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5

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18

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20 climate events, resilience.

21

22 **Abstract**

23 Extreme climate events such as late spring frosts (LSFs) negatively affect productivity
24 and tree growth in temperate beech forests. However, detailed information on how these
25 forests recover after such events are still missing. We investigated how LSFs affected
26 forest cover and radial growth in European beech (*Fagus sylvatica* L.) populations located
27 at different elevations at four sites in the Italian Apennines, where LSFs have been
28 recorded. We combined tree-ring and remote-sensing data to analyse the sensitivity and
29 recovery capacity of beech populations to LSFs. Using daily temperature records, we
30 reconstructed LSF events and assessed legacy effects on growth. We also evaluated the
31 role played by elevation and stand structure as modulators of LSFs impacts. Finally, using
32 satellite images we computed Normalized Difference Vegetation Index (NDVI),
33 Enhanced Vegetation Index (EVI) and LAI (Leaf Area Index) to evaluate the post-LSF
34 canopy recovery. The growth reduction in LSF-affected trees ranged from 36% to 84%.
35 We detected a negative impact of LSF on growth only during the LSF year, with growth
36 recovery occurring within 1-2 years after the event. LSF-affected stands featured low
37 vegetation indices until late June, i.e. on average 75 days after the frost events. We did
38 not find a clear relationship between beech forest elevation and occurrence of LSFs
39 defoliations. Our results indicate a high recovery capacity of common beech and no
40 legacy effects of LSFs.

41

42 **1. Introduction**

43 In temperate forests, a late spring frost (LSF) is an abrupt and severe temperature
44 drop during a period of mild weather (also known as false spring) which negatively
45 impact tree productivity and growth (Augspurger 2009, Chamberlain et al. 2020). In
46 European hardwood species such as European beech (*Fagus sylvatica* L.) below-zero
47 temperatures during spring can damage the recently unfolded leaves and cause a radial
48 growth reduction (Dittmar et al. 2003, 2006, Gazol et al. 2019, Vitasse et al. 2019,
49 Sangüesa-Barreda et al. 2021). In Mediterranean areas, growth and productivity of beech
50 forests could be also severely constrained by summer drought (Geßler et al. 2007,
51 Piovesan et al. 2008, Gazol et al. 2019, Tognetti et al. 2019), a factor designing the
52 southernmost xeric edge of beech distribution (Jump et al. 2006, Bolte et al. 2007, Serra-
53 Maluquer et al. 2019, Camarero et al. 2021). In Europe, the recent climate variability
54 significantly increased the frequency of extreme climate events such as LSFs
55 (Augspurger 2013, Bigler & Bugmann 2018, Zohner et al. 2020, Lamichhane 2021) and
56 summer droughts (Spinoni et al. 2018, Gazol & Camarero 2022, Dukat et al. 2022). In
57 widely distributed species such as beech the combined effects of these extreme climate
58 events pose several questions about forest productivity, tree growth and post-disturbance
59 recovery (Gazol et al. 2019, Vitasse et al. 2019, D'Andrea et al. 2020).

60 Beech in its juvenile phase is highly vulnerable to LSFs which can cause diffuse
61 seedling mortality, whereas survived individuals could increase their autumn
62 photosynthetic activity (Zohner et al. 2018). In mature beech trees, old carbohydrates can
63 rapidly be mobilized to produce a second cohort of leaves after LSF induced defoliations
64 (D'Andrea et al. 2019). However, new leaves and twigs of affected trees may be smaller
65 and less productive than in undamaged individuals (Rubio-Cuadrado et al. 2021b).

66 Moreover, LSFs occurring in two consecutive years may hamper growth resilience
67 (Rubio-Cuadrado et al. 2021a).

68 LSF induced defoliations largely depend on the timing of the event occurrence
69 and of the leaf unfolding. Most forest species including beech show earlier spring
70 phenology at lower elevation. Beech bud burst timing is mainly controlled by chilling and
71 forcing temperatures and influenced by the photoperiod length (Heide 1993; Vitasse et
72 al. 2014). Due to this interaction beech, compared to other co-occurring species, features
73 different timing in leaf unfolding according to the site elevation: later at lower and earlier
74 at higher elevation (Vitasse et al. 2009). Also, climate warming affects tree phenology
75 especially at high elevation sites, turning beech forest canopies more prone to LSFs
76 (Čufar et al. 2008, Menzel et al. 2011).

77 Leaf shedding after LSF is commonly reported in the beech distribution core area,
78 in Central Europe (e.g., Dittmar et al. 2006, Vitasse et al. 2019) and, in recent years, also
79 in Mediterranean mountains at the southernmost beech distribution limit (Gazol et al
80 2019). Recent studies, based on remote-sensing and tree-ring data, revealed that LSF
81 defoliation events on southern European beech forests were frequent from 1990 onwards
82 (Olano et al. 2021, Sangüesa-Barreda et al 2021). Nonetheless, this information could be
83 biased by the availability or quality of satellite images. We need complementary
84 information on how LSF affected beech radial growth in the last decades and across
85 extended ecological gradients, i.e. in sites at different altitudes or with different soil water
86 availability. The Italian Apennine range, due to its geographic layout almost
87 perpendicular to the direction of cold air masses from eastern Europe, provides a valuable
88 setting for such research because appears particularly sensitive to late frost events. Here,
89 beech forest is the most common forest type, spanning from the sub-montane belt up to
90 the upper treeline even at 1900 m a.s.l. (Vitali et al. 2018, Malandra et al. 2019).

91 In 2016 and 2017 two large-scale LSF events occurred along the Central and
92 Southern Apennines affecting approximately 5000 km² of forested area, around one third
93 of the beech forests extension in Italy (Nolè et al. 2018, Bascietto et al. 2018, 2019). LSFs
94 can differently affect beech canopies depending on site elevation and their phenology. A
95 remote-sensing study in Italy indicate that due to later leaf unfolding high-elevation beech
96 forests are less defoliated than mid- and low-elevation stands (Nolè et. al 2018). However,
97 high elevation stands could be more affected if a late frost occurs at the time of emerging
98 leaves, whereas at lower sites leaves would be more developed and frost resistant.

99 Lacking a clear relationship between beech forest elevation and occurrence of
100 LSF defoliations, we could reject the hypotheses that: (i) the forests located at higher
101 elevations are more sensitive to LSF disturbance, and (ii) their increased frequency may
102 in the longer term jeopardize the presence of beech from high-altitude sites in
103 Mediterranean mountains. We therefore tested this hypothesis by combining short-term
104 remote sensing information with long-term, retrospective tree-ring analyses at four sites,
105 two located on the wetter central Apennines and two on the drier southern Apennines.
106 The specific multispectral signature of brown-coloured affected foliage after LSF can be
107 detected by satellite imagery and used to assess the geographic extension and the severity
108 of such disturbances at broad spatial scales and in remote sites (Allevato et al. 2019,
109 Decuyper et al. 2020, Olano et al. 2021).

110 With tree-ring measurements, remote sensing and climatic data, we reconstructed
111 past LSFs and assessed their impacts on beech radial growth and canopy cover and
112 greenness. We aimed (i) to detect the effects of LSF on tree growth along altitudinal
113 gradients, and (ii) to assess the European beech post-LSF recovery and resilience in terms
114 of productivity and canopy greenness with remote sensed imagery.

115

116 **2. Material and methods**

117 *2.1. Study sites*

118 We studied four locations (Figure 1) located in central and southern Italy, all
119 within the European beech distribution range (Pott 2000). In this mountainous region,
120 beech is the most frequent species of the upper treeline ecotones ranging between 1600
121 and 1900 m a.s.l. (Vitali et al. 2018).

