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## The tempo of greening in the European Alps: Spatial variations on a common theme

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## **Title**

1 The tempo of greening in the European Alps: spatial variations on a common theme

## **Running Title:**

3 The tempo of greening in the European Alps

4

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mountain ecosystems - climate change - European Alps - greening - NDVI - remote sensing

## Abstract

20           The long-term increase of satellite-based proxies of vegetation cover is a well-  
21 documented response of seasonally snow-covered ecosystems to climate warming. However,  
22 observed greening trends are far from being uniform and substantial uncertainty remains  
23 concerning the underlying causes of this spatial variability. Here, we processed surface  
24 reflectance of the moderate resolution imaging spectroradiometer (MODIS) to investigate  
25 trends and drivers of changes in the annual peak values of the Normalized Difference  
26 Vegetation Index (NDVI). Our study focuses on the above treeline ecosystems in the  
27 European Alps. The NDVI changes of these ecosystems are highly sensitive to land cover and  
28 biomass changes and are marginally affected by anthropogenic disturbances. We found a  
29 widespread greening for the period 2000-2020, a pattern that is consistent with the overall  
30 increase of summer temperature. At the local scale, the spatial variability of greening was  
31 mainly due to the preferential response of north-facing slopes between 1900 m and 2400 m.  
32 Using high resolution imagery, we noticed that the presence of screes and outcrops  
33 exacerbated this response. At the regional scale, we identified hotspots of greening where  
34 vegetation cover is sparser than expected given the elevation and exposure. Most of these  
35 hotspots experienced delayed snowmelt and green-up dates in recent years. We conclude that  
36 the ongoing greening in the Alps primarily reflects the high responsiveness of sparsely  
37 vegetated ecosystems that benefitted the most from temperature and water-related habitat  
38 amelioration above treeline.  
39

## Introduction

40           The long-term increase of greenness in cold, seasonally snow-covered ecosystems is  
41 widely perceived as a consequence of climate change (Berner et al., 2020; Keenan & Riley,  
42 2018) . Arctic and alpine ecosystems have undergone particularly fast greening compared to  
43 other ecosystems and this is consistent with the accelerated warming documented for these  
44 regions (Callaghan et al., 2010; Pepin et al., 2015). However, this greening exhibits  
45 considerable spatial and temporal variability that is far from being understood (Berner et al.,  
46 2020; Cortés et al., 2021; Ju & Masek, 2016; Myers-Smith et al., 2020). The complex  
47 interaction between regional climate trends, topography, geomorphological and other  
48 disturbance regimes and vegetation dynamics contributes to these non-uniform patterns of  
49 greening (Ropars & Boudreau, 2012; Tape, Hallinger, Welker, & Ruess, 2012). Further  
50 studies are required to document the relative contribution of these drivers and to advance a  
51 more predictive understanding of greening and its consequences on ecosystem processes and  
52 services (Duveiller, Hooker, & Cescatti, 2018; Forzieri, Alkama, Miralles, & Cescatti, 2017;  
53 Myers-Smith et al., 2020; Zhu et al., 2016).

54           Temperate mountains have experienced warmer summers over the last decades  
55 (Beniston, 2006; Hock et al., 2019). Several studies have underlined the impact of these  
56 changes on land surface phenology (Asam et al., 2018; Dunn & de Beurs, 2011; Xie et al.,  
57 2020; Zhang, Zhang, Dong, & Xiao, 2013), ecosystem productivity (Choler, 2015; Jolly,  
58 Dobbertin, Zimmermann, & Reichstein, 2005), and species richness (Lamprecht, Semenchuk,  
59 Steinbauer, Winkler, & Pauli, 2018; Steinbauer et al., 2018). Other studies reported on the  
60 long-term increase of greenness in the south-western Alps (Carlson et al., 2017; Filippa et al.,  
61 2019), the Hindu Kush (Anderson et al., 2020) and underlined the particular responsiveness of  
62 sparsely vegetated areas located in the nival belt. However, none of these studies has provided  
63 a comprehensive analysis of the spatial variability of greening at the mountain range scale and

64 an investigation of its determinants. More specifically, the distinction between exposure to  
65 change (e.g. climate) and the responsiveness of ecosystems to change has remained elusive.  
66 Yet, well-documented case studies in the Arctic suggest that this fundamental question may  
67 underpin much of the observed spatial complexity of greening. For example, the preferential  
68 expansion of arctic shrubs in particular topographical situations - such as along streams or in  
69 floodplains, lead to local-scale greening heterogeneity (Tape, Sturm, & Racine, 2006), which  
70 in turn is possibly related to the snow-holding capacity of shrubs in winter (Sturm et al., 2005).  
71 The initial cover of *Betula glandulosa* in the 1950s explained part of the spatial variability of  
72 greening in Nunavik (Ropars & Boudreau, 2012; Ropars, Levesque, & Boudreau, 2015).  
73 These studies pointed out that land cover properties are pivotal to predict the responsiveness  
74 of the system to on-going changes and to identify the underlying ecological mechanisms of  
75 greening.

76         There is a growing body of evidence showing that mountain ecosystems of the Alps  
77 have undergone rapid changes in response to climate warming (Gottfried et al., 2012). Plot-  
78 based long-term surveys revealed increasing vegetation cover in mountain grasslands, mainly  
79 due to the expansion of graminoids (Rogora et al., 2018) and a colonization of scree and  
80 outcrops by shrubs and trees (Vittoz, Bodin, Ungricht, Burga, & Walther, 2008). While these  
81 studies are invaluable to inform on ecological mechanisms underpinning ecological changes,  
82 their paucity precludes tracking complex, non-linear responses along topographical,  
83 geomorphological and climate gradients. For example, winter snow duration - which is widely  
84 acknowledged as a key driver of vegetation dynamics - for the time being shows decreased  
85 sensitivity to global warming at elevations above 2000 m (Hantel & Hirtl-Wielke, 2007;  
86 Schoener, Koch, Matulla, Marty, & Tilg, 2019). Another issue is the overrepresentation of  
87 high summits in plot-based surveys, considering that the area they cover represents a minute  
88 fraction of the land above treeline. For these reasons, remote sensing offers a complementary

89 approach to probe ongoing land cover changes at a scale encompassing multiple  
90 environmental gradients and to examine their impacts on ecosystem services such as water  
91 provisioning, carbon sequestration or pastoral resources.

92 Here, we exploit available time series of the moderate resolution imaging  
93 spectroradiometer (MODIS) to provide a comprehensive picture of recent greening and its  
94 spatial variability in the European Alps and to improve our understanding of its drivers. Our  
95 study utilizes annual peak values of the Normalized Difference Vegetation Index (NDVI) as a  
96 proxy of land surface greenness (Tucker, 1979). We quantified the significance and  
97 magnitude of NDVI trends for high elevation ecosystems that are located between the treeline  
98 and the permanent snowline. This allows us to overcome two potential issues in such remote  
99 sensing studies. First, high elevation ecosystems are less affected by anthropogenic  
100 disturbances than other European habitats at lower elevation, which should facilitate the  
101 unraveling of a climate signal on greening trends (Filippa et al., 2019; Gehrig-Fasel, Guisan,  
102 & Zimmermann, 2007). Second, the NDVI range of these ecosystems lies in a range where it  
103 is highly sensitive to land cover and biomass changes, in contrast to closed canopies where  
104 NDVI no longer linearly depends on biomass or plant cover (Huete et al., 2002; Myneni &  
105 Williams, 1994).

106 We addressed the three following questions:

- 107 1. How widespread is the greening signal in above-treeline ecosystems of the  
108 European Alps?
- 109 2. Is the variability of greening spatially structured and what are its main drivers?
- 110 3. Are there fine scale land cover features that predispose to fast greening response?

## **Material and methods**

111 *Study area and selection of pixels*

112           The European Alps is a mountain range stretching over 1'200 km from Nice (France)  
113 to Vienna (Austria). Our study focuses on the uplands of the massif that are located between  
114 the treeline and the permanent snowline. This area includes shrublands, grasslands and  
115 sparsely vegetated ecosystems established on screes, debris, and outcrops. We first selected a  
116 set of 250-m resolution MODIS pixels having non-forested land cover classes with a tree  
117 cover density below 5%, an elevation above 1400 m and an average NDVImax above 0.15.  
118 To do so, we relied on a 25-m resolution Digital Elevation Model, a 100-m resolution Tree  
119 Cover Density of year 2018 ([https://land.copernicus.eu/pan-european/high-resolution-](https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/)  
120 [layers/forests/tree-cover-density/](https://land.copernicus.eu/pan-european/high-resolution-layers/forests/tree-cover-density/)) and the Corine Land Cover (CLC) product of year 2018  
121 (<https://land.copernicus.eu/pan-european/corine-land-cover/>), which is based on the visual  
122 photointerpretation of aerial images at a 100-m resolution. From the 44 CLC entries at level 3,  
123 we retained the following classes: Pastures (code 2.3.1), Natural grasslands (code 3.2.1),  
124 Moors and heathlands (code 3.2.2), Bare Rocks (code 3.3.2), Sparsely vegetated (code 3.3.3).  
125 We merged pastures and grasslands and we renamed the misleading “bare rocks” to “very  
126 sparsely vegetated” as we selected pixels with an average NDVImax above 0.15, i.e. not  
127 completely devoid of vegetation. We discarded pixels exhibiting more than 10% of  
128 settlements (ski resorts) or permanent water using data layers of European settlements  
129 (<https://land.copernicus.eu/pan-european/GHSL/european-settlement-map/>) and of permanent  
130 water ([https://land.copernicus.eu/pan-european/high-resolution-layers/water-wetness/status-](https://land.copernicus.eu/pan-european/high-resolution-layers/water-wetness/status-maps/water-wetness-2018)  
131 [maps/water-wetness-2018](https://land.copernicus.eu/pan-european/high-resolution-layers/water-wetness/status-maps/water-wetness-2018)). We also removed pixels for which we found significant abrupt  
132 changes of NDVImax within the period 2000-2020, as this might be indicative of a physical  
133 or anthropogenic disturbance unrelated to climate trend. This was done by using the Breaks  
134 For Additive Seasonal and Trend (BFAST) on 8-days NDVI time series. Breaks were  
135 identified after the time series decomposition into trend, seasonal and remainder component.

136 Abrupt changes were considered as break points when their uncertainty was found to be  
137 smaller than one year, consistent to a previous study in the south-western Alps (Filippa et al.,  
138 2019). This led to discard around 5 % of the total number of pixels. We ended up with  
139 511,375 pixels of which 284,346 (55.6%) exhibited an average NDVImax below 0.65. Our  
140 main findings are based on this data subset to avoid the annoying saturation effect of  
141 NDVImax for closed canopies (see Introduction and Figure S2). Figure S3 and Table S1 give  
142 the spatial distribution of these pixels and their breakdown by administrative units using the  
143 Nomenclature of territorial units for statistics (NUTS) classification at level 3  
144 ([https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-  
145 statistical-units/](https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/)). Figure S12 shows the distribution of pixels per elevation and DAH classes.  
146 We processed all spatial data using the raster, rgdal, sp and proj4 R packages (Venables &  
147 Ripley, 2002). We used the bfast R package to implement the BFAST analysis (Verbesselt,  
148 Hyndman, Newnham, & Culvenor, 2010).

