

Master Thesis

**Influence of snow cover on the spatial variation  
in abundance of the alpine marmot in the Swiss  
National Park**

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## Abstract

Snow cover is an important environmental variable influencing alpine marmots' physiology and vital rates. During hibernation, early snowfall ensures insulation of the burrow, which increases winter survival. But snow prolonging into spring delays vegetation growth, whereby less time remains for marmots to replenish their fat storages. Even though the effects of snow cover on vital rates are well known, its effect on the spatial pattern of abundance is not well understood. In this study I developed a hierarchical distance sampling model to investigate the environmental effects on the spatial variation in marmot abundance in the Swiss National Park while accounting for time-varying availability and imperfect detection. I found that in regions with delayed snowfall marmot abundance was lower, while snow prolonging into spring had no effect. The main drivers of the spatial variation in abundance were amount of meadows, maximum summer temperatures, and slope steepness. Abundance increased with the amount of meadow and decreased with steepness and extreme summer temperatures. These results indicate that shorter snow cover as a consequence of climate change may affect marmots negatively by reduced burrow insulation. However, the importance of the other environmental factors indicates that marmots may not be able to buffer the effects of altered snow conditions by quickly migrating to higher altitudes. This study gives new insights into drivers of spatial variation in marmot abundance and highlights the importance of the dynamic environment when investigating the effect of climate change on a species.

# 1 Introduction

Mountains belong to the habitats most affected by climate change [1]. Temperatures have risen faster compared to other habitats, and the same is predicted to continue in the future [2]. Precipitation patterns and their variance will change, increasing the frequency of extreme droughts and intense rainfalls [3]. Changes in temperature and precipitation translate to other processes, inducing changes in vegetation [4], snow conditions [5], and disturbance regimes [6].

Species react in various ways to the changing climate. Some species adjust their phenology, as for example birds in the UK. Advanced flowering resulted in an earlier peak in arthropods abundance, whereupon the birds laid their first eggs earlier in the season [7]. Climate change alters demographic rates such as survival or reproduction, which influence population dynamics. The effects on demographic rates are manifold and vary substantially among species [8]. Climate change can also indirectly affect species by modifying habitat quality and species interactions. For polar bears, the melting sea ice fragments their habitat and hampers their ability to feed, breed, and move [9]. Warmer temperatures facilitate the spreading of existing diseases or the emergence of new ones [10]. For example, higher temperatures increased the risk of tuberculosis outbreaks for meerkat populations [11]. The effects of climate change on individual species accumulate on the scale of the ecosystem, where they might get amplified or buffered by changes in community composition, material flow, and biogeochemical cycles [12].

Mountain-adapted species may cope with new conditions by shifting their distribution to higher altitudes [13–15]. However, the carrying capacity in high elevations is lower because the area with suitable habitat is reduced. Populations migrating upslope will become smaller and therefore face an increased extinction risk [16, 17]. For example, in a Peruvian bird community, abundance of species living at high elevations has declined, and some species living on the summits went extinct [18]. Additionally, upslope range shift may isolate populations genetically. For the American marten, gene flow between populations was substantially reduced under future climatic scenarios [19, 20]. Immigration of related species can cause silent extinctions by hybridization, as shown for example in plants [21].

One species especially sensitive to environmental conditions is the alpine marmot (*Marmota marmota*). The first marmot species arose in the cold environment of the Pleistocene [22]. Since then, climate was an important driver of their evolution [23]. This sensitivity to environmental conditions is enforced by the sessile lifestyle. While other species may buffer harsh conditions by temporal migration, marmots are locally bounded by their burrow system. To escape the harsh winter conditions, marmots evolved social hibernation to reduce energy expenditure [24]. In late September, alpine marmots convene in a chamber of the burrow, the hibernaculum. They reduce their metabolism to a fraction of the summer level [25]. By keeping their body temperature between 3 and 6°C, they reduce substantially the energy required to survive the winter [26]. As the family emerges in April from hibernation, the dominant pair starts mating. After five weeks, the pups are born and in July they leave the burrow for the first time. During the remaining summer, the marmots, and especially the pups, must replenish their fat storages to prepare for the next winter [27].

To elucidate how marmots may react to climate change, for example, by a shift in distribution, it is crucial to learn about their environmental and climatic requirements. Alpine marmots mainly live on alpine meadows [28–31] between 1800 and 2500 m.a.s.l. [29, 32]. They mainly feed on leaves of dicotyledonous herbs and if available, on flowers and seeds [33]. These plants contain essential linoleic acids, which, stored in the white fat tissue, help marmots to withstand lower temperatures during hibernation [34–36]. Besides herbal vegetation, some studies found that marmot habitats contain some amounts of scree [28, 30], as boulders provide hiding opportunities and rocks in the soil stabilize the tunnel systems [32].

Marmot occurrence is associated with intermediate slope steepness [28, 37], on which the danger of burrow floodings is minimized. Marmots occur less on slopes with northern exposures [29, 38]. One study reported that colonies on north-facing slopes had higher mass gains during summer but also lost more weight during winter than marmots on south-facing slopes [39]. Marmots prefer intermediate values of solar radiation [29, 37], which depends on the local topography and the surrounding mountain silhouette.

While the static environment, such as topography and ground cover, are important habitat characteristics, marmots are also sensitive to dynamic environmental conditions. Because marmots have few sweat glands [40], they cope poorly with heat. A study investigating behavioural responses to environmental temperatures found that above 25°C, marmots decreased their activity with increasing temperatures [41]. On hot days, marmots therefore show a diurnal activity pattern with two peaks in the morning and the afternoon [32, 42]. Because of the sensitivity to temperatures, it was proposed that high summer temperatures may determine the lower limit of alpine marmot's altitudinal distribution [41].

Marmots are also affected by snow cover conditions, even though they hibernate during winter. Adequate snow depth in winter ensures insulation of the burrow [27]. If the temperature in the hibernaculum falls below 5° C, marmots must increase their metabolism to keep their body temperature [25]. The increased energy expenditure has detrimental effects on winter survival and reproduction. Litter size in alpine marmots is associated positively with snow depth [43], indicating that after a hard winter, little energy is left for reproduction. Another study found that with more hard frost days in autumn, adult and pup survival decreased [44]. Pups were less likely to survive their first hibernation period in winters with thin snow cover, both in alpine [45] and in hoary marmots (*Marmota caligata*) [46]. In yellow-bellied marmots (*Marmota flaviventris*), litter size was higher in winters with more frost days and adult survival was higher in longer winters [47]. In alpine marmots, harsh winters in one year also decreased pup survival two years later [45], because the pups that died cannot support the future generations in warming during hibernation [25].

While adequate snow cover in winter is required, snow cover delaying into spring affects marmots negatively [27]. Delayed snow melt prevents vegetation green-up, which further shortens the already short vegetative period. In alpine marmot families with pups, winter mass loss increased with later snow thawing [48] and later snow melt correlated with lower juvenile survival [24]. Indirectly, this effect was also observed as the number of neighbouring families decreased with later snow melt [48]. In yellow-bellied marmots, female reproduction was limited by food availability [49] and earlier emergence from hibernation and earlier breeding allowed the animals to gain more weight during summer [50]. However, some studies found no association between spring snow and survival [44] or even the opposite pattern [46, 47]. In winters with thick snow-packs, snow melt also occurs later. This led to the hypothesis that the effect of insulation might be stronger than the effect of delayed vegetation greening [46].

While the effects of environmental conditions on marmots' physiology and vital rates have been addressed in various studies on several marmot species, their effects on the spatial variation of abundance are poorly understood.

In this study I aimed to answer the following questions: 1) How do environmental conditions, in particular snow cover conditions, influence the spatial pattern of alpine marmot abundance? Based on the effects of snow cover on vital rates, I hypothesized higher abundance where snow melts earlier and lower abundance where start of winter is delayed. 2) How do environmental factors influence the detection probability? 3) Are estimates for abundance, detectability, and environmental effects unbiased and if not, are there alternative modelling choices to minimize the bias? And 4) are the abundance estimates in line with estimates from a classical distance sampling analysis?

I analysed data from a marmot census in the Swiss National Park with a Bayesian hierarchical distance sampling model, which models marmot abundance as a function of the environment, while accounting for marmot availability and imperfect detection. I run simulations to investigate the model's performance under different conditions. Furthermore, I estimated marmot abundance following a classical distance sampling analysis to validate the abundance estimates.

Quantifying the relationship between snow conditions and abundance gives insights into how marmot populations may react to climate change. If marmot abundance is sensitive to the snow onset day, climate change may reduce marmot abundance. However, if marmot abundance is higher when snow melts earlier, climate change may affect marmots positively by advancing vegetation growth. Investigating the effects of other environmental variables may reveal other determinants of marmots' ability to shift their distributions as a response to climate change.

## 2 Methods

This study was divided into three parts: fieldwork, deriving environmental metrics, and statistical analysis. From July to September 2021, I censused the marmots in the region of the Swiss National Park. Next, I derived environmental covariates relevant for alpine marmots from remote sensing products. The statistical analysis included a classical distance sampling analysis to investigate the effect of covariates on the form of the detection function, a hierarchical distance sampling analysis to study the effect of the environment on marmot abundance, and a simulation study.

### 2.1 Study Area

I conducted this study in the region of the Swiss National Park near Zernez in the Canton of Grisons (Figure 1). The border of the study area is given by the HABITALP data (see Section 2.4.1), except for the southeast corner, where the border is defined by a rectangle surrounding the area of interest. The study area ranges from 1470 to 3170 m.a.s.l. and spans an area of 420 km<sup>2</sup>. Because of the inner Alpine location, the climate is shaped continentally with large temperature fluctuations and arid conditions. Average annual rainfall is 800 mm and average temperatures at the weather station Buffalora (1968 m.a.s.l.) range from -10°C in January to 10°C in June [51]. Habitats at lower elevations are dominated by coniferous forests, which are replaced by alpine meadows and finally by scree and rock at higher altitudes. The park is strictly protected from anthropogenic influence and can only be accessed on the various hiking paths. All agricultural and hunting activity is prohibited. Open areas outside the park are used for extensive grazing. Marmots occur mainly above the treeline on alpine meadows, but few colonies are also found in scree fields and clearings below the treeline.

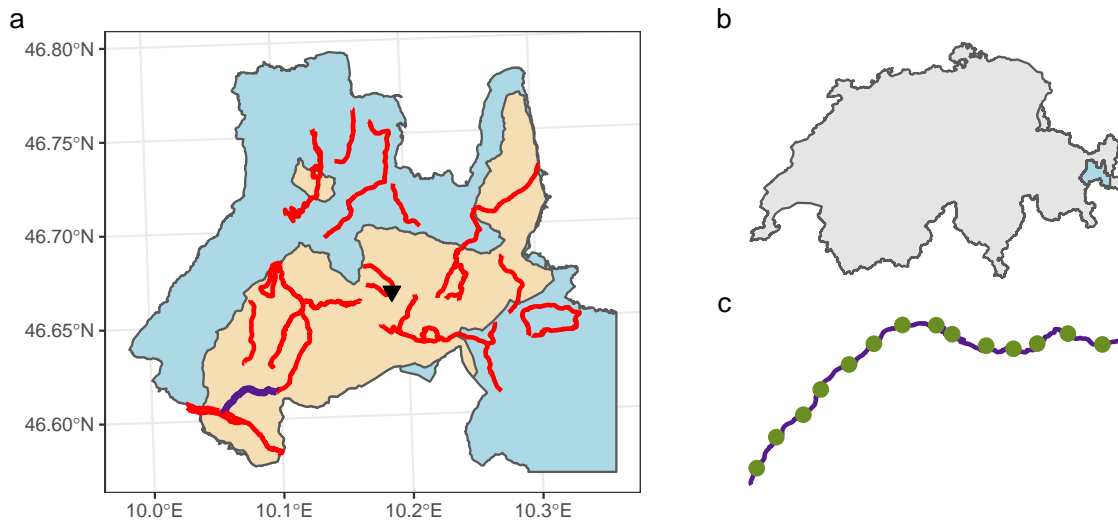


Figure 1: **a)** Transects (red) follow the main hiking paths in the study area (blue) around the Swiss National Park (light brown). **▼**: location of alp Grimmel, where the availability data was collected. **b)** Location of the study area (blue) in Switzerland. **c)** Along the purple transect in a), observation sites were placed every 330 m.



## 2.2 Fieldwork

Between July 29 and September 23, 2021, I censused the marmot populations in the region of the Swiss National Park following a point distance sampling approach [52]. I placed transects along the main hiking paths in and around the Swiss National Park (Figure 1a), with observation sites at 330 m intervals along these transects ( $n = 432$ ).

At each observation site I counted marmots for 10 minutes with binoculars, a thermal camera, and by eye. Until the end of August, I used a PULSAR CORE FXQ50 BW thermal scope and from September on a PULSAR Helion 2 XP50 Pro. I developed a custom app in the Field Maps app platform (ESRI) to facilitate the collection of locations and attributes of the animals surveyed. I distinguished between animals spotted by eye or with binoculars, and those spotted using the thermal camera. Former, I directly recorded in the app. As warm rocks also generate a thermal signature similar to marmots, I only recorded marmots seen using the thermal camera, if I saw them with binoculars as well. This also reduced any bias arising from the different sensitivities between the two thermal camera models. When the ground became too warm to spot marmots in the thermal camera, I ended the field day.

Some observation sites were unfortunately placed with little chance to spot marmots, because the habitat was not suitable for marmots (e.g., in forests or high altitudes), or the viewing range was restricted by topography or vegetation. If there was a better observation spot within 50 m, I surveyed from there and corrected the coordinates. Otherwise, I recorded that no survey would be carried out (Table 1). If I surveyed at an observation site, I noted the start and end times of the observation period. I remarked when I had no thermal camera with me, which was the case at three field days. Furthermore, I recorded the weather, temperature and the number of tourists within sight range during the observation period.

Table 1: Attributes for observation sites and values to select from.

Attribute	Values
Sampled	Yes, No
Time	Start, End
Gadget	ThermalCam, Binoculars
Disturbance	0, 1-3, 4-10, >10
Weather	sunny, cloudy, drizzle, fog, changeable
Temperature	cold (need for a jacket), chilly (need for a sleeve), warm

At each observation site, I recorded for 10 minutes the locations of marmots and their attributes (Table 2). Marmots that were separated by no more than 20 m as I considered as one group, for which I recorded the centre of the group with corresponding numbers of adults and pups. If individuals moved during the 10 minutes, I recorded their initial location. If it was not possible to record all groups during the 10 minutes, I spent additional time after the observation period to properly record the data. Any newly emerging marmots were not recorded.

