peaked later on, breeding birds just continued foraging on them.

When considering the habitat features, grassland and snow front provided the highest abundance and biomass of invertebrates for both methods (pitfalls and scratching), which was in line with previous studies showing that Snowfinches selected those habitats for foraging (Brambilla *et al.* 2017; Resano-Mayor *et al.* 2019). Overall, the most abundant invertebrates were Coleoptera adults, whilst larvae were most important when considering biomass. In a similar study, Resano-Mayor *et al.* (2019) found that Formicidae was the most abundant group and Orthoptera contributed with the highest biomass. This difference could be explained by different sampling years or even study site, as Resano-Mayor *et al.* (2019) considered several study sites within the Swiss Alps, whereas in this study we just focused at one. Coleoptera adults were previously suggested to play an important role in the diet of breeding birds (Resano-Mayor *et al.* 2019), but this was not confirmed in this study, where Coleoptera adults were much more abundant in the habitat than in the diet. Coleoptera adults are probably not an optimal prey for the chicks, as they have a thick chitin skin and are not easily digestible. However, they are still fed to the chicks and probably represent an alternative food resource when no larvae are found.

When looking deeper in the habitat preferences of all the larvae groups and Arachnida, snow (snow front) was often important. Additionally, new vegetation was also important for several groups by keeping rather low vegetation height. Unfortunately, we did not collect enough data to analyse the habitat requirements of Tipulidae larvae, which were previously shown to be important for the Snowfinches and relying on snow patches (Heiniger 1991b; Resano-Mayor *et al.* 2019). Interestingly, in a previous study it was found that Snowfinches selected habitats with snow front in the early season while preferring flower-rich grassy habitats later on, with overall high moisture values (Resano-Mayor *et al.*

2019). In this study, we did not find such a link between invertebrates and flower-rich habitats or soil moisture. A possible explanation for this difference could be that flower-rich and moistly habitats do not always support more invertebrates, but that vegetation was less dense and invertebrates were therefore more accessible there which was favourable for the Snowfinches.

In the wintering module, re-sighting data of colour-ringed Snowfinch individuals was collected. To avoid bird stress suffered when captured and handling, re-sighting was done visually by video recording and reading the ring code. Of course, during the previous years we had to do a capturing effort in order to mark the birds individually with colour rings. The video re-sightings proved to be a good method, although time consuming. Only few individuals could not be identified, especially when big groups of Snowfinches arrived at the feeder and hid one to each other. Therefore, this method looks promising for further data collection in order to monitor the population dynamic of wintering Snowfinches and estimate survival rates.

Relevance for conservation

Climate and land-use changes in the alpine ecosystem (Laiolo *et al.* 2004; Brunetti *et al.* 2009) are already altering the main breeding habitats of the Snowfinch. The alpine ecosystem is highly seasonal, with a relative short time span when the food resource availability is high (Martin 2001; Miller-Rushing *et al.* 2010). This seasonality was shown to be a major driver of the habitat selection of the Snowfinches in the Swiss Alps (Resano-Mayor *et al.* 2019). With rising temperature in spring, snow will be melting earlier (Laternser & Schneebeli 2003), which will change the whole phenology of the habitats (Keller, Goyette & Beniston 2005) and the associated invertebrates (Slatyer, Nash & Hoffmann 2017). This change in phenology needs to be synchronised with the breeding season of the birds so that the peak of food abundance is in line with their peak of energy requirements from their nestlings. If not, it would result in a phenological mismatch between the prey and predator, as the peak of food availability would not match with the reproductive effort resulting in lower or no reproductive success. This phenomenon has been already identified in an arctic *Pluvialis apricaria* population, where the chicks rely on adult Tipulidae. The study showed that the golden plover had advanced the egg laying date due to the warmer climate, but the Tipulidae phenology had not changed at the same rate, which could reduce the breeding success by 11% in the near future (Pearce-Higgins, Yalden & Whittingham 2005). This example shows the importance to gain data about the change in the breeding phenology of alpine birds such as the Snowfinch and its prey. Especially on the larvae stage, as they are the most preferred nestling diet and altogether are predicted to be largely affected by climate change.

As some main prey were most abundant at the snow front and it has been shown that Snowfinches positively select this habitat (Resano-Mayor *et al.* 2019), the future and impact of losing this key foraging habitat is unknown as climate change could alter in different ways habitat-prey relationships. There are studies suggesting that the spring snow melt will be occurring one month earlier in average in the Swiss Alps (Keller, Goyette & Beniston 2005), resulting in a complete habitat loss with its associated prey. Additionally, grassland with low vegetation height provided many invertebrates. Vegetation height should be kept low due to accessibility, so that foraging birds still get access to the main prey, which was already shown to be favourable for several passerines (Vickery *et al.* 2001; Douglas, Evans & Redpath 2008; Vickery & Arlettaz 2012). Therefore, it should be further investigated, whether management implications, such as actions to keep vegetation height low, could boost Snowfinch main prey and foraging habitat suitability (Brambilla et al. 2018). However, grazing was found to not boost breeding abundance of Snowfinches or other alpine birds (Laiolo *et al.* 2004). Finally, further studies on the wintering population dynamics of the species would be important to gain a better understanding of the survival and movement dynamics of the Snowfinches. The data gathered in this study will provide a valuable first approach for a better knowledge of the vital rates (survival) of this emblematic alpine passerine in Europe.

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Additional supporting information

Appendix A. Biomass estimates used for this study.

Appendix B. General overview of invertebrate abundance and biomass per habitat with scratching data.

Appendix C. Comparison of relative invertebrate biomass between sampling methods.

Table 1. List of explanatory variables used in the analyses for invertebrate availability and diet assessment.

Invertebrate availability	Diet assessment
Brood	Brood
Session	Session
Date	Date
Time (h)	Time (h)
Habitat	Sex
Old vegetation (%)	Cloud cover (%)
New vegetation (%)	
Snow (%)	
Mineral (%)	
Bare ground (%)	
Moss (%)	
Green superficial plants (%)	
Flowers (%)	
Water cover (%)	
Slope (°)	
Exposition (°)	
Vegetation height (cm)	
Distance to snow (m)	
Moisture (mV)	
Temperature (°C)	

Table 2. Invertebrate categories classified into order, suborder or family for the invertebrate availability estimates (three sampling methods) and the diet assessment. Invertebrate availability was estimated either in the field (visual observations) or later on in the lab, whereas diet assessment was done with the help of pictures.

Order	Invertebrate availability	Diet assessment
Arachnida	Araneae	Araneae
	Opilliones	Arachnida
	Acariformes	
Coleoptera	Adult	Adult
	Larvae	Larvae
Diptera	Brachycera	Diptera
	Tipulidae larvae	Tipulidae larvae
	Tipulidae adult	Tipulidae adult
	Nematocera	
Hemiptera	Homoptera	Hemiptera
	Heteroptera	
Hymenoptera	Formicidae	Hymenoptera
	Ichneumonidae	
	Other Hymenoptera	
Lepidoptera	Adult	Adult
	Larvae	Larvae
Larvae		Unidentifiable larvae
Orthoptera	Orthoptera	Orthoptera

Table 3. Multinomial analysis of diet composition compared with invertebrate availability based on data from the pitfalls (a) and scratching (b), showing the mean of the main invertebrate groups' abundance and its confidence interval for both diet and pitfalls estimates (see Fig. 8a) or scratching estimates (see Fig. 8b) .

(a)

	Diet			Pitfalls		
	Mean	Confidence interval		Mean	Confidence interval	
		2.50%	97.50%		2.50%	97.50%
Lepidoptera adult	0.103	0.077	0.131	0.036	0.028	0.045
Tipulidae adult	0.048	0.007	0.136	0.000	0.000	0.001
Coleoptera adult	0.093	0.067	0.124	0.345	0.297	0.395
Diptera	0.008	0.003	0.016	0.169	0.123	0.225
Hemiptera	0.004	0.001	0.010	0.033	0.022	0.047
Orthoptera	0.004	0.000	0.019	0.000	0.000	0.001
Hymenoptera	0.015	0.007	0.025	0.094	0.069	0.124
Arachnida	0.081	0.052	0.118	0.136	0.099	0.181
Larvae	0.643	0.556	0.717	0.187	0.145	0.234

(b)

	Diet			Scratching		
	Mean	Confidence interval		Mean	Confidence interval	
		2.50%	97.50%		2.50%	97.50%
Lepidoptera adult	0.098	0.068	0.131	0.062	0.039	0.090
Tipulidae adult	0.037	0.004	0.113	0.000	0.000	0.001
Coleoptera adult	0.088	0.053	0.131	0.213	0.140	0.294
Diptera	0.006	0.002	0.013	0.078	0.034	0.133
Hemiptera	0.003	0.001	0.008	0.119	0.042	0.233
Orthoptera	0.011	0.001	0.038	0.012	0.001	0.041
Hymenoptera	0.013	0.005	0.024	0.128	0.074	0.194
Arachnida	0.071	0.035	0.123	0.085	0.042	0.144
Larvae	0.673	0.573	0.765	0.303	0.212	0.402

Figures legends

Figure 1. Insight of fieldwork regarding monitoring and sampling. Each brood (one row and colour per brood) was divided into three sessions (for example, bright green) and in each session the same methods were applied. On the first day, habitat mapping at 300m and 5m radius was done, pitfalls were opened, and visual observation was carried out. Within the first session, one day the diet was monitored. The last day, habitat mapping at 5m radius, scratching, visual observation and closing pitfalls was carried out.

