

1 Stand structure, recruitment and growth dynamics in mixed subalpine spruce and Swiss stone
2 pine forests in the Eastern Carpathians

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12

13 **Abstract**

14 Natural subalpine forests are considered to be sensitive to climate change, and forest
15 characteristics are assumed to reflect the prevalent disturbance regime. We hypothesize that
16 stand history determines different stand structures. Based on large full inventory datasets
17 (including tree biometric data, spatial coordinates, tree age, and basal area increment) we
18 assessed the size structure, tree recruitment dynamics and radial growth patterns in three
19 permanent plots along an altitudinal gradient in a mixed coniferous forest (*Picea abies* and
20 *Pinus cembra*) in the Eastern Carpathians. Both discrete disturbances (large scale or small
21 scale) and chronic disturbances (climate change) were identified as drivers of stand structure
22 development in the studied plots. A stand replacing wind disturbance generated a unimodal
23 bell-shaped size and age distribution for both species characterized by a sharp increase in
24 post-disturbance recruitment. By contrast, small-scale wind-caused gaps led to a negative
25 exponential diameter distribution for spruce and a left-asymmetric unimodal for pine.
26 Climate-driven infilling processes in the upper subalpine forest were reflected as J-shaped
27 size and age distributions for both species, but with pine predating spruce. The growth
28 patterns for both species demonstrated an increased basal area increment since the early
29 1900s, with an emphasis in the last few decades, irrespective of stand history. Pine
30 demonstrated a competitive advantage compared to spruce due to the higher growth rate and
31 size at the same age. Recognition of combined discrete and chronic disturbances as drivers of
32 the tree layer characteristics in a subalpine coniferous forest is essential in both stand history
33 analyses and growth predictions.

34

35 Key words: high altitude forest, age structure, disturbance, Swiss stone pine, Norway spruce

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40 **1. Introduction**

41

42 Understanding forest structure dynamics in relation to natural disturbances and
43 climate change is essential from a sustainable management point of view, for both managed
44 and protected forests (Franklin et al., 2002; Kulakowski et al., 2016). The actual stand
45 structure of a natural subalpine forest is the result of centuries of interactions between
46 internal forest ecosystem drivers and external natural disturbance regimes (Frelich, 2002;
47 Kulakowski and Bebi, 2004; Čada et al., 2013).

48 Subalpine forest dynamics are sensitive to climate change, and growth responses and
49 stand density alterations close to the upper altitudinal occurrence are considered to be
50 reliable proxies of climate change effects (Kupfer and Cairns, 1996; Qi et al., 2015). A warming
51 temperature at a high altitude induces both shifts in the tree distribution and increased tree
52 growth (Wilmking et al., 2004; Camarero and Gutierrez, 2004; Bunn et al., 2005) as well as
53 changes in disturbance regimes (Čada et al., 2016). Episodic disturbances, such as extensive
54 wind throws, induce relatively homogeneous post-disturbance stand structures compared to
55 less-severe or small-scale disturbances. An uneven age structure with continuous
56 regeneration is a general characteristic of stands affected by low severity disturbances
57 (Frelich, 2002). Both large-scale and small-scale disturbances occur in natural forests and
58 generate a mosaic of even-aged and uneven-aged forests at the landscape level (Motta et al.,
59 1999; Čada and Svoboda, 2011). In temperate European forests, the main disturbance agents
60 that cause widespread damage are stem-felling winds and bark beetle attacks (Schelhaas et
61 al., 2003). The frequency of both small-scale and large-scale wind damage events has
62 increased over the last few decades both at the Central European level and in the Carpathians
63 (Seidl et al., 2014; Popa, 2010).

64 Numerous studies, in Europe and worldwide, have addressed the structure, dynamics
65 and physiological ecology of subalpine forests (Hofgaard, 1993; Motta et al., 2002; Carrer et
66 al., 2013; Svoboda et al., 2013). In Central Europe and the Balkans, disturbance regimes and
67 regeneration dynamics as well as their impacts on forest structure have been relatively well
68 studied in pure spruce and mixed spruce, silver fir and beech mountain forests (Svoboda and
69 Pouska, 2008; Zielonka and Malcher, 2009; Zielonka et al., 2010; Panayotov et al., 2011;
70 Svoboda et al., 2013; Kulakowski et al., 2016). However, few studies on forest dynamics have
71 been conducted in mixed subalpine forests of *Picea abies* (L.) Karst (Norway spruce,
72 henceforward spruce) and *Pinus cembra* L. (Swiss stone pine, henceforward pine) (Cenușă,

73 1996; Vlad et al., 2013; Carrer et al., 2013). Subalpine mixed spruce and pine forests are rare
74 forest types, but are found in the Romanian Carpathians (Blada, 2008; Casalegno et al, 2010).
75 Given the climate diversity and regional specificity of European subalpine forests, more
76 knowledge is needed to understand the effects of climate change in less studied regions, such
77 as the Romanian Carpathians.

78 The general objective of this study is to highlight how different developmental stages
79 in subalpine mixed coniferous forests that result from disturbances and climate change are
80 reflected in the stand structure, tree age distribution, and tree growth in the Eastern
81 Carpathians. Our specific research questions are: (1) What is the actual size structure
82 (diameter and height) of stands with different stand histories? (2) Is the tree age structure
83 related to the site-specific stand history? (3) Are tree growth patterns congruent with
84 regional warming trends?

