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RESEARCH ARTICLE

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Disturbance history is a key driver of tree life span in temperate primary forests

Jakob Pavlin[1] | Thomas A. Nagel[1,2] | Marek Svitok[3,4] | Joseph L. Pettit[1] | Krešimir Begović[1] | Stjepan Mikac[5] | Abdulla Dikku[6] | Elvin Toromani[7] | Momchil Panayotov[8] | Tzvetan Zlatanov[9] | Ovidiu Haruta[10] | Sorin Dorog[10] | Oleh Chaskovskyy[11] | Martin Mikoláš[1] | Pavel Janda[1] | Michal Frankovič[1] | Ruffy Rodrigo[1] | Ondřej Vostarek[1] | Michal Synek[1] | Martin Dušátko[1] | Tomáš Knížr[1] | Daniel Kozák[1] | Ondrej Kameniar[1] | Radek Bače[1] | Vojtěch Čada[1] | Volodymyr Trotsiuk[1,12,13] | Jonathan S. Schurman[1] | Mélanie Saulnier[1,14] | Arne Buechling[1] | Miroslav Svoboda[1]

[1]Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

[2]Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

[3]Department of Biology and General Ecology, Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, Zvolen, Slovakia

[4]Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic

[5]Department of Forest Ecology and Silviculture, Faculty of Forestry, University of Zagreb, Zagreb, Croatia

[6]PSEDA-ILIRIA Organization, Tirana, Albania

[7]Faculty of Forestry Sciences, Agricultural University of Tirana, Koder-Kamez, Albania

[8]Department of Dendrology, University of Forestry Sofia, Sofia, Bulgaria

[9]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria

[10]Forestry and Forest Engineering Department, University of Oradea, Oradea, Romania

[11]Institute of Forest Management, Ukrainian National Forestry University, Lviv, Ukraine

[12]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

[13]Department of Environmental Systems Science, Institute of Agricultural Sciences, ETH Zurich, Zurich, Switzerland

[14]Centre National de la Recherche Scientifique/French National Centre for Scientific Research, UMR 5602 Laboratoire Géode, Aix-Marseille University, Aix-en-Provence, France

Correspondence
Jakob Pavlin, Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcka 129, 165 21 Prague, Czech Republic.
Email: pavlinj@fld.czu.cz

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Abstract

Aims: We examined differences in life span among the dominant tree species (spruce, *Picea abies*; fir, *Abies alba*; beech, *Fagus sylvatica*; and maple, *Acer pseudoplatanus)* across primary mountain forests of Europe. We asked how disturbance history, life-time growth patterns, and environmental factors influence life span.

Locations: Balkan Mountains, Carpathian Mountains, Dinaric Mountains.

Methods: Annual ring widths from 20,600 cores from primary forests were used to estimate tree life spans, growth trends, and disturbance history metrics. Mixed models were used to examine species-specific differences in life span (i.e., defined as species-specific 90th percentiles of age distributions), and how metrics of radial

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growth, disturbance parameters, and selected environmental factors influence life span.

Results: While only a few beech trees surpassed 500 years, individuals of all four species were older than 400 years. There were significant differences in life span among the four species (beech > fir > spruce > maple), indicating life history differentiation in life span. Trees were less likely to reach old age in areas affected by more severe disturbance events, whereas individuals that experienced periods of slow growth and multiple episodes of suppression and release were more likely to reach old age. Aside from a weak but significant negative effect of vegetation season temperature on fir and maple life span, no other environmental factors included in the analysis influenced life span.

Conclusions: Our results indicate species-specific biological differences in life span, which may play a role in facilitating tree species coexistence in mixed temperate forests. Finally, natural disturbance regimes were a key driver of life span, which could have implications for forest dynamics if regimes shift under global change.

KEYWORDS

Disturbance, European beech, growth patterns, life span, longevity, Norway spruce, silver fir, site conditions, sycamore maple

1 | INTRODUCTION

Tree life span plays an important role in the structure and function of forest ecosystems. As a key life history trait, differences in the life span of competing species may contribute to tree coexistence in a variety of forest communities (Veblen, 1986; Lertzman, 1995; Lusk & Smith, 1998; Loehle, 2000). Tree life span also has important implications for carbon sequestration and residence time, particularly within the context of global change, whereby faster growth rates and tree turnover may shorten tree life span, thereby reducing long-term carbon storage in forests (Bugmann & Bigler, 2011; Körner, 2017; Büntgen et al., 2019; Martin-Benito et al., 2021). Finally, trees that approach their maximum longevity develop unique morphological characteristics and microhabitats (Van Pelt, 2007), features that provide important habitat for a variety of forest-dwelling species (Fritz & Heilmann-Clausen, 2010; Lindenmayer & Laurance, 2017).

Despite the fundamental importance of tree life span, determining whether there are biological differences in the life span of competing tree species in many forest communities remains a challenge. For example, among the common tree flora of the European temperate region, the widely accepted literature indicates that beech (*Fagus sylvatica* L.) and fir (*Abies alba* Mill.) are among the most long-lived species (e.g., 450 year maximum age), while maple (*Acer pseudoplatanus* L.) and spruce (*Picea abies* (L.) H.Karst.) are classified as moderately long-lived (e.g., 300 years) (Leuschner & Ellenberg, 2017; Leuschner & Meier, 2018). However, a number of site-specific studies carried out in old-growth remnants throughout temperate mountain forests in Europe often find individual stems that exceed these longevities (Biondi, 1992; Bigler & Veblen, 2009; Motta et al., 2011; Nagel et al., 2014; Di Filippo et al., 2015; Di Filippo et al., 2017; Piovesan et al., 2019).