Figure 2. Seasonal change of the main habitat variables (legend) at the 300m radius.

Figure 3. Total invertebrate abundance (a) and total invertebrate biomass (b) along the season separately per habitat based on pitfall data.

Figure 4. Total invertebrate abundance compared to new vegetation cover (a), moss cover (b) and date (c) based on pitfall data.

Figure 5. Total invertebrate biomass compared to snow cover (a), new vegetation cover (b) and date (c) based on pitfall data.

Figure 6. Minimum amount of invertebrates (a) and diversity of identified invertebrates (b) along the season (date), and beak load compared to week (c) based on diet data.

Figure 7. Total invertebrate biomass along the season (date) separately for the two dietary groups (All larvae and Lepidoptera larvae) based on diet data.

Figure 8. Results of the multinomial analysis with the mean relative abundance per invertebrate group and its confidence interval (2.50% and 97.50%) comparing diet and pitfall data (a) and diet and scratching data (b) separately.

Figure 9. Seasonal change of the total invertebrate biomass for each of the most important invertebrate groups contributing to the diet (legend) based on pitfall data.

Figure 10. All larvae biomass compared to snow cover (a), new vegetation cover (b) and date (c) based on pitfall data.

Figure 11. Lepidoptera larvae biomass compared to new vegetation cover (a), vegetation height (b) and northing (c) based on pitfall data. -1.0 in northing is south, whereas 1.0 is north.

Figure 12. Coleoptera larvae biomass compared to snow cover (a) and date (b) based on pitfall data.

Figure 13. Arachnida biomass compared to snow cover (a) and date (b) based on pitfall data.

Figure 14. Number of re-sighting events per colour banded video-recorded individual during the winter 2017/2018.

Figure 15. Individual re-sighting history during the winter 2017/2018 with colours indicating the number of re-sightings in the season (red = one re-sighting event, blue = several re-sighting events but not over the whole season, green = several re-sighting events over the whole season)

Figure 1

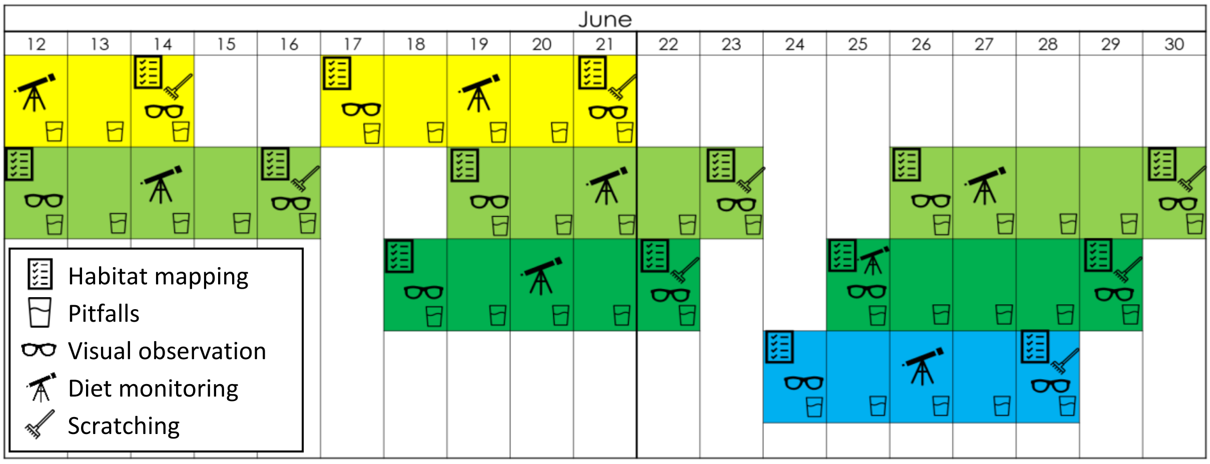
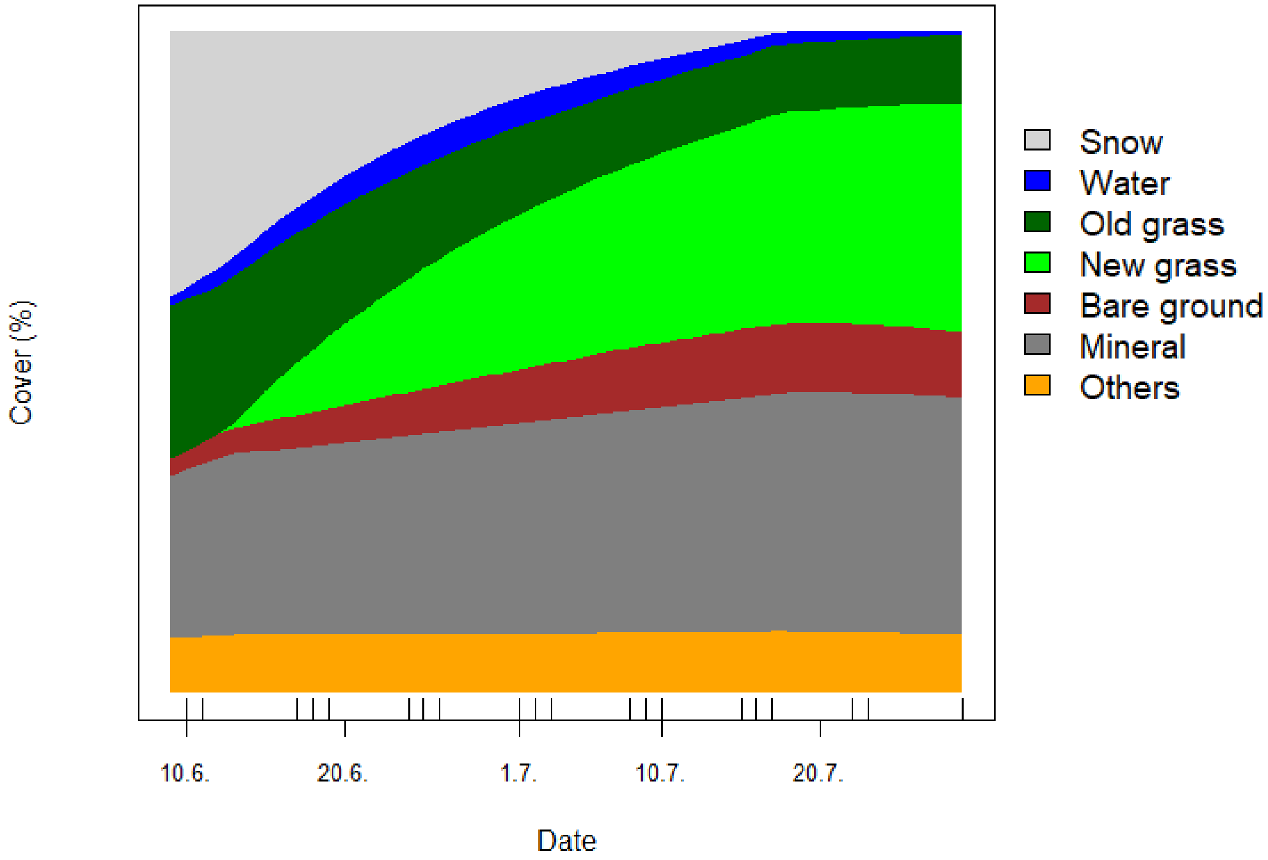

June
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
Habitat mapping
Pitfalls
Visual observation
Diet monitoring
Scratching

Figure 2



Cover (%)
10.6.
20.6.
1.7.
10.7.
20.7.
Date
Snow
Water
Old grass
New grass
Bare ground
Mineral
Others

