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7 **Legacies of past forest management determine current responses to severe drought**
8 **events of conifer species in the Romanian Carpathians**

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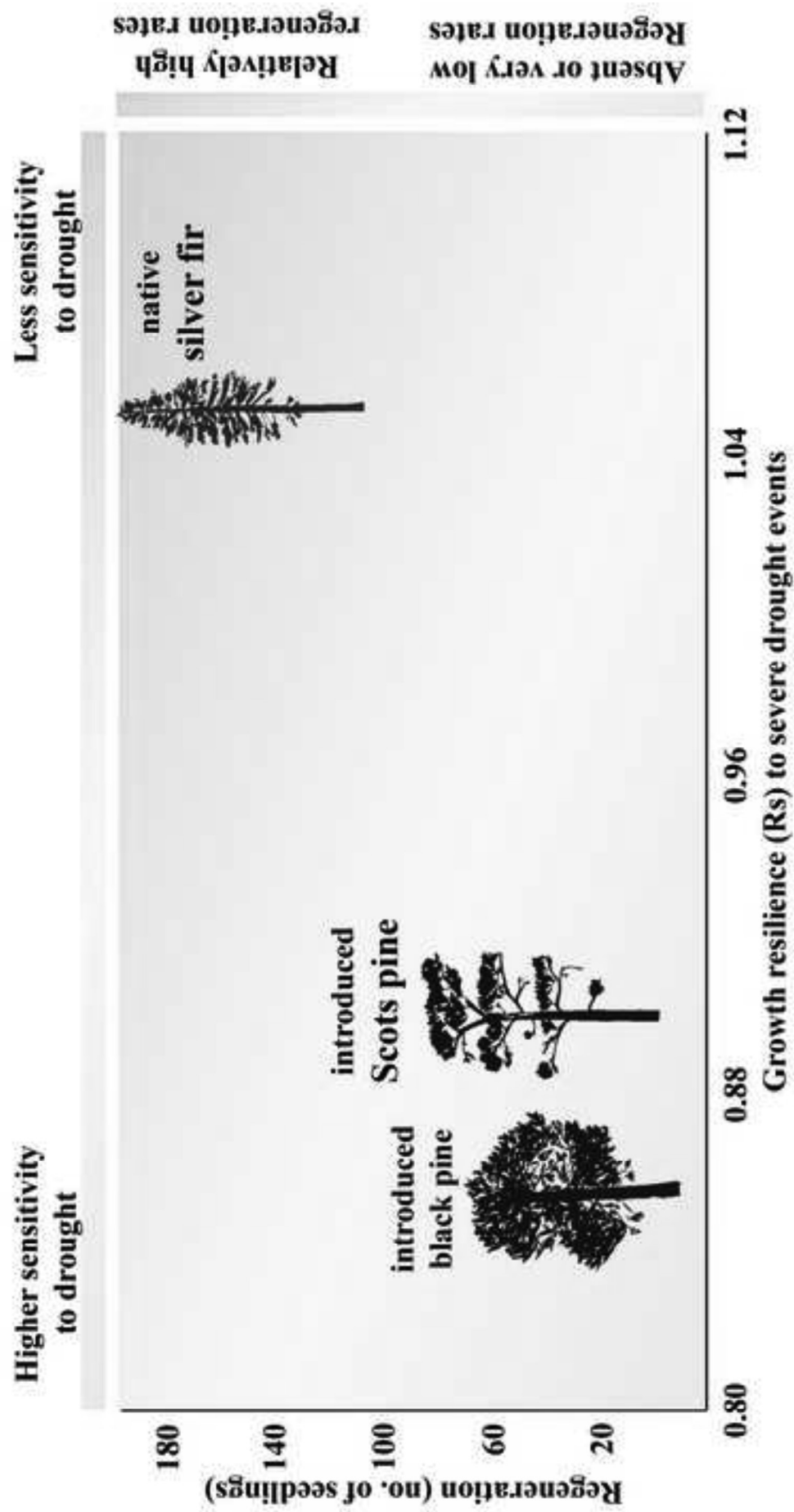
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58 This document is the Accepted Manuscript version of a Published Work that appeared in final form in:
59 *Hereş, A.M.; Petritan, I.C.; Bigler, C.; Curtu, A.L.; Petrea, Ş.; Petritan, A.M.; Polanco-Martínez, J.M.; Rigling, A.; Curiel Yuste, J..2020.*
60 **Legacies of past forest management determine current responses to severe drought events of conifer species in the**
61 **Romanian Carpathians.** SCIENCE OF THE TOTAL ENVIRONMENT. 751. DOI ([10.1016/j.scitotenv.2020.141851](https://doi.org/10.1016/j.scitotenv.2020.141851)).
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- Native silver fir is more resilient and regenerates better than introduced pines
- Growth decline of introduced pine species is related to high sensitivity to drought
- Silver fir dependence on precipitation is compensated by winter-spring temperatures
- Introduced pines are being replaced by native broadleaf species
- Legacies of past forest management underlie tree mortality and regeneration rates

1 **ABSTRACT**

2 Worldwide increases in droughts- and heat-waves-associated tree mortality events are
3 destabilizing the future of many forests and the ecosystem services they provide. Along
4 with climate, understanding the impact of the legacies of past forest management is key
5 to better explain current responses of different tree species to climate change. We
6 studied tree mortality events that peaked in 2012 affecting one native (silver fir;
7 growing within its natural distribution range) and two introduced (black pine and Scots;
8 growing outside their natural distribution range) conifer species from the Romanian
9 Carpathians. The three conifers were compared in terms of mortality events, growth
10 trends, growth resilience to severe drought events, climate-growth relationships, and
11 regeneration patterns. The mortality rates of the three species were found to be
12 associated with severe drought events. Nevertheless, the native silver fir seems to
13 undergo a self-thinning process, while the future of the remaining living black pine and
14 Scots pine trees is uncertain as they register significant negative growth trends. Overall,
15 the native silver fir showed a higher resilience to severe drought events than the two
16 introduced pine species. Furthermore, and unlike the native silver fir, black pine and
17 Scots pine species do not successfully regenerate. A high diversity of native broadleaf
18 species sprouts and develops instead under them suggesting that we might be witnessing
19 a process of ecological succession, with broadleaves recovering their habitats. As native
20 species seem to perform better in terms of resilience and regeneration than introduced
21 species, the overall effect of the black pine and Scots pine mortality might be
22 compensated. Legacies of past forest management should be taken into account in order
23 to better understand current responses of different tree species to ongoing climate
24 change.

25

26 **Keywords:** native; introduced; drought; mortality; resilience; regeneration

27

28 1. INTRODUCTION

29 Climate models predict an increase in the severity, frequency, and duration of droughts
30 and heat-waves mainly due to the effects of human-induced climate change and natural
31 climatic variability (Easterling et al., 2000; Schär et al., 2004; IPCC, 2013). In line with
32 global climate trends, worldwide forests are already showing worrisome drought- and
33 heat-waves-associated decline and mortality events (Allen et al., 2010, 2015; Hartmann
34 et al., 2018). Such scenarios destabilize the capacity of the forests to mitigate climate
35 change as they might be turned into carbon sources rather than carbon sinks (Lindner et
36 al., 2010; Naudts et al., 2016). Understanding tree decline and mortality within this
37 context is thus of utmost importance as forests provide essential ecosystem services
38 (Bonan, 2016; Castro-Díez et al., 2019).

39

40 Legacies of past forest management as e.g. *planting and favouring introduced tree*
41 *species at the expense of naturally regenerated native ones, thinning intensities, tree*
42 *species mixtures, horizontal structuring, but also forest pasturing or litter racking etc.*,
43 may play a critical role in determining how forests respond to severe droughts and heat-
44 waves (Gimmi et al. 2010; Munteanu et al., 2016; Perring et al., 2018). Throughout
45 history, extended areas of Europe have been reforested and afforested, these plantations
46 being mainly conversions from broadleaf to conifer forests (McGrath et al., 2015;
47 Bonan, 2016). This was done because conifer species are fast-growing, production-
48 orientated, and thus economically profitable (Naudts et al., 2016). Accordingly, legacies
49 of past forest management are imprinted in the current structure of most European
50 forests affecting their contemporary patterns (Munteanu et al., 2016). Nevertheless,

51 legacies of past forest management have been less considered as potential factors
52 involved in current tree decline and mortality trends, although they may also be
53 included as long-term predisposing factors (Camarero et al., 2011; Vilà-Cabrera et al.,
54 2011; Sánchez-Salguero et al., 2013) within the slow-decline framework on tree
55 mortality (Manion, 1991). The information regarding legacies of past forest
56 management is therefore of outermost importance to understand current drought
57 associated tree decline and mortality processes and to draw adaptation guidelines to
58 increase the resilience and the climate change mitigation capacity of our forests (Naudts
59 et al., 2016). Indeed, introducing non-native species might involve ecological
60 consequences that often become obvious when global climate change is putting forests
61 under enormous pressure (Bonan, 2016; Castro-Díez et al., 2019).

62

63 Tree rings faithfully register the events to which the trees have been exposed to during
64 their lifetime, representing a valuable tool to study their historical growth trends and
65 responses to past climatic variability. Retrospective analyses of how trees responded in
66 the past to climatic events such as droughts may give us clues about how they might
67 respond in the future to similar climatic conditions (Fritts, 1976; Vaganov et al., 2006).
68 Thus, tree rings are largely used as proxies to predict tree vulnerability, decline, or
69 mortality (Cailleret et al., 2007). On the other hand, patterns of current regeneration and
70 seedling survival of a species also provide valuable information on long-term forest
71 dynamics (Zhu et al., 2012). Regeneration rates and seedling survival and thus forest
72 successional dynamics are determined by multiple factors (Verdú et al., 2009), among
73 which legacies of past forest management also play a key role (Ruiz-Benito et al.,
74 2017). Combining the study of tree rings with the study of the capacity of a tree species

75 to regenerate, allows for an accurate estimation of the current vulnerability patterns of
76 this species and its long-term ability to survive under certain habitat conditions.