149

### 150 *Estimates of MODIS-derived NDVI metrics*

151 We downloaded the 250-m resolution 8-day composite of MOD09Q1/Terra collection  
152 6 products that are available in hdf format at the Land Processes Distributed Active Archive  
153 Center (<https://e4ftl01.cr.usgs.gov/>). Acquired dates covered the period from 18 February  
154 2000 to 27 December 2020. We assembled the tiles h18.v4 and h19v04, to cover the entire  
155 massif and re-projected red and near-infrared (NIR) surface reflectance values ( $\rho$ ) in the  
156 EPSG 3035 geometry. We retained reflectance values produced with high quality (according  
157 to the MOD09Q1 Quality Control flag) and calculated a NDVI according to  $(\rho_{\text{NIR}} - \rho_{\text{RED}})/(\rho_{\text{NIR}} + \rho_{\text{RED}})$ , where  $\rho$  is reflectance. We did not to use the 500m-resolution 16-day composite  
158 BRDF-corrected MODIS products (MCD43A4) as we needed a higher temporal and spatial  
159 resolution to best capture the peakiness of NDVI changes during the short growing season  
160



161 above treeline. Raw NDVI time series were processed in two steps. First, we used the Best  
162 Index Slope Extraction (BISE) algorithm to reduce the noise of the NDVI time series (Viovy,  
163 Arino, & Belward, 1992) with the parameters:  $n=0.2$  (i.e. a 20% acceptable difference in  
164 NDVI values within the sliding period) and  $p=3$  (the length of the forward sliding period).  
165 Second, we applied a low-pass filter using the Savitzky-Golay algorithm (Savitzky & Golay,  
166 1964) with the following parameters:  $n=3$  (the filter order) and  $p=7$  (the filter length). Smaller  
167 values of  $p$  would allow keeping track of more rapid changes whereas higher values would  
168 increase the smoothing. We also estimated a green-up date as the first date of the year where  
169 the NDVI amounts 50% of the  $NDVI_{max}$ . This was achieved using daily-interpolated time  
170 series of NDVI. This date is highly correlated to snow melting in the high-elevation mountain  
171 grasslands of the Alps (Choler, 2015; Fontana, Rixen, Jonas, Aberegg, & Wunderle, 2008).  
172 We used the non-parametric, rank based, Mann–Kendall (MK) monotonic test to assess the  
173 significance of NDVI time series trends. The significance was given by the approximately  
174 normally distributed  $z$  score with  $z$  values  $> 1.96$  indicating a significant increase ( $P$ -value  
175  $< 0.05$ ) and  $z$  values  $< -1.96$  a significant decrease (at  $P$ -value  $< 0.05$ ). To quantify change over  
176 the period 2000-2020 we fitted linear models based on Theil-Sen single median slope. The  
177 Theil-Sen estimator of the linear trend is much less sensitive to outliers than the least-squares  
178 estimator. The distribution of  $NDVI_{max}$  slopes for the different ranges of  $NDVI_{max}$  values is  
179 shown in figure S2. The decrease of the slopes in the highest ranges of  $NDVI_{max}$  was clearly  
180 indicative of a saturation effect. For further analyses, we retained pixels with a  $NDVI_{max}$   
181 value between 0.15 and 0.65. In this range, the pairwise mean difference of greenness slopes  
182 was below 0.005 (Figure S2). We randomly perturbed the RED and NIR raw reflectances by  
183 up to  $\pm 5\%$  to and recalculated 1000 times the MK trends and the Theil-Sen slopes for all  
184 pixels. The uncertainty of MODIS reflectance, and therefore of vegetation indices, arises from  
185 sensor calibration and the different steps of atmospheric correction (Vermote & Vermeulen,

186 1999). A perturbation of 5% lies in the upper range of the uncertainties associated with  
187 MODIS products(Miura, Huete, & Yoshioka, 2000). Our numerical simulation propagates  
188 this uncertainty into the estimates of NDVI trends and ensures a more robust analysis of the  
189 drivers of greening using random forest. We used the Kendall R package for estimating  
190 Mann-Kendall trends (McLeod, 2005) and the signal R package for the Savitzky-Golay  
191 function (signal developpers, 2013).

192

### 193 *Preparation of predictor datasets*

194 We estimated terrain indices from the 25 m resolution European Digital Elevation  
195 Model (EU-DEM, version 1.0, <https://land.copernicus.eu/imagery-in-situ/eu-dem/>). We  
196 resampled the EU DEM at a 250 m resolution and calculated the mean, range and standard  
197 deviation of elevation and the Diurnal Anisotropic Heating (DAH). The DAH index  
198 approximates the anisotropic heating of land surface to radiation (Böhner & Antonić, 2009).  
199 We computed DAH as  $\cos(\alpha_{\max} - \alpha) \cdot \arctan(\beta)$  where  $\alpha$  is the aspect,  $\beta$  is the slope and the  
200 parameter  $\alpha_{\max}$  corresponds to the aspect with the maximum total heat surplus. We used  $\alpha_{\max}$   
201 =  $212^\circ$  as we noticed that this SSW orientation corresponds on average to the earliest First  
202 Snow Free Day derived from Sentinel-2 products in the south-western Alps (unpublished  
203 results). Bedrock data were extracted from the 1:1 million OneGeology pan-European  
204 harmonized surface geological maps distributed by the European Geological Data  
205 Infrastructure (EGDI) portal (<http://www.europe-geology.eu/>). Surface geological units were  
206 aggregated into four categories: (i) igneous and metamorphic rocks including granite, gneiss  
207 etc., (ii) ferromagnesian rocks including serpentines, amphibolite, andesite, basalt etc., (iii)  
208 hard sedimentary rocks including dolomite, limestone etc. and (iv) clastic rocks including  
209 schist, mudstone, shale, flysch etc. For climate trends, we used the daily-based gridded  
210 datasets of E-OBS at a  $0.1^\circ$  resolution for the period 1995 onwards (version E-OBS v22.0e,

211 [https://surfobs.climate.copernicus.eu/dataaccess/access\\_eobs.php](https://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php)) (Cornes, van der Schrier,  
212 van den Besselaar, & Jones, 2018). For each year, we calculated Growing Degree Days  
213 (GDD) as the cumulative sum of daily average air temperature above 0°C during the summer  
214 months (June, July and August). As a complementary estimate of summer warming, we also  
215 extracted the average of daily maximum temperatures in July (T07). We computed a climatic  
216 water balance as the difference between precipitation (P) and a reference crop  
217 evapotranspiration ET<sub>0</sub>. We summed the P-ET<sub>0</sub> difference over the summer months to assess  
218 the dry-wet conditions of the growing season. ET<sub>0</sub> was estimated on a daily basis using the  
219 equation  $\lambda ET_0 = C (\Delta / (\Delta + \gamma)) Q$ , where Q is the global radiation (MJ m<sup>-2</sup> day<sup>-1</sup>), Δ the slope of  
220 the vapour pressure-temperature curve (kPa °C<sup>-1</sup>), γ the psychrometric constant (kPa °C<sup>-1</sup>), λ  
221 the latent heat of vaporization (MJ kg<sup>-1</sup>), and C an empirical coefficient (C=0.65). This is a  
222 simplified version of the Penman-Monteith equation originally proposed by Makkink and  
223 later modified by Hansen (Hansen, 1984). Maps of climate predictors are shown in figures S9  
224 and S10. For snow cover duration trends in the French Alps (Figure S11), we used the S2M  
225 meteorological and snow cover re-analysis for the period 1959-2019 (<https://www.aeris->  
226 [data.fr/catalogue/](https://www.aeris-data.fr/catalogue/)) (Vernay et al., 2019). As for NDVI time series, we used the non-parametric  
227 Mann-Kendall (MK) monotonic test and the Theil-Sen median slope to assess the  
228 significance and the magnitude of decadal trends of all meteorological variables.

229

### 230 *Random forest analysis.*

231 We implemented a random forest analysis to identify the best predictors of the spatial  
232 variability of greening. Based on the Mann-Kendall significance tests, we classified the  
233 greenness trends into three categories: no significant greening (P-value > 0.05), moderate  
234 greening (0.001 < P-value < 0.05) and strong greening (P-value < 0.001). There were not enough  
235 pixels exhibiting browning to include this response in the analysis. We randomly sampled

236 15 000 pixels in each category to balance the sample size among the greening responses and  
237 partitioned the data set into a model training subset (two thirds of pixels) and a model  
238 evaluation subset (one third of pixels). We repeated this procedure 1000 times, meaning that  
239 we assembled one random dataset for each perturbed simulation of MODIS reflectance and  
240 implemented one Random Forest model for each dataset. Predictor variables included  
241 elevation, Diurnal Anisotropic Heating, bedrock, NDVImax anomaly and decadal trends for  
242 the green-up date and the climate variables GDD and P-ET<sub>0</sub>. We calculated pair-wise  
243 correlations between predictors and checked that they were not highly correlated, i.e.  $r < 0.5$   
244 (Figure S13). We also implemented a Random Forest model including NDVImax to check for  
245 its influence on the classification probability and to further document the saturation effect  
246 (Figure S6). We relied on the out-of-bag classification accuracy to select the best Random  
247 Forest model. We assessed predictor importance using the mean decrease in accuracy metric,  
248 which is indicative of suitability of predictor, and the mean decrease in Gini, which is  
249 indicative of the homogeneity of nodes and leaves. Predictor importance was based on a  
250 permutation-based importance measure where one measures the effect of reshuffling each  
251 predictor on model accuracy. Last, we examined how classification probabilities depend on  
252 the values taken by each predictor by computing partial dependence plots. We computed  
253 empirical cumulative distribution function to determine the range of values where  
254 interpretation of partial dependence plots needs caution due to small sample size. We used the  
255 randomForest, caret, and pdp R packages to implement Random Forest models and evaluate  
256 its performance (Greenwell, 2017; Kuhn, 2020; Liaw & Wiener, 2002).

257

258 *Land cover assessment using very high-resolution imagery.*

259 Using the high-resolution imagery of Google Earth, we characterized the land cover  
260 features of a selection of 300 500m x 500m cells. First, we aggregated NDVImax anomaly at

261 a 500 m resolution. Then we performed a stratified random sampling of pixels using three  
262 classes of NDVImax anomaly - negative, around zero and positive values - and 100 pixels in  
263 each class (Figure S7). The visual photointerpretation of very high-resolution imagery from  
264 Google Earth allows us to distinguish 6 types of object: singular trees or tree patches, tall  
265 shrubs or shrublands (mainly composed of *Pinus mugho*), low shrublands (presumably  
266 *Ericaceae*-dominated), grasslands, screes and debris and finally outcrops. We assigned a  
267 percentage cover to these classes using the semi-quantitative ranges: <5%, 5%-25%, 25%-  
268 50%, 50%-75% and 75%-100%. Three authors of this paper (PC, EC, GF) conducted the  
269 photointerpretation independently and we retained the most frequent cover estimate for each  
270 land cover class. We did not try to standardize the year of satellite view, as there were no  
271 sufficient good quality images to do it.

