

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

Popa Ionel<sup>1,2\*</sup>, Nechita Constantin<sup>1</sup>, Hofgaard Annika<sup>3</sup>

Affiliation: <sup>1</sup> National Institute for Research and Development in Forestry "Marin Drăcea" (INCDS), Calea Bucovinei, 73bis, Câmpulung Moldovenesc, Romania

<sup>2</sup> Research Centre for Mountain Economy (CEMONT), Petreni 49, Vatra Dornei, Romania

<sup>3</sup> Norwegian Institute for Nature Research (NINA), NO-7485 Trondheim, Norway

\* Corresponding author: popaicas@gmail.com

### Abstract

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

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

Popa, Ionel; Nechita, Constantin; Hofgaard, Annika.

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

Science of the Total Environment 2017 ; Volum 598. s. 1050-1057

CC-BY-NC-ND

## 1. Introduction

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

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

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

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

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

85

## 86 **2. Material and methods**

87

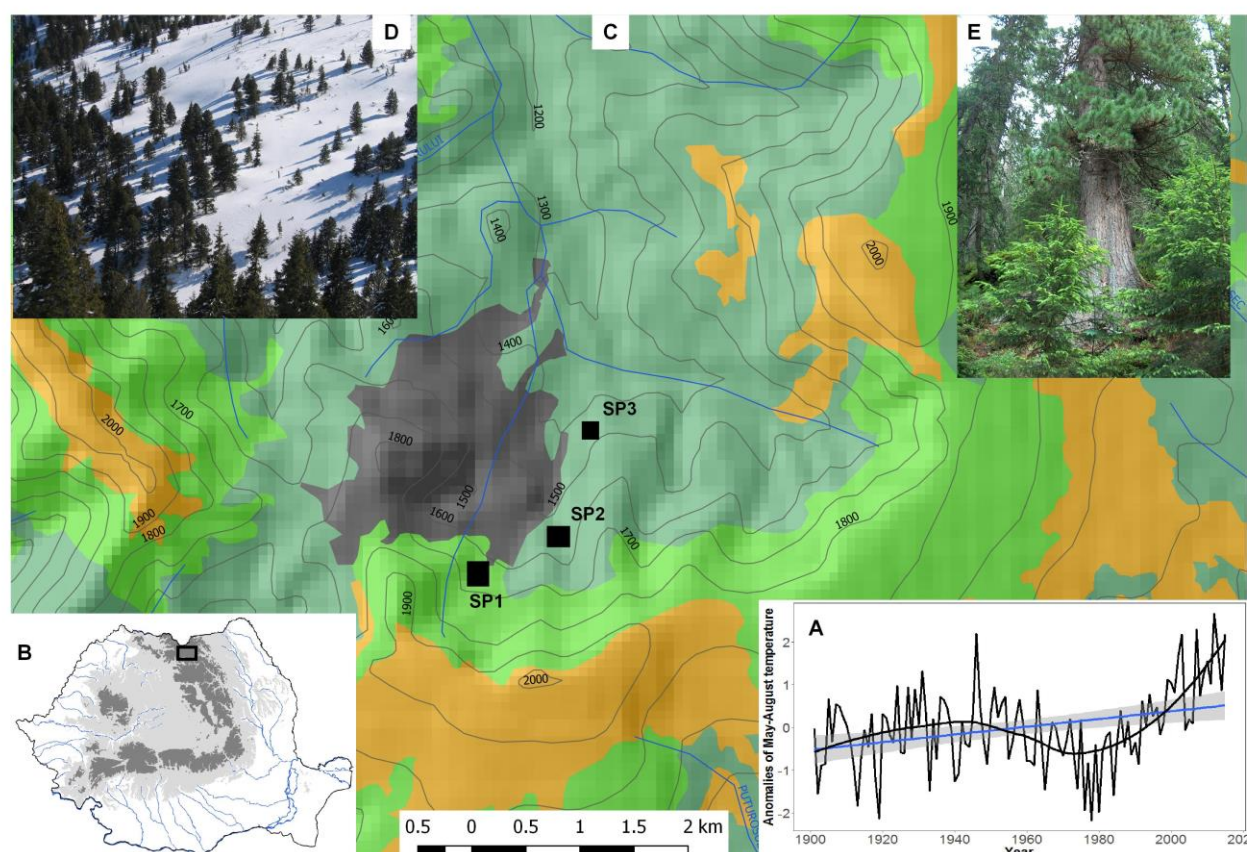
### 88 *2.1. Study area and sample plots*