77

78 Romania has an estimated forest surface of 7 million ha (IFN, 2018), 26% of it being
79 occupied by conifers. The Romanian forestry policy has historically promoted the
80 natural regeneration of native species (Munteanu et al., 2016). Still, following the
81 European trend (Naudts et al., 2016), plantations with non-native, fast-growing conifers
82 have been also established, many of them on areas naturally supporting broadleaves
83 (Barbu & Barbu, 2005). Conifer plantations proliferated mainly during the 1970s and
84 the 1980s, after World War II, but also at the end of the 19th century (i.e., following the
85 highest forest harvest registered in Romania), when extended pine plantations were
86 established (Munteanu et al., 2016). This is the case of black pine (*Pinus nigra* Arn.)
87 and Scots pine (*Pinus sylvestris* L.) which are mainly represented by plantations in
88 Romania (Șofletea & Curtu 2007; Bouriaud & Popa, 2009). In line with global climate
89 trends, drought is considered an important threat for the Romanian forests (Lindner et
90 al., 2010), high drought-related tree decline and mortality events being already observed
91 (Barbu & Popa, 2001; Sidor et al., 2019; Curiel Yuste et al., 2019).

92

93 Tree rings and a regeneration survey were used to investigate one native (silver fir,
94 *Abies alba* Mill.) and two introduced (black pine and Scots pine) conifer species
95 affected by high mortality events that peaked in 2012 in the Brașov region (Romanian
96 Carpathians; Fig. 1). Our aim was to compare the three conifer species in terms of
97 mortality events, growth trends, growth resilience to severe drought events, climate-
98 growth relationships, and regeneration patterns. To do so, the responses of these three
99 species to climatic conditions (i.e., temperature, precipitation, severe drought events)

100 were analysed considering that legacies of past forest management are imprinted in their
101 current performance including vitality, growth trends, growth resilience to severe
102 drought events, and regeneration patterns. Our hypothesis was that naturally regenerated
103 (i.e., native) species growing within their natural distribution range would perform
104 better than introduced species growing outside their natural distribution range.

105

106 **2. MATERIALS AND METHODS**

107 **2.1 Study sites**

108 Three silver fir, three black pine, and three Scots pine dominated sites were used in this
109 study. The nine study sites were within a maximum of 40 km from each other (Fig. 1).
110 At these sites, high mortality rates, which extended over large areas, were observed in
111 2013 and estimated in 2015 to have affected 19-23% of the silver fir trees, 16-27% of
112 the black pine trees, and 17-22% of the Scots pine trees (Curiel Yuste et al., 2019).
113 Silver fir sites were all natural, of high productivity, and located within the natural
114 distribution range of this species (Forest Management Plans of the Forest Districts
115 Sacele, Kronstadt, and Rasnov). Black pine and Scots pine sites instead were all
116 planted, of middle to low productivity, and established in areas naturally supporting
117 broadleaves (Forest Management Plans of the Forest Districts Kronstadt, Teliu, Codlea,
118 and Intorsura Buzaului). Black pine's natural distribution follows the Mediterranean
119 Basin (Farjon & Filer, 2013), being planted at the sites considered for this study (Schei,
120 Lempes, and Racadau; Forest Management Plans of the Forest Districts Kronstadt and
121 Teliu; Fig. 1). Although Scots pine is a species that occurs naturally in Romania
122 (Şofletea & Curtu, 2007), it has been planted at the sites considered for this study (i.e.,
123 Codlea, Lempes, and Teliu; Forest Management Plans of the Forest Districts Codlea,
124 Teliu, and Intorsura Buzaului; Fig. 1). Once the plantations had been established, using

125 seeds of unknown origin, the level of interventions has been low and consisted mainly
126 of sanitation harvesting according to the Forest Management Plans. All black pine and
127 Scots pine sites have an easy access, while the silver fir sites are less accessible.
128
129 Terrains are steep (17 to 37°) and slopes are S-, SE-, or SW-facing, except Rasnov
130 where the slope is NW-facing. The elevation varies between sites (Table 1). Soil pH is
131 acidic for all nine sites, while the soil type varies: Eutricambisols (Dambu Morii,
132 Kronstadt, Rasnov, Lempes and Codlea), Lytic-Rendzina (Schei), Leptosol (Racadau),
133 and Regosol (Teliu) (Curiel Yuste et al., 2019). The climate of the Braşov region, where
134 all nine study sites are located, is Dfb (i.e., wet and warm continental; Köppen-Geiger
135 map on climate classification; [link](#)). Mean annual temperatures and mean annual
136 precipitations (CRU TS v. 4; Harris et al., 2020) are relatively low and vary little
137 between sites, ranging from 6.3°C to 7.8°C and from 637 mm to 875 mm, respectively.
138

139 **2.2 Tree rings**

140 Tree rings were used to reconstruct past secondary growth rates (Fritts, 1976) of dead
141 and living silver fir, black pine, and Scots pine trees that were co-occurring, adult, and
142 dominant (i.e., canopy-level; see height in Table 1). At each of the nine study sites, 30
143 pairs of standing dead and living trees, with neither signs of biotic attacks (e.g., insects,
144 fungi) nor wind or snow damage, were selected. We used a paired sampling design
145 (Bigler & Bugmann, 2004), trying to assure that dead and living trees would have
146 similar DBH (diameter at breast height; Table 1), height (Table 1), competition level
147 ($CI_{Hegy\grave{i}}$; Table 1), apparent microsite conditions (Curiel Yuste et al., 2019), and a
148 distance of > 5 m between them. From each of the 540 selected trees, two radial wood
149 cores were extracted from opposite directions and perpendicular to the slope to account

150 for growth variability and to avoid reaction wood, respectively (Fritts 1976). Wood
151 cores were extracted at breast height (i.e., 1.3 m above ground) using increment borers
152 with an inner diameter of 5 mm (Haglöf, Sweden). Field sampling campaigns were
153 conducted in 2015 (early winter) and completed in 2016 (spring). Sampling started at
154 random locations and progressed until the required number of trees had been obtained.
155 Tree-ring chronologies ended in 2015 for all living trees, while the last assigned year for
156 the dead trees varied depending on their year of death (cf. *Section 2.3*). Following field
157 sampling, wood cores were air-dried, glued, and polished using a series of sand-paper
158 grits so tree-ring boundaries were clearly visible. Wood cores of both dead and living
159 trees were then visually crossdated using wide and narrow pointer years (Stokes &
160 Smiley, 1968), scanned to 1200 dpi (*Epson Expression 11000XL*), and measured to the
161 nearest 0.01 mm using the CooRecorder software (Cybis Elektronik & Data,
162 Saltsjöbaden, Sweden). Crossdating accuracy (Table 1) was repeatedly checked using
163 COFECHA, a program that calculates moving correlations between the mean site
164 chronology and each individual tree-ring chronology (Holmes, 1983). In total, 84 living
165 silver fir, 71 living black pine, and 81 living Scots pine trees were accurately crossdated
166 (Table 1). Different chronologies, one for each species and site, were obtained.

167

168 The cambial age (i.e., total number of tree rings at 1.3 m above ground) of all dead and
169 living silver fir, black pine, and Scots pine trees, was also estimated (Table 1). If the
170 centre of the tree was not hit, then the number of tree rings that were missing to the pith
171 was estimated using the “*distance to pith (DTP)*” function available from the
172 CooRecorder software (Cybis Elektronik & Data, Saltsjöbaden, Sweden).

173

174 **2.3 Dating of dead trees**

175 The years of tree mortality were established by attributing calendar years to the
176 outermost tree rings that could be measured on the previously visually crossdated wood
177 cores of the dead trees (cf. *Section 2.2*). This was done individually for each dead tree of
178 the three species using COFECHA (Holmes, 1983). Specifically, the individual tree-
179 ring series of the dead trees were run against the master chronologies built from the
180 accurately crossdated tree-ring series of living trees (cf. *Section 2.2*), separately for each
181 site. COFECHA suggested possible dating years for the outermost tree rings of the dead
182 trees (i.e., years of death; Grissino-Mayer, 2001). If different calendar years were
183 suggested for the two wood cores of each tree, the most recent one was considered as
184 the year of death (Bigler & Rigling, 2013). In total, 78 dead silver fir, 54 dead black
185 pine, and 71 dead Scots pine trees were accurately dated (Table 1). The confidence of
186 the dating process may have been influenced by the conservation status of the wood,
187 and by the fact that trees sometimes do not develop tree rings several years before death
188 (Amoroso & Daniels, 2010; Bigler & Rigling, 2013). Thus, we considered the year of
189 death to be year when the last tree ring was formed.

190

191 **2.4 Growth of silver fir, black pine, and Scots pine trees**

192 Only silver fir, black pine, and Scots pine trees for which both wood cores could be
193 accurately crossdated were considered for further analyses. The average of the two tree-
194 ring width (RW) series was used to represent growth of each dead and living tree. To
195 limit the *juvenile effect* (Richter, 2015), the first 20 years of growth of each accurately
196 crossdated dead and living tree were eliminated from further analyses. If the centre of
197 the tree was not hit, then the estimated number of tree rings that were missing to the pith
198 (cf. *Section 2.2*) was first rested and only the difference to the first 20 years of growth
199 was eliminated from further analyses.

200
201 Measured RW values of all dead and living trees were transformed into residual ring-
202 width index (RWI_{residual}) values that were used to estimate climate-growth relationships.
203 RWI_{residual} values were calculated to remove low-frequency fluctuations associated with
204 increasing stem size and tree age over time, and to have a better estimate of the overall
205 tree growth (Cook & Kairiukstis, 1990). To obtain RWI values, the *spline* detrending
206 method, available from the *dpLR* package (Bunn, 2008; Bunn et al., 2020) in the
207 software R (v. 4.0.0, 2020, R Core Team), was used by considering a 0.50 frequency
208 response cutoff and 30 years to define the rigidity of the smoothing spline. Then, the
209 resulting individual RWI values were prewhitened using an autoregressive model in
210 order to obtain residual chronologies (RWI_{residual}) separately for each species, site, and
211 tree condition (i.e., a total of 18 RWI_{residual} series).