In addition to species-specific life history, elucidating the drivers of life span within and among tree species has also proved challenging. A relatively large body of tree ring research has examined the longstanding hypothesized tradeoff between tree growth rates and life span (Schulman, 1954). Across multiple tree taxa spanning a range of shade tolerances, past work has generally documented a consistent negative relationship between radial growth rates and life span within species for both live (Black et al., 2008; Johnson & Abrams, 2009; Di Filippo et al., 2012; Castagneri et al., 2013; Di Filippo et al., 2015; Brienen et al., 2020) and dead trees (Bigler & Veblen, 2009; Rötheli et al., 2012; Bigler, 2016; Büntgen et al., 2019) In particular, many studies highlight that maximum tree ages are reached when trees experience a long period of suppressed growth during early life stages. Other studies, however, have not found support for a tradeoff between radial growth rates and life span (Ireland et al., 2014; Cailleret et al., 2017).

As previous authors have pointed out, it is not entirely clear to what extent the relationship between growth rates and life span is regulated by species-specific life history, genetics, or environmental constraints (Büntgen et al., 2019). Several of the studies highlighted above show substantial variation in growth rates and life span among individual trees within a species at the same site, which likely reflects the unique growth history and resource availability of trees in a given neighborhood of competitors (Black et al., 2008; Bigler, 2016). The growth history of a tree is largely a function of local disturbance history, which controls the trajectory of canopy accession. This is especially the case in multi-aged forests where gap scale and

periodic intermediate severity disturbances drive stand dynamics (Frelich & Lorimer, 1991; Nagel et al., 2014). In such forests, trees that avoid suppression, grow fast as juveniles and reach large canopy stature quickly, may be more likely to die early because residing in the canopy increases exposure to common disturbance agents (Di Filippo et al., 2015; Bigler, 2016). While it is generally assumed that trees will reach old ages on less productive sites sheltered from disturbance (Larson, 2001; Lanner, 2002; Di Filippo et al., 2015), few studies have quantified the relationship between local disturbance history and tree life span in multi-aged forests.

In addition to local constraints on growth regulated by stand dynamics, larger-scale environmental factors may also play a role in influencing life span within a species, such as climate and topography. Life span has been positively associated with north-facing slopes (Bigler & Veblen, 2009; Bigler, 2016), south-facing slopes on drier sites (Therrell & Stahle, 1998) slope steepness (Bigler, 2016), and elevation (Splechtna et al., 2000; Di Filippo et al., 2007; Di Filippo et al., 2012; Rötheli et al., 2012; Di Filippo et al., 2015), whereby harsher site conditions are thought to increase longevity via reduced growth rates. The link between temperature and life span is less clear; for broad-leaved species in the Northern Hemisphere, some late-successional shade-tolerant species (e.g., *Fagus* spp.) have been found to reach older ages in colder parts of their range, while this relationship was weak for shade-intolerant species (Di Filippo et al., 2015).

Previous work focusing on tree life span has often relied on data from the International Tree-Ring Data Bank (Black et al., 2008; Johnson & Abrams, 2009; Di Filippo et al., 2015; Brienen et al., 2020), in which the sampling objectives and strategy are not preserved in the metadata; in many cases, tree cores may have been subjectively sampled from large trees growing on extreme site conditions, or tree growth may have been influenced by past land use history. Other studies that have explicitly sampled live and dead trees to examine life span within species have often been limited to local sites (Larson, 2001) or regional scales (Bigler, 2016; Lorimer & Frelich, 1989), and do not permit assessment of environmental drivers at large scales or variation in life span across a species' range. Here, we take advantage of an unprecedented data set, consisting of plot-level forest structural data including randomly cored live trees (N = 20,600), sampled within extant primary-forest landscapes across the Carpathian Mountains and Balkan peninsula. The plot network covers the dominant mountain forest communities in Europe, spanning from beech to mixed beech–fir, to Norway spruce forest types. The data set allows a unique assessment of life span within and among tree species, across gradients of stand structure and disturbance history, and from local to subcontinental scales.

We ask if there are differences in life span among dominant tree species (i.e., spruce, fir, beech, and maple). We first find evidence that species-specific differences in adult life span are partly controlled by life history. We then ask how variation in life span within species is influenced by a variety of different drivers, including local disturbance history, lifetime radial growth patterns, and environmental factors available in our data set (i.e., slope, aspect, temperature). If life span is under strong environmental control, we predict that older trees will be found on less productive sites, characterized by higher elevation, lower temperature, and steep north-facing slopes. Alternatively, if local disturbance history controls life span, we predict that old trees will be found in areas with a history of low-intensity disturbance (i.e., gap dynamics) that lack evidence of more severe disturbance over the past few centuries. Individual tree growth histories in such stands typically show long periods of slow juvenile growth under the shaded understorey, followed by one or several growth releases during canopy accession caused by the death of overhead or nearby adult trees (Nagel et al., 2014). Finally, we examine how common exceptionally old trees are within these old-growth forest sites, which has implications for conservation of forest biodiversity.

2 | METHODS

2.1 | Study area and site selection

This study was conducted in primary temperate mountain forests of the Carpathian Mountains and the Balkan peninsula, spanning from beech-dominated and mixed forests (hereafter referred to as beech-dominated) at lower elevations to spruce-dominated forests at higher elevations. These two regions contain the largest remnants of primary forests in the temperate zone of Europe (Janda et al., 2019; Mikoláš et al., 2019; Nagel et al., 2014; Sabatini et al., 2018). Primary forests were characterized as unmanaged forests with natural stand composition, diverse horizontal, vertical, and age structure, and a significant amount and diversity of downed and standing dead trees in different stages of decomposition; most stands were typically in an old-growth stage of development, but early seral stages developing after more severe natural disturbances were also present in these primary-forest sites (Mikoláš et al., 2019). The data set used for this study is a part of the REMOTE network (for more details see www.remoteforests.org), which is focused on surveying remaining tracts of primary-forest landscapes in Europe and long-term study of their dynamics. The plot network has a hierarchical sampling scheme, with plots located within stands, and multiple stands organized in larger landscapes. For the purposes of this study, we split the data set into 11 landscapes, based on geographic location and forest type. They include seven beech-dominated landscapes (i.e., Albania, Bulgaria, Croatia, Central Slovakia beech, Eastern Slovakia beech, Northern Romania beech, and Southern Romania beech) and four spruce-dominated landscapes (i.e., Central Slovakia spruce, Ukraine spruce, Northern Romania spruce, and Southern Romania spruce). The landscapes comprise a total of 35 spruce-dominated stands, and 33 beech-dominated stands (Figure 1; Appendix S1.)

