Combined effects of topography, soil moisture and snow cover regimes on growth responses of grasslands in a low mountain range (Vosges, France)

Pierre-Alexis Herrault[1], Albin Ullmann[2], and Damien Ertlen[1]

[1]UMR LIVE 6554 CNRS; University of Strasbourg; 3, rue de l'Argonne 67000 Strasbourg
[2]UMR BIOGEOSCIENCE 6282 CNRS; University of Bourgogne; 6 bd Gabriel 21000 Dijon

Correspondence: Pierre-Alexis Herrault (pierre-alexis.herrault@live-cnrs.unistra.fr)

Abstract. Growth responses of low mountain grasslands to climate warming are poorly understood despite very large surfaces covered in Central Europe. They are characterized by still present agricultural exploitation and complex topographical features that limit species migration and increase differences in snow regimes. This study examined MODIS surface reflectances between 2000 and 2020 across the Vosges mountain grasslands to investigate trends and drivers of spatial patterns in annual maximum NDVI (Normalized Difference Vegetation Index). We found a majority of grasslands indicating no significant trends which possibly reveal several environmental and ecological compensatory effects to warming in the Vosges Mountains. We also noted hotspots of browning grasslands (a decrease of annual maximum NDVI), largely overrepresented compared to the greening ones (an increase of annual maximum of NDVI), a pattern in contradiction with most productivity signals highlighted in European high mountain grasslands. Spatial patterns of browning are enhanced on north-facing slopes and at low elevations (<1100m) where high producing grasslands with dominant herbaceous communities prevail. A low soil water recharge also appears pivotal to explain the probability of browning in the study site. Through the use of Winter Habitat Indices, we noted high responsiveness of low mountain grasslands to differences in intra seasonal snow regimes, partly modulated by topographic features. Prolonged and time-continuous snow cover promote higher productivity and shortened green-up period. High number of frost events result in lower productivity and prolonged green-up period. We hypothesize that observed growth responses in the Vosges Mountains are indicative of long term future responses to climate warming in high mountain ranges. With shorter and more discontinuous snow cover, we expect higher diversity of growth responses in European low mountain grasslands due to strong contextual effects and high terrain complexity.

1 Introduction

Climate warming is impacting the biodiversity and the functioning of mountain grasslands. They experienced warmer summers and longer snow-free periods over the last decades (Beniston, 2012; Zeeman et al., 2017; Möhl et al., 2022). The effects on

plant communities may be influenced by complex topographical characteristics (i.e. altitude, slope, and exposure; (Hua et al., 2022; Choler, 2015; Graae et al., 2018)). Moreover, agricultural practices such as mowing, grazing or fertilizing contribute to conditioning the species composition or modifying their physiology (Gillet et al., 2016)which potentially leads to a large
25   diversity of plastic responses at the community level (Bektaş et al., 2021). Thus, the effects of CC combined to agricultural abandonment in temperate mountain ranges, are multiple, such as higher plant productivity (Choler et al., 2021), longer growing seasons (Pepin et al., 2022; Möhl et al., 2022) or migration of plant species to higher altitudes (Lenoir et al., 2008; Scherrer and Koerner, 2010) with possible time lags in the responses (Alexander et al., 2018; Bektaş et al., 2021). In Europe, most of these studies are concentrated in the Alps and focused on alpine grasslands above tree line (nival, alpine, or high montane).
30   In contrast, very few studies are focused on low mountain range which cover vast areas in Europe and around the world and which present specificities regarding topography, biodiversity and snow regime.

These specificities can favor a large diversity of plastic responses in plant communities and present three main advantages for understanding mountain ecosystem's responses to CC:

1. Because of lower altitudes and shorter distances to farms, low mountain grasslands are strongly dependent on traditional
35   disturbance regimes such as mowing or grazing. Two opposite drivers tend to affect grassland vegetation, notably plant diversity (Butler et al., 2009). Abandonment of management in less productive sites can promote taller species shading and out-competing smaller species (Stevens et al., 2015). The intensification of practices (defoliation and fertilization) in the most productive sites can favor the species adapted to high levels of disturbance with fast-growing and competitive characteristics (Plantureux et al., 2005). A recent resampling study of semi-natural grasslands (2005-2019) above 600m
40   conducted in the Vosges and Jura mountains showed contrasted results between the two mountain range even if both are traditional low mountain regions devoted to dairy farming (Nicod and Gillet, 2021). In the Vosges Mountains, plant communities were not different in 2005 and 2019, contrary to the situation in the Jura Mountains mainly due to the intensification of agriculture in the recent years.

2. Species present in low mountain grasslands are limited in their ability to adjust to changing climatic conditions (**?**Keppel
45   and Wardell-Johnson, 2012). They are restricted to small isolated peaks that greatly limit their dispersion and/or thus their maintenance (Sauer et al., 2011; Keppel et al., 2017). Low mountain ranges can act as a "summit trap" for living species, while high mountain species have larger surfaces for migration (Sauer et al., 2011). Specific responses to warming are also likely to differ depending on plant traits, whether structural (i.e. Specific Leaf Area) or related to functional and reproductive strategies (Bucher et al., 2018; Siebenkäs et al., 2015).

50   For example, graminoids and forbs are likely to give different responses as they differ in functional and reproductive strategies

3. The temporal variability of the snow cover in low mountain environments (Schönbein and Schneider, 2003) and its decrease (Dong and Menzel, 2020) could strongly influence the growth cycle of plant species. In particular, earlier snow melt in spring (Choler, 2015; Cassou and Cattiaux, 2016),thus promoting earlier growth in the year, particularly exposes

55 plant communities to episodes of frost or abrupt temperature changes which in turn affects the productive capacity of certain species or phenology.

Among plastic responses, phenology has been widely studied and notably refers to the timing and duration of events in species plant growth. It can allow acclimation of plant communities, mainly for their essential functions such as productivity while remote sensing time-series (MODIS, Landsat) were widely considered for monitoring these parameters over large scales

60 (Carlson et al., 2017; Piao et al., 2006). The productivity of mountain grasslands is frequently monitored using the maximum NDVI (Normalized Difference Vegetation Index) as it captures the peak of greenness (the maximum of photosynthetic activity) during the growing season, providing a valuable metric for comparing productivity across different sites and years. In contrast, the green-up period may be characterized using the time to reach the peak of greeness (number of days between the Start of Season and the day of Peak) or the time-integrated NDVI during this stage (Tomaszewska et al., 2020). Thus, indicators

65 that capture the length of phenophases helps to better understand how plant communities adapt to environmental factors in term of growth strategies. For temperate mountain grasslands, recent works showed predominant increasing NDVImax trends (Greening) partly driven by topographical complexity such as altitude and exposure (Choler et al., 2021; Filippa et al., 2022). Browning trends (decreasing NDVI max trends) were also highlighted at lower altitudes but to a lesser extent(Gartzia et al., 2016) and few studies focused on the analysis of drivers that can explain spatial variability of the recorded signal at the

70 mountain range scale (Choler et al., 2021). Regarding plant growth strategies, recent finding showed that climate warming lead to earlier phenology (Winkler et al., 2019) and faster plant growth (Wang et al., 2020) but responses can differ according to the communities because of different functional and reproductive strategies (Bektaş et al., 2021).

Furthermore, complex interaction effects between snow and terrain complexity on vegetation expansion or growth were underlined in cold-related habitats such as shrubs and grasslands (Ropars and Boudreau, 2012; Tape et al., 2012; Choler et al.,

75 2021; Tomaszewska et al., 2020; Choler, 2015). Topographic complexity is a key determinant since it increases microclimatic heterogeneity according to climatic patchiness (or fragmentation) and the range of climatic conditions available (Graae et al., 2018). One challenge then consists of characterizing snow cover dynamics in complex topographic environments since climate warming is also often related to lower snow cover protection and more frequent exposure to freezing events resulting from early snowmelt, potentially limiting some species (Choler, 2015). Over the past decade, several studies combined MODIS

80 NDSI (Normalized Difference Snow Index) time series and climate data for providing functional measures of snow conditions, adapted to cold related species (Gudex-Cross et al., 2021; Zhu et al., 2017; Dietz et al., 2012) In particular, Winter Habitat Indices (WHIs) are composite indices measuring snow cover duration, the exposure to freezing which qualifies how plants lack thermal refugia (i.e., the subnivium) and identifies snow to rain dominated systems through monitoring snow cover variability. Low mountain ranges being affected by high intraseasonal snow cover variability or earlier snow melt, the latter variables

85 could be of high interest to understand snow phenology effects on growth response of mountain grasslands (Dong and Menzel, 2020).

In this study, MODIS time series (MOD09Q1) from 2000 to 2020 are used to assess the spatial variability of decennial productivity trends of mountain grasslands in a low mountain range. Then, statistical analysis is performed to understand the influence of climatic and topographic variables on the derived spatial patterns of productivity. Lastly, the influence of snow

cover dynamics on growth response of mountain grasslands was investigated through the use of Winter Habitat Indices and phenometrics. We sought to answer the following questions: (1) Do low mountain grasslands majorly express higher plant productivity in response to warming over time such as already demonstrated for high mountain grasslands? (2) Can the derived spatial patterns of productivity at the mountain range scale be explained by a combination of topoclimatic drivers? (3) How do contextual effects in snow cover regimes affect the growth response of grassland communities ?

2 Material and Methods

2.1 Study area

The Vosges mountains, located in the northeast of France, are low mountains range with altitudes varying from 200 to 1425 m a.s.l. (Figure 1). Due to the orientation of its primary drainage divide, which runs NNE-SSW, and depressions from the Atlantic Ocean, the region experiences a Foehn effect resulting in a climate that ranges from oceanic to (almost) semi-continental. This is evidenced by the significant rainfall gradient from west to east, with the main ridge of the Hautes Vosges receiving over 2300 mm/yr compared to the Upper Rhine Graben, which receives only 550 mm/yr in Colmar located directly 20 km to the east. Winters are typically cold while summers are mild (mean annual temperature = 11°c).

Our study area is located directly in the Hautes Vosges and is centered around the main central ridge extending from the Tanet site in the north to the Ballon d'Alsace in the south, representing around 3,500 hectares of high altitude mountain grasslands locally known as the Hautes Chaumes. They are inherited from ancestral grazing dating from at least the Middle Ages (Goepp, 2007) and are currently operated by around a hundred agricultural farms, mainly dairy cattle farms producing Munster cheese. They are largely colonized by forests on both sides (Lorraine to the east and Alsace to the west but pastures and hay meadows are still present on the summits. After agricultural abandonment (1980s), numerous landscape and pastoral reopening initiatives were implemented through the actions of the Regional Natural Park and the farmers'union. Finally, these grasslands are part of the Natura 2000 European network and exhibit a high species diversity (Ferrez, 2017). They are composed of both herbaceous vegetation (graminoids and forbs) such as *Nardus Stricta L, Meum Athamanticum Jacq,Festuca rubra* and *Festuca ovina L* and shrubs where three species of vaccinum are present, (*vaccinum myrtillus L, vaccinum uliginosum L,* and *vaccinum vitis-idaea*), as well as *Calluna vulagris L.* Their soils range from acidic brown soils to ochre podzolic soils, passing through humiferous ochre-brown soils (Goepp, 2007).