212
213 For the rest of the analyses, we used raw RW data as we wanted to detect when dead
214 and living trees diverged in terms of growth, which would have not been possible using
215 RWI_{residual} .

216

217 **2.5 Climatic data and severe drought events**

218 Monthly temperature (T, °C), precipitation (P, mm), and Standardized Precipitation-
219 Evapotranspiration Index (SPEI) data were available from 1901 to 2015 at 0.5°
220 resolution. T (°C) and P (mm) were obtained from the Climatic Research Unit (CRU TS
221 v. 4; Harris et al., 2020) and SPEI from the Global SPEI database ([link](#); Vicente-Serrano
222 et al., 2010; Beguería et al., 2010, 2014). Dambu Morii, Kronstadt, Schei, Lempes,
223 Racadau, and Teliu sites fell within the same grid, so they all had the same T (°C), P
224 (mm), and SPEI datasets. Rasnov and Codlea sites instead fell within two different

225 grids, so they had separate T (°C), P (mm), and SPEI datasets. The 0.5° resolution of the
226 CRU climatic dataset may be considered relatively coarse as topography and elevation
227 induce local climatic patterns. Still, in order to produce the CRU T (°C) and P (mm)
228 data of the three grids used in this study, meteorological data recorded at both low (i.e.,
229 Ghimbav meteorological station; 534 m a.s.l.; 45°41'44.55"N; 25°31'33.75"E) and high
230 (i.e., Predeal meteorological station; 1093 m a.s.l.; 45°30'21.98"N; 25°35'2.15"E)
231 elevations (Fig. 1), was also considered in the methodological process (Harris et al.,
232 2020). Accordingly, CRU provides reliable T (°C) and P (mm) data starting in 1901
233 across the nine study sites situated at different elevations.

234

235 SPEI is a multiscalar drought index that accounts for both T (°C) and evapotranspiration
236 effects on the water balance. It may take negative and positive values, indicating dry
237 and wet periods, respectively (Vicente-Serrano et al., 2010; Beguería et al., 2010, 2014).
238 Mean $SPEI_{\text{annual}}$ values were calculated from monthly SPEI01 (i.e., 1-month time scale)
239 and used to identify the most severe drought events, common to all nine sites, registered
240 since 1901 (i.e., $SPEI_{\text{annual}}$ values lower than -0.3). One such severe drought event was
241 selected per decade, if present. When two or more such events were identified per
242 decade, we selected the year with the lowest $SPEI_{\text{annual}}$. This was done to avoid
243 overlapping periods when calculating the components of resilience (cf. *Section 2.6*).
244 Accordingly, the following eight years were considered as being characterized by severe
245 drought events: 1903, 1929, 1934, 1948, 1953, 1986, 2000, and 2011.

246

247 **2.6 Components of resilience**

248 To quantify the growth responses of the three species to severe drought events, the
249 following indices (Lloret et al., 2011) were calculated: (1) resistance (Rt), which

250 estimates the capacity of the trees to overcome the effect of drought events; (2) recovery
 251 (Rc), which estimates the capacity of the trees to recover after the damage undergone
 252 during drought events; and (3) resilience (Rs), which estimates the capacity of the trees
 253 to reach pre-drought growth rates. These indices were calculated separately for each
 254 species using the annual RW values of the dead and living trees. Specifically, five (i.e.,
 255 1934, 1948, 1953, 1986, and 2000) out of the eight defined severe drought events (cf.
 256 *Section 2.5*) were used to calculate them. Rt, Rc, and Rs were calculated considering
 257 four years before and after the selected severe drought events in agreement with
 258 Anderegg et al. (2015). The first year of severe drought that entered the analyses was
 259 1934 as RW series of black pine were shorter (Table 1). Also, the 2011 severe drought
 260 event was not used for these analyses as most trees died in 2012.

261

262 **2.7 Competition and regeneration surveys**

263 Competition and regeneration data were collected during the 2016 (spring) field
 264 campaign. Both were estimated within a 5 m radius around each sampled dead and
 265 living tree (i.e., *reference trees* for the competition and regeneration surveys). To
 266 estimate the competition level, all trees with a DBH > 10 cm (i.e., *competitor trees*)
 267 were counted around each *reference tree*, and their species, DBH, and distance to the
 268 *reference trees* were recorded. These variables were then used to calculate competition
 269 indexes separately for each *competitor tree*, which were then summed in order to have a
 270 competition index for each *reference tree* ($CI_{Hegy\acute{i}} = \sum \left(\frac{DBH_{competitor\ tree}}{DBH_{reference\ tree}} * \right.$
 271 $\left. \frac{1}{distance\ to\ the\ reference\ tree} \right)$; Hegyi, 1974). To estimate the regeneration, all trees with a
 272 DBH < 10 cm and a minimum height of 10 cm, and shrubs were counted around each
 273 *reference tree* and identified at species level. All present species were considered,
 274 including the studied species (i.e., silver fir, black pine, and Scots pine).

275

276 **2.8 Statistical analyses**

277 T (°C) and P (mm) trends were analysed through simple linear regressions. Within-site
278 differences in DBH, height, age, RW, and CI_{Hegy_i} between vigour classes (i.e., living
279 and dead trees) were analysed through t-tests or Mann-Whitney U tests depending on
280 whether the data followed a normal distribution or not.

281

282 Pearson's chi-square tests followed by a Fisher's exact test were performed separately
283 for each species to investigate associations between severe drought events and years of
284 death. A five-year period (i.e., the severe drought year plus the four years following it)
285 was considered to account for lagged effects. As the earliest year of tree mortality was
286 1990, the severe drought events included in these analyses were 1986, 2000, and 2011.

287

288 A linear mixed-effects model (LME; “nlme” R package, Pinheiro et al., 2020) was run
289 to analyse the growth (RW) trends of the dead and living silver fir, black pine, and
290 Scots pine trees. The fixed part of the model included *Year*, and the interactions *Year* ×
291 *age*, *Year* × *DBH*, and *Year* × *vigour class* × *species*. Age and DBH were included in
292 the fixed part of the model to control for ontogenetic and tree-size effects. Tree
293 identities nested within sites were introduced as random effects. RW was log
294 transformed ($\log(RW+1)$) prior to analyses in order to meet normality assumptions. A
295 first-order autoregressive covariance structure was used to account for temporal
296 autocorrelation. To look for differences between vigour classes (i.e., dead and living
297 trees) the “lsmeans” R package (Lenth 2016) was used to run least-squares means with a
298 Tukey correction. The selection of the final model was based on the Akaike's
299 information criterion (AIC) (i.e., minimal models with the lowest AIC). The final

300 coefficients of the model were estimated using the restricted maximum likelihood
301 method (REML).

302

303 Climate-growth relationships were evaluated through Spearman correlations (“Hmisc”
304 R package, Harrell et al., 2020) between monthly T (°C) and P (mm) values and
305 RWI_{residual} data of dead and living trees of all species and sites. To do so, a 17-months
306 window of time (i.e., from June of the previous-to-growth year (t-1) to October of the
307 growth year (t)) was considered.

308

309 To test for differences in resistance (Rt), recovery (Rc), and resilience (Rs) indices
310 across species, we run generalized least squares models (GLS; “nlme” R package,
311 Pinheiro et al., 2020). Separate GLS were built for each of the three indices. To do so,
312 the values of each of the three indices were averaged over the five severe drought events
313 considered for these analyses (cf. *Section 2.6*). These averaged values were included in
314 the GLS as response variables, while species was introduced as an explaining factor.
315 When significant effects of species were found, least-square means based on Tukey
316 HSD tests (Lenth 2016) were used to analyse the differences between them.

317

318 All statistical analyses, if not otherwise mentioned, were carried out in R (v. 4.0.0,
319 2020, R Core Team). Statistical relationships were considered significant at $p < 0.05$
320 and marginally significant at $p < 0.1$.

321

322 **3. RESULTS**

323 **3.1 Climatic conditions**

324 Mean annual T (°C) increased significantly ($R^2 = 0.13$, $p < 0.001$) at the nine study sites
325 between 1901 and 2015, while mean annual P (mm) did not show any significant
326 temporal trend ($p > 0.05$) for the same time period (data not shown). Among the eight
327 severe drought events registered since 1901, the 1986 drought was the most severe,
328 being characterized by mean SPEI_{annual} values of -0.68 (Rasnov), -0.83 (Codlea), and -
329 0.74 (the other sites). Additionally, 2000 (mean SPEI_{annual} value of -0.67) was the
330 second driest year in Rasnov, while 2011 was the second driest year in Codlea (mean
331 SPEI_{annual} value of -0.56) and at the other sites (mean SPEI_{annual} value of -0.57).

332

333 **3.2 Mortality and severe drought events**

334 Tree mortality occurred between 2001 and 2015 for silver fir, between 2000 and 2014
335 for black pine, and between 1990 and 2015 for Scots pine, with a peak of mortality in
336 2012 for all three species (Fig. 2). High mortality was also registered in 2013, but only
337 for silver fir and Scots pine (Fig. 2). A clear association was found between the
338 registered severe drought events and the years of death of silver fir ($\chi^2(1) = 22.48$, $p <$
339 0.001), black pine ($\chi^2(1) = 6.82$, $p < 0.05$), and Scots pine ($\chi^2(1) = 10.57$, $p < 0.01$)
340 trees.

