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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 Change 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 no significant trends indicating 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 Change 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 Change (CC) 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

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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 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). 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 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 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 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). Their ability to adapt may also depend on their traits, whether structural (i.e. Surface Leaf Area) or related to their metabolism (Bucher et al., 2018); for these reasons, contextual effects are expected to be numerous, namely due to high terrain complexity (Hua et al., 2022).

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 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 (Carlson et al., 2017; Piao et al., 2006). For mountain grasslands, earliers works found 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). In term of performance, warming increased productivity when the soil water recharge present sufficient levels regarding air temperatures (Choler et al., 2021; Filippa et al., 2022). It also promoted longer plant growth due to increased early and late plant growth (Cao et al., 2015; Carlson et al., 2017; Yang et al., 2019; Wang et al., 2014).

Remote sensing studies are the most widespread to describe large-scale patterns of productivity and phenology for mountain grasslands (Choler, 2015; Xie et al., 2020; Filippa et al., 2022; Carlson et al., 2017). They also show a large spatial variability in the recorded signal at the mountain range scale both between and within-sites (Gartzia et al., 2016; Tomaszewska et al., 2020). Nonetheless, few studies focused on the analysis of drivers that can explain this spatial variability. Recently, an analysis conducted in the Alps by (Choler et al., 2021) demonstrated significant effects of several types of factors on greening trends such as topography (altitude and exposure), physiology (number of growing degree days), and climate (evapotranspiration/precipitation balance). Furthermore, complex interaction effects between climate and topography were already underlined (Ropars and Boudreau, 2012; Tape et al., 2012; Graae et al., 2018; Choler et al., 2021). Plant community responses of mountain grasslands are strongly dependent on the spatial structure of the massif mountain range in which they occur (Körner, 2004; Slavich et al., 2014).

MODIS time series have several advantages for jointly investigating large-scale snow and vegetation dynamics over a long time period. These products are available worldwide, have interesting temporal coverage (20 years), and have been used to reconstruct phenological variables in temperate mountain range (Filippa et al., 2022; Choler et al., 2021). Other studies have proposed their use to reconstruct dynamic variables such as Dynamic Habitat Indexes (DHI) or Winter Habitat Indexes (WHI), allowing the discrimination of unique biodiversity patterns through their combination (Radeloff et al., 2019; Gudex-Cross et al., 2021). This notably offers the potential to understand plant community processes at large scales which remains largely underdiscussed (Dronova and Taddeo, 2022). Interestingly, WHIs provide functional measures of snow conditions, adapted to cold related species. In addition to snow cover duration, it calculates Frozen Ground Without Snow by combining MODIS and temperature data, which approximates the frequency with which plants lack thermal refugia (i.e., the subnivium) and thus face functionally colder climates. Although exposure to freezing is widely discussed in studies dealing with productivity or phenology of grasslands, it is ultimately very poorly measured at large scales (Gudex-Cross et al., 2021). Snow cover variability is also calculated and describes the frequency with which an area switches from snow-covered to free of snow, quantifies freeze-thaw events, and identifies ecologically critical transition zones from snow to rain dominated systems. Low mountain ranges being affected by high intraseasonal snow cover variability, the latter variables could be of high interest to understand snow phenology effects on growth response of mountain grasslands.

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, 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, Meum Athamanticum Jacq. 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 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