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

Three permanent plots representing different development stages were established along an altitudinal gradient from closed forest to sparsely tree covered areas close to the timberline (Fig. 1). The selected plot locations lacked signs of historical wood logging or removal or other human disturbances. The uppermost plot (SP1) of 2.1 ha (140x150 m) was located at the transition between closed forest and treeless areas at 1750 m a.s.l. and was characterized by a sparse tree layer and climate-driven infilling processes. The plot was covered by a dense layer of dwarf mountain pine (*Pinus mugo* Turra) and juniper (*Juniperus communis* L.) over 50% of the plot area in addition to spruce and pine. The middle plot (SP2) (1.0 ha - 100x100 m, 1550 m a.s.l.) was established in a closed forest without signs of stand-level destructing disturbances. A spatial mosaic of gaps, regeneration patches and large sized trees characterized the plot. The lowermost plot (SP3) (0.49 ha - 70x70 m 1450 m a.s.l.) was established in a closed forest that was characterized by post-wind disturbance self-thinning 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 **Fig. 1.** Location and characteristics of the study area in the Calimani Mts. A - anomalies of  
 116 summer temperature (May-August) development and trend for 1900-2013 (CRU 3.2, Harris et  
 117 al., 2014); B - map of Romania, with the box indicating the study area; C - plot locations (dark  
 118 green - forest, light green - transitional woodland shrubs, orange - pasture, dark grey -  
 119 abandoned mining area); D-E show aspects from SP1 and SP2, respectively.