Figure 3

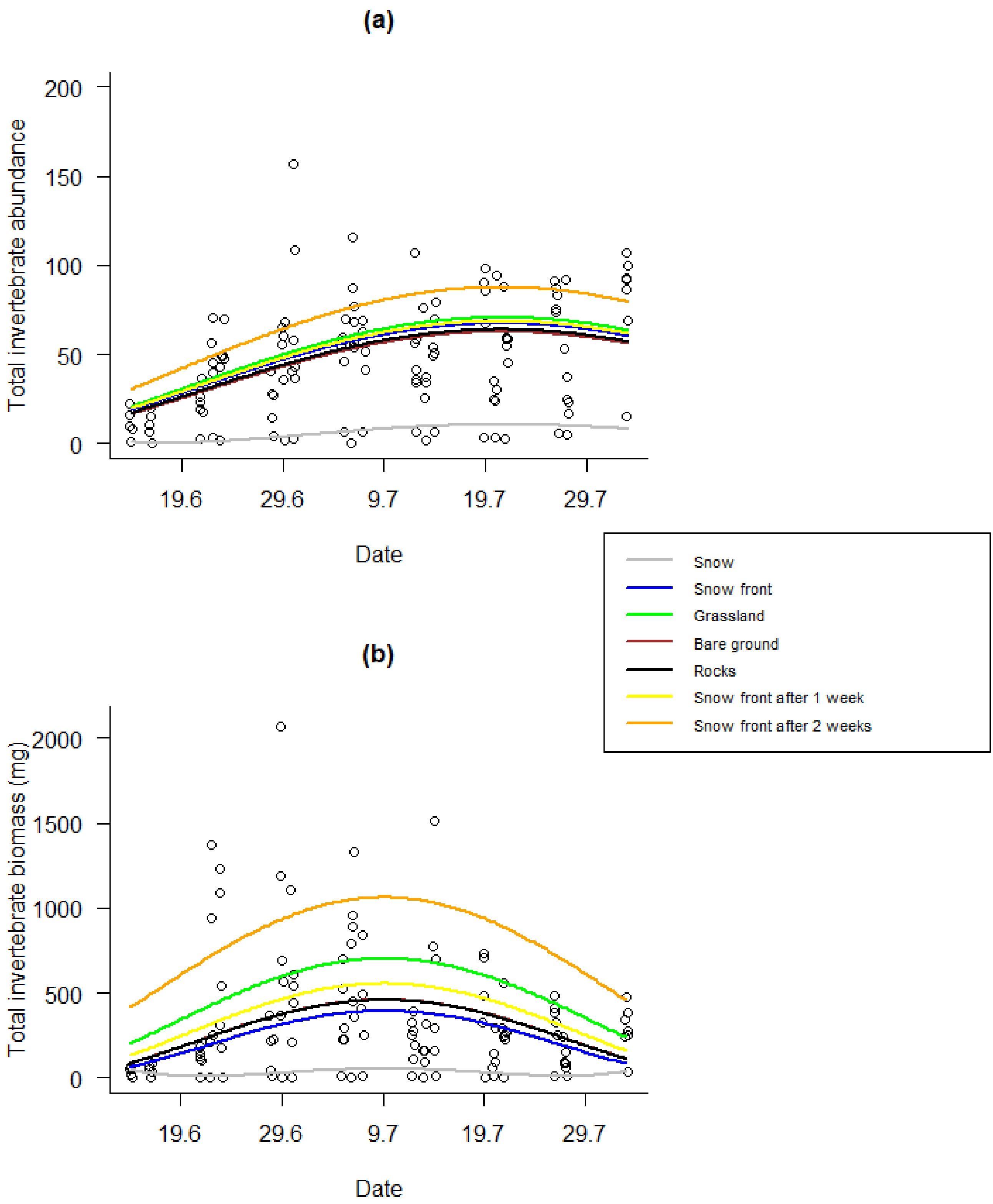
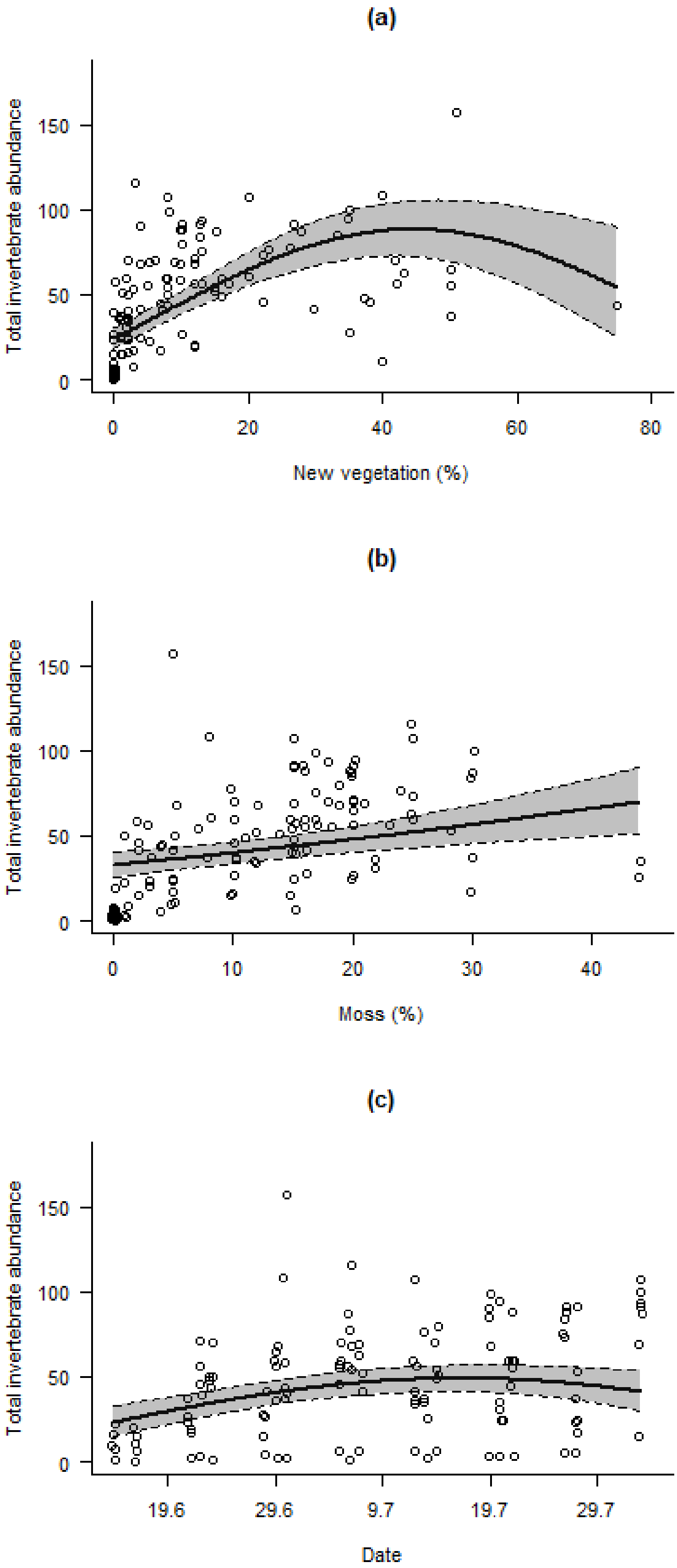

(a)
200
150
100
50
0
Total invertebrate abundance
19.6
29.6
9.7
19.7
29.7
Date
(b)
2000
1500
1000
500
0
Total invertebrate biomass (mg)
19.6
29.6
9.7
19.7
29.7
Date
Snow
Snow front
Grassland
Bare ground
Rocks
Snow front after 1 week
Snow front after 2 weeks

Figure 4



(a)
Total invertebrate abundance
0
50
100
150
0
20
40
60
80
New vegetation (%)
(b)
Total invertebrate abundance
0
50
100
150
0
10
20
30
40
Moss (%)
(c)
Total invertebrate abundance
0
50
100
150
19.6
29.6
9.7
19.7
29.7
Date

Figure 5

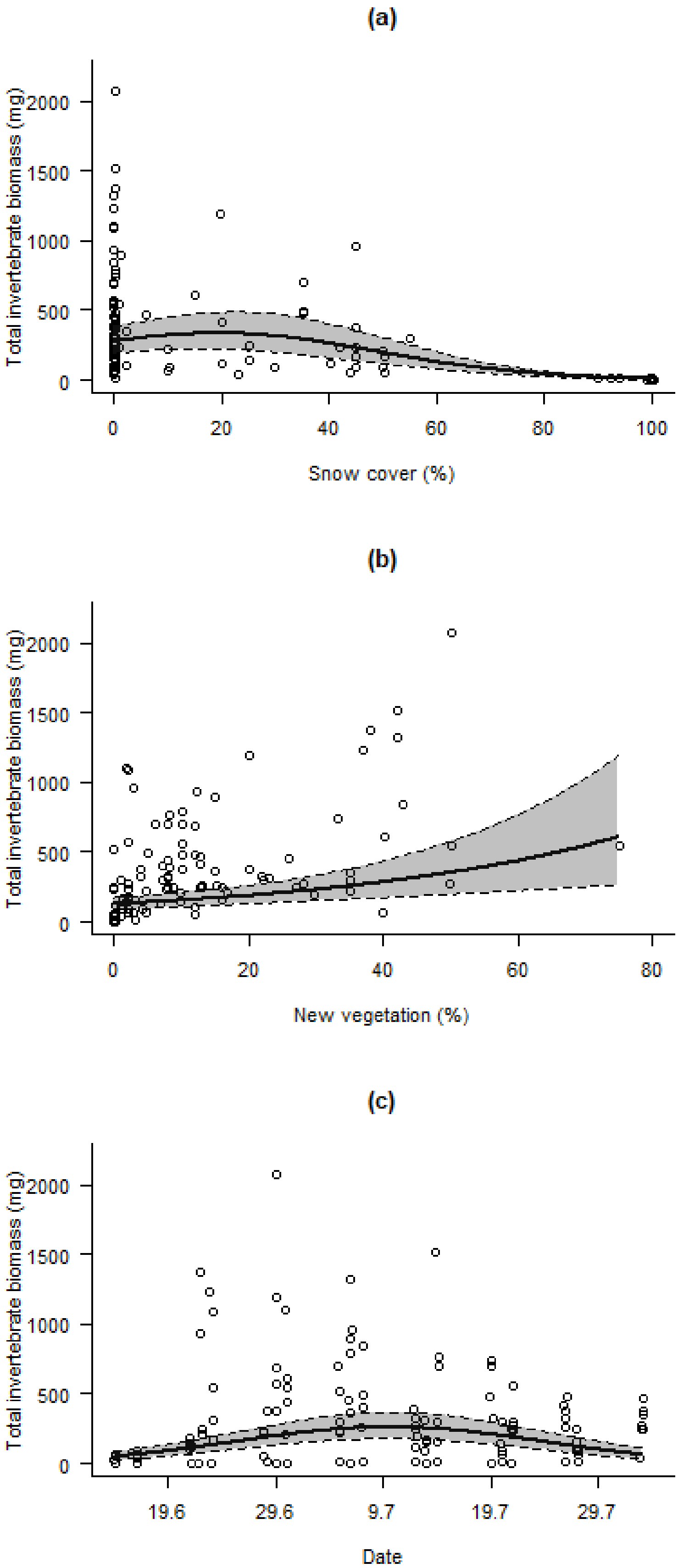

(a)
Total invertebrate biomass (mg)
0
500
1000
1500
2000
0
20
40
60
80
100
Snow cover (%)
(b)
Total invertebrate biomass (mg)
0
500
1000
1500
2000
0
20
40
60
80
New vegetation (%)
(c)
Total invertebrate biomass (mg)
0
500
1000
1500
2000
19.6
29.6
9.7
19.7
29.7
Date