85

86 **2. Material and methods**

87

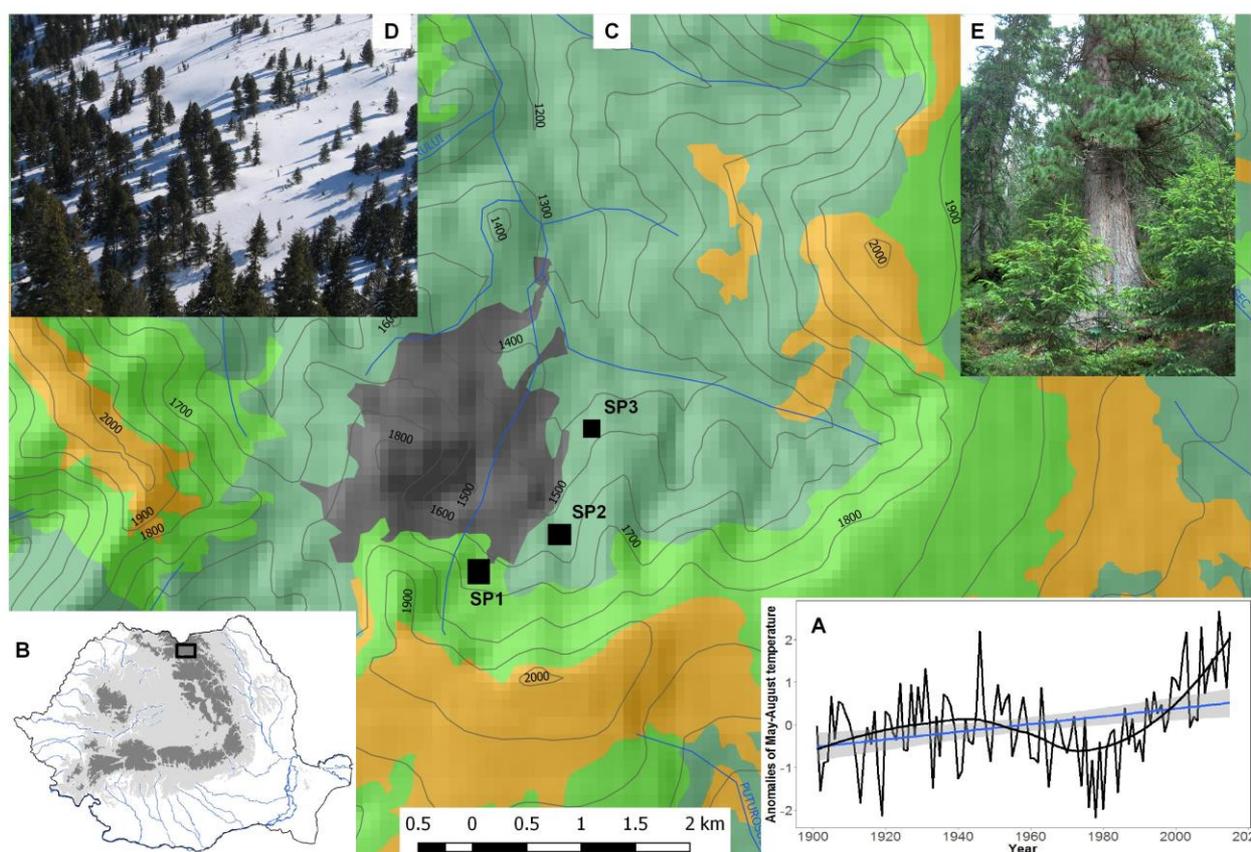
88 *2.1. Study area and sample plots*

89 Mixed pine and spruce subalpine forests are only present in two Eastern Carpathian
90 massifs: Ronda and Calimani (Blada, 2008). The study area is located on a north-western
91 slope of the Calimani Mts. (47° 06' N, 25° 14' E) (Fig. 1) and belongs to the Calimani National
92 Park. The area is a strict forest reserve with full protection status since 1971 (Seghedin,
93 1983).

94 Three permanent plots representing different development stages were established
95 along an altitudinal gradient from closed forest to sparsely tree covered areas close to the
96 timberline (Fig. 1). The selected plot locations lacked signs of historical wood logging or
97 removal or other human disturbances. The uppermost plot (SP1) of 2.1 ha (140x150 m) was
98 located at the transition between closed forest and treeless areas at 1750 m a.s.l. and was
99 characterized by a sparse tree layer and climate-driven infilling processes. The plot was
100 covered by a dense layer of dwarf mountain pine (*Pinus mugo* Turra) and juniper (*Juniperus*
101 *communis* L.) over 50% of the plot area in addition to spruce and pine. The middle plot (SP2)
102 (1.0 ha - 100x100 m, 1550 m a.s.l.) was established in a closed forest without signs of stand-
103 level destructing disturbances. A spatial mosaic of gaps, regeneration patches and large sized
104 trees characterized the plot. The lowermost plot (SP3) (0.49 ha - 70x70 m 1450 m a.s.l.) was
105 established in a closed forest that was characterized by post-wind disturbance self-thinning
106 processes.

107 In addition to spruce and pine, the tree layer of the three plots included sparse
108 occurrences of rowan (*Sorbus aucuparia* L.). The field vegetation layer was dominated by
109 *Vaccinium myrtillus* L., *Vaccinium vitis-ideae* L. and *Luzula sylvatica* in all three plots. The soil
110 was podzol, and the bedrock was andesites along the entire gradient (Seghedin, 1983).

111 The climate is typical montane climate with continental influence. The mean annual
112 temperature is +1.4°C, with the warmest period during July-August (+9.8°C) and coldest
113 during January-February (-6.8°C). Annual precipitation normally exceeds 1200 mm, with a
114 maximum in June-July (Popa and Kern, 2009).