122 Study sites were selected combining documental evidence of LSF events (e.g.,
123 forest reports) with satellite imagery verification (Figure 1c). Two sites are in the central
124 (Mt. Acuto -ACU and Mt. dei Fiori - MDF), and two in the southern Apennines (Mt.
125 Volturino - VOL and Mt. Pollino - POL), (Table 1, Figure 1a). At all sites, pure beech
126 forests extend continuously for at least 300-400 m along an elevation gradient from mid-
127 slope to the upper forestline.

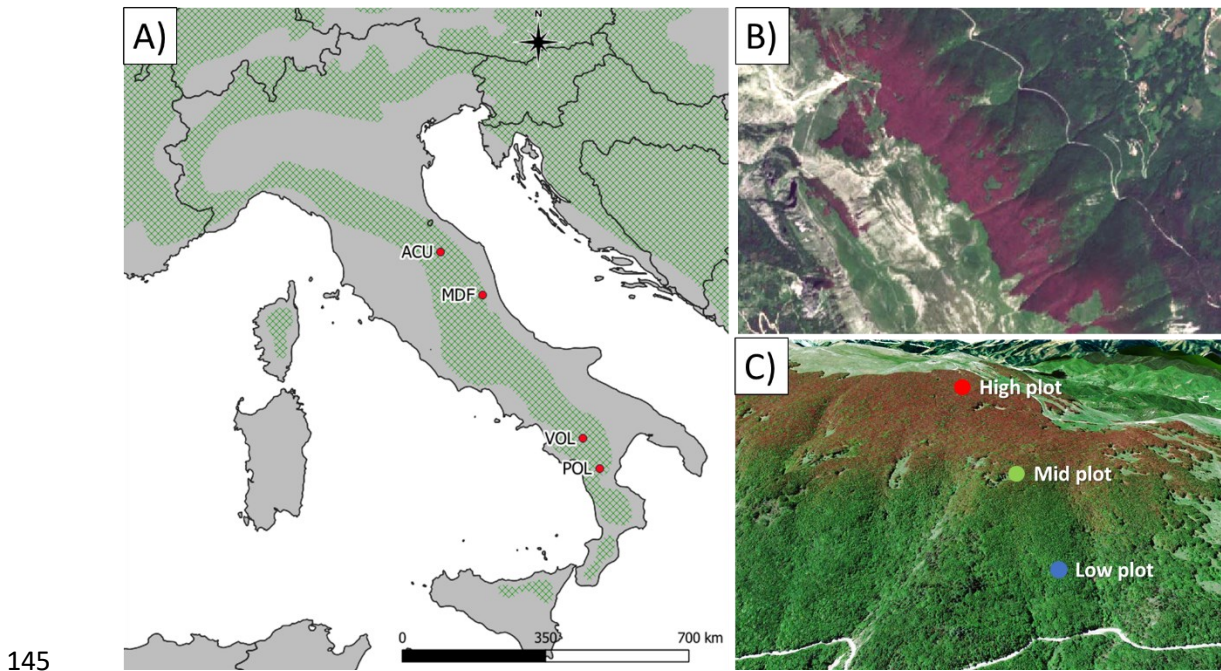
128 Mean annual temperatures range from 8.4 °C (ACU) to 5.0 °C at the coldest
129 location (POL), whereas annual precipitation varies from 754 mm in VOL to 1330 mm
130 in ACU (Table S1). According to the *Ecopedologic map of Italy* all sites are located on
131 calcareous substrates and share the same basic and deep soils (Italian Ministry for the
132 Environment, Land and Sea, <http://www.pcn.minambiente.it/viewer>). Slope steepness
133 ranges between 20 to 40%, and it increases upwards.

134

135 *2.2. Field data collection*

136 Between 2019 and 2020, in each study site, at high, mid, and low altitude we
137 placed two concentric circular sampling plots (Figure 1c). Along the slopes, sampling
138 plots have been located with an elevation difference of at least 100 m between one from
139 the others, i.e. the intermediate and high plots are located at elevations of at least 100 m
140 and 200 m, respectively, higher than the low plot. At each location we sampled beech

141 trees within a larger plot with variable radius between 20 and 30 m to guarantee the
 142 presence of at least 20 evenly distributed dominant healthy trees, with ≥ 30 cm diameter
 143 at breast height (DBH) and without crown damage. The inner plot radius was fixed at 10
 144 m.



145
 146 **Figure 1.** (A) Location of the four study sites in central and southern Apennines (Italy) within the
 147 *Fagus sylvatica* distribution range (green area) (Caudullo et al. 2019). (B) A true-colour Sentinel
 148 2A satellite image (May 26th, 2016) showing the beech forest sectors affected by a spring frost at
 149 MDF site. (C) Distribution of plot areas along the altitude gradient at MDF, (Google earth Pro V
 150 7.3.4.8248; May 22nd, 2016).

151
 152 **Table 1.** Geographic settings of the study sites and their forest structure variables. Forest structure
 153 abbreviations: OC, Overaged Coppice; CC, Coppice under Conversion; HF, High Forest.

| Site | Lat (°N) | Long (°E) | Plot | Elevation | Forest structure | Tree density (No stems ha ⁻¹) | Basal area (m ² ha ⁻¹) | DBH (cm) | Height (m) |
|------|-------------|--------------|------|-----------|---------------------|--|--|-------------|---------------|
| ACU | 43.48 | 12.68 | High | 1375 | OC | 7417 | 56.47 | 9.8 | 13.2 |
| | | | Mid | 1245 | CC | 1146 | 44.70 | 22.3 | 16.5 |
| | | | Low | 1080 | HF | 382 | 77.39 | 50.8 | 22.0 |
| MDF | 42.79 | 13.59 | High | 1584 | OC | 4170 | 51.68 | 12.6 | 14.9 |
| | | | Mid | 1423 | OC | 4520 | 53.98 | 12.3 | 15.2 |
| | | | Low | 1159 | OC | 3342 | 55.94 | 14.6 | 17.3 |
| VOL | 40.43 | 15.79 | High | 1600 | CC | 1401 | 54.69 | 22.3 | 21.8 |
| | | | Mid | 1405 | CC | 1655 | 49.75 | 19.6 | 25.3 |
| | | | Low | 1300 | CC | 1910 | 31.72 | 14.5 | 20.0 |

| | | | | | | | | | |
|-----|-------|-------|------|------|----|------|-------|------|------|
| | | | High | 1890 | OC | 4010 | 55.69 | 13.3 | 18.8 |
| POL | 39.93 | 16.16 | Mid | 1590 | CC | 2769 | 60.30 | 16.6 | 20.5 |
| | | | Low | 1450 | HF | 923 | 73.35 | 31.8 | 29.3 |

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168 *2.3. Cores processing and tree-ring width series*

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In the inner plots we measured the DBH (minimum threshold 2.5 cm) of all standing and living stems. In the larger plots we measured DBH and total height of the dominant individuals with a laser clinometer and rangefinder (TruPulse 360B, Laser Technology, Inc.). In each elevation plot, we extracted wood cores at breast height (1.3 m) orthogonally to the slope from at least 20 dominant trees using a Pressler increment borer. Globally, sample size of increment cores was 303 cores extracted from 244 trees. Basal area ranged from 31 to 77 m² ha⁻¹ and tree height from 13 to 29 m (Table 1). Values variability is partly related to different management systems: overaged coppices (e.g., ACU-high plot) have higher tree density and lower tree size (DBH, height) than high forests (e.g., POL-low plot). Coppices in conversion (e.g., ACU-mid plot) feature intermediate tree density, higher values than high forest and lower than the overaged coppices.

We mounted all cores on wooden supports and polished them with progressively finer sandpaper. We visually cross-dated each core and then measured ring widths using a semi-automatic system (LINTAB-TSAP) at 0.01 mm accuracy. We used the COFECHA software to check the visual cross-dating (Holmes 1983). Then we detrended the tree-ring width series by fitting cubic spline functions to remove the age- and disturbance-related trends and to emphasize the high-frequency growth variability (Cook et al. 1990). We set the smoothing spline's rigidity at 25 years and its wavelength cut-off value at 50%. We detrended all measured series dividing observed by fitted values to obtain dimensionless ring-width indices. We averaged individual tree-ring indexed series

178 using a bi-weight robust method to develop a mean chronology and obtained 12 mean
179 plot chronologies (Figure 2).

