Torresan et al. Annals of Forest Science (2024) 81:49
https://doi.org/10.1186/s13595-024-01264-5
INRAE
Annals of Forest Science

RESEARCH PAPER

Open Access

Changes in tree-ring wood density of European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), and Norway spruce (*Picea abies* (L.) H. Karst.) in European mountain forests between 1901 and 2016

Chiara Torresan[1*], Torben Hilmers[2], Admir Avdagić[3], Edmondo Di Giuseppe[4], Matija Klopčič[5], Mathieu Lévesque[6], Florian Motte[2], Enno Uhl[2,7], Tzvetan Zlatanov[8] and Hans Pretzsch[2]

Abstract

Key message We found a significant increase in the latewood density of European beech, and a decrease in the latewood and mean wood density of silver fir and Norway spruce in European mountain forests over the period 1901–2016. In the past century, drought did not directly influence the wood density trend of the three studied species. However, for both fir and spruce, drought indirectly affected the mean wood density *via* changes in the latewood to earlywood ratio, i.e., in the case of extreme drought, trees with high values of latewood to earlywood ratio experienced a slight attenuation in the declining trend of their mean wood density.

Context Century-long wood density measurements can provide novel information on tree response to climate change and the carbon sequestration potential of forest ecosystems. Still, the knowledge about long-term changes in wood density of European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), and Norway spruce (*Picea abies* (L.) H.Karst.) in European mountain forests needs to be further explored.

Aims We assessed long-term changes in tree-ring mean wood density, earlywood density, and latewood density in trees of the three species between 1901 and 2016. We investigated the influence of endogenous factors (i.e., tree-ring width, current tree diameter, and latewood to earlywood ratio) and drought events on wood density.

Methods In total, 150 tree cores were sampled from mountain forests in Bulgaria, Bosnia and Herzegovina, Slovenia, Switzerland, and Germany. The mean, early, and latewood density of these samples were measured with the LIGNOSTATION™ system. To address our research aims, we applied a linear mixed-effect modelling approach using the data from 101 correctly cross-dated cores that spanned the entire period of analysis.

Results In the absence of drought, the latewood density of European beech increased by 7.1%, the late and mean wood density of silver fir decreased by 16.8% and 11.0%, respectively, and the late and mean wood density of Norway spruce decreased by 16.1% and 7.2%, respectively, between 1901–2016. In the past century, drought influenced

Handling editor: Cyrille Rathgeber.

*Correspondence:
Chiara Torresan
chiara.torresan@cnr.it
Full list of author information is available at the end of the article

the trends of wood density through an effect mediated by changes in the latewood to earlywood ratio. Specifically, in cases of extreme drought, silver fir and Norway spruce trees with a latewood to earlywood ratio value 50% higher than the median experience a slight attenuation in the declining trend of their mean wood density, making the negative impact of drought marginally less severe.

Conclusions Our findings have significant implications for the accuracy of carbon stock assessments, national greenhouse gas inventories, and the utilization of wood from the three species. Given the fact that changes in wood density follow species-specific patterns and the expectation of more frequent drought events in Europe, in the future, it is essential to build further tree-ring density time series for other species and sites to improve our understanding of how climate change alters wood density and carbon sequestration of forest ecosystems.

Keywords Dendrochronology, Latewood to earlywood ratio, Drought, LIGNOSTATION™, Linear mixed-effects model

1 Introduction

Tree rings record environmental and climate variability, so have been widely used in dendrochronological studies to infer trees' response to environmental changes (Fritts 1976; Büntgen et al. 2010). Tree-ring analyses allow for detecting short-term and long-term responses of trees to climate (Büntgen et al. 2021). Tree-ring width (TRW) is a trait that can reveal changes in growing season temperature and soil water availability. For this reason, many studies have used (absolutely dated) tree-ring width as an indicator of tree response to climate conditions, such as drought (Rigling et al. 2002; Gazol et al. 2018; Pretzsch et al. 2020a; Schwarz et al. 2020).

Intra-annual changes in wood density are also good indicators of a tree's response to hydroclimate variability (Hoeber et al. 2014; De Micco et al. 2019; Camarero and Hevia 2020). Therefore, wood density at seasonal to annual scales can provide additional information on the climate sensitivity of tree species (Franceschini et al. 2013; Camarero and Hevia 2020). In deciduous and temperate angiosperm species, wood density is a functional trait that predicts the capacity to regulate seasonal water status (de Souza et al. 2020). In conifers, when water supply is abundant during the growing season, tracheids with wide lumens are formed, resulting in most of the annual ring having high hydraulic conductivity. However, under dry conditions, the tracheids develop narrower lumens with thicker cell walls, leading to a significant portion of the tree ring exhibiting low conductivity (Rathgeber et al. 2006; Rathgeber 2017). For conifers, particularly those growing in cooler high-latitude and high-elevation environments, the density of wood formed towards the end of the growing season is positively correlated to the growing season air temperature (Schweingruber et al. 1978; Björklund et al. 2019).

Wood density is influenced by several factors beyond just climate (Watt et al. 2008; Boakye et al. 2023). These factors include the tree species (Rozenberg and Cahalan 1997). Genetics, in turn, affect the size, shape, and chemical composition of wood cells, as well as the tree's longevity (Gryc et al. 2011). Changes in wood density over time can also result from the tree's age, as wood density varies during the tree ontogeny (Franceschini et al. 2013), as well as from microenvironmental and competition conditions. Early differences in growth among species might reflect intrinsic variations in tree physiology and shade tolerance, but changes in neighbourhood density and forest composition can alter or even reverse these early growth patterns, thereby influencing wood density (Boyden et al. 2009). Moreover, wood density is affected by the rate of xylogenesis, the timing of earlywood and latewood formation, and their interaction with climatic and edaphic factors (Bouriaud et al. 2005). Although the formation of earlywood and latewood is influenced by genotype or provenance (George et al. 2019; Klisz et al. 2016, 2019; Nabais et al. 2018), the latewood to earlywood ratio (LER)—calculated as the width of the latewood portion of a tree's annual ring divided by the width of the earlywood portion—is more prominently affected by climate (Klisz et al. 2019; Rozas et al. 2011). As LER is influenced by climate, it may also play a role in a tree's resistance to drought. This hypothesis was tested by Zhang et al. (2024) using a network of Dahurian larch (*Larix gmelinii* var. principis-rupprechtii (Mayr) Pilg.) earlywood and latewood width data from 1979 to 2018. Their results indicate that a higher proportion of latewood is formed during dry years, and this high drought sensitivity of LER, in turn, leads to increased drought resistance.

Wood density, which is also referred to as specific gravity (Williamson and Wiemann 2010), is defined as the amount of actual wood substance present in a given volume of wood. This property is crucial for several reasons. Investigating wood density is important because it is related to a tree's lifespan, its wood properties, and, consequently, the overall lifecycle of forests and the wood product supply chain. In standing trees, wood density determines mechanical stability and is closely associated with the risk of trunk breakage, embolism and pathogen invasion (Niklas and Spatz 2010). Additionally, wood density is a key contributor to forest biomass, making it an important measure of carbon storage (Chave et al. 2009; Larjavaara and Muller-Landau 2010). Wood density is also an important property for the quality of solid wood and fibre products in both conifers and hardwoods (Zobel and Jett 1995). In addition, wood density values affect the cost of transforming harvested wood into final products, affecting the entire wood product supply chain (Niklas and Spatz 2010).

Despite the recognized importance of wood density, long-term changes in wood density in European mountain forests have not yet been sufficiently studied. Previous research on trees in European lowland forests has shown that increased growth in several species is often associated with a decrease in wood density (Badeau et al. 1996; Franceschini et al. 2010; Bontemps et al. 2013; Pretzsch et al. 2018; Vannoppen et al. 2018). For example, studies using wood samples from long-term experimental plots in north-eastern France and Central Europe revealed that Norway spruce (*Picea abies* (L.) H. KARST.), the dominant tree species in that area, exhibited a significant decrease in wood density over the past 100 years (Franceschini et al. 2010; Pretzsch et al. 2018). Similar trends were observed in Central Europe for Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) (Pretzsch et al. 2018). However, to our knowledge, studies investigating the causal factors behind these changes in European mountain forest species are lacking. Therefore, it is essential to obtain reliable information on long-term trends in wood density and to understand the drivers of such changes, particularly in the context of climate conditions that have led to an increase in drought episodes across Europe (Vicente-Serrano et al. 2014; Spinoni et al. 2017; Grillakis 2019; Hänsel et al. 2022). Specifically, it is important to clarify how drought affects wood density and how factors such as tree-ring width, the ratio between earlywood and latewood in annual rings, and tree age or tree size modulate the effect of drought on wood density.