2.2 Selection of pixels

Several spatial databases were used to delimit study sites in the Vosges Mountains. The first source was the database of the Regional Natural Park, which identifies protected sites such as NATURA 2000 or Natural Reserve including natural classes such as forests and grasslands. We selected sites with elevations above 900 meters ASL in the Hautes Vosges regions which corresponds to the altitude where first mountain grasslands are above tree line. They were merged to form the study area for this paper. To make the study easier to interpret at a finer scale, we divided it into ten sites from North to South such as Le
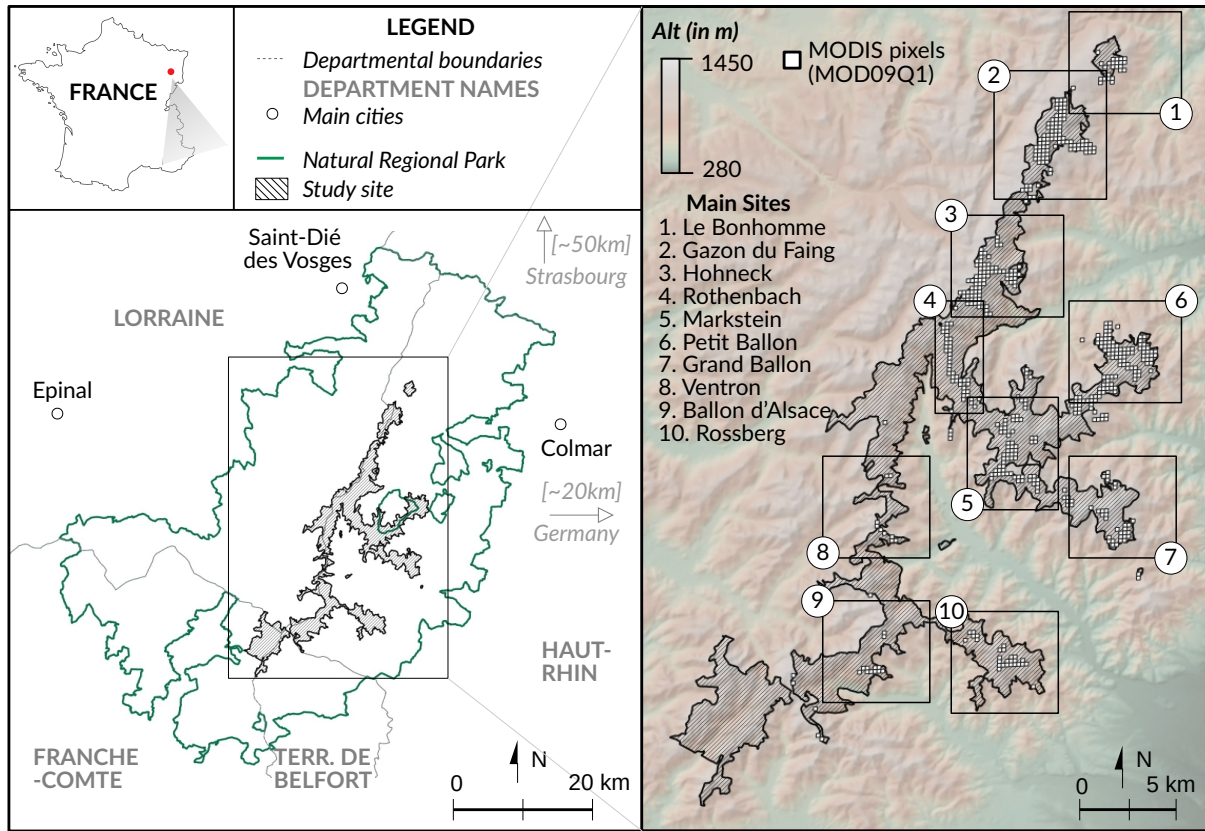
Figure 1. (Left) Location map of the study area; (Right) Distribution of the MODIS pixels selected across the ten sites in the Vosges mountains

Bonhomme, Gazon du Faing, Hohneck,Petit Ballon, Rothenbach, Markstein, Grand Ballon, Ventron, Rossberg and Ballon d'Alsace (Figure 1). Our second source was the CIGAL Land Cover database, which was produced by the Region Grand Est and includes 54 land cover classes at the level 4 (CIGAL – Product Description) based on the manula digitization of high resolution satellite images. We selected the "Mountain Grasslands" class and updated it with Very High-Resolution aerial images from 2020. We used a 1m resolution Digital Elevation Model (DEM) from the French National Mapping Institute (RGE IGN) to extract mountain grasslands located above 900 meters ASL. This spatial coverage was then intersected with the MODIS grid corresponding to MOD09Q1 product (250m spatial resolution, see section 2.3) to select candidate pixels. To ensure that each pixel was above the tree line, we removed pixels from the analysis pixels containing more than 10% of trees. In total, we selected 536 pixels for further analysis.

2.3 MODIS-derived metrics

We used the MOD09A1 and MOD09Q1 (version 6) surface reflectance products corresponding to the tile h18.v4 that were downloaded from the Land Processed Distributed Active Archive Center (LP DAAC) using the MODIStsp R package between 1st October 2000 and 31st December 2020. Surface reflectance in the red (RED), green (GREEN), near infrared (NIR), and mid infrared (MIR) were used to calculate a Normalized Difference Vegetation Index (NDVI= (NIR-RED)/(NIR+RED)) at a resolution of 250m (NDVI) and a Normalized Difference Snow Index (NDSI= (GREEN-MIR)/(GREEN+MIR)) at a resolution of 500m (Salomonson and Appel, 2004).

Missing or low-quality data were identified by examining quality insurance information contained in MOD09Q1 products and interpolated using cubic smoothing spline. Similarly to Choler (2016), NDVI and NDSI values that were two times larger or smaller than the average of the two preceding's and following values were considered as outliers and excluded. Time series were gap filled using cubic spline interpolation with a moving window of length = 2.

For each pixel, two phenological metrics providing indications of mountain grassland conditions during the growth season (approximately between April and September in the study site) were calculated:

1. The Peak of Value (PkV) is the maximum NDVI (NDVImax) registered during the growth season. Date of Peak (DOP) is the day where PkV was recorded.

2. Time to Peak (TTP, the duration of the green-up phase) corresponds to the number of days required to reach PkV from the Start of the Season (SOS). SOS was defined as the first day of year reaching 20% of the NDVI maximum amplitude and End Of the Season (EOS) is the first time point that exceeds 70% of the NDVI amplitude maximum.

The 'NDSI/NDVI>1' principle was used to detect the presence of snow. Our observation window starts on Day Of the Year 250 (DOY250) in the previous year and extends to DOY150 in the present year (DOY250 year-1 through DOY150), allowing us to characterize the snow cover each year and identify the first (First Snow) and last (Last Snow) appearances of snow cover during the winter season. Three Winter Habitat Indexes (WHI) were then calculated for every year from 2001 to 2020 for the winter season (Oct-June): i) Snow Season Length (SSL), ii) Spring Frozen Ground Without Snow (SFGWS), and iii) Snow Cover Variability (SCV). SSL is the difference in days between First Snow and Last Snow, while SCV is computed for the period [First Snow-Last Snow] by summing the snow days preceded by at least two snow-free days. We hypothesized that SCV may be responsible for abrupt variations of ground thermal regimes, which can alter the soil microorganisms. A high snow cover variability also indicates a low snowpack depth, leading to lower snow insulation for plant species. SFGWS is computed by summing the number of days < 0° recorded as snow-free (Guidex-Cross et al., 2020, see section 2.4. for the climatic datasets) and is summed for the period [SOS-DOP] for each year. We hypothesized that an increase in SFGWS may have detrimental effects on plant growth (Baptist et al., 2010; Inouye, 2000) resulting in a decrease of productivity (PkV) and an increase of the length of Green-Up (TTP). We examined the relationships between WHIs using Pearson's correlations and then created a multiband composite image with the final WHIs used in our analysis. This was done to identify sites with unique snow cover dynamics across the study area. We used the non parametric, rank-based Mann-Kendall (MK) monotonic test to
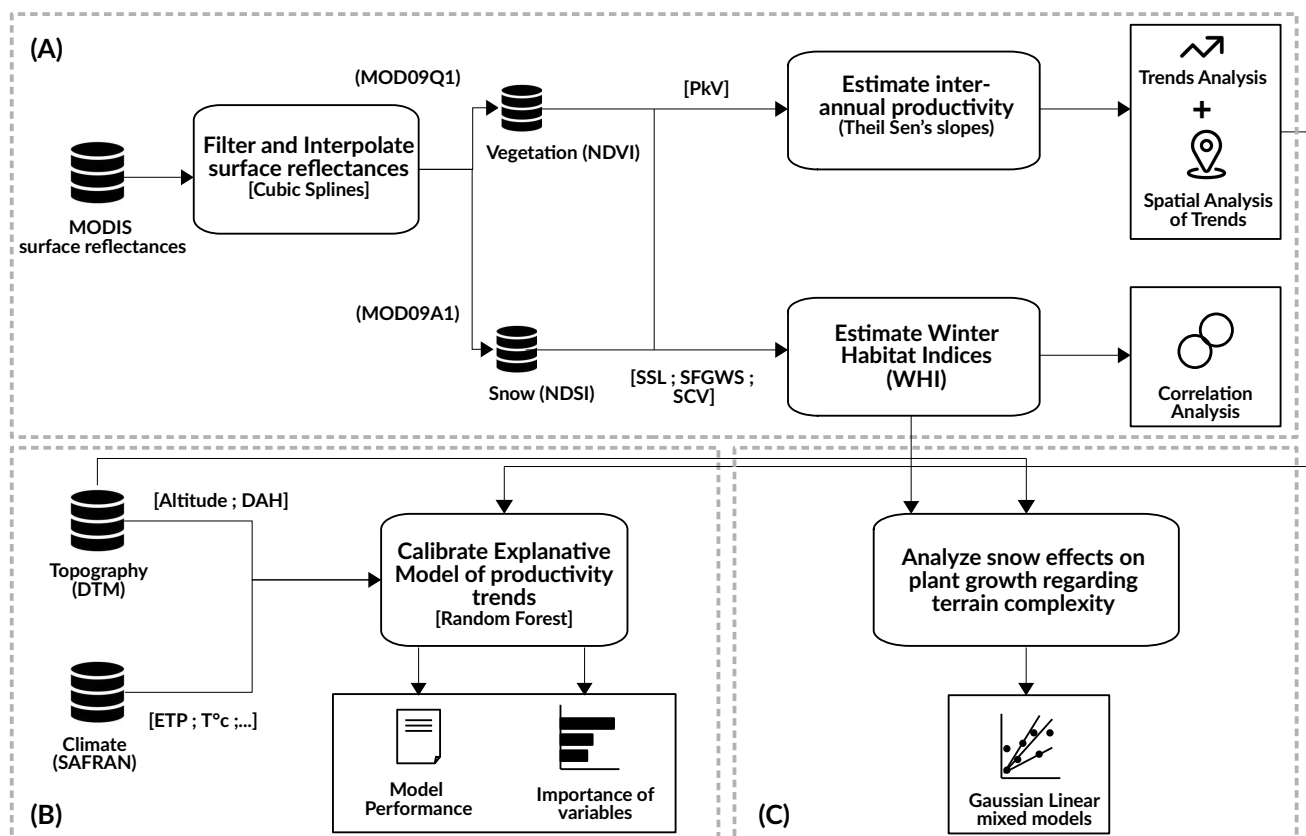
Figure 2. Detailed flowchart of the methodology applied in this study to understand the growth response of mountain grasslands in the Vosges mountains range. Three main stages were identified : the stage (A) aims at estimating phenological indicators and calculating interannual productivity trends; (B) corresponds to the calibration of the explanative model to identify drivers of the spatial variability of productivity trends and (C) has the objective of investigating contextual effects of intraseasonal snow regimes on plant growth.

assess the significance of NDVI trends (p-value <0.05). To investigate fluctuations over the period 2000-2020, we fitted linear models based on the Theil-Sen single median slope. Compared to the least squared method, the Theil-Sen estimator is more 165 robust against outliers by handling extremities in the data.

2.4 Climate and Topographical Metrics

We estimated terrain indices from the 1m resolution Digital Elevation Model (@RGE IGN). We calculated the mean, range, and standard deviation of elevation and the Diurnal Anisotropic Heat index (DAH). The DAH index takes into account the slope and the aspect and is calculated as: $DAH = cos(amax - a) * arctan(b)$ where $amax$ is the slope aspect receiving 170 the maximum amount of heat, a is the aspect, and b is the slope angle. We defined $amax$ = 198° (South South-West) as it corresponds, on average, to the earliest SOS over the study site in the past 20 years (Choler et al., 2021).