I followed several rules to minimize the influence of observer and tourists along the hiking paths on the number of counted marmots and their radial distance. On each field day I visited the first observation site between 7 and 8 am, providing enough time before the first tourists arrived. Once there were too many tourists in the area, I ended the field day. I approached each

Table 2: Attributes for observed marmots and values to select from.

Attribute	Values
ID	<i>unique ID of the observation site</i>
Habitat	AlpineMeadow, AlpineMeadow_Stones, Pasture, Forest, Forest_sparse, Forest_young, DwarfMountainPine, Scree, Rock, other
NoAdult	<i>number</i>
NoJuvenile	<i>number</i>

observation site calmly and slowly to not disturb the animals. I recorded marmots which fled during approach, if their initial location was visible from the next observation site.

### 2.3 Data cleaning and processing

I excluded observation sites and their corresponding marmot detections from further analysis, if they belonged to one of five categories: 1) The observation site was located outside the extent of the HABITALP data, 2) vegetation limited the sight range at the observation site, 3) the habitat in the surrounding of the observation site was unsuitable for marmots, 4) the observation site was in close proximity of another observation site and 5) I visited the observation site when some colonies already started hibernating.

Observation sites falling into category 2) and 3) often had the attribute `Sampled` set to `No`. I excluded few other sites based on remarks on the sight range taken during fieldwork. For case 4) I filtered observation sites closer together than 140 m. Out of two sites in proximity, I selected the site with the larger sight range. Observation sites further apart were often located in different terrain chambers, whereby the overlap between observed areas remained minimal. Case 5) applied to the last field day on the 29.9.2021, where I saw winter burrows with clogged entrances, indicating that the colony had started hibernating.

I performed all analysis in R 4.2.0 [53] on a Windows 10 x64 machine. I run time consuming calculations and Bayesian models on a Linux server running Ubuntu 20.04.4 LTS and R 4.1.3.

### 2.4 Deriving environmental metrics

I reviewed the literature on habitat characteristics of alpine marmots to find candidate covariates. The variable selection process is described in Appendix A.2. I derived ground cover, slope, solar radiation, temperature, and snow cover metrics. Variables from existing datasets were used where available, otherwise I derived variables from remote sensing products.

The year of a marmot is divided into hibernation and active period, and different environmental processes may play a role in each. I therefore estimated the mean emergence date and the mean hibernation date from marmot phenology data for the years 2003 to 2020 (Swiss National Park, unpublished data). The average emergence date was 18.4., the average hibernation date was 29.9. Solar radiation, temperature, and spring snow cover are environmental variables relevant during the active season. I derived these parameters between 18.4 and 28.9. To this time frame I refer to as “summer period”. Burrow insulation by snow is only relevant during hibernation, which is why I derived a metric for snow cover between 29.9. and 17.4. (“winter period”).

Dynamic environmental covariates such as snow cover or temperature underlie large year-to-year variations. Additionally, remote sensed indexes may show spatial artefacts due to the

flight pattern of the satellite. To average out these effects, I calculated dynamic environmental metrics for four years (preferably 2018 to 2021, the four years for which the snow cover product is available) and averaged the metrics across the four years. Averaging indices across years might also better explain marmot abundance, as winter conditions also influence vital rates over several years [45].

In ecological models, different pixel resolutions lead to different conclusions about the effect of environmental variables [54]. A fine resolution describes behavioural processes (e.g., feeding behaviour), whereas resolutions at home range scale describe how a colony chooses its territory. In this study, I aim to describe the latter. However, mountains are heterogeneous environments. The finer the resolution, the better the heterogeneity is captured by the data. I therefore resampled all environmental variables to  $100 \times 100$  m, which is on the lower end of a typical home range size of an alpine marmot family [55].

#### 2.4.1 Topography, radiation, habitat, and temperature

Topographical variables are often included in species distribution and abundance models because they combine effects of many environmental variables into a single parameter. I derived slope steepness from the digital terrain model (DTM) product SwissAlti3D from swisstopo [56] at a resolution of  $10 \times 10$  m.

From the same DTM resampled to  $20 \times 20$  m I derived a radiation map using the Solar Radiation Tool from ArcGIS Pro (ESRI). For each pixel I extracted the cumulative radiation over the summer period for the year 2021. As sky size I chose 200 cells, which is sufficient for time periods  $>14$  days [57]. For the remaining parameters, I chose the default settings, because I am not interested in precise radiation estimates but in relative differences across the landscape.

Table 3: Several habitat types were combined into the three categories meadow, scree, and unavailable. Habitat types are translated from German.

Category	Habitat Type	ID	Remark
<b>Meadow</b>	meadow	4200	
	resting spot	9392	in study area: always on meadows
	ruin	9160	in study area: overgrown by meadows
<b>Scree</b>	bare ground	5400	
	anthropogenic cairn	5520	
	snow through	5620	
	scree, boulders	5700	
	snow	5900	in study area: below is always scree
<b>Unavailable</b>	water	2000	
	bog	3000	
	agriculture	4000	
	cave	5100	
	retaining wall	5540	
	trees, bushes	6000	
	forest	7000	
	disturbed sites	8000	
	settlement, traffic, recreation	9000	without HT 9392 and HT 9160

To characterize ground cover, I calculated proportion of meadow, proportion of scree, and proportion of habitat unavailable for marmots per pixel from the HABITALP data set [58], a ground cover and vegetation data set from the Swiss National Park. As there are no distinct HABITALP categories for meadow, scree, and unavailable, I combined several habitat types (Table 3). For each  $100\times 100$  m pixel I calculated the proportion of each category covering the pixel area. I calculated the proportion of meadow and scree relative to the available area in the pixel. Pixels overlapping with the border of the HABITALP data were excluded from further analysis.

The category “unavailable” combines habitat types with two characteristics. First, marmots cannot occur in certain habitats (e.g., water, villages). Second, the snow and plant phenology metrics are only valid in open areas. Therefore, even though in rare cases marmots may occur in loose forests, I defined these habitat types as unsuitable for marmots.

As high summer temperatures may define the lower limit of marmot distribution [41], I derived temperature metrics for each pixel from downscaled Daymet data [59] at a resolution of  $100\times 100$  m. At the time I acquired the data, the DaymetCH data for the year 2021 was not yet processed. Therefore, I used daily temperatures of the summer periods of the years 2017 to 2020. For each year and pixel, I calculated the median of the daily maximum temperatures and averaged over the four years.

#### 2.4.2 Snow cover

Snow is hypothesized to have opposing effects on marmot abundance depending on the season. During the winter period, snow insulates the burrow, reducing energy expenditure of the hibernating marmots. In spring, delayed snow melt shortens the vegetation period.

I aimed to derive snow phenology metrics describing the insulating effect of snow in winter and the delaying effect of snow in spring. For the former, snow depth would be a convenient snow property. However, remote sensed snow depth measurements are not freely available. Instead, I used the Theia Snow Collection [60], a binary snow cover mask derived from Sentinel-2 and Landsat-8 images at a  $20\times 20$  m resolution, making the assumption that if snow is present, the ground is insulated. For snow melt, a binary snow cover is suitable, because vegetation starts growing two weeks after all snow has melted [61].

I downloaded level 2B snow masks with an average temporal resolution of 5-days for the period between 30.9.2017 and 29.9.2021 with the package theiaR [62]. I defined a hydrological year relevant for marmots starting from 29.9. until 28.9. of the following year. I derived all snow phenology metrics within one hydrological year and averaged across the four years.

For each pixel and year, I interpolated the binary snow/no snow values with a temporal nearest neighbour algorithm, where to each missing value in a pixel time series the value of the nearest measurement is assigned (Figure 2a). From the interpolated time series, I calculated two snow phenology metrics Snow Delay (SD) and Snow Prolongation (SP). SD is defined as the number of snow free days between 29.9. and the longest snow-covered period. Snow-free days beyond the longest period are not included in SD, because in spring the sun warms the burrow as soon as the ground is snow-free [24]. SP is the number of days snow prolongs beyond the emergence date on 18.4. until the longest snow-free period. Occasional snow-covered days in autumn are not included in SP, because they occur too late to affect vegetation growth.

The binary snow maps are only valid in open areas. In forest, the snow masks describe the state of the canopy rather than of the ground. I therefore masked out all  $20\times 20$  m pixels overlapping with unavailable habitat (section 2.4.1) before resampling to  $100\times 100$  m.

## 2.5 Statistical Analysis

Distance Sampling is a censusing method to estimate animal abundance by estimating a detection probability based on the distance of the animal [52]. The further away an animal is, the less likely it is spotted by an observer. To each animal spotted, the distance to the observer is recorded. To these distance measurements, a monotonically decreasing detection function is fitted, which is used to estimate a detection probability. However, distance sampling assumes that abundance is unknown, but constant across the study area [63]. Only if the study design is random with respect to animal abundance, one can extrapolate abundance to unobserved areas (“design-based abundance estimate”).

Recent efforts have been made to incorporate abundance effects into a distance sampling framework (“model-based abundance estimate”). Such approaches can be divided in two conceptual groups: two-stage and one-stage approaches [64]. Two-stage approaches are based on the count model of Hedley & Buckland (2004) [65]. First, the distance data informs a detection function, from which a detection probability is derived. Then, the individual observations are pooled to animal counts per transect segment or observation site. The pooled counts are modelled as a function of the environment, often by fitting generalized additive models (GAMs). One-stage approaches estimate parameters for the detection function and abundance jointly [66, 67].

However, both approaches only model changes in abundance at the level of the observation unit (observation site or transect segment). For mountain environments, this resolution is too coarse, as with a thermal camera marmots can be spotted beyond 300 m. The environmental variation within this radius is too large to yield useful models. Recently, Marc Kéry and Andrew Royle [68] proposed a Bayesian hierarchical model, which models abundance effects on a pixel unit smaller than the observation unit.

First, I analysed the data using a design-based analysis, to which I refer to as classical distance sampling (Section 2.5.1). To investigate the effect of environmental covariates on marmot abundance, I extended the Bayesian hierarchical model to account for time-varying availability (Section 2.5.2). I refer to this as the hierarchical distance sampling model. Furthermore, I conducted a simulation study using a simplified version of the hierarchical model to investigate its behaviour in different conditions (Section 2.5.3).

I wrote all Bayesian models in JAGS 4.3.1 [69] with the R interface jagsUI [70].

### 2.5.1 Classical distance sampling

I conducted a classical distance sampling analysis using the R package Distance [71]. I aimed to get estimates for average density, abundance, and for parameters describing the detection function. Furthermore, I wanted to explore the effect of covariates on the shape of the detection function.

To allow for comparisons with abundance estimates from the spatial distance sampling model, I set the area of the study area to the area of pixels used for the hierarchical model (section 2.5.2).

Large distances contribute little to the estimation of the detection function  $g(x)$  but may lead to high variance. It is recommended to exclude 10% of the detections [52], which corresponds to a truncation distance of 388.5 m for my data. However, goodness of fit assessments showed poor fit for large distances. I therefore truncated my data at 300 m.

I selected the most parsimonious model with a threshold of  $\Delta AIC > 2$ . AIC, however, tends to select overly complex models if the distance data is overdispersed [72], i.e., if there is higher

variability in the distance data than expected based on the model. In distance sampling, this arises if distance measurements are not independent, which is the case for marmots. Since marmots live in social groups, several individuals have similar distances. Therefore, I analysed the animals as spatial groups with a given size, which reduced overdispersion substantially. To convert the group abundance to individual abundance, the group size is regressed against distance. The group abundance is then multiplied by the average group size at distance 0, yielding the abundance of individual marmots. However, the marmot groups were still not completely independent, because one family may be split in several spatial groups.

I compared a model with a half-normal detection function (equation 1) against a model with a hazard-rate (equation 2). While AIC would have selected for the hazard-rate model, I proceeded with the half-normal model to keep the comparability to the hierarchical model. I iteratively added covariates to the previous best model (forward selection). The covariate vector  $\mathbf{z}$  influences the detection function by altering  $\sigma$  (half-normal: sigma, hazard-rate: scale, equation 3), which are the inflection points in both detection functions.

$$g(x) = \exp\left(-\frac{x^2}{2\sigma^2}\right) \quad \text{half-normal} \quad (1)$$

$$g(x) = 1 - \exp\left(-\left(\frac{x}{\sigma}\right)^{-b}\right) \quad \text{hazard-rate} \quad (2)$$

$$\sigma(\mathbf{z}) = \exp\left(\beta_0 + \mathbf{z}^\top \boldsymbol{\beta}\right) \quad \text{covariate effect} \quad (3)$$

I investigated the effect of habitat, weather, temperature, disturbance, time of day, and time of year on the shape of the detection function. To avoid overparameterization, I merged several factor levels of the categorical covariates. For habitat, I added `Pasture` to `AlpineMeadow`, and merged `Forest_sparse`, `Forest_young`, `Rock`, and `Scree` into the category `Other`. For weather, I merged the levels `changeable`, `Fog`, and `cloudy` into `cloudy`. I converted `disturbance` into a binary category (`yes`, `no`). Even though I would have expected an influence of `Gadget`, I only visited few observations sites without a thermal camera, so I did not test for an effect. I scaled the continuous variables `DayTime` and `YDay` to improve model fitting behaviour. I did not include any interactions, because for many factor combinations, there was no data. Since I included covariate effects, I did not add adjustment terms to the detection functions.

### 2.5.2 Hierarchical distance sampling

Covariates in classical distance sampling models only influence the shape of the detection function. Hierarchical distance sampling models contain an additional model component describing the abundance as a function of environmental covariates [64]. One attempt in a Bayesian framework, which models abundance on a pixel unit, was made by Marc Kéry and J. Andrew Royle in Applied Hierarchical Modeling in Ecology [68, 73]. I used their spatial model on pixel frequencies [73] as a basis and expanded the model to correct for time-varying availability of marmots.

The model corrects the marmot counts by accounting for three processes. The first process describes the abundance of marmots on a pixel (environmental process). The second process describes the availability of the marmots depending on the time of day (behavioural process), and the third process corrects for imperfect detection by filtering the number of available marmots depending on the distance (detection process).

