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Philippe Choler, Arthur Bayle, Bradley Carlson, Christophe Randin, Gianluca Filippa, Edoardo Cremonese

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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

List of authors & institutional affiliations

5 Philippe Choler^{1,*}, Arthur Bayle¹, Bradley Z. Carlson², Christophe Randin³, Gianluca

6 Filippa⁴, Edoardo Cremonese⁴

7 1- Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, F-38000 Grenoble,
8 France

9 2- Centre de Recherches sur les Écosystèmes d'Altitude (CREA), Observatoire du Mont-
10 Blanc, F-74400 Chamonix, France

11 3- Univ. Lausanne, Dept. of Ecology & Evolution / Interdisciplinary Centre for Mountain
12 Research (CIRM), Biophore, CH-1015 Lausanne, Switzerland

13 4- Environmental Protection Agency of Aosta Valley, Climate Change Unit, Loc. La
14 Maladière, 48, IT-11020 Saint-Christophe (AO), Italy

15

Contact Information

17 Philippe Choler, +33 6 76 51 48 96, philippe.choler@univ-grenoble-alpes.fr

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Key words

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 (ρ) 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 ρ 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 developers, 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 α is the aspect, β is the slope and the
200 parameter α_{\max} corresponds to the aspect with the maximum total heat surplus. We used α_{\max}
201 = 212° 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° resolution for the period 1995 onwards (version E-OBS v22.0e,

211 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_0 . We summed the $P-ET_0$ difference over the summer months to assess
218 the dry–wet conditions of the growing season. ET_0 was estimated on a daily basis using the
219 equation $\lambda ET_0 = C (\Delta/\Delta+\gamma) Q$, where Q is the global radiation ($MJ\ m^{-2}\ day^{-1}$), Δ the slope of
220 the vapour pressure-temperature curve ($kPa\ ^\circ C^{-1}$), γ the psychrometric constant ($kPa\ ^\circ C^{-1}$), λ
221 the latent heat of vaporization ($MJ\ kg^{-1}$), 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 ($P\text{-value} > 0.05$), moderate
234 greening ($0.001 < P\text{-value} < 0.05$) and strong greening ($P\text{-value} < 0.001$). 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-ET₀. 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.

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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.

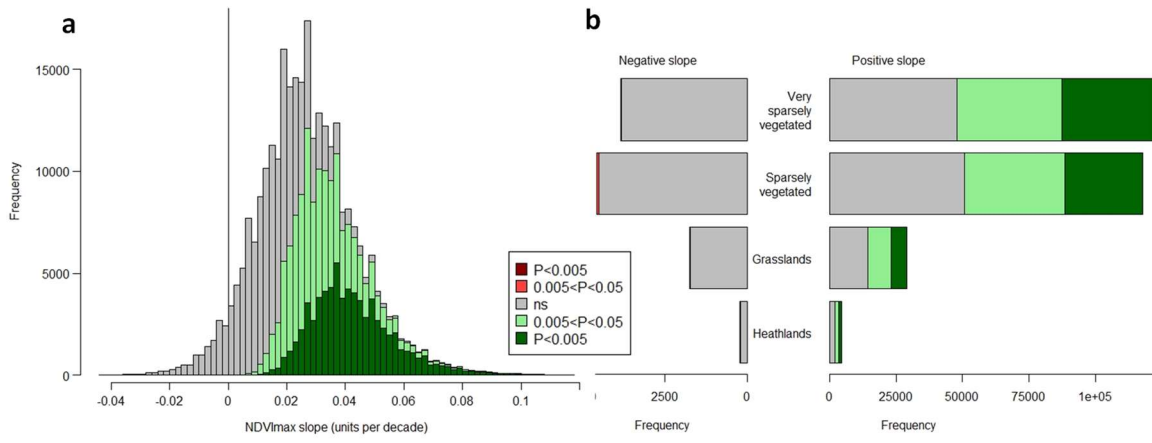
860

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.



