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The longevity of broadleaf deciduous trees in Northern Hemisphere temperate forests: insights from tree-ring series

Alfredo Di Filippo[1], *Neil Pederson*[2], *Michele Baliva*[1], *Michele Brunetti*[3], *Anna Dinella*[1], *Keiko Kitamura*[4], *Hanns D. Knapp*[5], *Bartolomeo Schirone*[1] *and Gianluca Piovesan*[1]*

[1] Department of Agriculture, Forest, Nature and Energy, Tuscia University, Viterbo, Italy, [2] Harvard Forest, Petersham, MA, USA, [3] Institute of Atmospheric Sciences and Climate, National Research Council, Bologna, Italy, [4] Hokkaido Research Center, Forestry and Forest Products Research Institute, Sapporo, Japan, [5] Federal Agency for Nature Conservation (BfN), Putbus, Germany

Edited by:
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Reviewed by:
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Canada

***Correspondence:**
Gianluca Piovesan,
Department of Agriculture, Forest,
Nature and Energy, Via SC de Lellis,
01100 Viterbo, Italy
piovesan@unitus.it

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Understanding the factors controlling the expression of longevity in trees is still an outstanding challenge for tree biologists and forest ecologists. We gathered tree-ring data and literature for broadleaf deciduous (BD) temperate trees growing in closed-canopy old-growth (OG) forests in the Northern Hemisphere to explore the role of geographic patterns, climate variability, and growth rates on longevity. Our pan-continental analysis, covering 25 species from 12 genera, showed that 300–400 years can be considered a baseline threshold for maximum tree lifespan in many temperate deciduous forests. Maximum age varies greatly in relation to environmental features, even within the same species. Tree longevity is generally promoted by reduced growth rates across large genetic differences and environmental gradients. We argue that slower growth rates, and the associated smaller size, provide trees with an advantage against biotic and abiotic disturbance agents, supporting the idea that size, not age, is the main constraint to tree longevity. The oldest trees were living most of their life in subordinate canopy conditions and/or within primary forests in cool temperate environments and outside major storm tracks. Very old trees are thus characterized by slow growth and often live in forests with harsh site conditions and infrequent disturbance events that kill much of the trees. Temperature inversely controls the expression of longevity in mesophilous species (*Fagus* spp.), but its role in *Quercus* spp. is more complex and warrants further research in disturbance ecology. Biological, ecological, and historical drivers must be considered to understand the constraints imposed to longevity within different forest landscapes.

Keywords: tree longevity, tree rings, old-growth forest, life history traits, temperate deciduous forest

Introduction

Identifying the biological and ecological drivers of forest tree longevity is a long-standing challenge. Exploring species longevity, i.e. the maximum lifespan of trees detected under specific environmental conditions, is an important step in the pursuit of a mechanistic understanding of tree life-history variation and plant geography, as they are related to morphological and physiological traits (e.g., Easdale and Healey, 2009; Stahl et al., 2014). Recent literature has revealed that within-species variation in traits is greater than previously supposed (Richardson et al., 2013), and such large within-species variation is also observed with tree longevity (Di Filippo et al., 2012). Although it is generally considered fixed for each species in ecological modeling, longevity appears to be tightly related to environmental features (e.g., Rotheli et al., 2012). While it has long been known that the age-size relationships are site-dependent (e.g., Suarez et al., 2008), we still have a poor understanding of how a species' longevity varies between forest stands and how it's driven by the environment (Di Filippo et al., 2012; Rohner et al., 2013). A quantitative understanding of the factors controlling tree growth and longevity in different environments is of utmost importance to (1) develop predictive models of tree longevity (Rohner et al., 2013) and forest demography (Stephenson et al., 2011), (2) comprehend ecosystem functioning under climate-change (Michaletz et al., 2014), and (3) develop sound environmental resource management and nature conservation strategies. Tree longevity's ecological counterpart is forest mortality, for which the causes of geographic variation have been explored only in a handful of studies (Stephenson et al., 2011).

Longevity studies are complex as they are intimately connected to the discovery of old-growth (OG) forests, a difficult task in the temperate forest biome where intense human activity has deeply transformed the natural landscape. Fragmentation and use of the forest landscape have affected the presence of OG forests, especially primary ones (Frelich and Reich, 2003). A macroecological approach based on large-scale ecological networks is thus required to better understand the drivers of tree longevity (Di Filippo et al., 2012). Over the last few decades, many dendroecological studies worldwide have generated a large amount of data from different species and environments. These campaigns are invaluable to explore the link between growth dynamics and longevity. Dendroecological studies of OG forests often require substantial scientific efforts, not only due to crossdating difficulties connected to competitive growth suppression and release (Black et al., 2008), but also due to increasing heart rot in older broadleaf tree species (Ranius et al., 2009). These factors limit our full comprehension of tree longevity under natural conditions.

Few meta-analysis studies have attempted to explore the patterns of longevity variation at the biome-scale (e.g., temperate deciduous forest) (Loehle, 1988; Bugmann and Bigler, 2011). In general, the maximum age found among temperate deciduous OG forests can vary widely, and do not seem to differ from other OG temperate and tropical forest types in terms of median age (∼300 years) and interquartile age range (200–400 years) (Wirth et al., 2009). Thousand-year old oak, plane, linden and chestnut trees are often reported in the gray literature (e.g., Plietzsch, 2009), even when pollarded in grazed woodland (Rozas, 2005; Drobyshev and Niklasson, 2010; Moir, 2012). In contrast, tree-ring studies have provided evidence that most deciduous tree species rarely exceed 4–5 centuries of age (e.g., OldList: www.rmtrr.org/oldlist.htm; Eastern Oldlist, www.ldeo.columbia.edu/∼adk/oldlisteast; Schweingruber and Wirth, 2009). In effect, studies on tree longevity must focus on measurement of tree age from annual growth rings so that a sound scientific assessment of longevity can be quantified.

Tree longevity patterns within-species can vary according to environmental (e.g., elevational) gradients (Di Filippo et al., 2012; Rotheli et al., 2012). It has long been known that there is a negative correlation between growth rates and longevity in both angiosperm and gymnosperm trees (Schulman, 1954; Black et al., 2008; Bigler and Veblen, 2009; Fritts, 2012). Indeed, this relationship appears to hold, even within-species growing along environmental gradients, as bioclimate and site fertility exert a strong control over tree growth (Di Filippo et al., 2012; Rotheli et al., 2012). Harsher environmental conditions seem to promote tree longevity via reduced tree growth, but the full understanding of their causal relationship, and the role of other life history traits (e.g., wood anatomy or mechanical properties; Loehle, 1988), is still missing. The availability of densely sampled tree-ring networks of widely distributed genera (such as *Fagus* or *Quercus*) allows us to investigate how environmental variations affect longevity in trees with similar life-history traits.

The aims of our study are to: (1) make a review of the longevity of the main genera of broadleaf deciduous (BD) trees living in closed-canopy temperate forests of different parts of the Northern Hemisphere using available tree-ring data; (2) identify the mechanisms controlling the expressed range of variation in tree longevity; and (3) explore the role of climate in controlling the expression of the realized maximum lifespan at biome scale.

Material and Methods

We created a dataset of maximum documented lifespan of BD trees from closed-canopy temperate forests in the Northern Hemisphere using tree-ring data and information from scientific literature or online databases. Original data consisted of tree-ring series already available in the laboratories of the coauthors of this manuscript (e.g., Piovesan et al., 2005; Di Filippo et al., 2007; Kitamura et al., 2007; Pederson, 2010; Martin-Benito and Pederson, 2015). Online data were retrieved by different sources, such as: OLDLIST (Brown, 1996; www.rmtrr.org/oldlist.htm); Eastern OLDLIST (http://harvardforest.fas.harvard.edu/oldlist-east); the International Tree-Ring Data Bank (ITRDB) (www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring).