## 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

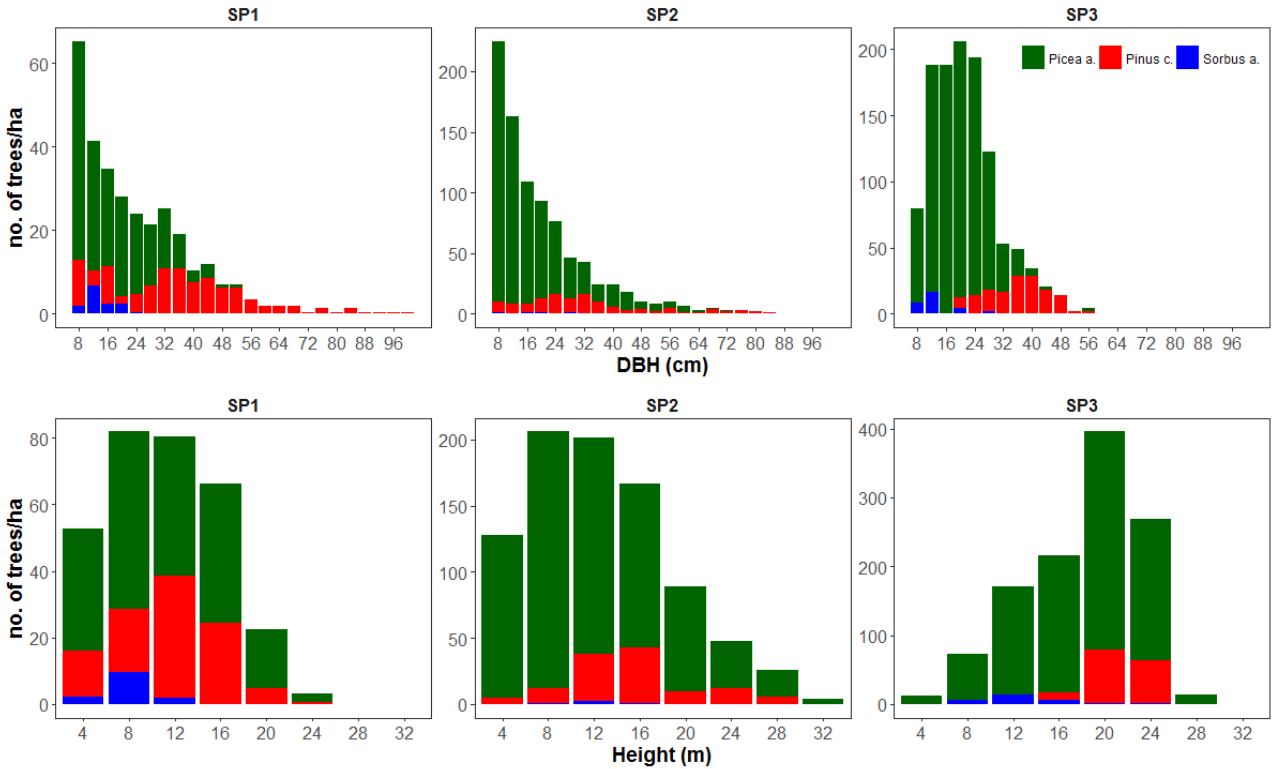
187 **Table 1**

188 Structural characteristics of the study plots

Species	Live trees		Standing dead trees		Mean DBH (cm)*	Mean	Mean
	Basal area	Stems	Basal area	Stems		height	age
	(m <sup>2</sup> ·ha <sup>-1</sup> )	(n·ha <sup>-1</sup> )	(m <sup>2</sup> ·ha <sup>-1</sup> )	(n·ha <sup>-1</sup> )		(m)*	(years)*
<i>SP1</i>							

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
<b>Total</b>	<b>20.55</b>	<b>311</b>	<b>0.62</b>	<b>15</b>	<b>24.1±16.3</b>	<b>11.2±4.8</b>	<b>81±41</b>
<b>SP2</b>							
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
<b>Total</b>	<b>40.74</b>	<b>873</b>	<b>3.76</b>	<b>82</b>	<b>20.0±13.9</b>	<b>12.6±6.2</b>	<b>119±67</b>
<b>SP3</b>							
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
<b>Total</b>	<b>50.11</b>	<b>1155</b>	<b>4.96</b>	<b>434</b>	<b>21.6±9.3</b>	<b>18.2±4.8</b>	<b>130±18</b>