180 We compared the mean chronologies by calculating descriptive statistics both on
181 single raw series, such as the first-order autocorrelation (AC) and the Gini coefficient
182 (Gini), and on indexed series as inter-series correlation (Rbar) and Expressed Population
183 Signals (EPS). The AC describes the influence of the previous growth on the current year
184 growth, and the Gini coefficient accounts for the percentage of variability in the widths
185 from one year to the next (Biondi & Qeadan 2008), similarly to the mean sensitivity (MS)
186 (Fritts 1976). Rbar and EPS assess respectively the mean correlation between the series
187 and the similarity degree of a given chronology with a correct reference chronology
188 (Briffa & Jones 1990; Wigley et al. 1984). We processed the raw series with the “dplr”
189 package (Bunn 2008) of R software (R Development Core Team, 2020). To assess the
190 similarity among plots’ indexed chronologies we calculated their Pearson correlations
191 and performed a Principal Component Analysis (PCA) on the covariance matrix.

192

193 *2.4. Inferring frost events from climate records*

194 To detect the potential LSF years, we used daily climate data from the E-OBS gridded
195 dataset, interpolating the temperature records from the grid elevation to the plot location
196 considering a mean lapse rate of $-6.5\text{ }^{\circ}\text{C km}^{-1}$ as the elevation increases. We used the
197 accumulated degree-days (ΣT) and chilling requirements (C) as proxies of leaf phenology
198 and then spring daily temperature anomalies (ΔT) to quantify the severity of the events.
199 ΣT is the cumulated daily mean temperature above a 5°C threshold from January 1st (Day
200 Of the Year - DOY 1) to the date of the minimum temperature recorded between DOY
201 111 and 131 (approximately from April 20th to May 10th). This method slightly differs
202 from the one in the literature (Vitasse et al. 2019), where accumulated degree-days are

203 accounted to the date of the last late frost day ($\leq -2^{\circ}\text{C}$). Yet, to avoid influences related
204 to temperature interpolation in gridded datasets, which are prone to large errors,
205 especially in daily records and across topographically complex areas, we decided to
206 consider the day with minimum temperatures rather than the temperature threshold of $-$
207 2°C . Chilling requirement was calculated as days with mean air temperature $<10^{\circ}\text{C}$
208 between November 1st to the date of the minimum temperature recorded between DOY
209 111 and 131 (the same period used for the calculation of the ΣT).

210 For the LSF detection, we computed spring temperature anomalies (ΔT) or the
211 difference between the mean minimum temperature from March 1st to April 30th and the
212 minimum temperature from April 20th to May 10th for each year. High values of ΣT and
213 ΔT lead to a higher probability for beech to suffer LSF events (Gazol et al. 2019, Vitasse
214 et al. 2019). We defined years with the highest risk of severe LSF when both ΣT and ΔT
215 exceeded the 3rd quartile computed for the reference period 1951–1990. While ΣT
216 temperatures cannot be effective if the chilling requirement is not reached, the years
217 selected must guarantee at least 120 days of C index (Dantec et al. 2014).

218 We then compared these three meteorological indices (ΣT , ΔT and C) and
219 validated them with available daily data collected by local meteorological stations (Table
220 S2). Again, temperature records were interpolated from station elevation to the plot
221 location considering a mean lapse rate of $-6.5^{\circ}\text{C km}^{-1}$. Local stations provide the daily
222 absolute minimum temperatures that we used to validate the calculated ΔT values
223 considering only the frost events (temperature $< 0^{\circ}\text{C}$).

224

225 2.5. *Quantifying frost impacts on tree growth*

226 In dendrochronology an event year is a dated tree-ring considerably wider or
227 narrower with respect to prior or subsequent rings, whereas a pointer year refers to several

228 trees that display synchronously an event year within the series (Schweingruber et al.
 229 1990). If LSFs are sufficiently severe, they can affect the cambial activity of trees and
 230 induce the formation of narrow rings detectable as negative event years and possibly as
 231 pointer years. We computed pointer years of all indexed individual tree-ring width series
 232 with the “Normalization in a moving Window” method (Cropper, 1979) using the R
 233 package PointRes (van der Maaten-Theunissen et al. 2015). This method delivers Cropper
 234 values (z_i) series by normalizing tree-ring width series in moving windows. We
 235 considered event years $|z_i|$ values of 0.75 in a 5-year moving window. We retained a
 236 pointer year when the event year occurred in 75% of the plot series. Then, we selected
 237 the negative pointer years (nPYs) matching with a LSF year, hereafter abbreviated as LSF
 238 ring.

239 We estimated the recovery time after the selected years on indexed tree-ring width
 240 series using the Superposed Epoch Analysis (SEA), with a time lag of 4 years and
 241 bootstrapped resampling (Lough & Fritts 1987, Rao et al. 2019), using the “sea” function
 242 of the “dplR” package (Bunn 2008). Then, we averaged and plotted the departures from
 243 the mean SEA value of each core for the 4 years prior to, and immediately after each LSF
 244 nPY, to determine the occurrence of significant growth deviations. This analysis allows
 245 detecting post-frost carryover or legacy effects on radial growth. For the SEA over recent
 246 LSFs occurring in 2016 and 2017 we considered only one or two years after each event,
 247 since tree-ring series end in 2018 (MDF site) or 2019 (ACU, VOL and POL sites).

248 As an additional analysis to assess the impact of LSF in nPY, we calculated
 249 resistance (R_t), recovery (R_c) and Resilience (R_s) indices following Lloret et. al (2011):

250

251 Resistance (R_t) = Ring width index $_t$ / Ring width index $_{t-2}$ [1]

252 Recovery (R_c) = Ring width index $_{t+2}$ / Ring width index $_t$ [2]

253 Resilience (Rs) = Ring width index $t+2$ / Ring width index $t-2$ [3]

254 We computed these indices using standard tree-ring width series and a 2-year lag to avoid
255 recovery underestimation due to consecutive LSFs, and to study the most recent LSFs.

256

257 2.6. *Tree variability to frost sensitivity*

258 The effect of various drivers of individual tree growth on frost sensitivity was
259 analysed at tree level. We assumed that beech sensitivity to spring frost could be
260 explained by individual tree characteristics, such as cambial age and topographic
261 elevation that could play an important role. The total number of LSF rings obtained by
262 climate data analysis were considered as an indicator of frost sensitivity. We fitted
263 Generalized Linear Mixed-effects Models (GLMMs) for predicting at each site the
264 number of LSF rings formed by each tree as a function of the following variables: cambial
265 age, mean tree-ring width, basal area increment (BAI), mean sensitivity and Gini index
266 computed for the period 1950–2019, and the growth trend (based on the slope of BAI) in
267 the period 1990–2019. From the analysis we removed BAI from the predictors because it
268 showed a high (≥ 4) Variance Inflation Factor, to avoid multicollinearity among the
269 independent variables. We rescaled all the predictors to account for differences on
270 measurement scale and we used a Poisson distribution family for the response count
271 variable (LSF rings). For each model, we also used the plot elevation as random factor to
272 search for different responses among plots.

273 We fitted two GLMMs for modelling the presence/absence of LSF rings in each
274 series in 1957 and 2016, the years with more trees affected by frost, as a function of
275 cambial age, mean tree-ring width, mean sensitivity, and Gini index. We used plots nested
276 in sites to focus on the explained variance. We rescaled all the predictors to account for
277 differences on measurement scale and we used a binomial distribution family for the

278 response variable (presence/absence of LSF rings). We performed all statistical analyses
279 within the R environment (R Development Core Team, 2020), using the “glm” function
280 of “stats” package (version 4.0.3) and the “glmer” function of “lme4” package (Bates et
281 al., 2015). BAI was calculated using the “bai.out” function of the “dplr” package (Bunn
282 2008).