Gathering Longevity Data from Tree-ring Studies

The criteria used to include a tree into the dataset can be summarized as follows:

- Age data came exclusively from tree-ring series developed through dendrochronological standards (Stokes and Smiley, 1996). Where samples without pith had estimated ages for those missing years, we excluded the estimated data. As heart rot is frequent in very old deciduous trees (Ranius et al., 2009), this restriction excludes ages derived through extrapolation rather than direct observation.
- Priority was given to trees living in OG forests (certified by our own field research or by the selected scientific literature).

OG forests contain old trees because they have not experienced recent stand-replacing disturbances. The identification of OG status is characterized by natural canopy tree mortality. Because wood decay often prevents the measurement of tree-rings on dead trees, maximum age from a sufficiently replicated dendroecological sampling can be used as a surrogate of maximum tree lifespan (i.e., longevity) within that forest. The occurrence of natural mortality connects maximum lifespan to local environmental conditions, and allows us to analyze longevity variations across different environments.

- When the OG status couldn't be certified, we used the oldest tree in sampling sites reported in online databases. Given that in warmer sites tree longevity is lower due to faster growth rates (Di Filippo et al., 2012) and turnover rates (Stephenson and van Mantgem, 2005), we used two different age thresholds for "old" trees to streamline the online database search: 400 years (i.e., above the 75th percentile in Wirth et al., 2009) in cool temperate forests and 200 years (i.e., above 25th percentile in Wirth et al., 2009) in warm temperate ones. Warm-cool temperate climate distinction was based on threshold values (mean annual temperature above 12°C or mean temperature of the warmest month above 21°C) reported in Holdridge's Life Zone system (Adams, 2010) and Box and Fujiwara (2015). Trees in the two climatic regimes with ages below these two thresholds (200 and 400 years) were not considered in our analyses.
- All data came from dendroecological studies, which require that samples are replicated enough to efficiently report a certain ecological information, e.g., the climatic signal or disturbance history (Stokes and Smiley, 1996). Tree-ring sampling generally requires large core replication (usually $\geq$20 cores per species) covering most of the study forest area. When multiple species were present in the same area, each species' maximum age was analyzed separately.
- When available, we retrieved the ring-width series of the oldest tree to characterize its growth history.

The website Dendrobox (www.dendrobox.org) was used as a tool to locate potential tree-ring studies involving BD trees in the Northern Hemisphere (Zang, 2015).

Retrieving Climate Data for Each Forest

We assessed the role of bioclimate (i.e., annual precipitation; mean temperature of the year, and of the coldest and the warmest month) in controlling the expression of maximum lifespan found at each site. To explore the lifespan-climate relationship, climate data for each site were retrieved via different methods, depending on data availability. In our initial screening, climate data was collected from either (1) climatic time series that were readily available for the site (all US and most European study sites) or (2) the nearest available weather station, which limited us to yearly or monthly climate averages.

Of the 136 sites, 30 (roughly 22%) of our sites did not have high-resolution climatic data. These sites were mostly comprised of those retrieved from literature, online databases and some Japanese sites. In these cases, we corrected for the difference in elevation between the study site and the meteorological station by applying a lapse rate of −0.55°C/100 m. Rolland (2003) reported for the European Alps an observed mean temperature lapse rate between −0.54 and −0.58°C/100 m. In Italy, considering an area spanning 12° latitude, the mean annual temperature lapse rate varied between −0.54°C/100 m in Northern Italy and -0.57°C/100 m in Southern Italy (Brunetti et al., 2014).

For the US and European (Italy and Austria) sites, we used high-resolution (30-arcsecond) temperature and precipitation (1981–2010) monthly climate normals. For the US, we used climate normals provided by the PRISM Group (Daly et al., 2008), based on a climate–elevation regression estimated for each 30-arcsecond digital elevation model (DEM) grid cell, where stations entering the regression are assigned weights based on the physiographic similarity between weather stations and the grid cell. Corresponding to the exact forest location, we estimated the local vertical gradient (using 21 × 21 PRISM grid boxes, about 400 km^2, centered on each site) of each meteorological variable and extrapolated its value to the site elevation. For Italy and Austria, normal climate data were obtained using a similar approach (e.g., Efthymiadis et al., 2006; Brunetti et al., 2012, 2014). In this case, thanks to the direct availability of source station data, the relationship between the meteorological variable and elevation was directly reconstructed for each site location using the nearby stations rather than surrounding grids (Brunetti et al., 2014). Both procedures provided reconstructed climate information with associated mean absolute error ranging between 0.5–1.0°C for mean monthly temperature and between 3 and 14 mm for total monthly precipitation, depending on the month considered (Daly et al., 2008; Brunetti et al., 2012, 2014).

The comparison among sites was based on annual temperature and precipitation, and mean temperature of the coldest/warmest months, as these variables are those generally reported in literature for describing site conditions.

Exploring the Factors Promoting Tree Longevity

The relationships between maximum tree lifespan and potential explanatory variables were first explored using a linear regression analysis for all species within our dataset. Next, we evaluated the most represented genera in our collection *(Fagus, Quercus*, *Liriodendron*) separately. When evaluating the maximum lifespan-climate relationships, we focused on *Quercus* and *Fagus* as both cover more continents. Since growth suppression can be an important factor promoting tree longevity (Black et al., 2008; Bigler and Veblen, 2009; Di Filippo et al., 2012), lifespan data were analyzed separately for shade-tolerant and shade-intolerant or intermediate species (see **Table 1**). In forests with many coexisting species, all species were considered separately when assessing the relationship between longevity and growth rate. However, only the oldest species was kept when assessing the temperature control over longevity. Given the established focus of the manuscript, our analyses excluded long-living trees of Mediterranean open dry woodland/shrubland (e.g., *Quercus douglasii, Q. canariensis*), which grow in severely moisture-stressed environmental conditions and may present a semi-deciduous habit.

TABLE 1 | The oldest tree found for each deciduous species in temperate forest of the Northern Hemisphere.