In the environmental process, I modelled the number of marmots  $N$  on a pixel  $g$  following a Poisson distribution with intensity function  $\lambda_g$ , which is linked to the habitat covariates  $\mathbf{x}_g$  by an intercept  $\beta_0$  and a parameter vector  $\boldsymbol{\beta}$ . The priors on the  $\beta$ 's were weak normal distributions

with mean  $\mu = 0$  and variance  $\sigma^2 = 100$ . Since not all the pixel area is suitable for marmots, I added an offset to the intensity function with the proportion of the pixel available for marmots  $A$ .

$$\begin{aligned}\beta_i &\stackrel{\text{iid}}{\sim} \mathcal{N}(0, 100) \\ \lambda_g &= \exp\left(\beta_0 + \mathbf{x}_g^\top \boldsymbol{\beta} + \log(A)\right) \\ N_g &\sim \mathcal{P}(\lambda_g)\end{aligned}$$

I modelled the effect of seven environmental covariates: proportion of meadow, proportion of scree, slope, snow prolongation (SP), snow delay (SD), radiation, and the median of the daily maximum temperatures (Tmax). For the last I included a quadratic effect, as I expect that marmots may prefer an optimum temperature. I standardized all covariates to improve run time and mixing of the models.

The number of marmots available depends on the time of day, as marmots show a diurnal availability pattern with two maxima [32]. Since I always started sampling in the valley bottom, the time of sampling is correlated with almost all environmental variables. By ignoring this effect, the model cannot disentangle if the observed abundance is a pattern in abundance or in availability. To incorporate information in availability, I used existing data from a study carried out in 2009 in the national park [74]. On Alp Grimmel (Figure 1a), the number of animals outside the burrow were counted every 10 minutes. I fitted a Bayesian spline with 9 knots to the available proportion of the marmot family (Figure 2b). For each observation site, I predicted the mean availability probability  $\mu_g$  and the corresponding standard deviation  $sd_g$ . In the behavioural process of the model, the number of available marmots  $M_p$  on a pixel follows a binomial distribution, where  $n = N_g$  and  $p$  follows a normal distribution with mean and standard deviation estimated from the spline for the nearest observation site.

$$\begin{aligned}p_g &\sim \mathcal{N}(\mu_g, sd_g^2) \\ M_g &\sim \mathcal{B}(N_g, p_g)\end{aligned}$$

In the detection process of the model, I modelled imperfect detection with a half-normal detection model, where the detection probability  $q_g$  decreases with distance  $d_g$  between the observation site and the pixel. Rather than using the distance to the pixel centre as proposed in [73], I used the expected distance of a pixel to the observation site (see Section 2.5.3). The parameter  $\sigma$  should be in  $\mathbb{R}^+$ , therefore I set the prior of  $\sigma$  to a wide, positive, uniform distribution. The number of animals detected on a pixel  $L_g$  then follows a binomial distribution with  $n = M_g$  and  $p = q_g$ .

$$\begin{aligned}\sigma &\sim \mathcal{U}(0, 20) \\ q_g &= \exp\left(-\frac{d_g^2}{2\sigma^2}\right) \\ L_g &\sim \mathcal{B}(M_g, q_g)\end{aligned}$$

While  $M_g$  and  $N_g$  are unknown properties which must be estimated,  $L_g$  is provided as data.  $L_g$  was calculated as the number of marmots on a pixel  $g$  seen from the nearest observation site during fieldwork. From these pixel-based metrics I derived total abundance and average density defined as

$$\begin{aligned}N_{\text{tot}} &= \sum_{g=1}^G N_g \\ D &= \frac{N_{\text{tot}}}{G}\end{aligned}$$

Similar to truncation in classical distance sampling, I only included pixels in the analysis that intersected with a buffer of 350 m around the observation sites. Additionally, I excluded pixels with missing environmental covariates. These were pixels mainly covered by unavailable habitat, for which the resampling had no values to average over. Marmots on such pixels were excluded as well, reducing the number of marmots from 571 to 550.

My data contains repeated observations of marmots, i.e., where I saw the same marmots from several observation sites. However, I did not allow the model to detect marmots from more than one observation site, but only evaluated each pixel with respect to the nearest observation site. This reduced the number of marmots for the analysis from 550 to 342 marmots on 170 pixels, on which abundance was bigger than 0.

### 2.5.3 Simulation Study

Before applying the model to my data, I tested the model on simulated data with the aim to compare the performance of different parametrizations and to investigate sources of bias. I simulated an imaginary marmot species *Marmota commenticius* on a virtual habitat. To analyse the simulated data I used a simplified version of the model described in sSection 2.5.2 without the behavioural process.

The simulated data is built in several steps with code modified from Applied Hierarchical Modeling in Ecology [68]. First, a plain is divided into pixels. To each pixel  $g$ , a spatially correlated habitat value  $x_g$  is assigned. Based on this habitat value, each pixel gets a probability to contain a marmot  $p_g = \exp(\beta x_g) / \sum_g \exp(\beta x_g)$ , where  $\beta$  describes the strength of the association between marmots and the habitat. Then,  $N$  marmots are distributed to the pixels following a categorical distribution with probability vector  $\mathbf{p}$ . Within a pixel, the coordinates of the marmots are uniformly distributed. Finally, each marmot is detected or not by a detection model (either half-normal or hazard-rate) depending on the distance between marmot and observation site. An example of a simulated data set is shown in Figure 2d).

There is a discrepancy between the simulated data and the model. In the simulated data, the marmots on a pixel are described by a Binomial point process (BPP), while the model describes them as a Poisson point process (PPP). Using a BPP in the simulations allows to fix the abundance, therefore making the estimates comparable to the true value. Using a BPP in the model would require augmenting the data, which will decrease the speed of the model drastically. While there are theoretical differences between BPP and PPP, in practice the two are indistinguishable with the exception that in the BPP the variances of the estimates will be slightly smaller [75].

I run four simulations to investigate the effect of four potential issues. In simulation 1 (SIM1) I compared a half-normal against a hazard-rate parametrization of the detection function. In simulation 2 (SIM2) I investigated the effect of spatial overlap between observation sites. In simulation 3 (SIM3) I examined the influence of pixel resolution on the estimates. And in simulation 4 (SIM4) I compared two distance measures for the distance between marmots and observation sites. If not stated otherwise, I set the true parameters to  $\beta = 1.2$ , abundance  $N = 400$ ,  $\sigma = 0.1$  for the half-normal model, pixel resolution =  $0.1 \times 0.1 \text{ km}^2$ , number of observation sites = 10, and distance between observation sites = 0.3 km.

In SIM1, I compared two parametrizations for the detection function, the half-normal model (HN, equation 1) and the hazard-rate model (HR, equation 2). In the classical distance sampling analysis, AIC selected for the hazard-rate detection model. However, previous runs of the hierarchical model with a hazard-rate detection model led to models where either the scale or shape parameter showed bad mixing behaviour (chains hitting against lower boundary of



parameter). To assess any differences between the two parametrizations, I simulated 100 data sets, 50 with a half-normal and 50 with a hazard-rate detection model, and analysed each data set with a model with the corresponding detection function.

Next, I investigated implications of the spatial overlap between observation sites. Each pixel is only evaluated with respect to the nearest observation site. As observation sites are closer together, the number of far pixel decreases. I therefore expected the detection function to decrease quicker when the observation sites are closer together. I simulated 50 data sets for each of seven distances between observation sites (0.1-0.7 km in 0.1 km steps) and analysed them with a half-normal model.

Furthermore, I wanted to investigate effects of the choice of pixel resolution. Distance models use continuous distance measures, whereas I used the distance to the pixel centre. The finer the grid, the better the approximation of the continuous space by the discrete raster. I simulated 50 data sets for each of 6 different pixel sizes (0.2, 0.15, 0.1, 0.08, 0.06, 0.04 km edge length) and run a half-normal model on each data set.

As a way to counteract the bias I found in the parameter estimates, I compared two different distance measures between pixel and observation site. The first is the Euclidean distance between site and pixel centre. The second is the expected distance between site and pixel. If the observation site is located on a pixel centre, the Euclidean distance is 0. However, the average distance of many uniformly distributed points on the pixel to the observation site will be  $> 0$  (Figure 2c). The expected distance accounts for this discrepancy. If a point within a pixel with edge length  $r$  is uniformly distributed

$$\begin{aligned} X &\sim \mathcal{U}(-r/2, r/2) \\ Y &\sim \mathcal{U}(-r/2, r/2) \end{aligned}$$

the distance between the point on the pixel with coordinates  $(x_1, y_1)$  and the observation site with coordinates  $(x_0, y_0)$  is

$$d = \sqrt{(x_1 + X - x_0)^2 + (y_1 + Y - y_0)^2}.$$

The expected distance of the focal pixel is then

$$\mathbb{E}[d] = \frac{1}{r^2} \int_{-r/2}^{r/2} \int_{-r/2}^{r/2} \sqrt{(x_1 + X - x_0)^2 + (y_1 + Y - y_0)^2} dX dY.$$

I simulated 50 data sets and analysed each twice with the two distance measurements.

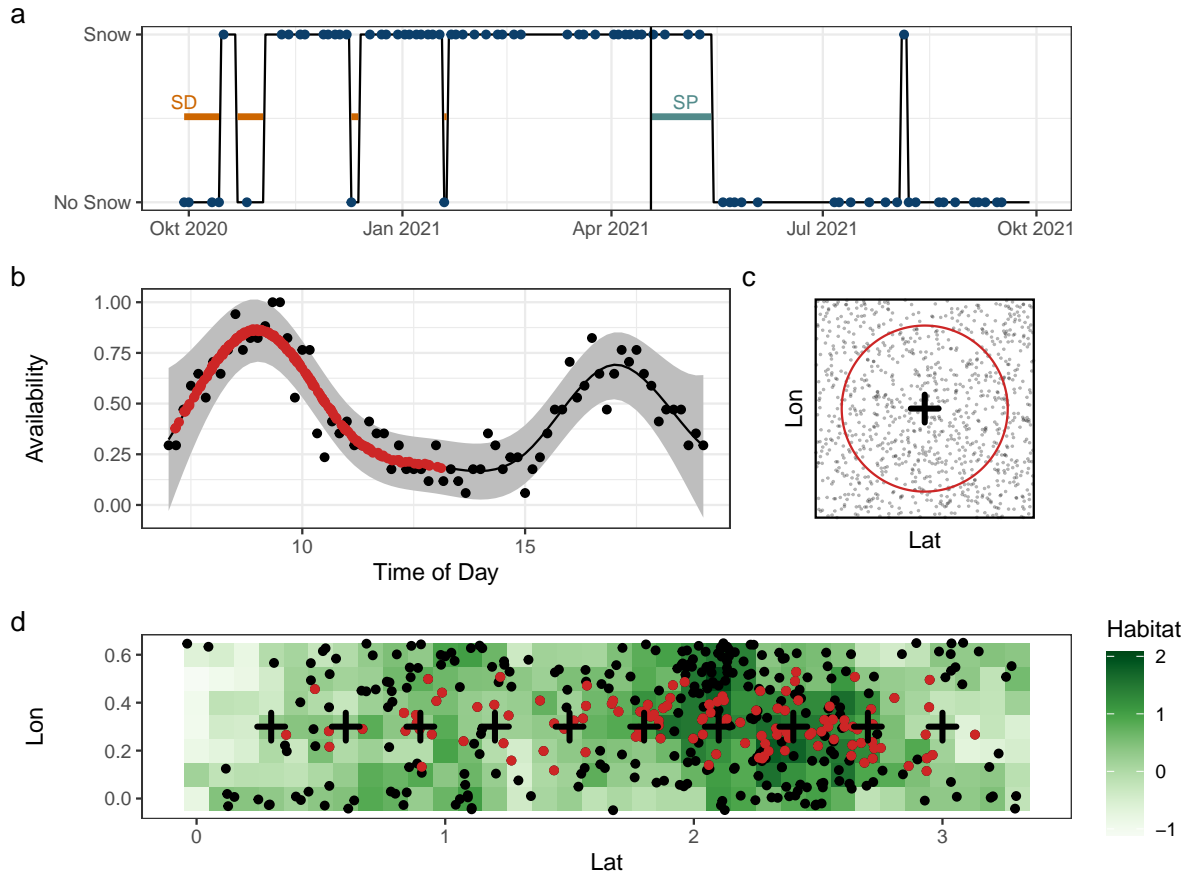


Figure 2: **a)** Illustration of the two snow cover metrics snow delay (SD) and snow prolongation (SP). The black line shows the interpolation from the theia snow cover product (blue points) for a random pixel. The vertical black line show the mean emergence date on 18.4. **b)** Bayesian spline fitted to the availability data of marmots on Alp Grimmels in the Swiss National Park with 95% credible interval. The red points are the mean predicted availability probabilities  $\mu_g$  for all observation sites. **c)** If the observation site (cross) is in the centre of a pixel, the distance to the pixel centre is zero, but the average distance of many uniformly distributed points is larger than zero (red circle). The expected distance accounts for this discrepancy. **d)** Example of a simulated data set. Crosses show the observation sites, black points the 400 marmots, and red points the marmots that were detected based on the detection model.

### 3 Results

#### 3.1 Classical distance sampling

From the two null models, the hazard-rate detection model had a lower AIC than the half-normal model (Table 4). However, since the hazard-rate detection function in the hierarchical model mixed poorly, I continued with the half-normal model to ensure comparability. The two best performing models were the ones with covariates Temperature + Weather and Temperature + Weather + YDay. Since the marmot observations are not independent, AIC tends to select overly complex models. Therefore, the model with fewer parameters should be preferred as the final model. While the detection probability  $P_a$  was in the same range for all half-normal models, it was considerably lower for the hazard-rate model.

Table 4: Results of the model selection process for the influence of covariates on the detection function. Key shows the family of the detection function (HN or hazard-rate), Formula shows the covariates in each model,  $P_a$  and  $se(P_a)$  is the detection probability and the corresponding standard deviation, and  $\Delta AIC$  is the difference in AIC to the best performing model.

Key	Formula	$P_a$	$sd(P_a)$	$\Delta AIC$
HN	Temperature + Weather	0.396	0.033	0
HN	Temperature + Weather + YDay	0.396	0.033	1.935
HN	Temperature + YDay	0.411	0.033	6.653
HN	Temperature	0.414	0.033	6.912
HN	YDay	0.421	0.033	10.788
HN	Weather	0.421	0.035	15.074
HR	1	0.243	0.075	16.675
HN	1	0.435	0.033	20.329
HN	Habitat	0.43	0.033	20.538
HN	DayTime	0.435	0.034	22.248
HN	Disturbance	0.435	0.033	22.286

The unweighted Cramer-von Mises goodness-of-fit test for the final model indicated sufficient model fit for the final model ( $p = 0.2409$ , where a significant p-value would indicate that the data origins from another model). However, for small distances, the observed distances were larger than the fitted distance, while the opposite was true for large distances (also seen in Figure 3).