Norway spruce comprised 99% of all trees in spruce-dominated stands, and was occasionally mixed with fir, *Pinus cembra* L., and *Sorbus aucuparia* L. In beech-dominated stands, beech accounted for 75% of all trees on average, followed by fir (14%), spruce (7%), and maple (2%); other less common species were sporadically present,

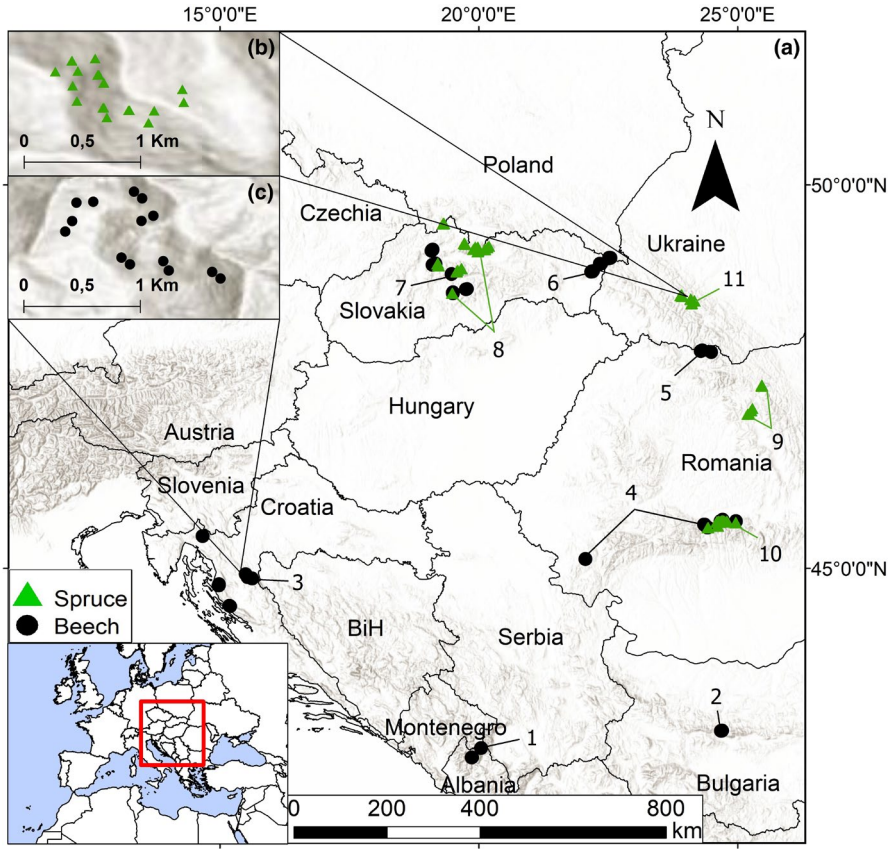

FIGURE 1 Hierarchical design and spatial distribution of study plots. The map shows the distribution of spruce stands and beech-dominated stands across the study region (a), including insets of plot locations within (b) spruce and (c) beech-dominated stands. The numbers mark the forest landscapes: 1, Albania; 2, Bulgaria; 3, Croatia; 4, South Romania beech; 5, North Romania beech; 6, East Slovakia; 7, Central Slovakia beech; 8, Central Slovakia spruce; 9, North Romania spruce; 10, South Romania spruce; and 11, Ukraine

such as *Acer platanoides* L., *Acer obtusatum* Waldst. & Kit. ex Willd., *Ulmus glabra* Huds., *Fraxinus excelsior* L., and *Fraxinus ornus* L.

2.2 | Data collection

Between 2010 and 2018, a network of circular permanent sampling plots was established within each primary-forest stand (Appendix S2). A stratified random sampling design was used for plot placement, whereby plots were randomly located within a regular grid laid over each stand, with grid size depending on the size of stands. In spruce landscapes, a grid with either a 1- or 2-ha cell size was used, and a circular plot of 1,000 m^2 (or occasionally 500 m^2 in recently disturbed areas where tree densities were high) was randomly located in the interior of every cell (0.25 or 0.5 ha). In beech-dominated landscapes, a 10-ha grid was used, and plots were either 1,500 or 2,000 m^2. A random point was generated in the 0.5–3.4 ha interior of each grid cell, and a pair of plots was established 40 m from either side of this point along the slope contour, such that plot centers were separated by 80 m.

The species and diameter at breast height (DBH) of all live trees ≥10 cm DBH were recorded in each plot, as well as the crown projection area (needed for the disturbance reconstruction described below) of 5–15 trees per plot. Slope, aspect, and elevation were also measured. Increment cores were extracted from randomly selected non-suppressed trees (i.e., at least half of the living crown area of the tree was exposed to direct sunlight) in each plot to obtain data on life spans, lifetime growth patterns, and disturbance history. We took an increment core from 15 (when smaller plots were used) to 30 randomly selected canopy trees over 10 cm DBH on every plot in spruce landscapes (for a mean of 24.1 cores/plot). In beech landscapes, we cored all the living trees ≥20 cm DBH and 25% randomly selected trees with DBH between 10 and 20 cm on each plot (for a mean of 33.9 cores/plot). All cores were taken 1 m above the ground, and perpendicular to the terrain slope direction to avoid reaction wood. Data from 13 plots affected by recent, stand-replacing disturbances were excluded from further analyses.

