New
Phytologist

Tansley review

On tree longevity

Gianluca Piovesan[1] (ID) **and Franco Biondi**[2] (ID)

[1]Dendrology Lab, Department of Agriculture and Forest Sciences (DAFNE), University of Tuscia, Viterbo 01100, Italy; [2]DendroLab,

Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89557, USA

Author for correspondence:
*Franco Biondi*
Email: fbiondi@unr.edu

Contents

Summary

Large, majestic trees are iconic symbols of great age among living organisms. Published evidence suggests that trees do not die because of genetically programmed senescence in their meristems, but rather are killed by an external agent or a disturbance event. Long tree lifespans are therefore allowed by specific combinations of life history traits within realized niches that support resistance to, or avoidance of, extrinsic mortality. Another requirement for trees to achieve their maximum longevity is either sustained growth over extended periods of time or at least the capacity to increase their growth rates when conditions allow it. The growth plasticity and modularity of trees can then be viewed as an evolutionary advantage that allows them to survive and reproduce for centuries and millennia. As more and more scientific information is systematically collected on tree ages under various ecological settings, it is becoming clear that tree longevity is a key trait for global syntheses of life history strategies, especially in connection with disturbance regimes and their possible future modifications. In addition, we challenge the long-held notion that shade-tolerant, late-successional species have longer lifespans than early-successional species by pointing out that tree species with extreme longevity do not fit this paradigm. Identifying extremely old trees is therefore the groundwork not only for protecting and/or restoring entire landscapes, but also to revisit and update classic ecological theories that shape our understanding of environmental change.

I. Introduction

Large, majestic trees are common iconic symbols of great age among living organisms, as popular claims of millennia-old individuals typically involve giant or monumental conifers and hardwoods (Lindenmayer & Laurance, 2017). Scientific dating tools have allowed for testing most such claims, but have not resolved debates on how tree age should be measured or on the ecological significance of extreme longevity. Because large old trees

may be threatened by ongoing and future global changes in climate, land use and disturbance regimes (Lindenmayer *et al.*, 2012; Faison, 2014), optimal conservation policies and management strategies must be grounded on solid scientific understanding of maximal tree lifespans. In this review we focus on cambial age, defined as the cumulative duration of secondary growth since pith formation at a specified height from the ground (Box 1). Our definition does not rule out trees resulting from asexual reproduction, but it purposely ignores the age of genetic material in clonal

Box 1 Dating old trees.
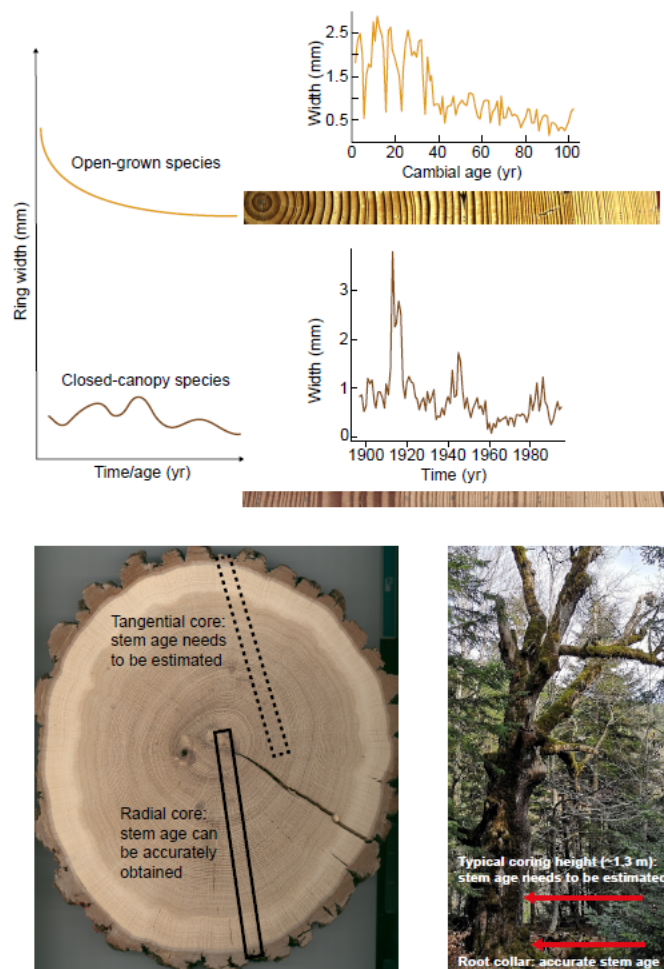
Dendrochronology provides accurately time-resolved (annual and subannual) data for measuring maximum tree lifespan and its associated growth history. Absolute tree age can be determined exactly by obtaining a wood sample that extends to the point of germination, which also corresponds to the root–shoot boundary (or root 'collar'). This can be located by either sectioning the stem immediately above and below a suspected root–shoot boundary (League & Veblen, 2006) or by splitting the stem vertically until the root–shoot boundary is found, and then analyzing radial growth at that point (Telewski, 1993). In some cases, however, the root collar is incorporated into the upper soil layers (i.e. the xylorhizome; Zaitsev et al., 2018). Accumulating leaf litter or a bryophyte layer can bury the root collar in the humus layer, where adventitious roots can develop, and therefore cross-dating below adventitious roots can add up to 20 yr to age estimates obtained at ground level (DesRochers & Gagnon, 1997). Seedlings of closed-canopy species established in soil may also form more adventitious roots than seedlings of the same species that become established on logs (Doi et al., 2008), further complicating the determination of true stem age.