272

273

## Results

274 Over the 2000-2020 period, we found significant ( $P<0.05$ ) positive temporal trends of  
275 NDVImax for 56% of the 284,346 analyzed pixels and significant negative trends for less  
276 than 0.1% of all pixels (Figure 1a and Table S1). Irrespective of significance, the ratio  
277 between positive and negative slopes was 26/1. These results were robust to uncertainty in  
278 MODIS data as more than two thirds of the pixels classified as fast ( $P<0.005$ ) and non-  
279 significant greening ( $P>0.05$ ) remained in these two classes when reflectance values were  
280 randomly perturbed (Figure S1). Sparse and very sparse vegetation contributed to 23% and  
281 26% respectively of the 56% of significant greening compared to 7% for grasslands and  
282 heathlands (Figure 1b). Figure S2 shows that there was no strong effect of the average  
283 NDVImax on the magnitude of greening in the selected range (0.15-0.65). By contrast, there  
284 was a marked decline in greening for higher values of NDVImax suggesting a saturation

285 effect (Figure S2 and Table S1). Only 31% of pixels exhibited a significant greening when the  
286 NDVImax value was above 0.65, the (Table S1).

287         Although widely distributed, the greening trends are not spatially uniform (Figure 2).  
288 We found a regional-scale component of this spatial variability, with hotspots of greening  
289 corresponding to southern parts of the French Alps (e.g. Haute-Provence and Maritime Alps,  
290 France), the southern part of the Central Alps (e.g. Sondrio, Italy and Tiroler Oberland,  
291 Austria) and the Northeastern-most part of the Alps (e.g. Pinzgau-Pongau, Austria; Figure 2,  
292 S3 and Table S1). At the local scale, topographical factors also modulate the greening trends  
293 (Figure 3a). First, there is a general tendency for the greening to increase with elevation  
294 (Figure 3a). Second, and on top of that, the greening is more noticeable for north-facing steep  
295 slopes i.e. for the most negative values of diurnal anisotropic heating (DAH), a proxy of the  
296 heating of land surface to radiation (Figure 3a). Consequently, we observed an overall upward  
297 shift of the isolines of NDVImax, meaning that the elevation of given value of NDVImax has  
298 increased steadily over the last two decades (Figure 3b). We estimated the median of this shift  
299 at 45 m per decade with strong regional disparities (Figure S4). It is worth noting that the  
300 magnitude of this elevational shift is higher for the first deciles of the distribution than for the  
301 last, and this difference is particularly striking at negative DAH values (Figure 3b). These  
302 results point out that greening is enhanced when the NDVImax is below the median of the  
303 distribution for a given elevation and DAH, leading to a reduction of the interdecile  
304 differences in the distribution of NDVImax along topographical gradients (Figure 3b).

305         These findings prompted us to quantify a per-pixel NDVImax anomaly and to assess  
306 its spatial distribution in the European Alps. The anomaly was calculated as the difference  
307 between the average NDVImax of a given pixel and the median NDVImax value of all pixels  
308 lying in the same class of DAH and elevation (Figure 4a). Negative anomalies are indicative  
309 of an “abnormally” low NDVImax value with respect to elevation and DAH. The mapping of

310 this anomaly revealed a clear regional-scale variability that was partly congruent with that of  
311 greening (Figure 4b). For example, the southern part of the French Alps, part of the south  
312 Central Alps and the Northeastern-most Alps are regions that present a combination of fast  
313 greening (Figure 2), negative NDVImax anomalies (Figure 4b), and high upward shift of  
314 NDVImax (Figure S4).

315 We evaluated the importance of this NDVImax anomaly in predicting the observed  
316 greening trends against two sets of predictors that are more widely used in greening studies,  
317 i.e. topographical predictors (elevation and DAH) and climate predictors pertaining to the  
318 growing season (summer). We used trends in the accumulation of growing degree-days  
319 (GDD) during summer as a proxy of temperature-related changes and trends in the difference  
320 between precipitation and potential evapotranspiration as a proxy of water balance-related  
321 changes (see Methods). We also estimated trends in the green-up date derived from the  
322 analysis of NDVI time series. Previous studies showed that the green-up date strongly  
323 depends on snow cover duration in high elevation temperate ecosystems (Choler, 2015). We  
324 built a random forest model to assess the usefulness of these variables for classifying pixels  
325 into three categories based on the Mann-Kendall significance test - no greening ( $P > 0.05$ ),  
326 moderate greening ( $P < 0.05$ ) and fast greening ( $P < 0.005$ ). The model classified the “no  
327 greening” and the “fast greening” classes with an accuracy of 61.5% and 62 % respectively  
328 corresponding to a kappa of 0.42 and 0.4 (Table S3). The values of the first and ninth deciles  
329 of the 1000 simulations differ by less than 2% from the mean. The performance of the random  
330 forest classifier for the “moderate greening” was low with an overall accuracy of 0.51 to be  
331 compared to a random accuracy of 0.33 (Table S3). The ranking of predictors shows that the  
332 NDVImax anomaly is as important as climate predictors (Figure 5a,b). Noticeably, its score is  
333 high for both the mean decrease accuracy and the mean decrease in Gini coefficient,  
334 indicating a high suitability as a predictor and a high contribution to the homogeneity of

335 nodes and leaves. By contrast, climate predictors show high decrease in permutation tests but  
336 do not exhibit a high contribution to the purity of nodes (low mean decrease in Gini), while  
337 topographical predictors show the reverse trend (Figure 5b). The greening trends did not  
338 change between bedrock types (Figure S5) and bedrock exhibited a very low variable  
339 importance in random forest. For these reasons, it was not retained in further analysis. Partial  
340 dependence plots (Figure 5c) reveal that greening was mostly associated with negative  
341 NDVImax anomalies, negative DAH, elevation between 2300 m and 2700 m and increasing  
342 green-up dates, and was marginally enhanced by a more positive trend in GDD and water  
343 balance. The lack of greening occurs more often at low and very high elevation, where  
344 NDVImax anomaly was positive and green-up dates decrease and, to a lesser extent, where  
345 climate amelioration was weak (Figure 5c). Given the positive correlation between snow  
346 melting date and green-up date above treeline, our results indirectly pointed out to a positive  
347 effect of delayed snow melt on the recent greening trends. We also implemented  
348 complementary random forest models for subsets of pixels lying in narrower ranges of  
349 NDVImax (0.15-0.4 and 0.4-0.65) and by adding NDVImax as a supplementary predictor  
350 (Figure S6). The ranking of variable importance was consistent for all these simulations,  
351 which also confirmed the overwhelming importance of the NDVImax anomaly for predicting  
352 the greening response whatever the NDVImax value (Figure S6). They also pointed out that  
353 adding the NDVImax as a supplementary predictor tends to lower the importance of the  
354 NDVImax anomaly (Figure 5a and S6a), which is explainable by the positive correlation  
355 between these two variables.

356         The strong link between negative NDVImax anomalies and significant greening trends  
357 led us to explore at a finer scale the land cover features associated with these contexts. Using  
358 very high-resolution satellite imagery from Google Earth, we performed a visual photo-  
359 interpretation of 300 randomly selected sites across the Alps (Figure S7). First, this analysis



360 indicated that NDVImax anomalies were consistently negative in the case of high cover of  
361 screes, debris and outcrops (Figure 6a). The reverse trend holds for grassland cover (Figure  
362 6c). Second, the magnitude of greening tend to increase with the cover of screes and debris  
363 and decreases with that of grasslands (Figure 6b,d). Last, we did not find evidence that the  
364 presence of nearby trees or tall shrubs was associated with more frequent greening, suggesting  
365 that the densification of non-woody vegetation is as important as the upward shift of trees to  
366 explain greening. This is illustrated by four examples of land cover dynamics using past and  
367 current very high-resolution color-infrared aerial photographs that are available for the French  
368 Alps (Figure S8).

369

## Discussion

370 The main findings of our study are threefold. First, more than half of the land surface  
371 occupied by above-treeline ecosystems in the European Alps has experienced significant  
372 greening over the last two decades. By contrast, the number of pixels showing significant  
373 browning trends is less than 1%. Second, this widespread greening is spatially non-uniform,  
374 and fast greening responses can be explained by a combination of local-scale factors - i.e.  
375 elevation and exposure - and regional-scale factors pertaining to anomalies of NDVImax and  
376 trends in green-up dates. Third, we provided substantial evidence for the high responsiveness  
377 of north-facing and sparsely vegetated areas that have clearly benefited the most from recent  
378 climate changes in the European Alps.

379 Our study investigated greening trends across a vast and highly heterogeneous  
380 landscape. Above-treeline ecosystems in the Alps include a wide range of geomorphological,

381 topographical and ecological situations that lead to a high turnover of plant communities over  
382 short distances. This fine-scale heterogeneity in plant cover inevitably calls into question the  
383 appropriateness of using moderate resolution remote sensing products to assess greening  
384 trends in mountainous landscapes. For example, it is entirely possible that contrasting trends  
385 of greenness are occurring within a 250 m resolution pixel because of habitat-specific  
386 responses (Matteodo, Ammann, Verrecchia, & Vittoz, 2016). While the use of moderate  
387 resolution remote sensing products certainly limits our ability to assign specific NDVImax  
388 trajectories to particular plant communities or habitats, our approach nonetheless provides a  
389 very valuable and comprehensive picture of vegetation shifts at the mountain range scale, and  
390 enables broad-scale investigation of land cover dynamics as demonstrated in previous studies  
391 (Zhao & Running, 2010). We acknowledge the potential of using high-resolution products  
392 such as the Landsat archive to complement our study. However, this will raise other  
393 difficulties. The most critical is the low frequency of available images, which makes it  
394 difficult to capture the peak of growth in alpine environments, and leads to large uncertainties  
395 in the estimate of NDVImax. In addition, calculating a finer grained greening response would  
396 exacerbate the mismatch between the spatial scale of remote sensing products and that of  
397 drivers of changes, especially climate (Randin et al., 2020). For these reasons, we believe that  
398 high-resolution remote sensing data would be more appropriate to examine the response of  
399 specific habitats or sites for which ground-truthing data are available. Similarly, the utilization  
400 of aerial photograph archives has an enormous, yet largely unexplored, potential to relate very  
401 fine-grained land cover dynamics to observed greening trends (see illustrative examples in  
402 Figure S8)

403 Another difficulty of our comparative analysis of greening trends pertains to the wide  
404 range of vegetation cover that is included. It is well known that NDVI exhibits a nonlinear  
405 response to aboveground biomass and plant cover, especially for planophilous canopies

406 (Myneni & Williams, 1994). The sensitivity of NDVI to an incremental change in biomass or  
407 cover decreases for dense canopies, as does our capacity to detect a significant greenness  
408 trend in these contexts. Thus, one may run the risk that the spatial variability of greening  
409 partly reflects the different sensitivity of the method used to detect greening. We paid  
410 particular attention to this issue and removed from our analysis all pixels with high NDVImax  
411 values ( $> 0.65$ ), as we had clear indications of a saturation effect on greening (Figure S2). The  
412 relationship between NDVImax and biomass or cover is linear in the NDVImax range we  
413 selected (Myneni & Williams, 1994). We also performed similar random forest analyses on  
414 subsets of pixels exhibiting very low NDVImax value and found similar conclusions (Figure  
415 S6). For these reasons, we are confident that the saturation of NDVImax with aboveground  
416 biomass did not blur our assessment of greening trends in the European Alps.