Max age	Species	CODE	Family	Site	Continent	Lat (°)	Long (°)	Elevation (m a.s.l.)	ST[a]	DT[a]	WT[a]	Leaf type	SDS	SB[b]	SW[b] (g)	PO[c]	WBD[d] (g/cm^3)	Reference/Author/ Source
679	Nyssa sylvatica	NYSY	Cornaceae	Blakes Hill Bog USA	N-America	–	–	–	Y	N	Y	S	B–O	O	145	DP	0.460	Sperduto et al., 2000
600	*Quercus robur*	QURO	*Fagaceae*	Sweden	Europe	57.3500	15.7900	100	N	N	Y	S	B	R	3378	RP	0.560	Drobyshev and Niklasson, 2010
559	*Fagus sylvatica subsp sylvatica*	FASY	*Fagaceae*	Valle Cervara, Italy	Europe	41.8285	13.7310	1763	Y	N	N	S	B	O	251	DP	0.585	This study
520	*Magnolia acuminata*	MAAC	*Magnoliaceae*	Cook Forest, USA	N-America	41.7000	−79.2500	448	N	N	N	S	O	O	88	DP	0.440	This study
509	*Liriodendron tulipifera*	LITU	*Magnoliaceae*	Forge Creek, USA	N-America	35.5300	−83.8300	670	N	N	N	S	A	O	54	DP	0.400	This study
501	*Acer pseudoplatanus*	ACPS	*Sapindaceae*	Parco Nazionale d'Abruzzo, Italy	Europe	41.8000	13.7833	1765	Y	N	N	Pa	A	R	97	DP	0.508	Biondi, 1992
464	*Quercus alba*	QUAL	*Fagaceae*	Blue Ridge Parkway Virginia, USA	N-America	37.5000	−79.5000	1100	N	Y	N	S	B	R	2997	RP	0.600	This study
461	*Quercus petraea*	QUPE	*Fagaceae*	Cavergno, Switzerland	Europe	46.3500	8.6000	900	N	N	N	S	B	R	2342	RP	0.560	Fonti et al., 2009
400	*Fagus sylvatica subsp. orientalis*	FASY	*Fagaceae*	Artvin, Turkey	Europe	41.3000	41.9000	1975	Y	N	N	S	B	O	251	DP	0.585	Kose and Guner, 2012
435	*Fagus crenata*	FACR	*Fagaceae*	Liyama, Japan	Asia	36.8230	138.5673	1275	Y	N	N	S	B	IN	147	DP	0.551	Nagano Regional Forest Office, 1989
427	*Quercus montana*	QUPR	*Fagaceae*	Uttertown New Jersy, USA	N-America	41.1000	−74.4300	350	N	N	N	S	B	R	4539	RP	0.570	Pederson et al., 2013
416	*Quercus mongolica*	QUMO	*Fagaceae*	Kunashir, Russia	Europe	43.8800	145.6000	65	N	N	N	S	B	R	2980	RP	0.644	ITRDB (Jacoby et al.)
407	*Aesculus flava*	AEFL	*Sapindaceae*	Gladie Creek,USA	N-America	37.8000	−83.6000	240	Y	N	N	Pa	B	R	12530	Dp	0.34	Cooper, 2011
405	*Quercus sp.*		*Fagaceae*	Braconne, France	Europe	45.7333	0.3000	11	N	N	N	S	B	R	3378	RP	0.560	Labuhn et al., 2014
405	*Quercus muehlenbergii*	QUMU	*Fagaceae*	Floracliff SNP, USA	N-America	37.9040	−84.3622	225	N	Y	N	S	B	R	1192	RP	-	Pederson et al., 2012
367	*Quercus stellata*	QUST	*Fagaceae*	Washington County, USA	N-America	35.8300	−94.0000	550	N	Y	N	S	B	R	1195	RP	0.721	ITRDB (Stahle)
357	*Kalopanax pictus*	KAPI	*Araliaceae*	Hokkaido, Japan	Asia	43.3333	143.7833	245	N	N	N	Pa	O	O	5	RP	0.389	Abrams et al., 1999
354	*Carya ovata*	CAOV	*Juglandaceae*	Fiddler's Green, USA	N-America	37.7694	−79.2415	640	N	N	N	Pin	B	O	4222	RP	0.640	Pederson et al., 2007
350	*Fagus grandifolia*	FAGR	*Fagaceae*	Warren Woods, USA	N-America	41.8200	−86.6200	350	Y	N	N	S	B	O	266	DP	0.560	Poulson and Platt, 1996
336	*Betula lenta*	BELE	*Betulaceae*	Mohonk, USA	N-America	41.7500	−74.2000	220	N	N	N	S	A	O	0.7	DP	0.600	Pederson et al., 2013
329	*Quercus lyrata*	QULY	*Fagaceae*	S Carolina, USA	N-America	33.1800	−80.4200	12	N	N	Y	S	B–H	R	3243	RP	0.570	ITRDB (Stahle and Sierzchula)
325	*Carya glabra*	CYGL	*Juglandaceae*	Sipsey Wilderness, USA	N-America	34.3300	−87.4500	225	N	Y	N	Pin	B	O	3502	RP	0.660	This study
322	Quercus rubra	QURU	Fagaceae	Wachusett Mountain, US	N-America	42.5000	−71.9000	550	N	N	N	S	B	R	3143	RP	0.560	Orwig et al., 2001

(Continued)

TABLE 1 | Continued

Max age	Species	CODE	Family	Site	Continent	Lat (°)	Long (°)	Elevation (m a.s.l.)	ST[a]	DT[a]	WT[a]	Leaf type	SDS	SB[b]	SW[b] (g)	PO[c]	WBD[d] (g/cm^3)	Reference/Author/ Source
313	*Acer saccharum*	ACSH	*Sapindaceae*	Big Reed Forest,, USA	N-America	46.3500	−69.0500	427	Y	N	N	Pa	A	O	55	DP	0.560	Chokkalingam and White, 2000
300	*Acer rubrum*	ACRU	*Sapindaceae*	Catskill Mountains, USA	N-America	41.8000	−74.2500	-	Y	N	N	Pa	A	O	24	DP	0.490	Pederson et al., 2007

Red, blue and black text indicates, respectively, species with maximum age above 500 years, between 400 and 500 years, less than 400 years.
ST, shade tolerace; DT, drought tolerance; WT, waterlogging tolerance. Leaf type: Pa, palmate compound; Pin, pinnate compound. S, simple; SDS, seed dispersal syndrome; A, anemocory; B, barocory; H, hydrochory; O, ornithochory; SB, storage behavior; IN, intermediate; O, orthodox; R, recalcitrant; SW, Mean 1000 Seed Weight; PO, porosity; DP, diffuse porous; RP, ring porous; WBD, Wood basic density.

[a] *Niinemets and Valladares (2006).*

[b] *Seed Information Database—Royal Botanic Gardens.*

[c] *Inside Wood—North Carolina State University.*

[d] *Global Wood Density Database—Dryad.*

Results

Our final dataset contained 136 dendrochronologically analyzed trees covering North America, Europe, and Asia, representing 25 species and 12 genera. Trees in this dataset covered a wide range of climatic conditions, with mean annual temperature spanning 4–18°C and mean annual precipitation varying between ~700 and 3000 mm (**Figure 1**). About 2/3 of our study sites came from our own research with the remaining being derived from literature or online databases (Table S1).

A wide variability in maximum age emerged within this large range of climatic conditions, either for the same species in different locations or for different species growing within the same forest (**Figure 2**). The maximum lifespan of most trees varied generally between 300 and 400 years (interquartile range in **Figure 2**). However, the full range of observed values was far wider, i.e., between 100 and circa 600 years. Latitude/elevation variations affected longevity (r is 0.36 for latitude and 0.43 for elevation, both $p = 0.05$; **Table 1**). The lowest ages were represented by low-elevation beech trees growing in warm temperate forests on highly fertile volcanic soils (e.g., *Fagus grandifolia* in Mexico or *F. sylvatica* in central Italy). The longest lifespan was reported in the eastern US for *Nyssa sylvatica* (679 years), a highly shade-tolerant species growing in wetlands that tolerates long suppression periods and commonly occupies an intermediate canopy position (Sperduto et al., 2000; Abrams, 2007). A distinguishing feature of this species is its extremely low growth rates (see **Figure 7**; Pederson, 2010). *N. sylvatica* was slightly older than a 600 year old Swedish oak (*Quercus robur*) reported by Drobyshev and Niklasson (2010), a 559 year old beech tree of the central Apennines in Italy, both growing in northern or high-mountain cold climates, and a 509 year old yellow poplar (*Liriodendron tulipifera*) in an acidic, north-facing, cove at low elevation in the Smoky Mountains of the southeastern US (Pederson, 2010). The most replicated genera (*Quercus*, *Fagus*, *Liriodendron*) in our study showed a similar median age. On average, oaks have a slightly higher maximum lifespan. But, the lower bound for the beech 25th percentile showed lower age expectations than for oak.

Among different sites, the maximum ages of the oldest trees belonging to each species were strongly and inversely related to their growth rate, as expressed by mean ring-width (**Figure 3**). The relationship also held for the most replicated genera, analyzed separately. *Fagus sylvatica* in southern Europe and *Liriodendron tulipifera* in the eastern US both exhibited highly significant negative growth-lifespan relationships (slopes respectively equal to −0.81 and −0.73, in both cases $P < 0.01$; see legend in **Figure 3**). *Nyssa* was not fully explored across its range in this study. *Fagus* and *Liriodendron* exhibited more negative slopes than *Quercus* (regression slope = −0.28; **Figure 3**), which was not able to reach the highest lifespan at slow growth rates, as predicted by the 600 years old Swedish oak (growth series not available; Drobyshev and Niklasson, 2010). Interestingly, oaks (especially *Quercus alba*) had older lifespans than the other species while sustaining growth rates over centuries.