115
116 **Fig. 1.** Location and characteristics of the study area in the Calimani Mts. A - anomalies of
117 summer temperature (May-August) development and trend for 1900-2013 (CRU 3.2, Harris et
118 al., 2014); B - map of Romania, with the box indicating the study area; C - plot locations (dark
119 green - forest, light green - transitional woodland shrubs, orange - pasture, dark grey -
120 abandoned mining area); D-E show aspects from SP1 and SP2, respectively.

121
122 *2.2. Stand data*

123 In the study plots, all living trees and standing dead trees with DBH (diameter at 1.3 m
124 above ground) >6 cm were identified, labelled and mapped in a 10x10 m grid network. The

125 following variables were recorded for each tree: species, DBH, status (live or dead), total
126 height, and spatial position in a local Cartesian system.

127 In addition, living trees with DBH >8 cm were cored to study the tree's establishment
128 period, age structure and radial growth patterns. Increment cores were taken at a 50 cm
129 height above ground, or in the case of stem rot at this sampling height, a second core was
130 taken at a 0.8-1.0 m height. Trees with DBH >8 cm accounted for 89%, 86% and 98%,
131 respectively, of sampled trees with DBH >6 cm in SP1, SP2 and SP3. In the laboratory all of the
132 cores were fixed to wood supports and sanded to highlight the tree ring boundaries. The tree
133 ring widths were measured to 0.01 mm accuracy with a Lintab sliding-stage measuring device
134 with TsapWin software (Rinntech, 2006). Each individual tree ring width series was
135 crossdated and checked for measurement error with the COFECHA program (Holmes, 1983).
136 For cores that did not include the pith, the number of missing rings was estimated based on
137 the mean growth rate of the last 5 to 10 years using the pith locator (Duncan, 1989). Trees
138 with rotten cores and cores for which a reliable estimation of the missing rings was not
139 possible were removed from future analysis. Following these procedures, the tree age was
140 successful determined for most of the trees, but the proportion of trees without an age
141 determination varied slightly between plots, 10% in SP1, 8% in SP2, and 6% in SP3.

142 As all of the age data refer to the stem age at 50 cm above ground, the difference
143 between the age at this height and age at the ground level, as given by seedling establishment
144 (Niklasson, 2002), is not included in the study. In this study, analysis of recruitment into the
145 stand is thus restricted to trees with DBH >8 cm that were cored at 50 cm above ground. The
146 age at core height is widely used in stand age analysis (Svoboda et al., 2010; Qi et al., 2015). In
147 this study, the stem ages are aggregated into 20-year age classes (where, e.g., the 1840 class
148 includes trees with ages between 1821 and 1840). Inventory and core sampling was
149 performed in 2006 (SP1), 2007 (SP2) and 2013 (SP3).

150 For growth pattern analysis, we used the basal area increment (BAI) instead of the tree
151 ring width as the BAI is more closely related to the tree biomass increment and net
152 productivity (Motta and Nola, 2001). We use the raw BAI as the growth indicator, which is a
153 conservative approach (Tognetti et al., 2000) that is less influenced by statistical techniques,
154 such as standardization, that are usually applied to tree ring width to remove age effects
155 (Cook and Kairiukstis, 1990). The BAI was thus based on the measured tree ring widths
156 assuming a circular stem section and calculated according to the following equation
157 (Monserud and Sterba, 1996):

158 $BAI_t = \pi(r_t^2 - r_{t-1}^2)$

159 where r_t is the radius at year t and r_{t-1} is the radius at year $t-1$. To show the influence of age on
 160 the growth pattern, the data set was split in three parts: trees with ages up to 50 years, 51-
 161 100 years and trees with ages of more than 100 years. The mean BAI chronology for each
 162 group was established by averaging of the individual tree-ring series.

163 All data processing was performed in R (R team, 2016).

164

165 3. Results

166

167 3.1. Stand structure

168 In terms of the number of trees, spruce is the dominant species in all of the plots (Table
 169 1), but the stand density of the species in SP1 is only 20-26% of the value of the lower altitude
 170 plots. The total basal area, on the other hand, is dominated by pine in SP1 (66% of the total)
 171 and by spruce in SP2 and SP3 (66% and 67%, respectively) (Table 1). Rowan is present at a
 172 low proportion in all of the plots. The frequency of standing dead trees, computed as the ratio
 173 of the basal area of living trees, is higher in SP2 and SP3 (9% and 10%, respectively)
 174 compared with SP1 (3%) and dominated by spruce in all plots. The highest number of
 175 standing dead trees is found in SP3 (27% of total tree number), and the small diameter of
 176 these trees (mean DBH: 10.9 cm) indicates an intensive on-going self-thinning process.

177 The mean stem diameter of living trees at the plot level is similar for all of the plots,
 178 with pine having twice the mean diameter of spruce in all cases (Table 1). The diameter
 179 distribution of pine is bimodal in SP1 (maximum at 16 cm and 36 cm), left asymmetric
 180 unimodal in SP2, and unimodal bell-shaped in SP3 (Fig. 2). Spruce shows a negative
 181 exponential diameter distribution in both SP1 and SP2, but is unimodal bell-shaped in SP3.

182 The mean tree height is largest in SP3 and dominated by pine in all three plots
 183 (although the pine and spruce heights are similar in SP1). The height distribution is unimodal
 184 both for spruce and pine in all three plots, with left asymmetry for spruce in SP2 and right
 185 asymmetry in SP3 (Fig. 2).