The half-normal model without covariates (Null) and the half-normal model with Temperature and Weather (Final) had similar abundance estimates (Table 5) and the uncertainties in abundance were considerably bigger than the difference between the models. The same was true for the density estimate  $D$  and its uncertainty. The distance to the inflection point of the detection function  $\sigma$  was 150.6 m for the null model. This was greater than  $\sigma$  in the final model (126.3 m) seen as the average across all factor level combinations.

Detection probability was lowest in warm temperatures and increased with cold and chilly temperatures (Figure 3a) for constant weather. The detection probability was lowest during drizzle, increased with cloudy weather and was highest for sunny weather (Figure 3b) for constant temperature. However, the category Drizzle had few samples and therefore, the decrease in  $P_a$  for this covariate level was not as robust as for the others.

Table 5: Comparison of the null model and the final model with temperature and weather effects.  $D$  and  $sd(D)$  are the density estimates and the standard deviations.  $N$  and  $sd(N)$  are the abundance estimates and their standard errors.  $\sigma$  is the distance in meters to the inflection point in the half-normal detection model.

Model	$D$	$sd(D)$	$N$	$sd(N)$	$\sigma$
Null	0.139	0.018	722.8	94.9	150.6
Final	0.143	0.021	743.7	107.8	127.3

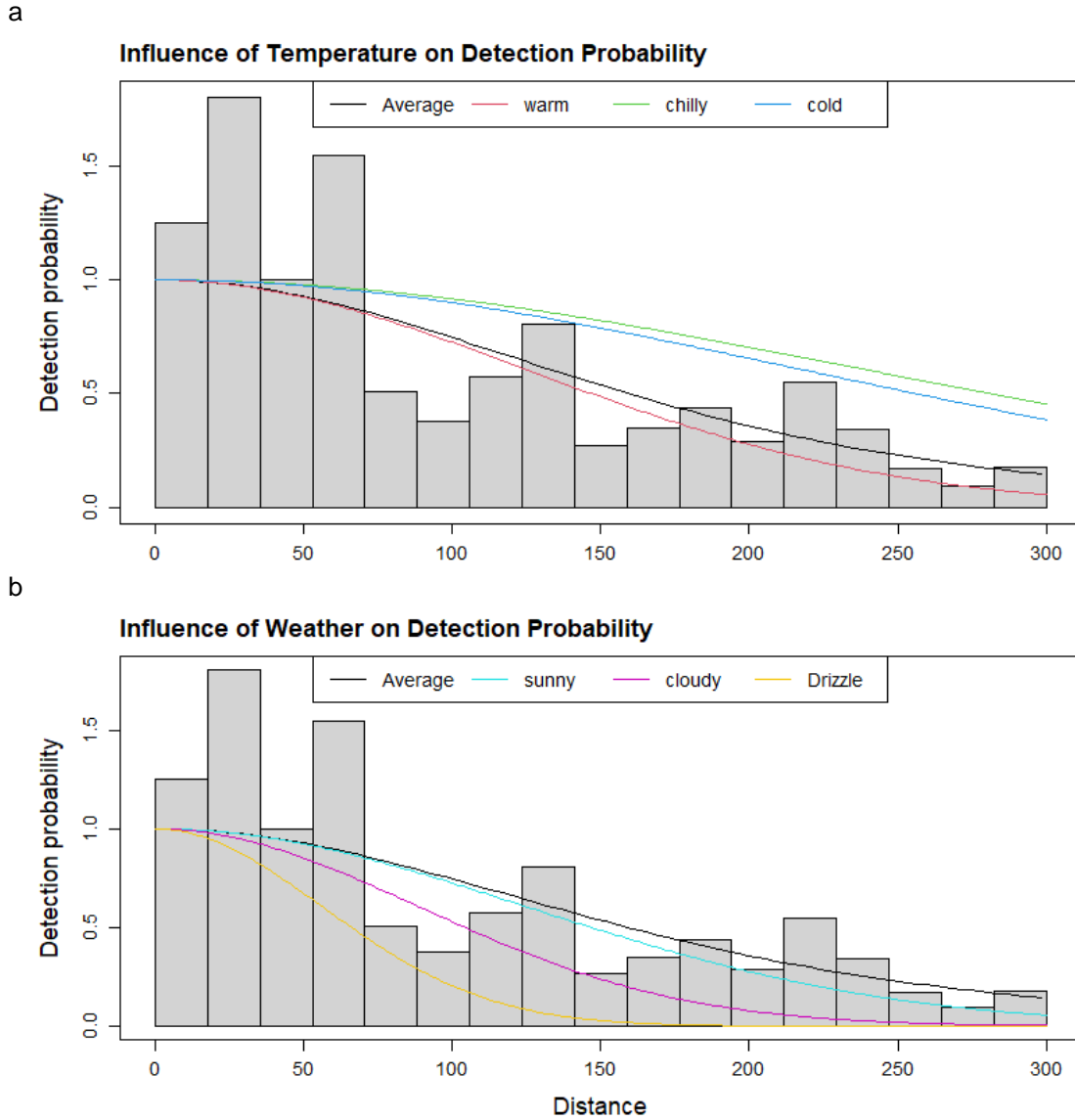


Figure 3: Result of the final model from the distance sampling analysis. Bars show the observed distances corrected for the increasing area observed with distance from the observation site. The lines show the predicted detection probabilities for a) the influence of temperature on the detection function (with weather being sunny) and b) the influence of weather on the detection function (with temperature being warm).

### 3.2 Simulation

I ran simulations to investigate the effects of a half-normal versus a hazard-rate parametrization of the detection function (SIM 1), biases arising from spatial overlap between observation sites (SIM 2), bias arising from the spatial resolution (SIM 3), and potential fixes for the bias (SIM 4). I estimated form parameters of the detection functions (sigma, scale, shape), the association with the environment (beta), and abundance (N) and compared them to the true simulated value.

Both the half-normal and hazard-rate detection model performed similarly (Figure 4, top row). However, all three form parameters for the detection functions were biased high, which lead to an overestimation of the detection probability. The bias in detection probability propagated to

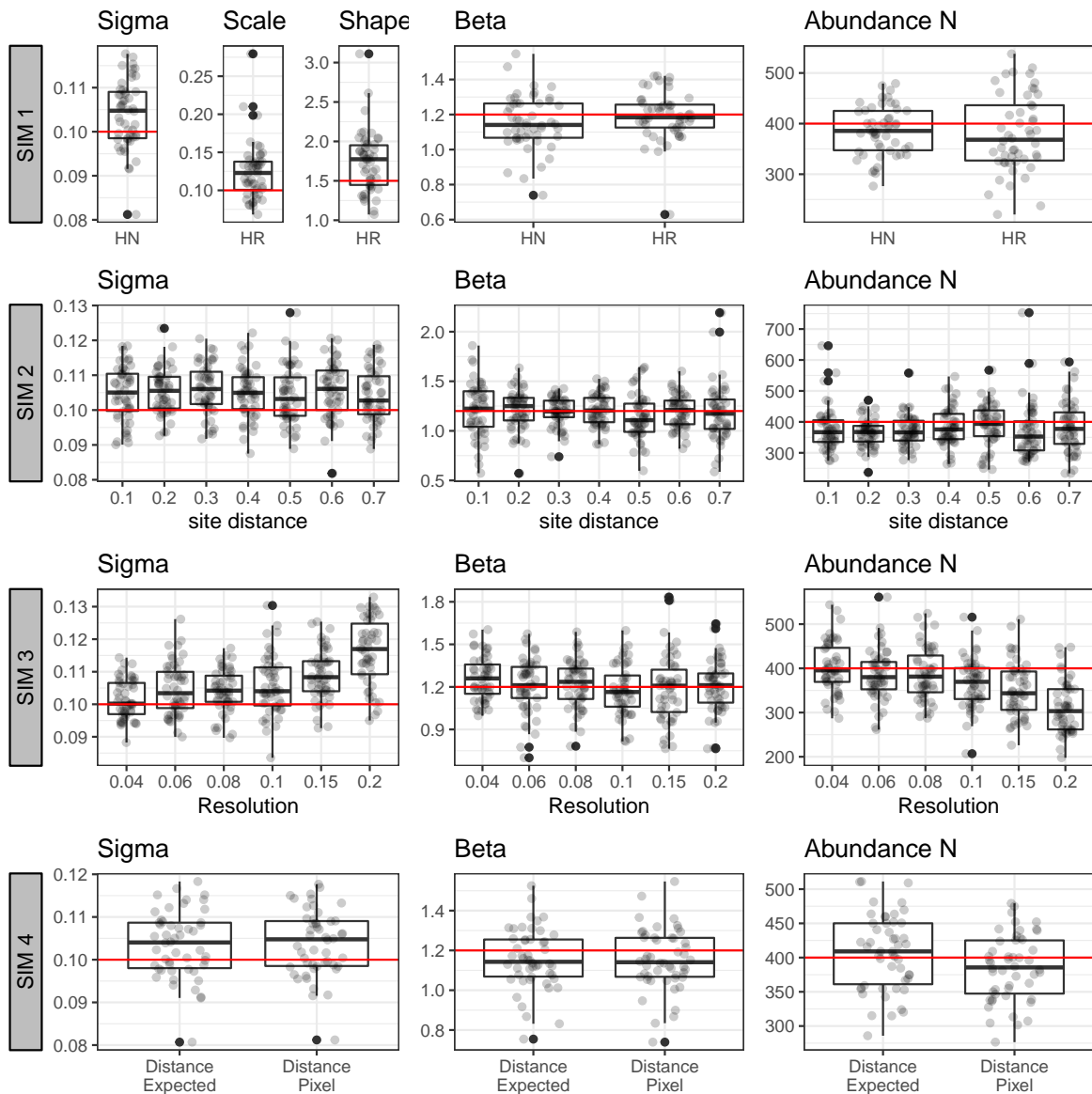


Figure 4: Estimated parameters for the four simulation runs (rows). Sigma, scale and shape define the form of the detection function. Beta is the association of *M. commenticus* with the environment. N is the abundance across all pixels and red lines show the true simulated values.

the abundance estimates, which were biased low. The beta parameters, however, were unbiased.

The biases in the detection function parameters were constant across varying distances between observation sites (Figure 4, second row). For all simulated distances, sigma estimates were biased high and abundance estimates were biased low. The beta parameters remained unbiased.

SIM 3 indicated that the bias arose from the decision on the spatial resolution of the environment. The finer the resolution, the smaller the bias in sigma (Figure 4, third row). The biases in the detection functions propagated into the abundance estimates, which were lower for coarser resolution. However, the beta parameters were not affected.

I expected the biases to arise from the difference between the distance to the pixel centre and the expected distance. However, both distance measures showed the same amount of bias in sigma and abundance estimate (Figure 4, bottom row).

### 3.3 Hierarchical Distance Sampling

I investigated the influence of environmental factors on marmot abundance with a Bayesian hierarchical distance sampling model correcting marmot count data for time-varying availability and incomplete detection.

The four MCMC chains converged successfully (visually and all Rhat values smaller than 1.003). Visual inspection of the chains showed that burn-in was sufficient. With 80'000 samples from the posterior distributions, the lowest effective sample size was 1003 for radiation. Some samples from the posterior distributions of the environmental parameters were unreasonably high. In combination with the exponential function in the environmental process, expected abundance estimates rocketed up, especially if the covariates were at their extreme values as well. To ensure robustness against these outliers, I calculated median estimates instead of mean estimates.

The effect size of the environmental covariates was largest for meadow, followed by Tmax2, slope, and SD (Table 6, Figure 5). For meadow, slope, and Tmax2, the 95% credible intervals (CI) did not overlap with zero, indicating a low probability for no effect. The CI for SD just

Table 6: Median of the samples of the posterior distribution of the parameter (Estimates), the standard deviation, and the corresponding 95% credible intervals (CI). The CI of bold environmental parameters do not overlap 0.

Parameter	Estimate	StDev	CI
Intercept	-1.402	0.118	[-1.63, -1.17]
<b>Meadow</b>	0.711	0.25	[0.25, 1.23]
Scree	-0.073	0.24	[-0.52, 0.42]
<b>Slope</b>	-0.222	0.088	[-0.39, -0.05]
SD	-0.103	0.056	[-0.21, 0.01]
SP	0.032	0.144	[-0.25, 0.31]
Radiation	0.026	0.096	[-0.16, 0.21]
Tmax	-0.012	0.13	[-0.26, 0.24]
<b>Tmax2</b>	-0.328	0.117	[-0.56, -0.1]
$\sigma$	0.183	0.01	[0.17, 0.2]
N	1142	73.87	[1007, 1296]
D	0.22	0.014	[0.19, 0.25]

barely overlapped with zero, while the rest of the parameters did not differ from zero (Figure 5).

The exponentiated intercept can be interpreted as the expected marmot abundance on a pixel in absence of habitat effects, which was 0.246 marmots per ha. With habitat effects, the median abundance was 1142 marmots across all pixels used for model fitting and with an average density of 0.22 marmots per ha. The classical analysis would have proposed a hazard-rate parametrization, which would have resulted in a lower detection probability. Therefore, the abundance estimate of the hierarchical model should be interpreted as a lower boundary rather than a precise estimate.

The median  $\sigma$  parameter of the half-normal detection function was with 0.183 km higher than the estimate from the regular distance sampling model (150.6 m) without covariates.

A model run without the behaviour model component showed similar environmental effect sizes. The median abundance of this model was 716 marmots, which was close to the estimate from the spatially-implicit distance sampling model without covariates (722.8).

Goodness-of-fit tests and investigating the residuals showed that the model overestimated abundance on pixels where no marmots were seen and underestimated abundance on pixels with high abundances (Appendix A.3). Two Bayesian p-values, computed with Pearson and Freeman-Tukey residuals respectively, indicated poor model fit (both  $p = 1$ ). A well-fitting model should simulate data similar to the observed data, which would be indicated by a Bayesian p-value of  $p = 0.5$ .

Based on the posterior samples I extrapolated median expected abundance with standard deviation to the whole study area (Figure 6). In the eastern part of the study area, the observed marmots were located where expected abundance was high as well. In the west, the observed marmots followed less the pattern in expected abundance. The standard deviation of expected abundance is influenced by two processes. Because of the Poisson model, the standard deviation is high in regions of high marmot abundance. Additionally, standard deviation is increased in parts of the study area which were not censused properly, for example, the low elevations in the west of the study area.