The daily based grids provided by the SAFRAN-SURFEX/Crocus-MEPRA model chain (S2M) developed by Meteo France (Durand et al., 2009; Noilhan and Mahfouf, 1996; Ledoux et al., 1989) were used to derive climatic variables. To characterize summer warming, we computed the average of daily maximum temperatures during the summer months (June, July, and August; noted as T-max). We computed the difference between precipitation (P) and evapotranspiration (ETP; noted as P-ETP). P-ETP differences were summed over the summer months to estimate fluctuations into the availability of rainwater for plants during the growing season. We also used the Soil Wetness Index (SWI) to measure the influence of soil moisture conditions on plant growth cycles (Soubeyroux et al., 2008). It represents the soil moisture level over a specific period in the two first meters of soil compared to its maximum water-holding capacity. Within the SAFRAN model, SWI is calculated based on meteorological inputs like precipitation, evapotranspiration, temperature, and wind. It is ranging from 0 (completely dry soil) to 1 (fully saturated soil). We first summed the number of day with SWI indexes lower than 0,7 (noted as SWIlow), over a period defined between SOS and DOP, as it corresponds to the upper limit of the third quantile. We considered that below this value, the water reserve in the soil was low for soils above 900m of the study area. Then, we calculated the ratio of SWIlow over the difference in days between DOP and SOS. The median Theil-Sen slopes of all climatic variables over the past 20 years have been used as statistical predictors. Pearson correlation coefficients were used to measure covariance between variables.

2.5 Statistical Analysis

2.5.1 Assessment of productivity trends and potential drivers

We used the nonparametric, rank-based Mann-Kendall (MK) monotonic test (significance at 5% level) to classify NDVImax trends into three categories: no significant greening, positive greening, and browning. To investigate potential drivers of the spatial distribution of NDVImax trends, we developed a Random Forest (RF) regression model. RF models are a widely accepted approach to study relationships between biological patterns and environmental variables, as they can address linear and non-linear effects (Revuelto et al., 2020; Choler et al., 2021; Revuelto et al., 2022). Due to the limited number of pixels belonging to the "positive greening" class, we excluded it from our analysis and we focused on explaining the categories "no significant greening" (NSG) and "negative greening" (NG). Additionally, we used a synthetic minority oversampling technique (SMoTE) to address the unbalanced dataset (NG= 67 and NSG=459). SMoTE is an oversampling technique which creates artificial synthetic samples for the minority class using nearest neighbor classification (Chawla, 2010). This helps to overcome the risk of overfitting in the classification model compared traditional random naive oversampling techniques. To evaluate the performance of the prediction models on similar datasets, we used a repeated holdout cross-validation method. Only non-synthesized candidates were used for this evaluation. For each run (100 in total), we randomly selected two-thirds of the training set to train the model and one-third for predictions. We computed the average Kappa score and average accuracy by class to evaluate the prediction results. We assessed predictor importance using the mean decrease in accuracy (MDA) and mean increase in Gini, which quantify the model's stability and the purity of nodes and leaves. We used a permutation-based importance measure to determine the relative importance of each predictor, and to quantify the effect of a dropped variable on model accuracy. Last, partial dependence plots were analyzed to investigate relationships between the classification

probabilities and the values taken of each predictor. In order to increase our understanding about negative trends of productivity, the drawn curves illustrate the predicted probability for the class "negative greening" (browning).

We used the *randomForest*, *caret*, *pdp* and *performanceEstimation* R packages.

2.5.2 Linking Winter Habitat Indices with Growth Response of Mountain Grasslands

We investigated the effects of Winter Habitat Indices on the growth response of mountains grasslands. Two linear mixed models were computed with pixel ID nested in year as random variables to control for spatial and temporal pseudoreplications (Pinheiro and Bates, 2000): the first one was used to measure the effects of snow metrics on PkV, and the second one was used to investigate similar effects on TTP. SFGWS, SSL, SCV, Altitude, and DAH were included as fixed factors. Interactions between the topographical variables (DAH and altitude) and SFGWS, SSL, or SCV were also calculated. All explanatory variables were standardized by retrieving means and dividing by standard deviations to compare the magnitude of model variables' responses directly. Correlations between covariates in full models were assessed with variance inflation factors (all VIF < 5; (Murray et al., 2012), see Table A1 and A2). We compared the Akaike information criterion (AIC values, (Burnham and Anderson, 2004)) of the full model with a null model including random effects only to test if the selected variables really improve the understanding of TTP or PkV variation. The model was run with the R *nlme* package (Lindstrom and Bates, 1990).

3 Results

Over the period 2000-2020, we found a majority of pixels showing non-significant temporal trends (N = 459, 85.6%). We also highlighted significant ($p < 0.05$) negative temporal trends (browning) in NDVI_{max} for 12.5% (N = 67) of the 536 pixels while only 1.9% of pixels (N = 10) exhibited significant positive trends (vegetation greening, Figure 3). Herbaceous vegetation is overrepresented among the significant browning pixels 76.1% (N = 51) and shrubs vegetation is dominant among the significant greening trends 90% (N = 9). Half of browning trends (50.7%, N = 34) exhibited a coefficient value higher than -0.002, and only 10.4% (N = 7) were lower than -0.003. Last, non-significant pixels were recorded all over the massif but significant trends were not spatially uniform, with hotspots of browning corresponding to the Hohneck, Petit Ballon, Markstein, and Rossberg sites. The few greening trends were rare and only recorded in Gazon du Faing, Petit Ballon, and Grand Ballon. They were quasiexclusively located in the highest elevations, (> 1300m).
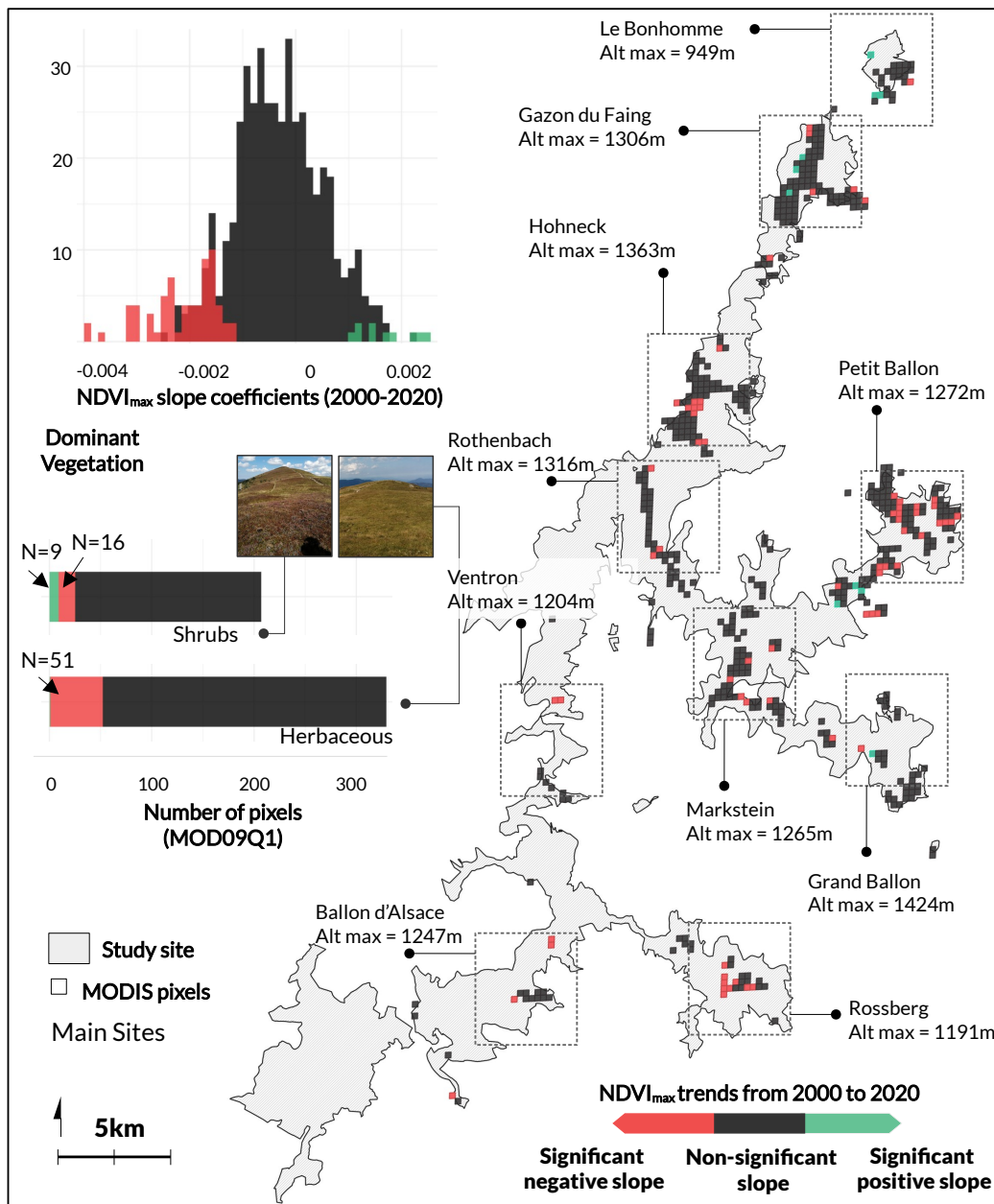
Figure 3. (a) Spatial distribution of $NDVI_{max}$ trends. The color represents the categories of $NDVI_{max}$ trends over the 2000-2020 period (red = significant negative $NDVI_{max}$ slope/browning; black = no significant $NDVI_{max}$ slope; green = significant positive $NDVI_{max}$ slope/-greening). Slopes were calculated using the Theil-Sen median slope. Level of significance were estimated using a nonparametric, rank based, Mann-Kendall monotonic test. (b) Frequency distribution of $NDVI_{max}$ trends for the 2000-2020 period. (c) Greening trends by dominant vegetation based on the CIGAL land cover class