2.3 | Data analysis

In total, 20,600 increment cores were processed using standard dendrochronological procedures. Each tree was represented by a single core. Ring-width series were measured with a LintabTM sliding-stage measuring system (Rinntech, Heidelberg, Germany; http://www.rinntech.ds), cross-dated using marker years (Yamaguchi, 1991), and verified with COFECHA (Holmes, 1983) and CDendro (Larsson, 2003). For samples that did not intersect the pith, the number of missing rings was extrapolated from the curvature and average growth rates of innermost rings (Duncan, 1989). We excluded all cores that had more than 20 estimated rings missing, or were of poor quality and therefore did not allow tree rings to be measured and cross-dated reliably. In total, 3,500 cores were omitted from further analyses (320 fir, 74 maple, 2,790 beech, and 316 spruce cores),

which resulted in a decrease in the overall mean diameter of cored trees for each species (from 31.4 cm to 28.0 cm for fir, 37.1 cm to 34.4 cm for maple, 36.4 mm to 31.6 cm for beech, and 36.6 cm to 36.4 cm for spruce).

Radial growth patterns of increment cores were analyzed for evidence of past disturbance events within each plot. Quantitative reconstructions of disturbance histories for different regions of the larger data set used here have been published previously (Standovár & Kenderes, 2003; Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017; Meigs et al., 2017; Nagel et al., 2017; Schurman et al., 2018; Janda et al., 2019; Schurman, Babst, Björklund, et al., 2019; Čada et al., 2020; Frankovič et al., 2020), and provide detailed descriptions of dendroecological methods. We therefore only briefly summarize the methods used to reconstruct disturbance below. We used the original approach of Lorimer and Frelich (1989), in which each core is screened for (a) abrupt, sustained increases in radial growth (i.e., releases) and (b) rapid early growth rates (i.e., gap-recruited trees), both of which provide indirect evidence of mortality of a former canopy tree. Following Lorimer and Frelich (1989), we only included release events before trees reached a diameter threshold, such that only mortality events that provided access to the canopy were counted. The diameter threshold was based on comparisons of diameters of currently suppressed vs released trees in the plot data. Multiple releases were allowed as long as they occurred before the diameter threshold. The severity of disturbance was based on the relative canopy area removed on each plot calculated from the current crown area of trees containing evidence of past disturbance; this approach makes the assumption that the sum of the current crown areas of such trees is representative of the proportion of the plot disturbed in the past (Lorimer & Frelich, 1989).

Disturbance history reconstruction and lifetime growth patterns of trees were used to derive several variables that may influence longevity. These included the timing and severity (i.e., percent plot canopy area killed) of the reconstructed maximum severity disturbance event on each plot (Meigs et al., 2017) (hereafter referred to as disturbance severity and disturbance year), as well as the number of release events per core. To assess the influence of growth rates on longevity, we used the average growth rate of the first 50 years following Bigler (2016) (hereafter referred to as early growth). As such, we excluded all cores that had less than 50 rings measured or estimated. We also included metrics of the minimum and maximum 10-year average growth periods for each tree ring series following Orwig and Abrams (1994) (hereafter referred to as minimum and maximum growth), as well as the number of releases detected throughout the series.

Several different environmental variables were also compiled to test their influence of longevity. We used raw values of slope steepness for each plot, while values of slope aspect were transformed into northness following the formula: northness = cosine [(aspect in degrees * π)/180] (Janda et al., 2019). To avoid problems with multicollinearity, we excluded altitude because it was strongly correlated with temperature ($r = -0.752$). Mean temperature of the vegetation season for each plot was calculated for the period from the 1 May until 31 October, by downscaling the Worldclim gridded data (Fick & Hijmans, 2017) for the period 1970–2000; this was done by building a linear model of temperature vs the product of altitude, longitude, and latitude. Given that we use the 1970–2000 period, which is likely not representative of the temperatures experienced during early life stages of old trees, our temperature variable is more of an index of relative temperature across the study region. Finally, there are several broad-scale differences between the Balkan and Carpathian study sites that may influence tree growth and longevity, including higher annual precipitation and temperature in the Balkan region, as well as differences in bedrock (Kozák et al., 2018); we therefore included raw values of latitude for each plot to further explore if there are differences in life span across the region.

To estimate life span within a species, we simply use the 90th percentile of age distributions for each species from pooled data across the entire study (Nagel et al., 2014). To compare life span among species, we used a negative binomial generalized linear mixed model (GLMM) with the ages of trees ≥ the species-specific 90th percentile (hereafter referred to as the oldest trees) as the response variable and species as the explanatory variable. We applied a four-level random-effects structure to account for the potential effects of geographical variability: a plot nested within a pair of plots (in beech-dominated regions), a pair of plots nested within a stand, and a stand nested within a landscape. Wald tests were performed to assess statistical significance. We used Tukey pairwise comparisons to test for differences among individual species.

To identify the most influential drivers of life span, a binomial GLMM was fit for each species. To facilitate interpretation, we converted the 90th percentile ages to a binary variable, such that the age status of a given tree age was either ≥ species-specific 90th percentile or <species-specific 90th percentile. Age status was used as a response variable and disturbance history, growth rate, and environmental variables were included as fixed effects. In the spruce GLMM, forest type (spruce or beech-dominated) was used as an additional fixed factor that may cause potential differences in longevity of spruce growing in these two forest types. The mean values and ranges of all the variables included in these models are listed per species in Appendix S3. In the maple model, some variables were strongly correlated (i.e., early growth with maximum and minimum growth, latitude with the average temperature of the vegetation season, and disturbance year with disturbance severity). To avoid multicollinearity issues, we assembled a simpler model excluding disturbance year, early growth, number of releases, and latitude from the model. None of the final models showed problems associated with multicollinearity (all variance inflation factors were <3.00) (Zuur et al., 2009). We used the same random-effects structure as described above. We calculated marginal determination coefficients (R^2_m) and conditional determination coefficients (R^2_c) for each GLMM to assess the relative contribution of fixed effects and all effects respectively (Nakagawa et al., 2017).

All the analyses were performed in R language version 3.5.1 (R Core Team, 2019) using the following libraries: *glmmTMB* (Brooks et al., 2017) to run the models, *car*(Fox & Weisberg, 2019) for analysis-of-variance calculation, *emmeans* (R Core Team, R Foundation for

Statistical Computing, Vienna, Austria) to perform Tukey pairwise comparisons, *DHARMa*(R Core Team, R Foundation for Statistical Computing, Vienna, Austria) to perform residual diagnostics, *performance*(R Core Team, R Foundation for Statistical Computing, Vienna, Austria) to calculate VIF values, *MuMIn*(R Core Team, R Foundation for Statistical Computing, Vienna, Austria) to calculate the determination coefficients, and *ggplot2* (Wickham, 2016) for plotting.