341

342 **3.3 Growth (RW) trends**

343 According to the LME results, dead and living silver fir, black pine, and Scots pine trees
344 showed different RW trends (Table S1, Fig. 3). Specifically, dead silver fir trees showed
345 a significant negative RW trend, while living silver fir trees showed a significant
346 positive RW trend (Fig. 3). The results of the least-square means with a Tukey
347 correction further confirmed significant differences between the RW trends of dead and
348 living silver fir trees ($p < 0.001$). Black pine and Scots pine trees instead showed

349 significant negative RW trends independent of the vigour class (i.e., dead and living
350 trees) (Fig. 3). The results of the least-square means with a Tukey correction further
351 confirmed that there were no significant differences between the RW trends of the dead
352 and living black pine ($p = 0.999$) and Scots pine trees ($p = 0.879$).

353

354 **3.4 Climate-growth relationships**

355 Overall, silver fir (Fig. S1) showed a strong negative growth response to the previous
356 year summer and autumn temperature (i.e., July (t-1), August (t-1), and September (t-1))
357 and a positive growth response to precipitation during July (t-1) and August (t-1).
358 Instead, during the late autumn and winter period (i.e., from November (t-1) to February
359 (t)), the growth response of silver fir to temperature was constantly positive. This
360 positive growth response to temperature continued until spring (i.e., March (t)), when a
361 positive growth response was also found with precipitation (i.e., March (t) and April
362 (t)). Silver fir growth response to May (t) temperature was negative, while responses to
363 May (t) and July (t) precipitation were positive.

364

365 Black pine (Fig. S1) also showed a negative growth response to the previous year
366 summer and autumn temperature (i.e., August (t-1) and September (t-1)) and a positive
367 growth response to precipitation for the same period. During winter (i.e., December (t-
368 1) to February (t)), its response to temperature was also positive and remained positive
369 until March (t). Nevertheless, most of the climate-growth relationships of black pine
370 concentrated during the spring and summer seasons (i.e., from April (t) to August(t)),
371 when this species responded positively to precipitation. Negative climate-growth
372 relationships were found for temperature in May (t) and August (t).

373

374 The climate-growth relationships of Scots pine (Fig. S1) concentrated mainly during
375 spring and summer of the growth year. Specifically, growth of Scots pine responded
376 positively to precipitation from March (t) to July (t). Growth responses to temperature
377 were spread over the previous-to-growth and growth years: positive (December (t-1),
378 February (t), and March (t)) and negative (April (t), May (t), and August (t-1)).

379

380 **3.5 Components of resilience**

381 No significant differences were found between the native silver fir and the two
382 introduced pine (i.e., black pine and Scots pine) species in terms of resistance (Rt)
383 (Table 2, Fig. 4). In terms of recovery (Rc), only one marginally significant ($p < 0.1$)
384 difference was found between silver fir and black pine (Table 2, Fig. 4), with silver fir
385 showing a better recovery than black pine. In terms of resilience (Rs) instead, silver fir
386 differed statistically significant from black pine ($p < 0.05$; Table 2, Fig. 4) and
387 marginally significant from Scots pine ($p < 0.1$; Table 2, Fig. 4). In both cases, silver fir
388 showed higher resilience than the two pine species. No significant differences were
389 found between black pine and Scots pine in terms of Rt, Rc, and Rs (Table 2, Fig. 4).

390

391 **3.6 Regeneration**

392 The native silver fir showed relatively high regeneration rates (Fig. 5A). Nevertheless,
393 black pine and Scots pine species showed either no regeneration (Fig. 5B) or very low
394 regeneration rates (Fig. 5C). The rest of the species that regenerated under silver fir,
395 black pine and Scots pine *reference trees* were mainly native broadleaves and shrubs.
396 Specifically, species such as *Fagus sylvatica* L., *Fraxinus ornus* L., or *Fraxinus*
397 *excelsior* L. predominated among the broadleaf tree species. Species such as *Crataegus*
398 *monogyna* L. or *Sambucus nigra* L. predominated among the shrub species (Fig. 5).

399 Nevertheless, the diversity of broadleaves and shrubs that regenerated under silver fir
400 *reference trees* was low compared with the diversity of broadleaves and shrubs that
401 regenerated under black pine and Scots pine *reference trees* (Fig. 5).

402

403 4. DISCUSSION

404 We studied one native (i.e., silver fir) and two introduced (i.e., black pine and Scots
405 pine) conifer species affected by high drought-associated mortality events that peaked in
406 2012. These mortality events, registered in the Braşov region, have been previously
407 reported by Curiel Yuste et al. (2019) and are in line with global trends of forest decline
408 and mortality events following severe droughts and heat-waves (Allen et al., 2010,
409 2015; Hartmann et al. 2018). Indeed, the peak of mortality registered in 2012 followed a
410 succession of years characterized by droughts and heat-waves (2010, 2011, and 2012;
411 Barriopedro et al., 2011; Ionita et al., 2016; Marcu & Borz, 2013; Sidor et al., 2019).
412 Nevertheless, to the best of our knowledge, this is the first study in the Romanian
413 Carpathians that compares native with introduced tree species in terms of mortality
414 events, growth trends, growth resilience to severe drought events, climate-growth
415 relationships, and regeneration patterns. As both introduced pine species register high
416 mortality events, significant negative growth trends among the living trees, low
417 resilience, as well as no regeneration, we suggest that we might be witnessing a process
418 of ecological succession through which native broadleaves are recovering their habitats
419 (Ruiz-Benito et al., 2016). The observed increase in broadleaves at the expense of
420 conifers in temperate forests (Alfaro Reyna et al., 2018) might be therefore, at least
421 partially explained by the fact that many native broadleaves have been replaced in the
422 past with introduced conifer species (McGrath et al., 2015; Bonan, 2016; Naudts et al.,
423 2016). Thus, it becomes evident that understanding the role of legacies of past forest

424 management on current forest growth, resilience, and seedlings establishment could
425 help us better explain climate-associated impacts on forests (Gimmi et al., 2010;
426 Camarero et al., 2011; Vilà-Cabrera et al., 2011; Sánchez-Salguero et al., 2013;
427 Munteanu et al., 2016; Perring et al., 2018).

428

429 Black pine and Scots pine showed significant negative growth trends for both dead and
430 living trees. Silver fir instead showed a significant negative growth trend for the dead
431 trees and a significant positive trend for the living trees (Fig. 3). This indicates that
432 living black pine and Scots pine trees might not be healthy and that they might face a
433 higher risk to succumb to death in the coming years (Cailleret et al., 2017), while silver
434 fir seems to undergo a self-thinning process. The significant negative growth trends of
435 the living black pine and Scots pine trees might be explained by the fact that these two
436 introduced species showed a high sensitivity to drought. Indeed, both pine species
437 showed a common and strong response to spring and summer precipitation during the
438 growth year (t), indicating their dependence on this climatic variable. These results are
439 in agreement with Bouriaud & Popa (2009) and Sánchez-Salguero et al. (2013) who
440 also showed that Scots pine and black pine, respectively, largely depend on
441 precipitation during the growth year. Silver fir growth also showed dependence on the
442 previous-to-growth ($t-1$) summer precipitation (i.e., when temperature had a strong
443 negative effect) and on the spring and summer precipitation of the growth year (t),
444 otherwise forming extremely narrow tree rings (Gazol et al. 2015). However, this spring
445 and summer drought sensitivity gets compensated by the strong positive responses to
446 winter and early spring temperatures, as previously found for silver fir (Popa, 2003;
447 Kern & Popa, 2007; Bouriaud & Popa, 2009; Gazol et al., 2015). Thus, it seems that
448 silver fir might benefit from the significant increase of temperature (Gazol et al., 2015)

449 at least on the short- to medium-term. All these results may be further explained by
450 factors such as elevation (Barbu & Barbu, 2005), although this local contingency of
451 climate-growth relationships may also be related to legacies of past forest management
452 (Gazol et al., 2015). In spite of their different elevations, all species responded
453 negatively to May (t) temperatures. For Scots pine, such negative responses were also
454 found with April (t) and August (t) temperatures, results that are in line with those
455 found by Sidor et al. (2019) who reports that warm conditions from April to August
456 may reduce Scots pine growth and trigger its decline and mortality.

457

458 The high sensitivity to drought of the two introduced pine species is further supported
459 by the fact that they showed lower growth resilience to severe drought events than the
460 native silver fir. In line with these results, in a study that included Scots pine forests
461 across whole Romania, Sidor et al. (2019) also found that this conifer species has a low
462 capacity to recover pre-drought growth rates, and a low resilience. These results are of
463 outmost importance given that climatic models predict an increase in the severity,
464 frequency, and duration of heat-waves and droughts (Easterling et al., 2000; Schär et al.,
465 2004; IPCC, 2013). Reduced resilience to droughts has been further related to an
466 increased risk of mortality (DeSoto et al., 2020). Indeed, Scots pine has been found to
467 be more vulnerable to severe drought events, showing a reduced growth resilience when
468 growing at mid-elevation sites characterized by low productivity (Bose et al., 2020).

469

470 The significant negative growth trends of the living black pine and Scots pine trees
471 might also be explained by the fact that these species face non-optimal growth
472 conditions as they have been introduced at these sites. Legacies of past forest
473 management may be thus considered as a predisposing factor within the slow-decline

474 framework on tree mortality (Manion, 1991; Sánchez-Salguero et al., 2013). Indeed, for
475 black pine, it has been found that it performs much better in natural (i.e., less vulnerable
476 and more drought resilient) than in planted stands, even within its natural distribution
477 range (Sánchez-Salguero et al., 2013). Also, the resilience of Scots pine to drought
478 events largely depends on where it grows (i.e., the type of site) and on how it performs
479 in terms of growth during the pre-drought period (Bose et al., 2020). Although we
480 acknowledge that we did not directly analyse legacies of past forest management, we do
481 have indirect evidence regarding them through the regeneration survey.