The model classified "browning" and "no significant" pixels with an accuracy of 0.89±0.05% and 0.83±0.03%, respectively,
corresponding to a global kappa of 0.52±0.06 and accuracy of 0.84±0.03%. The ranking of predictors shows that topographical
variables such as elevation and DAH were important predictors, as well as the SOS and SWI slopes (Figure 4). They exhibited
high Mean Decrease Accuracy (MDA) and Mean Decrease Gini (MDG), indicating high suitability as predictors and a high
contribution to the homogeneity of nodes and leaves. Partial dependence plots showed that the probability of detecting browning
trends decreased with positive DAH (SSW) and increased with elevation between 900m and 1100m (Figure 5). However, it
continuously decreased with increasing elevation after 1100m. Results also showed that browning trends were enhanced by
positive SOS slopes and higher SWI slopes. In fact, as the number of days with low soil humidity (SWI < 0.7) increases, so
does the probability of finding browning tendencies. Lastly, a low MDG and/or MDA for T-max slopes and P-ETP slopes were
found, meaning marginal or insignificant effects in the classification procedure.
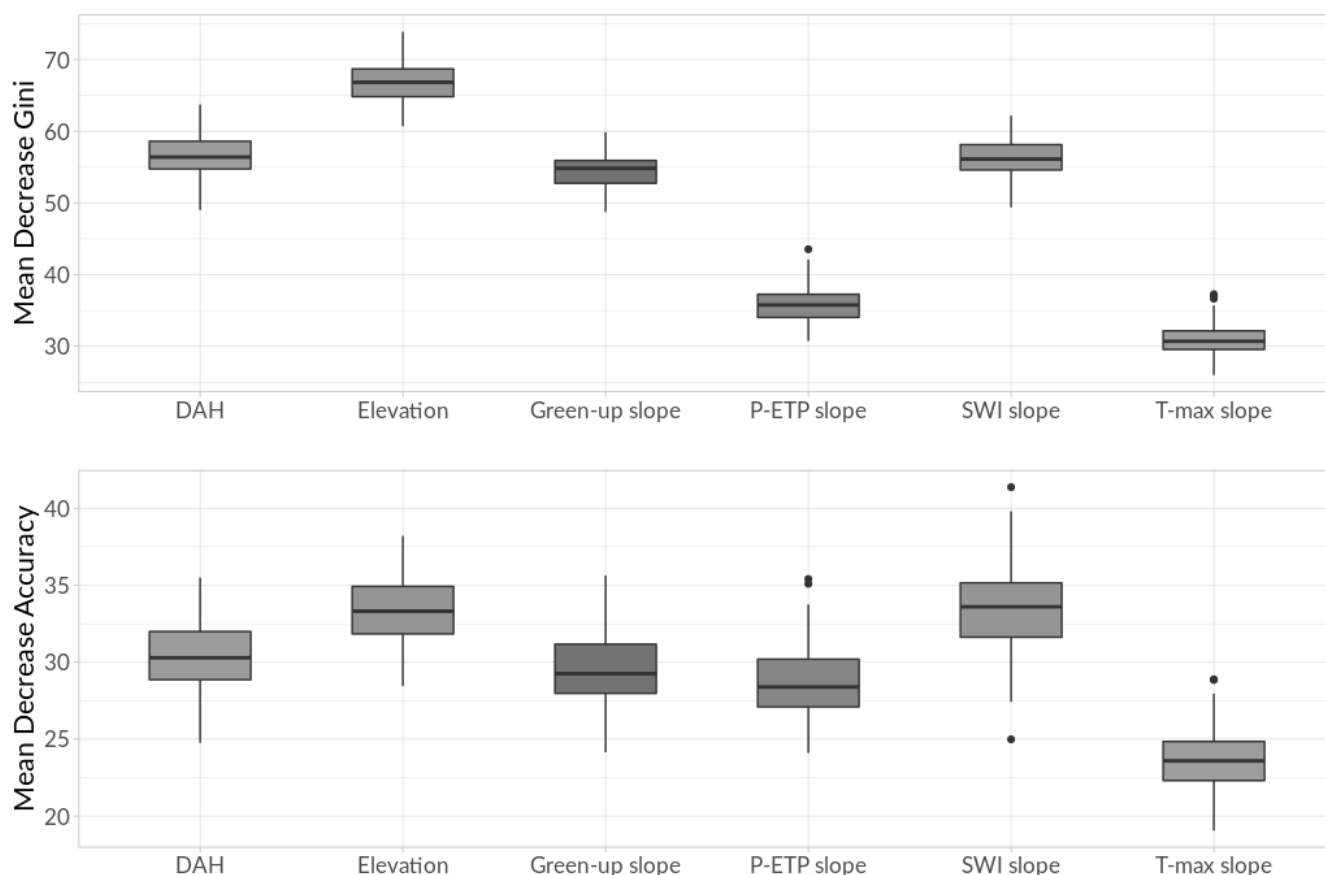
Figure 4. ((A) Contribution of predictors to the purity of nodes and leaves based on Mean Decrease Gini coefficient. (B) Predictor importance
ranking based on Mean Decrease in Accuracy (MDA) scores.
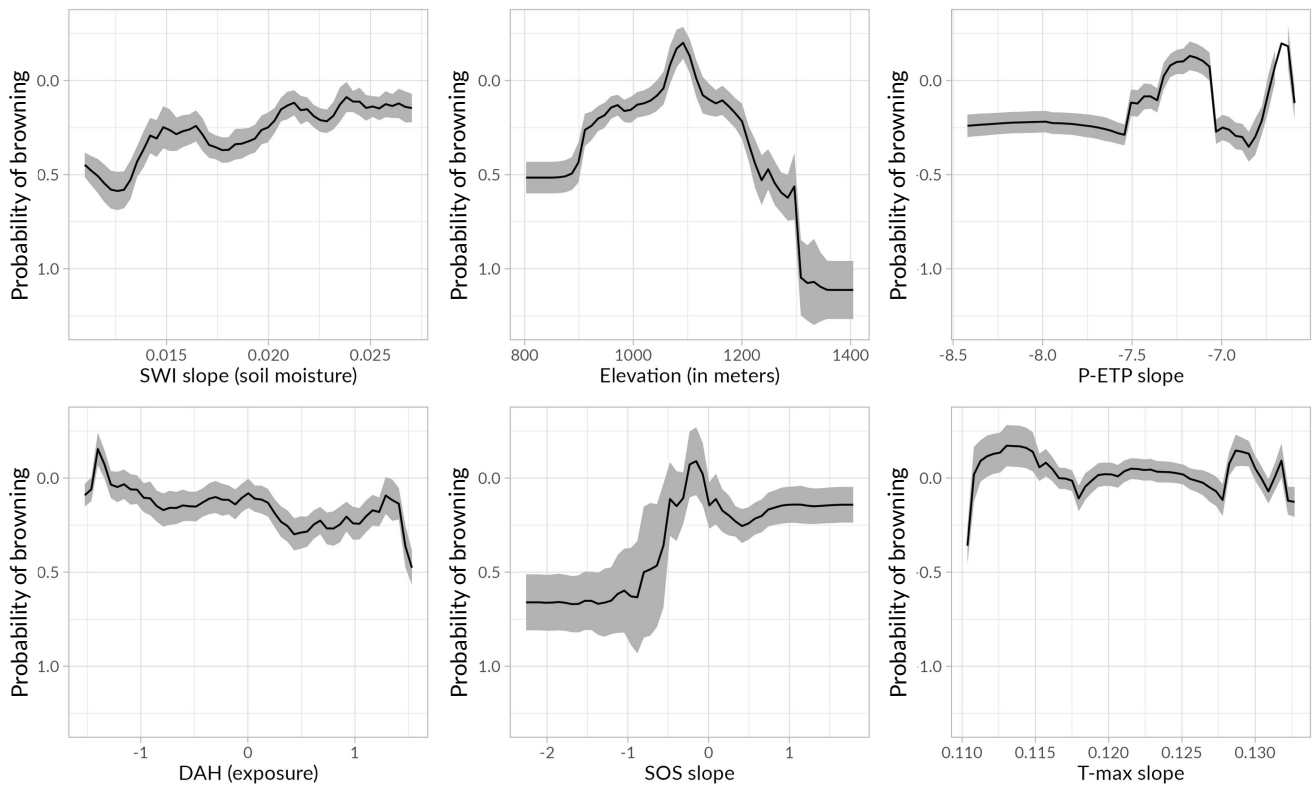
Figure 5. Partial dependence plots illustrating the feature contribution of the six predictors to the browning class (the significant negative NDVImax slope). Each graph represents the influence (intensity and direction, positive or negative) of each predictor. The x-axis represents the value of the predictor. The y-axis represents the feature contribution, or the change in predicted browning class probability for a specific value of the predictor. The fitted line was estimated with a k-nearest neighbors' function with Gaussian distance weighting.

MODIS WHI showed low to moderate correlations (Figure A2). Snow Season Length and Snow Cover Variabilty had the strongest correlation (Rho = 0.64, $p < 0,001$), followed by Spring Frozen Ground Without Snow and Snow Season Length (Rho = -0.14, $p < 0,001$), then Snow Cover Variability and Spring Frozen Ground Without Snow (Rho = -0.02, $p < 0,05$). The combination of WHIs in a composite image highlight distinct zones of different snow cover dynamics dominated by either one WHI or a combination of them (Figure 6). Hohneck, Rothenbach, Markstein and the southern part of Rossberg sites are some of the harshest (as well as some pixels of Grand Ballon) and are dominated by long snow seasons with near continuous snow cover or low snow cover variability. Gazon du Faing is also dominated by high snow season lengths but with larger snow cover variability and moderate spring frozen ground without snow. However, Petit Ballon, Le Bonhomme, Ballon d'Alsace and the northern part of Rossberg are dominated by pixels exhibiting frequent spring frozen ground without snow, high snow cover variability and relatively low snow season length.

S1

Table 1. Summary table of model output (degrees of freedom (numDF), Slope estimates (and standard errors) of fixed variables, t-values and p-value

Variables	Phenometrics							
	Time to Peak (TTP)				Peak of Value (PkV)			
	numDF	Slope estimates (standard error)	t-value	p-value	num DF	Slope estimates (standard error)	t-value	p-value
(Intercept)	10689	-0.01 (0.06)	-0.18	0.85	10689	-0.003 (0.09)	-0.02	0.97
Snow Season Length (SSL)	10689	-0.37 (0.01)	-23.12	***	10689	0.07 (0.02)	3.66	***
Spring Frozened Ground Without Snow (SFWGS)	10689	0.24 (0.01)	23.67	***	10689	-0.06 (0.01)	-6.40	***
Snow Cover Variability (SCV)	10689	0.34 (0.01)	28.76	***	10689	-0.06 (0.01)	-4.59	***
Elevation (Ele)	10689	-0.24 (0.009)	-25.91	***	10689	0.03 (0.01)	3.12	**
DAH	10689	-0.0007 (0.008)	-0.008	0.99	10689	-0.017 (0.009)	-1.91	0.05
SSL*Ele	10689	0.20 (0.011)	16.92	***	10689	0.022 (0.01)	1.63	0.10
SFGWS*Ele	10689	0.09 (0.009)	10.83	***	10689	0.001 (0.01)	0.17	0.86
SCV*Ele	10689	-0.12 (0.01)	-11.76	***	10689	-0.017 (0.01)	-1.41	0.15
SSL*DAH	10689	-0.007 (0.01)	-0.64	0.51	10689	0.02 (0.01)	1.73	0.08
SFGWS*DAH	10689	0.02 (0.007)	2.89	**	10689	0.003 (0.009)	0.34	0.72
SCV*DAH	10689	0.01 (0.01)	1.25	0.21	10689	-0.04 (0.01)	-3.32	***
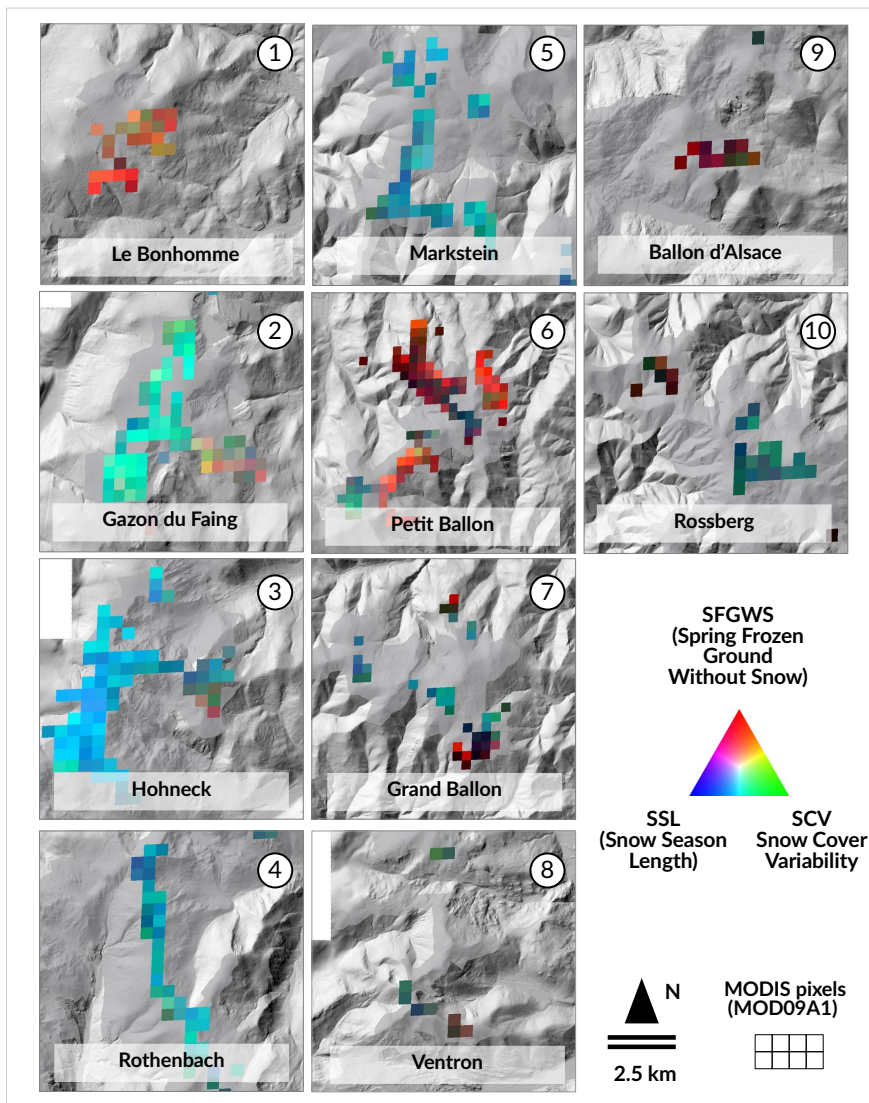
Figure 6. Composite spatial patterns in the MODIS WHIs from 2000-2001 to 2019-2020 highlighting areas with distinct snow cover dynamics across the Vosges mountains. The Spring Frozen Ground Without Snow (SFGWS) is in red, the Snow Season Length (SSL) is in blue and the Snow Cover Variability (SCV) is in green