186

187 **Table 1**

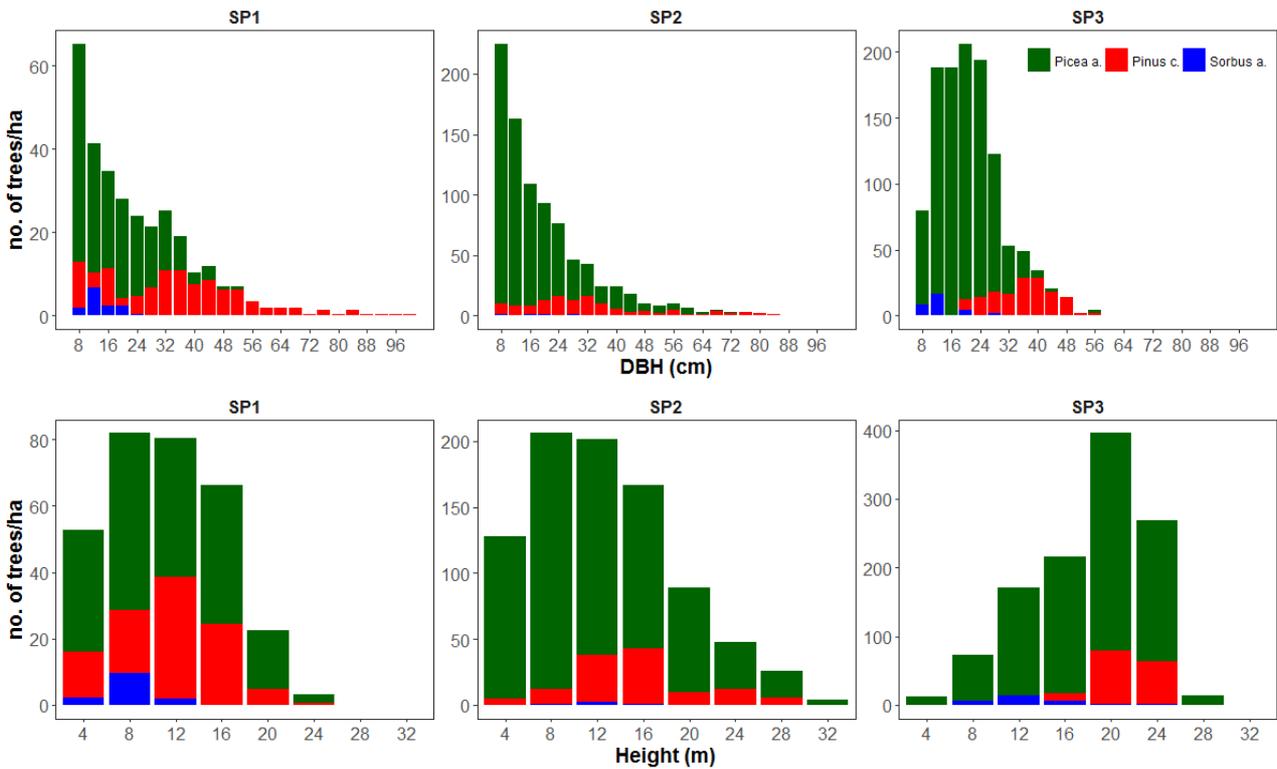
188 Structural characteristics of the study plots

Species	Live trees		Standing dead trees		Mean DBH (cm)*	Mean height (m)*	Mean age (years)*
	Basal area (m ² ·ha ⁻¹)	Stems (n·ha ⁻¹)	Basal area (m ² ·ha ⁻¹)	Stems (n·ha ⁻¹)			

SP1

Picea abies	6.81	195	0.20	11	18.5±10.2	11.2±5.2	69±32
Pinus cembra	13.54	102	0.41	3	36.2±19.6	11.7±4.3	105±46
Sorbus aucuparia	0.20	14	0.01	1	13.9±4.2	8.0±1.9	48±14
Total	20.55	311	0.62	15	24.1±16.3	11.2±4.8	81±41
<hr/>							
<i>SP2</i>							
Picea abies	26.82	745	2.89	77	17.8±11.8	12.2±6.2	112±56
Pinus cembra	13.80	124	0.87	5	32.8±18.5	15.2±5.5	159±100
Sorbus aucuparia	0.12	4	-	-	17.7±9.5	11.9±2.8	92±14
Total	40.74	873	3.76	82	20.0±13.9	12.6±6.2	119±67
<hr/>							
<i>SP3</i>							
Picea abies	33.33	975	4.30	404	19.6±7.1	17.8±4.9	131±18
Pinus cembra	16.28	149	0.53	14	36.4±8.3	21.3±2.0	126±14
Sorbus aucuparia	0.50	31	0.13	16	13.2±6.0	8.6±5.4	106±19
Total	50.11	1155	4.96	434	21.6±9.3	18.2±4.8	130±18

* Mean±standard deviation; values refer to living trees.



190
 191 **Fig. 2.** Distribution of the number of trees by diameter (upper panels) and height classes
 192 (lower panels). The total bar height represents the cumulative values of the numbers of trees
 193 for all species. The X-axis tick marks represent the centre of the 4 cm and 4 m classes (i.e., the
 194 first diameter class includes trees with DBH 6.1-10 cm, and the first height class 2.1-6 m
 195 trees).