3 | RESULTS

3.1 | Interspecific differences in life span

The ages of the oldest trees decreased from beech (291–578 years), silver fir (218–456 years), spruce (218–449 years), to maple (192–412 years) (Figure 2; Appendix S4). The GLMM showed significant differences in mean age of the oldest individuals among the four tree species ($\chi^2 = 280.41$, $p < 0.001$). The oldest beech trees were significantly older than all the other three species. The oldest fir trees were significantly older than spruce trees, while the differences between the oldest maple and spruce trees, and maple and fir trees, were not statistically significant (Appendix S5).

3.2 | Drivers of tree life span

The influence of disturbance-related variables on reaching the 90th percentile ages varied among the four tree species (Table 1; Appendices S6, S7). Maximum severity of plot-level disturbance had a significant negative effect on life span (i.e., the plot-level presence of trees above the 90th percentile age thresholds) for spruce and maple, while the calendar year of this maximum severity event had a significant negative influence on beech and spruce (i.e., plots with more recent maximum severity events had less trees reaching old age (Appendices S6, S7). Neither of the two disturbance variables were significant in the fir model. The number of releases had a significant positive effect on life span in all models.

Growth rate variables had strong and consistent effects on life span among the species (Table 1; Appendixes S8–S10). Minimum ten-year average growth showed a significant negative influence for each species, while early growth rate had a significant negative influence on life span for beech and fir, but not spruce. Maximum growth was not significant in any of the models.

The models did not show strong evidence of environmental control on tree life spans. Both the plot level (northness and slope)

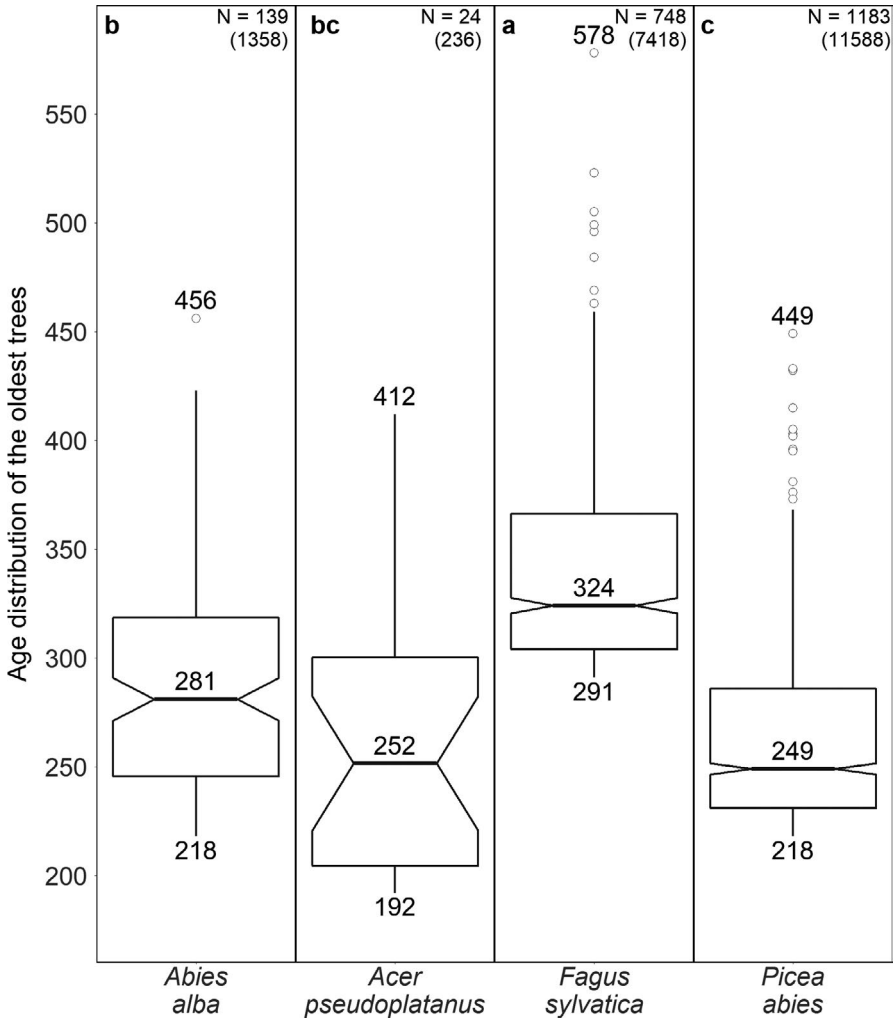

FIGURE 2 Age distribution of the oldest trees (≥species-specific 90th percentile of age) of four dominant species pooled across all study sites. Boxes represent the interquartile range, with the median age of the oldest trees given by a horizontal line within each box, and notches showing 95% confidence intervals of the median. The lower whisker of each box extends to the species-specific 90th percentile of age, while upper whiskers extend 1.5 times the interquartile range, and points show outliers. Numbers in the upper right corners indicate the number of trees above the species-specific 90th percentile, including the total numbers of all trees per species in parentheses. The letters in the upper left position of each plot indicate significant differences among species ($p < 0.05$) based on Tukey's pairwise comparisons

TABLE 1 Summary of generalized linear mixed models (GLMMs) examining the effect of environmental, growth, and disturbance factors on the age of the oldest individuals of four tree species