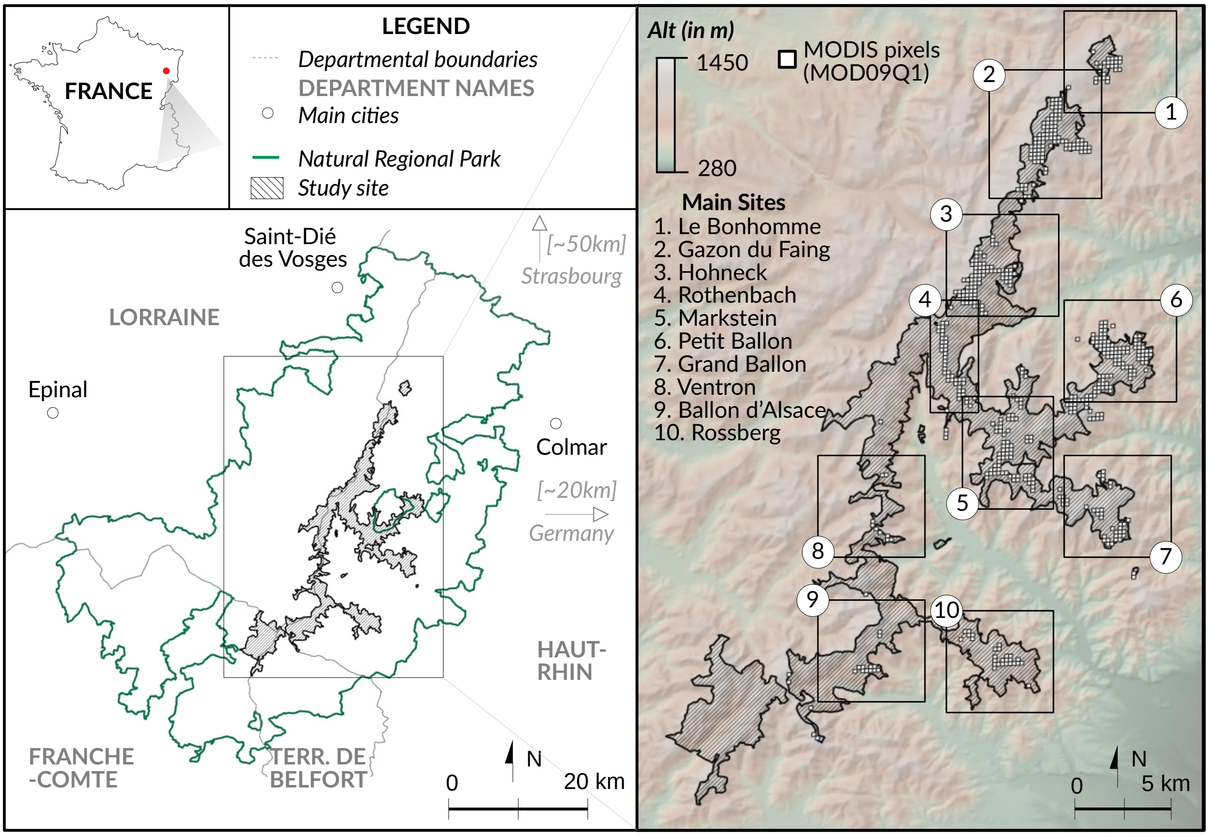

Figure 1. (Left) Location map of the study area; (Right) Distribution of the MODIS pixels selected across the ten sites in the Vosges mountains

ten sites from North to South such as Le 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 were calculated:

1. The Peak of Value (PkV) is the maximum NDVI (NDVImax) registered during the year. 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 ff 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