482

483 Unlike the native silver fir, a very-shade tolerant species (Şofletea & Curtu, 2007) that
484 showed relatively high regeneration rates, both introduced black pine and Scots pine
485 species showed absent or very low regeneration rates (Fig. 5; Curiel Yuste et al., 2019).
486 Most of the species that regenerated well under silver fir, black pine, and Scots pine
487 *reference trees* are native broadleaves (e.g., *Fagus sylvatica* L., *Fraxinus ornus* L., or
488 *Fraxinus excelsior* L.) and shrubs (e.g., *Crataegus monogyna* L. or *Sambucus nigra* L.).
489 Nevertheless, their diversity is low under silver fir comparing with the high diversity of
490 species that sprouts and develops under black pine and Scots pine. At the silver fir sites,
491 *Fagus sylvatica* L. is the most abundant species in terms of regeneration, but this pattern
492 is not surprising as the natural distribution areas of those two species overlap (Şofletea
493 & Curtu, 2007). At the black pine and Scots pine sites instead, the native broadleaves
494 that regenerate are likely to be the local species, as both pine species have been planted
495 at sites naturally supporting broadleaves, which now seem to register a steady increase
496 of their advance regeneration (Zlatanov et al., 2010). Black pine and Scots pine
497 regeneration in plantations is known to be limited by the advance regeneration of native
498 broadleaves which outcompete pine seedlings (Zlatanov et al., 2010). Low regeneration

499 rates associated with high levels of decline and mortality have been previously reported
500 for black pine and Scots pine, interactions between structural and climatic factors being
501 also considered as a possible cause (Vilà-Cabrera et al., 2011; Rigling et al., 2013;
502 Ruiz-Beniro et al., 2016). All pine sites considered for this study are mainly located on
503 S-facing slopes, summer droughts being previously found to lead to high mortality rates
504 among pine seedlings growing on slopes with south exposure (Zlatanov et al., 2010).
505 Finally, both black pine and Scots pine are light demanding species (Şofletea & Curtu,
506 2007), their regeneration in plantations largely depending on silvicultural interventions.
507

508 To conclude, the results of this study show that the naturally regenerated silver fir
509 growing within its natural distribution range performs better in terms of resilience and
510 regeneration rates than the two introduced black pine and Scots pine species growing
511 outside their natural distribution range. Although high mortality rates have been
512 registered for all three species, silver fir seems to undergo a self-thinning process, while
513 living black pine and Scots pine trees, given their significant negative growth trends,
514 might face a higher risk to succumb to death in the coming years. Indeed, and unlike
515 silver fir that showed dependence on spring and summer precipitations compensated by
516 winter and spring temperatures, black pine and Scots pine showed a high sensitivity to
517 drought. Moreover, the absent or very low regeneration rates of the two introduced pine
518 species and the high regeneration rates of native broadleaves suggest that we might be
519 witnessing a process of ecological succession, with broadleaves recovering their
520 habitats. Thus, the overall effect of the black pine and Scots pine mortality might be
521 compensated by native species, which seem to cope better with challenging climate
522 change conditions. Along with climate, legacies of past forest management should be
523 taken into account in order to better understand current responses of different tree

524 species to climate change as the decisions taken in the past affect the future of the
525 forests and the ecosystem services they provide.

526

527 **ACKNOWLEDGMENTS**

528 We thank the Forest District staff of Sacele, Kronstadt, Rasnov, Teliu, Codlea, and
529 Intorsura Buzaului for all their support and for giving us access to the Forest
530 Management Plans. This work was financed by the NATivE (PN-III-P1-1.1-PD-2016-
531 0583) and TreeMoris (PN-II-RU-TE-2014-4-0791) projects through UEFISCDI ([link](#);
532 Romanian Ministry of Education and Research) and supported by the BERC 2018-2021
533 (Basque Government), and BC3 María de Maeztu Excellence Accreditation 2018-2022,
534 Ref. MDM-2017-0714 (Spanish Ministry of Science, Innovation and Universities). We
535 also thank Antonio Gazol for interesting discussions on the study and Ionela-Mirela
536 Medrea, Andrei Apafaiian, Maria Băluț, and Florin Dinulică for assistance during field
537 and laboratory campaigns. Silver fir, black pine, and Scots pine figures included in the
538 graphical abstract are reproduced with the authorization of the designer Luiza Anamaria
539 Pop (©2020) who drew the three conifer species and processed the drawings in Adobe
540 Illustrator® CS5 (v. 15.0.0).

541

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750

1 **Figure captions:**

- 2 **Fig. 1.** Location of the nine study sites in the Braşov region (Romanian Carpathians): silver fir (Dambu Morii, Kronstadt, and Rasnov; empty
3 triangles), black pine (Schei, Lempes, and Racadau; empty squares), and Scots pine (Codlea, Lempes, and Teliu; empty diamonds). The location
4 of the meteorological stations Ghimbav (534 m a.s.l.) and Predeal (1093 m a.s.l.) is also given (North star symbol). The location of the city of
5 Braşov (simple star symbol) is shown as a reference.
- 6 **Fig. 2.** Mortality rates of silver fir, black pine, and Scots pine. The number of dead trees per species were summed across their three sites (Table
7 1). The 1990-2015 SPEI_{annual} (Standardized Precipitation-Evapotranspiration Index) trends are also shown. The diamond black symbol indicates
8 the 2011 severe drought event.
- 9 **Fig. 3.** Results of the linear mixed-effects model (LME) showing the growth (i.e., ring-width, RW) trends of dead and living silver fir, black
10 pine, and Scots pine trees. For ease of interpretation, the results of the LME (for which $\log(RW+1)$ was used as a response variable) were
11 backtransformed to the original scale (i.e., RW).
- 12 **Fig. 4.** Results of the generalized least squares models (GLS), followed by least-square means based on Tukey HSD tests, showing differences
13 between tree species in terms of resistance (Rt), recovery (Rc), and resilience (Rs). Different letters indicate significant ($p < 0.05$) or marginally
14 significant ($p < 0.1$; marked with *) differences between species (i.e., silver fir, black pine, and Scots pine).

- 15 **Fig. 5.** Regeneration (i.e., number of trees) of different tree and shrub species under silver fir (A), black pine (B), and Scots pine (C) reference
- 16 trees: **Aa** = *Abies alba* Mill.; **Fs** = *Fagus sylvatica* L.; **Cb** = *Carpinus betulus* L.; **Pa** = *Picea abies* Karst.; **Sorbus** = *Sorbus* sp. L.; **Ca** = *Corylus*
- 17 *avellana* L.; **Sn** = *Sambucus nigra* L.; **Crm** = *Crataegus monogyna* L.; **Tb** = *Taxus baccata* L.; **Rc** = *Rosa canina* L.; **Lonicera** = *Lonicera* sp. L.;
- 18 **Pn** = *Pinus nigra* Arn.; **Qr** = *Quercus robur* L.; **Tilia** = *Tilia* sp. L.; **Ap** = *Acer pseudoplatanus* L.; **Ac** = *Acer campestre* L.; **Pc** = *Prunus*
- 19 *cerasifera* Ehrh.; **Jr** = *Juglans regia* L.; **Ulmus** = *Ulmus* sp. L.; **PrAv** = *Prunus avium* L.; **Lv** = *Ligustrum vulgare* L.; **Cs** = *Cornus sanguinea* L.;
- 20 **Euonymus** = *Euonymus* sp. L.; **Sv** = *Syringa vulgaris* L.; **Fe** = *Fraxinus excelsior* L.; **AcPI** = *Acer platanoides* L.; **Qp** = *Quercus petraea* (Matt.)
- 21 Liebl.; **Rubus** = *Rubus* sp. L.; **Vo** = *Viburnum opulus* L.; **Salix** = *Salix* sp. L.; **Vl** = *Viburnum lantana* L.; **Cm** = *Cornus mas* L.; **Fo** = *Fraxinus*
- 22 *ornus* L.; **Ps** = *Pinus sylvestris* L.; **Pp** = *Pyrus pyraeaster* L.; **Pt** = *Populus tremula* L.

Table 1. Main characteristics of the dead and living silver fir, black pine, and Scots pine trees from the nine study sites.

Species	Site (elevation)	Vigour class	No. of trees	Corr. with Master	DBH (cm)	Height (m)	Age (years)	Growth period	RW (mm)	CI _{Hegyvi}
silver fir	Dambu Morii (825 m a.s.l.)	dead	28	0.619	51.73 ^a (12.73)	25 ^a (5.98)	139 ^a (29.06)	1901- 2015	1.69 ^a (0.44)	0.48 ^a (0.31)
		living	27	0.634	54.04 ^a (9.16)	30 ^b (3.56)	133 ^a (31.34)	1901- 2015	1.88 ^a (0.67)	0.42 ^a (0.30)
	Kronstadt (945 m a.s.l.)	dead	28	0.685	49.16 ^a (9.17)	30 ^a (4.71)	150 ^a (10.99)	1901- 2015	1.40 ^a (0.43)	0.63 ^a (0.41)
		living	29	0.692	51.02 ^a (7.61)	31 ^a (4.27)	155 ^a (11.41)	1901- 2015	1.44 ^a (0.30)	0.59 ^a (0.47)
	Rasnov (1250 m a.s.l.)	dead	22	0.573	53.61 ^a (7.48)	27 ^a (7.89)	187 ^a (48.62)	1901- 2013	1.32 ^a (0.65)	0.52 ^a (0.33)
		living	28	0.570	54.29 ^a (10.01)	32 ^b (5.25)	161 ^a (55.87)	1901- 2015	1.78 ^b (0.45)	0.45 ^a (0.26)
black pine	Schei (456 m a.s.l.)	dead	15	0.674	43.50 ^a (7.47)	24 ^a (4.22)	98 ^a (4.27)	1929- 2012	1.26 ^a (0.53)	1.03 ^a (0.51)
		living	21	0.690	45.21 ^a (6.11)	27 ^a (3.40)	103 ^b (3.40)	1928- 2015	1.19 ^a (0.51)	0.88 ^a (0.42)
	Lempes (561 m a.s.l.)	dead	18	0.689	36.69 ^a (7.06)	23 ^a (3.96)	98 ^a (5.83)	1927- 2012	1.10 ^a (0.45)	1.17 ^a (0.60)
		living	27	0.741	40.56 ^a (5.17)	24 ^a (3.76)	105 ^b (3.15)	1927- 2015	1.22 ^a (0.49)	1.13 ^a (0.44)
	Racadau (753 m a.s.l.)	dead	21	0.660	38.29 ^a (6.40)	23 ^a (4.35)	92 ^a (14.88)	1927- 2014	1.15 ^a (0.50)	1.09 ^a (0.80)
		living	23	0.698	40.50 ^a (5.31)	25 ^a (3.90)	99 ^a (8.55)	1927- 2015	1.17 ^a (0.49)	1.14 ^a (0.63)