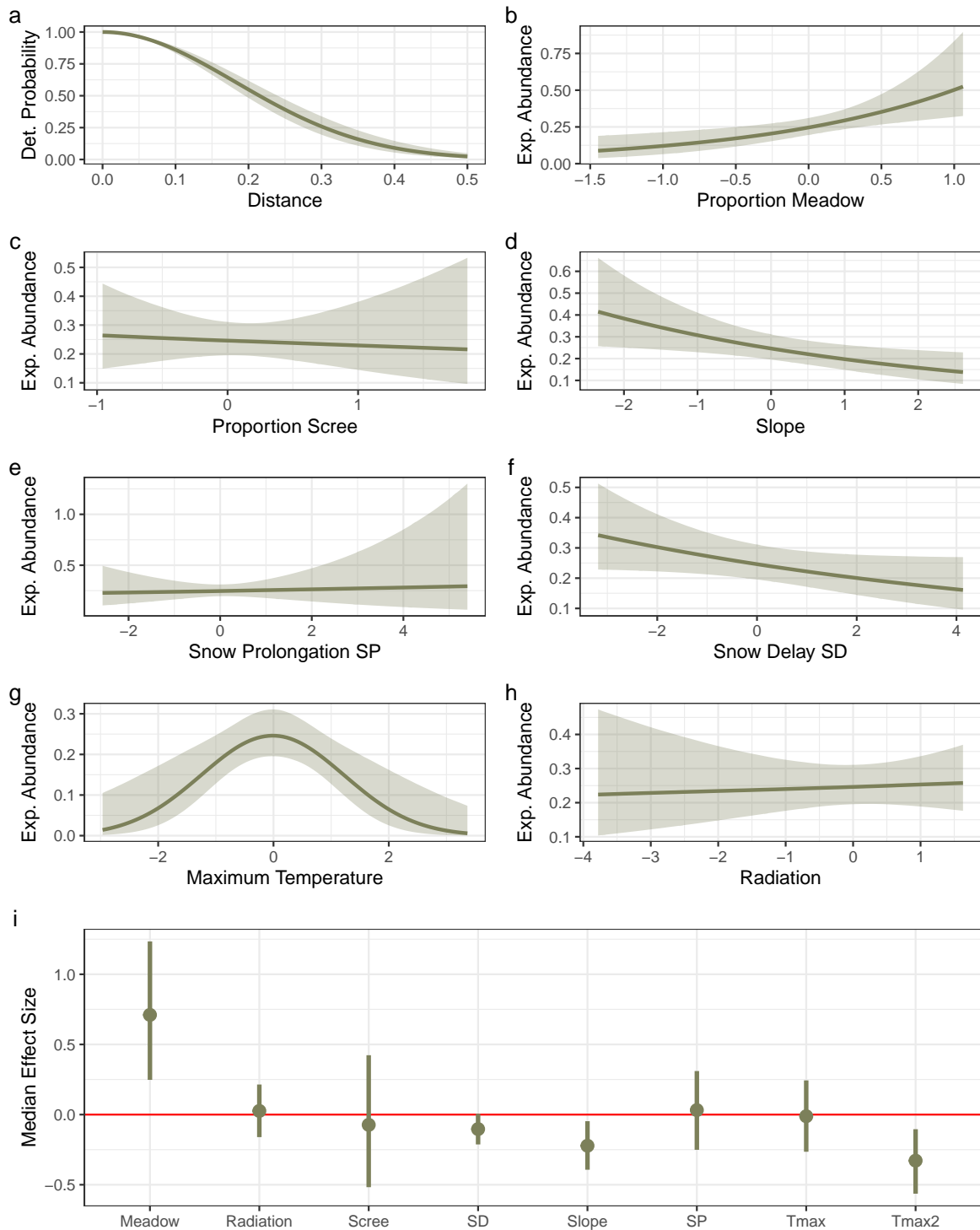


Figure 5: **a)** Half-normal detection function proposed by the model. **b-h)** Effect plots of the environmental covariates on the expected abundance per pixel. For each covariate  $x$ , the effect plot shows  $\exp(\beta_0 + \beta_x \cdot x)$ . The rest of the covariates are kept constant at their mean value (0). The dark line shows the median expected abundance surrounded by a 95% credible interval. **i)** Median of the samples of the posterior distribution for each environmental parameter with 95% credible intervals.



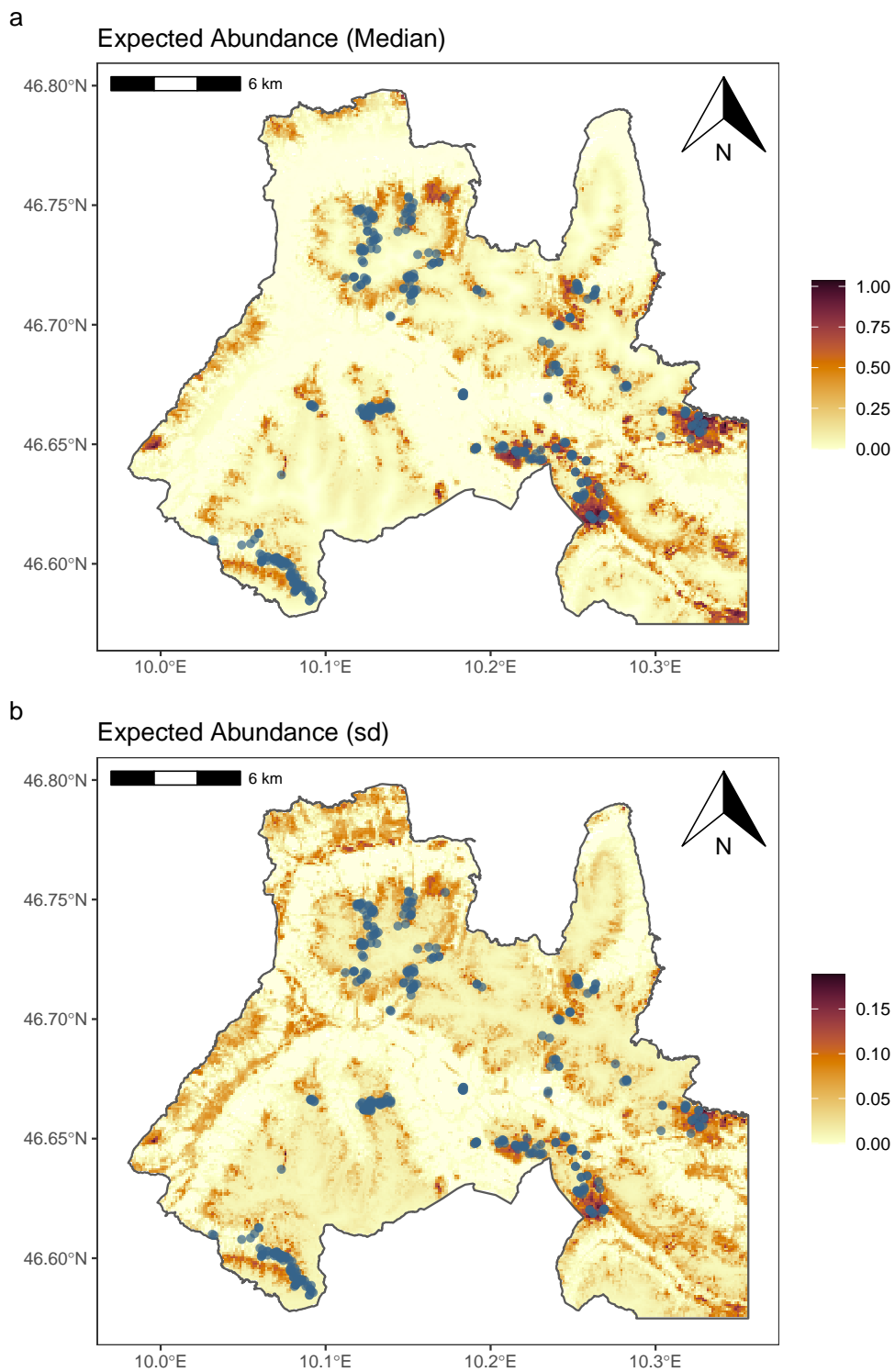


Figure 6: Extrapolation of the model predictions to the study area with recorded marmots (blue points). **a)** Median expected marmot abundance per ha. The darker a pixel, the higher the expected abundance per pixel. **b)** Standard deviation of expected marmot abundance. The darker, the higher the uncertainty.

## 4 Discussion

In this study I analysed the effect of environmental conditions on the spatial pattern of marmot abundance with a focus on snow cover conditions. In summer 2021 I collected marmot abundance data in the Swiss National Park. I developed a Bayesian hierarchical model to study environmental effects on marmot abundance while accounting for imperfect detection and time-varying availability. I tested different model in simulations to investigate its performance under several parametrizations and technical variations. Additionally, I compared the results of the hierarchical model to abundance estimates from a classical distance sampling analysis.

Model selection between different distance sampling models revealed an effect of temperature and weather on the detection probability. For warm temperatures, warmed rocks appeared in thermal camera. Marmots, especially at large distances, became harder to detect, which is represented in the faster drop of the detection function for warm temperatures. In chilly and cold temperatures, the thermal cameras did unfold their full potential. Out of the different weather conditions, detection probability was lowest for drizzle, because water in the atmosphere absorbed the thermal signals of distant marmots. However, the sample size in this category was low, which weakens the strength of this finding. In the hierarchical model, I ignored environmental effects on the form of the detection function to keep the model simple. Ignoring temperature and weather effects biases abundance estimates in some regions. But across the whole study area, distance sampling models are pooling robust [76], meaning that even though there are factors influencing detection probability, analysis of the pooled data across all factors still produce reliable abundance estimates.

Simulations showed that abundance estimates from the hierarchical model are biased low because of the spatial resolution of the environmental variables. The finer the resolution, the better the approximation of continuous space. This discrepancy might be responsible for the higher  $\sigma$  estimates from the hierarchical model compared to the one from the classical model. However, choosing a finer resolution would change the interpretation of the environmental effect. Coarse resolutions reflect how marmots choose their home range, while fine resolutions would mirror behavioural processes [54]. Nevertheless, the simulations showed that the association with the environment, the main objective of this study, is unbiased. The bias in abundance can therefore be accepted if abundance estimates are only interpreted as a lower boundary. Two ideas to reduce the bias are discussed in Appendix A.5.

In line with many studies on habitat characteristics of marmots, proportion of meadow was the strongest predictor for abundance in the hierarchical model [28–31]. Meadows provide several benefits for marmots. Dicotyledonous herbs contain essential linoleic acids, which were shown to improve survival during hibernation [34–36]. Additionally, the shallow vegetation allows vigilant marmots to spot predators earlier than in shrubs or forests. Proportion of scree had no effect on abundance, even though some colonies in the study area had their main burrows in scree fields (personal observation). This might be reflected in the large uncertainties in the effect of scree amount, as some scree fields may support large colonies while others do not. Steep slopes had a negative effect on abundance. Steep slopes occur mainly in high altitudes, which are unsuitable due to lack of vegetation, low temperature, or long snow cover. Previous studies showed that armots select intermediate slopes to prevent burrow floodings [28, 37]. However, the exact burrow locations is influenced by micro-topographical characteristics not captured by the coarse resolution of  $100 \times 100$  m. Radiation had no effect in contrast to two studies [29, 37]. Both studies do not provide biological explanations why radiation should be important. I used radiation to replace aspect because it captures sun exposure effects more realistically. However, radiation effects change considerably across the landscape and may only play a role on smaller scales than  $100 \times 100$  m. Abundance was highest for intermediate maximum temperatures. DmyetCH temperatures are interpolated between weather stations using a digital elevation model [59].

Therefore, microclimatic effects, which are known to influence marmot physiology [25], are not captured. The effect of temperature should therefore be interpreted with care, as it is mainly an effect of elevation, with which many other processes are correlated. For future applications, one might consider remote-sensed surface temperatures or microclimatic models [77].

Abundance decreased with longer snow delay (SD), as proposed by studies showing a negative effect of late autumn snow fall on survival and reproduction [25, 27, 43–46]. SD is derived from binary snow cover maps, but to describe burrow insulation snow depth would be better suited. Since SD had a small, but clear negative effect on abundance, snow depth is expected to influence abundance even more. Snow prolongation (SP) had no effect on abundance, contradicting other studies [24, 27, 48]. However, also other studies, which tested explicitly for an effect of prolonged snow cover, found no or opposite effects [44, 46]. Marmots keep their body mass constant after emergence until snow melts, rather than losing more weight [32]. This may suggest that marmots can buffer the negative effects of prolonged snow cover. Moreover, snow melt in mountains is a heterogeneous process. Directly after emerging from hibernation, marmots feed on the few snow-free patches in their territory (Domenic Godly, personal comment). Therefore, rather than averaging SP values within a  $100 \times 100$  m pixel, the minimum SP value per pixel might be more important for marmots.

I derived snow cover metrics relevant to the life cycle of marmots. The metrics could be improved by a more sophisticated interpolation algorithm. Gapfill [78] interpolates missing pixel values both spatially and temporally, but it is not straight forward to apply for binary data. Additionally, it should be checked that SD and SP indeed reflect the two processes of interest: burrow insulation and delay of vegetation greening. To dilute remote sensing artefacts from the flight pattern of the satellite, I averaged all dynamic environmental metrics over four years. But even though environmental effects may propagate over several years, the effect of the current year on marmot abundance is expected to be stronger [45].

The hierarchical model was not flexible enough to model the many pixels with zero marmot abundance. Zero-inflation is a well-known problem in quantitative ecology and a biological understanding of the source of zeros is required [79, 80]. Imperfect detection is one process inflating the number of false zeros. The detection model component of the hierarchical model assumes that each pixel was perfectly visible from the observation site. However, some pixels were hidden because topography or vegetation limited the visibility. Excluding such pixels would improve the model, but automation of this process is challenging. Zero-inflation can also arise if important environmental covariates were missed in the model. For example, marmot abundance may be influenced by geology, vegetation quality, or the presence of key plant species. Also, marmot distribution and abundance may underlie different processes. While the distribution of dominant pairs may be explained by static environmental factors, abundance of a colony with sub-adults and pups might be largely influenced by the dynamic environment. A zero-inflated Poisson model would allow to disentangle the two processes.