There are several techniques available for measuring tree-ring wood density in the laboratory, which differ from the standard wood density measurement method. The standard method involves calculating the ratio of the dry weight of wood to its fresh volume, yielding a value known as basic density (Tsoumis 1991), or specific gravity, which measures the amount of structural material a tree species allocates for support and strength (Williamson and Wiemann 2010). Laboratory techniques offer the advantage of differentiating relative changes in earlywood and latewood density, which is why density is often reported as relative density. The main techniques used include (i) high-frequency densitometry (Schinker et al. 2003), (ii) hyperspectral imaging (Fernandes et al. 2013), (iii) X-ray microdensitometry (Björklund et al. 2019), (iv) X-ray computer tomography (Steffenrem et al. 2014; De Mil et al. 2016), (v) microwave scanning (Johansson et al. 2003), and (vi) blue intensity (Björklund et al. 2014). The merits and challenges associated with these various techniques for measuring relative wood density have been thoroughly discussed (e.g., Baetting et al. 2017; Björklund et al. 2019; Ravoajanahary et al. 2022).

In our study, we used the high-frequency densitometric technique to measure the annual wood density of increment cores taken from European beech (hereafter beech), silver fir (hereafter fir), and Norway spruce (hereafter spruce) in European mountain forests across Bulgaria, Bosnia and Herzegovina, Slovenia, Switzerland, and Germany. We analysed the changes in the relative earlywood density (EWD), latewood density (LWD), and mean wood density (MWD) of the annual rings of these three species over the past century (for readability, we will refer to these densities without the term "relative" from here on). Our analysis involved developing a model that predicts the wood density for each species using dendrometric, dendrochronological, and climate data. Unlike simple trend detection analysis, which only identifies whether changes occurred over time, our approach allows us to understand the factors driving these variations. By considering multiple causal factors and their relationship, we sought to determine whether wood density could serve as an indicator of the sensitivity of the three studied species to drought (Bouriaud et al. 2004; Koprowski and Duncker 2012; Rosner et al. 2014). Additionally, our modelling approach enabled us to infer how wood density might have changed in the absence of drought or under conditions of severe and extreme drought events. By applying this approach, we aimed to address the following research questions: RQ1—Did tree-ring wood density, including earlywood and latewood density, and the latewood to earlywood ratio of beech, fir, and spruce in European mountain forests change over the last century? RQ2—Are long-term changes in the wood density of beech, fir, and spruce in mountain forests across Europe influenced by drought?

2 Material and methods

2.1 Study sites and tree core collection

The tree cores analysed in this study were collected in plots of mixed forests in European mountainous regions belonging to long-term forest monitoring programmes of Bulgaria, Bosnia and Herzegovina, Slovenia, Switzerland, and Germany (Fig. 1). Mixed forests are forest units where at least two tree species coexist at any developmental stage, sharing common resources (Bravo-Oviedo et al. 2014). In Europe, mixed forests cover large

Fig. 1 Location of the mixed mountain forest stands in Bulgaria, Bosnia and Herzegovina, Slovenia, Switzerland and Germany where the tree cores were collected

proportions of the Alps, Balkan and Carpathian mountain ranges. They are biodiversity hotspots and provide important ecosystem services far beyond the mountain regions themselves (MEA 2005; Estreguil et al. 2012; Gret-Regamey et al. 2012).

The plots are prevalently located on steep slopes, at elevations between 900 and 1600 m a.s.l., and are exposed between northwest and northeast (Table 1). More information about the plots can be found in Hilmers et al. (2019), Pretzsch et al. (2020b, 2021) and Gillerot et al. (2021).

The tree cores used for this study were collected from dominant trees of beech, fir and spruce in 2017 in all countries except those from Switzerland, which were taken in 2018. For each tree, stem diameter at breast height (DBH) was measured, and two cores with a diameter of 5 mm were taken using an increment borer (Haglöf, Långsele, Sweden) at breast height on the side of the trunk where no compression or tension wood was formed. The tree cores were glued on wooden supports, sanded and stored in specific rooms until use to avoid differences in humidity and temperature that might influence wood density.

2.2 Tree-ring wood density measurement through high-frequency densitometry

For measurement of the wood density, we used the LIGNOSTATION™ system (Rinntech-Metriwerk Gmbh & Co, Heidelberg, Germany). With this system, a small high-frequency transmitting electrode emits a sinusoidal signal at 10 MHz that propagates through the wood sample to a receiving electrode, which grabs the received signal, allowing a tree-ring wood density profile to be produced (Schinker et al. 2003). A synthesis of the main variables that describe the LIGNOSTATION™ system is reported in Table 7 of the Appendix.

Before starting wood density measurement, we visually inspected the two cores collected per tree and chose the one that showed fewer defects, such as cracks or loss of

Table 1 Geographic location and morphological characteristics of the study sites

Site	Country	Latitude (°)	Longitude (°)	Elevation (m a.s.l.)	Slope (%)	Aspect (°)
Velingrad	Bulgaria	41.92	23.84	1569	18	339
Igman	Bosnia and Herzegovina	43.76	18.25	1270	23	59
Jelovica	Slovenia	46.25	14.04	1375	7	59
		46.25	14.04	1421	37	25
		46.25	14.04	1443	16	322
Dürsrüti	Switzerland	46.96	7.77	890	21	340
Kreuth	Germany	47.60	11.66	1091	27	5

bark. In total, we selected and measured 150 tree cores, resulting from 10 cores per species and study site, which were analysed following these steps: (i) fixing of the tree cores on the LIGNOSTATION™ table; (ii) optical microscope scanning and image acquisition of the cores after defining the path along which the scanning microscope must move; (iii) milling of the cores by an ultra-precise fly cutter (Spiecker et al. 2000) after having defined the tracks for the mill; (iv) optical microscope scanning of milled cores; (v) tree-ring wood density measurement along three tracks after defining the paths for the high-frequency probe. The complete procedure for wood density measurements includes the creation of wood calibration standards measuring wood samples with different densities from the same group of species. If the procedure is not executed, the LIGNOSTATION™ system does not provide calibrated wood density values. However, it provides reliable information about the relative changes in the wood density along the increment core. For our study, we did not build a calibration curve before performing wood density measurements. Despite that, given that in our study, we were interested in the trends of the tree-ring wood density, the values provided by the LIGNOSTATION™ system and used in our analysis conserved the suitable features to answer our research questions. Since the values of wood density obtained using the LIGNOSTATION™ system are not calibrated, we decided to report the values of wood density as earlywood-density index (EWDI), latewood-density index (LWDI), and mean wood-density index (MWDI) in the tables and figures of this paper.

2.3 Tree-ring boundary setting and cross-dating

After measuring the wood density for each core, the tree-ring boundaries were set using the LIGNOSTATION™ software to align the wood density values with individual annual tree rings. This process involved setting the tree-ring borders based on photos of the sanded cores, while photos of the milled cores were used to check for any potential wood loss due to the milling process, particularly in areas with cracks. Once the tree-ring boundaries were established, a peak filter was applied to address any outlier values in the density measurements. A deviation factor of 4 was used as the maximum threshold to remove extreme values. As a result of the tree-ring analysis, a comma-separated file was produced by the LIGNOSTATION™ software with the values of the tree-ring width, earlywood width, latewood width, earlywood density, latewood density, and mean wood density. Specifically, the software determines the transition between earlywood and latewood at the point where the local wood density reaches 50% of the maximum wood density of a given tree ring.

Cross-dating was performed to assign a calendar year to each tree ring. The TSAP-WinTM software (Rinntech-Metriwerk Gmbh & Co, Heidelberg, Germany) was used for the on-screen cross-dating, which was supported by statistics obtained with the tests available in the software. For each species and each site, the process was conducted by correlating the width of the measured segments of a single tree-ring series to the master chronology composed of the remaining series of the same species and same site. We used the t-statistic method for cross-dating and a t-value of 4 as a minimum value to consider a series sufficiently correlated to the master chronology, as suggested by Baillie and Pilcher (1973). The on-screen visual analysis using the TSAP-WinTM software also allowed us to identify missing or false rings and, consequently, to make the changes needed in the ring border setting. Regarding beech, very narrow or even missing rings were found in many samples, which made the tree-ring border setting complicated. Therefore, at the end of the cross-dating process, not all samples were suitable for the subsequent analysis. Due to this high uncertainty, we decided to use a precautionary approach and preserve as much of the common climatic signal as possible with a minimum of "noise" introduced through errors (Sedmáková et al. 2016). In this way, 26 out of 50 cores of beech (5 from Bulgaria, 3 from Bosnia and Herzegovina, 5 from Slovenia, 7 from Switzerland and 6 from Germany) were correctly cross-dated and measured using the LIGNOSTATION™ system. In the case of spruce from the Dürsrüti site in Switzerland, only 2 out of 10 cores were highly correlated despite the certainty that no dating errors were included in the tree-ring border setting. The reason for the almost absence of correlation between the tree-ring time series of spruce from Dürsrüti is due to suppression periods, typical in mountain forests for trees in their young and juvenile stages (Magin 1959). Despite the low inter-series correlations for these spruce samples, we kept all the cores collected in Dürsrüti in our analysis. At the end of the tree-ring boundary setting and cross-dating, 39 out of 50 cores of spruce (7 from Bulgaria, 6 from Bosnia and Herzegovina, 10 from Slovenia, 10 from Switzerland and 6 from Germany) were included in further analysis.

Regarding fir, 36 out of 50 cores (5 from Bulgaria, 10 from Bosnia and Herzegovina, 7 from Slovenia, 7 from Switzerland and 7 from Germany) were included in the further analysis. The characteristics of the cores that were fully cross-dated and used in further analysis are reported in Table 2.