The slope of the relationship between TTP or PkV, and significant variables of the linear mixed models were examined (Table 1). AIC values of full models were substantially smaller than those of null models (Full model AIC values: 25560.03 and 28687.59; null model AIC values: 28744.08 and 28744.08, respectively for TTP and PkV), suggesting that explanatory variables used in the full model improved the understanding of the main drivers of phenometrics. The elevation of the pixel

was associated with an increase of PkV (slope estimate = 0.03; $p < 0.001$), and a decrease of the TTP (slope estimate = -0.24; $p < 0.001$). DAH had no independent significant effect on PkV and TTP. Snow Discontinuity was the variable with the largest

255   effect (positive) on TTP (slope estimate = 0.34; $p < 0.001$). This effect was larger when the pixels are located in lower altitudes (Figure 7a). It also had a positive effect on the peak of productivity (slope estimate = 0.04; $p < 0.001$). The latter effect was enhanced in pixels with higher DAH values, therefore situated on SSW-facing slopes (Figure 7b). Snow Discontinuity was associated with a decrease of TTP (slope estimate = -0.37; $p < 0.001$). This effect was greater when the pixels are located in lower elevations (i.e. < 1000m; Figure 7a). It was also an important driver of PkV (slope estimate = 0.07; p < 0.001). Lastly,

260   SFGWS showed a positive association with TTP (slope estimate = 0.24; $p < 0.01$). This effect was more important in pixels located on east-facing slopes and higher altitudes (Figure 7a,b). The number of frozen days without snow in spring was also negatively associated with PkV (slope estimate = -0.06; $p < 0.001$).
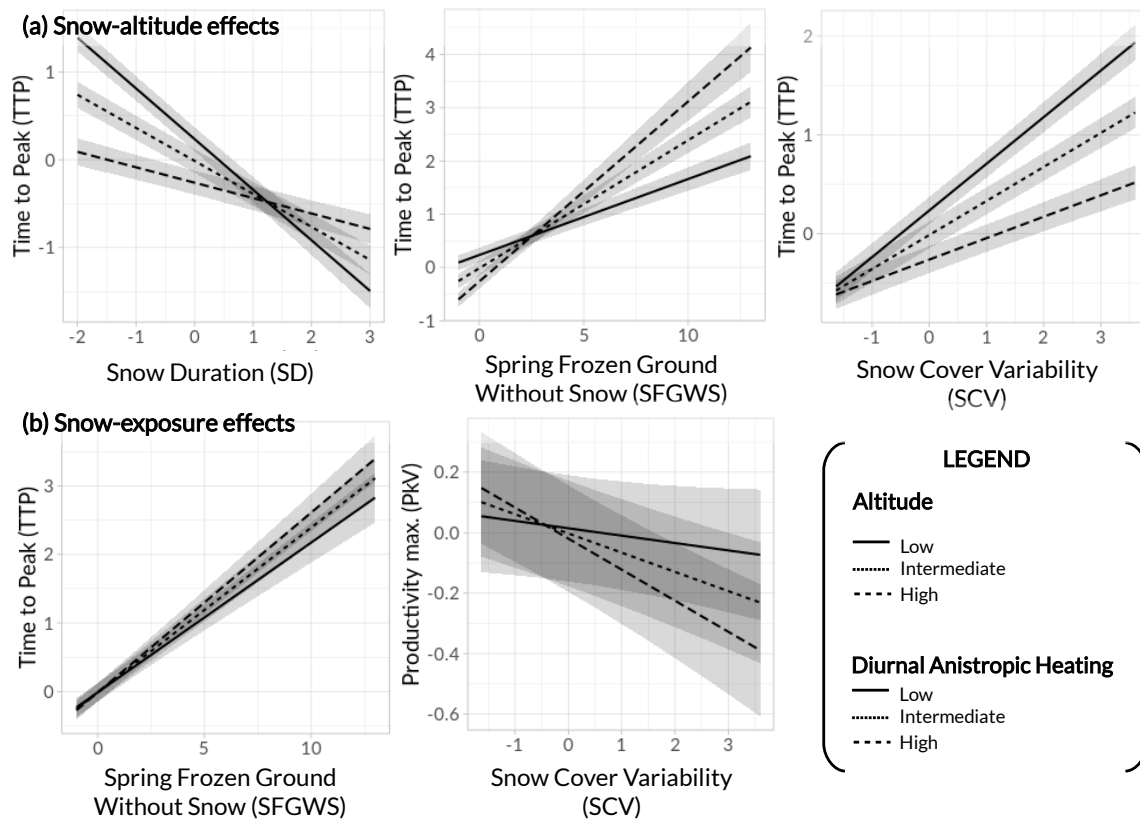
Figure 7. Predicted effects of significant snow-terrain variables interaction on the growth response of mountain grasslands. Estimates resulting from linear moxed models; see Table 1. SFGWS* = Spring Frozen Ground Without Snow

4 Discussion

4.1 Vosges mountain grasslands predominantly exhibit non-significant trends and hotspots of decrease in productivity

The majority of 536 pixels in the study area between 2000 and 2020 demonstrated no significant trends. Overrepresentation of non-significant trends over significant ones is a common "statistical effect" in similar studies (Choler et al., 2021; Filippa et al., 2022) but this could also demonstrate several compensatory effects to warming in the Vosges Mountains. Soil temperatures, nutrients and moisture can limit plant reactions to rising air temperature (Tape et al., 2012; Myers-Smith et al., 2015) while genetic adaptation can also help in protecting from changing environmental conditions (Bjorkman et al., 2017). Then, stable productivity trends may also indicate compensatory effects due to traits of local plant communities. A larger niche selection can increase phenotypic plasticity in local populations which has strong implications on their ability to respond to environmental changes (Chevin and Lande, 2010; Jump and Peñuelas, 2005; Nicotra et al., 2010). Lastly, a twenty year period remains relatively short to investigate the ecosystem's responses to climate warming. This could explain a large part of non-significance in our results. Linear trend tests can also mask nonlinear responses over the studied time period, such as temporal reversal in productivity trends (decrease-increase or increase-decrease). Polynomial-based methods should thus further be considered to expand the range of trends detected (Rigal et al., 2020).

Overrepresentation of browning trends over greening contradicts most of studies in European or Asian high mountain grasslands in the recent decades (Choler et al., 2021; Carlson et al., 2017; Cao et al., 2015; Yang et al., 2019; Tomaszewska et al., 2020). However, they are in line with recent works highlighting not uniform greening trends at the mountain range scale (Gartzia et al., 2016; Brookshire and Weaver, 2015). Interestingly, several analogies between the latter studies and our results can be drawn, notably because of the lower elevation range of the monitored grasslands. In particular, (Gartzia et al., 2016) found browning trends in the Pyrenees from 1980 to late 2000s preferentially in mountain grasslands at the lowest elevation of their study site (mean elevation = 1900m). Explanative factors are cattle grazing that occur preferentially on most productive dense grasslands at gentle slopes while lower precipitation in late summer probably reduce soil water availability thus affecting biomass and greenness. Our findings show that pixels indicating decrease in greeness also mostly occurred in lowest elevation grasslands (.i.e high producing grasslands) comprising dominant herbaceous communities. We hypothetize that low elevation also naturally exposes them to summer droughts that are less and less compensated by soil water availability due to reduced snowpack (Herberich et al., 2023; Brilli et al., 2011). Overall, our results support a high vulnerability of low mountain grasslands in response to climate warming, even more at lower altitudes whose species compositions are strongly dependent on grazing or mowing intensities.

Monitoring browning trends in low mountain ranges is of interest for several reasons. Firstly, this indicates that vegetation growth of low mountain plant communities can be weakened and even inhibited by climate warming-derived factors. Indeed, our results don't corroborate NDVI trends estimated by Kempf et al. (2023) at the European scale whose apparent trends showed increase in greenness over most of the European mountains. This strengthen the need of adapted spatial scales in satellite-based studies to investigate phenology or productivity trends in specific ecological habitats. The spatial resolution of satellite data is

obviuolsy a key point, but not the only one. The selection of monitored pixels, delimited and consistent study area and spatially aligned data (DEM, land cover maps) are all factors that play a major role in further studies and consequently in our ability of observing exact trends (Cortés et al., 2021; Lewińska et al., 2023). Secondly, our findings support the assumption that similar trends could likely occur for plant communities located in similar elevations at the European scale, leading to wide-ranging implications for ecological functionning and land management (Grignolio et al., 2003; Duparc et al., 2013). This could modify the spatial distribution and available amount of grazing resources for domestic or wild herbivore. Recent works also showed that strong modifications in phenology or productivity of mountains grasslands may have implications for different trophic levels such as soil microorganisms or insects (Frei and Isotta, 2019; Frenzel, 2022). Thirdly, our results allow to project further responses in higher mountain grasslands as the temperature continues to rise. Indeed, the recorded signal for plant communities whose the vertical migration is limited could be an expected response in high mountain massif since possibilities for migrating will reduce in the future (Frei et al., 2014; Opedal et al., 2015). Previous studies showed that topographic complexity may favor horizontal migration but its degree of compensation is currently unknown (Bickford et al., 2011; Hua et al., 2022).

Lastly, we found very few pixels (N = 10) exhibiting greening trends over the studied time period. They share same sites than pixels exhibiting browning trends but tend to be located in higher elevation and to be dominated by low stature shrubs vegetation. Increasing productivity trends in grasslands mountains due to shrubs has already been described in the past (Carlson et al., 2017; Dullinger et al., 2003; Cannone et al., 2007). We observed this mechanism on the Gazon du Faing site (7) in the form of local increases of ericaceous plants (*vaccinum myrtillus L*) possibly provoked by the collapse of grazing due to the creation of a Natural Reserve.

4.2 Spatial patterns of browning grasslands are preferentially explained by topographic and soil water content variables

We found significant effects from the topographical variables on the probability of finding browning trends. They corroborate previous studies demonstrating the differential effects of topography in the timing or the performance of mountain grasslands (Tomaszewska et al., 2020; Choler et al., 2021; Graae et al., 2018). The elevation, despite a little amplitude (900-1424m) within our study area was the most explaining factor with a tipping line around 1100m. Beyond this altitude, the probability of finding browning progressively declined until the summit. Two explanations can be found : (1) 1100m is the average rain-snow limit in the Vosges mountains (Goepp, 2007) explaining benefits arising from snow cover by plant communities above this line. Furthermore, a large part area above 1100m include summit with flat or gentle slopes facilitating snow accumulation. (2) Pixels selected above this line comprise a large part of low producing grasslands with low grazing/mowing intensities and shrubs. Consequently, their profile was less favourable to browning. Exposure was the second significant topographical factor. Pixels showing browning trends were more probable on north-facing slopes than in south-facing exposures. One possible explanation would be that grasslands communities located in these aspects were the most impacted by snow cover reduction and the most responsive to changing environmental conditions because of shorter acclimatation. This situation was already noted by (Choler et al., 2021)in the Alps with a higher responsiveness to warming of ecosystems exhibiting lower NDVI than expected given the topography.