The strongest lifespan relationship with climate was with the temperature of the warmest month (in terms of regression significance and variance explained; **Figure 4**, Figures S1, S2; Di Filippo et al., 2012). The shade-tolerant *Fagus* and *Acer* species showed a consistent, highly significant relationship characterized by a steep decrease of maximum lifespan with increasing temperature. We found a relationship for these two species where trees can be 30 years younger in longevity for each Celsius degree increase during the warmest month of the year (see legend in **Figure 4**). *Nyssa sylvatica* and *Aesculus flava* did not yield significant model fits, which might be due to the limited amount of data across their distributions. For oaks, and in general for shade-intolerant species, the regression was weaker and essentially maintained by the oldest Swedish oak tree of 600 years. Correlation between growth-rates and climate confirmed these results. In fact, among all species used in the regressions of **Figure 3**, *Fagus sylvatica* was the only one with available ring-width data that showed a significant correlation with temperature ($r = 0.75$, $P \leq 0.001$).

Within the OG *Fagus sylvatica* forests growing from the Alps to the Southern Apennines studied to date, the oldest trees were significantly smaller in diameter and slow growing in comparison to the larger ones in the same stand (**Figure 5**). Slower growth rates in the oldest beech trees are generally associated with long and repeated suppression phases (**Figure 6**). It is remarkable that the oldest beech trees (**Figure 6**) are found in primary forests of the Central Apennines (see Ziaco et al., 2012), where the longest

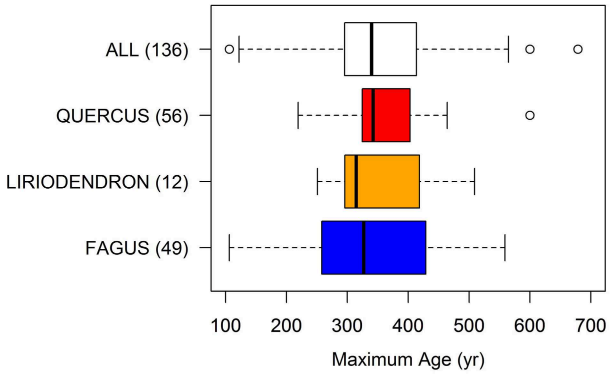

FIGURE 2 | Boxplots of the maximum age found for all temperate deciduous trees in our dataset and separately for the main genera. Within parentheses, the number of trees in each boxplot. The central bar is the median, the margins of each box are the first and third quartile, the whiskers are at ± 1.57 interquartile range and external points are outliers.

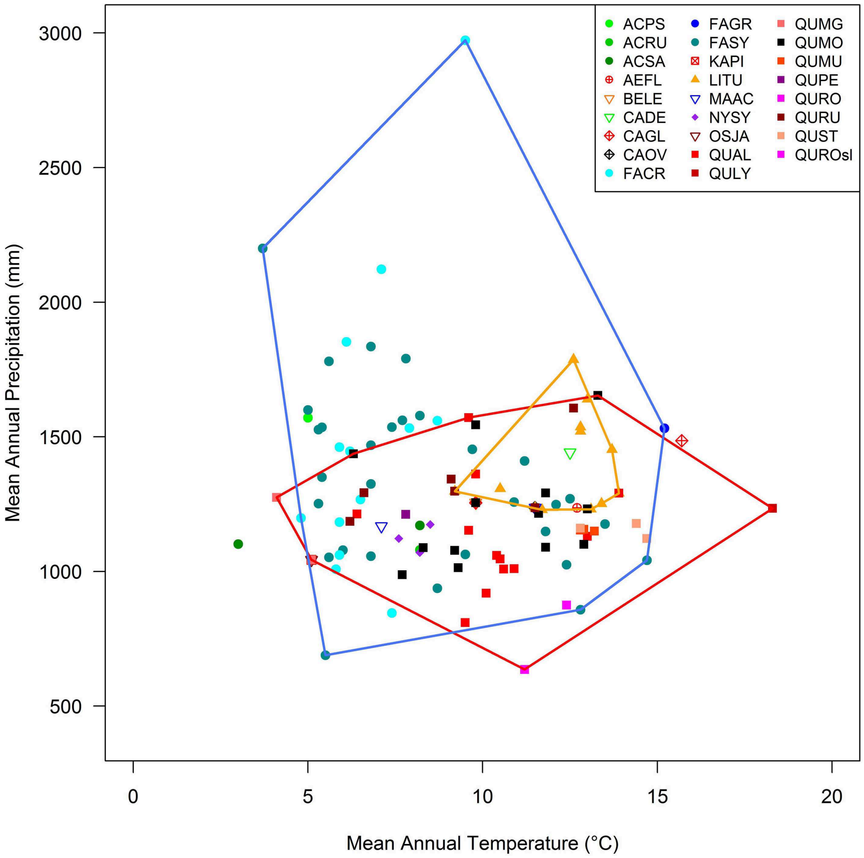

FIGURE 1 | Precipitation–temperature space occupied by the temperate deciduous forests analyzed. Symbols-colors refer to different genus-species. Convex hulls for *Quercus*, *Fagus,* and *Liriodendron* are drawn in red, blue and orange, respectively. Acronyms in **Table 1**.

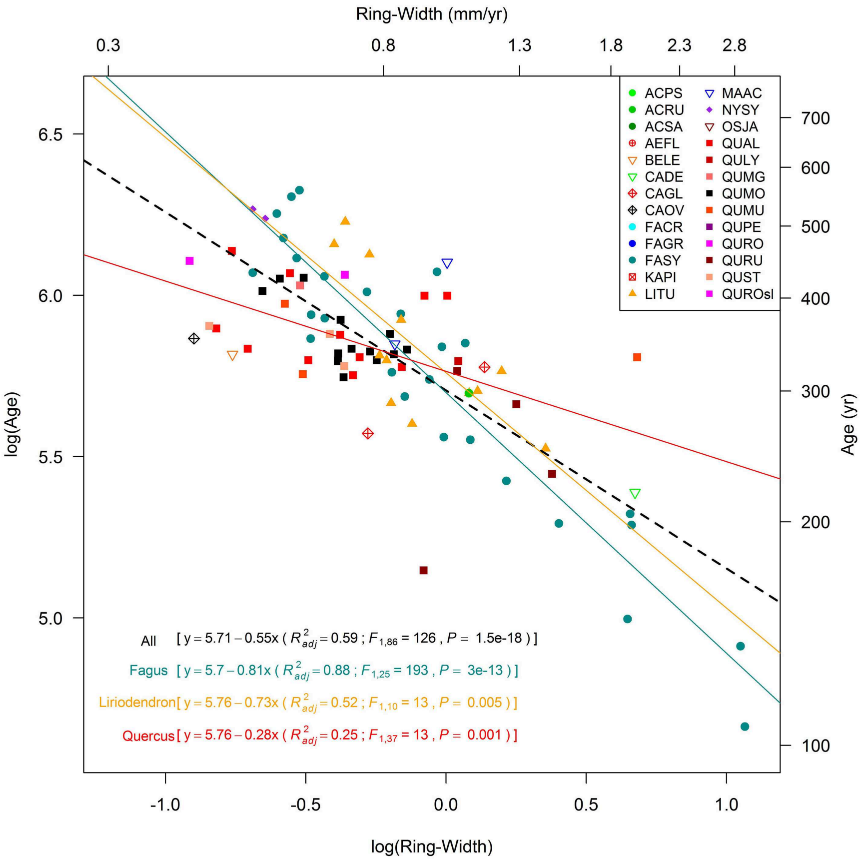

FIGURE 3 | Relationships between the age of the oldest deciduous tree within each temperate old-growth forest and its mean ring-width. Values are represented using log-transformed scales, regression lines were developed for all sites together and separately for the main *genera* (within parentheses: R^2_{adj}, adjusted R^2; *F*, value of the *F* statistic; *P*, significance of the *F*-test). Species code in **Table 1** (QUROsl = *Quercus robur sensu latu*, i.e., the exact species not reported in the literature paper). The oldest NYSY couldn't be plotted because the tree-ring series was not available.