The complete time series of tree-ring width, MWDI, EWDI, and LWDI of beech, fir and spruce for the period 1901–2016 are reported in Fig. 5 of the Appendix, while the time series of tree-ring width, MWDI, EWDI, and

Table 2 Characteristics of the trees and cores used in this study. DBH and height are referred to the year when the trees were sampled, TRW = tree-ring width, EWDI = earlywood density index, LWDI = latewood density index, MWDI = mean wood density index, LER = latewood to earlywood ratio. min, mean, max, and CV are the minimum, mean, and maximum values and coefficient of variation of each variable, respectively

Species	Number of cores		DBH (cm)	Height (m)	TRW (mm)	EWDI	LWDI	MWDI	LER (%)
Beech	26	min	31.1	20.8	0.05	72	186	124	3.0
		mean	46.0	28.5	1.7	636.7	860.2	733.9	107.9
		max	66.7	36.2	9.3	1220	1365	1286	135.0
		CV (%)	20.5	13.3	72.8	26.5	19.5	21.7	87.7
Fir	36	min	37.0	22.3	0.02	105	136	122	3.0
		mean	60.0	31.2	2.2	399.9	962.8	567.1	52.9
		max	103.1	47.7	12.0	937	1660	994	90.0
		CV (%)	21.2	20.2	73.5	26.1	21.0	22.5	79.8
Spruce	39	min	42.6	25.7	0.06	69	178	96	3.3
		mean	59.2	35.3	2.1	446.3	953.4	585.8	47.5
		max	81.3	47.7	18.4	1011	1575	1215	95.0
		CV (%)	16.5	15.0	70.3	23	20.5	19.8	80.8

LWDI for the three species averaged across all sites for the period 1901–2016, with the Pearson correlation test results, are reported in Fig. 6 of the Appendix.

2.4 Climate data and standardized precipitation evapotranspiration index computation

For the German site, we used climate data from the German Meteorological Service (DWD Climate Data Center 2023). Gridded climate data included monthly precipitation and monthly mean temperature in a spatial resolution of 1 km × 1 km from 1901 to 2016. For the Swiss site, we used climate data spatially interpolated (100 m resolution) from the closest MeteoSwiss weather stations based on the Daymet algorithm (Thornton et al. 1997). For the Bulgarian, Bosnian and Slovenian sites, monthly precipitation and monthly mean temperature were obtained from the weather stations nearest to the sites. Table 8 of the Appendix reports the list of weather stations from which the data have been collected with the period of data availability.

To extend the climate time series from the weather station to the period 1901–2016, data were imputed with monthly data from the Climatic Research Unit (CRU) Time-Series (TS) Version 4.03 database (Harris et al. 2020) at a spatial resolution of 0.5° × 0.5°. More specifically, based on site coordinates, the four closest pixels were selected from CRU, and the monthly time series of precipitation and temperature were averaged with weights by distance. As there were common periods in station data and CRU, CRU data were fitted to station data, and then the shifting and scaling factors were used to align the CRU series to that of the weather station for the period that was out of the common period. The mean annual temperature (MAT) and cumulative annual precipitation (CAP) were computed from the monthly data.

We used the Standardized Precipitation Evapotranspiration Index (SPEI) to quantify drought at the study sites.

SPEI is usually calculated based on the difference between precipitation and potential evapotranspiration at different time scales (Vicente-Serrano et al. 2010; Tegos et al. 2023). In our study, the SPEI was calculated for each month of the year at a 3-, 6, and 12-month timescale, i.e., using the data of the given month and the past 2, 5, and 11 months, respectively. A correlation analysis between SPEIs and tree-ring chronologies showed that the most suitable SPEI time window across all sites was the 6-month window for August, meaning that the 6-month SPEI for August captures the temporal frequency of periods of drought and moisture over the entire growing period in European mountain forests considered in our study (Manrique-Alba et al. 2022). The SPEI package (Beguería and Vicente-Serrano 2023) in R (R Core Team 2022) was used to process the climate data. The SPEI value is usually classified according to drought severity. For example, Alam et al. (2022) propose the classification into mild, 0 to -0.84; moderate, from -0.85 to -1.27; severe, -1.28 to -2.05; and extreme, < -2.06.

2.5 Statistical analysis

2.5.1 Analysis of LER trend of beech, fir and spruce over the past century

To test if LER had changed between 1901 and 2016, we employed the nonparametric Mann–Kendall trend test. To determine the magnitude of these trends, we used Sen's slope estimator, denoted as β, which represents the median of all possible slopes calculated from pairs of points in the time series (Sen 1968). It is crucial to acknowledge that yearly time series of LER may be influenced by autocorrelation due to multi-annual cycles. When positive autocorrelation is present, the null hypothesis (β = 0) tends to be rejected more frequently than if autocorrelation was absent (von Storch 1999). To account for autocorrelation and correct the time series before applying the trend test, we utilized the method proposed by Zhang et al. (2000). This iterative approach begins with an initial estimate of autocorrelation, which is then used to obtain a de-correlated series using a first-order autoregressive model. The initial estimate of β is calculated on this de-correlated series. Subsequently, this estimate is used to de-trend the time series. The autocorrelation coefficient is re-estimated on the de-trended series, and the process is repeated iteratively. This procedure continues until the differences in the estimated parameters between successive iterations become negligible. This analysis was done both for each site separately and for all sites together.

The R package "zyp" (Bronaugh and Schoeneberg 2023) was used for this analysis.

2.5.2 Analysis of SPEI trend in the last hundred years in the study sites

We made a trend assessment of the 6-month SPEI for August in the periods 1901–2016, following the same approach, assuming that a decreasing trend of SPEI would lead to an increase in severe drought episodes. In addition, we analysed if drought events, particularly severe events, have increased in frequency over the last century.

2.5.3 Model building

To answer our research questions, we built a model that incorporates i) calendar year (i.e., YEAR) ii) current DBH (i.e., cDBH), iii) tree-ring width (i.e., TRW), iv) latewood to earlywood ratio (i.e., LER) and v) drought index (i.e., SPEI).

The variable calendar year allows us to understand if changes in wood density occurred in more than a hundred years and if these changes were significant at the set significance level. Tree ring width is a proxy for annual variation in forest productivity in temperate forests (Xu et al. 2017), and hence tree size, and must be considered to correlate with wood density. Current DBH, computed as the difference between the DBH of the tree in the year when the core was taken and the cumulative tree-ring width referred to the specific year, is a proxy for tree size and allows us to detect the effect of ontogeny on wood density. Trouillier et al. (2019) advocated that the cumulative ring-width method is the best approach to assess the effect of ontogenetic changes on a tree's climate sensitivity. The relevance of including LER in our model for studying the density of tree rings comes from the evidence from previous studies. Tree ring wood density is typically linked to the overall ring width, which is the sum of earlywood and latewood widths. The density might, therefore, also be expected to relate to the widths of these individual portions (earlywood and latewood) and their relative proportions (i.e., LER). Kern et al. (2013) found that earlywood width in pedunculate oak (*Quercus robur* L.) displayed a weak correlation with environmental factors (precipitation and temperature) and did not strongly contribute to common variance. In contrast, latewood width showed a stronger signal, implying its greater sensitivity to environmental variables. Thus, LER allows us to interpret these differences in relation to climatic conditions and translate them into effects on wood density. Pretzsch et al. (2018) highlighted that the earlywood ratio (i.e., the inverse of LER) is a significant factor influencing wood density values and trends in spruce but not in beech. For spruce, changes in the earlywood ratio directly impacted wood density, whereas, for beech, the relationship was more complex and did not solely depend on this ratio. Including LER may also help to test hypotheses derived from the findings of Pretzsch et al. (2018), such as whether LER influences wood density independently of ring width or whether changes in LER over time might correlate with changes in density for the three species.

We included in the model as well the interaction of cDBH, TRW, and LER with SPEI because we assumed that drought has an indirect effect on wood density, limiting the width of the tree ring, mediating the latewood to earlywood ratio, and acting as an ontogenic factor.

We used a linear mixed-effect modelling approach (LMM). In particular, we considered two nested levels of data higher than a single observation, i.e., the plot and the tree core, and we included random effects on them.

For each species and MWDI, EWDI, and LWDI, separately, we developed the following model:

$$\begin{aligned} MWDI/EWDI/LWDI_{pcr} = \beta_0 + \beta_1 YEAR_{pcr} + \beta_2 TRW_{pcr} + \beta_3 \mathrm{cDBH}_{pcr} + \beta_4 \mathrm{LER}_{pcr} + \beta_5 SPEI_{pcr} \\ + \beta_6 TRW * SPEI_{pcr} + \beta_7 cDBH * SPEI_{pcr} + \beta_8 LER * SPEI_{pcr} + \eta_p + \eta_{pc} + \epsilon_{pcr} \end{aligned} \quad (1)$$

where the β_s are the estimated coefficients of the explanatory variables, p stands for sites (p = 1, ..., 7), c indicates tree cores (c = 1, ..., 101), and r stands for annual growth rings (r = 1, ..., 10,215). The model includes two random intercepts for the plot and tree core to account for the data hierarchy, which are η_p and η_{pc}, respectively. In the framework of LMM, random intercepts are assumed to be independent and normally distributed with means zero and constant, positive variances. Moreover, they are independent of the residual random errors ϵ_{pcr}.