Figure 6

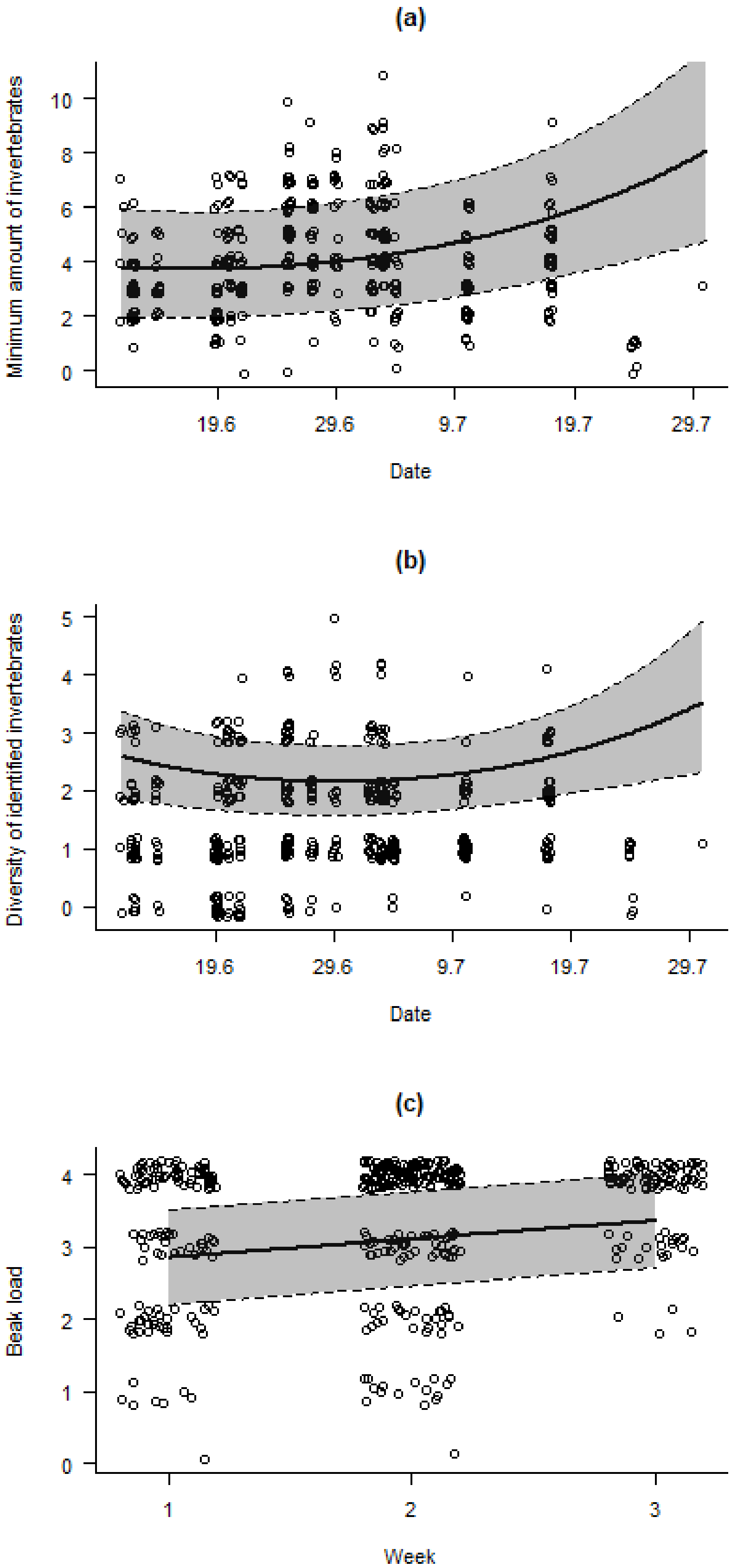
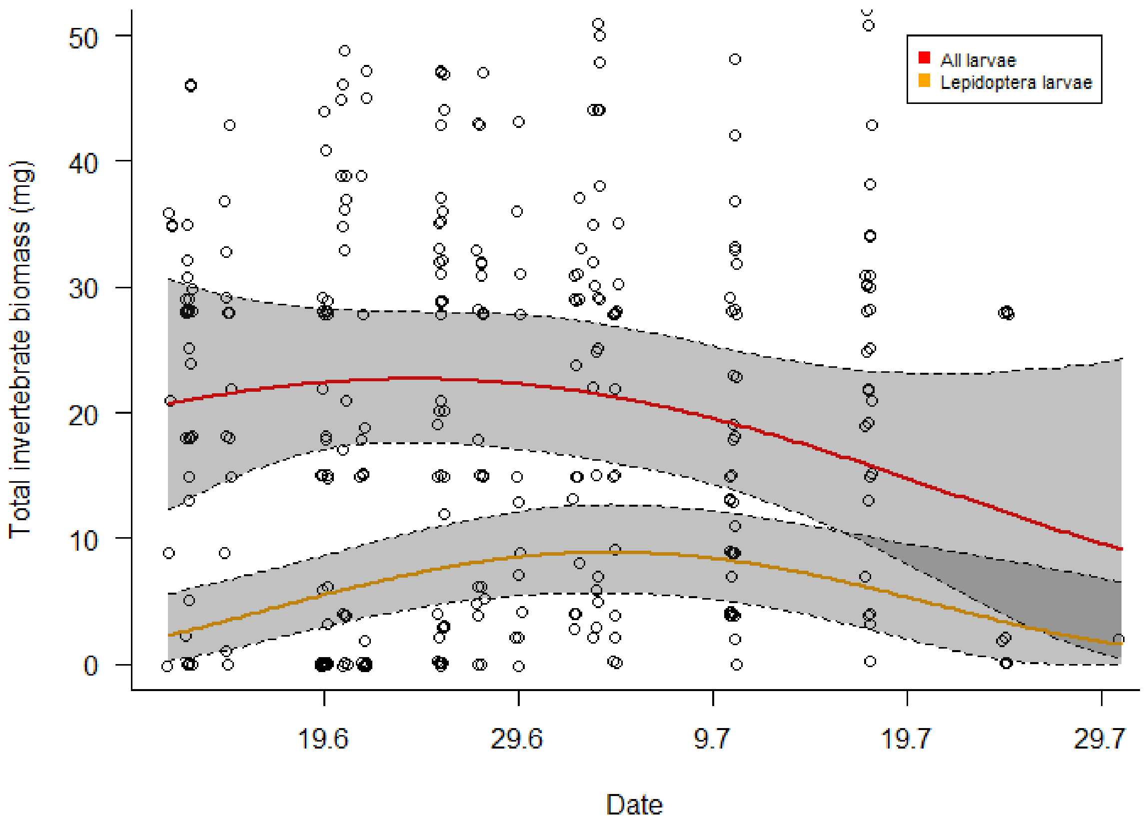
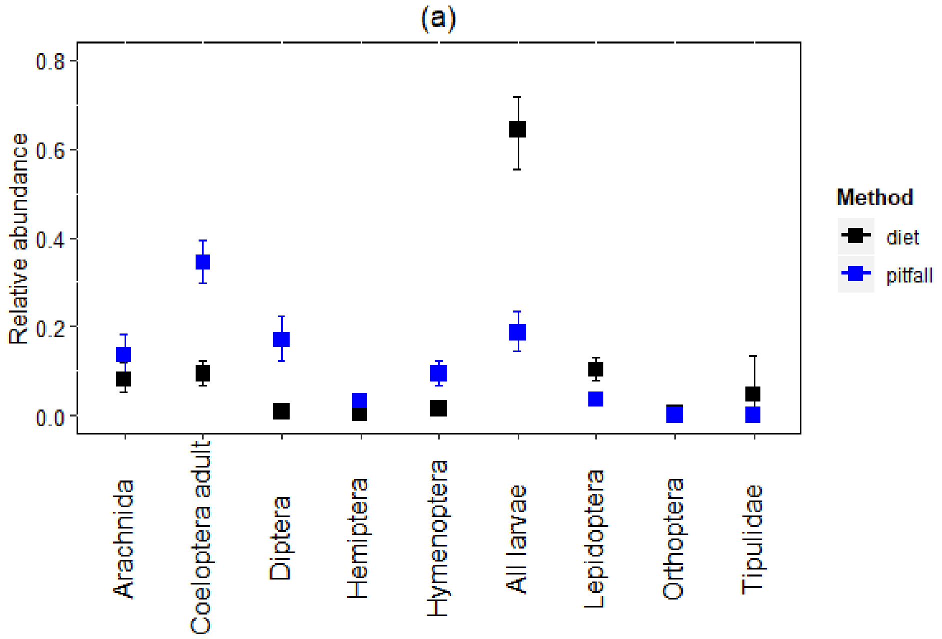