Another interesting outcome of this research is that the Soil Wetness Index slope is an important predictor of browning to explain the presence of browning trends. Higher is the number of "stressed" days, higher is the probability of meeting browning trends. Our findings support the conclusion of previous studies highlighting the soil moisture as a key control variable to explain the productive capacity of mountain plant communities (Luo et al., 2021; Marchin et al., 2018). Indeed, for grasslands with abundant soil water caused by abundant snowpack) (longer snow season in early and late winter and/or spring/summer precipitation), warming had positive effect on plant productivity (Corona-Lozada et al., 2019; Grigulis and Lavorel, 2020). Our results rather indicate that for a large part of grasslands with probable insufficient soil water recharge, warming caused water limitation and affected negatively their productivity. This could be explained by the high soil porosity of the area which is dominated by sandy soils. In line with these results and surprinsingly, our findings also showed that browning pixels exhibit stable or slighlty later SOS . It is important to note that we did not find any significant SOS slopes over the time period revealing strong interannual variation in the onset of vegetation, partly driven by snow melt (R = 0,52, p < 0,001). We hypothetize that, in a situation of delayed SOS provoked by delayed snow melt, plants can be immediately exposed to high temperatures leading to a decrease in productivity (Revuelto et al., 2022; Jonas et al., 2008).

Pixels showing browning were not significantly associated with climatic drivers, .i.e summer air temperature and the climatic balance variable. Our results are in line with previous studies showing inconsistencies between the recorded signal in productivity and climatic patterns derived from climatic gridding datasets (Choler et al., 2021). First, Safran Crocus datasets rely on a few meteorological stations above 1000m which explain difficulties to reproduce climatic variables along the topographic gradient (Frei and Isotta, 2019; Vionnet et al., 2019). Second, the spatial resolution of Safran Crocus (8km) do not provide sufficient spatial variability over the Vosges mountains regarding the small size of the massif. Growth responses of mountain plant communities are dependent on subtle thermic variations enhanced by local landforms and soil characteristics (Giaccone et al., 2019; Huelber et al., 2011). The latter contextual effects could be even strenghtened by the small size of the mountain range such as the Vosges. Third, mountain plant communities can express possible time lags in response to changing climatic conditions. Indeed, there may have been a plant recruitment provoked by warming events whose the effects are not yet visible (Alexander et al., 2018). This can also depend on plant traits communities such as dispersal mobility (Engler et al., 2009). Another example is a recent transplant experiment of mountain grassland communities in the Alps showing that forbs have longer acclimatation than graminoids probably due to vernalization (flower bud) or allocation capacity of resources to stomatic growth (Bektaş et al., 2021).

4.3 Growth response of low mountain grasslands showed high sensitivity to intra and inter seasonal fluctuations in snow cover that can be modulated by topographical effects

This study primarily focused on the productivity of mountain grasslands and its determinants but the analysis of the snow cover effects combined with topography allow for a better understanding of contextual effects occuring in mountain environments (Figure 6). Gazon du Faing, Hohneck, Rothenbach and Markstein sites have the longest snow season. This can be explained by their higher altitude but also by their position on the main ridge directly exposed to the main western atmospheric flux and receiving the highest quantity of precipitations. In contrast, the Grand Ballon that is the highest point of the range but more

365 sheltered from westerly winds present a shorter snow season. Similarly, sites away from the main ridge (Petit Ballon, Ventron, Immerlin, Rossberg) present a shorter season length and more exposure to frozen grounds. At a finer scale, the main ridge sites are also bordered on the east side by cirque of glacial origin where locally the snow accumulates in cornices and can remain until July (Wahl et al., 2007). However, it is difficult to quantify the influence of this phenomenon in pixels 250m apart. Spectacular snow accumulation in the past are also documented along the "route des crêtes", the road that follows the main

370 ridge (Figure A3).

We found a positive effect of the Snow Season Length (SSL) on the productivity. Our results are in line with studies showing direct and indirect benefits provided by snow cover to regulate soil temperature, soil water content, light and nutrient availability (Starr and Oberbauer, 2003; Welker et al., 2005; Convey et al., 2018). Furthermore, we found a significant positive association between SSL and snow melt (Pearson = 0,83, p < 0,001) which means that positive effects of SSL on plant growth also reflects

375 the positive effects of snow timing such as the last presence of snow. The latter variable has been largely identified as an essential predictor of interannual variations of the onset of vegetation which can be independent of the snow season length (Choler, 2015; Revuelto et al., 2022; Francon et al., 2020). Then, our results demonstrated that longer SSL promoted shorter growth period. This is consistent with apparent strategies for alpine plant communities that reduce their growing seasons with faster plant growth (Körner, 1999). In our study, this effect is stronger at lower altitudes. We hypothetize that higher air

380 temperature after snow melt promoted by lower altitudes and associated to sufficient soil water recharge (due to longer SSL and/or delayed snowmelt) can accelerate plant growth (Jonas et al., 2008; Convey et al., 2018).

Our results also corroborate previous studies showing detrimental effects of freezing events on plant growth (Klein et al., 2018; Liu et al., 2018) into multiple ways such as roots damages, limitations in roots uptakes of nitrogen and carbon allocation and storage (Pardee et al., 2018). Consistently, they support that an increase in frost days after the start of season have negative

385 effects on productivity and promote longer growth period. With warming, snowmelt is earlier which induce potential spring freezing events that can damage flower buds and leaves of frost sensitive species (Inouye, 2000, 2008). These findings are also in line with previous studies indicating that root growth of alpine species can be slowed by low soil temperatures which could possibly result into later maximal plant growth due to numerous spring freezing events (Nagelmüller et al., 2017). Furthermore, it is important to note that the latter effect is enhanced at lower altitudes and in south -facing slopes. One explanation is that

390 earlier snowmelts mostly occur in pixels with high sun radiation levels while higher altitudes can favor more spring frost episodes because of lower air temperature.

Lastly, we found a negative effect of the Snow Cover Variability on the productivity of plant communities with stronger relationships for grasslands located on south-facing slopes. We hypothesize that because of high sun radiation levels associated to shallow snowpack, these grasslands firstly experience fluctuations in snow cover. Consequently, similarly to spring frost

395 episodes, abrupt change variation in ground thermal regimes can affect the growth rate of plant communities, notably in the early growing season. In line with this, future consequences of high snow cover variability in low mountain ranges could be also bi-modal seasonal patterns because of two favourable sequences for growing season. For instance, a previous study conducted in the Central Norwegian Mountains showed earlier onset of radial stem for different shrub species closely linked to the rise of available soil moisture associated with thawing soils or snow melt and rising temperatures. A first phase of stem growth was

400 then followed by a period of radial stem shrinkage before starting the main growth phase (Dobbert et al., 2022). Furthermore, it is important to note that the effects of snow depth on plant growth vary between studies with significant (Wipf et al., 2009) or non-significant impact (Revuelto et al., 2022). In the latter study, authors demonstrated effects of the melt-out dates without observing significant effect of snow depth on plant response in the Pyrenees. This could explain lower statistical associations found between SCV and productivity for pixels located in north-facing slopes because of more continuous remaining snowpack,
405 even with low depth, caused by lower sun radiation levels.

5 Conclusion

We established that Vosges mountain grasslands exhibited predominant stable productivity trends between 2000 and 2020. Several environmental and ecological compensatory effects can be advanced to explain such results. Interestingly, grasslands showing positive trends in productivity were largely underrepresented compared to those with a negative signal. These latter
410 grasslands are preferentially located in the lowest range of our study area. They are also covered by dominant herbaceous (graminoids and forbs) communities revealing that high producing grasslands are mostly impacted by these phenomenon. Elevation and exposure are essential to explain spatial patterns of productivity and phenology at the mountain range scale while soil water content is pivotal to understand the productive capacity of species, notably in earlier growing season. We also found considerable differences in intraseasonal snow regimes with strong effects from snow duration, snow cover variability
415 and freezing events on plant growth.

We encourage the mountain ecology community to deeply investigate low mountain range ecosystems. Limitations in term of vertical migration for species could indicate future plasticity or adaptation mechanisms in high mountain plant communities with rising air temperature. Moreover, strong contextual effects in snow regimes and dwindling snow are likely to provoke a large diversity of growth responses, both in magnitude and temporal lags.

420 Finally, future works about benefits arising from microrefugia by plant communities in low mountain ranges should be considered, notably for cold-related species. Observation data allowing to investigate these microecological habitats at large scales such as UAV and/or phenocam will be essential to perform these researches.

Code and data availability. All data required to analyze the results and replicate the research are available as separate
425 .csv in a Zenodo repository (https://zenodo.org/doi/10.5281/zenodo.10204065; (Herrault et al., 2024a)). Software code and tutorials describing how to perform the statistical analysis are available in a GitHub repository (https://github.com/herrault/Article-Phenology-of-Low-Mountain-Grasslands/tree/main; (Herrault et al., 2024b)).

Coompeting interest. The contact author has declared that none of the authors has any competing interests.

Table A1. Variation Inflation Factors (VIF) of all explanative variables in the linear mixed models

Explanative Variables	VIF
Snow Season Length (SSL)	2.38
Spring Frozen Ground Without Snow (SFGWS)	1.64
Snow Cover Variability (SCV)	1.94
Altitude	1.57
Diurnal Anisotropic Heating (DAH)	1.00
SSL:Altitude	2.13
SGWGS:Altitude	1.60
SCV:Altitude	1.98
SSL:DAH	1.78
SFGWS:DAH	1.04
Snow Season Length:DAH	1.75
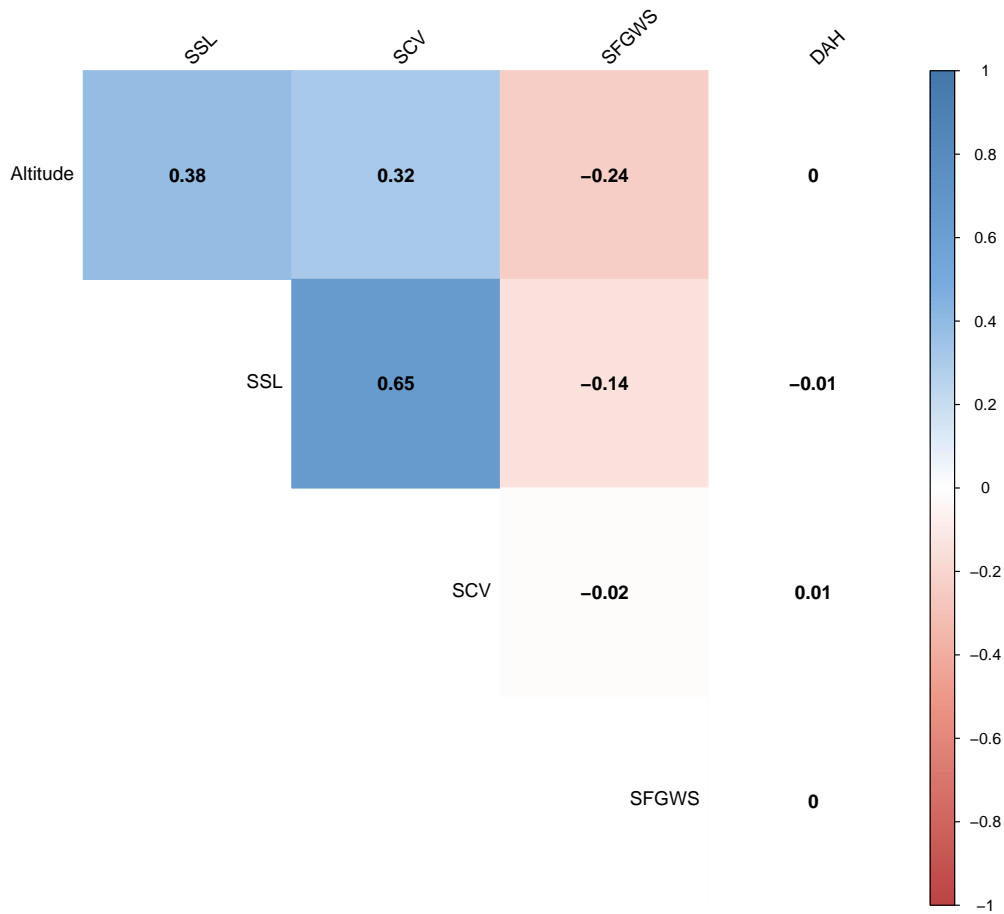
Figure A1. Pearson Correlation matrix between covariates included in the linear mixed models. Two digits after comma are shown. Blue squares represent significant positive associations between two variables, red squares the significant negative associations while the white squares indicate no significant relationships between two covariates. Significance level at 0.05 was used.
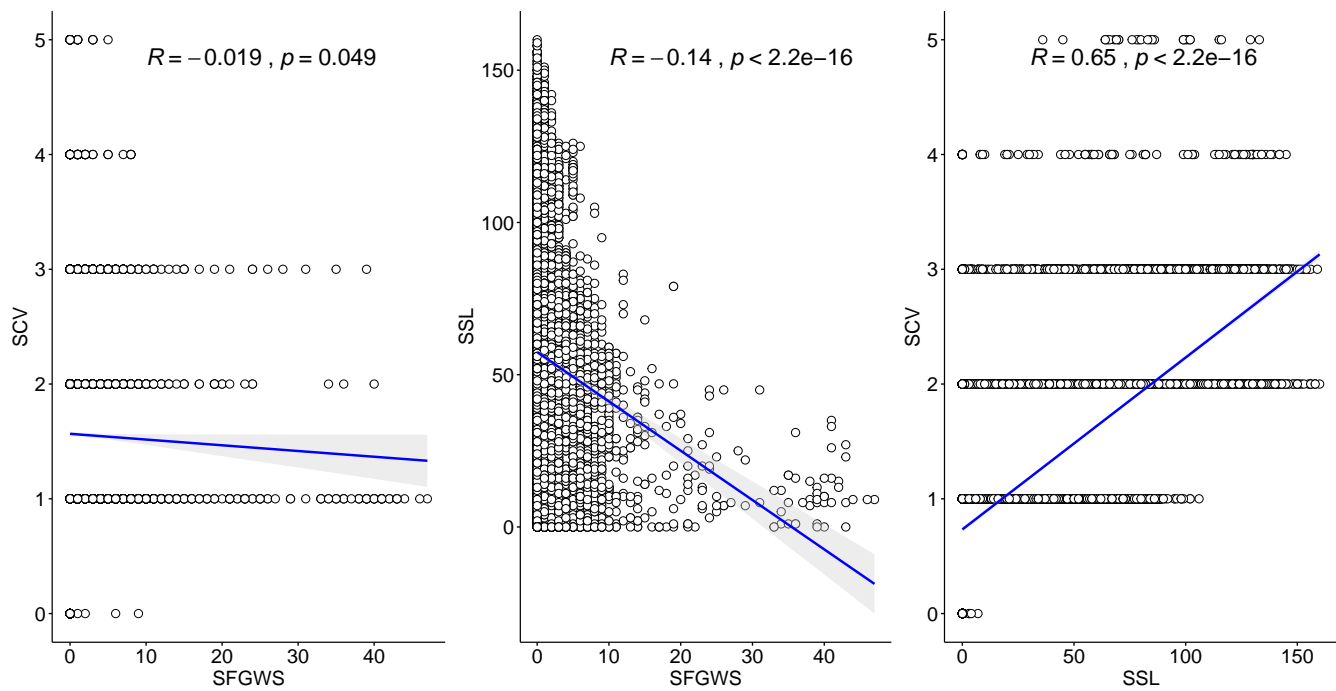
Figure A2. Scatterplot of WHI indices. R corresponds to Pearson's Rho and p is the p-value of the significance test