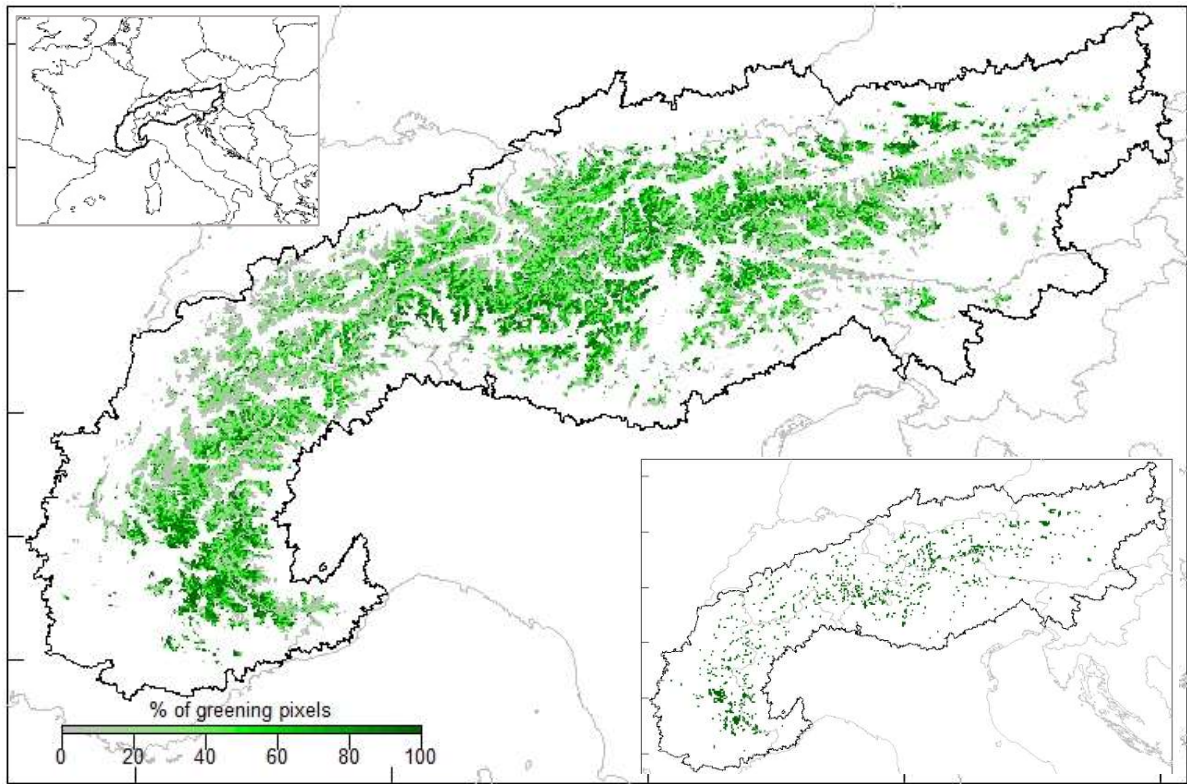
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Figure 1

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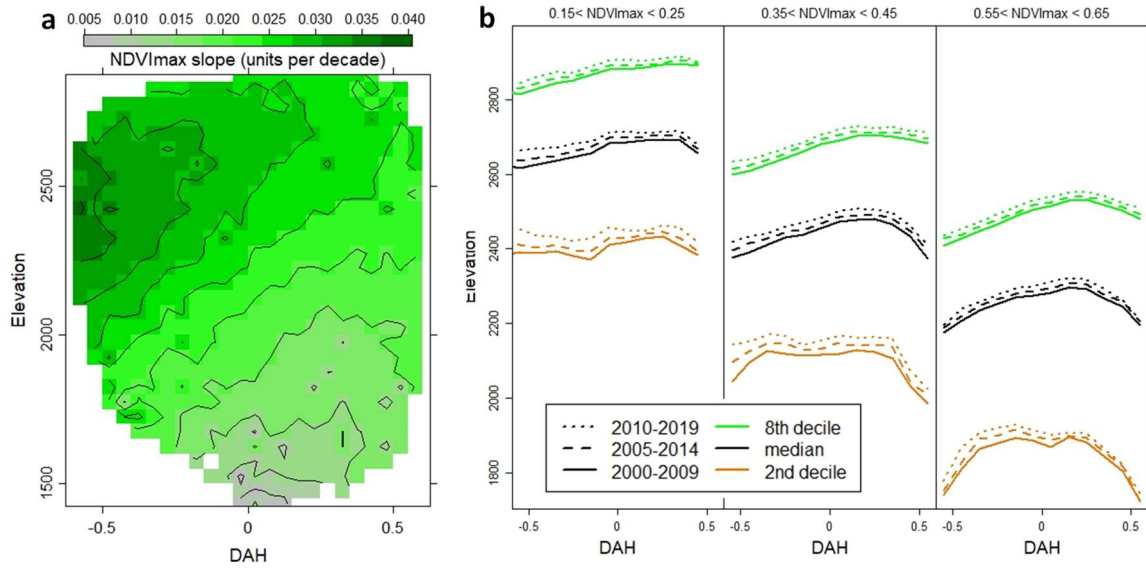
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Figure 2