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



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

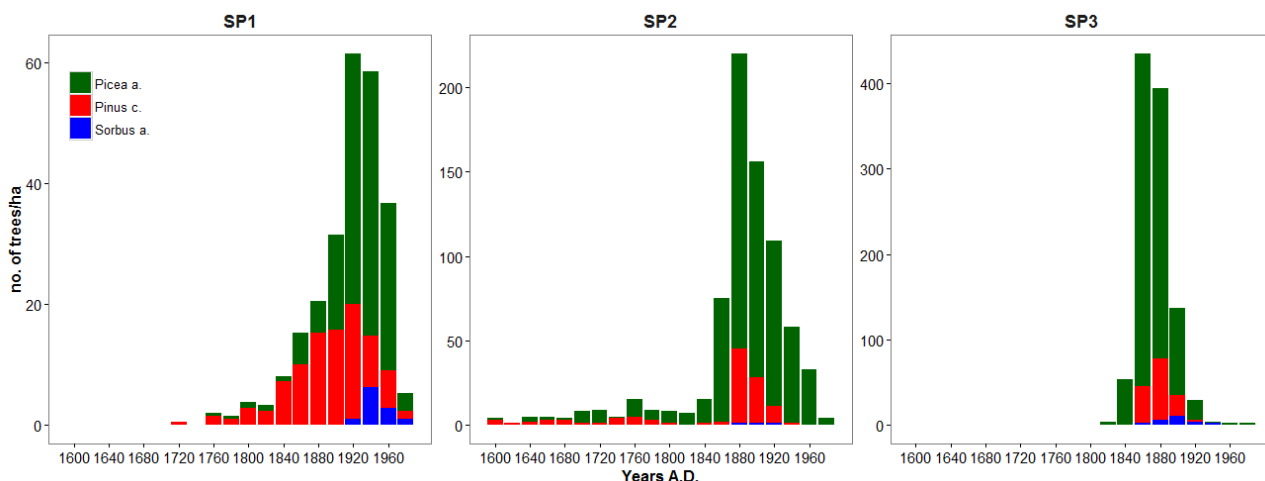
### 3.2. Tree recruitment

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-18<sup>th</sup> century at SP1 (Fig. 3). After these initial  
204   recruitments, both pine and spruce recruited at low frequency until the mid-19<sup>th</sup> 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.

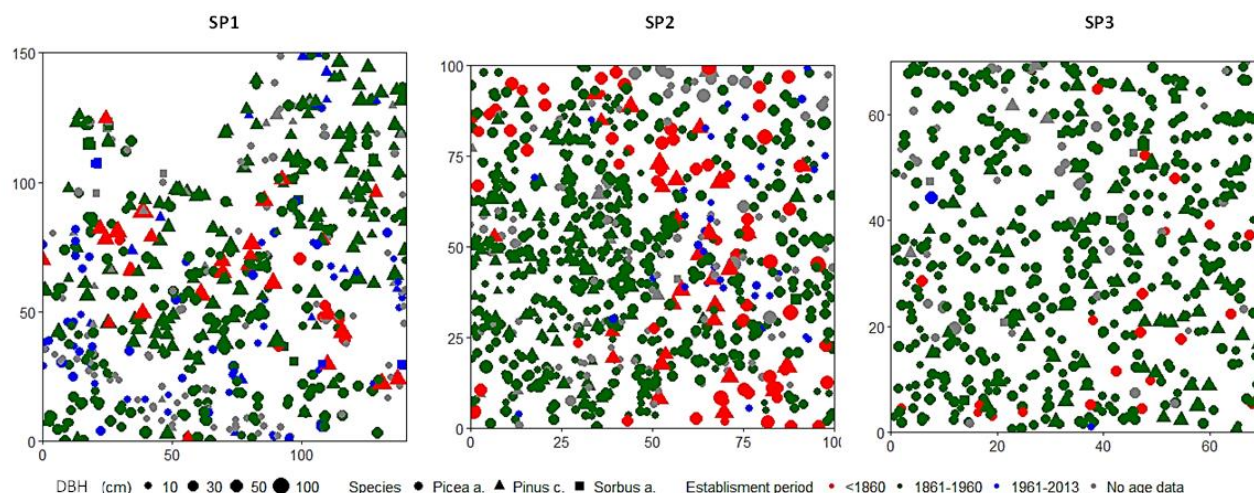
212           In SP2, two clear age groups can be distinguished. A first group of old trees with an age  
213   between 180 and 400 years (Fig. 3) consisting of both pine and spruce was located as a matrix  
214   in the right half of the plot (Fig. 4). The frequency of trees recruited before 1840 is 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).