417         Our report on widespread greening in above-treeline ecosystems of the Alps is  
418 consistent with previous studies on arctic and alpine ecosystems (Berner et al., 2020; Ju &  
419 Masek, 2016; Krakauer, Lakhankar, & Anadon, 2017; Xie et al., 2020). As in other cold parts  
420 of the earth, high elevation ecosystems of the Alps have experienced a more pronounced  
421 warming than lowlands (Palazzi, Mortarini, Terzago, & von Hardenberg, 2019; Pepin et al.,  
422 2015) and, not surprisingly, these temperature-limited ecosystems are benefitting from this  
423 increased temperature. However, and by comparison to a recent report from the Arctic  
424 (Berner et al., 2020), we found very few significant browning trends. A plausible explanation  
425 is that all regions of the Alps have experienced warmer summers, albeit to varying degrees,  
426 over the last decades (Figure S9). This led us to consider that, at least for the Alps, the  
427 knowledge gap is less about the detection of significant greening trends than it is about the  
428 causes of its spatial variability in a warmer climate. Our study provides new perspectives on  
429 this matter, given that we unraveled the pivotal role of the anomaly of NDVImax to capture  
430 part of this greening complexity. Ecosystems exhibiting a lower NDVImax than expected

431 given the topography, i.e. a negative anomaly, have been the most responsive over the last  
432 two decades, and this is the reason why we observe today a reduced dispersion of NDVImax  
433 values for a given elevation x DAH compared to the years 2000 (Figure 4b) as well as  
434 reduced regional heterogeneity (Figure 2). We can refer to this trend as a *catching-up*  
435 *phenomenon* and we assert that it is the most important facet of the ongoing greening in the  
436 Alps.

437 To further understand this phenomenon, we paid particular attention to land cover  
438 properties using high-resolution images. Clearly, the presence of very sparsely vegetated  
439 surfaces - such as screes, talus and outcrops - is a predisposing factor to negative anomalies  
440 and greening (Figure 6). In this regard, our findings extend at a broader mountain range scale  
441 conclusions that were drawn from more localized studies (Carlson et al., 2017). The  
442 increasing vegetation cover in initially sparsely vegetated areas is being documented through  
443 long-term surveys (Rixen, Wipf, Frei, & Stoeckli, 2014; Steinbauer et al., 2018) and remote  
444 sensing (Carlson et al., 2017). Noticeably, several reports have underlined the preferential  
445 expansion of tall shrubs and trees on screes and debris compared to nearby grasslands. In  
446 addition to forest ingrowth caused by land-use abandonment, this upward shift of trees is the  
447 other dimension of tree expansion documented in the Alps (Gehrig-Fasel et al., 2007; Vittoz,  
448 Rulence, Largey, & Frelechoux, 2008), and diffuse treelines can be highly responsive to  
449 climate warming (Harsch, Hulme, McGlone, & Duncan, 2009). Forest dynamics at the  
450 treeline have also been influenced by the constant decline of pastoralism and the related  
451 human activities due to the land abandonment since the Industrial Revolution (1850), making  
452 it difficult to disentangle climate influence and human impacts (Motta & Nola, 2001). In the  
453 southern part of the Alps, these dynamics occur well above the treeline, which is mainly  
454 constituted by the European larch (*Larix decidua* L.) and the stone pine (*Pinus cembra* L.).  
455 For example, the systematic survey of alpine ridges and cliffs in the south-western Alps led to

456 report on the occurrence of isolated individuals or stands of *Pinus cembra* at very high  
457 elevation (André, Lavergne, & Carcaillet, 2020). This is consistent with the hypothesis that  
458 the upward shift of the treeline may be more pronounced in the inner part of the Alps where  
459 trees take advantage of the more continental, warmer and drier, climate (Körner, 1999). Our  
460 study did not allow to precisely relate tree cover dynamics with greening because of the  
461 coarse resolution and the focus on high elevation sites. Nonetheless, we noticed that the  
462 greening trends are more accentuated on north-facing slopes that are generally more forested  
463 and more densely covered by heathlands than southern aspects. Further studies should  
464 associate the different magnitudes of increase in NDVImax to well-documented colonization  
465 of pioneer shrubs and trees. Our mapping of hotspots and coldspots of greening can provide  
466 the foundations for such an investigation coupling remote sensing and plant population  
467 models.

468 Another ecological dynamic that is consistent with our findings is the increasing cover  
469 of dwarf shrub - mainly *Ericaceous* species - in north-facing grasslands. Expanding low shrub  
470 cover in recent decades has been reported in the central Italian Alps at elevations up to 2500  
471 m (Cannone, Sgorbati, & Guglielmin, 2007). Coupled with climate change, the transition  
472 from an agro-pastoral socio-economic model to an economy based on tourism and skiing has  
473 enabled a pronounced expansion of trees and shrubs into mountain grasslands in numerous  
474 locations throughout the Alps since the 1950s, including for example the Chamonix valley  
475 (unpublished data). In addition to the expansion of woody vegetation, increasing grass cover  
476 in sparsely vegetated areas is probably contributing to the observed trends, both in the context  
477 of screes and talus as well as glacier forelands in the wake of glacier retreat (Mainetti et al.,  
478 2021).

479 Our study allowed for distinction between external drivers of greening such as climate  
480 and predisposing factors that pertain to the initial state of the responding system. Overall, the

481 regional-scale variability of the greenness response did not strongly reflect spatial variation in  
482 climate change. Several reasons may explain this phenomenon. First, the climate data we used  
483 may be poor predictors because they fall short to capture surface conditions in high elevation  
484 complex terrain. There are a limited number of weather stations above 2000 m in the Alps,  
485 and some variables like precipitation are notoriously difficult to model along topographical  
486 gradients (Frei & Isotta, 2019; Vionnet et al., 2019). Second, plant growth and community  
487 dynamics primarily respond to fine-scale thermal and moisture regimes that depend on  
488 landforms and soil factors (Giaccone et al., 2019; Liberati, Messerli, Matteodo, & Vittoz,  
489 2019; Matteodo et al., 2016; Suding, Farrer, King, Kueppers, & Spasojevic, 2015), and these  
490 factors are not accounted for in continental-scale gridded datasets. Third, high-elevation  
491 ecosystems may respond to different temporal scales of climate such as extreme events or past  
492 climate shifts. For example, previous studies have underlined the positive response of alpine  
493 primary productivity to heat waves (Corona-Lozada, Morin, & Choler, 2019; Jolly et al.,  
494 2005). There is also strong evidence that the most significant rise of temperature in the Alps  
495 occurred in the late eighties (EEA, 2009), i.e. a decade before the start of the MODIS  
496 observations. It is possible that these particularly favorable years lead to massive plant  
497 recruitment and that we are tracking the consequences of these events years later.

498         An example of a physical variable that we can track at the pixel scale is the green-up  
499 date, which strongly depends upon the first snow free date. At first glance, our findings are  
500 counter-intuitive as the likelihood of greening is predominantly associated with a delayed  
501 green-up date (Figure 4), as illustrated by the situation in the south-western Alps and the  
502 south-central Alps (Figure S10). Using the regional climate re-analysis available for the  
503 French Alps, we confirmed that the positive trend of the green-up date is consistent with  
504 delayed snow melt-out during the last 20 years especially in the southern-most ranges and  
505 above 2000 m (Figure S11). A significant decrease in snow-melt-out dates in the 1980s and

506 1990s has been reported, mostly for sites below 2000 m (Durand et al., 2009; Klein, Vitasse,  
507 Rixen, Marty, & Rebetez, 2016; Matiu et al., 2021). Recent reports highlighted that these  
508 trends tend to vanish in the recent period, especially at high elevation (Matiu et al., 2021;  
509 Vorkauf, Marty, Kahmen, & Hiltbrunner, 2021). In line with these findings, there is evidence  
510 that high elevation sites in European Alps have experienced an increase in the precipitation  
511 over the last decades (Avanzi et al., 2020; Napoli, Crespi, Ragone, Maugeri, & Pasquero,  
512 2019). We hypothesize that the combination of snowy winters and warm summers may be  
513 particularly favorable for alpine vegetation, especially where vacant niches are available for  
514 recruitment. This was suggested by Corona et al. (2019) who showed that among the four  
515 main heat waves that hit the Alps in the last 20 years, the only one that did not translate into  
516 increased productivity was that of 2015 because a strong water deficit coincided with  
517 increased temperature. Recent work also indicated that earlier snowmelt can be detrimental to  
518 the growth of *Rhododendron ferrugineum* shrubs that preferentially occur on north-facing  
519 slopes (Francon et al., 2020). It is therefore plausible that a delayed snowmelt ameliorates the  
520 summer soil water balance and acts synergistically with warm summer temperatures to boost  
521 plant productivity and colonization, especially on north-facing slopes that may previously  
522 have been too cold to support dense vegetation cover. Further studies are needed to confirm  
523 that this association between prolonged snow cover and greening is not simply coincidental  
524 but is reflecting ecological mechanisms that are beneficial to plant recruitment and growth.

525 Finally, our findings call into question whether changes in pastoral management may  
526 have contributed to the negative NDVImax anomalies and more generally to the contrasting  
527 regional greening trends. Unfortunately, consistent long-term data on mountain livestock  
528 systems are not available at the scale of the European Alps. A socio-economic analysis led  
529 Tappeiner & al. (2008) to identify regions of the European Alps where agriculture receded in  
530 recent years. Most of the Italian Alps and the North-easternmost Austrian Alps were

531 described as “forgotten rural areas” experiencing sharp decline in agriculture, which  
532 demonstrates substantial spatial consistencies with our delineation of greening hotspots.  
533 However, the analysis aggregated many different socio-economic variables at the scale of  
534 administrative districts, and it was not possible to include it in our analysis of the drivers of  
535 greening. There is certainly no simple relation between greening trends and changes in  
536 agricultural practices. For example, there has been a remarkable resilience of mountain  
537 livestock farming systems in the southern part of the French Alps which is a greening hotspot,  
538 and this was observed despite many adverse factors such as demography, poor profitability,  
539 extreme events and return of the large predators (Hinojosa, Napoleone, Moulery, & Lambin,  
540 2016). Recent trends even point toward an increasing demand for high-elevation pastures to  
541 overcome the detrimental effects of droughts in lowlands and southernmost mountain ranges,  
542 leading shepherds to bring their flocks to high-elevation pastures for extended summer  
543 periods (Nettier, Dobremez, Coussy, & Romagny, 2010). The greening trends we have  
544 documented here may further encourage such practices. This highlights that livestock farming  
545 systems cannot be solely envisaged as potential drivers of greening trends but that pastoral  
546 practices will also have to adapt to the changing productivity and spatial distribution of  
547 mountain pastures (Jager, Peratoner, Tappeiner, & Tasser, 2020).