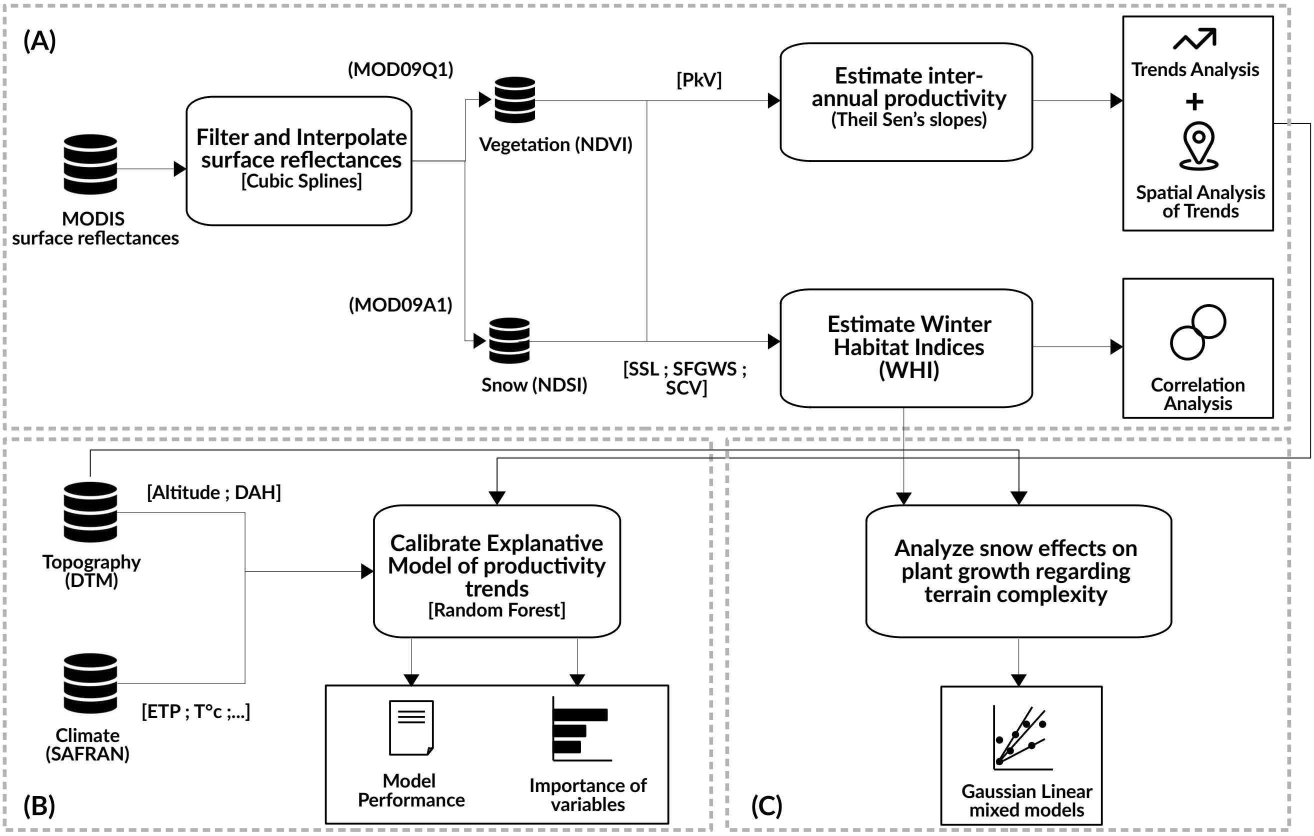

Figure 2. Detailed flowchart of the methodology applied in this study to understand the growth response of mountain grasslands in the Vosges mountains range. Three main stages were identified : the stage (A) aims at estimating phenological indicators and calculating interannual productivity trends; (B) 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 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 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).

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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). 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 first 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 to classify NDVImax trends into three categories: no significant greening, positive greening, and negative greening (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).

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

2.5.2 Linking Winter Habitat Indices with Phenometrics

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).