suppression events are experienced (Di Filippo et al., 2012). In Europe and in the US (**Figure 7**), the oldest trees found in temperate deciduous forests showed a mean ring-width close to 0.5 mm/year, a threshold generally reported to track suppression phases in ring-width series in temperate trees (Canham et al., 1990). Interesting exceptions were provided by *Fagus sylvatica* in the Northern Apennines (**Figure 6**) and *Magnolia acuminata* and *Quercus rubra* in the US (**Figure 7**), where trees experienced long periods of sustained growth, especially in the early stages of life. The oldest *Liriodendron tulipifera* was truly a surprising and exceptional finding, since this 509 years old tree has faster growth rates in comparison to other species of similar maximum age (*Fagus sylvatica* and *Nyssa sylvatica*; **Figure 3**), and is the tallest *L. tulipifera* so far measured in the eastern US (N. Pederson, *personal communication*). This underlines that many ways can exist to attain the maximum lifespan in different tree species and environment.

Discussion

Several BD tree species growing in different sites of the temperate biome of the Northern Hemisphere showed longevities of 500–600+ years (**Table 1**). Amazingly, species from evolutionary distant families and genera—*Fagus*, *Quercus*, *Nothofagus* (Pollmann, 2005), *Acer*, *Magnolia*, *Nyssa*, *Liriodendron*—converge to similar age limits. These species do not show outstanding commonalities in life history traits (**Table 1**), suggesting that functional traits (e.g., wood density) may not always be the dominant determinants of longevity (see Loehle, 1988). Our findings suggest that much remains to understand how biological (e.g., wood properties, anatomy) and ecological (e.g., r-K selection) properties can definitively influence tree longevity. Since intraspecific plant trait variation could be driven by the environment (Richardson et al., 2013), future exploration of their influence on the realized tree longevity must also consider their simultaneous variability along wide environmental gradients.

The maximum lifespan realized by the BD trees in our overall dataset showed a remarkable variability (100–650 years; see also Wirth et al., 2009). In this study, the lower quartile of age distribution was 300 years, which is higher than the previously reported quartile age of 200 years (see Wirth et al., 2009). This could be related to the exclusive use of rigorously dated tree ages through dendrochronological techniques, or to the

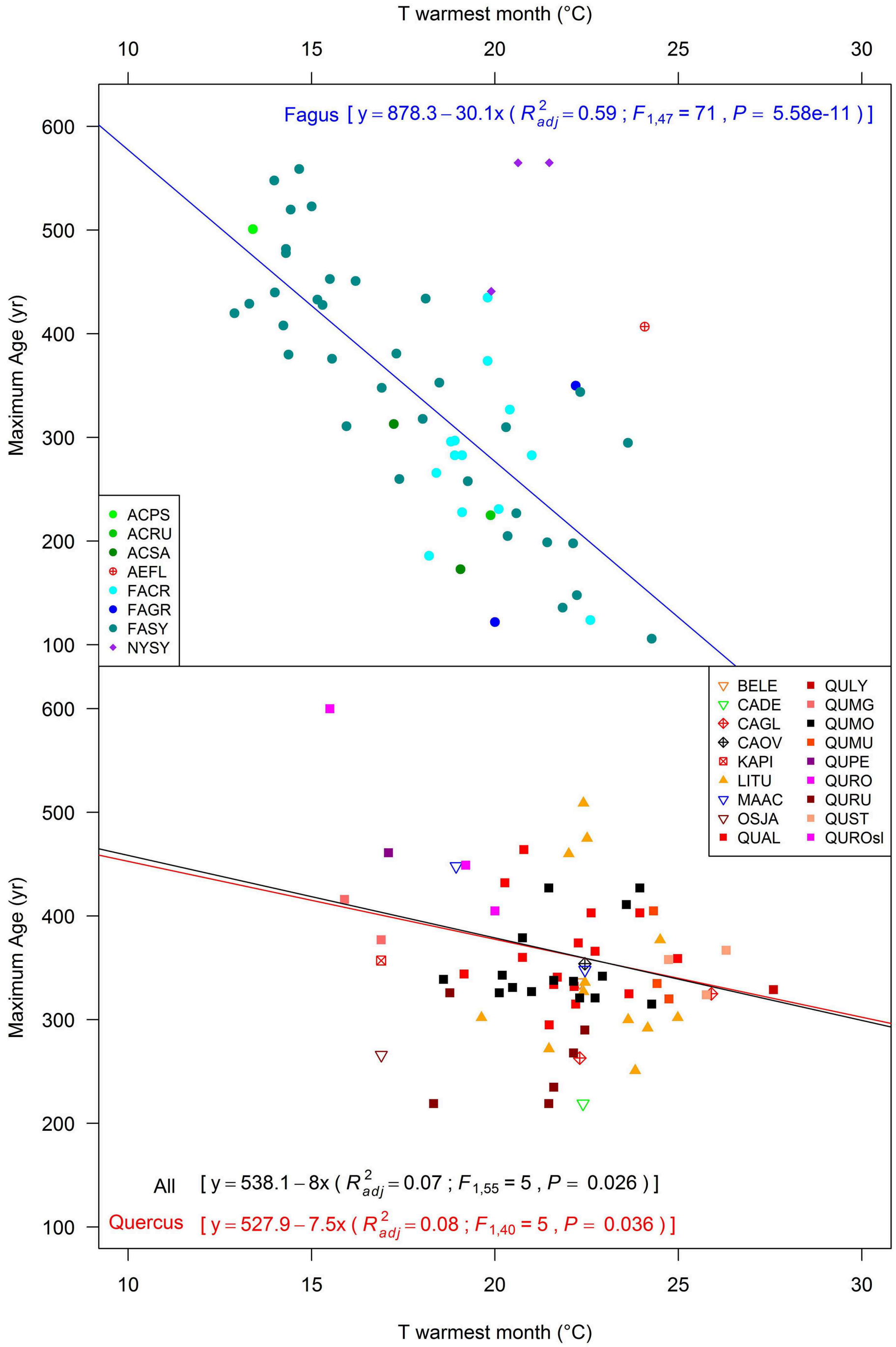

FIGURE 4 | Relationships between the age of the oldest deciduous tree within each temperate old-growth forest and its mean ring-width. Values are represented using log-transformed scales, regression lines were developed for all sites together and separately for the main *genera* (within parentheses: R^2_{adj}, adjusted R^2; *F*, value of the *F* statistic; *P*, significance of the *F*-test). Species code in **Table 1** (QUROsl = *Quercus robur sensu latu*, i.e., the exact species not reported in the literature paper).

fact that we used maximum age rather than other forest age indicators (e.g., mean canopy age, mean age of the oldest 10 trees). According to our results, 300–400 years can be baseline values for most temperate deciduous OG forests. These baseline values hold even when analyzing the most represented genera separately, and verify reported lifespans in tropical forests, where large trees over 300 years old may be relatively abundant (Metcalf et al., 2009).