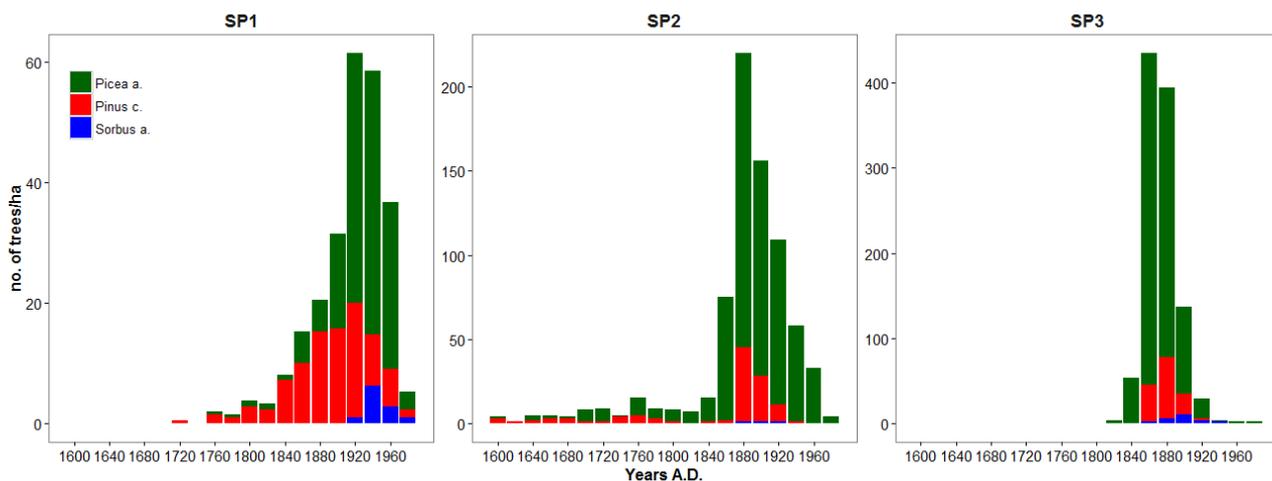
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197 *3.2. Tree recruitment*

198 The stem age distribution of trees (age at 50 cm height) varied between plots (Fig. 3).
199 In SP1, the maximum age is 285 years for pine, 231 years for spruce, and less than 100 years
200 for rowan. The oldest trees are found in SP2, where pine reached a maximum age of 546 years
201 and spruce reached a maximum age 450 years. In SP3, the maximum age is similar for both
202 spruce (180 years) and pine (152 years). According to these maximum ages, pine and spruce
203 have been present since the early or mid-18th century at SP1 (Fig. 3). After these initial
204 recruitments, both pine and spruce recruited at low frequency until the mid-19th century,
205 when pine recruitment first increased around 1840, followed by spruce around 1860. This
206 recruitment increase continued for both species until the 1920s. The resulting age structure is
207 unimodal for both species, but the mean age differs at ca. 35 years (Table 1). The first wide-
208 aged cohort of pine starting from 1720 was mainly located in the middle part of the plot (Fig.
209 4) and for spruce in the left part of the plot. In comparison with pine and spruce, rowan
210 recruitment occurred over a much shorter time period and is only recorded for age classes
211 since the 1920s, with a maximum between 1931 and 1940.

212 In SP2, two clear age groups can be distinguished. A first group of old trees with an age
213 between 180 and 400 years (Fig. 3) consisting of both pine and spruce was located as a matrix
214 in the right half of the plot (Fig. 4). The frequency of trees recruited before 1840 is low, but a
215 sharp change in regeneration is observed after 1840 (spruce) and 1860 (pine) (Fig. 3). This
216 wave of recruitment reaches its maximum between 1861 and 1880 for both species. After
217 1920, the regeneration is mainly represented by spruce. The age structures are bimodal for
218 both pine and spruce, but the mean age differs by ca. 45 years (Table 1).

219 In SP3, few trees (spruce) regenerated before 1840, but an apparent recruitment
220 increase took place in both species between 1841 and 1900. The increase was characterized
221 by spruce predating pine. No pine and very few spruce trees were recruited after 1920.
222 Rowan recruitment occurred at a low frequency from 1860 to 1940. The age structure has a
223 unimodal bell-shape with low variability for all three species (Fig. 3). The mean age difference
224 between spruce and pine is only 5 years (Table 1). The spatiotemporal recruitment pattern is
225 similar for spruce and pine (Fig. 4), but spruce is dominating in all classes (Fig. 3).



226

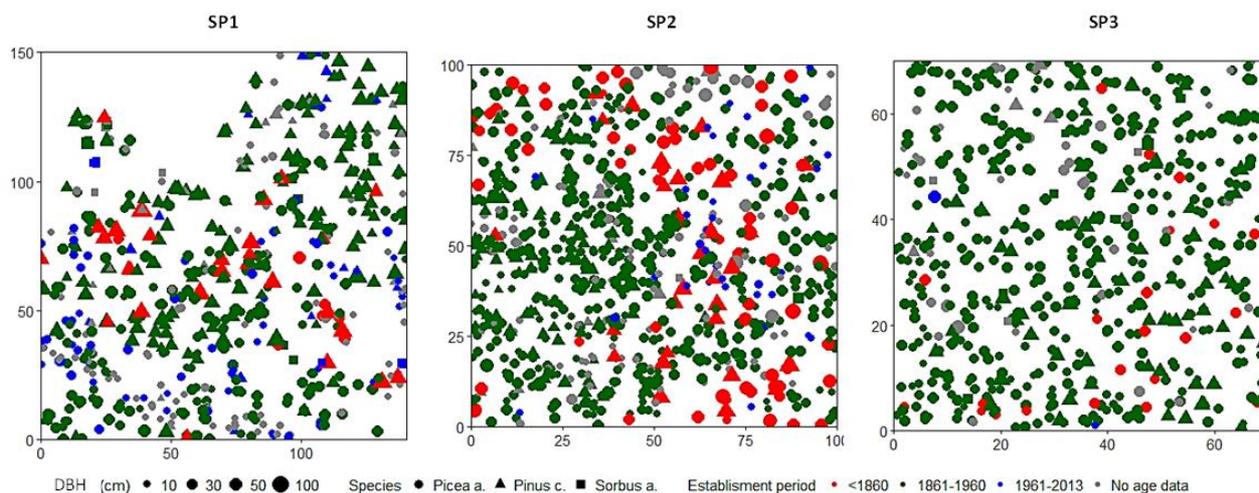
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Fig. 3. Recruitment pattern of trees >8 cm DBH and recorded at 50 cm above ground presented in 20-year age classes (breaks represent the end of the classes, e.g., the 1840 age class includes trees with an age between 1821 and 1840). Note the differences in the y-axis scales.