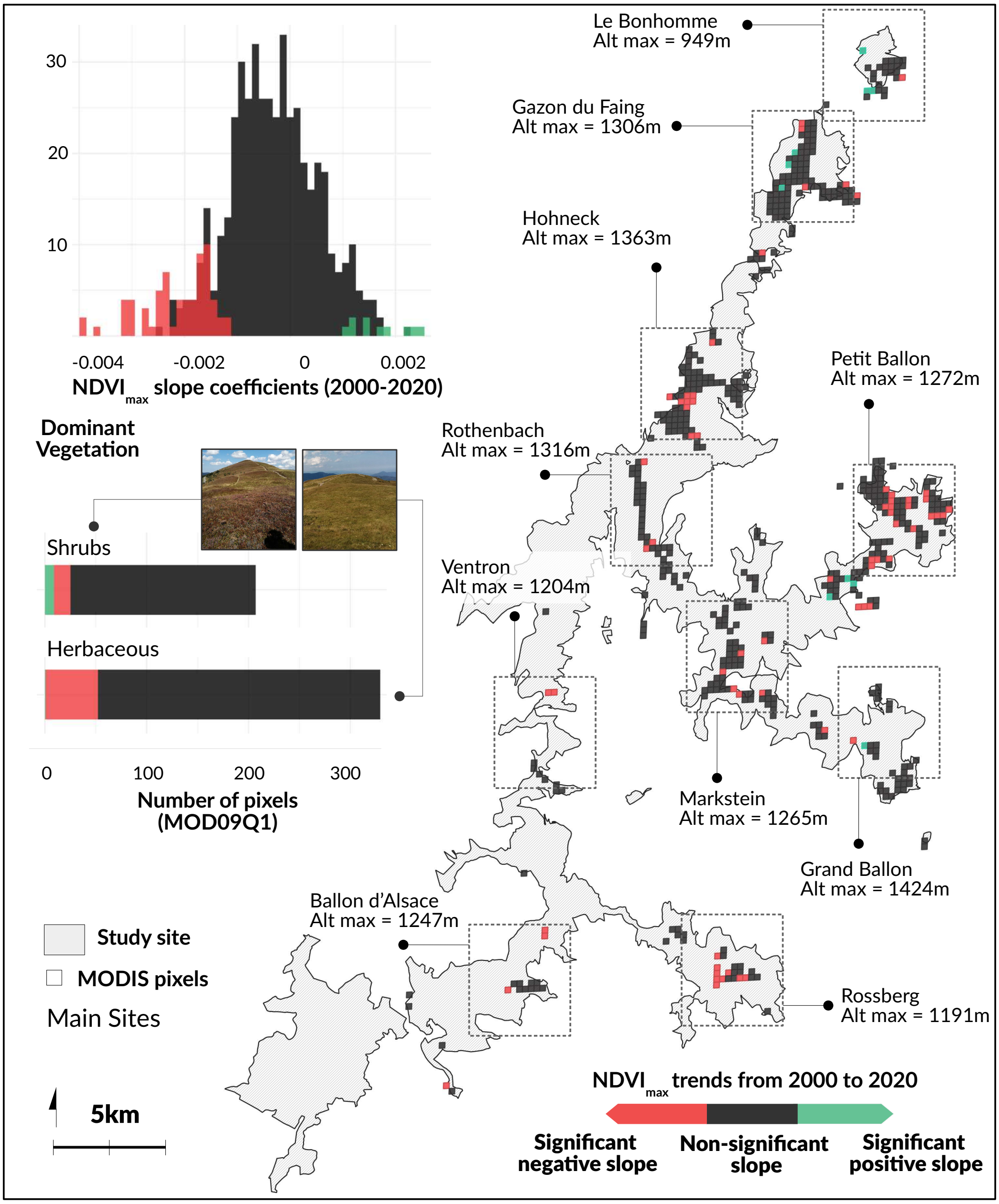

Figure 3. (a) Spatial distribution of NDVI$_{max}$ trends. The color represents the categories of NDVI$_{max}$ trends over the 2000-2020 period (red = significant negative NDVI$_{max}$ slope/browning; black = no significant NDVI$_{max}$ slope; green = significant positive NDVI$_{max}$ slope/-greening). 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.