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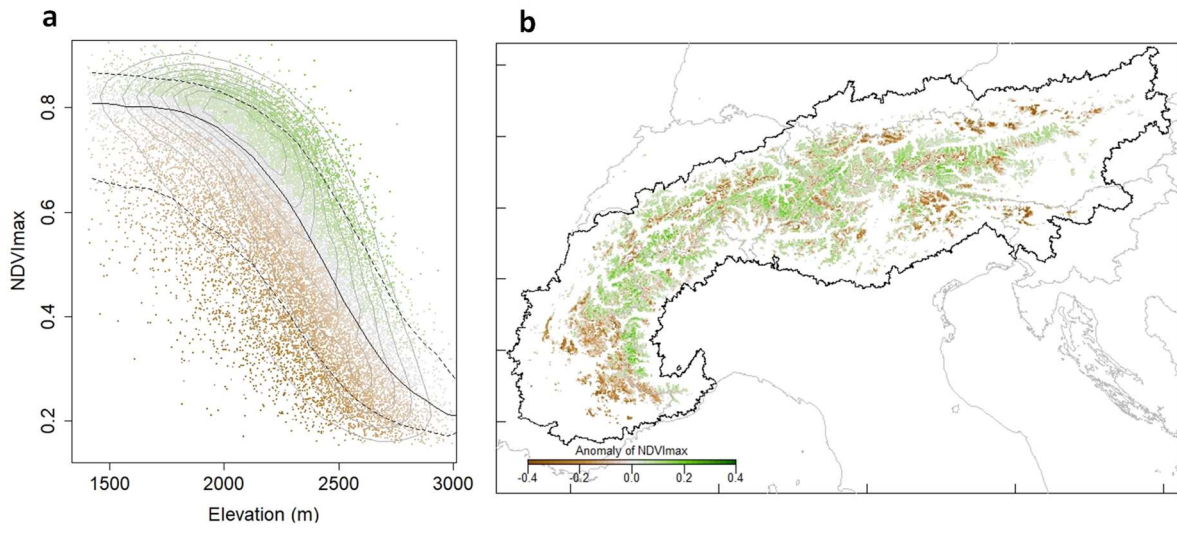
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Figure 3

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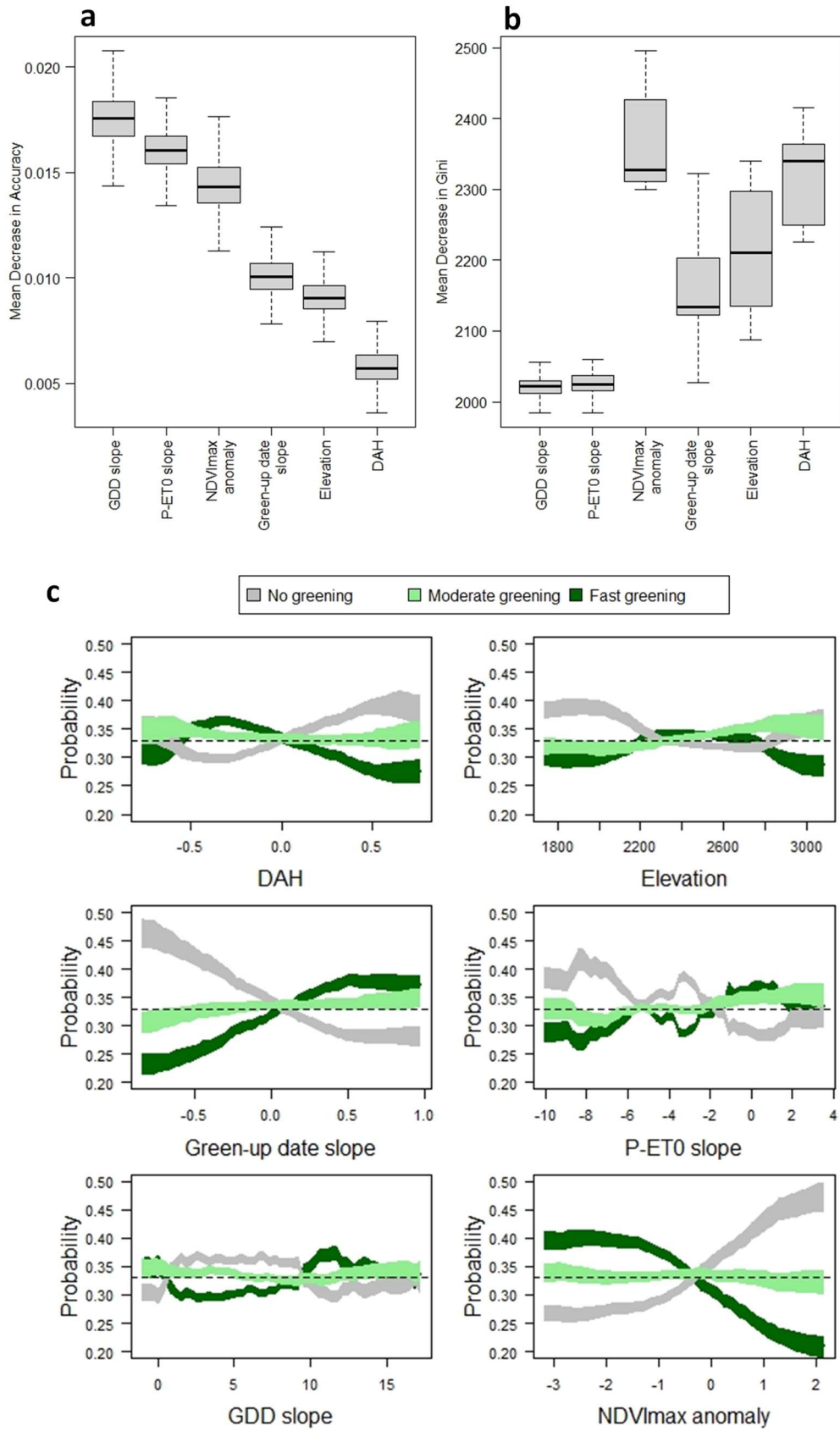