548

## **Conclusion**

549 In summary, the uplands of the European Alps have undergone widespread albeit non-  
550 uniform greening over the last two decades. High-elevation ecosystems have positively  
551 responded to ongoing summer warming with varying degrees of sensitivity. This conclusion  
552 is supported by the importance of predisposing factors such as the NDVImax anomaly, i.e. an  
553 abnormally low initial greenness, which explains a substantial portion of the spatial variability  
554 of greening. Sparsely vegetated ecosystems on north-facing slopes and experiencing



555 prolonged snow cover duration are the most highly responsive to ongoing warming, possibly  
556 because the positive effect of increased temperature is not dampened by limiting water supply  
557 and density-dependent plant competition. Our findings call for further studies examining why  
558 certain areas of the European Alps exhibit negative NDVImax anomalies and whether this  
559 determines specific ecological mechanisms underpinning observed greening trends.

560

561

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571

### **Supporting Information**

572 Additional supporting information - three tables and 13 figures - may be found online in the  
573 Supporting Information section.

## References

- 574 Anderson, K., Fawcett, D., Cugulliere, A., Benford, S., Jones, D., & Leng, R. L. (2020).  
575 Vegetation expansion in the subnival Hindu Kush Himalaya. *Global Change Biology*,  
576 26(3), 1608-1625. doi:10.1111/gcb.14919
- 577 André, G., Lavergne, S., & Carcaillet, C. (2020). Unsuspected prevalent tree occurrences in  
578 high elevation sky-islands of the western Alps. *bioRxiv*, 2020.2007.2008.193300.  
579 doi:10.1101/2020.07.08.193300
- 580 Asam, S., Callegari, M., Matiu, M., Fiore, G., De Gregorio, L., Jacob, A., . . . Notarnicola, C.  
581 (2018). Relationship between Spatiotemporal Variations of Climate, Snow Cover and  
582 Plant Phenology over the Alps-An Earth Observation-Based Analysis. *Remote*  
583 *Sensing*, 10(11). doi:10.3390/rs10111757
- 584 Avanzi, F., Ercolani, G., Gabellani, S., Cremonese, E., Pogliotti, P., Filippa, G., . . . Cauduro,  
585 M. (2020). Learning about precipitation orographic enhancement from snow-course  
586 data improves water-balance modeling. *Hydrology and Earth System Sciences*  
587 *Discussions*, 1-37.
- 588 Beniston, M. (2006). Mountain weather and climate: A general overview and a focus on  
589 climatic change in the Alps. *Hydrobiologia*, 562, 3-16. doi:10.1007/s10750-005-1802-  
590 0
- 591 Berner, L. T., Massey, R., Jantz, P., Forbes, B. C., Macias-Fauria, M., Myers-Smith, I., . . .  
592 Goetz, S. J. (2020). Summer warming explains widespread but not uniform greening  
593 in the Arctic tundra biome. *Nature Communications*, 11(1). doi:10.1038/s41467-020-  
594 18479-5
- 595 Böhner, J., & AntoniĆ, O. (2009). Land-surface parameters specific to topo-climatology.  
596 *Developments in soil science*, 33, 195-226.

597 Callaghan, T. V., Bergholm, F., Christensen, T. R., Jonasson, C., Kokfelt, U., & Johansson,  
598 M. (2010). A new climate era in the sub-Arctic: Accelerating climate changes and  
599 multiple impacts. *Geophysical Research Letters*, 37. doi:10.1029/2009gl042064

600 Cannone, N., Sgorbati, S., & Guglielmin, M. (2007). Unexpected impacts of climate change  
601 on alpine vegetation. *Frontiers in Ecology and the Environment*, 5(7), 360-364.  
602 doi:10.1890/1540-9295(2007)5[360:UIOCCO]2.0.CO;2

603 Carlson, B. Z., Corona, M. C., Dentant, C., Bonet, R., Thuiller, W., & Choler, P. (2017).  
604 Observed long-term greening of alpine vegetation-a case study in the French Alps.  
605 *Environmental Research Letters*, 12(11). doi:10.1088/1748-9326/aa84bd

606 Choler, P. (2015). Growth response of temperate mountain grasslands to inter-annual  
607 variations in snow cover duration. *Biogeosciences*, 12(12), 3885-3897.  
608 doi:10.5194/bg-12-3885-2015

609 Cornes, R. C., van der Schrier, G., van den Besselaar, E. J. M., & Jones, P. D. (2018). An  
610 Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. *Journal of*  
611 *Geophysical Research-Atmospheres*, 123(17), 9391-9409. doi:10.1029/2017jd028200

612 Corona-Lozada, M. C., Morin, S., & Choler, P. (2019). Drought offsets the positive effect of  
613 summer heat waves on the canopy greenness of mountain grasslands. *Agricultural and*  
614 *Forest Meteorology*, 276. doi:10.1016/j.agrformet.2019.107617

615 Cortés, J., Mahecha, M. D., Reichstein, M., Myneni, R. B., Chen, C., & Brenning, A. (2021).  
616 Where are Global Vegetation Greening and Browning Trends Significant?  
617 *Geophysical Research Letters*, 48(6), e2020GL091496.

618 Dunn, A. H., & de Beurs, K. M. (2011). Land surface phenology of North American  
619 mountain environments using moderate resolution imaging spectroradiometer data.  
620 *Remote Sensing of Environment*, 115(5), 1220-1233. doi:10.1016/j.rse.2011.01.005

621 Durand, Y., Giraud, G., Laternser, M., Etchevers, P., Mérindol, L., & Lesaffre, B. (2009).  
622 Reanalysis of 47 Years of Climate in the French Alps (1958–2005): Climatology and  
623 Trends for Snow Cover. *Journal of Applied Meteorology and Climatology*, 48(12),  
624 2487-2512. doi:10.1175/2009jamc1810.1

625 Duveiller, G., Hooker, J., & Cescatti, A. (2018). The mark of vegetation change on Earth's  
626 surface energy balance. *Nature Communications*, 9. doi:10.1038/s41467-017-02810-8

627 EEA. (2009). Regional Climate Change Adaptation. The Alps Facing the Challenge of  
628 Changing Water Resources. *European Environment Agency: Copenhagen, Denmark*.

629 Filippa, G., Cremonese, E., Galvagno, M., Isabellon, M., Bayle, A., Choler, P., . . .  
630 Migliavacca, M. (2019). Climatic Drivers of Greening Trends in the Alps. *Remote*  
631 *Sensing*, 11(21). doi:10.3390/rs11212527

632 Fontana, F., Rixen, C., Jonas, T., Aberegg, G., & Wunderle, S. (2008). Alpine grassland  
633 phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series - a  
634 comparison with in situ measurements. *Sensors*, 8(4), 2833-2853.  
635 doi:10.3390/s8042833

636 Forzieri, G., Alkama, R., Miralles, D. G., & Cescatti, A. (2017). Satellites reveal contrasting  
637 responses of regional climate to the widespread greening of Earth. *SCIENCE*,  
638 356(6343), 1140-1144. doi:10.1126/science.aal1727

639 Francon, L., Corona, C., Till-Bottraud, I., Choler, P., Carlson, B. Z., Charrier, G., . . . Stoffel,  
640 M. (2020). Assessing the effects of earlier snow melt-out on alpine shrub growth: The  
641 sooner the better? *Ecological Indicators*, 115. doi:10.1016/j.ecolind.2020.106455

642 Frei, C., & Isotta, F. A. (2019). Ensemble Spatial Precipitation Analysis From Rain Gauge  
643 Data: Methodology and Application in the European Alps. *Journal of Geophysical*  
644 *Research-Atmospheres*, 124(11), 5757-5778. doi:10.1029/2018jd030004

645 Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps:  
646 Climate change or land abandonment? *Journal of Vegetation Science*, *18*(4), 571-582.  
647 doi:10.1111/j.1654-1103.2007.tb02571.x

648 Giaccone, E., Luoto, M., Vittoz, P., Guisan, A., Mariethoz, G., & Lambiel, C. (2019).  
649 Influence of microclimate and geomorphological factors on alpine vegetation in the  
650 Western Swiss Alps. *Earth Surface Processes and Landforms*, *44*(15), 3093-3107.  
651 doi:10.1002/esp.4715

652 Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barancok, P., Alonso, J. L. B., . . .  
653 Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate  
654 change. *Nature Climate Change*, *2*(2), 111-115. doi:10.1038/nclimate1329

655 Greenwell, B. M. (2017). pdp: An R Package for Constructing Partial Dependence Plots. *The*  
656 *R Journal*, *9*, 421-436.

657 Hansen, S. (1984). Estimation of Potential and Actual Evapotranspiration. *Nordic Hydrology*,  
658 *15*(4-5), 205-212.

659 Hantel, M., & Hirtl-Wielke, L. M. (2007). Sensitivity of Alpine snow cover to European  
660 temperature. *International Journal of Climatology*, *27*(10), 1265-1275.  
661 doi:10.1002/joc.1472

662 Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines  
663 advancing? A global meta-analysis of treeline response to climate warming. *Ecology*  
664 *Letters*, *12*(10), 1040-1049. doi:10.1111/j.1461-0248.2009.01355.x

665 Hinojosa, L., Napoleone, C., Moulery, M., & Lambin, E. F. (2016). The "mountain effect" in  
666 the abandonment of grasslands: Insights from the French Southern Alps. *Agriculture*  
667 *Ecosystems & Environment*, *221*, 115-124. doi:10.1016/j.agee.2016.01.032

668 Hock, R., Rasul, G., Adler, C., Cáceres, B., Gruber, S., Hirabayashi, Y., . . . Steltzer, H.  
669 (2019). Chapter 2: High Mountain Areas.

670 [http://report.ipcc.ch/srocc/pdf/SROCC\\_FinalDraft\\_Chapter2.pdf](http://report.ipcc.ch/srocc/pdf/SROCC_FinalDraft_Chapter2.pdf). In *In IPCC Special*  
671 *Report on Ocean and Cryosphere in a Changing Climate*.

672 Huete, A., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002).  
673 Overview of the radiometric and biophysical performance of the MODIS vegetation  
674 indices. *Remote Sensing of Environment*, 83(1-2), 195-213. doi:10.1016/s0034-  
675 4257(02)00096-2

676 Jager, H., Peratoner, G., Tappeiner, U., & Tasser, E. (2020). Grassland biomass balance in the  
677 European Alps: current and future ecosystem service perspectives. *Ecosystem*  
678 *Services*, 45. doi:10.1016/j.ecoser.2020.101163

679 Jolly, W. M., Dobbertin, M., Zimmermann, N. E., & Reichstein, M. (2005). Divergent  
680 vegetation growth responses to the 2003 heat wave in the Swiss Alps. *Geophysical*  
681 *Research Letters*, 32(18), NIL\_1-NIL\_4.