	Fagus sylvatica				*Picea abies*				*Abies alba*				*Acer pseudoplatanus*			
Parameter	**Est.**	***SE***	***z***	***p***	**Est.**	***SE***	***z***	***p***	**Est.**	***SE***	***z***	***p***	**Est.**	***SE***	***z***	***p***
(Intercept)	**−3.74**	**0.20**	**−19.14**	**<0,001**	**−4.12**	**0.36**	**−11.40**	**<0,001**	**−3.70**	**0.56**	**−6.66**	**<0,001**	**−22.36**	**6.98**	**−3.20**	**0.001**
Disturbance severity	−0.11	0.09	−1.22	0.224	**−0.70**	**0.09**	**−7.60**	**<0,001**	−0.06	0.17	−0.33	0.738	**−9.19**	**3.81**	**−2.41**	**0.016**
Disturbance year	**−0.39**	**0.08**	**−4.72**	**<0,001**	**−0.29**	**0.06**	**−4.73**	**<0,001**	0.25	0.16	1.61	0.108				
Early growth	**−0.63**	**0.11**	**−5.73**	**<0,001**	0.07	0.08	0.86	0.389	**−0.98**	**0.25**	**−3.90**	**<0,001**				
Maximum growth	−0.05	0.07	−0.70	0.482	0.00	0.08	−0.04	0.967	0.06	0.17	0.36	0.719	2.87	1.90	1.51	0.131
Minimum growth	**−1.13**	**0.14**	**−7.99**	**<0,001**	**−1.99**	**0.10**	**−20.60**	**<0,001**	**−1.11**	**0.32**	**−3.48**	**0.001**	**−13.10**	**5.15**	**−2.55**	**0.011**
Number of releases	**1.11**	**0.06**	**19.70**	**<0,001**	**0.58**	**0.04**	**14.27**	**<0.001**	**1.08**	**0.15**	**7.42**	**<0,001**				
Latitude	−0.34	0.20	−1.72	0.086	−0.06	0.13	−0.45	0.650	−0.01	0.45	−0.01	0.990				
Northness	−0.09	0.10	−0.85	0.393	0.00	0.07	0.05	0.961	−0.28	0.17	−1.62	0.106	−2.54	2.47	−1.03	0.304
Slope	0.04	0.11	0.39	0.694	−0.03	0.08	−0.35	0.726	0.18	0.20	0.90	0.370	1.49	1.53	0.97	0.331
Mean T of vegetation season	−0.20	0.16	−1.25	0.211	0.13	0.10	1.27	0.204	**−0.50**	**0.25**	**−2.00**	**0.045**	**−6.45**	**3.17**	**−2.04**	**0.042**
Forest type					0.29	0.37	0.79	0.432								
$\tau_{00\ \text{plot:(pairplot:(stand:landscape))}}$	0.57				0.47				0.00				464.87			
$\tau_{00\ \text{pairplot:(stand:landscape)}}$	0.37				0.57				0.41				0.00			
$\tau_{00\ \text{stand:landscape}}$	0.69				0.34				1.85				0.00			
$\tau_{00\ \text{landscape}}$	0.00				0.00				0.84				0.01			
R_m^2[%]	48.03				54.56				42.65				40.93			
R_c^2 [%]	65.25				68.07				70.49				99.59			

Note: Results show explanatory variables used in the models, estimates of the regression coefficients (Est.), standard errors (*SE*), *z*-values (*z*), probabilities (*p*), variances of all four levels of random effects (τ_{00}), marginal determination coefficients R^2_m, and conditional determination coefficients R^2_c. The significant model parameters are displayed in bold.

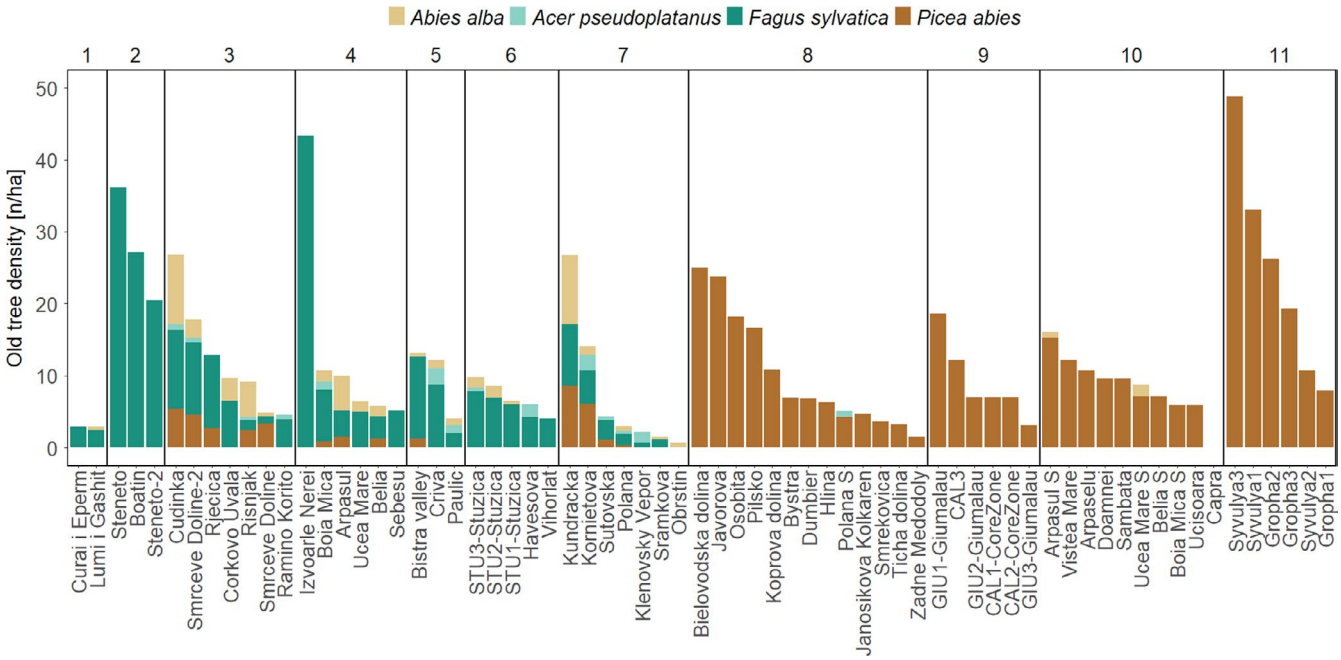

FIGURE 3 Densities of oldest trees (≥species-specific 90th percentile of age) by species within each stand across the study region. The numbers indicate the forest landscape names: 1, Albania; 2, Bulgaria; 3, Croatia; 4, South Romania beech; 5, North Romania beech; 6, East Slovakia; 7, Central Slovakia beech; 8, Central Slovakia spruce; 9, North Romania spruce; 10, South Romania spruce; 11, Ukraine

and large-scale drivers (latitude and temperature of the vegetation season) were insignificant for most species-level models. The only exceptions were the models for fir and maple, in which temperature of the vegetation season had a weak but significant negative effect on life spans (Table 1, Appendix S11).