The properties of the identified models were assessed by testing for colinearity, calculating the variance inflation factor (VIF), statistics that indicate how much larger the standard error would be due to colinearity, and for homoscedasticity, by using residual plots, histograms of residuals, and applying a studentized Breusch-Pagan test (Breusch and Pagan 1979) to the standardized residuals to evaluate whether the independent variables explain our model errors variance. We used the 'nlme' package for linear mixed-effects modelling in R (Pinheiro et al. 2023).

We utilized the model estimates to make inferences to understand if the effect of drought on wood density depends on the value of the earlywood to latewood ratio. This analysis was conducted to test the hypotheses emerging from the results of the study by Pretzsch et al. (2018), i.e., the LER is a driver of wood density trend, and to evaluate the impact of combined levels of SPEI and LER on the variation of wood density. With this aim, we set SPEI to 0, -1.28, and -2.06 to represent mild (i.e., normal), severe and extreme drought conditions, respectively, and we changed LER from its median value per species (i.e., 0.79, 0.44 and 0.39 for beech, fir and spruce, respectively) to the median value increased by 50% and decreased by 50%. Hence, we estimated the trend of mean, early and latewood density under normal, severe and extreme conditions at a median value of LER, an increase of 50% of LER and a decrease of 50% of LER.

3 Results

3.1 Changes in tree-ring wood density of beech, fir and spruce in European mountain forests over the last century

3.1.1 LER trends

The results of the Mann–Kendall trend test show that LER changed significantly over the period 1901–2016 in almost all species and sites, specifically in 11 out of 15 cases (Table 3). In detail, LER of beech increased at Jelovica in Slovenia and Kreuth in Germany (mean increase equal to 0.26 and 0.54 respectively). LER of fir increased in all sites (mean increase ranging from 0.18 to 0.44) except for Igman in Bosnia and Herzegovina where the test highlighted a mean decrease of 0.23. LER of spruce changed in all sites except Jelovica (Slovenia). It increased at Velingrad in Bulgaria and Kreuth (mean increase equal to 0.36 and 0.19 respectively) and decreased significantly at Igman in Bosnia and Herzegovina and Dürsüti in Switzerland (mean decrease equal to 0.18 and 0.36 respectively).

When LER was averaged across the sites and then regressed against time, the trend was positive for fir and beech and negative for spruce (Fig. 2).

Table 3 Trend in LER from 1901 to 2016, with values of the lower and upper bounds (i.e., lb; ub) and the *p*-value. Significant (i.e., *p*-value < 0.05) trends are in bold

Species	Site	Country	LER trend (lb; ub)	*p*-value
Beech	Velingrad	Bulgaria	No trend	0.580
	Igman	Bosnia and Herzegovina	No trend	0.110
	Jelovica	Slovenia	0.26 (0.04; 0.48)	**0.025**
	Dürsüti	Switzerland	No trend	0.760
	Kreuth	Germany	0.54 (0.20; 0.86)	**0.003**
Fir	Velingrad	Bulgaria	0.32 (0.24; 0.41)	**< 0.001**
	Igman	Bosnia and Herzegovina	-0.23 (-0.40; -0.06)	**0.009**
	Jelovica	Slovenia	0.18 (0.11; 0.24)	**< 0.001**
	Dürsüti	Switzerland	0.26 (0.08; 0.43)	**0.005**
	Kreuth	Germany	0.44 (0.35; 0.53)	**< 0.001**
Spruce	Velingrad	Bulgaria	0.36 (0.30; 0.41)	**< 0.001**
	Igman	Bosnia and Herzegovina	-0.18 (-0.28 – -0.09)	**< 0.001**
	Jelovica	Slovenia	No trend	0.550
	Dürsüti	Switzerland	-0.36 (-0.56; -0.17)	**< 0.001**
	Kreuth	Germany	0.19 (0.13; 0.25)	**< 0.001**

3.1.2 Changes in wood density

Between 1901 and 2016, the latewood density of beech changed significantly (*p*-value = 0.007), as well as the latewood and mean wood density of fir and spruce (*p*-value < 0.001 of the coefficient of YEAR for both types of density and both species) (Table 4). For beech trees, we found that tree-ring width, current DBH and LER influenced long-term changes in latewood density. Specifically, from 1901 to 2016, latewood density increased with increasing tree-ring width and decreasing current DBH and LER. In fir, the latewood density decreased from 1901 to 2016 with increasing tree-ring width and current DBH and decreasing LER. In spruce, from 1901 to 2016, the decrease in latewood density was influenced by the increase in tree-ring width and tree size and the decrease

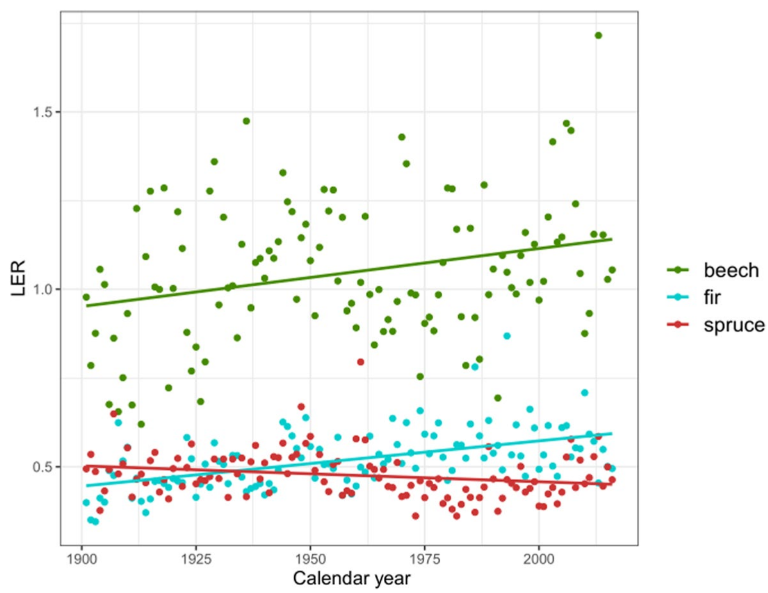

Fig. 2 Latewood to earlywood ratio (LER) in beech, fir and spruce from 1901 to 2016. The trend lines are based on a linear regression of calendar year and mean LER

in the LER. A decrease in LER leads to a decrease in the density of latewood of all species.

SPEI was not significant in all species. Thus, imposing normal hydroclimatic conditions (i.e., SPEI equal to 0) from 1901 to 2016 and considering a median tree in terms of tree-ring width, current DBH and latewood to earlywood ratio of each species using the model estimates, we inferred (i) for beech, an increase of latewood density of 7.1%, suggesting that even without significant changes in water stress, beech trees have been producing denser latewood over time, (ii) for fir, a decrease of latewood and mean wood density equal to 16.8% and 11.0%, respectively, suggesting that fir trees have been producing less dense wood over time, and (iii) for spruce, a decrease of the latewood and mean wood density equal to 16.1% and 7.2%, respectively, indicating that spruce, like fir, has been experiencing a decline in wood density (Fig. 3).

3.2 Influence of drought on wood density changes for beech, fir and spruce in European mountain forests over the last century

3.2.1 *SPEI trends*

Over the last century, SPEI decreased for Jelovica (Slovenia) and Igman (Bosnia and Herzegovina) by 1.93 and 0.93, respectively (Table 5, Fig. 4). This means that only in the Jelovica and Igman sites there was a worsening of the drought conditions, in the last hundred years. However, the percentage of cases with an SPEI value equal to or below -1.28, which indicates severe drought, has generally increased in all sites, except for Dürsüti (Switzerland), starting from 1980 (Table 5, Fig. 4). This finding aligns with the results from Monteiro nnnnnnnnnnnnand Costa (2023), which identified a significant change point in temperature trends in the Northern Hemisphere during the 1980s. In addition, the latest Intergovernmental Panel on Climate Change (IPCC) assessment stated, with high confidence, that the Northern Hemisphere springtime snow water equivalent has "generally declined" since 1981 (Masson-Delmotte et al. 2021). Then, by synthesizing our findings with the results from previously cited studies, we can argue that Europe's mountain forests have likely experienced increasing water deficits over the last century.

3.2.2 *Influence of drought on wood density*

In beech, drought did not affect the long-term variation of mean, early and latewood density either through interaction with TRW or current DBH (Table 4, coefficients of TRW*SPEI and cDBH*SPEI not significant). Drought enhanced the influence of LER on the mean wood density of beech (i.e., the coefficient of the LER went from 15.05 to 22.41) and attenuated the decreasing effect of LER on latewood density (i.e., the coefficient of the LER went from -12.03 to -4.95).