682 Ju, J., & Masek, J. G. (2016). The vegetation greenness trend in Canada and US Alaska from  
683 1984-2012 Landsat data. *Remote Sensing of Environment*, 176, 1-16.  
684 doi:10.1016/j.rse.2016.01.001

685 Keenan, T. F., & Riley, W. J. (2018). Greening of the land surface in the world's cold regions  
686 consistent with recent warming. *Nature Climate Change*, 8(9), 825-+.  
687 doi:10.1038/s41558-018-0258-y

688 Klein, G., Vitasse, Y., Rixen, C., Marty, C., & Rebetez, M. (2016). Shorter snow cover  
689 duration since 1970 in the Swiss Alps due to earlier snowmelt more than to later snow  
690 onset. *Climatic Change*, 139(3-4), 637-649. doi:10.1007/s10584-016-1806-y

691 Körner, C. (1999). *Alpine Plant Life*. Berlin: Springer Verlag.

692 Krakauer, N. Y., Lakhankar, T., & Anadon, J. D. (2017). Mapping and Attributing  
693 Normalized Difference Vegetation Index Trends for Nepal. *Remote Sensing*, 9(10).  
694 doi:10.3390/rs9100986

695 Kuhn, M. (2020). Caret: classification and regression training. R package version 6.0-86.  
696 <https://CRAN.R-project.org/package=caret>.

697 Lamprecht, A., Semenchuk, P. R., Steinbauer, K., Winkler, M., & Pauli, H. (2018). Climate  
698 change leads to accelerated transformation of high-elevation vegetation in the central  
699 Alps. *New Phytologist*, 220(2), 447-459. doi:10.1111/nph.15290

700 Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R news*, 2(3),  
701 18-22.

702 Liberati, L., Messerli, S., Matteodo, M., & Vittoz, P. (2019). Contrasting impacts of climate  
703 change on the vegetation of windy ridges and snowbeds in the Swiss Alps. *Alpine*  
704 *Botany*, 129(2), 95-105. doi:10.1007/s00035-019-00223-5

705 Mainetti, A., D'Amico, M., Probo, M., Quaglia, E., Ravetto Enri, S., Celi, L., & Lonati, M.  
706 (2021). Successional Herbaceous Species Affect Soil Processes in a High-Elevation  
707 Alpine Proglacial Chronosequence. *Frontiers in Environmental Science*, 8.  
708 doi:10.3389/fenvs.2020.615499

709 Matiu, M., Crespi, A., Bertoldi, G., Carmagnola, C. M., Marty, C., Morin, S., . . . De  
710 Gregorio, L. (2021). Observed snow depth trends in the European Alps: 1971 to 2019.  
711 *The Cryosphere*, 15(3), 1343-1382. doi:10.5194/tc-15-1343-2021

712 Matteodo, M., Ammann, K., Verrecchia, E. P., & Vittoz, P. (2016). Snowbeds are more  
713 affected than other subalpine-alpine plant communities by climate change in the Swiss  
714 Alps. *Ecology and Evolution*, 6(19), 6969-6982. doi:10.1002/ece3.2354

715 McLeod, A. I. (2005). Kendall rank correlation and Mann-Kendall trend test. R package  
716 version 2.2. <https://CRAN.R-project.org/package=Kendall>.

717 Miura, T., Huete, A. R., & Yoshioka, H. (2000). Evaluation of sensor calibration uncertainties  
718 on vegetation indices for MODIS. *Ieee Transactions on Geoscience and Remote*  
719 *Sensing*, 38(3), 1399-1409. doi:10.1109/36.843034

720 Motta, R., & Nola, P. (2001). Growth trends and dynamics in sub-alpine forest stands in the  
721 Varaita Valley (Piedmont, Italy) and their relationships with human activities and  
722 global change. *Journal of Vegetation Science*, 12(2), 219-230. doi:10.2307/3236606

723 Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J.,  
724 . . . Wipf, S. (2020). Complexity revealed in the greening of the Arctic. *Nature*  
725 *Climate Change*, 10(2), 106-117. doi:10.1038/s41558-019-0688-1

726 Myneni, R. B., & Williams, D. L. (1994). On the Relationship between FAPAR and NDVI.  
727 *Remote Sensing of Environment*, 49(3), 200-211. doi:10.1016/0034-4257(94)90016-7

728 Napoli, A., Crespi, A., Ragone, F., Maugeri, M., & Pasquero, C. (2019). Variability of  
729 orographic enhancement of precipitation in the Alpine region. *Scientific Reports*, 9.  
730 doi:10.1038/s41598-019-49974-5

731 Nettier, B., Dobremez, L., Coussy, J.-L., & Romagny, T. (2010). Attitudes of livestock  
732 farmers and sensitivity of livestock farming systems to drought conditions in the  
733 French Alps. *Revue De Geographie Alpine-Journal of Alpine Research*, 98(1-4), 383-  
734 400. doi:10.4000/rga.1307

735 Palazzi, E., Mortarini, L., Terzago, S., & von Hardenberg, J. (2019). Elevation-dependent  
736 warming in global climate model simulations at high spatial resolution. *Climate*  
737 *Dynamics*, 52(5-6), 2685-2702. doi:10.1007/s00382-018-4287-z

738 Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., . . . Mt Res  
739 Initiative, E. D. W. W. G. (2015). Elevation-dependent warming in mountain regions  
740 of the world. *Nature Climate Change*, 5(5), 424-430. doi:10.1038/nclimate2563

741 Randin, C. F., Ashcroft, M. B., Bolliger, J., Cavender-Bares, J., Coops, N. C., Dullinger, S., . . .  
742 . Payne, D. (2020). Monitoring biodiversity in the Anthropocene using remote sensing  
743 in species distribution models. *Remote Sensing of Environment*, 239.  
744 doi:10.1016/j.rse.2019.111626



745 Rixen, C., Wipf, S., Frei, E., & Stoeckli, V. (2014). Faster, higher, more? Past, present and  
746 future dynamics of alpine and arctic flora under climate change. *Alpine Botany*,  
747 *124*(2), 77-79. doi:10.1007/s00035-014-0141-z

748 Rogora, M., Frate, L., Carranza, M. L., Freppaz, M., Stanisci, A., Bertani, I., . . . Matteucci,  
749 G. (2018). Assessment of climate change effects on mountain ecosystems through a  
750 cross-site analysis in the Alps and Apennines. *Science of the Total Environment*, *624*,  
751 1429-1442. doi:10.1016/j.scitotenv.2017.12.155

752 Ropars, P., & Boudreau, S. (2012). Shrub expansion at the forest-tundra ecotone: spatial  
753 heterogeneity linked to local topography. *Environmental Research Letters*, *7*(1).  
754 doi:10.1088/1748-9326/7/1/015501

755 Ropars, P., Levesque, E., & Boudreau, S. (2015). Shrub densification heterogeneity in  
756 subarctic regions: the relative influence of historical and topographic variables.  
757 *Ecoscience*, *22*(2-4), 83-95. doi:10.1080/11956860.2015.1107262

758 Savitzky, A., & Golay, M. J. E. (1964). Smoothing and Differentiation of Data by Simplified  
759 Least Squares Procedures. *Analytical Chemistry*, *36*, 1627-1639.

760 Schoener, W., Koch, R., Matulla, C., Marty, C., & Tilg, A.-M. (2019). Spatiotemporal  
761 patterns of snow depth within the Swiss-Austrian Alps for the past half century (1961  
762 to 2012) and linkages to climate change. *International Journal of Climatology*, *39*(3),  
763 1589-1603. doi:10.1002/joc.5902

764 signal developpers. (2013). signal: Signal processing. [http://r-forge.r-](http://r-forge.r-project.org/projects/signal/)  
765 [project.org/projects/signal/](http://r-forge.r-project.org/projects/signal/).

766 Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., . . . Wipf,  
767 S. (2018). Accelerated increase in plant species richness on mountain summits is  
768 linked to warming. *Nature*, *556*(7700), 231-+. doi:10.1038/s41586-018-0005-6

769 Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., . . .  
770 Romanovsky, V. E. (2005). Winter biological processes could help convert arctic  
771 tundra to shrubland. *Bioscience*, 55(1), 17-26. doi:10.1641/0006-  
772 3568(2005)055[0017:wbpchc]2.0.co;2

773 Suding, K. N., Farrer, E. C., King, A. J., Kueppers, L., & Spasojevic, M. J. (2015). Vegetation  
774 change at high elevation: scale dependence and interactive effects on Niwot Ridge.  
775 *Plant Ecology & Diversity*, 8(5-6), 713-725. doi:10.1080/17550874.2015.1010189

776 Tape, K. D., Hallinger, M., Welker, J. M., & Ruess, R. W. (2012). Landscape Heterogeneity  
777 of Shrub Expansion in Arctic Alaska. *Ecosystems*, 15(5), 711-724.  
778 doi:10.1007/s10021-012-9540-4

779 Tape, K. D., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern  
780 Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686-702.  
781 doi:10.1111/j.1365-2486.2006.01128.x

782 Tappeiner, U., Borsdorf, A., & Tasser, E. (2008). *Mapping the Alps: Society - Economy -*  
783 *Environment*. Heidelberg: Spektrum Akademischer Verlag.

784 Tucker, C. J. (1979). Red and photographic infrared linear combinations for monitoring  
785 vegetation. *Remote Sensing of Environment*, 8(2), 127-150. doi:10.1016/0034-  
786 4257(79)90013-0

787 Venables, W., & Ripley, B. (2002). *Modern applied statistics (Fourth S., editor) New York:*  
788 *Springer*.

789 Verbesselt, J., Hyndman, R., Newnham, G., & Culvenor, D. (2010). Detecting trend and  
790 seasonal changes in satellite image time series. *Remote Sensing of Environment*,  
791 114(1), 106-115. doi:10.1016/j.rse.2009.08.014

792 Vermote, E., & Vermeulen, A. (1999). Atmospheric correction algorithm: spectral  
793 reflectances (MOD09). *ATBD version, 4*, 1-107.

794 Vernay, M., Lafaysse, M., Hagenmuller, P., Nheili, R., Verfaillie, D., & Morin, S. (2019).  
795 The S2M meteorological and snow cover reanalysis in the French mountainous areas  
796 (1958 - present). Dataset. <https://doi.org/10.25326/37>.

797 Vionnet, V., Six, D., Auger, L., Dumont, M., Lafaysse, M., Queno, L., . . . Vincent, C. (2019).  
798 Sub-kilometer Precipitation Datasets for Snowpack and Glacier Modeling in Alpine  
799 Terrain. *Frontiers in Earth Science*, 7. doi:10.3389/feart.2019.00182

800 Viovy, N., Arino, O., & Belward, A. S. (1992). The Best Index Slope Extraction (BISE) - a  
801 method for reducing noise in NDVI time-series. *International Journal of Remote*  
802 *Sensing*, 13(8), 1585-1590. doi:10.1080/01431169208904212

803 Vittoz, P., Bodin, J., Ungricht, S., Burga, C., & Walther, G. R. (2008). One century of  
804 vegetation change on Isla Persa, a nunatak in the Bernina massif in the Swiss Alps.  
805 *Journal of Vegetation Science*, 19(5), 671-U628. doi:10.3170/2008-8-18434

806 Vittoz, P., Rulence, B., Largey, T., & Frelechoux, F. (2008). Effects of climate and land-use  
807 change on the establishment and growth of cembra pine (*Pinus cembra* L.) over the  
808 altitudinal treeline ecotone in the Central Swiss Alps. *Arctic Antarctic and Alpine*  
809 *Research*, 40(1), 225-232. doi:10.1657/1523-0430(06-010)[vittoz]2.0.co;2

810 Vorkauf, M., Marty, C., Kahmen, A., & Hiltbrunner, E. (2021). Past and future snowmelt  
811 trends in the Swiss Alps: the role of temperature and snowpack. *Climatic Change*,  
812 165(3), 1-19.