Scots pine	Codlea (712 m a.s.l.)	dead	24	0.579	42.96 ^a (7.62)	21 ^a (6.68)	114 ^a (10.54)	1904-2015	1.19 ^a (0.58)	0.73 ^a (0.46)
		living	30	0.618	47.38 ^b (8.88)	26 ^b (6.73)	117 ^a (10.52)	1905-2015	1.40 ^b (0.70)	0.74 ^a (0.42)
	Lempes (545 m a.s.l.)	dead	22	0.678	37.50 ^a (5.69)	21 ^a (5.78)	108 ^a (5.55)	1921-2014	1.12 ^a (0.52)	0.65 ^a (0.46)
		living	25	0.695	37.34 ^a (6.63)	20 ^a (6.87)	109 ^a (7.08)	1921-2015	1.08 ^a (0.49)	0.59 ^a (0.37)
	Teliu (606 m a.s.l.)	dead	25	0.664	38.44 ^a (6.30)	24 ^a (3.74)	110 ^a (5.11)	1915-2014	1.06 ^a (0.50)	1.28 ^a (0.71)
		living	26	0.686	42.69 ^b (4.41)	26 ^b (3.50)	117 ^b (3.31)	1915-2015	1.19 ^b (0.47)	1.11 ^a (0.51)

25 Values in brackets represent standard deviations; **Corr. with Master**, correlation with the master dating series (COFECHA); **DBH**, mean

26 diameter at breast height; **height**, the height of the trees; **Age**, mean cambial age (i.e., total number of tree rings at 1.3 m above ground),

27 including the first 20 years; **Growth period**, period after removing the first 20 years of growth (cf. Section 2.4); **RW**, mean ring-width; **CI_{Hegy}**,

28 competition index. Different letters indicate significant differences ($p < 0.05$) between dead and living trees from the same site in terms of DBH,

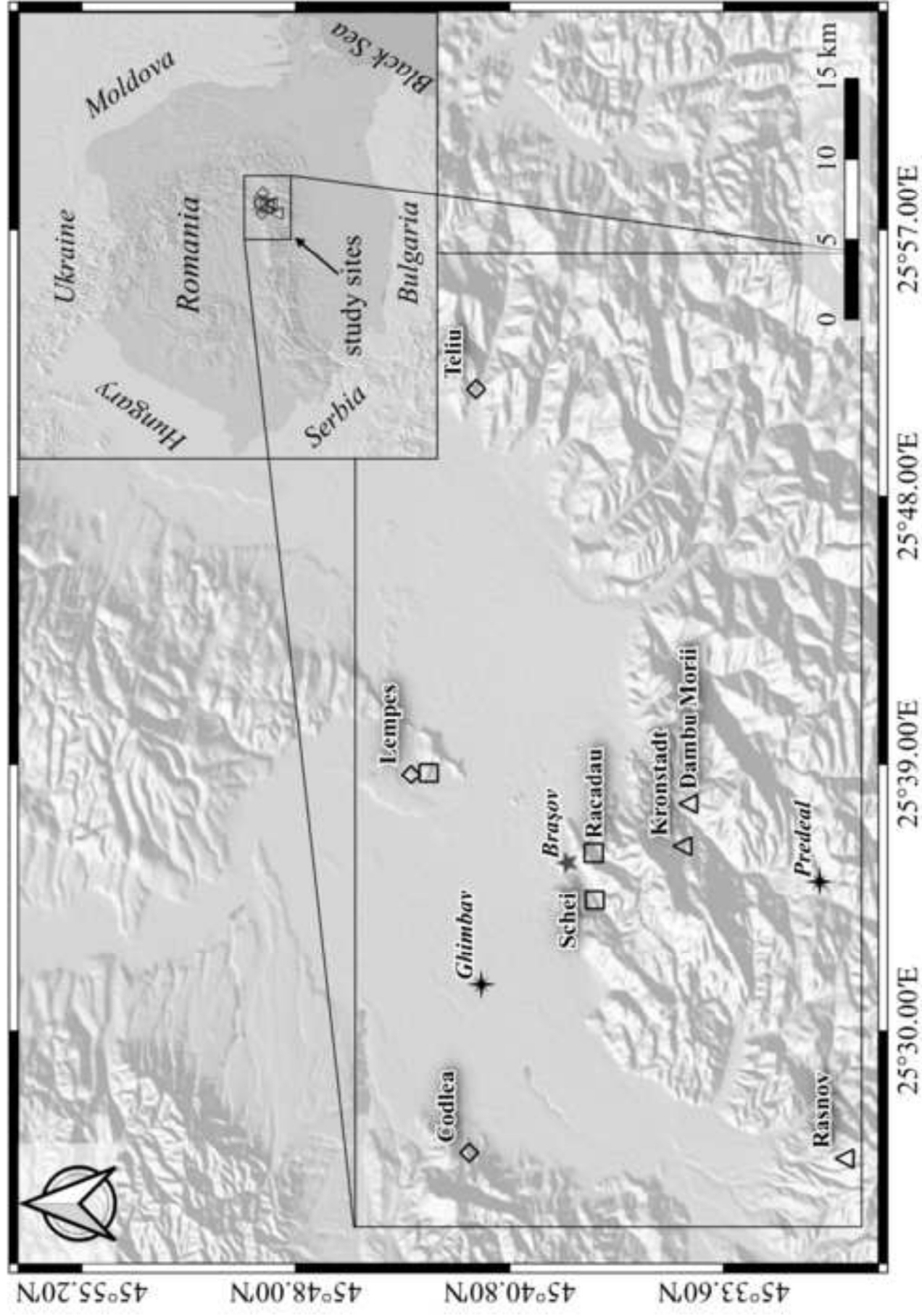
29 height, age, RW, and CI_{Hegy}.

31 **Table 2.** Summary of the generalized least squares models (GLS), followed by least-square means based on Tukey HSD tests, showing
32 differences between tree species in terms of resistance (Rt), recovery (Rc), and resilience (Rs). The contrasts between species are shown together
33 with their estimates, associated standard errors (SE), t-statistic, and p-values. Significant ($p < 0.05$) and marginally significant ($p < 0.1$)
34 differences between species are marked in bold.

GLS	Contrast	estimate	SE	t-ratio	p-value
Rt	silver fir – black pine	0.017	0.07	0.248	0.97
	silver fir – Scots pine	0.049	0.07	0.700	0.76
	black pine – Scots pine	0.032	0.07	0.452	0.89
Rc	silver fir – black pine	0.143	0.07	2.147	0.09
	silver fir – Scots pine	0.107	0.07	1.610	0.25
	black pine – Scots pine	-0.036	0.07	-0.537	0.85
Rs	silver fir – black pine	0.195	0.07	2.840	<0.05
	silver fir – Scots pine	0.151	0.07	2.204	0.08
	black pine – Scots pine	-0.044	0.07	-0.636	0.80

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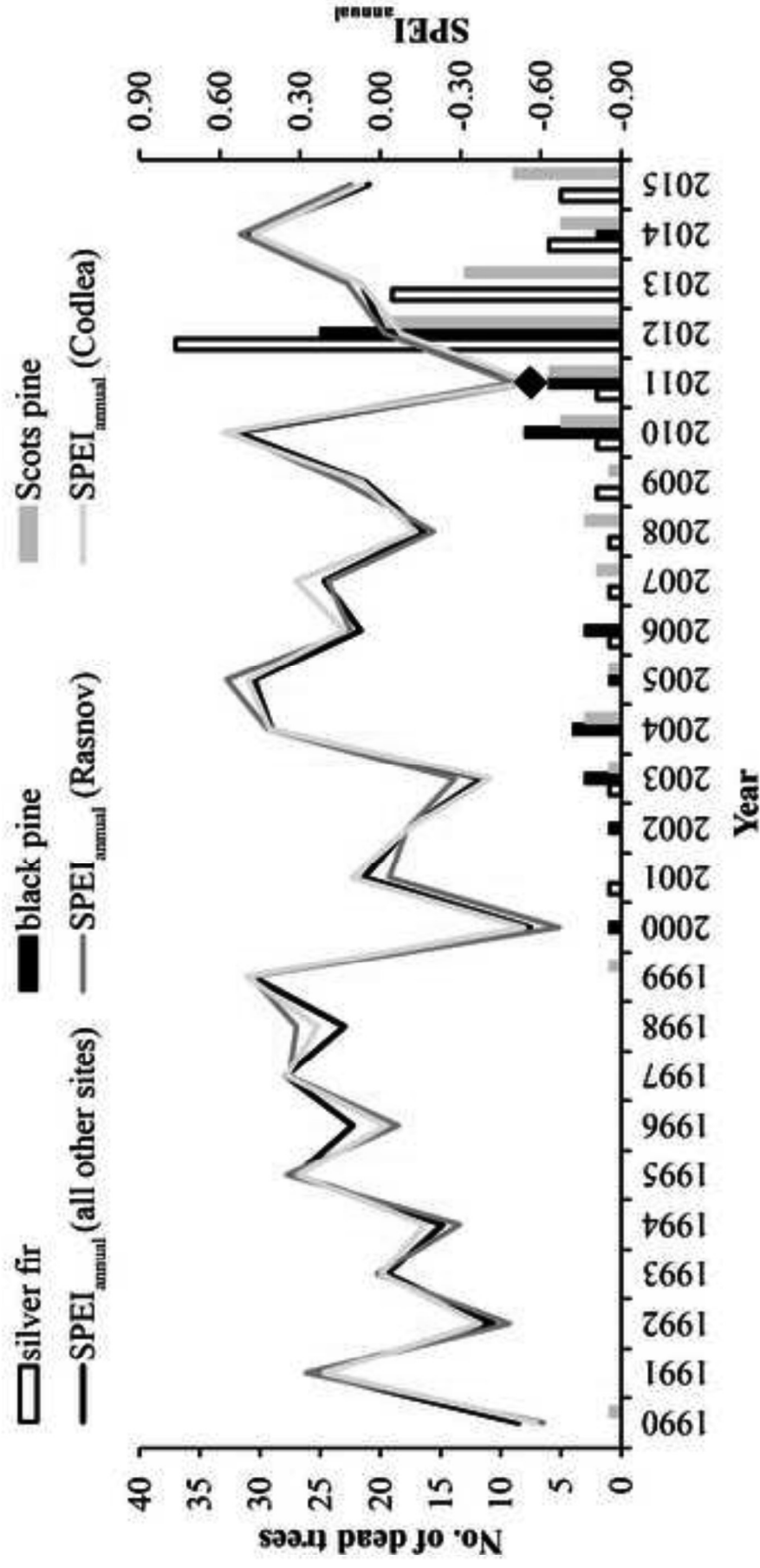