Figure A3. Regional news clipping from 2021-05-08 in DNA (Dernières Nouvelles d'Alsace) illustrating spectacular snow accumulation on 1970-05-19, in the Markstein site, located on the main ridge of the study area. The snow drift has been measured about 10 meters.

References

Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., et al.: Lags in the response of mountain plant communities to climate change, Global change biology, 24, 563–579, 2018.

Bektaş, B., Thuiller, W., Saillard, A., Choler, P., Renaud, J., Colace, M.-P., Della Vedova, R., and Münkemüller, T.: Lags in phenological acclimation of mountain grasslands after recent warming, Journal of Ecology, 109, 3396–3410, 2021.

Beniston, M.: Environmental change in Mountain regions, Environmental Change, 2012.

Bickford, C. P., Hunt, J. E., and Heenan, P. B.: Microclimate characteristics of alpine bluff ecosystems of New Zealand's South Island, and implications for plant growth, New Zealand Journal of Ecology, 35, 273, 2011.

Bjorkman, A. D., Vellend, M., Frei, E. R., and Henry, G. H.: Climate adaptation is not enough: warming does not facilitate success of southern tundra plant populations in the high Arctic, Global Change Biology, 23, 1540–1551, 2017.

Brilli, F., Hörtnagl, L., Hammerle, A., Haslwanter, A., Hansel, A., Loreto, F., and Wohlfahrt, G.: Leaf and ecosystem response to soil water availability in mountain grasslands, Agricultural and Forest Meteorology, 151, 1731–1740, 2011.

Brookshire, E. and Weaver, T.: Long-term decline in grassland productivity driven by increasing dryness, Nature communications, 6, 7148, 2015.

Bucher, S. F., König, P., Menzel, A., Migliavacca, M., Ewald, J., and Römermann, C.: Traits and climate are associated with first flowering day in herbaceous species along elevational gradients, Ecology and Evolution, 8, 1147–1158, 2018.

Burnham, K. P. and Anderson, D. R.: Multimodel inference: understanding AIC and BIC in model selection, Sociological methods & research, 33, 261–304, 2004.

Butler, A. B., Martin, J. A., Palmer, W. E., and Carroll, J. P.: Winter use of south Florida dry prairie by two declining grassland passerines, The Condor, 111, 511–522, 2009.

Cannone, N., Sgorbati, S., and Guglielmin, M.: Unexpected impacts of climate change on alpine vegetation, Frontiers in Ecology and the Environment, 5, 360–364, 2007.

Cao, R., Chen, J., Shen, M., and Tang, Y.: An improved logistic method for detecting spring vegetation phenology in grasslands from MODIS EVI time-series data, Agricultural and Forest Meteorology, 200, 9–20, 2015.

Carlson, B. Z., Corona, M. C., Dentant, C., Bonet, R., Thuiller, W., and Choler, P.: Observed long-term greening of alpine vegetation—a case study in the French Alps, Environmental Research Letters, 12, 114 006, 2017.

Cassou, C. and Cattiaux, J.: Disruption of the European climate seasonal clock in a warming world, Nature Climate Change, 6, 589–594, 2016.

Chawla, N. V.: Data mining for imbalanced datasets: An overview, Data mining and knowledge discovery handbook, pp. 875–886, 2010.

Chevin, L.-M. and Lande, R.: When do adaptive plasticity and genetic evolution prevent extinction of a density-regulated population?, Evolution, 64, 1143–1150, 2010.

Choler, P.: Growth response of temperate mountain grasslands to inter-annual variations in snow cover duration, Biogeosciences, 12, 3885–3897, 2015.

Choler, P., Bayle, A., Carlson, B. Z., Randin, C., Filippa, G., and Cremonese, E.: The tempo of greening in the European Alps: Spatial variations on a common theme, Global Change Biology, 27, 5614–5628, 2021.

Convey, P., Coulson, S., Worland, M., and Sjöblom, A.: The importance of understanding annual and shorter-term temperature patterns and variation in the surface levels of polar soils for terrestrial biota, Polar Biology, 41, 1587–1605, 2018.

Corona-Lozada, M., Morin, S., and Choler, P.: Drought offsets the positive effect of summer heat waves on the canopy greenness of mountain grasslands, Agricultural and Forest Meteorology, 276, 107 617, 2019.

470 Cortés, J., Mahecha, M. D., Reichstein, M., Myneni, R. B., Chen, C., and Brenning, A.: Where are global vegetation greening and browning trends significant?, Geophysical Research Letters, 48, e2020GL091 496, 2021.

Dietz, A. J., Wohner, C., and Kuenzer, C.: European snow cover characteristics between 2000 and 2011 derived from improved MODIS daily snow cover products, Remote Sensing, 4, 2432–2454, 2012.

Dobbert, S., Albrecht, E. C., Pape, R., and Löffler, J.: Alpine shrub growth follows bimodal seasonal patterns across biomes–unexpected
475 environmental controls, Communications Biology, 5, 793, 2022.

Dong, C. and Menzel, L.: Recent snow cover changes over central European low mountain ranges, Hydrological Processes, 34, 321–338, 2020.

Dullinger, S., Dirnböck, T., Greimler, J., and Grabherr, G.: A resampling approach for evaluating effects of pasture abandonment on subalpine plant species diversity, Journal of Vegetation Science, 14, 243–252, 2003.

480 Duparc, A., Redjadj, C., Viard-Crétat, F., Lavorel, S., Austrheim, G., and Loison, A.: Co-variation between plant above-ground biomass and phenology in sub-alpine grasslands, Applied Vegetation Science, 16, 305–316, 2013.

Durand, Y., Laternser, M., Giraud, G., Etchevers, P., Lesaffre, B., and Mérindol, L.: Reanalysis of 44 yr of climate in the French Alps (1958–2002): methodology, model validation, climatology, and trends for air temperature and precipitation, Journal of Applied Meteorology and Climatology, 48, 429–449, 2009.

485 Engler, R., Randin, C. F., Vittoz, P., Czáka, T., Beniston, M., Zimmermann, N. E., and Guisan, A.: Predicting future distributions of mountain plants under climate change: does dispersal capacity matter?, Ecography, 32, 34–45, 2009.

Ferrez, Y.: Guide phytosociologique des prairies du massif des Vosges et du Jura alsacien, Conservatoire botanique national de Franche-Comté, 2017.

Filippa, G., Cremonese, E., Galvagno, M., Bayle, A., Choler, P., Bassignana, M., Piccot, A., Poggio, L., Oddi, L., Gascoin, S., et al.: On
490 the distribution and productivity of mountain grasslands in the Gran Paradiso National Park, NW Italy: A remote sensing approach, International Journal of Applied Earth Observation and Geoinformation, 108, 102 718, 2022.

Francon, L., Corona, C., Till-Bottraud, I., Choler, P., Carlson, B., Charrier, G., Améglio, T., Morin, S., Eckert, N., Roussel, E., et al.: Assessing the effects of earlier snow melt-out on alpine shrub growth: the sooner the better?, Ecological Indicators, 115, 106 455, 2020.

Frei, C. and Isotta, F. A.: Ensemble spatial precipitation analysis from rain gauge data: Methodology and application in the European Alps,
495 Journal of Geophysical Research: Atmospheres, 124, 5757–5778, 2019.

Frei, E. R., Ghazoul, J., and Pluess, A. R.: Plastic responses to elevated temperature in low and high elevation populations of three grassland species, PLoS One, 9, e98 677, 2014.

Frenzel, T.: Effects of grassland management on arthropod diversity, 2022.

Gartzia, M., Perez-Cabello, F., Bueno, C. G., and Alados, C. L.: Physiognomic and physiologic changes in mountain grasslands in response
500 to environmental and anthropogenic factors, Applied Geography, 66, 1–11, 2016.

Giaccone, E., Luoto, M., Vittoz, P., Guisan, A., Mariéthoz, G., and Lambiel, C.: Influence of microclimate and geomorphological factors on alpine vegetation in the Western Swiss Alps, Earth Surface Processes and Landforms, 44, 3093–3107, 2019.

Gillet, F., Mauchamp, L., Badot, P.-M., and Mouly, A.: Recent changes in mountain grasslands: a vegetation resampling study, Ecology and Evolution, 6, 2333–2345, 2016.

505 Goepp, S.: Origine, histoire et dynamique des Hautes-Chaumes du massif vosgien. Déterminismes environnementaux et actions de l'Homme, Ph.D. thesis, Université Louis Pasteur-Strasbourg I, 2007.

Graae, B. J., Vandvik, V., Armbruster, W. S., Eiserhardt, W. L., Svenning, J.-C., Hylander, K., Ehrlén, J., Speed, J. D., Klanderud, K., Bråthen, K. A., et al.: Stay or go–how topographic complexity influences alpine plant population and community responses to climate change, Perspectives in Plant Ecology, Evolution and Systematics, 30, 41–50, 2018.

510 Grignolio, S., Parrini, F., Bassano, B., Luccarini, S., and Apollonio, M.: Habitat selection in adult males of Alpine ibex, Capra ibex ibex, FOLIA ZOOLOGICA-PRAHA-, 52, 113–120, 2003.

Grigulis, K. and Lavorel, S.: Simple field-based surveys reveal climate-related anomalies in mountain grassland production, Ecological Indicators, 116, 106 519, 2020.