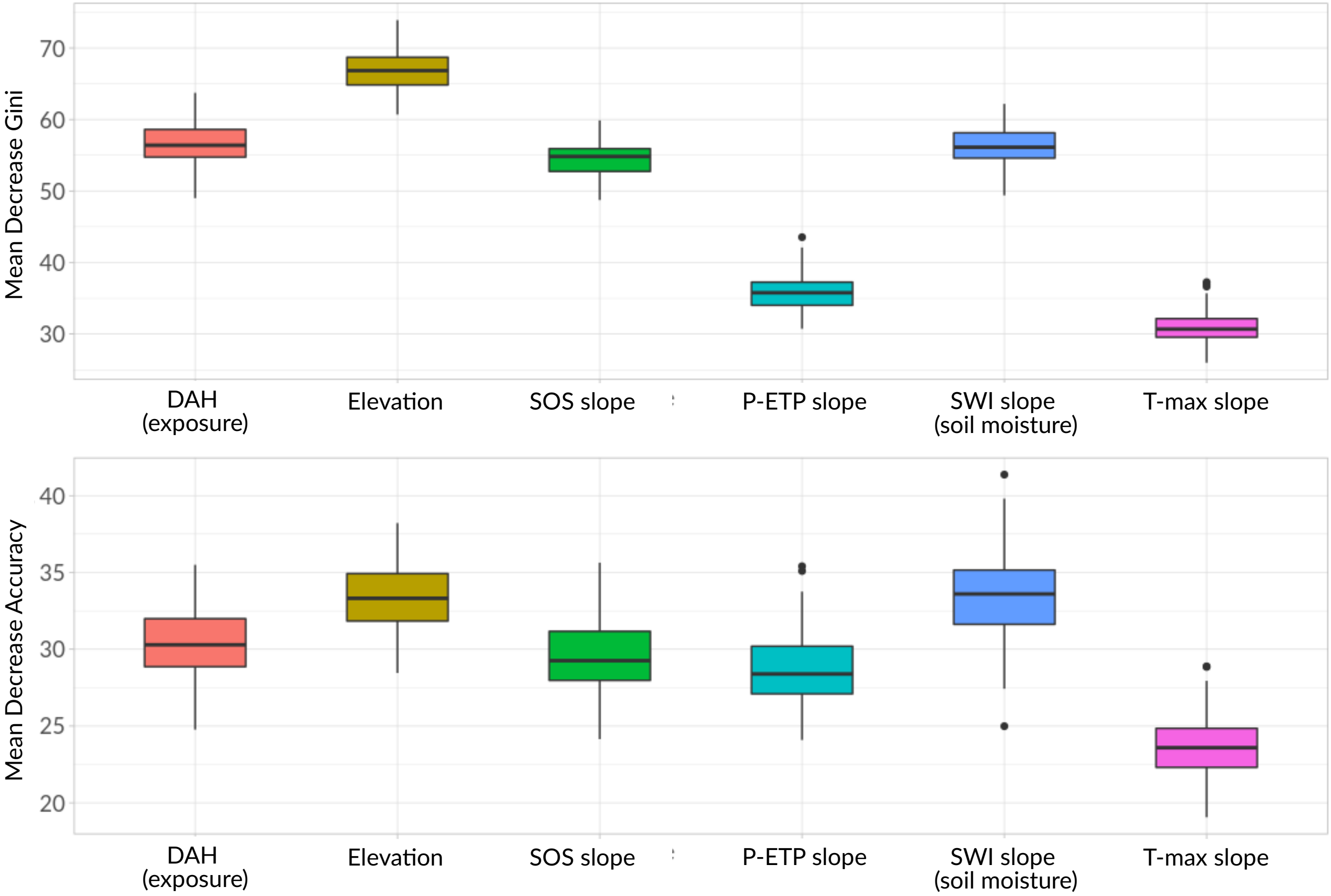

Figure 4. (at the top) Contribution of predictors to the purity of nodes and leaves based on Mean Decrease Gini coefficient. (at the bottom) Predictor importance ranking based on Mean Decrease in Accuracy (MDA) scores.

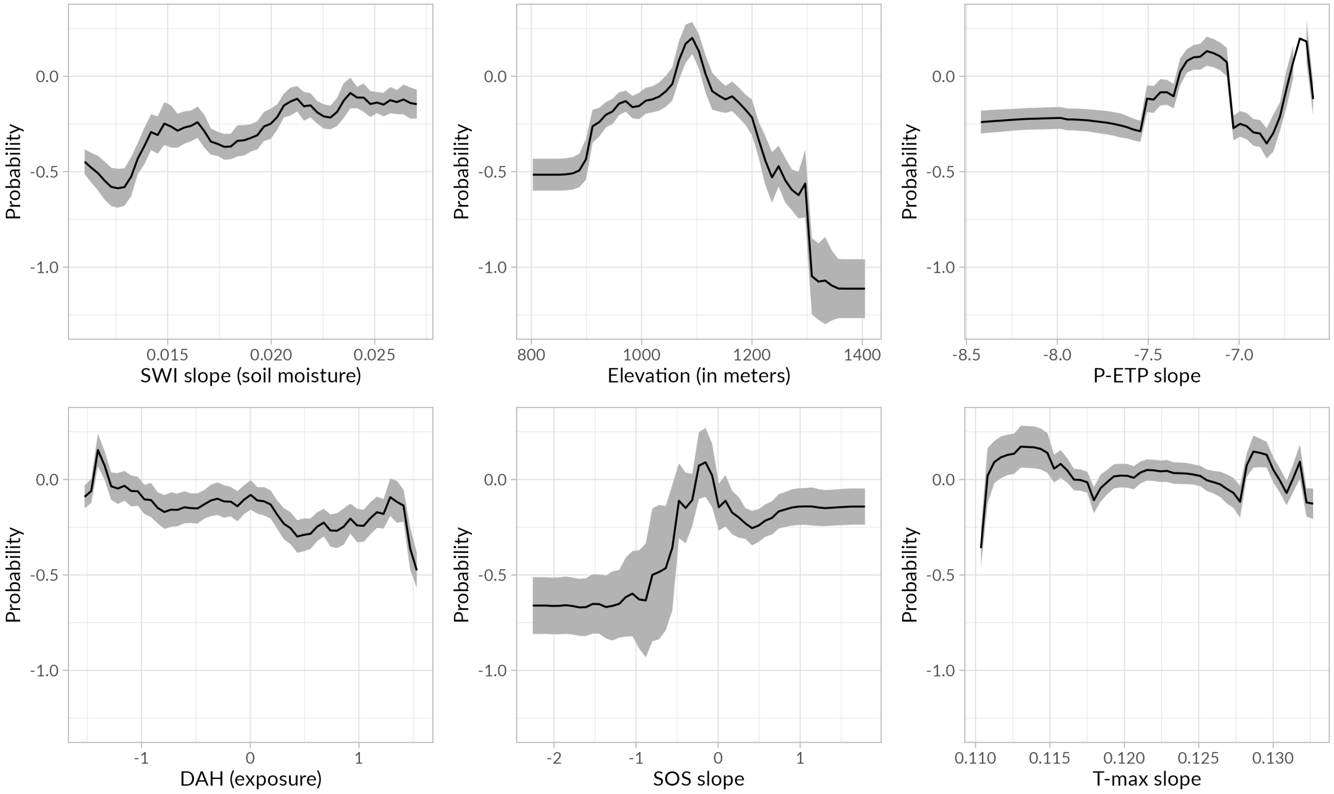

Figure 5. Partial dependence plots illustrating the feature contribution of the six predictors to the browning class (the significant negative NDVImax slope). Each graph represents the influence (intensity and direction, positive or negative) of each predictor. The x-axis represents the value of the 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	***