283

284 *2.7. Frost events detected through remote sensed imagery*

285 We used multispectral satellite Copernicus Sentinel-2 imagery to estimate the
286 incidence of late frost and the recovery time of beech at the different plots. We used
287 images from the twin satellites Sentinel-2A and Sentinel-2B. These platforms carry a
288 Multi-Spectral Instrument (MSI) that samples thirteen spectral bands (Drusch et al. 2012).
289 The EO Browser service (<https://www.sentinel-hub.com/explore/eobrowser/>) allowed
290 satellite images selection with cloud-free areas over the study sites for the time interval
291 ranging from March 2016 to December 2018. We selected images only for ACU and VOL
292 sites due to (i) the least cloud contamination over their plots, and (ii) the occurrence of
293 two consecutive LSF events in 2016 and 2017. We collected 62 images of the same time
294 interval and downloaded the corresponding products from the Copernicus Scientific Data
295 Hub (<https://scihub.copernicus.eu/>) as a Level-1C (Top-of-atmosphere reflectance –
296 orthoimage products) and Level-2A (Bottom-of-atmosphere reflectance –
297 atmospherically corrected), when available (Table S3).

298 We processed twenty-six Sentinel-2 Level-1C images performing the atmospheric
299 corrections using the SNAP 8.0 and Sen2Cor V2.8 software provided by the European
300 Space Agency. We used the classification mask, built from the scene classification layer
301 produced by Level 2A-processing, or provided in the Level 2 product acquired, to remove
302 pixels classified specifically as cloud shadows, water, intermediate and high-probability

303 of cloud cover, thin cirrus, and snow. All images were calibrated to convert Digital
304 Number into units of surface reflectance applying their respective scale factor. Then we
305 calculated three vegetation indices: (i) Normalized Difference Vegetation Index (NDVI),
306 (ii) Enhanced Vegetation Index (EVI), and (iii) Leaf Area Index (LAI). NDVI is the most
307 widely used vegetation index and it is not only related to canopy structure and LAI, but
308 also to canopy cover and greenness (Xue & Su 2017). NDVI ranges between -1 and 1
309 (Rouse et al. 1974) and is computed as follows:

$$310 \quad \text{NDVI} = (\text{NIR} - \text{Red}) / \text{NIR} + \text{Red} \quad [4]$$

311 where NIR and Red are reflection values in the near-infrared and red ranges of the
312 electromagnetic spectrum. Positive NDVI values between 0.3 and 0.8 usually refer to
313 vegetation canopy with a high cover and greenness values. Since NDVI is sensitive to
314 soil brightness and atmosphere conditions, EVI can simultaneously correct these noises
315 (Liu & Huete 1995, Huete et al. 2002). EVI is expressed as:

$$316 \quad \text{EVI} = G * (\text{NIR} - \text{Red}) / (\text{NIR} + \text{C1} * \text{Red} - \text{C2} * \text{Blue} + \text{L}) \quad [5]$$

317 Where G is the gain factor, L the soil adjustment parameters, C1 and C2 are the
318 coefficients used to correct the aerosol influences in the red band, and Blue are reflection
319 values from the blue band. For the Sentinel 2 products, according to Henrich et al. (2009),
320 we adopted the following coefficients: L=1, C1 = 6, C2 = 7.5, and G = 2.5.

321 For each selected image, we computed NDVI and EVI in a 40-m radius buffer
322 zone from each plot centroids. A minimum of 30 pixels falling within the 40-m buffer
323 were used to extract NDVI and EVI mean values for each low, mid, and high elevation
324 plots at both ACU and VOL sites.

325 Finally, effective Leaf Area Index (LAI_{eff}) was estimated from satellite
326 observations using the biophysical processor in SNAP 8.0. This function is proposed to
327 use neural networks for the estimation of biophysical variables (Weiss & Baret 2016).

328 We calculated the LAI_{eff} at ACU and VOL sites on the date of maximum LSF severity
329 and on the date of the following full recovery time.

330

331 **3. Results**

332 *3.1. Tree growth*

333 Mean tree age varied from 61 years to 132 years, with the oldest tree (216 years)
334 sampled at the VOL-high plot (Table 2). The mean tree-ring width ranged from 1.39 to
335 2.10 mm. At ACU, trees at low elevation showed the highest mean growth rate, but the
336 rate decreased with increasing elevation (Table 2, Figure S1). The MDF, VOL and POL
337 plots have similar growth rates within each site with no evident effects due to elevation,
338 although the POL-low showed lower growth rates after 1990 (Figure S1). At MDF, we
339 found wider rings in the lowest plot, whereas in VOL and POL at the mid-elevation plots.

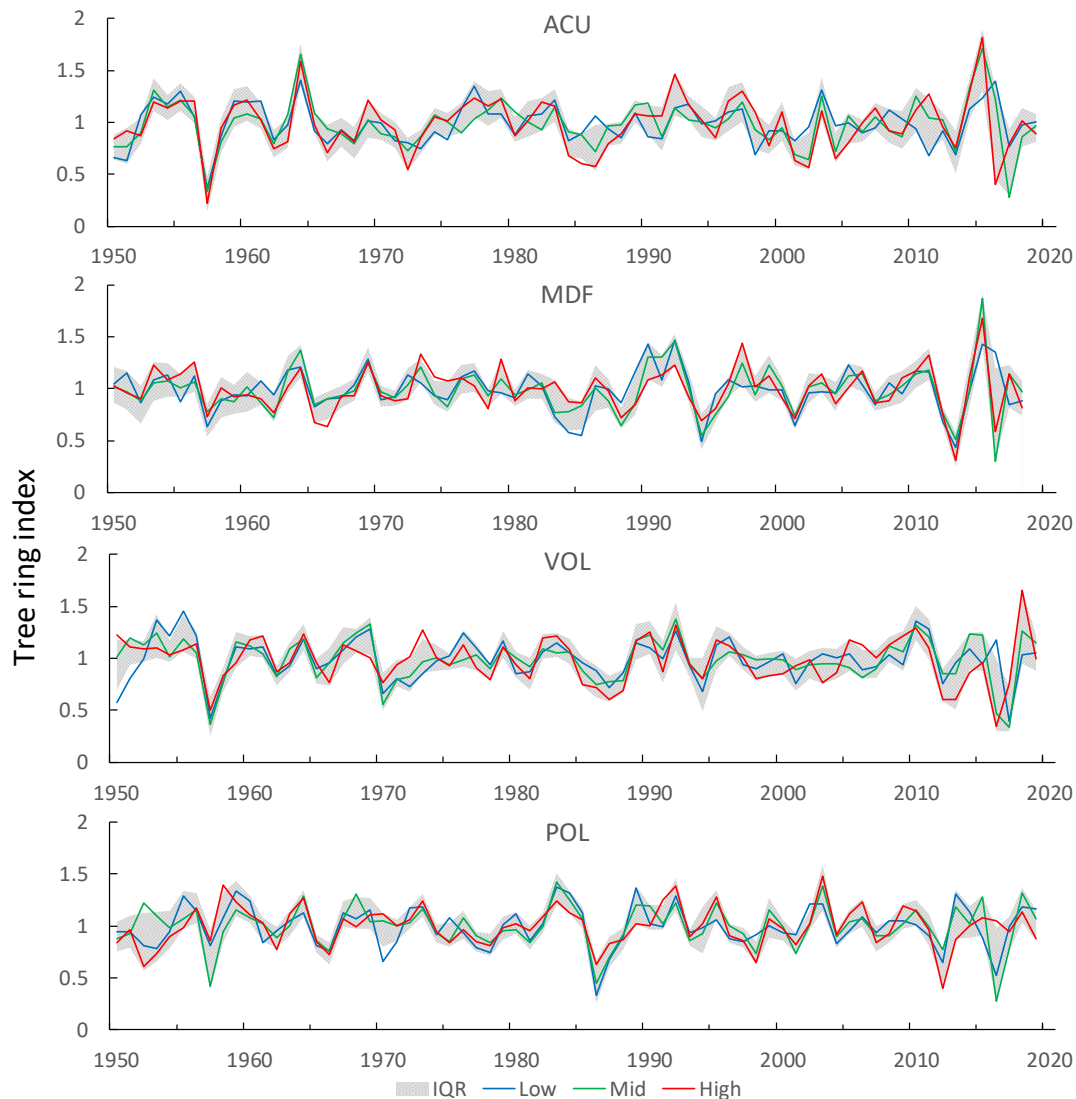
340 First order autocorrelation values (AC1) in tree-ring width series are similar and
341 ranging between 0.51 and 0.74 (Table 2). High Gini coefficients indicate sensitive series
342 with high year-to-year growth variability. The EPS and Rbar values are high at all sites
343 suggesting a large inter-annual growth variation and synchrony, i.e., a common growth
344 signal shared among trees. Tree-ring chronologies developed at each site at different
345 elevations are positively correlated with high and significant ($p < 0.01$) correlation values
346 (Table S4). Similarly, the PCA discriminates two groups of plots mean chronologies
347 corresponding to the central and southern Apennines (Figure S2). Their yearly
348 interquartile range (IQR) reached the highest values in years of LSF occurrence, such as
349 2016 and 2017 (Figure 2). In these two years, very cold spring temperatures reduced
350 growth rates of several trees. We also observed other abrupt growth reductions in most
351 trees related to LSFs in 1957, 1986–1987 and 2013 (Figure 2).