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Fig. 4. Spatial distribution of tree recruitment (DBH classes: <10 cm, 11 – 30 cm, 31 – 50 cm, 51 – 100 cm)

3.3. Growth pattern

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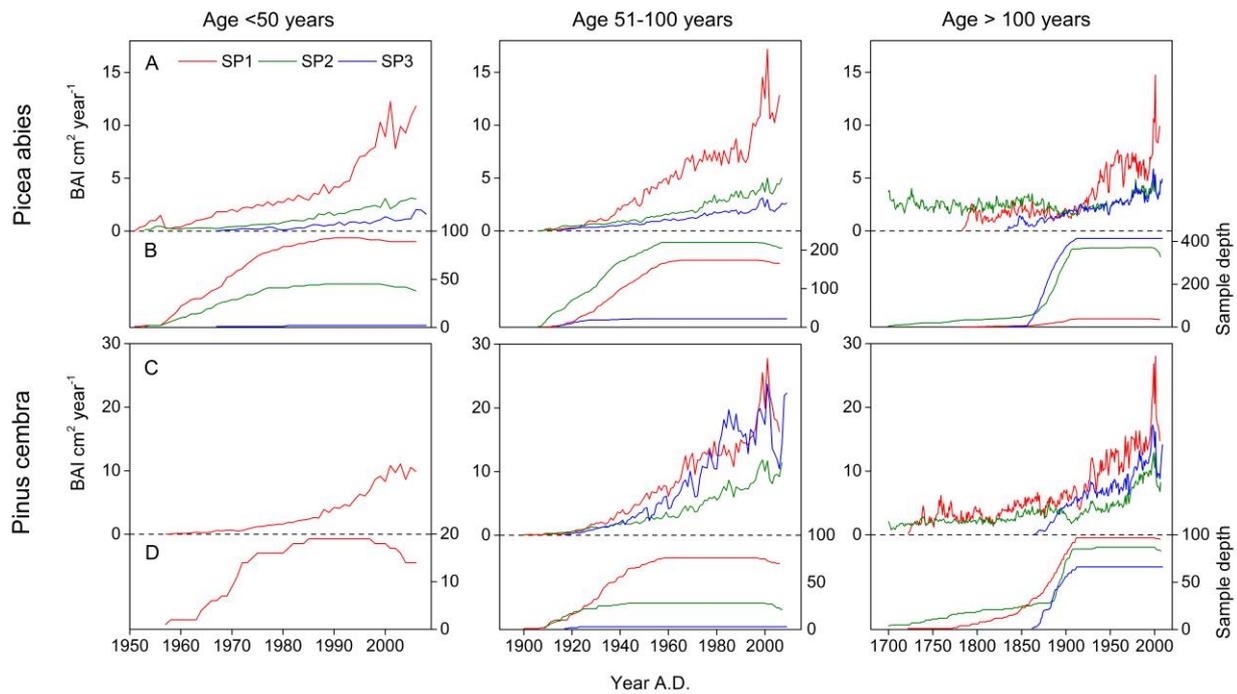
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243

Growth patterns expressed as BAI values show apparent differences between plots and species (Fig. 5). Pine has a higher growth rate compared with spruce in all plots and both age groups, but no apparent difference was observed between plots (although growth of old pine trees was highest in SP1). For spruce for all age classes trees showed a higher growth rate in SP1 in the last century compared to SP2 and SP3 (2-3 times higher in SP1 than in SP2 or SP3). In SP2, the growth rate of old spruce has been more or less constant over the last 300 years, with some inter-annual and decadal variation. The results show an evident BAI peak during 1990-2000 for all plots and species followed by the growth drop after 2000.



244
 245 **Fig. 5.** Basal area increment (BAI) development in the three study plots separated into spruce
 246 (*Picea abies* Karst L.) and pine (*Pinus cembra* L.), and trees with stem age <50 years, age
 247 between 51 and 100 years and age>100 years. A – BAI for spruce; B – sample depth for
 248 spruce; C – BAI for pine; D – sample depth for pine.

249
 250 **4. Discussion**

251
 252 Our results highlight climate- and disturbance-driven tree layer changes that
 253 characterize subalpine mixed coniferous forests in three different stand history areas. The
 254 long-term regional increase in temperature, particularly since the 1980s, is likely a main
 255 driver of documented recent growth rate increase across sites and the apparent infilling
 256 process at the timberline. However, it cannot explain the observed age structure differences.
 257 A spatiotemporal combination of small- and large-scale disturbances characterizes the forest
 258 below the timberline, although the entire studied subalpine forest area has had apparent tree
 259 cover since the early 19th century. In addition, the presence of more than 500-year-old trees
 260 and large amounts of dead wood is indicative of a naturally developed forest that is suitable
 261 for stand history analyses (Popa and Kern, 2009).