(a)
Minimum amount of invertebrates
0
2
4
6
8
10
19.6
29.6
9.7
19.7
29.7
Date
(b)
Diversity of identified invertebrates
0
1
2
3
4
5
19.6
29.6
9.7
19.7
29.7
Date
(c)
Beak load
0
1
2
3
4
1
2
3
Week

Figure 7



All larvae
Lepidoptera larvae
Total invertebrate biomass (mg)
50
40
30
20
10
0
19.6
29.6
9.7
19.7
29.7
Date

Figure 8


(a)
Relative abundance
0.8
0.6
0.4
0.2
0.0
Arachnida
Coeloptera adult
Diptera
Hemiptera
Hymenoptera
All larvae
Lepidoptera
Orthoptera
Tipulidae
Method
diet
pitfall

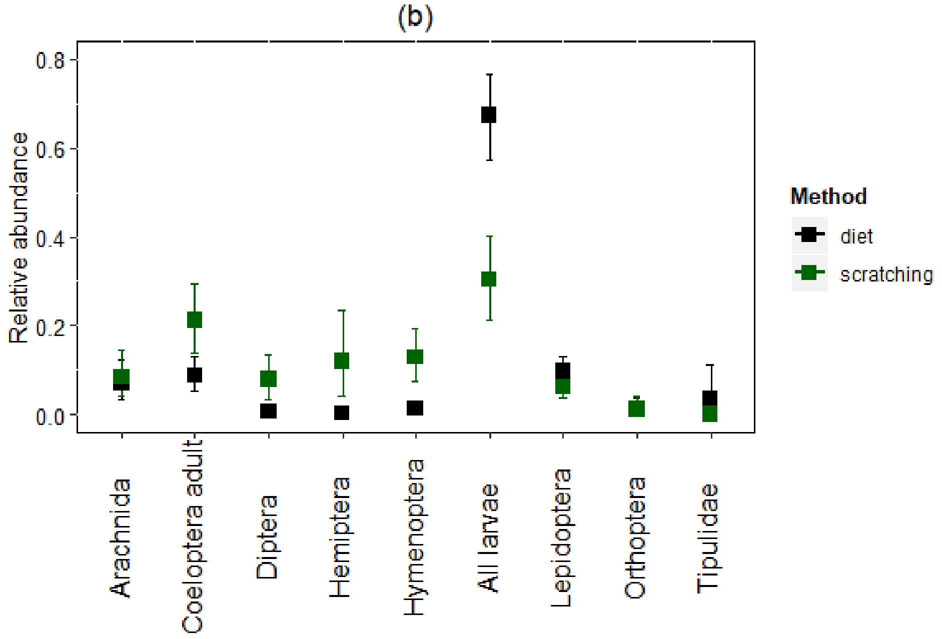

(b)
Relative abundance
0.8
0.6
0.4
0.2
0.0
Arachnida
Coeloptera adult
Diptera
Hemiptera
Hymenoptera
All larvae
Lepidoptera
Orthoptera
Tipulidae
Method
diet
scratching

Figure 9

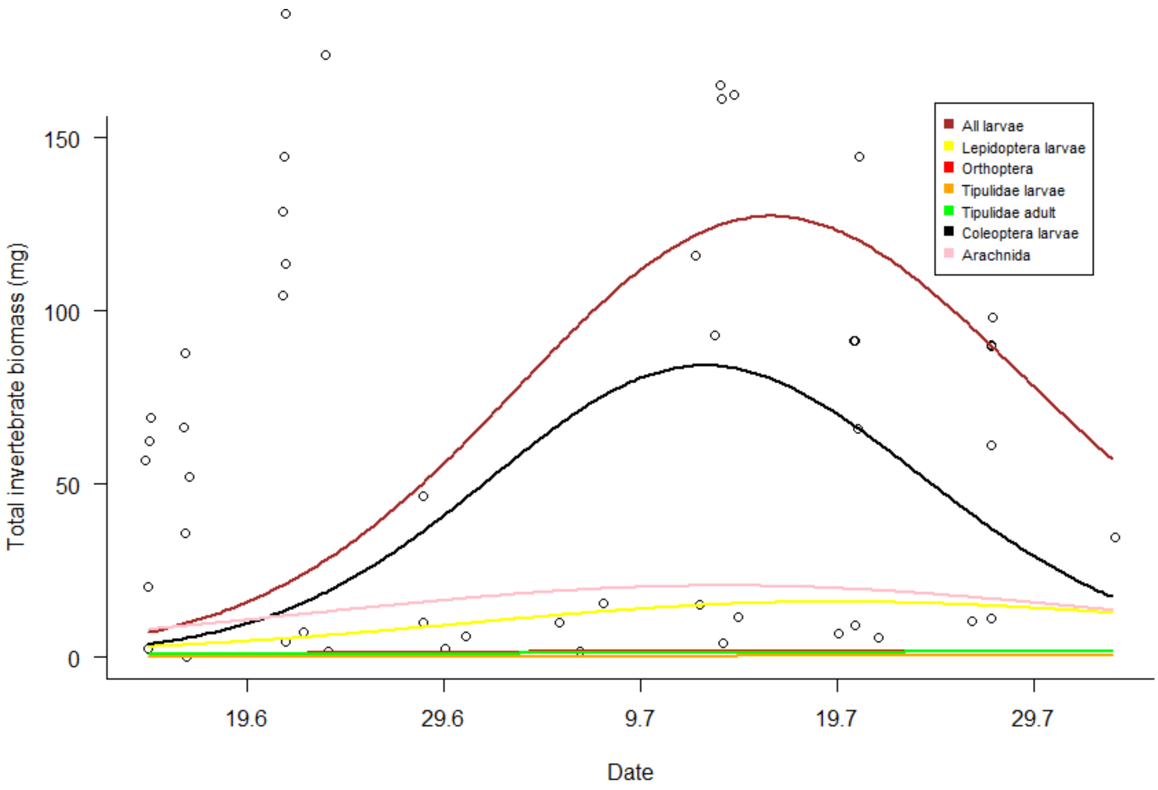

All larvae
Lepidoptera larvae
Orthoptera
Tipulidae larvae
Tipulidae adult
Coleoptera larvae
Arachnida
Total invertebrate biomass (mg)
150
100
50
0
19.6
29.6
9.7
19.7
29.7
Date