In fir, drought episodes influenced latewood density through the current DBH. Specifically, drought attenuated the positive effect of tree size on latewood density (i.e., the coefficient of the current DBH went from 2.19

Table 4 Summary statistics of the model [1] investigating the long-term trend in mean wood, earlywood and latewood density for the period 1901–2016. MWDI = mean wood density index, EWDI = earlywood density index, LWDI = latewood density index, YEAR = calendar year, TRW = tree-ring width, SPEI = Standardized Precipitation Evapotranspiration Index, cDBH = current DBH, LER = latewood to earlywood ratio, value = coefficient values, SE = standard error, significant (i.e., *p*-value < 0.05) parameter estimates are in bold

Beech										
Density type		**Intercept**	**YEAR**	**TRW**	**SPEI**	**cDBH**	**LER**	**TRW*SPEI**	**cDBH*SPEI**	**LER*SPEI**
MWDI	**value**	467.25	0.13	14.69	-8.35	-1.44	15.05	0.20	-0.05	7.36
	SE	324.95	0.17	2.22	6.33	0.51	2.47	1.70	0.18	2.54
	***p*-value**	0.151	0.432	**< 0.001**	0.188	**0.005**	**< 0.001**	0.904	0.788	**0.004**
EWDI	**value**	946.15	-0.15	10.03	-5.63	-0.68	-12.03	-0.46	-0.05	7.08
	SE	342.62	0.18	2.34	6.67	0.54	2.60	1.79	0.19	2.67
	***p*-value**	**0.006**	0.402	**< 0.001**	0.399	0.210	**< 0.001**	0.799	0.788	**0.008**
LWDI	**value**	-99.48	0.51	24.24	-11.12	-2.36	-18.63	-0.26	0.13	3.78
	SE	361.06	0.19	2.47	7.07	0.57	2.75	1.90	0.20	2.83
	***p*-value**	0.783	**0.007**	**< 0.001**	0.116	**< 0.001**	**< 0.001**	0.892	0.524	0.183
Fir										
Density type		**Intercept**	**YEAR**	**TRW**	**SPEI**	**cDBH**	**LER**	**TRW*SPEI**	**cDBH*SPEI**	**LER*SPEI**
MWDI	**value**	1567.20	-0.57	0.47	-1.62	1.82	83.60	0.42	-0.41	25.98
	SE	206.70	0.11	1.22	4.99	0.26	4.15	0.94	0.09	3.25
	***p*-value**	**< 0.001**	**< 0.001**	0.702	0.745	**< 0.001**	**< 0.001**	0.651	**< 0.001**	**< 0.001**
EWDI	**value**	73.85	0.14	4.05	0.28	0.63	30.02	-0.90	-0.14	13.53
	SE	185.39	0.10	1.10	4.51	0.23	3.74	0.85	0.08	2.93
	***p*-value**	0.690	0.155	**< 0.001**	0.951	**0.007**	**< 0.001**	0.290	0.967	**< 0.001**
LWDI	**value**	3848.92	-1.53	23.31	16.13	2.19	-68.40	-2.43	-0.61	1.14
	SE	351.80	0.19	2.08	8.54	0.44	7.09	1.60	0.16	5.56
	***p*-value**	**< 0.001**	**< 0.001**	**< 0.001**	0.059	**< 0.001**	**< 0.001**	0.130	**< 0.001**	0.837
Spruce										
Density type		**Intercept**	**YEAR**	**TRW**	**SPEI**	**cDBH**	**LER**	**TRW*SPEI**	**cDBH*SPEI**	**LER*SPEI**
MWDI	**value**	1257.24	-0.38	-2.71	-0.60	1.00	71.29	0.26	-0.09	9.02
	SE	218.45	0.12	1.14	5.09	0.29	4.44	1.01	0.10	4.05
	***p*-value**	**< 0.001**	**< 0.001**	**0.018**	0.907	**< 0.001**	**< 0.001**	0.801	0.349	**0.026**
EWDI	**value**	366.44	0.04	-0.45	5.61	-0.10	18.30	0.05	-0.10	-0.38
	SE	203.73	0.11	1.07	4.76	0.27	4.15	0.95	0.09	3.79
	***p*-value**	0.072	0.727	0.676	0.238	0.707	**< 0.001**	0.962	0.256	0.921
LWDI	**value**	3792.97	-1.49	15.85	-3.55	2.84	-77.49	-0.54	0.06	-10.89
	SE	353.90	0.19	1.85	8.25	0.46	7.20	1.64	0.16	6.57
	***p*-value**	**< 0.001**	**< 0.001**	**< 0.001**	0.667	**< 0.001**	**< 0.001**	0.744	0.713	0.097

to 1.58). Drought episode also attenuated the effect of tree size (i.e., the coefficient of the current DBH dropped from 1.82 to 1.41, Table 4) and enhanced the influence of LER (i.e., the coefficient of the LER went from 83.60 to 109.58) in the mean wood density.

In spruce, drought events in the past century did not affect late and earlywood density either indirectly in interaction with TRW, current DBH or latewood to earlywood ratio. In contrast, drought impacted the mean wood density by enhancing the LER effect (i.e., the coefficient of the LER increased from 71.29 to 80.31).

Table 6 reports the wood density trends resulting from the scenarios of possible combinations of drought severity and LER levels developed through the what-if analysis (Sect. 2.5.3).

In the case of beech, under severe drought conditions, LER did not significantly influence the trend of the mean wood density. Even in the case of extreme drought events in the past century, changes in LER (whether an increase or decrease by 50%) did not alter the trend in mean wood density for beech trees. This suggests that factors other than LER are more

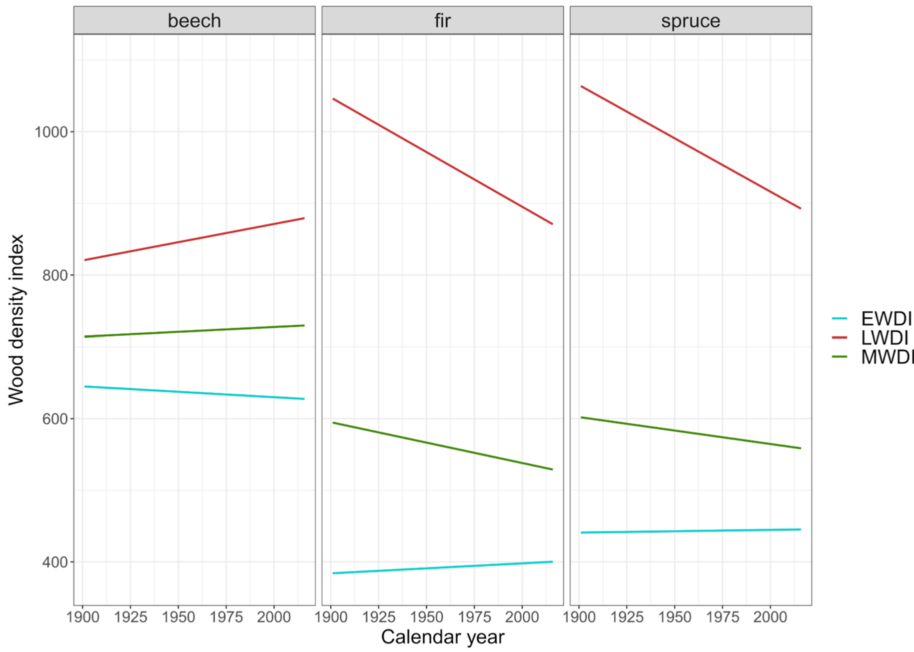

Fig. 3 Modelled trends of mean wood density, earlywood density and latewood density (MWDI, EWDI, and LWDI respectively) for the period 1901–2016 for a median tree in terms of tree-ring width, current DBH, and latewood to earlywood ratio of beech (TRW = 1.35 mm, cDBH = 27.45 cm, LER = 0.79), fir (TRW = 1.79 mm, cDBH = 40.02 cm, LER = 0.44) and spruce (TRW = 1.73 mm, cDBH = 36.76 cm, LER = 0.39), in normal hydroclimatic conditions (i.e., SPEI = 0)

Table 5 SPEI trend from 1901 to 2016, with values of the lower and upper bounds (lb and ub, respectively) and the *p*-value (significant, i.e., *p*-value < 0.05, trends are in bold). In the last two columns, the percentage of cases with an SPEI value equal to or below -1.28 are reported for the periods 1901 to 2016 and 1980 to 2016

Site	Country	SPEI trend (lb; ub)	*p*-value	Percentage of years with SPEI value equal to or below -1.28 (%)	
				1901 to 2016	1980 to 2016
Velingrad	Bulgaria	No trend	0.390	11.2	16.2
Igman	Bosnia and Herzegovina	-0.93 (-1.69; -0.23)	**0.012**	11.2	18.9
Jelovica	Slovenia	-1.93 (-2.6; -1.34)	**< 0.001**	13.8	35.1
Dürsüti	Switzerland	No trend	0.750	8.6	8.1
Kreuth	Germany	No trend	0.26	10.3	13.5

influential in determining the mean wood density of beech under drought conditions.

For fir, without the influence of higher LER (i.e., at median LER value), the mean wood density decreased to 10.8% under extreme drought conditions. With LER values 50% higher than the median, the decrease in mean wood density was slightly mitigated to 10.7%.

In the case of spruce, without higher LER, the mean wood density remained equal to 7.2% under extreme drought conditions. With LER values 50% higher than the median, the mean wood density decreased to 7.0%.