262
 263 **4.1. Climate-driven stand development**

264 The natural subalpine forests, including the timberline areas, of the studied northern
 265 slope of the Calimani Mts. are well preserved and without apparent human disturbance (e.g.,

266 grazing, wood logging) since the establishment of Calimani National Park and experienced
267 low or negligible disturbances prior to the park's establishment (Kern and Popa, 2008).
268 Historical records from the early 20th century indicate the presence of dense areas of dwarf
269 mountain pine with a sparse tree layer of pine and spruce in the upper part of the studied
270 subalpine area (Fekete and Blattny, 1913), which is indicative of low or absent herding
271 activity. The current presence of dwarf mountain pine with maximum age over 130-150
272 years, lack of typical wind disturbance signs (e.g. pits and mounds), and low amount of dead
273 stems confirms the dominance of a non-land-use and non-event driven succession. Instead,
274 based on the field inventory and historical records, a significant climate-driven upward shift
275 of the timberline (65 m in altitude) and krummholz tree form (95 m in altitude) limits is
276 indicated for the 20th century (Kern and Popa 2008).

277 In spite of this altitudinal advance, the current forest structure still shows
278 characteristics typical for a colonization/infilling phase and ongoing transition from dwarf
279 mountain pine cover to mixed pine and spruce forest with a low stand density and low tree
280 layer competition with specific spatial structure (Popa and Sidor, 2013). The mixed spruce
281 and pine recruitment is mediated by combined wind (spruce) and avian (pine) seed dispersal,
282 in which the feeding behaviour of the Eurasian nutcracker (*Nucifraga caryocatactes*) plays a
283 central role (Zong et al., 2010). The most important food source of this bird is pine seeds, and
284 surplus seeds are stored for winter use. Open areas, such as ridges, rock outcrops and
285 subalpine forest gaps, are preferred sites to hide cones and seed batches (Tomback et al.,
286 1993; Zong et al., 2010), and dismissed seeds might germinate and form recruits for a future
287 tree layer. The survival of these seedlings might be climate dependent, but the behaviour of
288 the nutcracker jointly explains the ongoing increase in pine recruitment.

289 The significant basal area increment increase shown since the 1980s is a consistent
290 pattern irrespective of tree age and stand history (although emphasized at timberline for
291 spruce). Growth The consistency of the pattern calls for a common, possibly climatic,
292 explanation. The significant and positive correlation between the radial growth and summer
293 temperature shown for the study region (Popa and Kern, 2009) indicates warming and the
294 length of the growing season as plausible important factors. The main limitation at high
295 altitude is the capacity to form new wood tissues during the short growing season (Körner,
296 2003; Holtmeier, 2009). The positive effects of a warmer temperature on radial growth
297 depend on the capacity to compensate for increased transpiration (Paulsen et al., 2000),
298 which in the Calimani Mountains, is accomplished by high annual precipitation levels. Similar
299 recent climate-dependent radial growth increases have been observed in other central and

300 south European subalpine areas (Motta and Nola, 2001; Vittoz et al., 2008; Rolland et al.,
301 1998).

302 In addition to warming, the low stand density in the timberline part of the subalpine
303 forest may explain the higher growth rate compared to the lower altitude subalpine forest,
304 where competition in the tree layer is important. Further and hypothetically, the recorded
305 increased growth rate could be associated with rising CO₂ (Spiecker, 1999; Pretzsch et al.,
306 2014), but no information is available regarding this factor for our study area. However, a
307 growth-promoting increase in nitrogen deposition (Pretzsch et al., 2014) might have had a
308 local effect in the study area, as nitrogen-based explosives were used in an opencast mine
309 close to the study area. Reducing of the growth after 2000 may be linked to the reduction in
310 nitrogen fertilization due to the closure of mining activity. This mining activity occurred in the
311 1970s and 1990s, and dendroclimatological studies reveal somewhat of a divergence of the
312 radial growth response to the summer temperature during this period (Popa and Kern, 2009).

313 *4.2. Small-scale disturbance-driven stand development*

314 The magnitude and frequency of disturbances in subalpine forests determine the size
315 and spatiotemporal distribution of canopy gaps available for tree regeneration (Frelich,
316 2002). Consequently, analyses of the tree size and age structure lead to a better
317 understanding of the stand disturbance history. For a subalpine forest, small-scale wind
318 disturbances generate dead wood and canopy gaps (Holtmeier, 2009). This stand
319 heterogeneity, including single tree falls, blow-down tree groups, wind uprooting, and
320 standing and downed dead trees, mediates a spatiotemporal tree recruitment pattern that is
321 typical for stands with frequent small-scale disturbances. This type of spatial heterogeneity, in
322 terms of gap openings and the presence of dead wood at different decay stages, represents a
323 sustainable environment for tree establishment and diversity (Khakimulina et al., 2015). In
324 particular, spruce regeneration in a subalpine forest is strongly related to the abundance of
325 dead wood at different decay stages, as evidenced in a variety of European natural spruce
326 forests (Hofgaard, 1993; Kuuluvainen, 1994; Motta et al., 2006). Pine regeneration, on the
327 other hand, is favoured by open spaces with low tree layer competition and good light
328 conditions (Hattenschwiler and Korner, 1995; Risch et al., 2003; Carrer et al., 2013). However,
329 small gaps will be dominantly regenerated by spruce, which is tolerant to low light availability
330 over long periods (Čada et al., 2013; Popa and Sidor, 2013).