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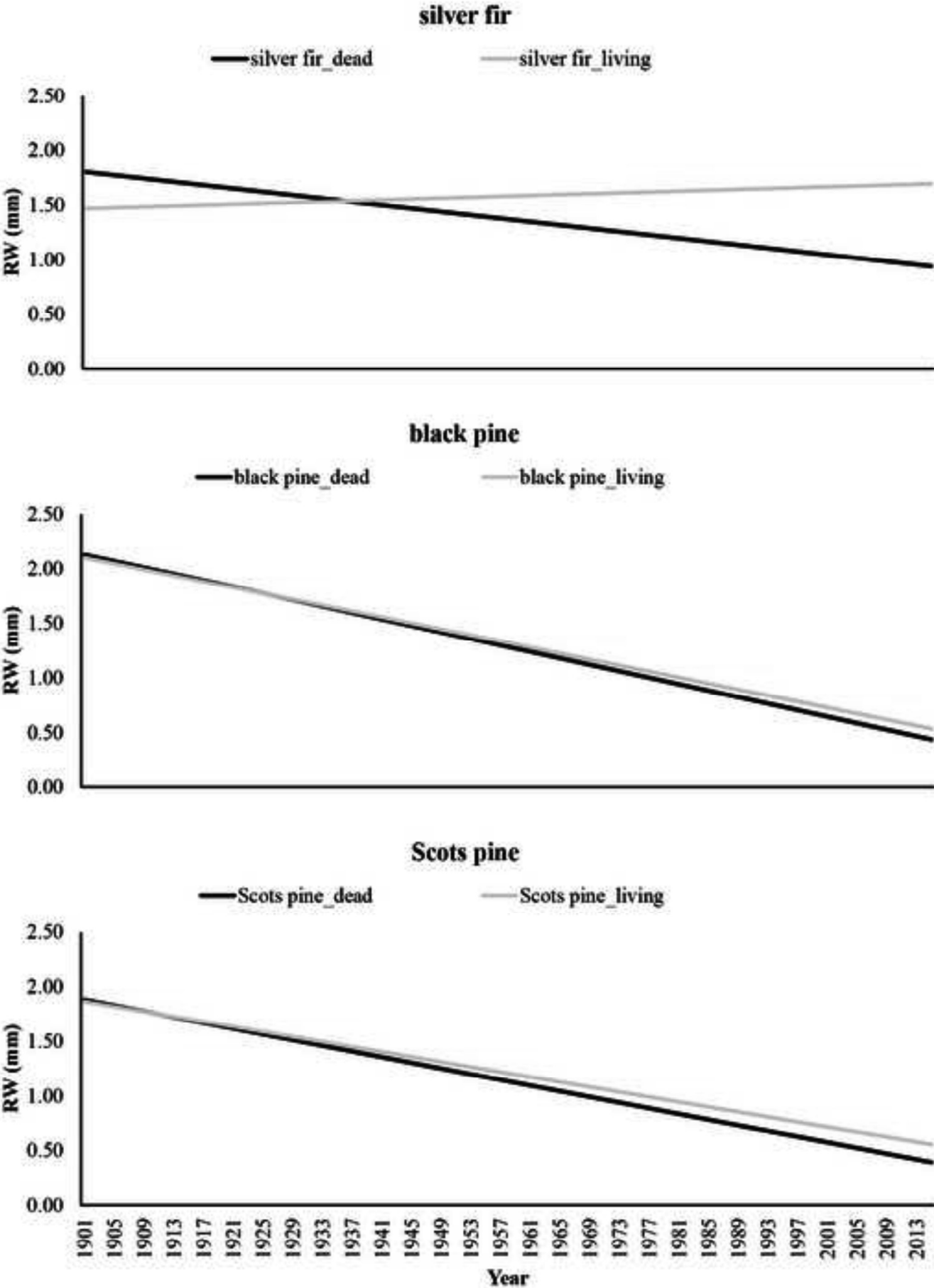


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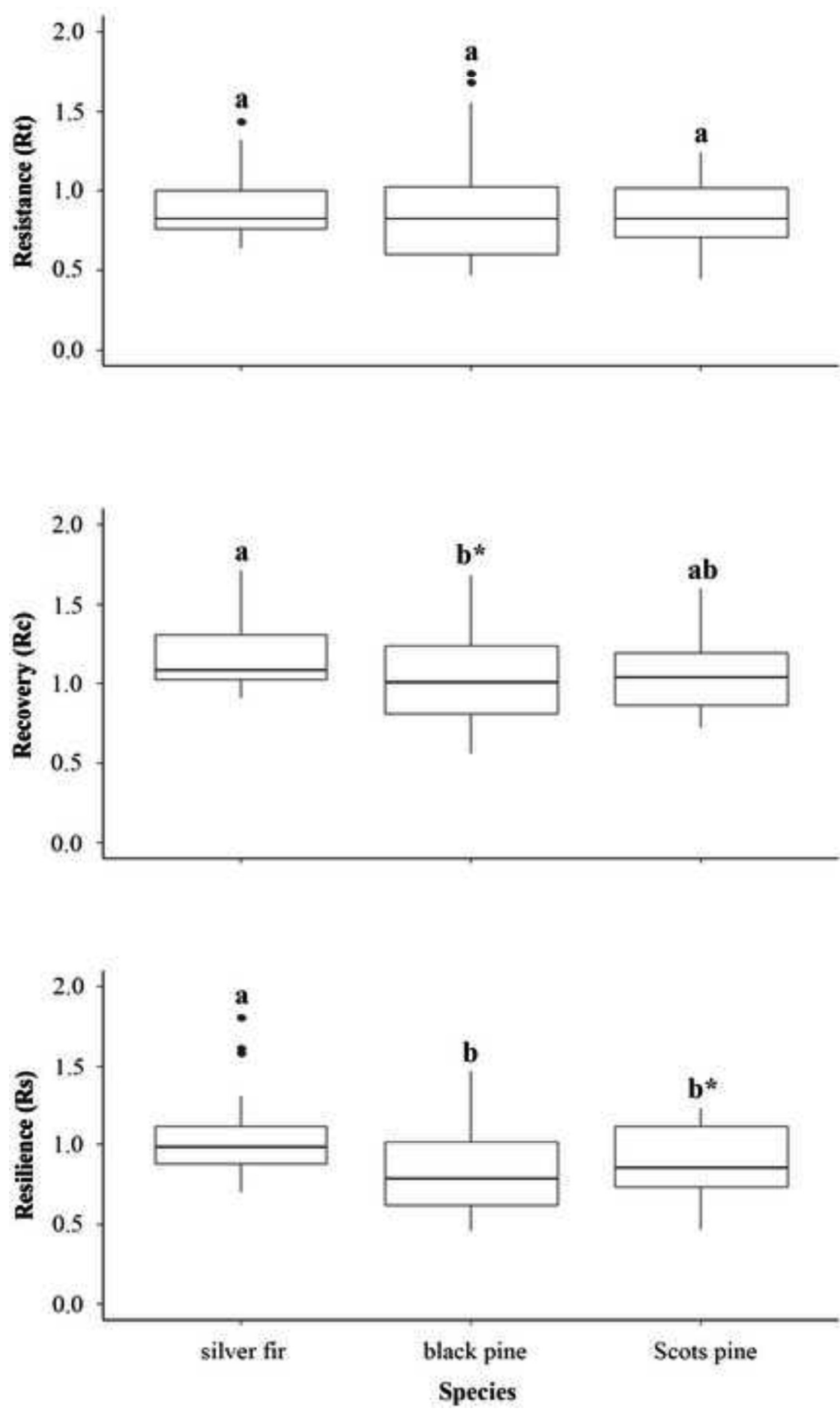