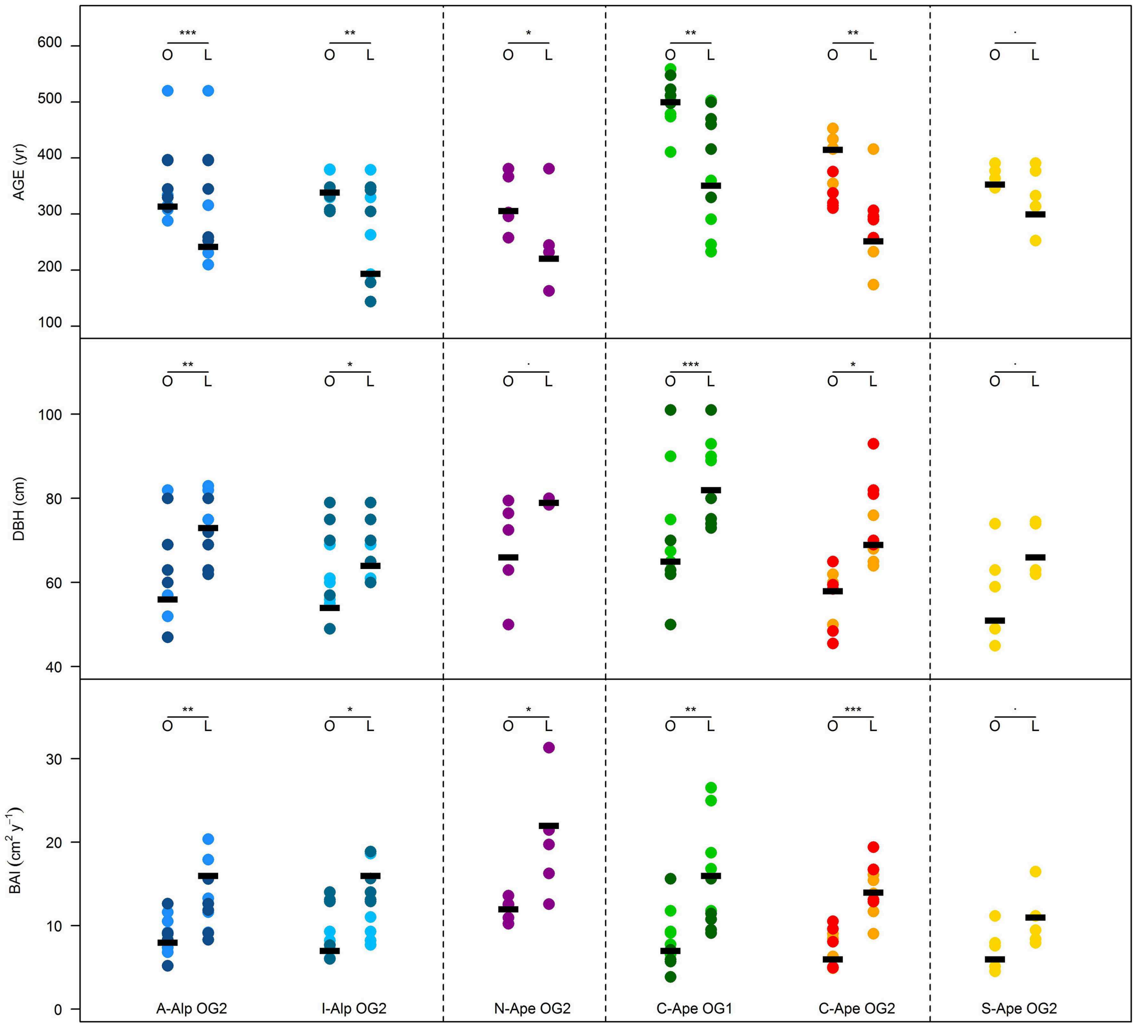

FIGURE 5 | Comparison between the age, DBH and overall Basal Area Increment (BAI) of the 5 oldest (O) and largest (L) beech trees within high-elevation forests. The difference in mean (thick black lines) was tested by a Welch's *t* test (***: $P \leq 0.001$; **: $P \leq 0.01$; *: $P \leq 0.05$; ".": $P \leq 0.1$). Stands (represented in different colors) are grouped according to location (A-Alp and I-Alp: Austrian and Italian Alps; N-Ape, C-Ape, S-Ape: northern, central, southern Apennines) and naturalness degree (primary and secondary old-growth forest: OG1, OG2).

Different ecological site conditions can affect tree longevity through controls over tree growth rates (Di Filippo et al., 2012). Within and between different species, maximum lifespan decreased with increasing growth rates along continental-scale ecological gradients, from cool temperate to warm temperate. In *Fagus sylvatica*, the maximum lifespan had a threefold increase from hilly to high-mountain sites (200–600 years along an elevation range of ~1500 m), following a three to 4-fold growth rate decrease (Di Filippo et al., 2012). This relationship was evident in previous studies on different genera such as oak, chestnut, spruce, fir, pine, and beech (Black et al., 2008; Bigler and Veblen, 2009; Briffa and Melvin, 2011; Reynolds and Burke, 2011; Di Filippo et al., 2012; Rotheli et al., 2012; Seim et al., 2012; Cooper et al., 2013). Bioclimate (Di Filippo et al., 2012), soil fertility (e.g., Robichaud and Methven, 1993), and early suppression (Black et al., 2008; Bigler and Veblen, 2009; Di Filippo et al., 2012) have been proposed as prominent ecological factors in conferring longevity to forest trees. The dependence of longevity on growth rates can thus be observed from the community-level to landscape- (e.g., elevation transects) and biome scales.

At the hemispheric level, the meta-analysis conducted for the temperate deciduous forest biome highlighted convergent geographic patterns in maximum lifespan and temperature variability. Latitude/elevation variations can affect longevity (r is 0.36 for latitude and 0.43 for elevation, both $p \leq 0.05$; **Table 1**) by controlling tree growth rates (Rotheli et al., 2012). The dependence of maximum lifespan on temperature is prominent in *Fagus* forests, which cover large geographic transects, but generally selecting well-drained mesic sites (Peters, 1997). Temperature positively affects *Fagus* growth, primarily through the growing season length (Alessandrini