In summary, in cases of extreme drought, fir and spruce trees with LER values 50% higher than the median experienced a slight attenuation in the declining trend of their mean wood density, making the negative impact of drought less pronounced.

4 Discussion

4.1 Century-long changes in wood density

For beech in mountain forests, the changes in wood density observed from 1901 to 2016 differ from those reported in other studies. For example, Pretzsch et al.

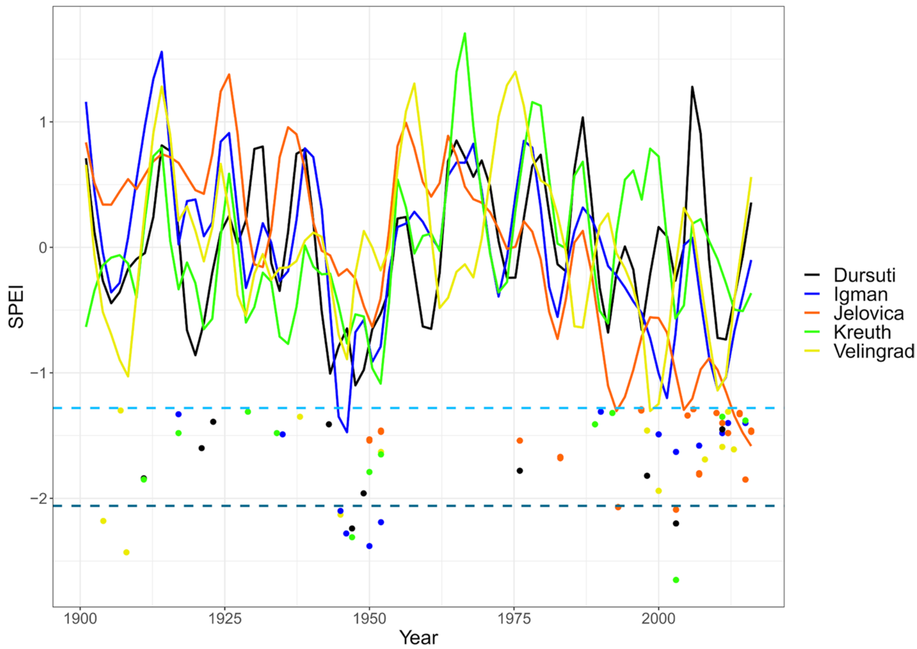

Fig. 4 6-month SPEI for August in the periods 1901–2016 in the study sites (smoothed lines are based on a span factor equal to 0.1). The dots, coloured according to the site, correspond to severe (i.e., 6-month SPEI for August equal to or below -1.28, dashed light blue line) and extreme drought (i.e., 6-month SPEI for August equal to or below -2.06, dashed dark blue line)

(2018) analysed beech trees that were, on average, 30 years older and sampled from some of the oldest existing experimental plots in the lowlands of Central Europe. Using a similar linear mixed-effect modelling approach, albeit with a different model structure, they found a decrease in the latewood density of beech (i.e., -12.1%) from 1900 to 2015. In contrast, our study highlights a 7.1% increase in the latewood density. We did not find changes in the earlywood density of beech, whereas Pretzsch et al. (2018) reported a 10.8% decrease. Additionally, we found no variation in the mean wood density of beech, while Pretzsch et al. (2018) identified an 11.2% decrease. Bontemps et al. (2013), using a linear mixed-effect modelling approach, found a 7.5% decrease in latewood density of beech from 1911 to 1983 in northeastern France. For fir, latewood density and mean wood density decreased by 16.8% and 11.0%, respectively, over the last century. However, due to the lack of comparable wood-density studies on this species, we cannot directly compare these trends with other research. The decrease in latewood wood density of spruce in our study is consistent with the findings of Pretzsch et al. (2018), although our results indicate a greater decline (-16.1% versus -4.2%). The decrease in mean wood density that we observed aligns closely with the results of Pretzsch et al. (2018), with our study showing a 7.2% decrease compared to their 7.7% decrease.

4.2 Causal factors of century-long changes in wood density

In beech, tree ring width, current DBH and LER collectively influence how the latewood density has evolved from 1901 to 2016. Referring to drought, despite the number of severe and extreme episodes generally increasing after 1980 (Table 5), drought events did not significantly influence latewood density in beech, nor were their influence mediated by tree-ring width, current diameter at breast height, or LER. In beech, the effect of drought was mediated by LER only on mean and latewood density. Bouriaud et al. (2004) highlighted the complexities in understanding wood density variability in beech trees, revealing that even with sophisticated models that account for water balance, a significant portion of the annual density variability remains unexplained. This led the authors to propose that a considerable part of the variability in tree-ring density is governed by internal tree factors rather than external climatic influences. They also observed notable differences between individual trees, suggesting that tree-specific factors play a role in density variability, although these factors did not significantly

Table 6 Predicted trend of wood densities according to a combination of different drought conditions (i.e., SPEI / Drought intensity) and levels of LER for all species. MWDI, EWDI, and LWDI columns identify the trend estimated by the model by fixing TRW = 1.35 mm, cDBH = 27.45 cm in the case of beech, TRW = 1.79 mm, cDBH = 40.02 cm in the case of fir, and TRW = 1.73 mm, cDBH = 36.76 cm in the case of spruce. The values of MWDI, EWDI and LWDI in bold refer to the cases when the estimated coefficients of LER*SPEI resulted as statistically significant in our models

Species	SPEI / Drought intensity	LER	MWDI (%)	EWDI (%)	LWDI (%)
Beech	0 / Mild	Median	**2.2**	**-2.7**	7.1
		1.5 of median	**2.1**	**-2.7**	7.2
		0.5 of median	**2.2**	**-2.7**	7.1
	-1.28 / Severe	Median	**2.1**	**-2.7**	7.1
		1.5 of median	**2.1**	**-2.7**	7.2
		0.5 of median	**2.2**	**-2.6**	7.0
	-2.06 / Extreme	Median	**2.1**	**-2.7**	7.0
		1.5 of median	**2.1**	**-2.7**	7.1
		0.5 of median	**2.1**	**-2.6**	7.0
Fir	0 / Mild	Median	**-11.0**	**4.2**	-16.8
		1.5 of median	**-10.7**	**4.1**	-17.0
		0.5 of median	**-11.4**	**4.2**	-16.5
	-1.28 / Severe	Median	**-10.9**	**4.2**	-16.5
		1.5 of median	**-10.7**	**4.1**	-16.8
		0.5 of median	**-10.7**	**4.1**	-16.8
	-2.06 / Extreme	Median	**-10.8**	**4.1**	-16.4
		1.5 of median	**-10.7**	**4.1**	-16.6
		0.5 of median	**-10.9**	**4.1**	-16.1
Spruce	0 / Mild	Median	**-7.2**	1.0	-16.1
		1.5 of median	**-7.0**	1.0	-16.3
		0.5 of median	**-7.4**	1.0	-15.9
	-1.28 / Severe	Median	**-7.2**	1.0	-16.0
		1.5 of median	**-7.1**	1.0	-16.2
		0.5 of median	**-7.1**	1.0	-16.2
	-2.06 / Extreme	Median	**-7.2**	1.0	-15.9
		1.5 of median	**-7.0**	1.0	-16.6
		0.5 of median	**-7.3**	1.0	-15.7

impact how trees respond to climate. Building on these findings, van der Maaten et al. (2012) used wood density profiles from beech cores collected in southwestern Germany to investigate these patterns further. Their research supported the notion that climatic influences on wood density are not confined to the late growing season. Instead, they demonstrated that climate-related associations with wood density could occur throughout the growing season. This study refined the understanding of how climate affects wood density, suggesting that the timing and duration of climatic influences are more complex and widespread than previously thought.

In fir, the decrease in latewood density was associated with increasing tree-ring width, larger current DBH, and a decreasing LER. The effect of drought on the decrease of latewood density was mediated by tree diameter and the LER. Considering the effect of tree size, our results are in line with those of Oggioni et al. (2024), who found a decline in fir growth responses to drought under extreme drought conditions, showing that, beyond certain climatic thresholds, the ability of the species to respond to drought is limited by physiological processes. The current DBH and LER were the two factors that influenced the decrease of mean and latewood density of fir in the past century, and these two factors mediated the effect of drought on the mean wood density. Higher-than-median LER values in fir trees help to buffer the impact of extreme droughts on mean wood density, reducing the extent of the decline that would otherwise occur. This suggests that LER plays a protective role in maintaining wood density under harsh environmental conditions.

In spruce, we found that the decrease in latewood density over the last century was due to an increase in tree-ring width, a tree diameter effect, and a decrease in the LER. Drought did not directly influence changes in latewood density, nor did it have an indirect effect through tree ring width, current DBH or LER. This suggests that the variability in latewood density is not strongly driven by drought conditions or mediated by these specific tree growth parameters. These findings do not agree with that of Jyske et al. (2008). In their study, they assessed the effect of artificially induced drought on the wood properties of spruce and found that in drought-exposed trees, cell wall proportion within an annual ring increased and, consequently, led to higher wood density. According to our results, drought had only an effect on mean wood density in spruce, mediated by the LER. Under extreme drought conditions, spruce trees with LER values 50% higher than the median experience a slight reduction in the declining trend of their mean wood density. This means that the negative impact of drought on mean wood density is marginally less severe for these trees, suggesting that higher LER values help mitigate the adverse effects of extreme drought on spruce mean wood density.