3.3 | Commonness of old trees

The densities of the oldest trees (≥species-specific 90th percentile of age) were highly variable across the stands and landscapes, ranging from 0 to 48.8 trees/ha (Figure 3). Fifteen out of 68 stands had 10–20 old trees/ha, and 11 stands had densities greater than 20 old trees/ha. We identified 893 trees that were at least 300 years old, and 113 trees older than 400 years, of which two were maple (0.084% of all maple trees), four were fir (0.29% of all fir trees), nine were spruce (0.08% of all spruce trees), and 98 were beech (1.32% of all beech trees). Three beech trees were older than 500 years (0.04% of all beech trees). When calculated as a proportion of the canopy layer trees, the oldest trees made up from 0% to 23.9% of the canopy per stand (Appendix S12).

4 | DISCUSSION

We found compelling evidence of biological differences in life span among the four coexisting trees species across mountain regions of Europe, yet these differences are not entirely consistent with published literature on the ecology of European tree species. We also found that local disturbance history, rather than plot-scale and broad-scale environmental factors, was a key driver of life span. The particular history of local disturbance likely contributes to the highly variable density of the oldest trees that was documented across the study region. Before we elaborate on these main findings, we highlight several caveats that are important for the discussion that follows.

The estimates of tree life span used in our study, in particular the ages of the oldest living stems above the species-specific 90th percentiles, provide an indication of the longevity of a given individual, but not actual longevity, or the number of years from seed germination to death of an adult tree. Because we cored trees at 1 m in height, we underestimate the number of years required to reach 1 m, which could range from years to decades depending on light conditions, particularly for shade-tolerant species (Wong & Lertzman, 2001; Nagel et al., 2006). We also only worked with live trees, mainly due to the challenges of obtaining a large sample of recently dead trees with intact wood for tree coring. The species sampled in our study, especially the broad-leaved species, have relatively fast decay rates, such that tree ring counts of dead and declining trees are often extremely difficult (Di Filippo et al., 2012). Finally, given that larger trees often had bole decay, more larger stems were excluded from the sample compared to smaller stems, which is an additional reason why our data set may underestimate life span. Despite these limitations, the large population-based data set of randomly sampled trees in remaining primary forests across a subcontinental scale should provide a robust estimate of interspecific differences in tree life span.

Beech, the dominant broad-leaved species, was markedly older than the other species, and fir was older than spruce, but there were no significant differences in life span between maple and the two

conifer species. As previous studies have pointed out, interspecific differences in life history traits at both juvenile and adult life stages may contribute to tree coexistence, whereby adult longevity may compensate for lower competitiveness of juveniles compared to co-occurring species (Veblen, 1986; Lusk & Smith, 1998). In temperate mixed mountain forests of Europe, beech is both one of the most shade-tolerant species as a juvenile and long-lived as an adult, likely contributing to its dominance across the region. Compared to juveniles of beech and fir, maple and spruce are less tolerant of shade, but grow more rapidly in larger gaps with higher light levels (Stancioiu and O'hara, 2006; Petritan et al., 2007; Leuschner & Meier, 2018). For example, in a mixed mountain forest in the Dinaric region, (Nagel et al., 2010) found that maple required relatively large gaps (>400 m^2) to access the canopy, while smaller gaps were captured by beech and fir, which were often present prior to gap formation. Although the lower shade tolerance of maple may be a disadvantage in forests that lack moderate-severity disturbance for long time periods, its relatively high longevity likely contributes to its persistence in the landscape. Indeed, there are likely other interspecific trait differences associated with various life stages that may contribute to the coexistence of these species (Nakashizuka, 2001), such as long-distance dispersal of maple seeds or the tall canopy stature of fir and spruce. However, further research is required to better understand the life history traits and life stages that contribute to tree species coexistence in these forests.

It is important to point out that our findings are not consistent with the classic literature on life span of European tree species. For example, Korpel' (1995) reported life spans of 230 and 350 years for beech and fir, respectively, which is in complete contrast to our findings. Leuschner and Ellenberg (2017) report maximum ages of 450 years for both beech and fir, and 300 years for spruce and maple. However, the maximum ages found in our data set are considerably older than the median ages of trees above the 90th percentile ages; these median ages are a better predictor of expected tree life spans in forests regulated by natural disturbance processes. We believe that the range of life span estimates provided here may serve as an important reference for future studies that must prescribe values for them, such as simulation models of forest dynamics. Relying on estimates from earlier work may lead to spurious conclusions regarding long-term forest dynamics. In support of our findings, other recent dendroecological studies that focused on local sites or other regions in Europe have reported similar values of maximum life span for the four species studied here (Bigler & Veblen, 2009; Motta et al., 2011; Nagel et al., 2014; Di Filippo et al., 2015; Piovesan, Biondi, Baliva, Dinella, et al., 2019).

In addition to life history differences, we also sought to identify drivers of longevity across the large gradient of environmental conditions and disturbance histories present in the data set. The analyses indicated significant links between disturbance metrics and longevity in three of the four species-level models. There was a higher probability of finding old trees on plots with a lower maximum severity of plot-level disturbance, or where the maximum severity event occurred further back in time. These findings are not at all surprising given that both the beech- and spruce-dominated primary forests studied here experience a disturbance regime characterized by relatively frequent moderate-severity, partial canopy disturbances that are likely to remove susceptible individuals (i.e., large, old trees) in the canopy layer (Nagel et al., 2014; Čada et al., 2020; Frankovič et al., 2020).