331 These species-specific responses to gap conditions are also evident in the present
332 study, with spruce showing spatiotemporal dominance in areas controlled by small-scale
333 disturbance regimes. The continued coexistence of spruce and pine will depend on the

334 frequency of large gap-creating disturbances. Successive events of disturbance-regeneration
335 that generate almost exclusively small-scale windthrow gap formations are beneficial to
336 spruce and for maintaining uneven-age mountain forests (Svoboda et al., 2010).

337

338 *4.3. Large-scale disturbance-driven stand development*

339 The coinciding mid- to late-19th century recruitment period, which was shown for both
340 small-scale and large-scale disturbed areas, points to a disturbance event with relevance
341 beyond the study site scale. The unimodal bell-shaped age structure indicates tree
342 recruitment in open spaces after a large-scale catastrophic windthrow event dated to
343 approximately 1840-1850 (Nechita et al., 2013). Information about a high magnitude wind
344 damage event in the Eastern Carpathians during this time is both noted in historical records
345 (December 1843) (Popa, 2007) and evidenced by disturbance reconstruction based on spruce
346 radial growth data (Svoboda et al., 2014). In the studied area, this disturbance event produced
347 a typical wind uprooting geomorphology with mounds and pits (Nechita et al., 2013). These
348 edaphic structures and the presence of decaying coarse wood promote high frequency
349 regeneration of both spruce and pine trees during relatively short post-disturbance periods
350 (Ulanova, 2000). Consequently, a typical homogeneous post-disturbance stand development
351 phase is produced (Oliver and Larson, 1996; Čada and Svoboda, 2011; Svoboda et al., 2010)
352 that is characterized by an even-aged high tree density, bell-shaped diameter distribution,
353 large basal area of living trees, and high density of standing dead trees, as was found in the
354 studied area. Although the recruitment periods of pine and spruce overlap, the pine trees
355 have a larger DBH and are taller compared to spruce of the same age. This growth pattern and
356 associated high competitiveness of pine ensure a long-term presence for the species in old
357 stands (Oliver and Larson, 1996).

358 In the next few decade(s) the homogeneous post-disturbance stand structure will
359 likely change due to an increasing self-thinning process characterised by death of individual
360 trees, evolving small-scale disturbance events, and subsequent gap development allowing for
361 new regeneration. The process would thus hypothetically lead to structural dynamics
362 characterizing areas driven by small-scale canopy perturbations. A second scenario might be
363 a new large-scale catastrophic wind damage event that will reset (re-initialization) the stand
364 dynamics. The probability of a large wind damage event in the study region is high, taking into
365 account the recent history of windthrow and forecasted climate change (Popa, 2007; Seidl et
366 al., 2014).

367 Same disturbance event may have varying impact on stand structure dynamics as a
368 consequence of deviating pre-event stand structures. The climate-growth relationships in
369 spruce mountain forest from Calimani NP differ among altitude with influence on
370 regeneration processes (Primicia et al., 2015). The slowest regeneration was at the SP1 (the
371 very harsh climate limiting tree growth), faster regeneration processes were at the SP2 and
372 SP3, where is the lowest impact of climate.

373

374 *4.4. Methodological implications*

375 The age structure combined with tree ring width data is frequently used to date tree
376 layer destroying disturbances and post-disturbance tree establishment patterns (Lorimer and
377 Frelich, 1989; Nowacki and Abrams, 1994; Carrer et al., 2013). However, when the stand
378 structure, recruitment, and growth analyses are restricted to trees larger than a given DBH,
379 interpretations of stand dynamics do not include processes linked to smaller size classes. The
380 presented structure for the studied plots reflects the pattern of tree layer trees that survived
381 up to the sampling time. This structure does not reflect the mortality rate or other life history
382 processes during the time between tree regeneration and study-specific size requirements
383 (Motta et al., 2002). Further, age structure analysis based on the age at a 50 cm height,
384 without extrapolation to the ground level, results in a systematic underestimation of the tree
385 age. Although the size of this underestimation is unknown, any interpretation has to consider
386 this bias. In subalpine spruce forest, the time necessary to reach a coring height of 50 cm is at
387 least 20 years (Szewczyk et al., 2011). A high stand density, shading and frequent snow
388 breakage can increase that period considerably. Consequently, the number of years needed to
389 attain the coring height will be species and site dependent (Wong and Lertzman, 2001).
390 Species differences in the height growth of small/young trees are pronounced in subalpine
391 forest due to species-specific differences in stem elasticity. Consequently, spruce is more
392 frequently affected by snow breakage compared to pine. In subalpine forests, large gaps
393 determine faster sapling growth (diameter and height) compared with that in small gaps or
394 under a dense canopy (Svoboda et al., 2011). However, there are also examples that show no
395 significant difference between open conditions and below canopy conditions for spruce
396 sapling growth to reach 50 cm height (Tsvetanov et al., 2016).

397

398 **5. Conclusion**

399

400 Recognition of combined discrete and chronic disturbances as drivers of the tree layer
401 characteristics in a subalpine coniferous forest is essential for both stand history analyses and
402 growth predictions. Our results highlight the importance of wind disturbances and climate
403 change as drivers of stand structure dynamics and associated tree recruitment dynamics in
404 Eastern Carpathian subalpine mixed coniferous forests. These forests represent an important
405 European forest biome, and further investigations focusing on disturbance effects, stand
406 structure dynamics, and spatiotemporal regeneration patterns are needed. Better knowledge
407 of combined warming and disturbance effects in high altitude forest ecosystems can be
408 obtained by coupling altitudinal advance information with tree growth and stand structure
409 analyses. Networks of permanent plots provide prominent conditions in this respect through
410 production of high quality information on stand dynamics driven by interplaying disturbance
411 regimes, including climate change.

412

413

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