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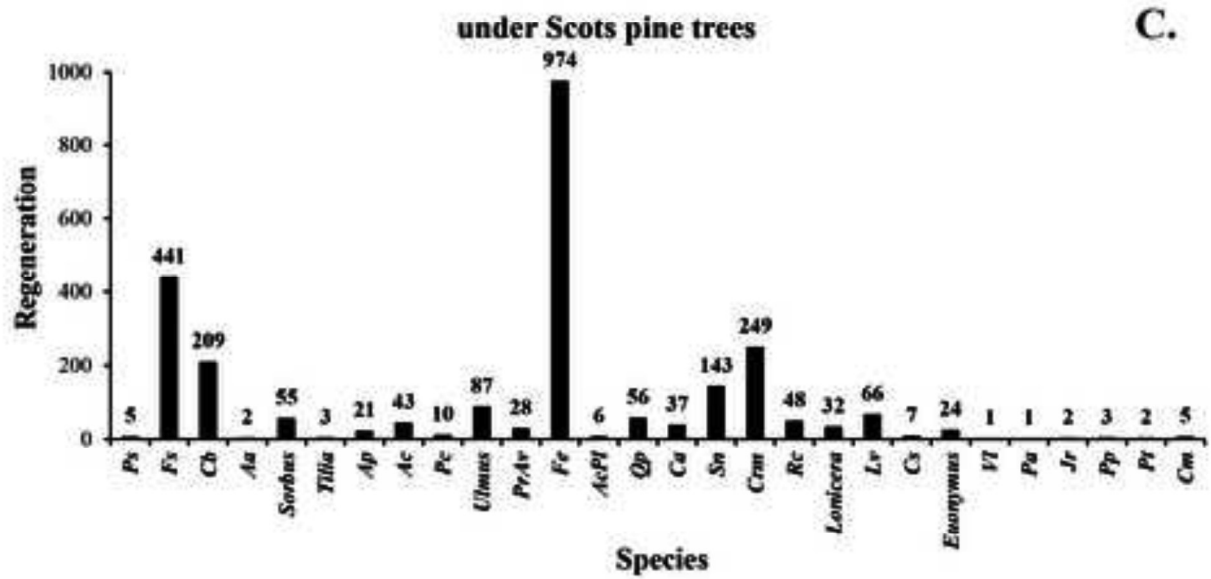
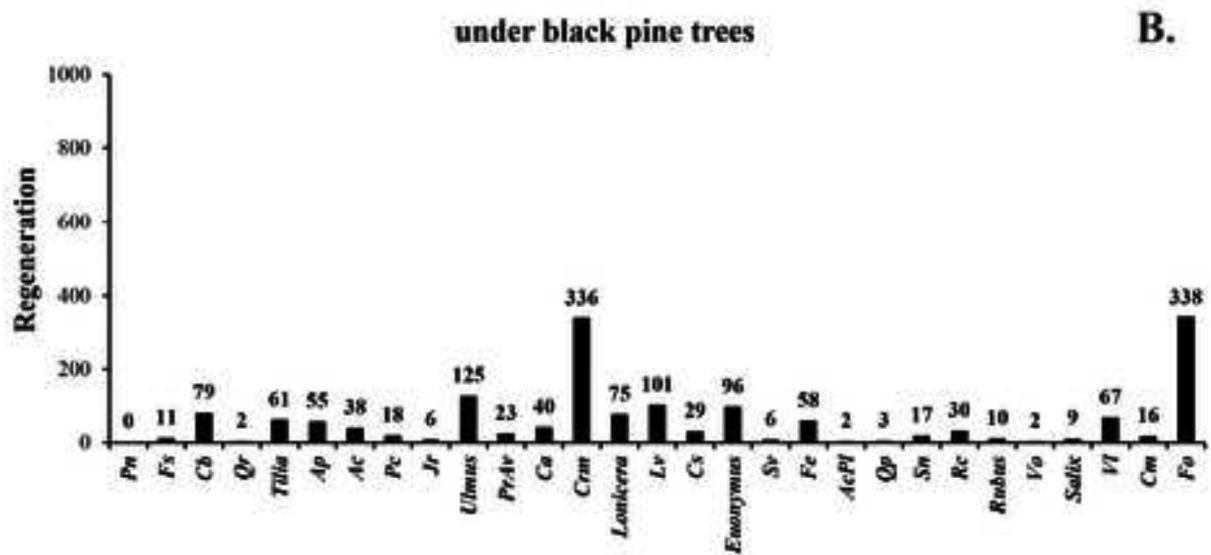
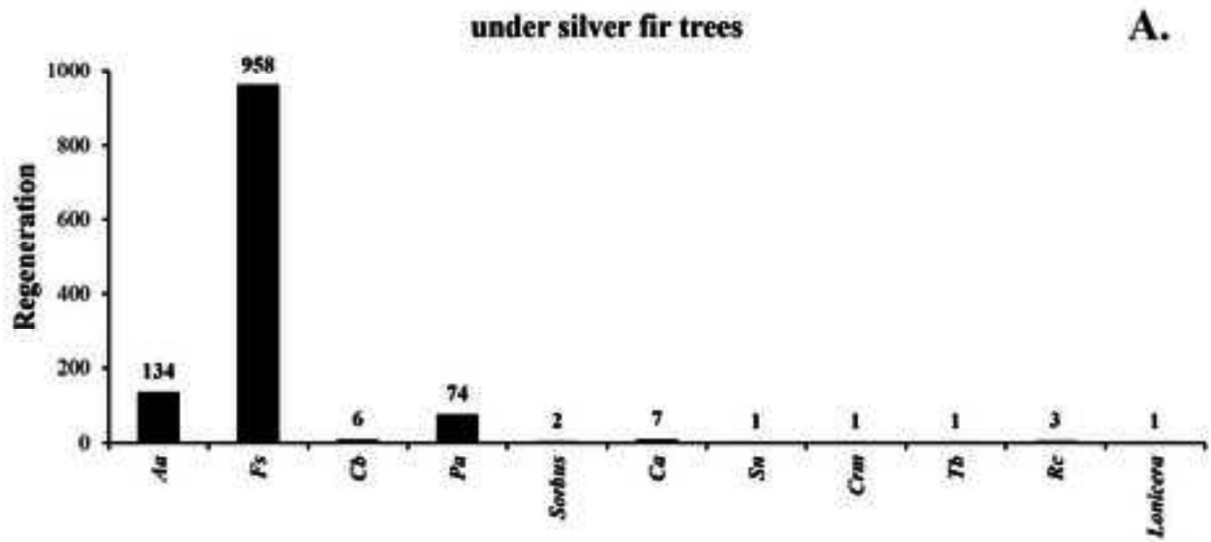
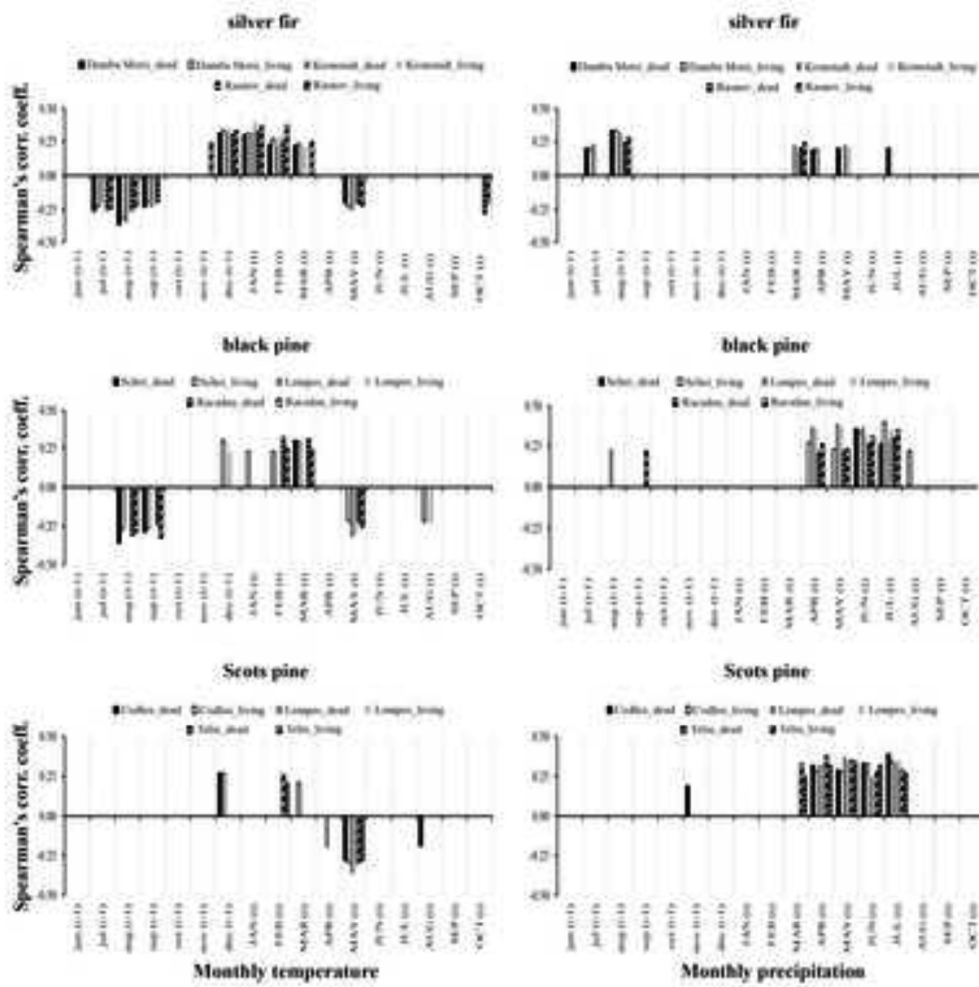


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AUTORS' CONTRIBUTIONS

A.-M. Hereş, J. Curiel Yuste, and I.C. Petritan conceived the ideas and designed the methodology; I.C. Petritan and A.-M. Petritan measured the tree-rings and compiled the final ring-width database; A.-M. Hereş and J.M. Polanco-Martínez performed statistical analyses; A.-M. Hereş drafted and led the manuscript writing and revision with continuous inputs from all authors J. Curiel Yuste, J.M. Polanco-Martínez, I.C. Petritan, C. Bigler, A. Rigling, A. L. Curtu, A.-M. Petritan, and Ş. Petrea. All authors agreed with the final version of the manuscript.

*Declaration of Interest Statement

The authors (A.-M. Hereş, I. C. Petritan, C. Bigler, A. L. Curtu, Ş. Petrea, A.-M. Petritan, J.M. Polanco-Martínez, A. Rigling, J. Curiel Yuste) of the manuscript titled “*Legacies of past forest management determine current responses to severe drought events of conifer species in the Romanian Carpathians*” declare no conflict of interest.