The model developed in this study only accounts for environmental effects on abundance. While the environment does influence abundance, so do dispersal, predation, density dependence, and spatial structure. Sub-adult alpine marmots disperse between the age of two and four [48]. Limited dispersal is one reason why some suitable pixels may not be inhabited by marmots. Predation pressure for marmots mainly originates from the golden eagle and the fox, though the latter only preys on pups. But considering the large home ranges of both predators, the mortality by predation is negligible compared to winter mortality [32]. Density dependence in alpine marmots exhibits different effect directions within and between colonies. Within a colony, larger families have higher survival during winter [25]. But the pattern between colonies is less clear. A recent study found that juvenile survival and reproduction decreased with number of families in the surrounding [81], while another study found that recruitment rate was higher for

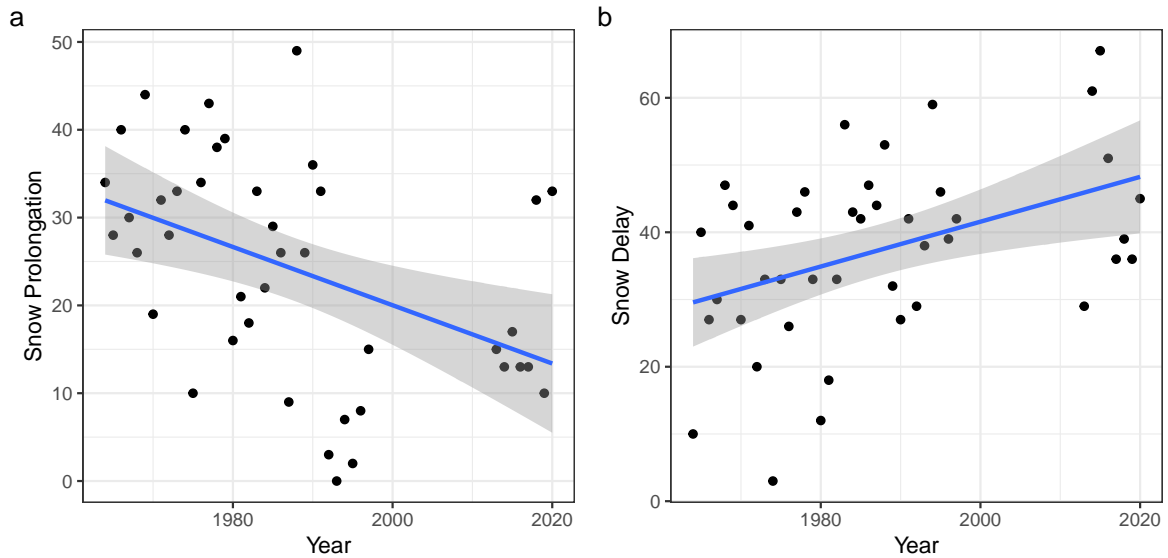


Figure 7: Change in a) Snow Prolongation and b) Snow Delay between 1964 and 2020 at the weather station Buffalo (1958 m.a.s.l.).

well-connected colonies [82].

While the environment may not explain all the variance in abundance, an environment-only model can be interpreted with respect to climate change under the assumption that other non-environmental drivers of abundance will remain constant. The weather station in Buffalo (1968 m.a.s.l.) measures snow depths since 1963 with a break from winter 1998/1999 until winter 2012/2013 (Figure 7). Average snow prolongation decreased from 32 to 13 days, while the average snow delay increased from 30 to 48 days. With high certainty, this pattern will also continue in the future. A study investigated the effects of climate change on the snow conditions in Grisons (Switzerland) under the IPCC A1B emission scenario. For the years 2070-2095, the snow season is expected to shorten by five to nine weeks compared to 2000-2010, which corresponds to an elevational shift of 400-800 m [83]. Two other studies modelling snow cover changes in Alpine catchments in Grisons suggested 900 m and 700-1000 m elevational shift respectively over the same time period [84, 85]. A study investigating snow cover changes for Switzerland found that already in near future, elevations between 1000-1700 m.a.s.l. will show the greatest reduction in snow depth [86].

Even though snow conditions may indicate an elevational shift by several hundred meters, marmots will certainly not follow this shift at the same speed. This is indicated by the strong association with meadow and slope. The upper limit of vegetation shifts by 17 to 40 m per decade [87], at a slower pace than the one for snow conditions change. Additionally, the plant species marmots rely most on may not follow the migration to higher altitudes. Altered interactions in the plant community can lead to local and even global extinctions [88, 89], making the future plant community difficult to predict. Because meadow is such a strong driver of abundance, climate-induced changes in vegetation must be considered for future climate change assessments for marmots.

My study, however, does not elucidate if and how marmots will adapt to climate change, because it does not account for buffering of changing environmental conditions. For example, marmots may buffer high summer temperatures by adjusting the daily activity pattern [32].

Snow cover effects may be buffered by altering hibernation phenology, a topic not yet studied for alpine marmots. Harsher snow conditions may be compensated for by warmer winter temperatures or higher vegetation quality. These limitations show the importance of temporal studies, which can account for many of these effects.

I demonstrated how a spatially explicit distance model can elucidate environmental effects on the spatial variation in abundance. For marmots, previous distance sampling attempts often were limited by the availability problem [90, 91]. If the model accounts for availability, distance sampling provides a cheap and effective way to census marmot populations. It neither requires expensive gear such as traps or tags nor legal approval and it can be conducted by few trained field assistants. Spatial distance sampling models can be extended to model individual based covariates, such as sex or stage [68]. A logical development is to allow abundance to vary over time. Such an approach would combine the best of two worlds: the precision of spatial models and the valuable information from long-term time series.

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## A Appendix

### A.1 Discriminating between active and inactive burrows

Marmots use three different types of burrows. The largest ones are winter burrows, consisting of a labyrinth of tunnels and cavities in which the colony hibernates. In front of the main entrance is a large ejection mound. Smaller, but often with an equally large mound are summer burrows, which are used by parts of the colony during nights. The third category are escape burrows; short tunnels between 50 cm and a few meters that are used to protect marmots from acute danger.

From distance, only summer and winter burrows are visible because of the large mound and the altered vegetation (Figure 8c). A burrow in the data always referred to a summer or a winter burrow, whereas the discrimination between the two is not possible from the distance and even challenging from up close.

Burrows remain visible beyond a local colony extinction and might later be recolonized by dispersing animals. I used several rules to decide if a burrow was occupied during summer 2021. Some hints were visible from distance, for others I had to inspect the burrow up close. I considered a burrow as active, if at least one of the following signs was seen:

- A marmot was seen near the burrow at any time during fieldwork (not only during the 10 min observation period)



Figure 8: a) Fresh faeces next to a marmot burrow. b) Den grass in front of the main burrow entrance. c) Changed vegetation structure around the marmot burrow. d) Marmot “highways” connecting burrow entrances.

- In front of the burrow lied freshly digged soil.
- The entrance tunnel was plant free (not used as the only criteria)
- Rocks in the burrow entrance were small and the soil was loose (vs. big rocks and consolidated soil). Attention: rain consolidates the soil too.
- Fresh faeces (Figure 8a).
- Den grass in front of the burrow entrance (Figure 8b).
- Vegetation in front of the entrance was squashed (not used as the only sign).
- Entrance holes were connected by traces (“highways”) in the vegetation (Figure 8d).

## A.2 Deriving and selection of environmental variables

Based on a literature review on habitat characteristic of alpine marmots, I derived environmental metrics for ground cover, topographical variables (altitude, slope, aspect), temperature, radiation, snow cover, and plant phenology metrics. Here, I describe the metrics which I did not use in the final analysis and the covariate selection process.

### A.2.1 Snow cover metrics

After interpolation of the Theia snow cover maps (Section 2.4.2), I derived 7 snow phenology metrics relevant for the winter period and 6 metrics relevant for the summer period (Table 7 and Figure 10b).

The metrics for the summer period were all correlated (Figure 9), indicating that using one metric for spring snow cover is sufficient. I selected Snow Prolongation (SP) because of two considerations. First, the metric should not be strongly influenced by few snow free days in spring, which is the case for SMD, SPC, and LSD. Furthermore, it should not count snow-covered days in autumn, as these do not affect vegetation green-up. This would be the case for all remaining metrics except for Snow Prolongation (SP).

The metric for the winter period should only account for snow-free days in early winter, since towards spring, the sun warms the burrow as soon as the ground is snow free [24]. This is not the case for WiD, SCD, and SCDW. Additionally, it should account for snow-rethaw cycles. FSD would ignore long snow-free periods, and SOD would be strongly influenced by long snow-covered periods interrupted by short snow-free periods. Snow Delay (SD) is the metric which satisfies these requirements best. Other metrics were uncorrelated with SD (e.g., SCD), however, these metrics were strongly correlated with SP (only indirectly shown via strong correlation with SCD in both plots of Figure 9).

### A.2.2 Vegetation Phenology metric

Another way to measure the delaying effect of prolonging snow is to extract start of growing season from satellite-based NDVI measurements. In seasonal environments NDVI follows a cyclic pattern over a year (Figure 10c). As snow melts and vegetation grows, NDVI increases, reaches a plateau during summer, and decreases in autumn as vegetation becomes brown. The double-logistic function in equation 4 models this behaviour [92].  $mn$  is the NDVI value during winter (minimum NDVI),  $mx$  is the NDVI during summer (maximum NDVI),  $sos$  is the first inflection point (start of season) with the corresponding slope  $s_1$ , and  $eos$  is the second inflection point (end of season) with slope  $s_2$ .

$$NDVI(t) = mn + (mx - mn) \cdot \left( \frac{1}{1 + \exp(-s_1 \cdot (t - sos))} + \frac{1}{1 + \exp(s_2 \cdot (t - eos))} - 1 \right) \quad (4)$$

In Google Earth Engine, I used the 5-day composite tiles of Sentinel-2 for the year 2018 to 2021. By masking the tiles with the quality band, I removed pixels covered by clouds and cirrus. Then, I calculated NDVI as the normalized difference between Band 8 (NIR) and Band 5 (red). For the remaining calculations, I exported the raster tiles to proceed with R.

As negative NDVI values reduce the fit of the double-logistic curve, Beck et al. (2006) proposed to reclassify them to the minimal NDVI value in absence of snow cover [92]. Since I was not able to estimate such a threshold, I set all negative NDVI values to 0. In Figure 10c), the empty circles are values that were reclassified to 0.



Table 7: Snow phenology metrics derived from the Theia Snow Collection. The top 7 metrics describe processes during hibernation, the lower 6 metrics describe processes after end of hibernation.

Metric	Full Name	Description
FSD	First Snow Day	First snow-covered day after 29.9.
SOD	Snow Onset Day	First day of the longest snow-covered period.
SD	Snow Delay	Number of snow-free days between 29.9. and SOD.
SDC	Snow Delay Cycles	Number of snow-thaw cycles between 29.9. and SOD.
WiD	Winter Duration	Duration of the longest snow-covered period.
SCD	Snow Cover Duration	Total number of snow-covered days in the year.
SCDW	Snow Cover Duration Winter	Total number of snow-covered days between 29.9. and 18.4.
SMD	Snow Melt Day	Last Day of longest snow-covered period.
LSD	Last Snow Day	Last snow-covered day of the year.
SP	Snow Prolongation	Number of snow-covered days after 18.4 and longest snow-free period.
SPC	Snow Prolongation Cycles	Number of thaw-snow cycles between 18.4. and the longest snow-free period.
SuD	Summer Duration	Duration of the longest snow-free period.
SCDS	Snow Cover Duration Summer	Snow-covered days after 18.4.

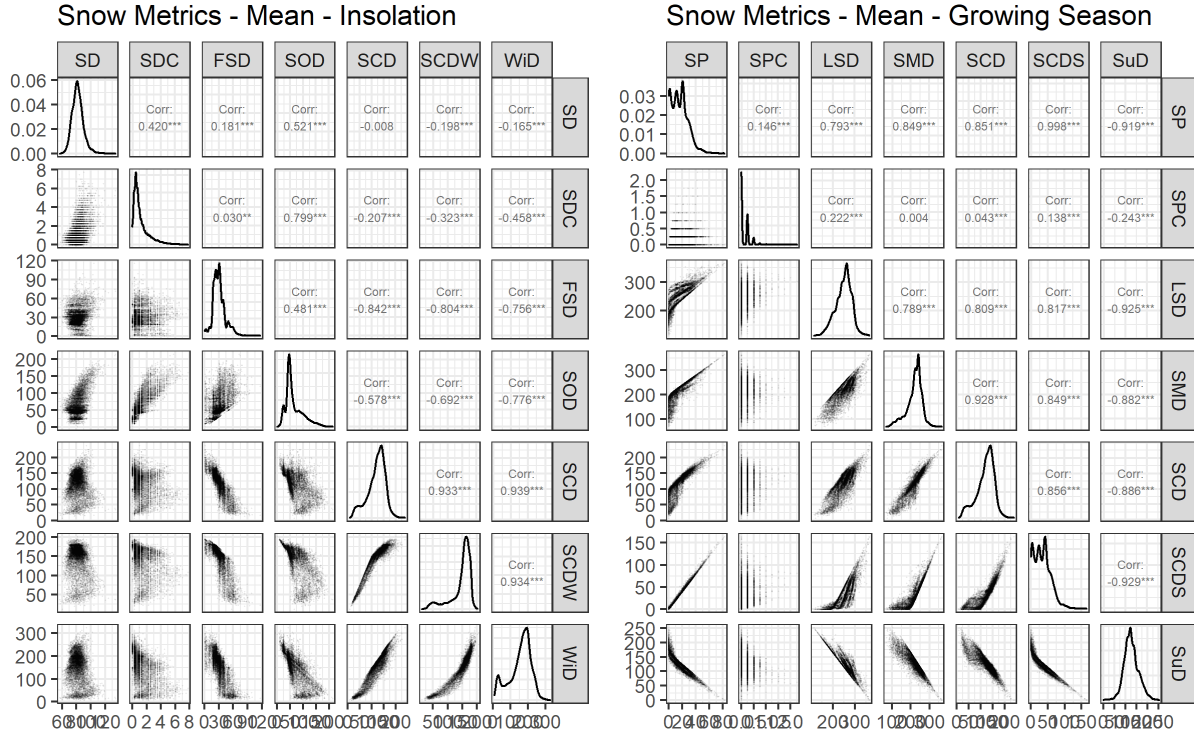


Figure 9: Correlations between the derived snow phenology metrics for the winter period (left) and the summer period (right).