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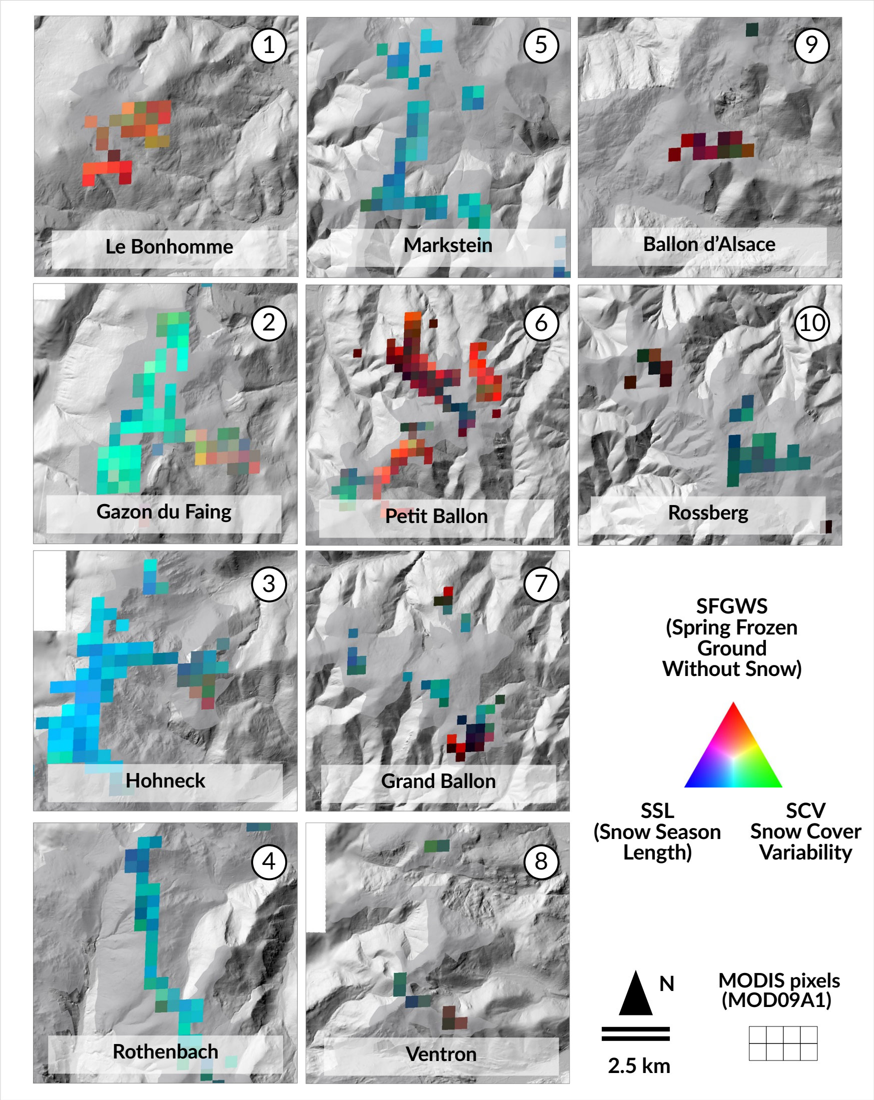

Figure 6. Composite spatial patterns in the MODIS WHIs from 2000-2001 to 2019-2020 highlighting areas with distinct snow cover dynamics across the Vosges mountains. The Spring Frozen Ground Without Snow (SFGWS) is in red, the Snow Season Length (SSL) is in blue and the Snow Cover Variability (SCV) is 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

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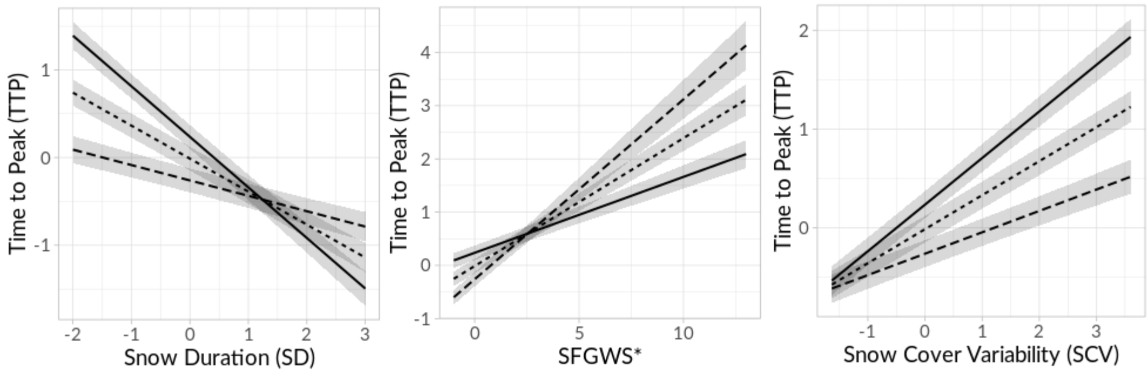
was associated with an increase of PkV (slope estimate = 0.03; $p < 0.001$), and a decrease of the TTP (slope estimate = -0.24; $p < 0.001$). DAH had no independent significant effect on PkV and TTP. Snow Discontinuity was the variable with the largest effect (positive) on TTP (slope estimate = 0.34; $p < 0.001$). 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, 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; $p < 0.001$).