352

353 **Table 2.** Dendrochronological statistics of sampled trees. First-order autocorrelation (AC1) and
 354 Gini (Gini) coefficients refer to the raw series, whereas inter-series correlation (Rbar) and
 355 Expressed Population Signal (EPS) refer to indexed ring-width series. Values are means \pm SD.
 356

| Site plot | No. trees | Series length (yrs.) | Ring width (mm) | AC1 | Gini | Rbar | EPS |
|-----------|-----------|----------------------|-----------------|------|------|------|------|
| ACU-High | 23 | 75 \pm 11 | 1.03 \pm 0.48 | 0.51 | 0.25 | 0.50 | 0.94 |
| ACU-Mid | 18 | 85 \pm 14 | 1.51 \pm 0.66 | 0.57 | 0.25 | 0.34 | 0.88 |
| ACU-Low | 17 | 104 \pm 14 | 2.18 \pm 0.93 | 0.61 | 0.24 | 0.37 | 0.90 |
| MDF-High | 18 | 75 \pm 19 | 1.56 \pm 0.66 | 0.50 | 0.23 | 0.43 | 0.90 |
| MDF-Mid | 20 | 71 \pm 8 | 1.42 \pm 0.65 | 0.57 | 0.25 | 0.43 | 0.92 |
| MDF-Low | 20 | 61 \pm 6 | 1.80 \pm 0.82 | 0.63 | 0.25 | 0.44 | 0.93 |
| VOL-High | 26 | 120 \pm 46 | 1.66 \pm 0.80 | 0.62 | 0.28 | 0.35 | 0.88 |
| VOL-Mid | 27 | 75 \pm 28 | 2.10 \pm 1.08 | 0.62 | 0.28 | 0.34 | 0.86 |
| VOL-Low | 26 | 111 \pm 58 | 1.54 \pm 0.86 | 0.69 | 0.32 | 0.37 | 0.87 |
| POL-High | 25 | 108 \pm 48 | 1.59 \pm 0.81 | 0.67 | 0.29 | 0.35 | 0.88 |
| POL-Mid | 27 | 84 \pm 33 | 1.87 \pm 0.81 | 0.55 | 0.25 | 0.40 | 0.90 |
| POL-Low | 22 | 133 \pm 30 | 1.39 \pm 0.77 | 0.74 | 0.31 | 0.32 | 0.88 |

357



358

359 **Figure 2.** Mean indexed, ring-width chronologies at high (red), mid (green) and low (blue)
 360 elevation plots in the four study sites. The grey shadow is the interquartile range (IQR) of each
 361 site series. Chronologies are truncated in 1950 for matching the common period used for the
 362 detection of LSF years (1950–2019).

363

364 3.2. Detection of LSF years using temperature data

365 The analysis of climate records revealed eleven potential LSF years (1955, 1957,
 366 1962, 1967, 1970, 1977, 1989, 1991, 2001, 2016 and 2017). In these years, accumulated
 367 degree days (ΣT) and spring temperature anomalies (ΔT) exceeded the threshold values
 368 of the third quartile computed for the 1951–1990 reference period (Figure S3, Table S5)
 369 while the chilling requirements (C) exceeded 120 days. In four years (1957, 1991, 2016

370 and 2017) there is documented evidence of frost events, and local climate records confirm
371 the abrupt drop of temperatures (Table S6). In 1957, 1991 and 2017, high temperature
372 anomalies were recorded at all sites, whereas in 2016 E-OBS data underestimated the
373 frost risk for the southern VOL and POL sites. Above average ΣT and ΔT values following
374 the LSF events in years 1957, 2016 and 2017 are recorded in most sites and plots, whereas
375 in 1991 high ΣT and ΔT occurred only at ACU site.

376

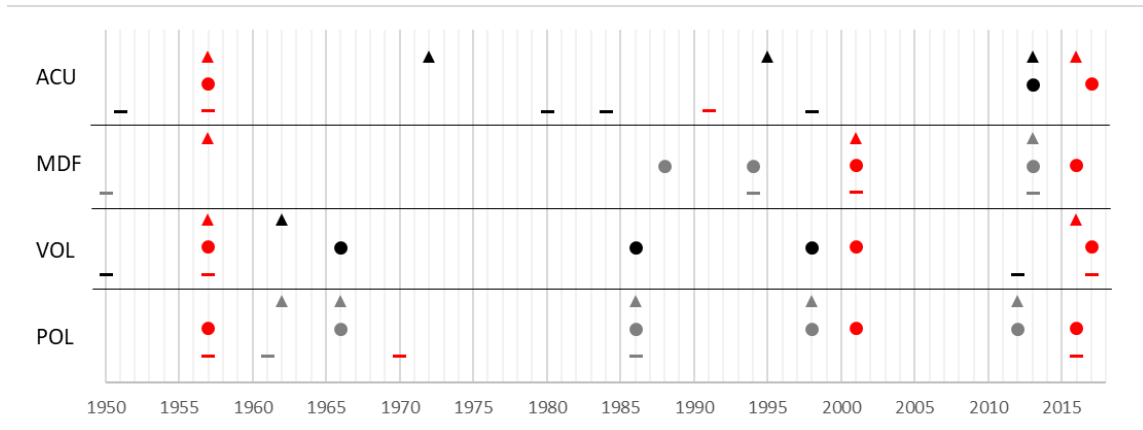
377 *3.3. Impact of LSF on radial growth*

378 Within the common period 1950–2019 we detected 56 nPYs distributed in 21
379 different calendar years (Figure 3). In particular, 24 nPYs were associated to LSF events
380 detected in previous analyses. LSF rings occurred in 1957, 1970, 1991, 2001, 2016 and
381 2017. All trees from ACU and VOL sites showed the 1957 nPY, as well as the MDF-
382 high, POL-low and POL-mid plots. The LSF events in 1970 and 1991 lead to nPYs only
383 in POL-low and ACU-low plots, respectively. All MDF plots shared a LSF ring in 2001,
384 as well as VOL-mid and POL-mid plots. According to local climate station data, the mean
385 values of ΣT , C and absolute minimum temperatures in years of LSF ring occurrence were
386 302°C, 168 days and -3.9 °C respectively (Figure S4).