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Figure 4



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Figure 5

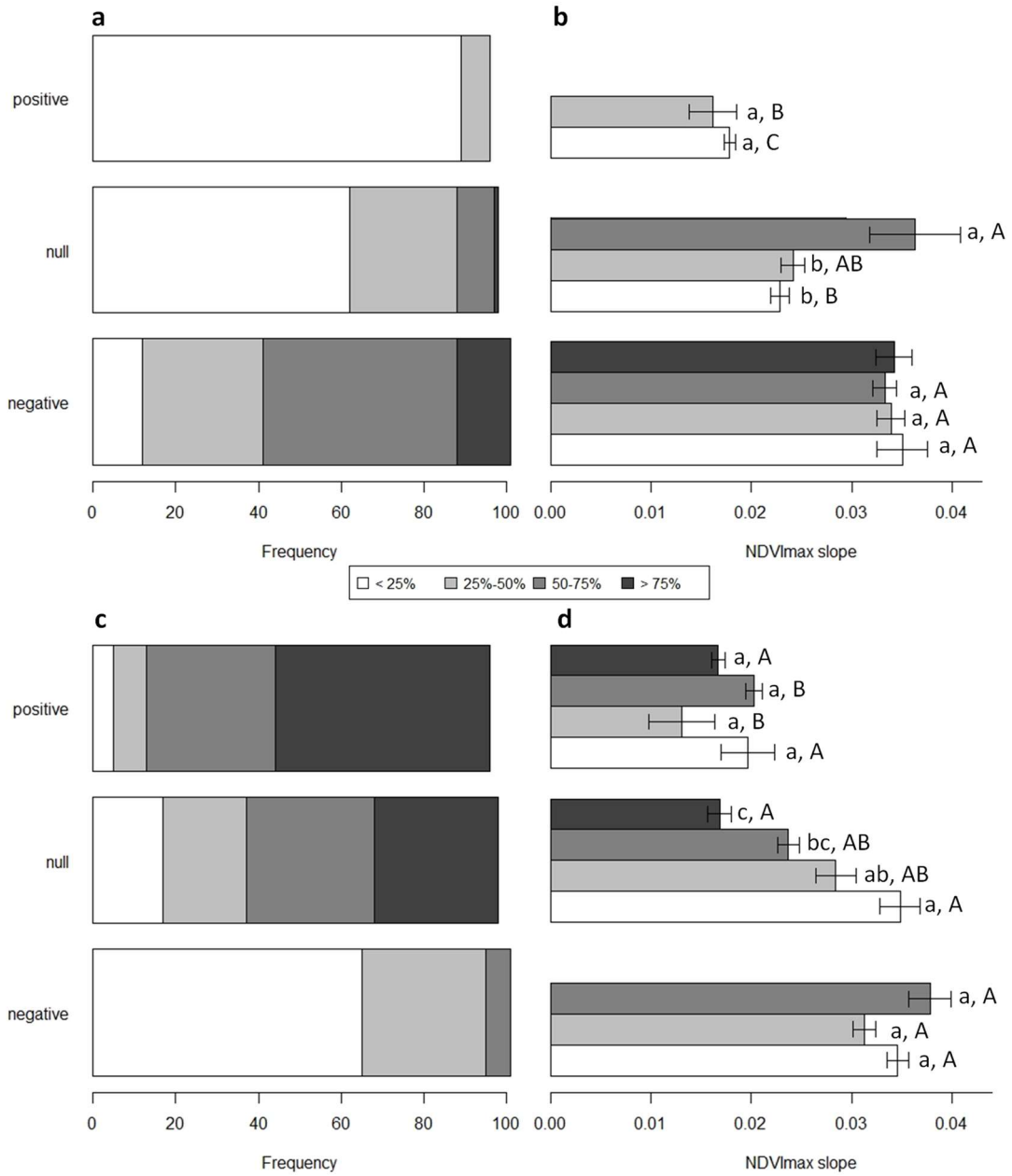


Figure 6