Figure 10

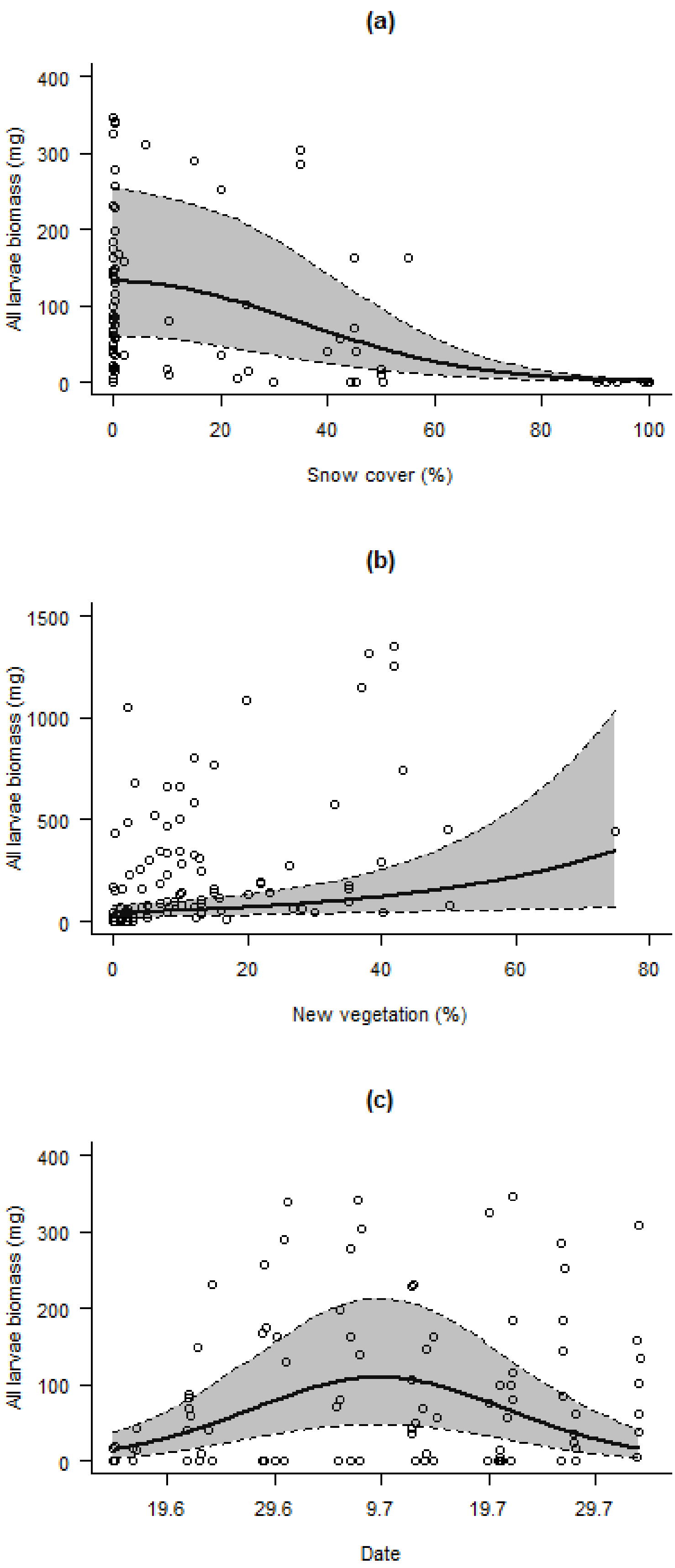
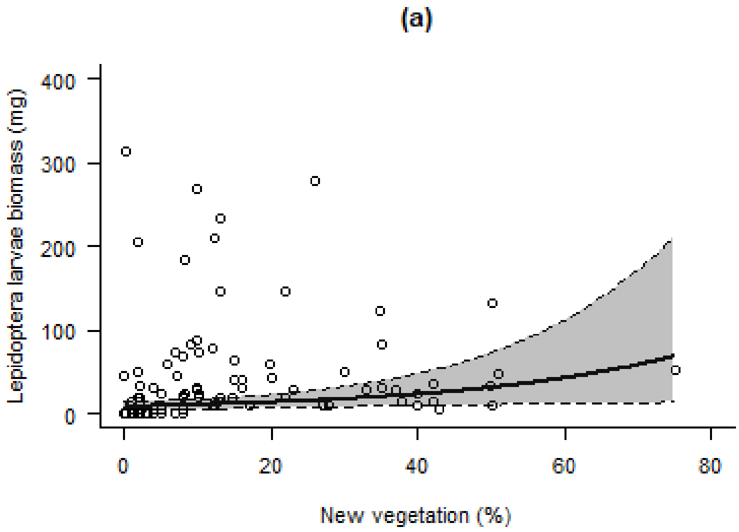
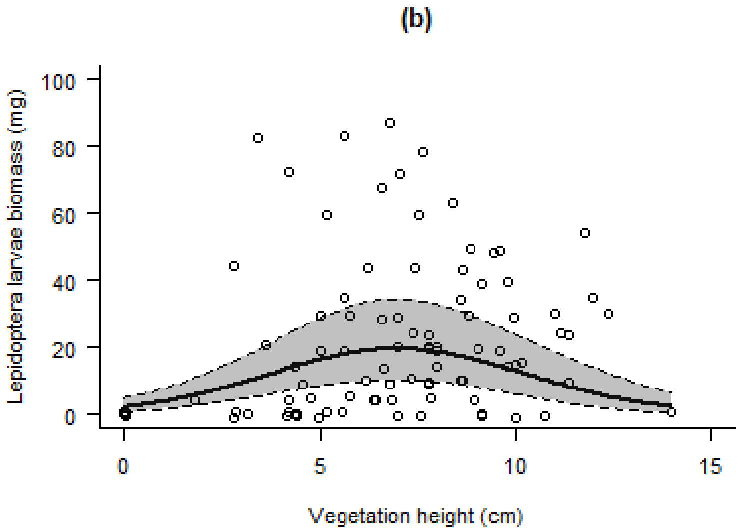

(a)
All larvae biomass (mg)
400
300
200
100
0
0
20
40
60
80
100
Snow cover (%)
(b)
All larvae biomass (mg)
1500
1000
500
0
0
20
40
60
80
New vegetation (%)
(c)
All larvae biomass (mg)
400
300
200
100
0
19.6
29.6
9.7
19.7
29.7
Date

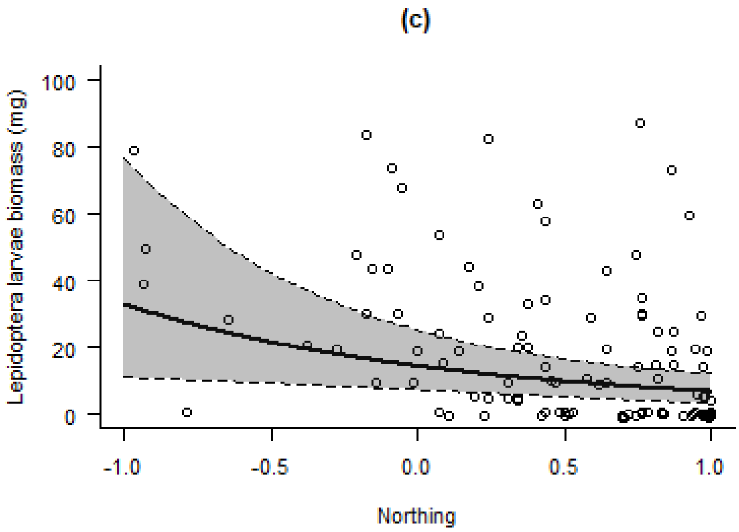
Figure 11



(a)
Lepidoptera larvae biomass (mg)
400
300
200
100
0
0
20
40
60
80
New vegetation (%)



(b)
Lepidoptera larvae biomass (mg)
100
80
60
40
20
0
0
5
10
15
Vegetation height (cm)



(c)
Lepidoptera larvae biomass (mg)
100
80
60
40
20
0
-1.0
-0.5
0.0
0.5
1.0
Northing

Figure 12

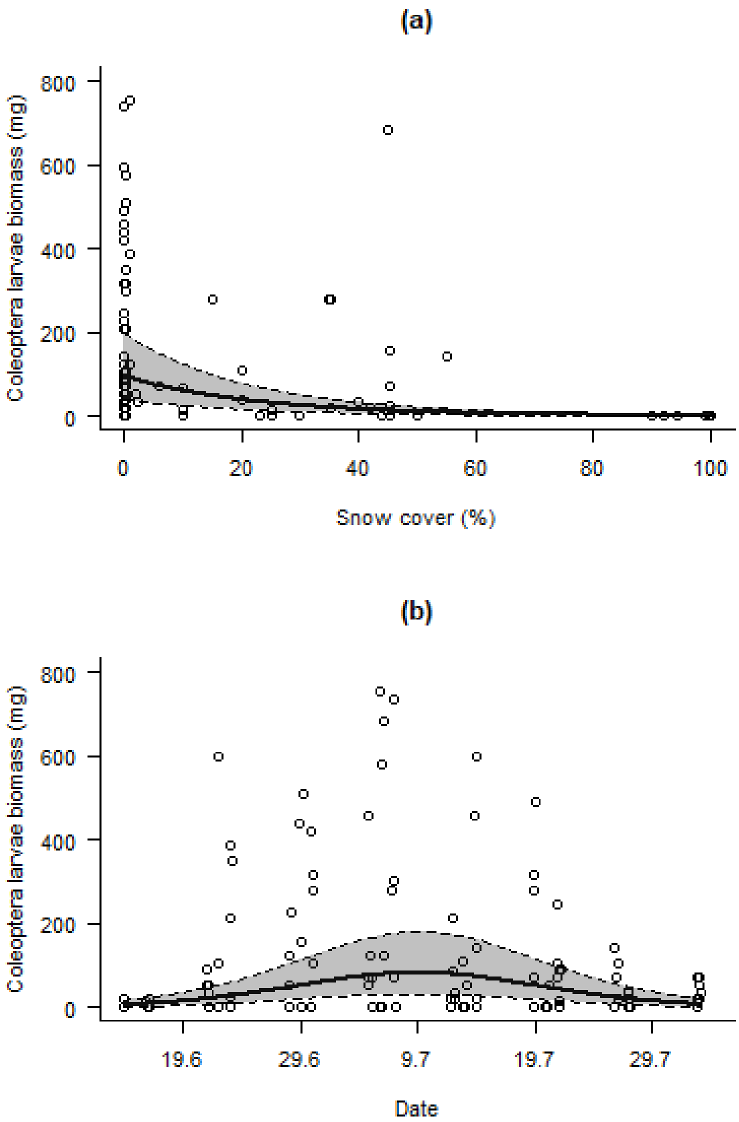
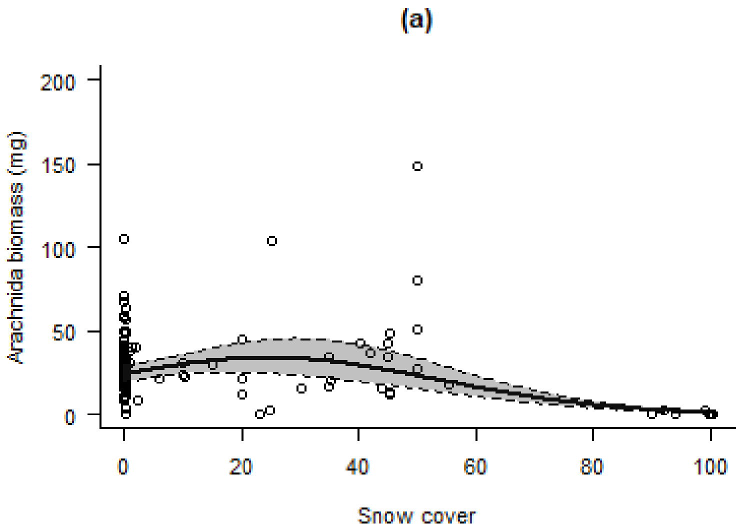
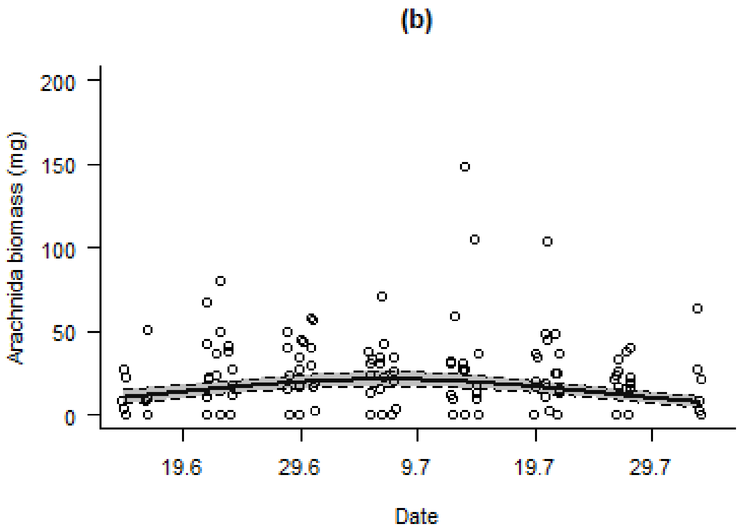