387 The SEA of ring-width indexed series revealed a significant ($p < 0.05$) growth
388 reduction in 71% of the series during the LSF years (Figure 4). One year after each LSF
389 event growth was recovering since reduction occurred in only 4.9 % of the trees. In
390 affected trees average growth was 54 and 84 % lower than the two preceding years (Table
391 S7). At all plots, growth series showed high levels of recovery. Two years after (t_{+2}) the
392 LSFs, tree rings were 2.49-4.81 times wider than in the year of the event. The resilience
393 index was around 1 or even higher in most cases, meaning that ring-width indices were

394 equal or higher in t_{+2} compared to t_{-2} . Only at ACU, the resilience index showed low
 395 values, in high- and mid-elevation plots after the 2016 LSF.

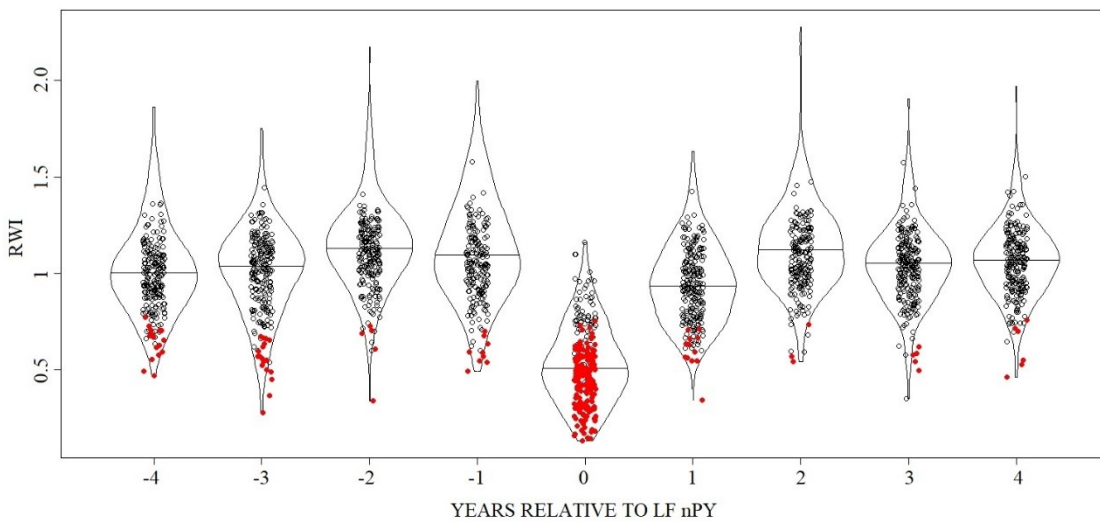
396



397

398 **Figure 3.** Negative pointer years (nPYs) detected at high (▲), mid (●) and low (-) elevation plots
 399 of the four study sites in the period 1950–2019. In red the nPYs occurred in LSF years when ΔT
 400 and ΣT exceeded the third quartile threshold.

401



402

403 **Figure 4.** SEA beech growth response to spring late frosts (LSFs) in 1950-2019. The y axis shows
 404 the number of years before and after LSF negative pointer years (nPY). Horizontal lines inside
 405 the “violins” indicate median ring-width indices (RWI), whereas red dots correspond to
 406 significant ($p < 0.05$) RWI reductions.

407 3.4. Variability factors in growth sensitivity to LSFs

408 Several trees featured some narrow rings related to spring frost (LSF rings). The
409 frequency of LSF rings ranged from zero to five in the period 1960–2019, with most trees
410 (41.8%) showing two LSF rings in their tree-ring series (Figure S5). The estimated
411 number of LSF rings tends to be higher at mid- than at low- and high-elevation plots
412 (Figure S6), but between-plot differences tend to be significant only at MDF site ($p =$
413 0.11). We did not find any significant contribution of tree parameters such as age, mean
414 TRW, MS, Gini, and BAI trend as predictors of the LSF rings number using the GLMMs
415 modelling approach (Table S8). We found only two significant predictors using binomial
416 models with random effects (GLMMs) to predict presence/absence of frost in 1957 (Age)
417 and 2016 (Gini). For the 1957 events, the sites explained 66% of variance, while plot
418 elevation only 6% (Table S6).

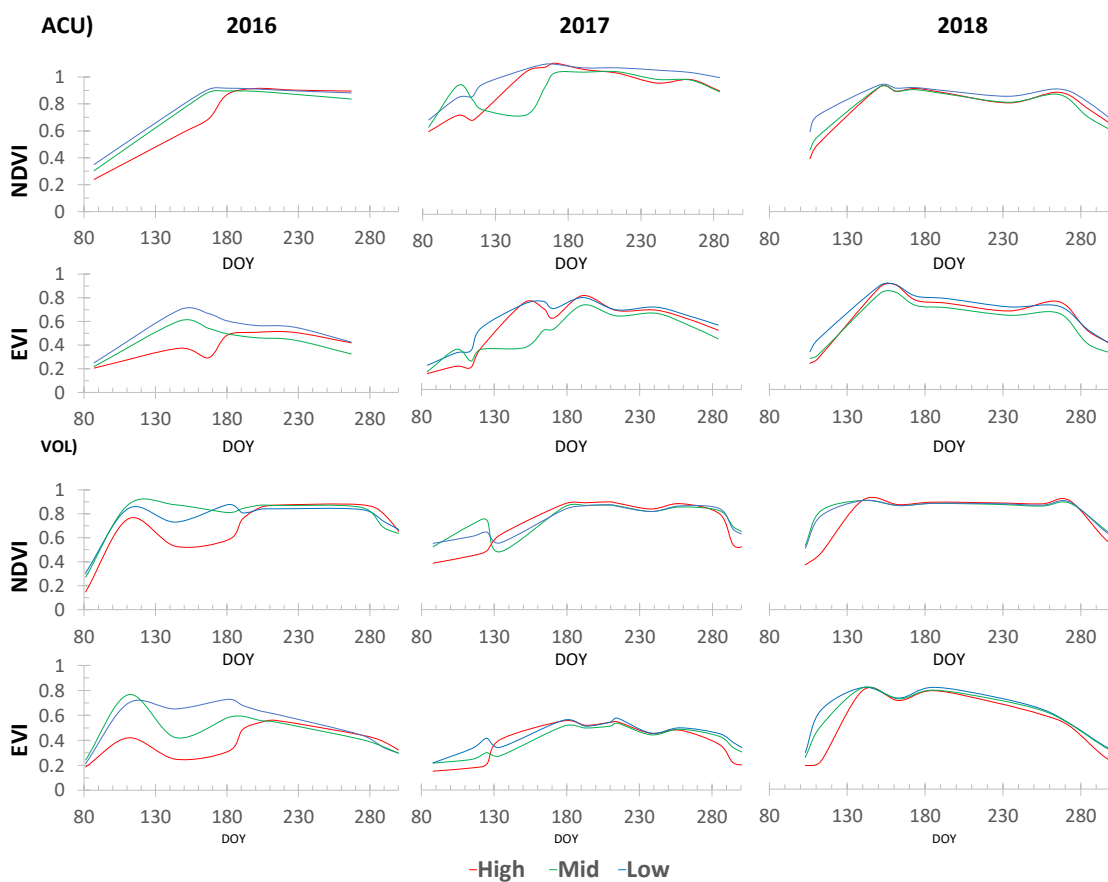
419

420 3.5. Late frost detection from remote sensing data

421 We computed vegetation indices (NDVI, EVI and LAI) at each elevation plot in
422 ACU and VOL sites to assess the canopy reflectance trend throughout the growing
423 seasons in 2016 and 2017 (years with LSF) as compared with 2018, a LSF free year (Figs.
424 5 and 6). At ACU, the 2016 frost occurred on April 26th (DOY 116) and affected only the
425 high-elevation plot. NDVI and EVI values were respectively 25% and 43% lower than
426 unaffected plots at DOY 147. EVI and NDVI values recovered over two months (DOY
427 180). At the same site, in 2017 the LSF occurred on April 22nd (DOY 112) and affected
428 only the mid-elevation plot, with NDVI and EVI values respectively 65% and 51% lower
429 than undisturbed plots at DOY 151. At ACU in 2017 beech canopies fully recovered the
430 LSF event after 79 days (DOY 191), when spectral vegetation indices assume the same
431 levels as the unaffected plots. The LSF occurred at VOL in 2016 (DOY 116) affected the