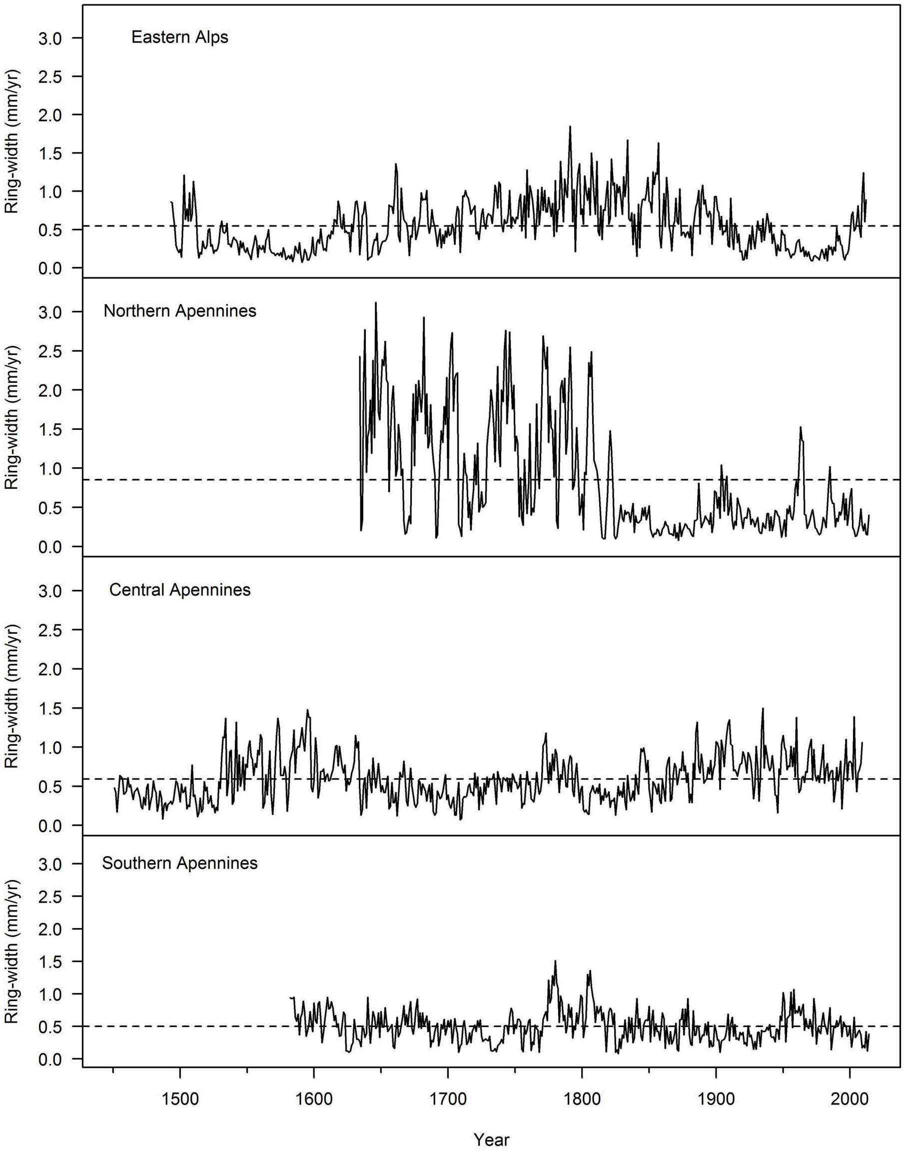

FIGURE 6 | Ring-widths series of the oldest *Fagus sylvatica* trees living in (top to bottom). The eastern Alps, northern, central, and southern Apennines (trees sampled, respectively, in the following National Parks: Kalkalpen NP, Foreste Casentinesi NP, Abruzzi NP, and Pollino NP). The dotted line represents the average ring width of the tree.

et al., 2010). The relationship of deciduous *Quercus* spp. with temperature is instead weaker and more complex to interpret. This interpretation might be related to oaks' capacity to adapt to extremely dry, wet, or unfertile site conditions (Jones, 1959). Deciduous oaks have evolved to occupy the drier and wetter ecological spaces left by other tree species with higher competitive capabilities in mesic conditions, i.e., *Fagus* or *Acer* spp. (Ellenberg, 1988; Johnson et al., 2009). Since water balance issues have a great impact on their growth (Martin-Benito and Pederson, 2015), they may assume a central role in controlling their expression of longevity. More broadly, some oak species are well adapted to dry environments, like *Quercus douglasii*, which can live 500–600 years in warm temperate open woodlands under the Mediterranean climate of California (Stahle et al., 2013), while old oak trees can even be found at the opposite side of the wetness gradient, as the 600 year old *Quercus robur*, growing in the wet forests of northern Europe (Drobyshev and Niklasson, 2010).

The oldest trees maintain remarkably low growth rates for their entire lifespan (Black et al., 2008; Johnson and Abrams, 2009), especially when young (Bigler and Veblen, 2009). This well-known phenomenon to dendrologists (Schulman, 1954; Loehle, 1988; literature cited in Bugmann and Bigler, 2011) seems to support the metabolic theory of ecology (e.g., Issartel

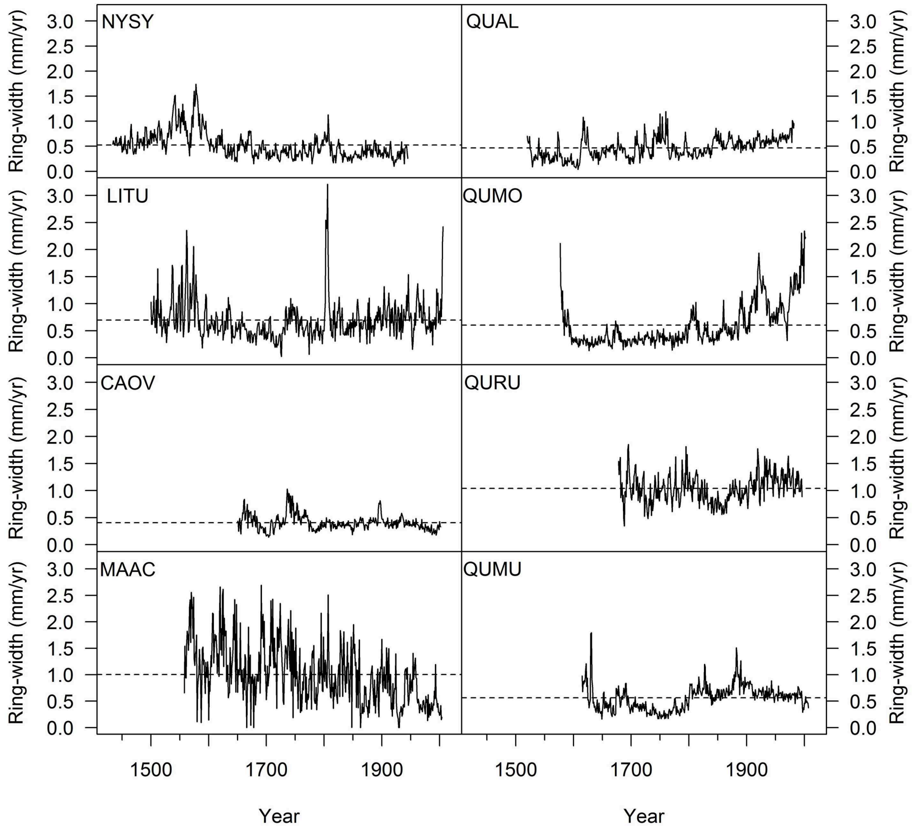

FIGURE 7 | Ring-widths series of the oldest species (≥300 years old) found in the eastern US. The dotted line represents the average ring width of the tree. [NYSY, *Nyssa sylvatica*; LITU, *Liriodendron tulipifera*; CAOV, *Carya ovata*; MAAC, *Magnolia acuminata*; QUAL, *Quercus alba*; QUMO, *Quercus montana*; QURU, *Quercus rubra*; QUMU, *Quercus muehelebergii*).

and Coiffard, 2011). For a given species, the oldest trees can thus be found in sites characterized by a colder climate, lower soil fertility, and in advanced OG forests with several, long phases of suppression (Di Filippo et al., 2012). Protracted suppression can contribute to denser and more durable wood in some species (Bigler and Veblen, 2009). Fast-growing trees can instead be subject to trade-offs, such as reduced investment in defenses and a lower mechanical wood strength, which can reduce their life expectancy (Bugmann and Bigler, 2011). Slow growth rates confer smaller dimensions to trees, a factor that can delay the onset of hydraulic limitations imposed by size (Mencuccini et al., 2005). Smaller trees can even cope more efficiently with mechanical damages by sustaining lower repairing costs (Peñuelas and Munné-Bosch, 2010). Multiple suppression and release events are frequent in natural closed-canopy temperate forests (Canham et al., 1990), and the oldest trees found in Europe and the eastern US have consistent suppression phases followed by release even in old age (**Figures 6**, **7**; Black et al., 2008). This demonstrates that these old trees must be characterized by an incredible plasticity to survive under harsh environmental conditions.

Slow growth can also confer reduced size (i.e., DBH), a factor with important ecological implications for survival under different disturbance regimes. In structurally complex forests, the oldest trees are usually not the largest, and maintain significantly slower growth rates. This phenomenon has also been observed in species living in different forest types, such as *Sequoiadendron giganteum* in California (N. Stephenson, *personal communication*) or *Pinus heldreichii* in Italy (Monte Pollino, *data not shown*). In natural temperate deciduous forests, rapidly growing trees are more likely to reach earlier the "high-risk" (i.e., large) DBH (Melvin, 2004), associated with the U-shaped mortality curve (e.g., Lines et al., 2010). In contrast, protracted growth suppression postpones canopy accession and, potentially, exposure to disturbance. Our results only partially follow the reported effect of temperature on mortality rates within temperate deciduous forests of the eastern US (Lines et al., 2010). This finding might result from the fact that specific mortality rates may not always correlate with the maximum lifespans observed in this study. Correspondence is good for beech, but weaker for *Quercus*, *Liriodendron*, *Betula*, *Carya*, and greatly underestimated for *Nyssa sylvatic*a. Understanding longevity in trees will require integration of the biological and ecological aspects governing slow growth.