(a)
Coleoptera larvae biomass (mg)
800
600
400
200
0
0
20
40
60
80
100
Snow cover (%)
(b)
Coleoptera larvae biomass (mg)
800
600
400
200
0
19.6
29.6
9.7
19.7
29.7
Date

Figure 13

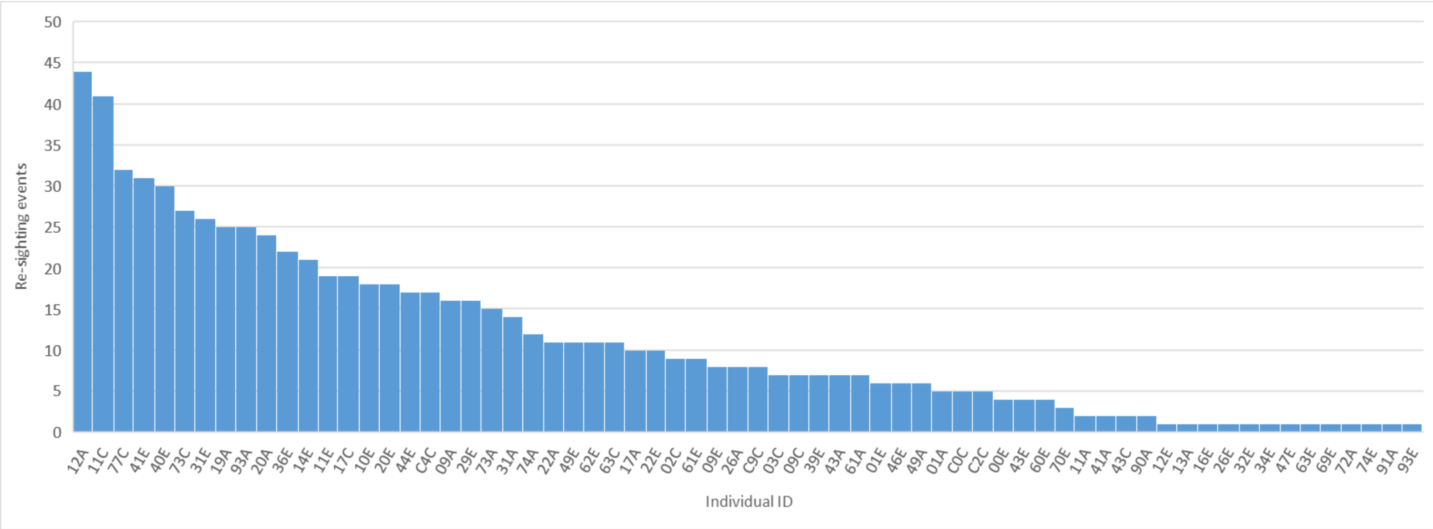


(a)
200
150
100
50
0
Arachnida biomass (mg)
0
20
40
60
80
100
Snow cover



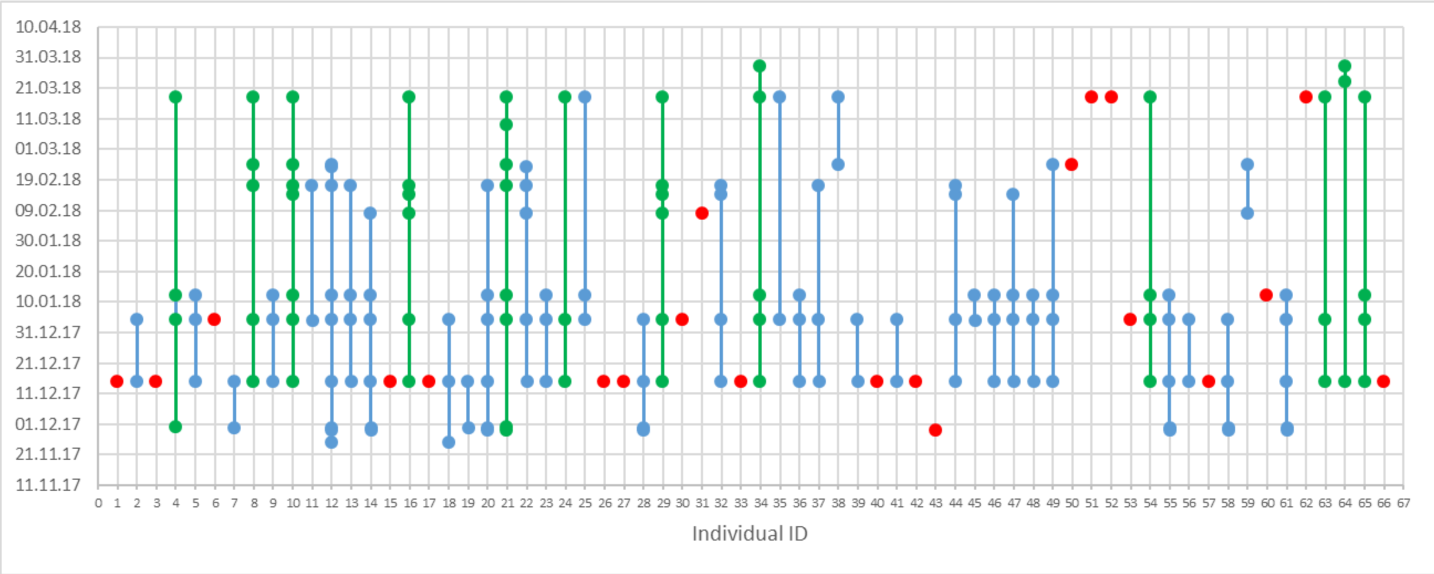
(b)
200
150
100
50
0
Arachnida biomass (mg)
19.6
29.6
9.7
19.7
29.7
Date

Figure 14



50
45
40
35
30
25
20
15
10
5
0
Re-sighting events
12A 11C 77C 41E 40E 73C 31E 19A 93A 20A 36E 14E 11E 17C 10E 20E 44E C4C 09A 29E 73A 31A 74A 22A 49E 62E 63C 17A 22E 02C 61E 09E 26A C9C 03C 09C 39E 43A 61A 01E 46E 49A 01A C0C C2C 00E 43E 60E 70E 11A 41A 43C 90A 12E 13A 16E 26E 32E 34E 47E 63E 69E 72A 74E 91A 93E
Individual ID

Figure 15


10.04.18
31.03.18
21.03.18
11.03.18
01.03.18
19.02.18
09.02.18
30.01.18
20.01.18
10.01.18
31.12.17
21.12.17
11.12.17
01.12.17
21.11.17
11.11.17
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67
Individual ID

Appendix A. Biomass estimates used for this study.

Table A1. Biomass estimates from (Resano-Mayor *et al.* 2019). Profitability estimates were used for this MSc thesis.