432 high-elevation plot, with NDVI and EVI values respectively 34% and 54% lower than
 433 undamaged plots at DOY 144. On the contrary, the 2017 LSF (DOY 111) affected only
 434 the low- and mid-elevation VOL plots, with NDVI and EVI values respectively 17% and
 435 23% lower than at unaffected high-elevation plot at DOY 134. At VOL LSF in affected
 436 plots EVI and NDVI reached normal values after 88 days in 2016 and after 67 days in
 437 2017.

438



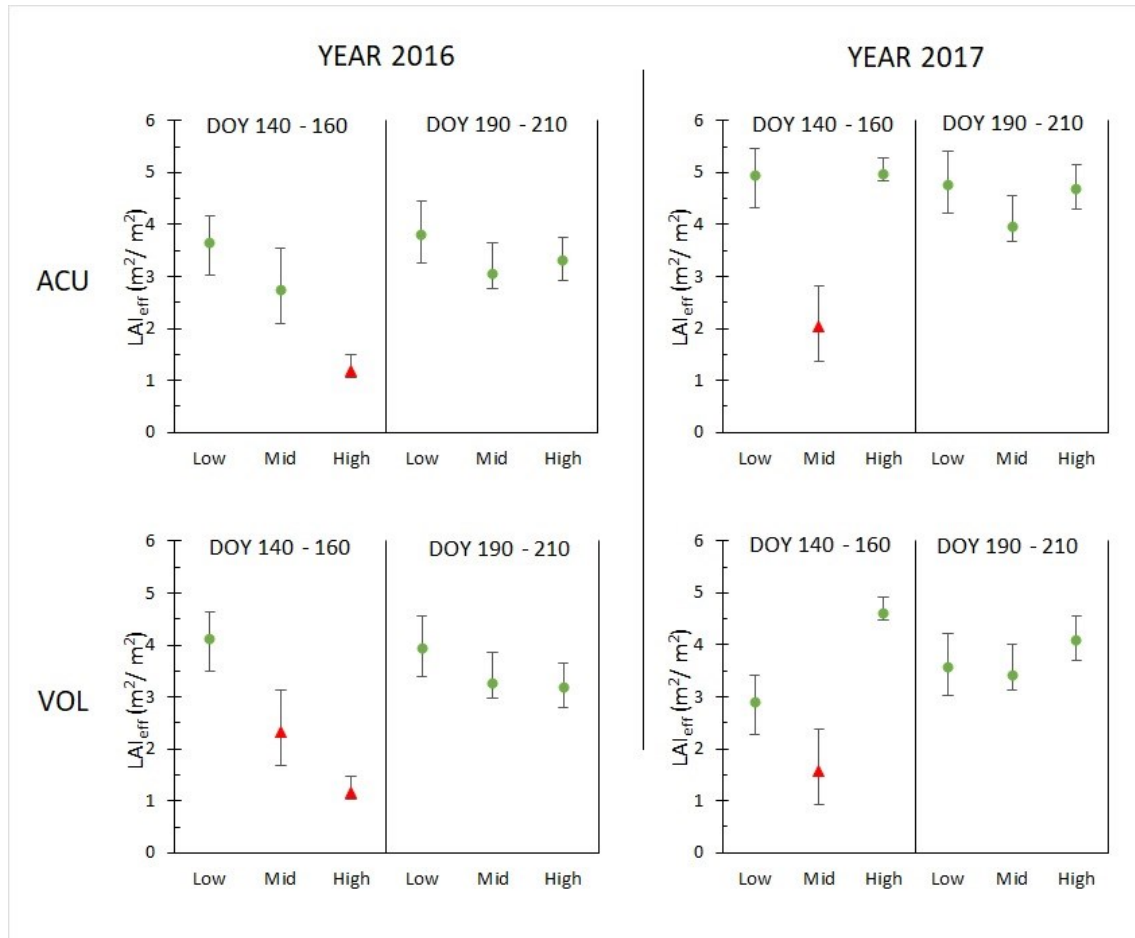
439

440 **Figure 5.** The averaged NDVI and EVI trend curves throughout the growing seasons in 2016 and
 441 2017 (LSF years) and 2018 (no-LSF year) at the three elevation plots at ACU and VOL sites.
 442 DOY (day of the year) is reported in x axes.

443

444 Late spring frost effect on LAI_{eff} is evident at both ACU and VOL in 2016 and
 445 2017. We found differences comparing mean values of affected and unaffected plots and
 446 between post-frost (DOY 140-160) and recovery periods (DOY 190-210). In affected

447 plots, the LAI_{eff} values are nearly half of those recorded in unaffected plots (1.2 to 2.3 m^2
 448 m^{-2} vs. 2.8 – 5.0 $m^2 m^{-2}$) (Figure 6). As expected, in the latter plots LAI_{eff} values of post-
 449 frost and recovery periods were very similar, whereas in affected plots LAI_{eff} increased
 450 until mid-July and reached 3.2 – 4.0 $m^2 m^{-2}$ values. However, in disturbed plots estimated
 451 LAI_{eff} in the recovery period are in most cases slightly lower than in undisturbed plots.



452

453 **Figure 6.** LAI_{eff} values at ACU and VOL sites in two LSF years (2016 and 2017). The whiskers
 454 represent the minimum and maximum values within each plot. Mean LAI_{eff} values were compared
 455 between plots using a two-sided Wilcoxon test. Significantly ($p < 0.01$) low LAI_{eff} values in
 456 affected plots are marked with a red triangle.

457

458 4. Discussion

459 The Apennines range, where beech shares over 10% of the total forested area, is
 460 a transition zone where cold and wet air masses coming from Northern and Eastern
 461 Europe are merging with warm and dry masses from Northern Africa. These conditions

462 can induce important regional or local phenological variability of beech and increase its
463 sensitivity to LSF events. Here we focused on detection and assessment of LSF effects
464 on beech stands in Central and Southern Apennines. We used diverse but complementary
465 approaches to quantify, date, and spatially define the occurrence and the effects of major
466 LSFs on beech forest productivity and growth. The results confirmed our hypothesis of
467 the absence of a clear relationship between beech forest elevation and the incidence of
468 LSF-induced defoliation. More severe growth reduction was found at mid-elevation plots
469 (Figs. 3 and S6), although this may depend on LSF severity and time of occurrence. The
470 POL-high plot (in southern Apennines) revealed the most resistant beech stand to LSFs
471 without nPYs potentially associated to LSF impacts. In several cases, a defoliation-free
472 portion of beech forest occurred above a defoliated one (e.g. at POL in 2016 or ACU and
473 VOL in 2017). In these cases, the possibility of temperature inversions cannot be
474 excluded, but the defoliation observed only at the intermediate zone of the slope
475 suggested its relationship with the interannual thermal conditions and with the elevation
476 dependent variations of bud burst timing.