813 Xie, J., Jonas, T., Rixen, C., de Jong, R., Garonna, I., Notarnicola, C., . . . Kneubuehler, M.  
814 (2020). Land surface phenology and greenness in Alpine grasslands driven by  
815 seasonal snow and meteorological factors. *Science of the Total Environment*, 725.  
816 doi:10.1016/j.scitotenv.2020.138380

817 Zhang, G., Zhang, Y., Dong, J., & Xiao, X. (2013). Green-up dates in the Tibetan Plateau  
818 have continuously advanced from 1982 to 2011. *Proceedings of the National Academy*

819            *of Sciences of the United States of America*, 110(11), 4309-4314.  
820            doi:10.1073/pnas.1210423110

821    Zhao, M., & Running, S. W. (2010). Drought-Induced Reduction in Global Terrestrial Net  
822            Primary Production from 2000 Through 2009. *SCIENCE*, 329(5994), 940-943.  
823            doi:10.1126/science.1192666

824    Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., . . . Zeng, N. (2016).  
825            Greening of the Earth and its drivers. *Nature Climate Change*, 6(8), 791-+.  
826            doi:10.1038/nclimate3004

827

## Figure legends

828           **Figure 1 Sign and magnitude of greenness trends in above-treeline ecosystems of**  
829 **European Alps. a** Frequency distribution of linear trends of NDVImax over the period 2000-  
830 2020. Slopes were estimated using the Theil–Sen median slope analysis. Levels of  
831 significance were assessed by a non-parametric, rank based, Mann–Kendall (MK) monotonic  
832 test. Positive [negative] values correspond to greening [browning] trends. The analysis was  
833 performed on 284 546 pixels at 250 m resolution. **b** Greenness trends by land cover class. The  
834 European-scale product Corine Land Cover (CLC) was utilized. Note that the CLC class  
835 “bare rocks” was renamed “very sparsely vegetated” as the average NDVImax of selected  
836 pixels was above 0.1. Note the different scale for positive and negative trends.

837

838           **Figure 2 Spatial distribution of greenness trends.** To ease reading, we applied a 5x5  
839 pixels moving window to the original 250 m resolution map. The color scale represents the  
840 percentage of pixels showing significant greening ( $P < 0.05$ ) over the period 2000-2020. The  
841 bold line delineates the European Alps whose location is shown in the upper left insert. The  
842 lower right insert allows visualizing regional hotspots of greening by aggregating the 250 m  
843 resolution map at 2.5 km and by coloring pixels for which more than 80% of the 250 m pixels  
844 exhibited fast greening ( $P < 0.005$ ).

845

846           **Figure 3 Variation of greenness trends along gradients of elevation and diurnal**  
847 **anisotropic heating (DAH). a** Heatmap of the mean value of NDVImax slopes per class of  
848 elevation and DAH. Only combinations representing more than 5% of the total number of  
849 pixels are shown. **b** Elevational distribution of three ranges of NDVImax along the gradient of  
850 DAH. Lines indicate the second decile, the median and the eighth decile of the distribution.  
851 Average NDVImax values are shown for three 10-year sliding windows.

852

853 **Figure 4 Anomalies of NDVImax.** **a** An example of the variation of NDVImax along  
854 elevation for DAH values in the interval  $]-0.25;-0.2]$ . NDVImax values are averages for the  
855 period 2000-2020. Black lines indicate the first, the fifth (median) and the ninth deciles of the  
856 distribution. The color palette from brown to green allows visualizing the NDVImax anomaly,  
857 i.e. the difference between NDVImax and the median value of the corresponding elevation x  
858 DAH combination. **b** Spatial distribution of the NDVImax anomaly in the European Alps. To  
859 ease reading, we applied a 5x5 moving window to the original 250 m resolution map.

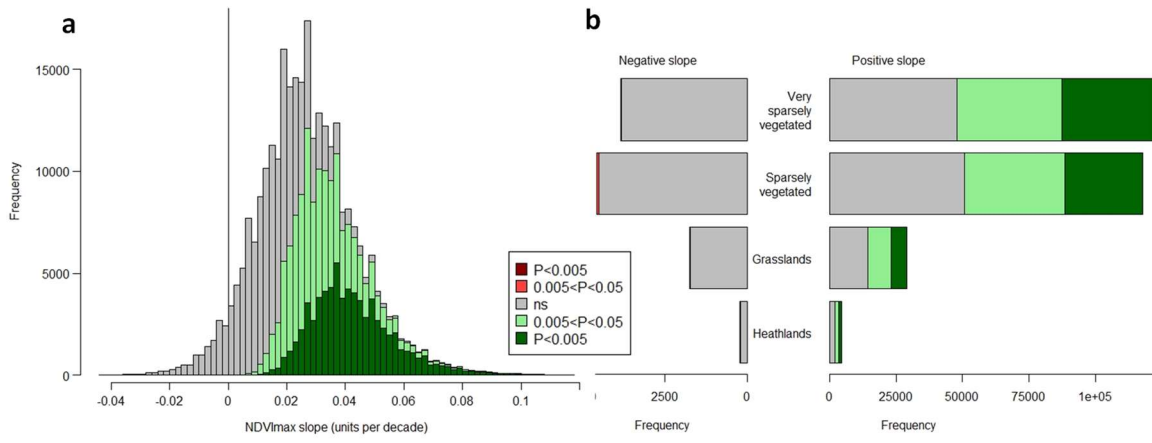
860

861 **Figure 5 Predictors of greenness trends.** We classified pixels into three categories -  
862 no greening, moderate greening ( $0.005 < P < 0.05$ ) and fast greening ( $P < 0.005$ ) - and  
863 implemented a random forest model to assess the importance of predictors. **a** Usefulness of  
864 the predictor for classification measured by the mean accuracy decrease in classification  
865 following permutation of variables. **b** Contribution of a predictor to the purity of nodes  
866 measured by the decrease in the Gini coefficient. **c** Partial dependency analyses showing the  
867 classification probability as a function of the set of values taken by the predictors. We created  
868 1000 perturbed datasets of MODIS reflectances for the 284,346 pixels and then randomly  
869 selected 30,000 pixels in each dataset. These subsets of pixels were split into training (66%)  
870 and validation (33%) to implement the random forest model. Envelopes show the first and  
871 ninth deciles of the distribution.

872

873 **Figure 6 Relationships between land cover, NDVImax anomalies and greenness**  
874 **trends.** We randomly selected 100 pixels (500 m resolution) in three data subsets exhibiting  
875 negative, null and positive NDVImax anomalies (see Figure S7) and visually photo-  
876 interpreted land cover using very high resolution Google Earth imagery. Cover of

877    screes/outcrops (a) and grasslands (c) per class of NDVImax anomaly. NDVImax slopes  
878    (mean +/- se) for each class of NDVImax anomaly distinguishing the cover of screes/outcrops  
879    (c) and grasslands (d). Results of a post-hoc Tukey tests are denoted with letters. Different  
880    lower case letters indicate a significant ( $P<0.05$ ) difference within NDVImax anomaly class.  
881    Different upper case letters indicate a significant ( $P<0.05$ ) difference between NDVImax  
882    anomaly class.



883

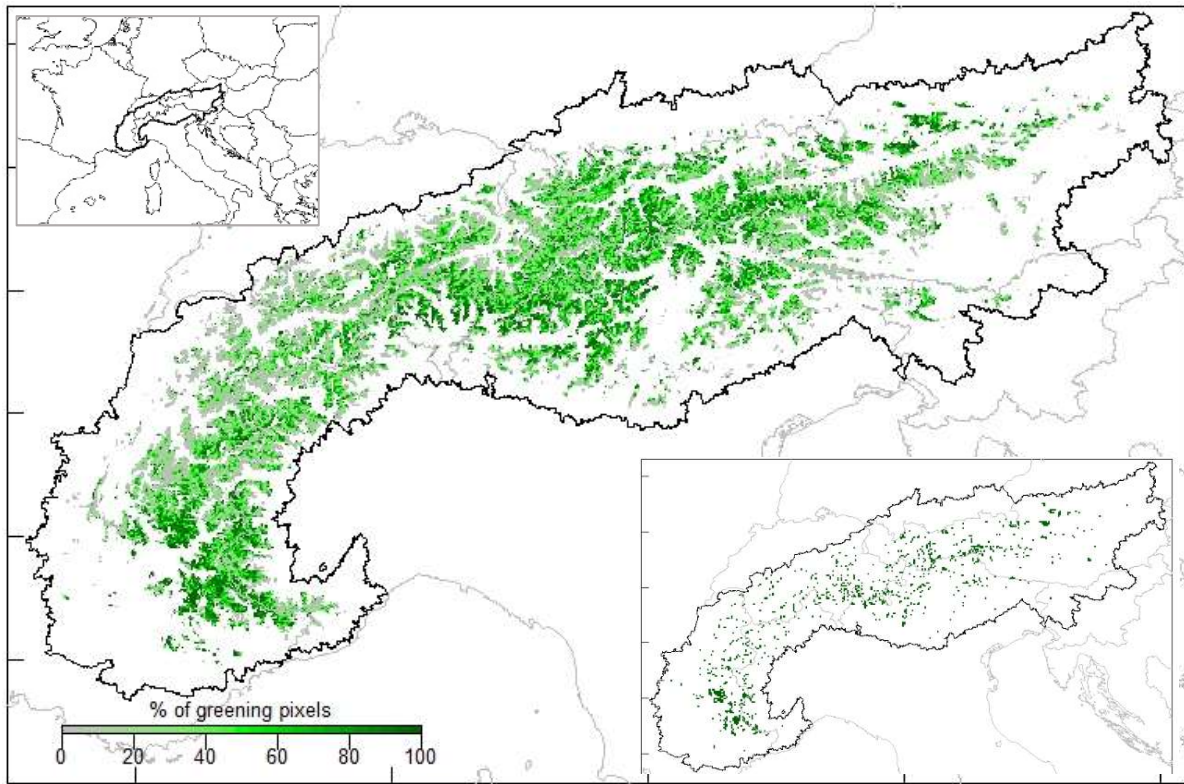
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**Figure 1**