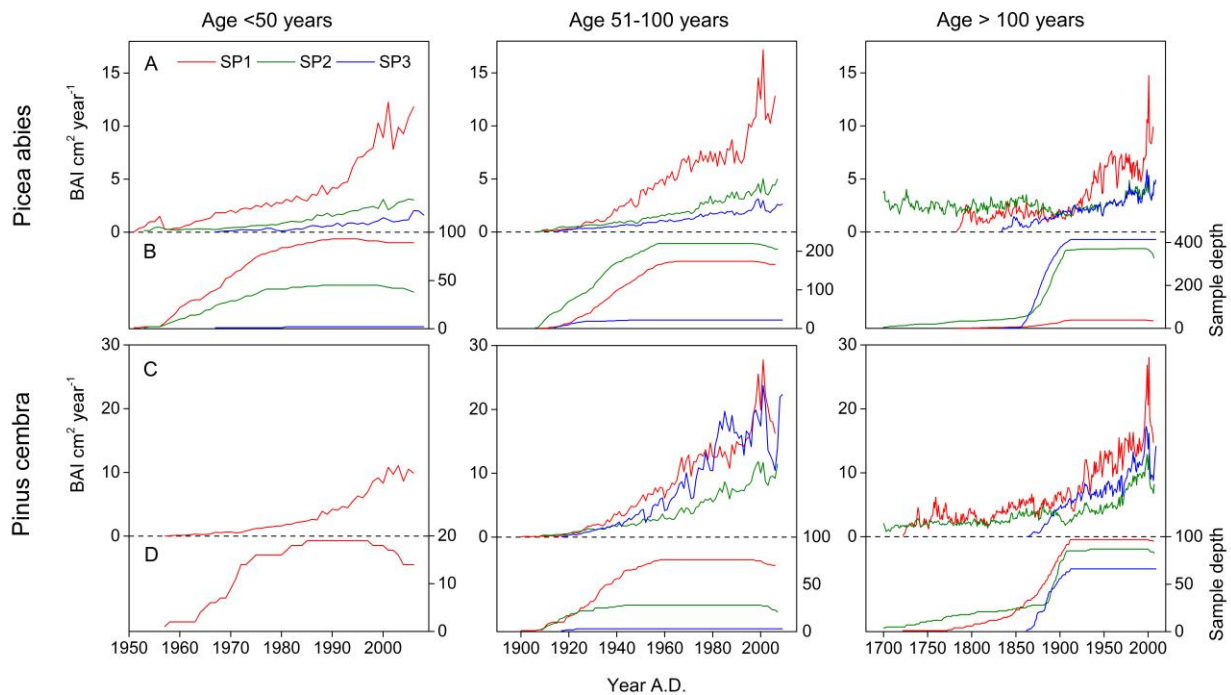
**Fig. 3.** Recruitment pattern of trees >8 cm DBH and recorded at 50 cm above ground presented in 20-year age classes (breaks represent the end of the classes, e.g., the 1840 age class includes trees with an age between 1821 and 1840). Note the differences in the y-axis scales.



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

### 3.3. Growth pattern

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.



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

#### 4. Discussion

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

##### 4.1. Climate-driven stand development

The natural subalpine forests, including the timberline areas, of the studied northern 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 20<sup>th</sup> 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 20<sup>th</sup> 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 CO<sub>2</sub> (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-19<sup>th</sup> 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 (Tsuetanov 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

#### 414 **Acknowledgements**

415 The research leading to these results has received funding from EEA Financial Mechanism  
416 2009–2014 under the project CLIMFOR contract no. 18SEE/2016, the Research Council of  
417 Norway (grant no. 160022/F40 and 244557/E50), and ANCS grant no. TE40. We would like  
418 to thank C. Sidor, R. Vlad and D. Vladeanu for assistance in the field.

419

420

#### 421 **References**

422

- 423 • Blada, I., 2008. *Pinus cembra* distribution in the Romanian Carpathians. Annals of  
424 Forest Research. 51:115-132.
- 425 • Bunn, A.G., Graumlich, L.J., Urban, D.L., 2005. Trends in twentieth-century tree growth  
426 at high elevations in the Sierra Nevada and White Mountains, USA. Holocene. 15:481–  
427 488.
- 428 • Čada, V., Svoboda, M., 2011. Structure and origin of mountain Norway spruce in the  
429 Bohemian Forest. Journal of Forest Science. 57:523–535.
- 430 • Čada, V., Svoboda, M., Janda, P., 2013. Dendrochronological reconstruction of the  
431 disturbance history and past development of the mountain Norway spruce in the  
432 Bohemian Forest, central Europe. Forest Ecology and Management. 295:59-68.
- 433 • Čada, V., Morrissey, R. C., Michalová, Z., Bače, R., Janda, P., Svoboda, M., 2016. Frequent  
434 severe natural disturbances and non-equilibrium landscape dynamics shaped the  
435 mountain spruce forest in central Europe. Forest Ecology and Management. 363:169-  
436 178.
- 437 • Camarero, J.J., Gutierrez, E., 2004. Pace and pattern of recent treeline dynamics:  
438 response of ecotones to climatic variability in the Spanish Pyrenees. Climatic Change.