Invertebrates		**n**	**% Abundance**	**Biomass (g)**	**% Biomass**	**Mean size (range) (mm)**	**Profitability (mg/item)**
Diptera	Tipulidae adult	375	12.29	1.66	9.68	10.97 (4.67-23.02)	4.43
	Tipulidae larvae	82	2.69	1.44	8.40	17.19 (7.00-24.11)	17.56
	Other Nematocera	94	3.08	0.04	0.23	3.18 (1.71-8.56)	0.43
	Brachycera	228	7.47	0.45	2.60	5.73 (1.56-10.50)	1.97
	Other larvae	18	0.59	0.06	0.33	12.35 (4.98-28.00)	3.33
	Pupae	13	0.43	0.42	2.44	14.58 (11.67-19.44)	32.31
	Total	**810**	**26.55**	**4.07**	**23.68**		5.02
Hymenoptera	Formicidae	649	21.27	0.49	2.83	4.26 (3.18-11.36)	0.76
	Ichneumonoidea	31	1.02	0.05	0.30	5.27 (2.64-15.56)	1.61
	Symphyta	17	0.56	0.03	0.17	6.03 (2.02-8.87)	1.76
	Other	2	0.07	0.00	0.00	1.32 (0.93-1.71)	0.00
	Total	**699**	**22.91**	**0.57**	**3.30**		0.82
Arachnida	Araneae	341	11.18	2.18	12.65	5.04 (1.63-9.18)	6.39
	Opiliones	271	8.88	0.57	3.30	3.95 (0.93-7.39)	2.10
	Acariformes	10	0.33	0.01	0.04	2.88 (2.33-3.58)	1.00
	Total	**622**	**20.39**	**2.75**	**16.00**		4.42
Coleoptera	Carabidae	171	5.60	0.41	2.38	4.98 (3.27-12.13)	2.40
	Other	166	5.44	0.66	3.84	6.06 (2.64-17.89)	3.98
	Larvae	23	0.75	1.21	7.02	11.52 (2.96-20.22)	52.61
	Total	**360**	**11.80**	**2.28**	**13.24**		6.33
Orthoptera	**Total**	**205**	**6.72**	**5.22**	**30.36**	15.31 (4.20-27.69)	25.46
Lepidoptera	Adults	66	2.16	0.14	0.83	6.15 (2.18-12.76)	2.12
	Larvae	106	3.47	1.55	9.00	13.27 (4.04-21.78)	14.62
	Total	**172**	**5.64**	**1.69**	**9.83**		9.83
Hemiptera	Heteroptera	120	3.93	0.19	1.09	4.42 (3.50-8.40)	1.58
	Aphididae	16	0.52	0.00	0.01	2.07 (1.40-3.19)	0.00
	Other	4	0.13	0.00	0.00	2.37 (1.24-3.27)	0.00
	Total	**140**	**4.59**	**0.19**	**1.11**		1.36
Annelida	**Total**	**19**	**0.62**	**0.25**	**1.44**	30.47 (15.56-49.78)	13.16
Myriapoda	**Total**	**11**	**0.36**	**0.09**	**0.53**	16.94 (7.31-21.78)	8.18
Collembola	**Total**	**8**	**0.26**	**0.00**	**0.01**	1.06 (0.70-1.87)	0.00
Dermaptera	**Total**	**5**	**0.16**	**0.09**	**0.51**	14.93 (13.53-15.40)	18.00
TOTAL		**3051**	**100**	**17.19**	**100**		

Appendix B. Comparison of relative invertebrate biomass between sampling

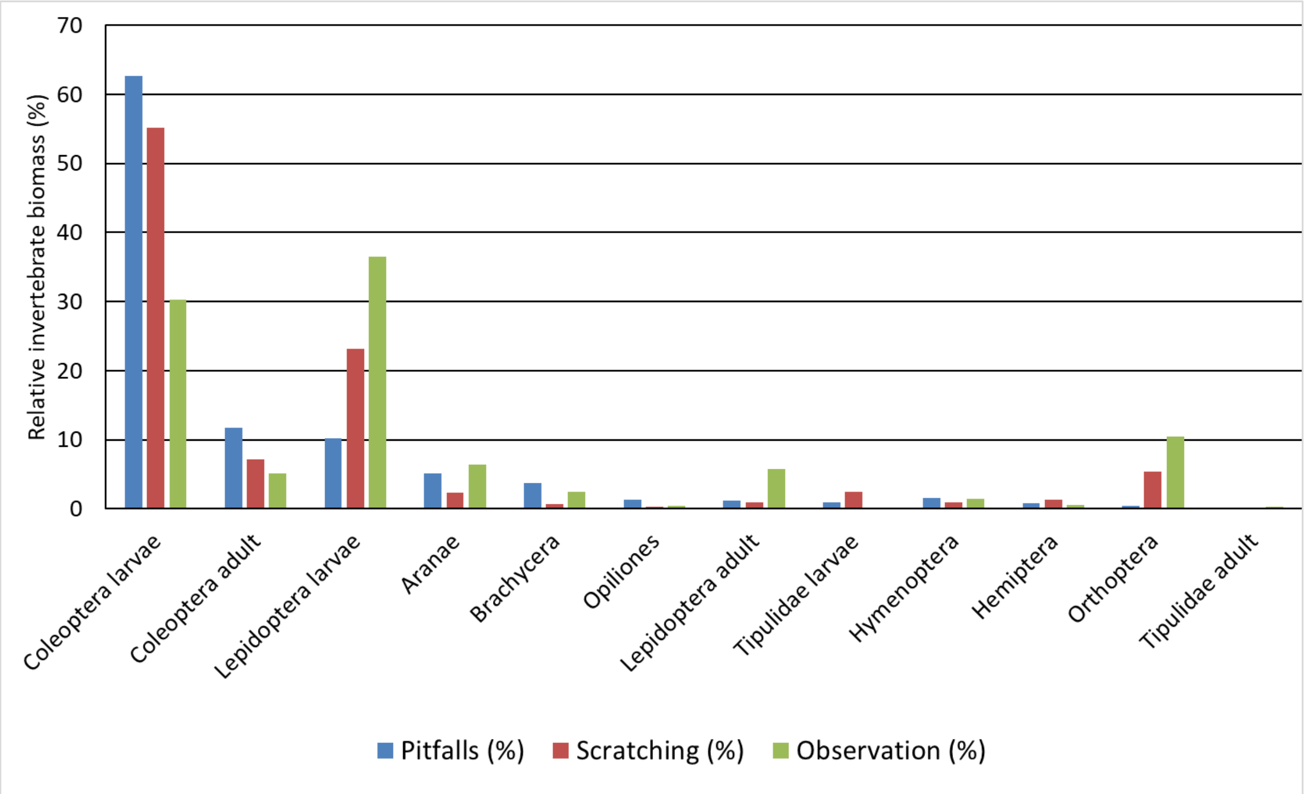


Fig. B.1 Histogram of relative invertebrate biomass of the different invertebrate groups separately per sampling method.

methods.

Appendix C. General overview of invertebrate abundance and biomass per

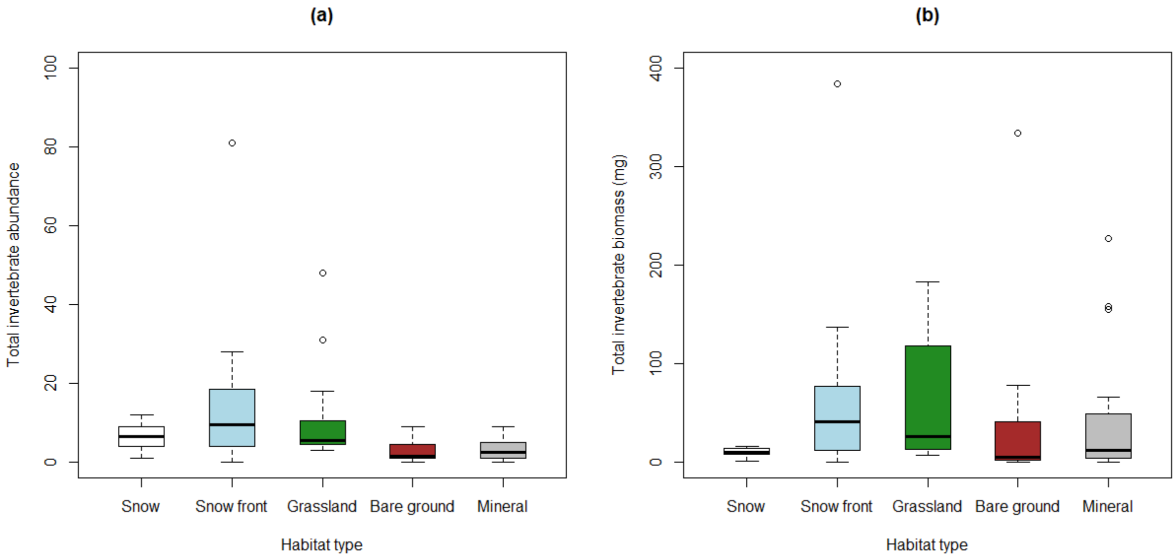


Fig. C.1 Boxplot of total invertebrate abundance (a) and biomass (b) per habitat type with scratching data.

habitat with scratching data

Declaration of consent

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

Name/First Name: Besimo Julia

Registration Number: 14-109-706

Study program: Ecology and Evolution

Bachelor ☐ Master ☐ Dissertation ☐

Title of the thesis: Foraging ecology and wintering monitoring of the White-winged Snowfinch (Montifringilla nivalis) in the Swiss Alps.

Supervisor: Dr. Jaime Resano-Mayor, Prof. Raphaël Arlettaz

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

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