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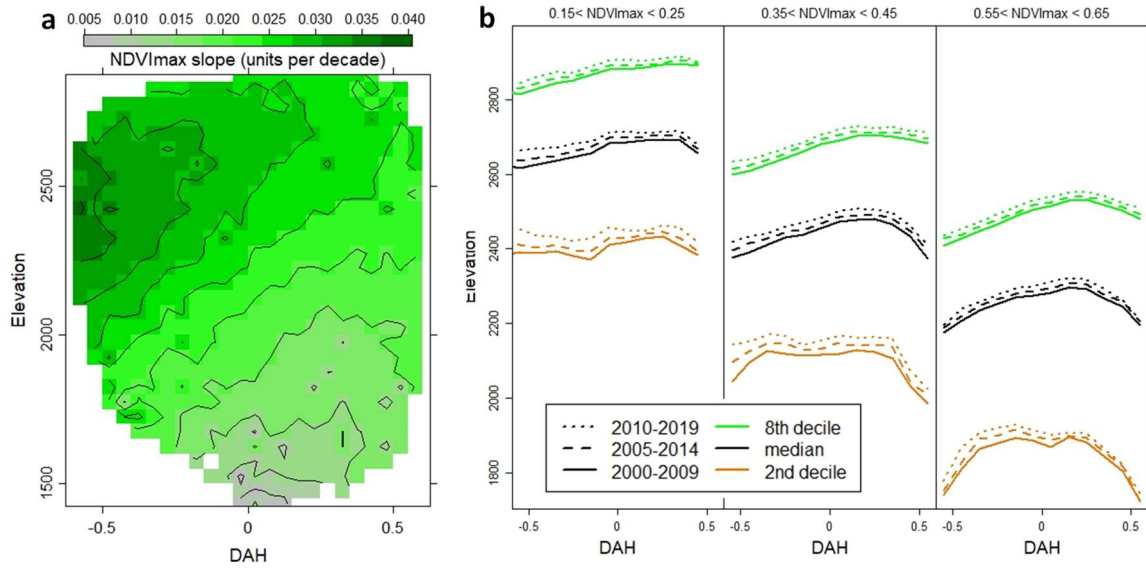
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**Figure 2**

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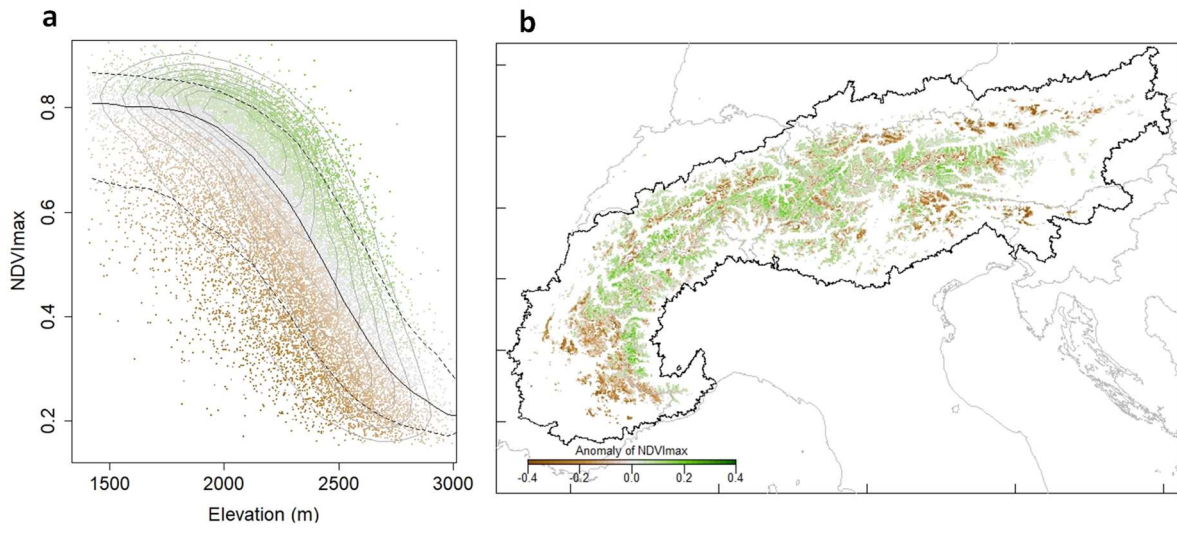
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Figure 3

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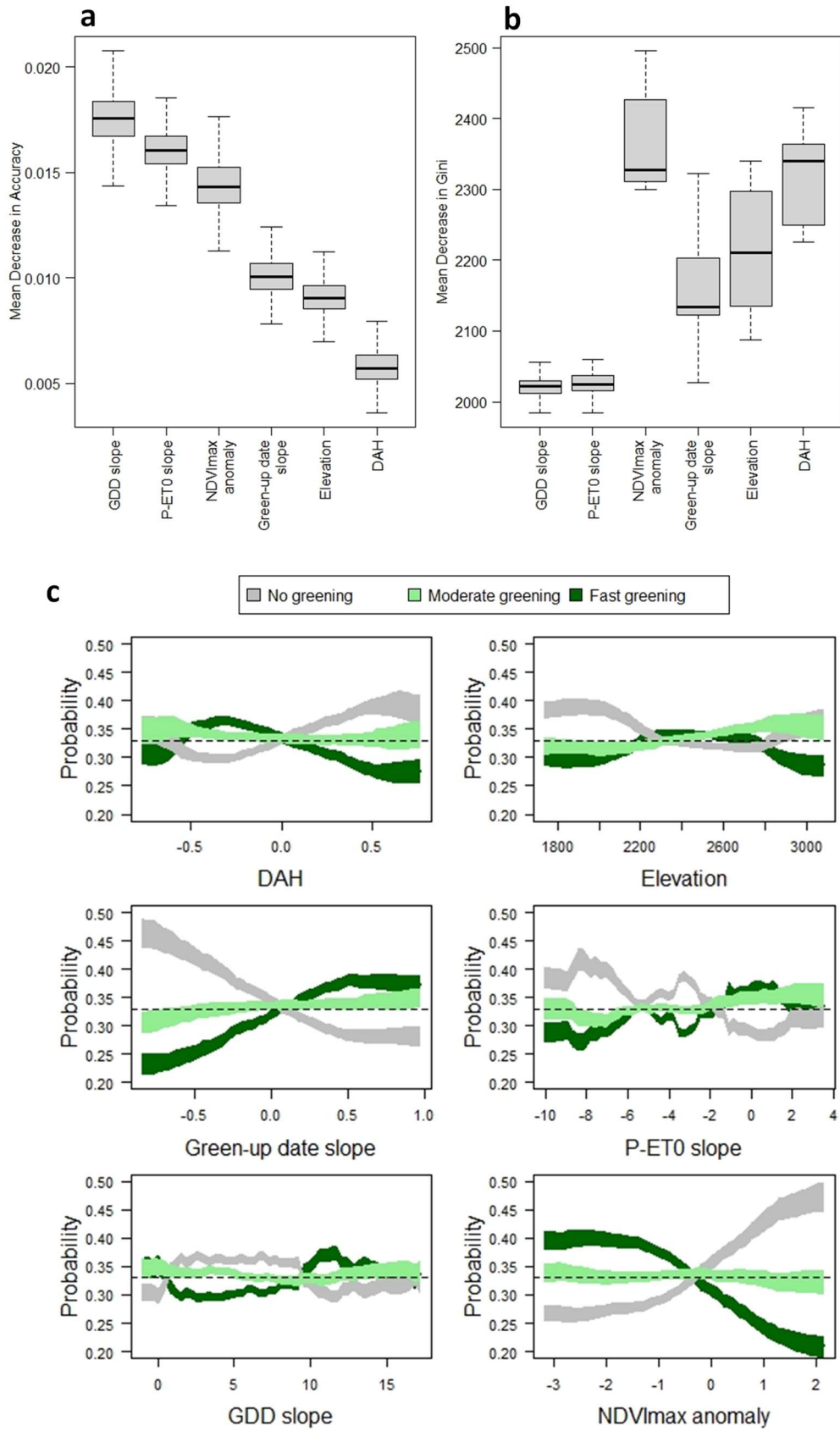


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**Figure 4**



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Figure 5

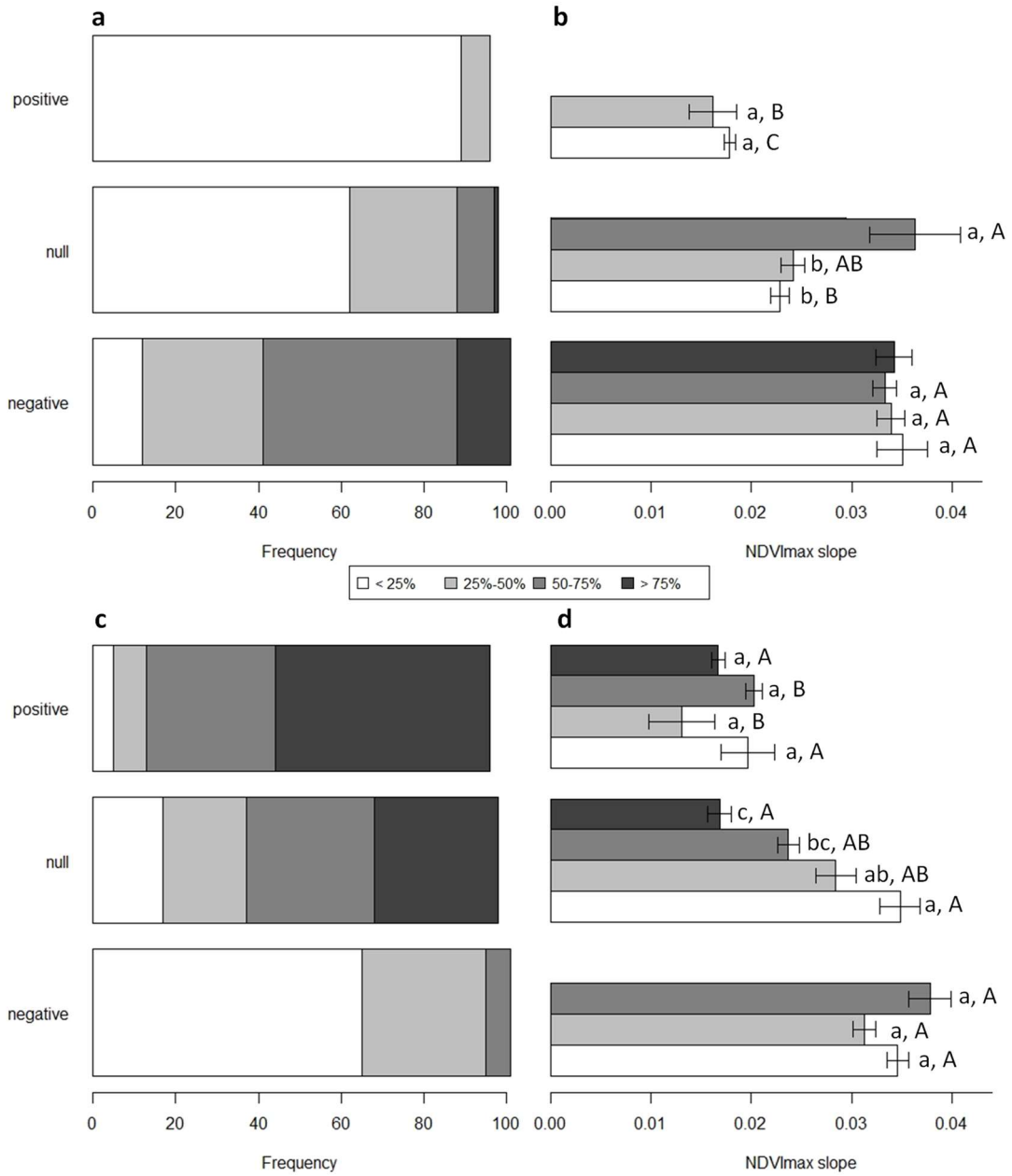


Figure 6