Analysing Fig. 6 in Appendix, we note that since the 1970s, the fraction of earlywood increased while the latewood density decreased in spruce. At the same time, observing Fig. 2, we notice that the LER of spruce decreased since the beginning of the past century: a decrease in LER suggests that, with the latewood portion remaining the same (Fig. 6 in Appendix), the earlywood portion has increased. This implies that the tree produced less latewood relative to earlywood in that period, potentially resulting in lower overall wood density. This was already reported for the same species in Central Europe by Pretzsch et al. (2018). In the region of their study, the average N-deposition increased in the first decade of the twenty-first century, and during the twentieth century, mean annual air temperature and precipitation increased. In the same area, temperature data indicated that the length of the growing season increased by 22 days during the last 110 years. Pretzsch et al. (2018) supposed that the observed extension of the growing season and the fertilization effect of dry N deposition are the main causes of the decrease in latewood density. The results of many studies conducted in fertilization trials showed that added nitrogen supply can strongly reduce wood density (Jozsa and Brix 1989; Cao et al. 2008; Mäkinen et al. 2002; Minikaev et al. 2024) and other research indicated that a rise in temperature entails a decrease of mean wood density in general and latewood density in particular (e.g., D'Arrigo et al. 1992; Thomas et al. 2004, 2007; Bouriaud et al. 2005; Ivković et al. 2013). Although we did not analyse the changes in mean temperature, length of the growing season and N deposition in our study area, it is plausible to suggest that the increase in temperature and N deposition could be additional factors contributing to the decline in latewood density observed over the past century.

4.3 Implications of changes in wood density for forest monitoring and management

Our findings may contribute to better monitoring of trees and stand vitality under climate change. A broad range of angiosperm and gymnosperm tree species with lower wood density show higher mortality responses (Chao et al. 2008; Martinez-Meier et al. 2008; Woodall et al. 2015; López et al. 2021) across biomes (Kraft et al. 2010; Greenwood et al. 2017; Liang et al. 2021). Considering that our study found a decrease in the mean wood density of fir and spruce from 1901 to 2016, it is crucial to pay more attention to tree-ring wood density measurements as a means for monitoring tree vitality and forest health.

A reduction in wood density may impact the management of stands where tree mortality needs to be addressed. Indeed, silvicultural interventions may attenuate the decrease in wood density by keeping higher stand densities. Many studies assessed the effects of thinning on wood density (Mörling 2002; Jaakkola et al. 2005, 2006; Peltola et al. 2007). For instance, strong stand density reductions applied to spruce in two long-term thinning experiments in southeastern Finland resulted in a reduction (1%–4%) of mean wood density compared with low thinning intensity (Jaakkola et al. 2005). Thus, keeping higher stand densities may counteract the decrease in wood density. Mitigating the reduction in wood density could potentially be achieved by encouraging the development of mixed species stands, which often have higher stand density (Pretzsch and Biber 2016). However, in their study, which aimed to determine whether tree species mixing modifies tree-ring wood density, Zeller et al. (2017) found that tree-ring wood density was lower in mixed stands of Scots pine (*Pinus sylvestris* L.) and beech compared to pure stands of the same species. Furthermore, they found that wood density was not influenced by stand density or tree size. It is important to note that the study of Zeller et al. (2017) was carried out in lowland forests in southern and eastern Germany and northern Spain, which have different climatic conditions compared to our mixed mountain forest stands.

The outcomes of our study should be considered when using tree standing volume or biomass to estimate the carbon stock of forest stands. Typically, wood density and carbon content are often assumed to be constant across regions, forest types and time (Woodall et al. 2015; Clough et al. 2017). However, our study demonstrates that the wood density of the main species of European mountain forests has varied over time and across species. Precisely quantifying the wood density of the species that make up a forest type and updating the values currently in use could positively impact the accuracy of carbon stock assessments and associated national greenhouse gas inventories (Clough et al. 2017). The revealed century-long reductions in wood density are not negligible in forest carbon balance calculations (Pretzsch et al. 2018). This consideration would also improve carbon sequestration estimates under current and future climate conditions (Alvarez et al. 2016).

4.4 Implications of the changes in wood density for wood utilization

When the wood density of living trees decreases, they may maintain their mechanical stability through structural and morphological acclimation (Mattheck and Mattheck 1998, Pretzsch et al. 2018), which reduces the risk of tree mechanical failure and uprooting by snow (Peltola et al. 2000) and wind (Putz et al. 1983; Dunham and Cameron 2000; Meyer et al. 2008). However, higher density values are not only crucial for the mechanical stability of trees but also for ensuring quality wood (Pretzsch and Rais 2016). As wood density provides a simple measure of the total amount of solid-wood substance in a piece of wood, it provides an excellent means for predicting end-use characteristics of wood such as strength, stiffness, hardness, heating value, machinability (Jozsa and Middleton 1994). These parameters, in turn, determine the end use of the wood, i.e., the type of product obtainable and practical implications for wood processing (Hacke et al. 2001; Olivar et al. 2015). The trend that emerged from our study suggests that the mechanical stability and strength of fir and spruce wood may change with consequences on the timber properties of these species. At the same time, if the wood is less dense, its thermal insulation properties improve because thermal conductivity declines as the wood density decreases (Le Duong and Zoltán 2021).

An additional implication of the changes in wood density for wood utilization is related to the use of wood for energy purposes, being a relatively carbon-balance-friendly renewable energy material. The energy content and calorific value are proportional to the wood density and carbon content and the energy yield is a relevant criterion for using biomass as fuel. Thus, the trends of wood density found reflect the species-specific changes in energy content and calorific value (Günther et al. 2012).

5 Conclusion

Our study provides valuable insights into long-term changes in the wood density of beech, fir and spruce in mountain forests across Europe. By analysing data from 1901 to 2016 using model inference, we observed an increase in latewood density for beech and a decline in both latewood and mean wood density for fir and spruce. For beech, these changes appeared to be driven by endogenous factors rather than the increase in drought events recorded since 1980. In contrast, for fir, drought played a role in shaping mean wood density by influencing the growth rate and latewood to earlywood ratio, although its impact was relatively minimal. For spruce, drought influenced the mean wood density through an effect mediated by the latewood to earlywood ratio. Given the expectation of more frequent drought events in Europe, our findings have significant implications for the accuracy of carbon stock assessments, national greenhouse gas inventories, and the utilization of wood from these species.