(a) Snow-altitude effects



(b) Snow-exposure effects

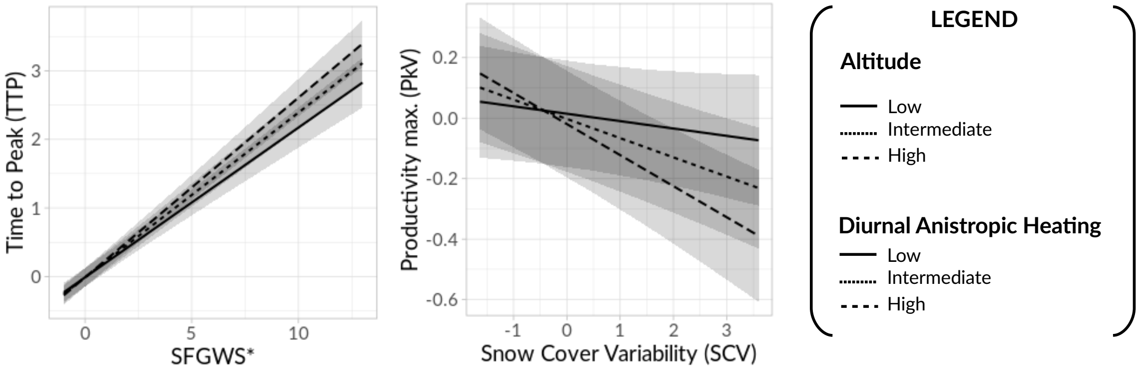


Figure 7. Predicted effects of significant snow-terrain variables interaction on the growth response of mountain grasslands. Estimates resulting from linear moxed models; see Table 1. SFGWS* = Spring Frozen Ground Without Snow

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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 Change. 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 Change, 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 obvioulsy 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 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 porososity 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

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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 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 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 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 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 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 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 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, 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 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 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.

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 .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.