Gudex-Cross, D., Keyser, S. R., Zuckerberg, B., Fink, D., Zhu, L., Pauli, J. N., and Radeloff, V. C.: Winter Habitat Indices (WHIs) for the
515 contiguous US and their relationship with winter bird diversity, Remote Sensing of Environment, 255, 112 309, 2021.

Herberich, M. M., Schädle, J. E., and Tielbörger, K.: Plant community productivity and soil water are not resistant to extreme experimental drought in temperate grasslands but in the understory of temperate forests, Science of The Total Environment, p. 164625, 2023.

Herrault, P.-A., Ullmann, A., and Ertlen, D.: Statistical analysis to investigate phenology of low mountain grasslands [Data]. https://zenodo.org/doi/10.5281/zenodo.10204065, Zenodo repository, 2024a.

520 Herrault, P.-A., Ullmann, A., and Ertlen, D.: Statistical analysis to investigate phenology of low mountain grasslands [Software]. Github. https://github.com/herrault/Article-Phenology-of-Low-Mountain-Grasslands/tree/main, Github repository, 2024b.

Hua, X., Ohlemüller, R., and Sirguey, P.: Differential effects of topography on the timing of the growing season in mountainous grassland ecosystems, Environmental Advances, 8, 100 234, 2022.

Huelber, K., Bardy, K., and Dullinger, S.: Effects of snowmelt timing and competition on the performance of alpine snowbed plants, Per-
525 spectives in Plant Ecology, Evolution and Systematics, 13, 15–26, 2011.

Inouye, D. W.: The ecological and evolutionary significance of frost in the context of climate change, Ecology letters, 3, 457–463, 2000.

Inouye, D. W.: Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers, Ecology, 89, 353–362, 2008.

Jonas, T., Rixen, C., Sturm, M., and Stoeckli, V.: How alpine plant growth is linked to snow cover and climate variability, Journal of
530 Geophysical Research: Biogeosciences, 113, 2008.

Jump, A. S. and Peñuelas, J.: Running to stand still: adaptation and the response of plants to rapid climate change, Ecology letters, 8, 1010–1020, 2005.

Keppel, G. and Wardell-Johnson, G. W.: Refugia: keys to climate change management, Global change biology, 18, 2389–2391, 2012.

Keppel, G., Robinson, T. P., Wardell-Johnson, G. W., Yates, C. J., Van Niel, K. P., Byrne, M., and Schut, A. G.: A low-altitude mountain
535 range as an important refugium for two narrow endemics in the Southwest Australian Floristic Region biodiversity hotspot, Annals of Botany, 119, 289–300, 2017.

Klein, G., Rebetez, M., Rixen, C., and Vitasse, Y.: Unchanged risk of frost exposure for subalpine and alpine plants after snowmelt in Switzerland despite climate warming, International Journal of Biometeorology, 62, 1755–1762, 2018.

Ledoux, E., Girard, G., De Marsily, G., Villeneuve, J., and Deschenes, J.: Spatially distributed modeling: conceptual approach, coupling
540 surface water and groundwater, Unsaturated flow in hydrologic modeling: Theory and practice, pp. 435–454, 1989.

Lenoir, J., Gégout, J.-C., Marquet, P. A., de Ruffray, P., and Brisse, H.: A significant upward shift in plant species optimum elevation during the 20th century, science, 320, 1768–1771, 2008.

Lewińska, K. E., Ives, A. R., Morrow, C. J., Rogova, N., Yin, H., Elsen, P. R., de Beurs, K., Hostert, P., and Radeloff, V. C.: Beyond "greening" and "browning": Trends in grassland ground cover fractions across Eurasia that account for spatial and temporal autocorrelation, Global Change Biology, 2023.

Lindstrom, M. J. and Bates, D. M.: Nonlinear mixed effects models for repeated measures data, Biometrics, pp. 673–687, 1990.

Liu, Q., Piao, S., Janssens, I. A., Fu, Y., Peng, S., Lian, X., Ciais, P., Myneni, R. B., Peñuelas, J., and Wang, T.: Extension of the growing season increases vegetation exposure to frost, Nature communications, 9, 426, 2018.

Luo, M., Meng, F., Sa, C., Duan, Y., Bao, Y., Liu, T., and De Maeyer, P.: Response of vegetation phenology to soil moisture dynamics in the Mongolian Plateau, Catena, 206, 105 505, 2021.

Marchin, R. M., McHugh, I., Simpson, R. R., Ingram, L. J., Balas, D. S., Evans, B. J., and Adams, M. A.: Productivity of an Australian mountain grassland is limited by temperature and dryness despite long growing seasons, Agricultural and Forest Meteorology, 256, 116–124, 2018.

Möhl, P., von Büren, R. S., and Hiltbrunner, E.: Growth of alpine grassland will start and stop earlier under climate warming, Nature Communications, 13, 7398, 2022.

Murray, L., Nguyen, H., Lee, Y.-F., Remmenga, M. D., and Smith, D. W.: Variance inflation factors in regression models with dummy variables, 2012.

Myers-Smith, I. H., Elmendorf, S. C., Beck, P. S., Wilmking, M., Hallinger, M., Blok, D., Tape, K. D., Rayback, S. A., Macias-Fauria, M., Forbes, B. C., et al.: Climate sensitivity of shrub growth across the tundra biome, Nature climate change, 5, 887–891, 2015.

Nagelmüller, S., Hiltbrunner, E., and Körner, C.: Low temperature limits for root growth in alpine species are set by cell differentiation, AoB Plants, 9, plx054, 2017.

Nicod, C. and Gillet, F.: Recent changes in mountain hay meadows of high conservation value in eastern France, Applied Vegetation Science, 24, e12 573, 2021.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., et al.: Plant phenotypic plasticity in a changing climate, Trends in plant science, 15, 684–692, 2010.

Noilhan, J. and Mahfouf, J.-F.: The ISBA land surface parameterisation scheme, Global and planetary Change, 13, 145–159, 1996.

Opedal, Ø. H., Armbruster, W. S., and Graae, B. J.: Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape, Plant Ecology & Diversity, 8, 305–315, 2015.

Pardee, G. L., Inouye, D. W., and Irwin, R. E.: Direct and indirect effects of episodic frost on plant growth and reproduction in subalpine wildflowers, Global Change Biology, 24, 848–857, 2018.

Pepin, N., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., Seibert, P., Serafin, S., Schöner, W., et al.: Climate changes and their elevational patterns in the mountains of the world, Reviews of Geophysics, 60, e2020RG000 730, 2022.

Piao, S., Mohammat, A., Fang, J., Cai, Q., and Feng, J.: NDVI-based increase in growth of temperate grasslands and its responses to climate changes in China, Global Environmental Change, 16, 340–348, 2006.

Plantureux, S., Peeters, A., and McCracken, D.: Biodiversity in intensive grasslands: Effect of management, improvement and challenges, Agronomy research, 3, 153–164, 2005.

Revuelto, J., Billecocq, P., Tuzet, F., Cluzet, B., Lamare, M., Larue, F., and Dumont, M.: Random forests as a tool to understand the snow depth distribution and its evolution in mountain areas, Hydrological Processes, 34, 5384–5401, 2020.

Revuelto, J., Gómez, D., Alonso-González, E., Vidaller, I., Rojas-Heredia, F., Deschamps-Berger, C., García-Jiménez, J., Rodríguez-López, G., Sobrino, J., Montorio, R., et al.: Intermediate snowpack melt-out dates guarantee the highest seasonal grasslands greening in the Pyrenees, Scientific Reports, 12, 18 328, 2022.

Rigal, S., Devictor, V., and Dakos, V.: A method for classifying and comparing non-linear trajectories of ecological variables, Ecological Indicators, 112, 106 113, 2020.

Ropars, P. and Boudreau, S.: Shrub expansion at the forest–tundra ecotone: spatial heterogeneity linked to local topography, Environmental Research Letters, 7, 015 501, 2012.

Sauer, J., Domisch, S., Nowak, C., and Haase, P.: Low mountain ranges: summit traps for montane freshwater species under climate change, Biodiversity and Conservation, 20, 3133–3146, 2011.

Scherrer, D. and Koerner, C.: Infra-red thermometry of alpine landscapes challenges climatic warming projections, Global Change Biology, 16, 2602–2613, 2010.

Schönbein, J. and Schneider, C.: Snow cover variability in the Black Forest region as an example of a German low mountain range under the influence of climate change, in: EGS-AGU-EUG Joint Assembly, p. 5993, 2003.

Siebenkäs, A., Schumacher, J., and Roscher, C.: Phenotypic plasticity to light and nutrient availability alters functional trait ranking across eight perennial grassland species, AoB Plants, 7, plv029, 2015.

Soubeyroux, J.-M., Martin, E., Franchisteguy, L., Habets, F., Noilhan, J., Baillon, M., Regimbeau, F., Vidal, J.-P., Le Moigne, P., and Morel, S.: Safran-Isba-Modcou (SIM): Un outil pour le suivi hydrométéorologique opérationnel et les études, La Météorologie, pp. PP–40, 2008.

Starr, G. and Oberbauer, S. F.: Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance, Ecology, 84, 1415–1420, 2003.

Stevens, C. J., Lind, E. M., Hautier, Y., Harpole, W. S., Borer, E. T., Hobbie, S., Seabloom, E. W., Ladwig, L., Bakker, J. D., Chu, C., et al.: Anthropogenic nitrogen deposition predicts local grassland primary production worldwide, Ecology, 96, 1459–1465, 2015.

Tape, K. D., Hallinger, M., Welker, J. M., and Ruess, R. W.: Landscape heterogeneity of shrub expansion in Arctic Alaska, Ecosystems, 15, 711–724, 2012.

Tomaszewska, M. A., Nguyen, L. H., and Henebry, G. M.: Land surface phenology in the highland pastures of montane Central Asia: Interactions with snow cover seasonality and terrain characteristics, Remote Sensing of Environment, 240, 111 675, 2020.

Vionnet, V., Six, D., Auger, L., Dumont, M., Lafaysse, M., Quéno, L., Réveillet, M., Dombrowski-Etchevers, I., Thibert, E., and Vincent, C.: Sub-kilometer precipitation datasets for snowpack and glacier modeling in Alpine terrain, Frontiers in Earth Science, 7, 182, 2019.

Wahl, L., Planchon, O., and David, P.-M.: Névés, corniches et risque d'avalanche dans les Hautes-Vosges. En hommage à Laurent Wahl, décédé le 18 décembre 2008, Revue Géographique de l'Est, 47, 2007.

Wang, H., Liu, H., Cao, G., Ma, Z., Li, Y., Zhang, F., Zhao, X., Zhao, X., Jiang, L., Sanders, N. J., et al.: Alpine grassland plants grow earlier and faster but biomass remains unchanged over 35 years of climate change, Ecology Letters, 23, 701–710, 2020.

Welker, J., Fahnestock, J., Sullivan, P., and Chimner, R.: Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska, Oikos, 109, 167–177, 2005.

Winkler, D. E., Lin, M. Y.-C., Delgadillo, J., Chapin, K. J., and Huxman, T. E.: Early life history responses and phenotypic shifts in a rare endemic plant responding to climate change, Conservation Physiology, 7, coz076, 2019.

Wipf, S., Stoeckli, V., and Bebi, P.: Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing, Climatic change, 94, 105–121, 2009.

Yang, J., Dong, J., Xiao, X., Dai, J., Wu, C., Xia, J., Zhao, G., Zhao, M., Li, Z., Zhang, Y., et al.: Divergent shifts in peak photosynthesis timing of temperate and alpine grasslands in China, Remote Sensing of Environment, 233, 111 395, 2019.

Zeeman, M., Mauder, M., Steinbrecher, R., Heidbach, K., Eckart, E., and Schmid, H.: Reduced snow cover affects productivity of upland temperate grasslands, Agricultural and Forest Meteorology, 232, 514–526, 2017.

620   Zhu, L., Radeloff, V. C., and Ives, A. R.: Characterizing global patterns of frozen ground with and without snow cover using microwave and MODIS satellite data products, Remote Sensing of Environment, 191, 168–178, 2017.