Appendix

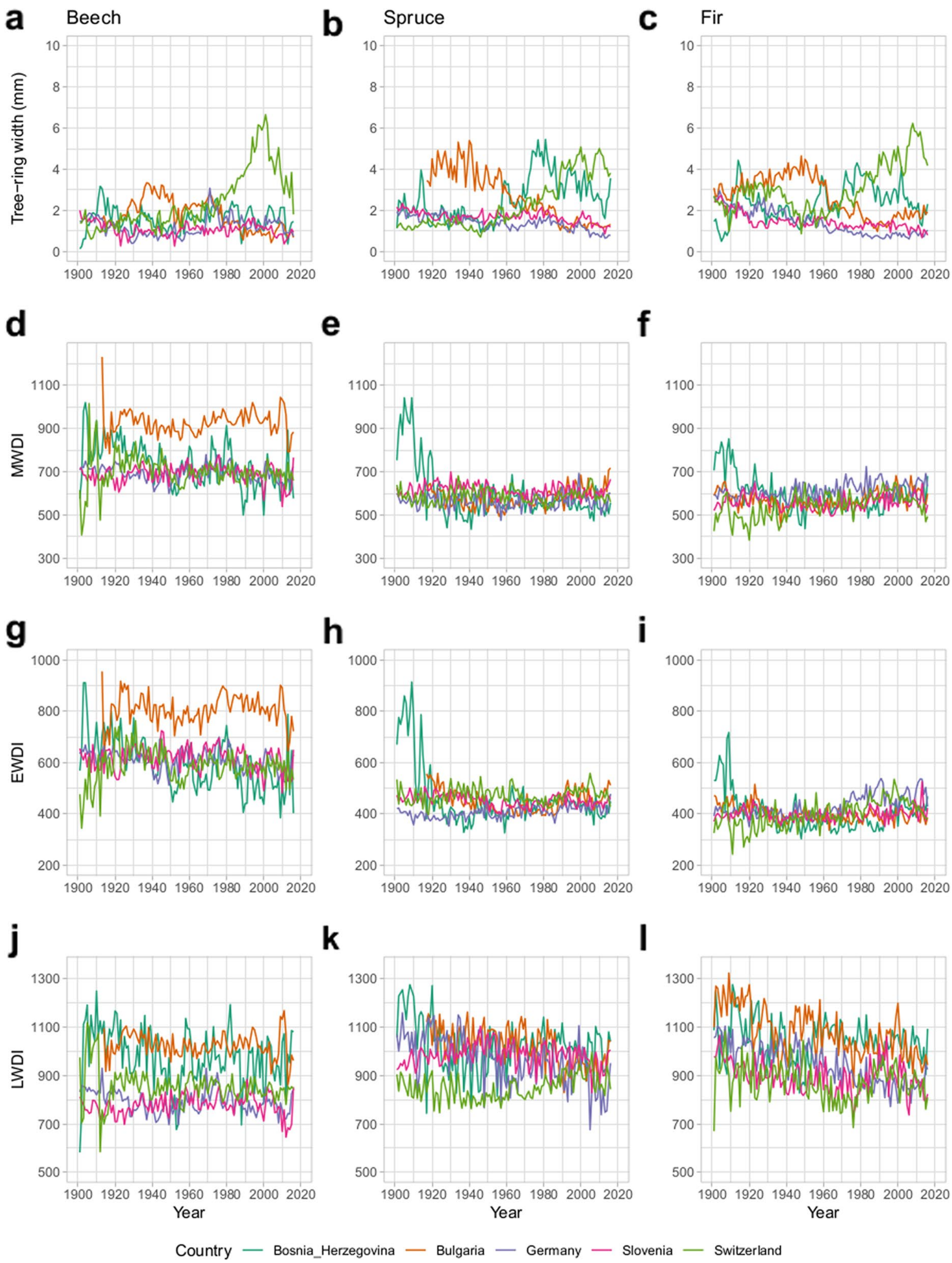

Fig. 5 Time series of tree-ring width (TRW), mean wood density index (MWDI), earlywood density index (EWDI) and latewood density index (LWDI) for beech (**a**, **d**, **g**, **j**), spruce (**b**, **e**, **h**, **k**) and fir (**c**, **f**, **i**, **l**) for the period 1901–2016

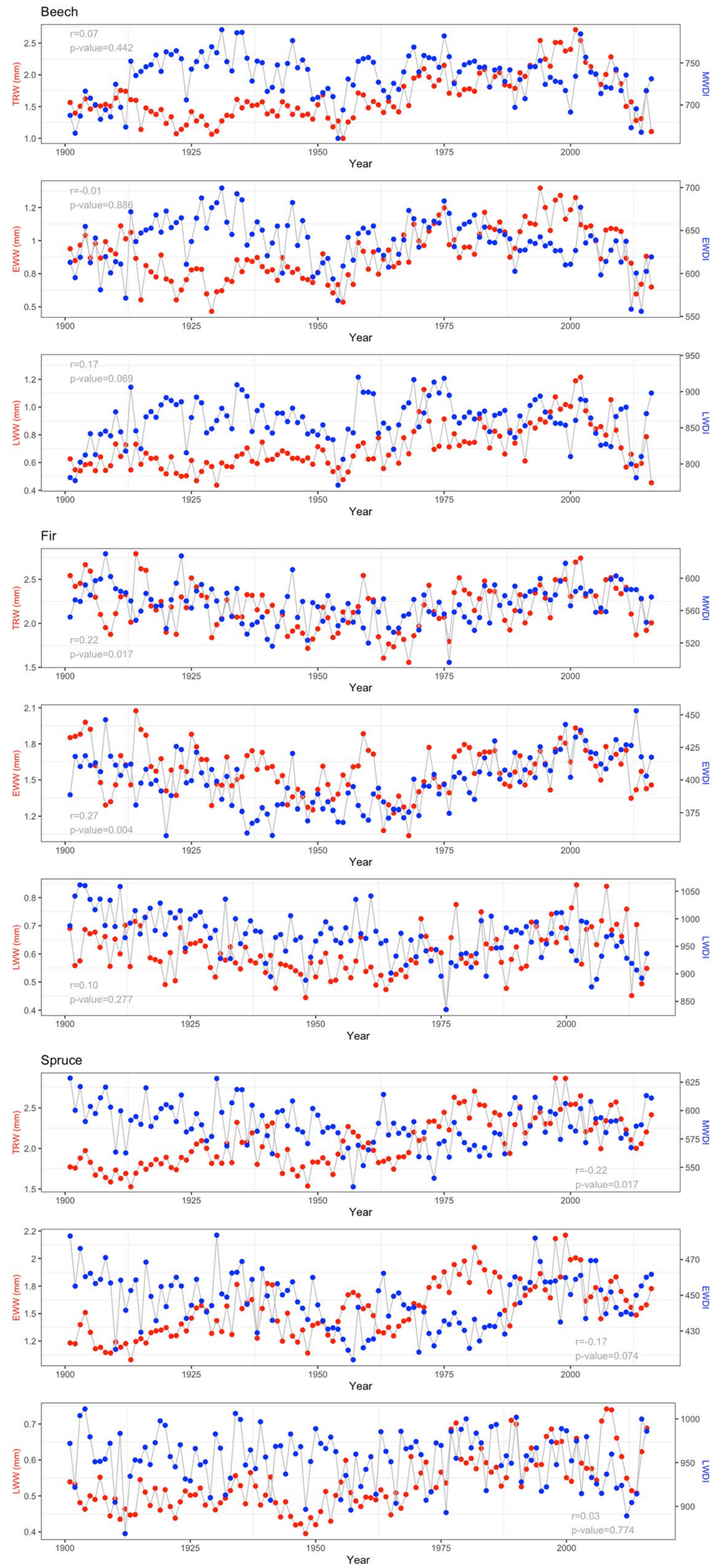

Fig. 6 Time series of tree-ring width (red) and wood density (blue) for beech, fir and spruce averaged across all sites for the period 1901–2016 with the Pearson correlation test results reported in each panel. TRW = tree-ring width; MWDI = mean wood density index; EWW = earlywood width; EWDI = earlywood density index; LWW = latewood width; LWDI = latewood density index; r= Pearson correlation coefficient; *p*-value = significance of correlation test

Table 7 Synthesis of the main variables that described the LIGNOSTATION™ system

Frequency of the sinusoidal signal produced by the high-frequency generator	Power of the sinusoidal signal produced by the high-frequency generator	Pressure of the high-frequency probe on the wood surface	X and Y resolution of the high-frequency probe	Spot measured by the tip of the high-frequency probe	Recording frequency of the signal received by the receiving electrode
10 MHz	50 mW	1 N	2/100 mm	20 µm x 20 µm	1 kHz

Table 8 List of weather stations from which the data, used in this study, have been collected with the period of data availability for the monthly mean temperature and monthly precipitation

Country	Locality	Latitude (°)	Longitude (°)	Elevation (m a.s.l.)	Time range of climate data availability
Bulgaria	Yundola	42.02	23.66	1383	1931-2007
Bosnia and Herzegovina	Bjelašnica	43.70	18.26	2067	1954-2016
Slovenia	Zgornja Sorica	46.22	14.02	846	1970-2016

Acknowledgements
We thank Florian Motte of TUM for his help with the dendrochronological laboratory work, Gerhard Schmied of TUM for his support with the climate data, and Mauro Bernabei of IBE-CNR for his help with tree ring cross-dating.

Authors' contributions
Conceptualization: [Chiara Torresan]; Methodology: [Chiara Torresan, Torben Hilmers, Edmondo Di Giuseppe, Enno Uhl], Formal analysis and investigation: [Chiara Torresan, Florian Motte, Edmondo Di Giuseppe], Writing—original draft preparation: [Chiara Torresan]; Writing—review and editing: [Torben Hilmers, Admir Avdagić, Edmondo Di Giuseppe, Matija Klopčič, Mathieu Lévesque, Florian Motte, Enno Uhl, Tzvetan Zlatanov, Hans Pretzsch], Funding acquisition: [Chiara Torresan]; Resources: [Torben Hilmers, Enno Uhl, Hans Pretzsch]; Supervision: [Torben Hilmers, Hans Pretzs, Enno Uhl].
The authors read and approved the final manuscript.

Funding
The activity in the dendrochronology laboratory of the Technical University of Munich in Freising in December 2021 was carried out thanks to the funding obtained by Chiara Torresan through the Short-Term Mobility—CALL 2021 of the National Research Council of Italy, a special program for the promotion of international collaboration between National Research Council of Italy and foreign research institutions through the short-term mobility of Italian and foreign scholars.

Data availability
The datasets generated and/or analysed during the current study are available in ETH Zurich Research Collection (Torresan et al., 2024) at this permanent link https://doi.org/10.3929/ethz-b-000642511.

Code availability (software application or custom code)
The custom code and/or software application generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors gave their informed consent to this publication and its content.

Competing interests
The authors declare that they have no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Author details
[1]Institute of BioEconomy, National Research Council of Italy, San Michele All'Adige, Italy. [2]Chair of Forest Growth and Yield Science, Department of Life Science Systems, TUM School of Life Sciences, Technical University of Munich, Freising, Germany. [3]Faculty of Forestry, University of Sarajevo, Sarajevo, Bosnia and Herzegovina. [4]Institute of BioEconomy, National Research Council of Italy, Rome, Italy. [5]Biotechnical Faculty, Department of Forestry and Renewable Forest Resources, University of Ljubljana, Ljubljana, Slovenia. [6]Silviculture Group, Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland. [7]Department of Biodiversity and Nature Conservation, Bavarian State Institute of Forestry (LWF), Freising, Germany. [8]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria.

Received: 20 December 2023 Accepted: 3 October 2024
Published: 2 December 2024

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