Disturbance history is also intrinsically linked to lifetime growth of trees in that it regulates canopy structure, and thereby the growth of understorey trees via changes in light. Depending on the size, location, and timing of disturbance relative to a given understorey tree, some individuals will gain access to the forest canopy quickly, others will reach the canopy after multiple periods of suppression and release, and yet others will die due to prolonged periods of suppression. Across all four of the species studied here, trees that survived periods of very suppressed growth were more likely to reach old age. For example, average annual growth rates during the minimum 10-year growth periods for all the trees older than 300 years was <0.62 mm/year, <0.36 mm/year for all the trees older than 400 years, and <0.17 mm/year for all the trees older than 500 years (Appendix S1: Figure S6). Likewise, trees that had slow early growth rates were also more likely to reach old age (Appendix S1: Figure S5). These findings are consistent with previous literature for a number of different species (Larson, 2001; Di Filippo et al., 2015; Bigler, 2016; Piovesan, Biondi, Baliva, Dinella, et al., 2019), including beech (Piovesan et al., 2005; Di Filippo et al., 2012; Piovesan et al., 2019) and spruce (Bigler & Veblen, 2009; Rötheli et al., 2012; Castagneri et al., 2013). Finally, the results show a positive relationship between the number of suppression-release periods experienced by a tree and longevity (Appendix S1: Figure S7). Trees with multiple suppression-release periods persist in the understorey for a large proportion of their life span, while trees that access the canopy quickly, such as those that establish in large gaps, spend a longer proportion of their life in the canopy. These results lend support to the idea that time spent in the canopy, where there is higher risk of disturbance, may have a stronger influence on longevity than other factors, such as environmental constraints or genetics.

Indeed, one of the more surprising findings was that we did not identify a consistent relationship between life span and environmental factors, such as temperature and elevation, which has been documented in previous studies of the same species (Rötheli et al., 2012; Di Filippo et al., 2015; Bigler, 2016). Aside from the negative correlation between the mean temperature of the vegetation season and longevity for fir and maple, none of the other environmental factors (i.e., slope, northness, latitude) were related to longevity across the four species. The strong influence of disturbance and slow growth rates on longevity documented here may simply override the influence of other environmental factors. In a study on mountain pine in Switzerland, Bigler (2016) also suggested that a lack of an expected temperature effect on the early growth of mountain pines was likely due to superimposing effects of stand structure. Furthermore, past studies that have documented extremely old trees for a given species were often located within extreme site conditions (Larson et al., 2000), whereas our data set is likely to be more representative of site conditions found across mountain forests in the region.

A notable drawback of our study is that we cannot tease apart how various drivers influence longevity. Previous work has often hypothesized that slow-growing trees invest more in defense, such as chemicals or other wood properties that promote resistance to decay (Loehle, 1987), or that slow radial growth may incur greater mechanical resistance to canopy disturbance (Larson, 2001). For the species studied here, the literature does not provide clear evidence on how slow growth or other wood properties may increase longevity. Previous research does not indicate a clear or consistent relationship between radial growth and wood density for beech (Bouriaud et al., 2004; Diaconu et al., 2016), while faster radial growth has been found to decrease wood density in spruce (Piispanen et al., 2014). Moreover, in a study of deadwood decay across temperate tree species in Europe, wood density was positively correlated with decay rates for beech, maple, and spruce, whereas chemicals such as phenolic organic extractives were negatively correlated with decay rate (Kahl et al., 2017). However, if understorey trees are growing slowly due to light limitation, then presumably they have limited resources to invest in chemical defense (Herms & Mattson, 1992). Finally, it is important to note that we cannot rule out genetic control on intraspecific variation in life span, or other trade-offs between growth and longevity related to physiology (Roskilly et al., 2019).

A final objective of our study was to quantify the commonness of old trees across the primary-forest landscapes sampled in the study region. In general, very old trees are exceptionally rare; out of 20,600 cores dated to ≥50 years of age, only 115 were dated to more than 400 years. Although these exceptionally old trees are rare, 26 out of the 68 stands had more than 10 trees ha^{-1} that reached the species-specific 90th percentile age. Moreover, the remarkable variation in the density of these trees across the stands likely highlights how tree longevity is strongly influenced by local disturbance histories, which cover a gradient from low-intensity gap dynamics, to partial canopy disturbance, to severe stand replacement in the study region (Svoboda et al., 2014; Trotsiuk et al., 2014; Janda et al., 2017; Schurman et al., 2018; Čada et al., 2020; Frankovič et al., 2020). Our results imply that disturbance and phenotypic plasticity play a strong role in controlling tree life span. As a consequence, if disturbance regimes shift toward larger and more intense events under global change (Seidl et al., 2017), speeding up canopy accession, then future forests may support fewer long-lived trees.

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AUTHORS CONTRIBUTIONS

JP, TAN, and MSvo conceived the idea for this study. JP, TAN, MSvi, and JLP designed the study. SM, AD, ET, MP, TZ, OH, SD, OC, MM, and MSvo located the study sites and dealt with acquiring permissions for data collection. KB, MM, PJ, MF, RR, MSy, MD, TK, DK, OK, RB, VČ, VT, MSvo, and MSa collected the tree cores and structural data. JP, KB, MM, PJ, MF, RR, MSy, MD, TK, DK, OK, RB, VČ, and VT processed and analyzed the tree cores. MM, PJ, OV, RB, VČ, VT, MSvo, JSS, and AB conceptualized and calculated the disturbance parameters. JP, MSvi, and OV analysed the data. JP and TAN wrote the draft of the manuscript. All authors have approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available at the Dryad Digital Repository (https://doi.org/10.5061/dryad.1ns1rn8ts).

ORCID

Jakob Pavlin https://orcid.org/0000-0001-8514-3446
Thomas A. Nagel https://orcid.org/0000-0002-4207-9218
Ondřej Vostarek https://orcid.org/0000-0002-0657-0114
Radek Bače https://orcid.org/0000-0001-6872-1355

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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