63:181–200.

- Carrer, M., Soraruf, L., Lingua, E., 2013. Convergent space–time tree regeneration patterns along an elevation gradient at high altitude in the Alps. *Forest Ecology and Management*. 304:1-9.
- Casalegno, S., Amatulli, G., Camia, A., Nelson, A., Pekkarinen, A., 2010. Vulnerability of *Pinus cembra* L. in the Alps and the Carpathian mountains under present and future climates. *Forest Ecology and Management*. 259:750-761.
- Cenusă, R., 1996. Probleme de ecologie forestieră – Aplicații la molidișurile naturale din Bucovina. Editura Universitatea Ștefan cel Mare din Suceava. 165 p.
- Cook, E.R., Kairiukstis, L. (eds.), 1990. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer. 408 p.
- Duncan, R.P., 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Natural Sciences*. 16:1-37.
- Fekete, L., Blattny, T., 1913. Az erdészeti jelentőségű fák és cserjék elterjedése a Magyar Állam területén. [Distribution of trees and shrubs significant in forestry in Hungary.] vol. I, *Selmechánya*, 793 p.
- Franklin, J., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*: 155: 399–423.
- Frelich, L.E., 2002. *Forest Dynamics and Disturbance Regimes*. Cambridge University Press, Cambridge. 266 p.
- Harris, I., Jones, P.D., Osborn, T.J., Lister, D.H. 2014. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *International Journal of Climatology*: 34:623–642.
- Hättenschwiler, S., Körner, C., 1995. Responses to recent climate warming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. *Journal of Vegetation Science*. 6:357-368.
- Hofgaard, A., 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. *Journal of Vegetation Science*. 4:601–608.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43:69–78.
- Holtmeier, F.K., 2009. *Mountain Timberlines: Ecology, Patchiness and Dynamics*. Springer. 437 p.
- Kern, Z., Popa, I., 2008. Changes of Frost Damage and Treeline Advance for Swiss Stone Pine in the Calimani Mts. (Eastern Carpathians, Romania). *Acta Silvatica Lignaria Hungarica*. 4:39-48.
- Khakimulina, T., Fraver, S., Drobyshv, I., 2015. Mixed-severity natural disturbance regime dominates in an old-growth Norway spruce forest of northwest Russia. *Journal of Vegetation Science*. 27:400–413.
- Körner, C., 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems*. Springer Science and Business Media. 220 p.
- Kulakowski, D., Bebi, P., 2004. Range of variability of unmanaged subalpine forests. *Forum für Wissen: Schutzwald und Naturgefahren*. Davos, Switzerland. p. 47–54.
- Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T. A., Panayotov, M., Svoboda M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T., Bebi, P., 2016. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecology and Management* (in press). <http://dx.doi.org/10.1016/j.foreco.2016.07.037>