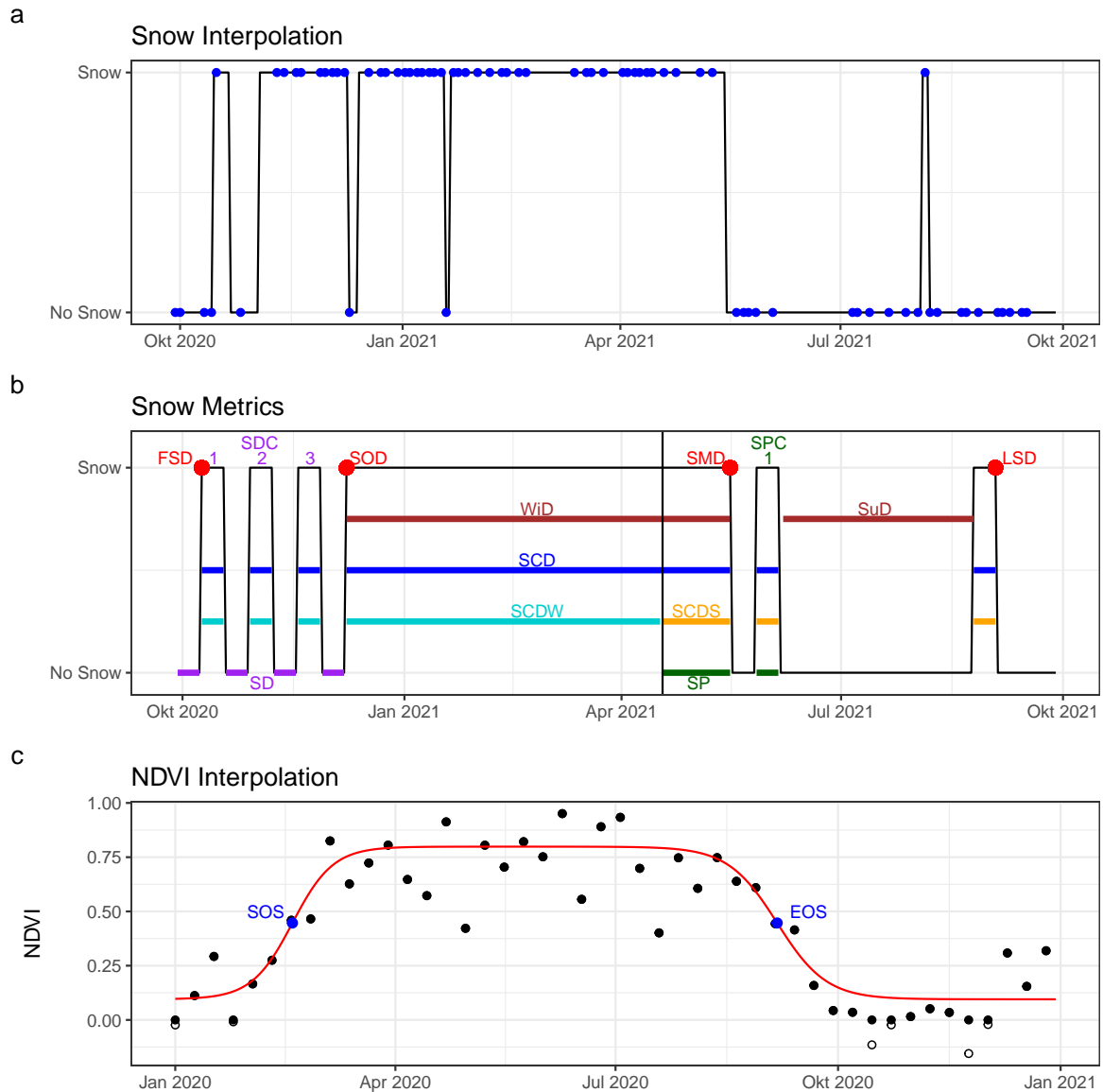


Figure 10: **a)** Nearest neighbour interpolation of the Theia Snow Collection L2B tiles for one pixel and one year. Blue points are measured snow cover conditions, the black line shows the interpolated values. **b)** Snow metrics for an artificial snow cover interpolation showing the 13 snow phenology metrics (Table 7). The black line shows the mean end of hibernation on 18.4. **c)** Artificial data showing the cyclic behaviour of the NDVI over a year. The red curve shows the fitted double-logistic curve with the two inflection points SOS and EOS.

To fit the double-logistic curve from equation 4 to the processed NDVI values I used the R package phenofit [93]. For each pixel and year, I saved the value of the inflection point *sos*. This resulted in four maps for the years 2018 to 2021 with start of season (SOS) in Julian days. I then averaged SOS across the four years.

### A.2.3 Variable selection

SOS describes the same process as SP, and indeed the two metrics were correlated ( $r = 0.63$ ,  $p < 0.001$ ). However, SOS is only valid for habitats with a certain amount of green vegetation. If,

because of low vegetation cover, the maximum NDVI ( $mx$ ) is low, uncertainty in SOS increases. I therefore believe that SP describes the process of vegetation delay better, because it is also informative for marmot populations living in habitats dominated by scree fields.

Median maximum summer temperature was very strongly correlated with altitude ( $r = -0.99$ ,  $p < 0.001$ ), as the temperature was interpolated using a DTM. Since I was more interested in the mechanistical relationships, I excluded altitude as a covariate, aware of the strong influence of altitude on the metric.

Both radiation and aspect describe the process sun exposure. Since aspect is a circular variable, it has to be transformed to the continuous scale to be included in a model. Cosine of aspect would describe the “northernness” of the pixel, sine of aspect the “easterness”. For sun exposure, northernness is the more important variable and indeed, the cosine of aspect was correlated with radiation ( $r = -0.5817$ ,  $p < 0.001$ ). However, aspect contains way less information on sun exposure than radiation. As some south exposed slopes may barely get sun because of the topography. Therefore, I used radiation instead of aspect, because it describes the process of interest more directly.

Because of these considerations, the remaining environmental covariates for the spatially explicit model were ground cover (proportion of meadow, scree, and unavailable), slope, snow prolongation, snow delay, radiation, and median maximum summer temperature.

#### A.2.4 Qualitative validation of phenology metrics

I compared the snow and plant phenology metrics qualitatively with two other data sources: snow water equivalent (SWE) maps, and soil temperatures from the national park.

DaymetCH [59] provides daily interpolated maps of SWE. SWE describes the amount of liquid water stored within the snowpack. It uses empirical relationships between temperature and precipitation to determine if precipitation falls as snow and to model snow melt rates [94]. I defined  $SWE > 0$  as snow covered and  $SWE = 0$  as snow free. I compared the Theia interpolation and SWE time series for 25 random points in the study area of 5 habitat types (forest, scree, rock, water, meadow). Two plots for points on alpine meadows are shown in Figure 11d) and e). Often, the snow fall for SWE was later than the snow fall for Theia. It is expected that the empirical association for snow fall predicts the snow fall better than the linearly interpolated Theia data. However, for snow thaw, SWE often overestimated the thaw date drastically, even though several satellite images without snow were recorded. This shows the limitation of the empirical snow melt rules to model small scaled topographical effects influencing snow melt. Additionally, SWE does not show small snow spikes or short snow free cycles. However, it remains unclear if these spikes and dips are not only artefacts because of how Theia determines if a pixel is snow covered.

I compared the Theia interpolation with soil temperature data from the park during winter 2020/21 (unpublished data, TMS-4 Standard loggers). The temperature at -6 cm is always around  $0^{\circ}\text{C}$  if covered by snow. Because the creeping snowpack destroyed many loggers, only two were available in open terrain. In Figure 11a), Theia predicted the snow fall in November too early. In the snow free period after the first snow fall, the temperature decreases below  $0^{\circ}\text{C}$  as the insulating snow is missing. Snow thaw is quite adequately predicted by the Theia interpolation. In Figure 11b), the first snow peak aligns precisely with the dip in temperature. However, the snow melt during the long period without satellite data is predicted half a month too early. If interpreting these plots, one should consider that the temperature at  $-6$  cm shows the snow cover status and not temperatures within a hibernaculum (compare to Appendix D in Tafani et al. (2013) [43]).

I compared the correlation between SOS and time of full bloom for four plant species. For the years 2018 to 2021 I plotted the day of full bloom against the corresponding SOS value. The full bloom was almost always after SOS, because flowers bloom after the main vegetative burst. Additionally, years and locations within one plant species with later full bloom also had a higher SOS, indicating that SOS indeed captures delays in vegetation phenology.

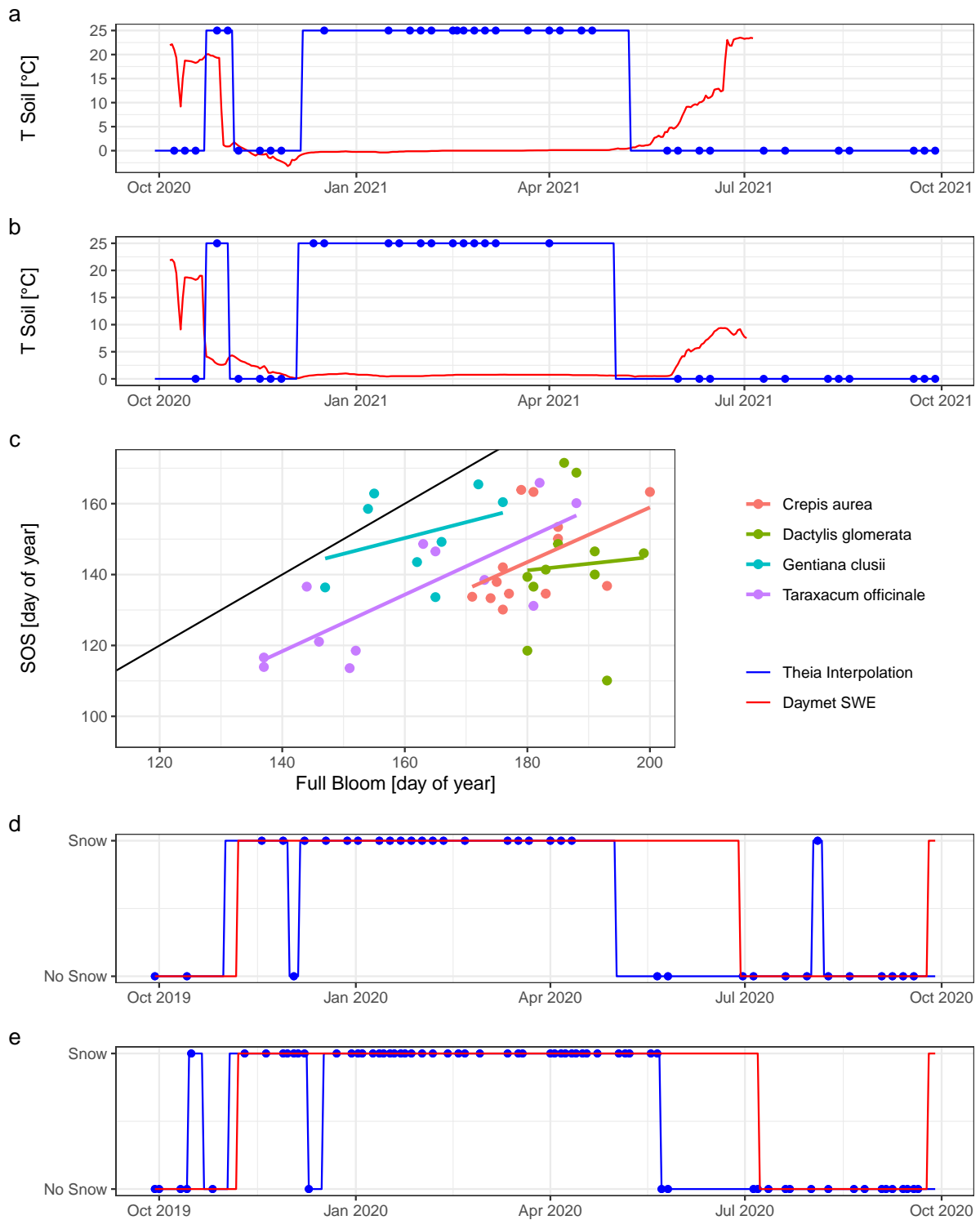


Figure 11: **a, b**) Theia snow cover interpolation (blue) plotted against two soil temperature measurements on alpine meadows in the Swiss National Park (red). **c**) Correlation between the NDVI derived start of season SOS and plant phenology data of the Swiss National Park. **d, e**) Theia snow cover interpolation (blue) plotted against snow water equivalent (SWE) metrics from DaymetCH interpolations for two random points on alpine meadows.

### A.3 Goodness of Fit assessment and residual checks of hierarchical model

Based on the fitted model parameters, one would expect to observe the following number of marmots on a pixel  $g$ :

$$L.\text{exp}_g = \lambda_g \cdot p_g \cdot q_g$$

With  $e = 0.0001$  to avoid dividing by zero, the Pearson residual for pixel  $g$  between observed marmots  $L_g$  and expected marmots is then

$$r_g = \frac{(L_g - L.\text{exp}_g)}{\sqrt{L.\text{exp}_g + e}}$$

Considering the estimated parameters, a realisation of observed marmots on pixel  $g$  is

$$\begin{aligned} N.\text{new}_g &\sim \mathcal{P}(\lambda_g) \\ L.\text{new}_g &\sim \mathcal{B}(N.\text{new}_g, q_g \cdot p_g) \end{aligned}$$

The two fit statistics for observed and expected (simulated) number of marmots based on the Pearson residuals are

$$\begin{aligned} T.\text{exp} &= \sum_g \frac{(L.\text{new}_g - L.\text{exp}_g)^2}{L.\text{exp}_g + e} \\ T.\text{obs} &= \sum_g \frac{(L_g - L.\text{exp}_g)^2}{L.\text{exp}_g + e} \end{aligned}$$

For Freeman-Tukey residuals, the two test statistics are

$$\begin{aligned} D.\text{exp} &= \sum_g \left( \sqrt{L.\text{new}_g} - \sqrt{L.\text{exp}_g} \right)^2 \\ D.\text{obs} &= \sum_g \left( \sqrt{L_g} - \sqrt{L.\text{exp}_g} \right)^2 \end{aligned}$$

The Bayesian p-value is then the posterior probability  $\mathbb{P}(T.\text{obs} > T.\text{exp})$  for the Pearson fit statistic and  $\mathbb{P}[D.\text{obs} > D.\text{exp}]$  for the Freeman-Tukey fit statistic respectively.

The residuals are not uniformly distributed around zero (Figure 12a,b). Most residuals are below zero. These residuals stand for pixels, in which no marmots were observed, but where the model would have expected some to be observed. Above zero are residuals for pixels on which more marmots were seen than expected by the model. Neither the spatial arrangement (Figure 12c) nor the expected abundance (Figure 12d) explain patterns in the residuals.