The oldest temperate deciduous trees were mainly found in mountainous and remote areas of USA and Europe. Trees over

500 years were often found where geographical features and historical dynamics have discouraged intensive human activities. Despite millennia of intensive land-use, relict primary OG forests can still be found in Europe and North America (e.g., Carpathian Mountains; Abruzzi National Park in the Apennines; Dinaric Mountains; Appalachian Mountains, Adirondacks Mountains; various wetlands in the eastern US; e.g., Sperduto et al., 2000; Piovesan et al., 2005; Stahle et al., 2006; Trotsiuk et al., 2012). "Remote" can either mean distant from large urban settlements (e.g., *Nothofagus spp.* in the Andes and Patagonia; Gutiérrez et al., 1991; Pollmann, 2005), or limited to economically marginal sites, like those documented in ecotonal oak forests of the eastern US (Stahle, 1996) and the high-mountain Apennines beech forests (Abruzzi National Park; Piovesan et al., 2005). It is remarkable that European OG beech forests (e.g., Carpathian Mts., eastern Alps, Pyrenees, Dinaric, and Apennines Mts.) contain a large stock of trees 400–600 years old (Piovesan et al., 2011; Trotsiuk et al., 2012). In the last decade, the 500–600 year old trees, often living in small, but widespread patches of primary forests in the Abruzzi National Park, have been an unexpected discovery (Piovesan et al., 2005, 2011). This area is distinguished by hosting some among the oldest montane mesophilous deciduous forests in the Northern Hemisphere. Interestingly, trees living in these primary forests are (on average) 100 years older than those living in secondary OG forests.

Deciduous oaks approaching 500 years are currently very rare both in the eastern US and in the European landscape. Given the pristine nature of several oak OG forests in the eastern US (Stahle, 1996), this general lack of very old trees could be ascribed to limits imposed by recurring severe natural disturbance like fires and severe drought spells (e.g., Cook et al., 2007). In central Europe, oak forests are instead mostly remnants of pasture woodlands from the Middle Age, shaped by grazing and impacted by pigs, or hunting reserves (like Fontainbleau Forest). The lack of very old deciduous oaks can be related to historical landscape modifications. However, among hundreds of sub-fossil oak trees extracted from bogs in central Europe, very few samples reached 500–600 years (**Figure 8**; Leuschner et al., 2002; Spurk et al., 2002; Friedrich et al., 2004). This would lead us to conclude that, at least for a large part of lowlands in west and central Europe, oaks were not able to surpass the limit of 500–600 years even in the Neolithic period. An emblematic example is the Fointainebleau Forest, protected since the late Middle Age, where windstorms have been a major force driving stand dynamics so as beech and oak trees are no older than 400 years (Pontailler et al., 1997). Interestingly, central-western Europe is impacted by a higher risk of windstorms/flood (see Map 11 in Schmidt-Thomé, 2005). Winter storms, flooding and fires can act as major large-scale environmental stressors for longevity.

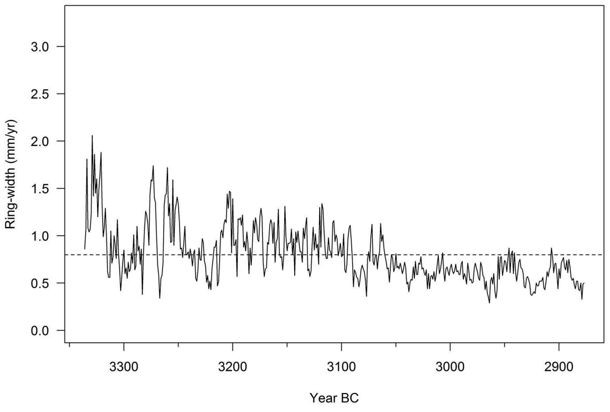

FIGURE 8 | Ring-width series of the "bog oak Methusalem," one of the oldest central European sub-fossil bog oaks (3336–2877 BC). The sample has 460 tree rings, but sapwood was missing: estimated age is circa 500 years (courtesy of Dr. Hanns Hubert Leuschner). The dotted line represents the average ring width of the tree.

The 600 year age limit may also be explained by human history and climate change. The Black Death in the mid-14th century contributed to a substantial reduction in the human impact on natural ecosystems (~50% human population died in Western Europe), so that beech and oak forests re-colonized, especially in mountainous areas (Mensing et al., 2013). Similarly, there appeared to be a remarkable pulse of regeneration in the late-1600s across the broadleaf dominated forest of the eastern US (Pederson et al., 2014). A spike in recruitment in a light-limited forest suggests large-scale canopy gaps (Lorimer and Frelich, 1989). Factors that open canopies include windstorms, ice storms, severe fire, and climate variations, specifically drought. Most of these factors are not known to operate at subcontinental scales (Vanderwel et al., 2013). Paleoclimate records suggest dry conditions around this time (Pederson et al., 2014) and that regional to pan-continental droughts have occurred over the last 1000 years in the continental US (Cook et al., 2007). Thus, some of the maximum longevities narrowly exceeding 300 years in this region could also be related to severe disturbance pulses from repeated or intense drought.

In some cases, cultural practices could contribute to the conservation of old trees in different cultural landscapes. Moreover, the discovery of 300 year old trees in hilly beech forests (Foreste Casentinesi National Park and Pollino National Park) have been unexpected. How these old trees have survived at low elevation in one of the cradles of Western cultures is difficult to fully understand. Despite these limitations, there are some clues in the cultural history of the region. Most of the remnant forests survived close to towns as hunting reserves or parkland forests for cattle and pig grazing. Romans had a strong tradition for hunting edible dormouse (*Glis glis*), considered a delicacy, and this practice has persisted up to recent times in local communities like the Pollino National Park (Aldo Schettino, *personal communication*). Such a tradition may have contributed to preserve those habitats, containing older trees with hollow trunks (wildlife trees).

Conclusion

The relationship between size (i.e., stem diameter), age, and life expectancy in different forest environments is still poorly understood. Slow growth is the only life-history functional trait clearly linked to longevity, and correlating it with environmental features. The dendrochronologically verified age limit of 600–700 years can be considered a maximum lifespan reference for the deciduous temperate biome. Considering the increased growth rates maintained by trees at great ages, we believe that this is not a biological limit (i.e., meristem senescence; Mencuccini et al., 2014). A central theme for future studies will be to understand how the geography of rare, severe disturbance agents impacts tree survivorship.

The oldest trees were living in subordinate canopy conditions for extended periods and/or within primary forests in European cool temperate mesic environments, generally in harsh areas outside storm tracks characterized by extremely infrequent catastrophic stand replacing disturbance events like hurricanes and fires (Piovesan et al., 2011; Trotsiuk et al., 2012; Nagel et al., 2014). It is difficult to find a single mechanism linking forest net primary productivity (NPP), as inferred from radial growth rates, and mortality rates to climate, edaphic and structural state conditions (Stephenson et al., 2011). Site features that constrain tree growth rates and longevity demonstrated to control the velocity of OG recovery in mesic (*Fagus*) forests; in this ecosystem the structural cycle is faster in warm, fertile environments, rather than in cool ones (Ziaco et al., 2012).

The ecological importance of the Apennines OG beech sites is testified by their candidature—under the criterion IX—to UNESCO World Heritage List (Knapp and Fichtner, 2011), as already acknowledged for the serial sites of Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany (http://whc.unesco.org/en/list/1133) and Shirakami-Sanchi *Fagus crenata* forests in Japan (http://whc.unesco.org/en/list/663). The protection of the ecological integrity under UNESCO will guarantee the conservation of some of the oldest BD trees on Earth.

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Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2015.00046/abstract

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