- Kupfer, J.A., Cairns, D.M., 1996. The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography*. 20:253–272.
- Kuuluvainen, T., 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland—a review. *Annales Zoologici Fennici*. 31:35–51.
- Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research*. 19:651–663.
- Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even-and uneven-aged forest stands in Austria. *Forest Ecology and Management*. 80:57–80.
- Motta, R., Nola, P., Piussi, P. 1999. Structure and stand development in three subalpine Norway spruce (*Picea abies* (L.) Karst.) stands in Paneveggio (Trento, Italy). *Global Ecology and Biodiversity*. 8:455–473.
- Motta, R., Nola, P., 2001. Growth trends and dynamics in sub-alpine forest stands in the Varaita Valley (Piedmont, Italy) and their relationships with human activities and global change. *Journal of Vegetation Science*. 12:219–230.
- Motta, R., Nola, P., Piussi, P., 2002. Long-term investigations in a strict forest reserve in the eastern Italian Alps: spatio-temporal origin and development in two multi-layered subalpine stands. *Journal of Ecology*. 90:495–507.
- Motta, R., Berretti, R., Lingua, E., Piussi, P., 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. *Forest Ecology and Management*. 235:155–163.
- Nechita, C., Popa, I., Roibu, C., 2013. Disturbance history in a stone-pine (*Pinus cembra*) multicentury tree-ring chronology from Calimani Mountains (Eastern Carpathians). *Advances in Agriculture & Botany*. 5:91–95.
- Niklasson, M., 2002. A comparison of three age determination methods for suppressed Norway spruce. Implications for age structure analysis. *Forest Ecology and Management*. 161:279–288.
- Nowacki, G.J., Abrams, M.D., 1994. Forest composition, structure, and disturbance history of the Alan Seeger Natural Area, Huntington Country, Pennsylvania. *Bulletin of Torrey Botanical Club*. 121:277–291.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. Wiley. 520 p.
- Panayotov, M., Kulakowski, D., Laranjeiro Dos Santos, L., Bebi, P., 2011. Wind disturbances shape old Norway spruce-dominated forest in Bulgaria. *Forest Ecology and Management*. 262:470–481.
- Paulsen, J., Weber, U. M., Korner, C., 2000. Tree growth near timberline: abrupt or gradual reduction with altitude? *Artic, Antarctic, and Alpine Research*. 32:14–20.
- Popa, I., 2007, *Managementul riscului la doborâturi produse de vânt (Windthrow risk management)*. Tehnică Silvică. Bucharest. 235 p.
- Popa, I., Kern Z., 2009. Millennial summer temperature reconstruction inferred from tree ring records for Calimani Mts. (Eastern Carpathians, Romania). *Climate Dynamics*. 32:1107–1117.
- Popa, I., Sidor, C., 2013. Serii dendrocronologice seculare pentru pădurile virgine din lanțul carpatic din România. In Giurgiu, V. (eds.). *Pădurile virgine și cvasivirgine ale României*. Romanian Academy Publishing House. p. 310–318.
- Popa, I., Sidor, C., 2013. Structura spațială a unei păduri naturale de limită altitudinală superioară din Munții Călimani (Carpații Orientali, România). In Giurgiu, V. (eds.), 2013, *Padurile virgine și cvasivirgine ale României*. Romanian Academy Publishing House. p. 257–276.

- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature communications*. 5.
- Primicia, I., Camarero, J. J., Janda, P., Čada, V., Morrissey, R. C., Trotsiuk, V., Bace, R., Teodosiu, M., Svoboda, M., 2015. Age, competition, disturbance and elevation effects on tree and stand growth response of primary *Picea abies* forest to climate. *Forest Ecology and Management*. 354:77-86.
- Qi, Z., Liu, H., Wu, X., Hao, Q., 2015. Climate-driven speedup of alpine treeline forest growth in the Tianshan Mountains, Northwestern China. *Global Change Biology*. 21: 816-826.
- Rinntech, 2006. LINTAB: Precision Ring by Ring. (<http://www.rinntech.com>)
- Risch, A.C., Nagel, L.M., Schutz, M., Krusi, B.O., Kienast, F., Bugmann, H., 2003. Structure and long-term development of subalpine *Pinus montana* Miller and *Pinus cembra* L. forests in the central European Alps. *Forstwissenschaftliches Centralblatt*. 122:219-230.
- Rolland, C., Petitcolas, V., Michalet, R., 1998. Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees*. 13:40-53.
- Schelhaas, M.J., Nabuurs, G.J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*. 9:1620-1633.
- Seghedin, T., 1983. Rezervatile naturale din Bucovina. Sport-Turism. Bucharest. 127p.
- Seidl, R., Schelhaas, M.J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*. 4: 806-810.
- Spiecker, H., 1999. Overview of recent growth trends in European forests. *Water, Air, and Soil Pollution*. 116:33-46.
- Svoboda, M., Pouska, V., 2008. Structure of a central-European mountain spruce old-growth forest with respect to historical development. *Forest Ecology and Management*. 255:2177-2188.
- Svoboda, M., Fraver, S., Janda, P., Bače, R., Zenáhlíková, J., 2010. Natural development and regeneration of a Central European montane spruce forest. *Forest Ecology and Management*. 260:707-714.
- Svoboda, M., Janda, P., Nagel, T.A., Fraver, S., Rejzek, J., Bače, R., 2012. Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. *Journal of Vegetation Science*. 23:86-97.
- Svoboda, M., Janda, P., Bače, R., Fraver, S., Nagel, T. A., Rejzek, J., Mikolas, M., Douda, J., Boublik, K., Samonil, P., Čada, V., Trotsiuk, V., Teodosiu, M., Bouriaud, O., Biris, I., Sykora, O., Uzel, P., Zelenka, J., Sedlak, V., Lehejcek, J., 2014. Landscape-level variability in historical disturbance in primary *Picea abies* mountain forests of the eastern Carpathians, Romania. *Journal of Vegetation Science*. 25:386-401.
- Szewczyk, J., Szwagrzyk, J., Muter, E., 2011. Tree growth and disturbance dynamics in old-growth subalpine spruce forests of the Western Carpathians. *Canadian Journal of Forest Research*. 41:938-944.
- Tognetti, R., Cherubini, P., Innes, J.L., 2000. Comparative stem growth rates of Mediterranean trees under background and naturally enhanced ambient CO<sub>2</sub> concentrations. *New Phytologist*. 146:59-74.
- Tomback, D.F., Holtmeier, F.K., Mattes, H., Carsey, K.S., Powell, M.L., 1993. Tree clusters and growth form distribution in *Pinus cembra*, a bird-dispersed pine. *Arctic and Alpine Research*. 25:374-381.
- Tsvetanov, N., Panayotov, M., Yurukov, S., 2016. Age estimation of Norway spruce saplings: analysis of the cambial age at various stem heights. *TRACE*. 14:128-133.

- Ulanova, N.G., 2000. The effects of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management*. 135:155-167.
- Vittoz, P., Rulence, B., Largey, T., Freléchoux, F., 2008. Effects of climate and land-use change on the establishment and growth of cembra pine (*Pinus cembra* L.) over the altitudinal treeline ecotone in the Central Swiss Alps. *Arctic, Antarctic, and Alpine Research*. 40:225-232.
- Vlad, R., Sidor, C., Popa, I., 2013. High mountain forest structure in Calimani Mts. (Eastern Carpathians). *Analele Universității din Oradea*. 20:179-186.
- Wilmking, M., Juday, G.P., Barber, V.A., Zald, H.S.J., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology*. 10:1724–1736.
- Wong, C.M., Lertzman, K.P., 2001. Errors in estimating tree age: implications for studies of stand dynamics. *Canadian Journal of Forest Research*. 31:1262-1271.
- Zielonka, T., Malcher, P., 2009. The dynamics of a mountain mixed forest under wind disturbances in the Tatra Mountains, central Europe – a dendroecological reconstruction. *Canadian Journal of Forest Research*. 39:2215–2223.
- Zielonka, T., Holeksa, J., Fleischer, P., Kapusta, P., 2010. A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. *Journal of Vegetation Science*. 21:31–42.
- Zong, C., Wauters, L.A., Van Dongen, S., Mari, V., Romeo, C., Martinoli, A., Preatoni, D., Tosi, G., 2010. Annual variation in predation and dispersal of Arolla pine (*Pinus cembra* L.) seeds by Eurasian red squirrels and other seed-eaters. *Forest Ecology and Management*. 260:587–594.