477 At global scale, Zohner et al. (2020) found that the LSF risk for plants increases
478 with elevation, due to higher daily temperature variations, as it occurs in mountain areas.
479 However, at our study sites with constrained elevation ranges, beech does not seem to
480 present this pattern. The Apennine beech forests show similar risk of LSF damage along
481 the elevational gradients as described in Lenz et al. (2013). Although beech in the
482 Apennines rarely grows above the studied elevation range, we cannot exclude the
483 possibility that below 1000 m a.s.l the LSF frequency induced defoliation could be lower.
484

485 Using two climate indices, we detected warm springs followed by frost events in
486 eleven years. However, plots' mean chronologies showed an abrupt growth decrease in

487 only six of those years. Ten out of the twelve plots were exposed by at least two extreme
488 events in the 1950–2019 period (Figure 3), with an average return time of 39 years,
489 irregularly ranging from 13 to 60 years. Consecutive frost events occurred at the same
490 site but causing damages at different elevations (e.g., ACU and VOL sites in 2016 and
491 2017 LSFs). No plots featured negative pointer years related to frosts in consecutive
492 years; however, in the VOL-mid 67% of the series showed a negative event year in 2016
493 and 75% of series in 2017. The estimation of the return time is highly influenced by the
494 thresholds used to define a pointer year in tree-ring chronologies. Sangüesa-Barreda et al.
495 (2021) calculated a reduced return time from 33 to 14 years before and after 1990,
496 respectively. We found that most LSFs also occurred after 1990 (in 1991, 2001, 2016 and
497 2017), excluding the 1957 event which affected all sites (Figure 4) and the 1970 event
498 detected only at POL-low. In our stands the most severe LSFs occurred in 1957, 2016 and
499 2017, causing a radial growth reduction ranging between 36% and 84%. Even if in VOL-
500 mid several trees were affected by consecutive frost events, their resilience values
501 remained high even after the 2017 event.

502 LSFs can also occur at the beginning of dry growing seasons, a particular
503 combination that occurred at the ACU site in 2017, with defoliation being observed only
504 at mid elevation. Trees at ACU-mid show low resistance and resilience under the 2017
505 stressful conditions, with averaged values of 0.16 and 0.56 respectively (Tab. S7). Very
506 dry summer periods can also reduce beech radial growth in the following years (Decuyper
507 et al 2020, Hacket-Pain et al. 2016).

508 However, excluding this effect at ACU site, we did not find significant growth
509 reductions in the years following the LSFs (Figure 4), suggesting a good recovery of
510 beech to this disturbance, in accordance with recent studies (D’Andrea et al. 2019, Rubio-
511 Cuadrado et al. 2021a, 2021b).

512 Not only LSF and drought events can cause negative pointer years in beech trees,
513 but also masting years and insect outbreaks (Hackett-Pain et al. 2015; Camarero et al.
514 2018; Nussbaumer et al. 2021). The 2013 negative pointer year could be related to a mast
515 year recorded across beech forests in central Italy (Mancini et al. 2016); however, the
516 general lack of long-term, detailed data on seed production cannot confirm this
517 hypothesis. In the same year, southern Apennine beech forests featured a radial growth
518 reduction which was attributed to unusually cold summer conditions (Šimůnek et al.
519 2021).

520 GLMMs did not detect significant elevation-dependent differences in LSF
521 frequency. However, results suggest that the frequency of LSF rings could be more related
522 to elevation rather than to individual tree parameters. A greater number of study sites and
523 LSF events detected (by extending the analysis time period) is required to answer this
524 question. In this sense, large remote-sensing analyses applied to relatively long periods
525 can compensate the spatio-temporal biases (Bascietto et al. 2019). In the southern
526 Apennines beech forests located within the altitudinal range of 1250-1500 m) was the
527 most exposed to the 2016 LSF (Nolè et al. 2018). This range corresponds to our mid-
528 elevation plots (1245-1590 m) suggesting a high LSF sensitivity of this altitudinal belt in
529 Apennine beech forests to for the.

530 Detection and assessment of the LSFs impact on forest canopy cover and
531 greenness can be efficiently conducted with remote sensing data and related indices
532 (Bascietto et al. 2018, 2019, Nolè et al. 2018, Rubio-Cuadrado et al. 2021a, Olano et al.
533 2021). We found EVI being a more sensitive index than NDVI to detect LSF effects on
534 beech canopies (Figs. 5 and 6). In the affected beech stands of our study in 2016 the
535 average NDVI and EVI were respectively 30% and 48% lower than in unaffected forests,
536 whereas in 2017 32% and 47% lower. The forest canopy on average recovered after 75

537 days from the frost events. However, the estimated recovery period can be biased by the
538 time resolution of the used satellite data, and on cloud cover levels, challenging a correct
539 daily resolution at population scale. The 2016 frost at VOL site was confirmed by the
540 remoted sensed data, local meteorological records, and abrupt growth reductions, but not
541 by the E-OBS gridded climate data that appeared to overestimate the minimum
542 temperatures over the late frost period. The availability of suitable long-term *in situ*
543 meteorological data would have helped to deepen into these analyses. However,
544 microclimatic conditions play an important role in regulating the budburst timing in
545 spring while temperature of buds and leaves can be much lower than the temperature
546 recorded by standard climate stations during clear nights due to radiative cooling (Vitasse
547 et al., 2021).

548 Software applications based on artificial intelligence can estimate the biophysical
549 components of vegetation such as LAI, but they could underestimate higher LAI values
550 such as those observed over dense forests (Brown et al. 2021, Filipponi 2021). In our
551 beech forests, LAI_{eff} values ranged between 2.8 and 5.0 $m^2 m^{-2}$ in relation to the stand
552 structure. LSFs in ACU and VOL sites resulted in an estimated loss of LAI_{eff} values of
553 2.4-3.0 $m^2 m^{-2}$ compared to undamaged neighbouring plots. In many cases, affected plots
554 showed lower LAI_{eff} values until mid-July, probably due to the presence of smaller leaves
555 (Rubio-Cuadrado et al. 2021a, 2021b). These findings demonstrate an intra-annual legacy
556 effect which could be further investigated in terms of productivity or reduction in carbon
557 uptake of the most affected stands by performing quantitative wood anatomy studies.
558 Interestingly, such intra-annual legacy effects of reduced LAI_{eff} did not turn into inter-
559 annual growth legacy effects. The use of both high-resolution satellite and aerial
560 multispectral images and LiDAR based sensors could provide more information to study
561 forest disturbances at finer spatial and temporal scales.

562 Our findings cannot confirm that LSF severity increased in the 1990s, given the
563 widespread and great impact of the 1957 LSF across the Apennines. Nonetheless, we
564 demonstrated the high resilience capacity of beech forests after LSFs. In addition, we
565 cannot discard that an increasing frequency of LSFs could alter such resilience capacity,
566 particularly in Mediterranean mountains prone to a forecasted warming but also to more
567 variable thermal conditions which could increase the frequency of adverse climate
568 extremes such as frost and drought events (Giorgi & Lionello 2008).

569

570 **5. Conclusions**

571 European beech low growth rates caused by LSF-induced leaf shedding depend on site
572 spring phenology and abrupt spring temperature drop. However, beech trees affected by
573 spring frost appeared to be resilient and rapidly recovering their growth rates, showing
574 no year-to-year legacy or carryover effects. Nonetheless, late frosts remain a threat to
575 Apennine beech forests, especially if combined with summer drought, another major
576 climate induced stressor for this species. These extreme climate events and their potential
577 synergy within globally warmer and more variable climate scenarios should be certainly
578 considered in the future forest management and planning of mountain beech forests. The
579 combination of remote sensing at broad scale and the finer tree-ring analyses could be
580 applied to improve the detection of late spring frosts and to assess the LSFs impact and
581 recovery time. In the context of climate change, the multiscale approach could improve
582 the forecasting capacity of growth and canopy cover simulations after disturbances and
583 climatic stressors.

584

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