The Bayesian p-value is one for both the Pearson and the Freeman-Tukey fit statistic (Figure 12e,f). The point cloud does not intersect the diagonal line, which would indicate that the observed and expected fit statistics are equal.

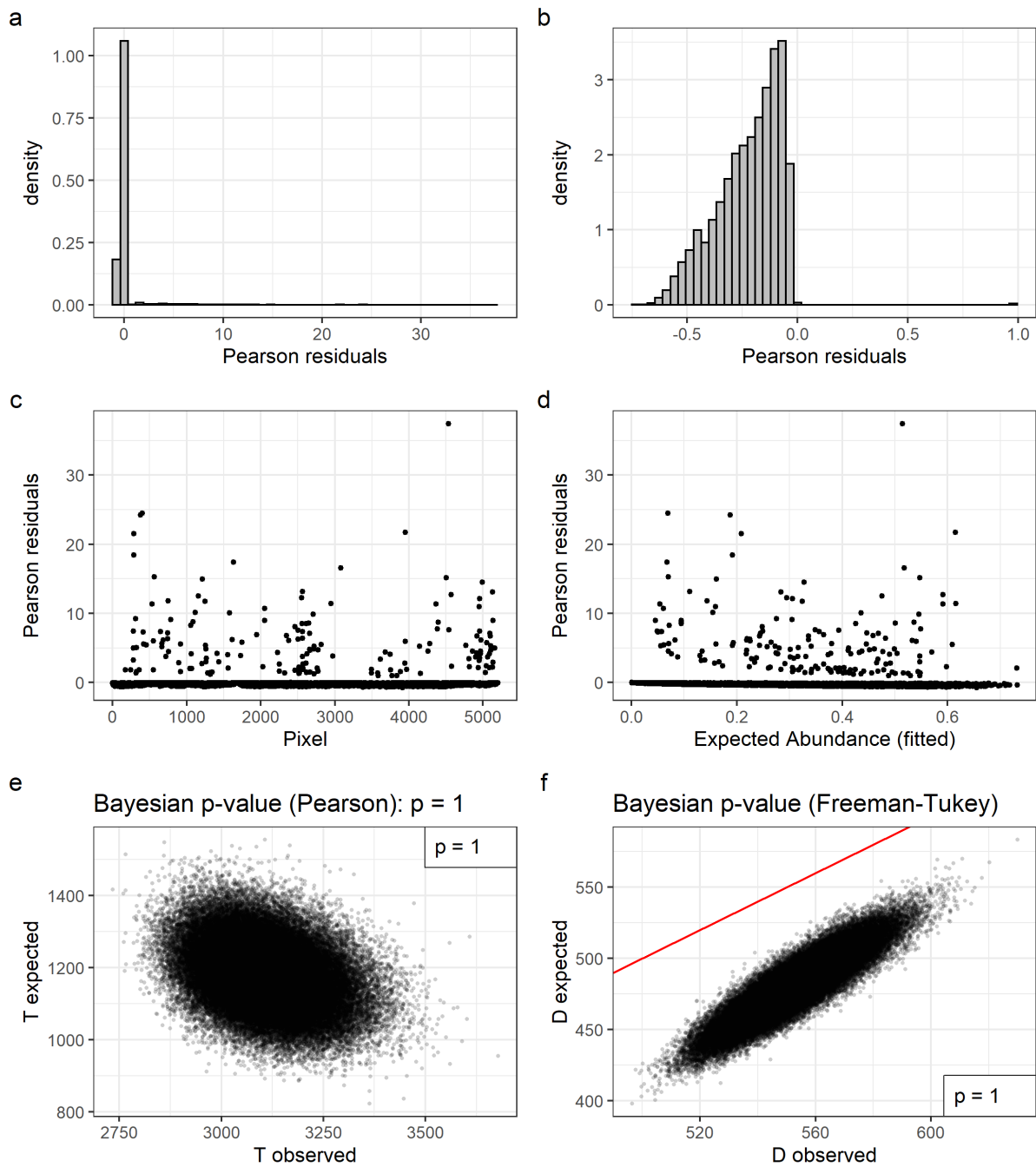


Figure 12: **a)** Distribution of the Pearson residuals between observed and expected number of marmot. **b)** Distribution of the Pearson residuals lower than 1, by which the pattern for the negative residuals is better visible. **c)** Pearson residuals against pixel index. **d)** Expected abundance against Pearson residuals. **e)** Posterior distribution of  $T_{\text{obs}}$  against posterior distribution of  $T_{\text{exp}}$ . **f)** Posterior distribution of  $D_{\text{obs}}$  against posterior distribution of  $D_{\text{exp}}$ . The red line is where the expected equals the observed fit statistic.

## A.4 Discussion of Distance Sampling Assumptions

In distance sampling literature, four assumptions are discussed [52]. 1) Animals are independently distributed of the observation sites and do not respond to the observer, 2) detection probability at distance zero is one, 3) distance measurements are exact, and 4) detections are independent.

If animals are not independently distributed from the observation site, several issues may arise. In ordinary distance sampling, extrapolation of abundance to the rest of the study area is not valid. For spatial approaches, this effect problem is solved by model-based abundance estimates. In this study, observation sites were placed on hiking paths. Marmots may show responsive movement to tourists and the observer, which skews distance measurements. However, marmots living near hiking paths are habituated to humans, which reduces their fleeing distance [95]. To reduce bias in the distance measurements, I avoided times with many tourists, approached observation sites calmly and recorded fleeing animals if they would have been spotted from the next observation site. A design independent from hiking paths would have not been possible, as researchers leaving trails in the Swiss National Park must minimize disturbance of ungulates. A study with many observation sites as this would have caused inadmissible disturbance.

Distance sampling requires perfect detection at distance zero. For marmots, two processes may violate this assumption. The first is responsive movement, which is discussed in the previous paragraph. The second are marmots in burrows, which are not available for detection. Ignoring this effect would bias abundance estimates low and if availability is correlated with environmental variables, bias inference about environmental effects. I estimated availability probabilities and uncertainties from availability data from a marmot colony on Alp Grimmel. Doing so assumes that the behaviour expressed on Alp Grimmel is representative for other populations as well. The dip in activity around noon was mainly due to disturbance by tourists and hot temperatures. It is expected that other censused colonies show similar activity patterns due to tourists, as they were censused next to hiking paths. However, activity dips are not as pronounced on cold days [32]. In this respect, the availability model component is too simplistic, but the data from Alp Grimmel does not allow to account for weather and temperature effects. Availability of marmots also changes across the year, with little activity at the beginning and end of season (Peter Lattmann, unpublished data). However, availability over the year is not correlated with environmental effects and therefore do not bias the habitat parameters.

In distance sampling, rounding of angles or distances may lead to biased detection probabilities. Since I recorded marmot locations in a mobile GIS application, rounding of distances is not an issue. Even though the recorded locations were never correct, the error was equal in all direction, which does not affect the form of the detection function.

Finally, distance sampling requires independent detections. In the hierarchical model, marmot observations are aggregated per pixel, ignoring the exact spatial locations of the marmots. Therefore, independence is not an issue. In ordinary distance sampling, violation of independence (overdispersion) has little effects on abundance estimates, but AIC tends to select overly complex distance functions. I analysed marmots as the spatial groups they were recorded in, which reduced the issue of overdispersion considerably, but not fully. Therefore, I selected the less complex model out of the two competing models based on AIC.



## A.5 Accounting for abundance bias in the hierarchical distance sampling model

Simulations indicated that abundance estimates are biased because the pixel resolution of  $100 \times 100$  m is too coarse to approximate continuous space. Here I present two ideas on how to account for this bias.

In this study, I used the spatial distance sampling model based on pixels frequencies [68]. Kéry and Royle also present a model using data augmentation. In short, for each observation site  $s$  a fixed number of marmots are distributed across the adjacent pixels. A model, where the location of a marmot  $i$  was uniformly distributed within a pixel did not exhibit the bias in  $\sigma$  and abundance  $N$ . However, the model run too slow and mixed poorly, why the model was not useful for the analysis data.

Using the presented model on pixel frequencies, one could model individual distances for each individual from  $M_g$ . However, in combination with the Poisson model, the parameter space would not be closed anymore. Therefore, one should consider letting  $N_g$  follow a binomial distribution.  $n$ , the maximum number of marmots per pixel, should be chosen large enough. The probability in the binomial distribution would be defined as  $\phi_g = \lambda_g/n$ . This is also a form of data augmentation, but in contrast to the model discussed in the previous paragraph, at the pixel level rather than at the level of the observation site. The advantage is that to calculate  $\phi_g$ , the model would not have to consider all pixels belonging to the same observation site. However, the model behaviour should be tested in simulations, as mixing or run time issues may arise.

## Statement of Authorship

I declare that I have used no other sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicated as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Place, Date

Signature

# Influence of snow cover on the spatial variation in abundance of alpine marmots in the Swiss National Park



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## Background

Snow cover is an important environmental variable in the life of alpine marmots.

- A thick snowpack in winter ensures **insulation of the burrow** during hibernation.
- Snow cover in spring **delays vegetation growth**, leaving less time for marmots to fill their fat storages.

Under climate change, winters will become drastically shorter. Studying the effect of snow on marmot abundance will give insights into how marmots may respond to climate change.



## Question

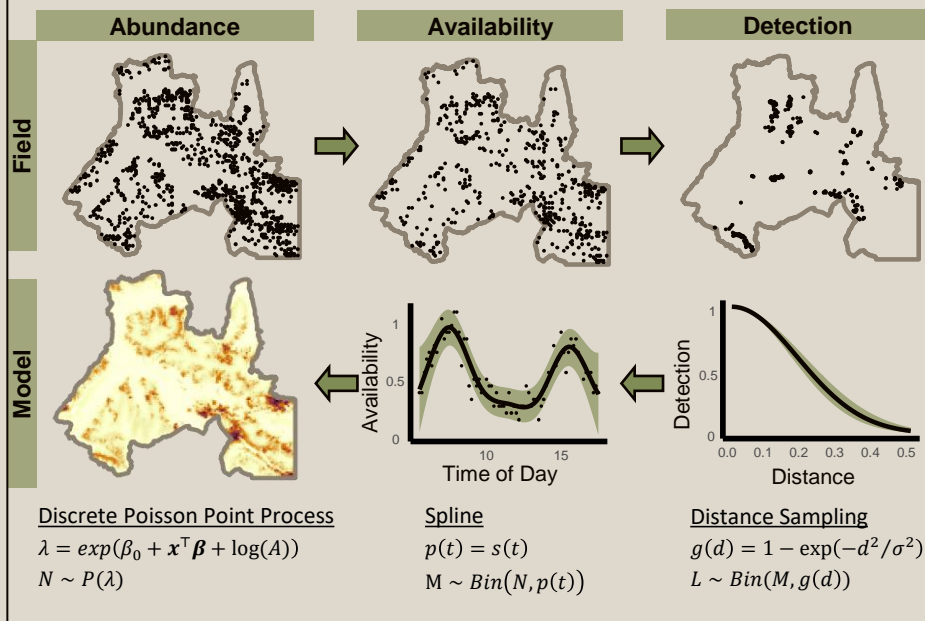
- How does **delayed snowfall (SD) in winter** affect the spatial pattern in marmot abundance?
- How does **snow prolongation (SP) in spring** affect the spatial pattern in marmot abundance?
- How do other environmental variables influence the spatial pattern in abundance? (ground cover, temperature, topography)

## Methods

Counting marmots provides special challenges:

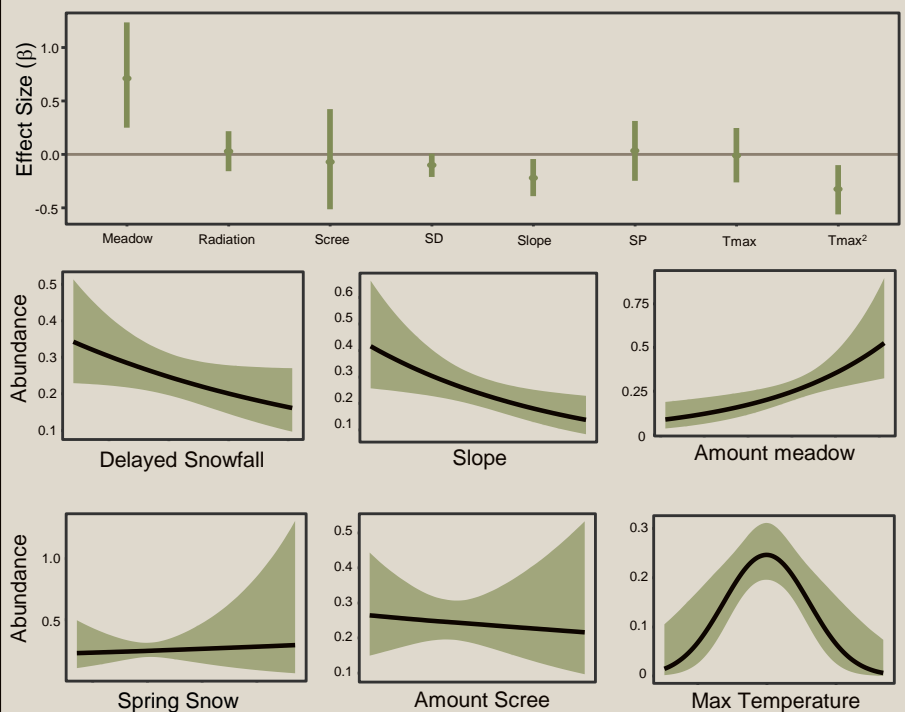
- **Availability:** From all marmots present in the study area (abundance), only a part is outside of the burrow.
- **Detection:** From the available marmots, some will be missed.

While modelling abundance with respect to the environment, one must correct marmot counts for time-varying availability and incomplete detection.



## Results

- Marmot abundance per ha was mainly explained by the amount of meadow, slope, and max. summer temperature.
- Snow delay had a small but clear negative effect.
- Snow prolongation and radiation had no effect on abundance.



## Conclusion

- The negative effect of delayed snowfall on abundance highlights the importance of burrow insulation.
- Prolonging snow in spring had no effect on the spatial pattern of abundance, indicating that delayed vegetation green-up is of little importance or can be buffered by marmots.
- Under climate change, snow cover will close later and melt earlier. For marmots, snow conditions in higher altitudes will become more suitable.
- However, the strong association with meadow and slope questions the ability of marmots to follow this rapid change in snow conditions.