Appendix A: Appendix

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

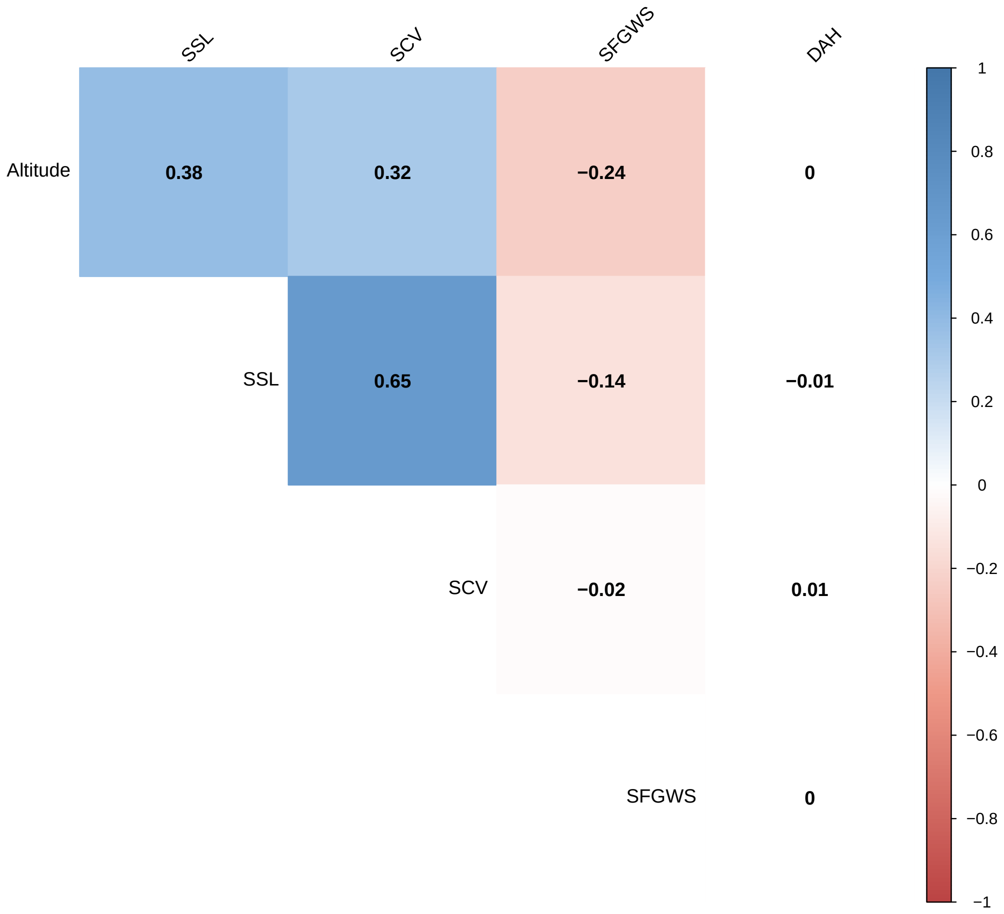

Figure A1. Pearson Correlation matrix between covariates included in the linear mixed models. Two digits after comma are shown. Blue squares represent significant positive associations between two variables, red squares the significant negative associations while the white squares indicate no significant relationships between two covariates. Significance level at 0.05 was used.

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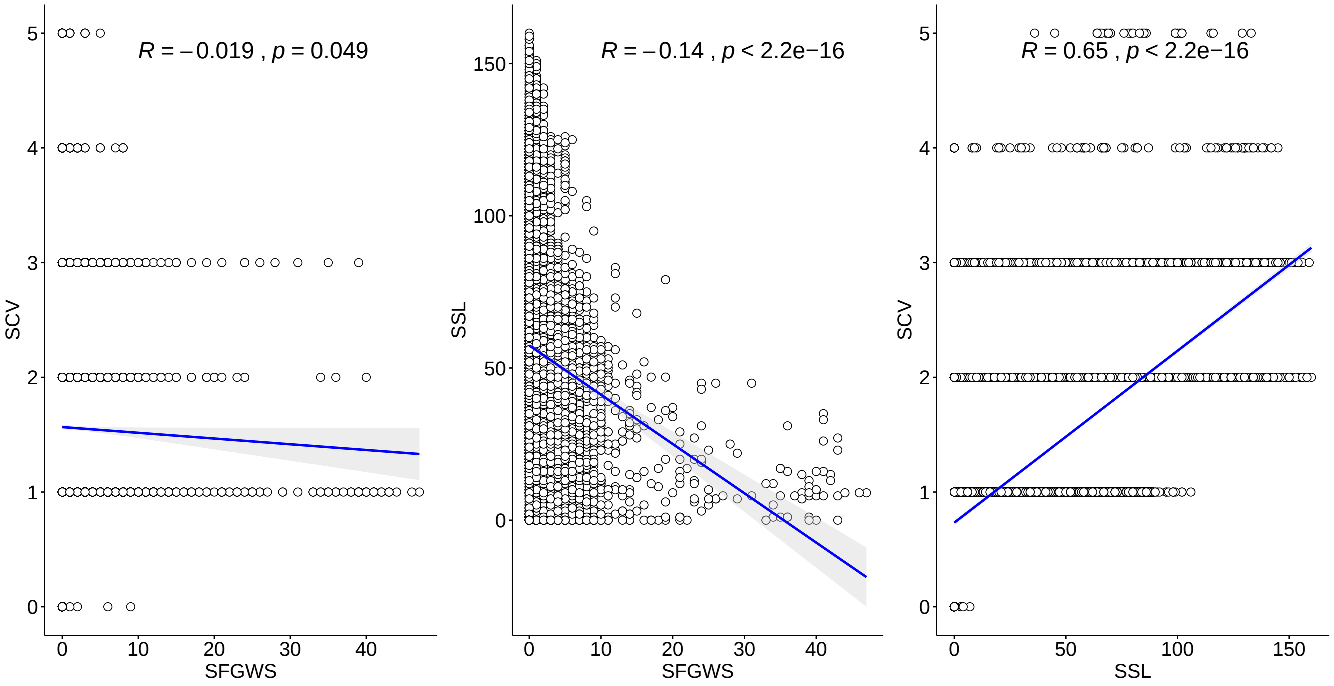

Figure A2. Scatterplot of WHI indices. R corresponds to Pearson's Rho and p is the p-value of the significance test

Le dégagement de la route des Crêtes : 4.000 m^3 de neige déblayés au Markstein

La phase finale pour la percée du Markstein entre deux murs de neige et de glace de 10 m de haut.
(PHOTO·DN)

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.

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