A simple modification to the handle of an increment borer allows for coring the tree stem near the base (Brown, 2007). For practical reasons, however, most tree-ring samples are increment cores collected using standard tools at 'breast height', which is *c.* 1.3–1.5 m from the ground. In those cases, an estimate of the number of years required to reach the sampling height has to be provided based on local average growth patterns (e.g. see Piovesan et al., 2019b). This estimation is more prone to errors for closed-canopy species (Gutsell & Johnson, 2002), which can form extremely small or even locally absent rings during the suppression phase in their early life (Parent et al., 2002). Shade-tolerant trees may already be older than 150 yr when they reach a height of 1.3 m (Antos et al., 2005). In comparison, open-canopy species form larger rings when young, and also display a monotonically decreasing trend of ring width with age (Biondi & Qeadan, 2008).

For accurate age determination, wood samples must also include the pith, as shown in the figure by the 'radial core' drawn on top of a *Quercus gambelii* Nutt. cross-section. Often the pith is not easily attainable with increment cores, especially for relatively large stems with root buttresses. Regardless of available specimens, age data are most reliable when based on cross-dating of the tree-ring series among themselves and with the site chronology for the species (Stokes & Smiley, 1996). By means of proper visual and numerical cross-correlation of growth patterns, it is possible to identify locally absent and false rings in species that experience seasonally distinct growing seasons (Speer, 2010).

When annual growth layers cannot easily be separated, as typically occurs for woody species in tropical climates, radiocarbon dating must be used (Ogden, 1981; Chambers et al., 1998; Patrut et al., 2007). Besides providing age estimates, radiocarbon dating allows for independent validation of dendrochronological dates through the application of ^{14}C bomb-pulse dating (Biondi & Fessenden, 1999; Andreu-Hayles et al., 2015). In addition, when trees are hollow and root samples are available, cross-dating can be enhanced through its combination with radiocarbon dating (Piovesan et al., 2018a; see also the middle panel of Fig. 3).

plants (genet age; de Witte & Stöcklin, 2010) to be consistent with society's everyday experience and perception of tree longevity. Such a framework, especially in the context of assessing the ecological role of large old trees, is steeped in the field of dendrochronology, which can be defined as the study and reconstruction of past changes that impacted tree growth (Speer, 2010; Biondi, 2020).

As will be discussed, the capacity to exceed 2000 yr of age has been demonstrated so far for six conifer genera: *Fitzroya*, *Juniperus*, *Pinus*, *Sequoia*, *Sequoiadendron* and *Taxodium* (Figs 1, 2). Other conifer genera include dendrochronologically tested individuals with ages in excess of 1000 yr, such as *Agathis*, *Chamaecyparis*, *Cupressus*, *Lagarostrobus*, *Pseudotsuga* and *Thuja* to name just a few. These genera are adapted to widely different environments, but several studies have highlighted some common requirements for maximizing longevity. Besides differences among species with regard to life history traits that lead to longevity, we also address factors leading to long-lived individuals within a tree species. Because flowering trees are characterized by a markedly lower longevity than conifers, the environmental context and growth

behavior of hardwood species was taken into consideration mostly when considering the factors that favor intraspecific differences in lifespans.

Radial, woody growth of stems is the product of secondary growth from vascular cambia (Spicer & Groover, 2010). The cambial meristem appears immune to senescence, which is defined as the intrinsic age-dependent increase in mortality or deterioration in performance under the control of an endogenous biological clock (Thomas, 2013). Theoretically, trees can therefore be immortal organisms (Peñuelas & Munné-Bosch, 2010), and gene expression analyses are starting to uncover the processes that maintain a balance between growth and aging processes in old trees (Wang *et al.*, 2020). At the same time, maximal tree lifespans reported in plant trait databases (e.g. TRY; Kattge *et al.*, 2020), in reviews of tree longevity (e.g. Table 1 of Thomas, 2013) or in articles published in prestigious scientific journals (e.g. Major, 1967) are not always supported by scientific evidence. For instance, Huon pine (*Lagarostrobos franklinii* (Hook.f.) Quinn – scientific names taken from the World Flora Online (WFO,
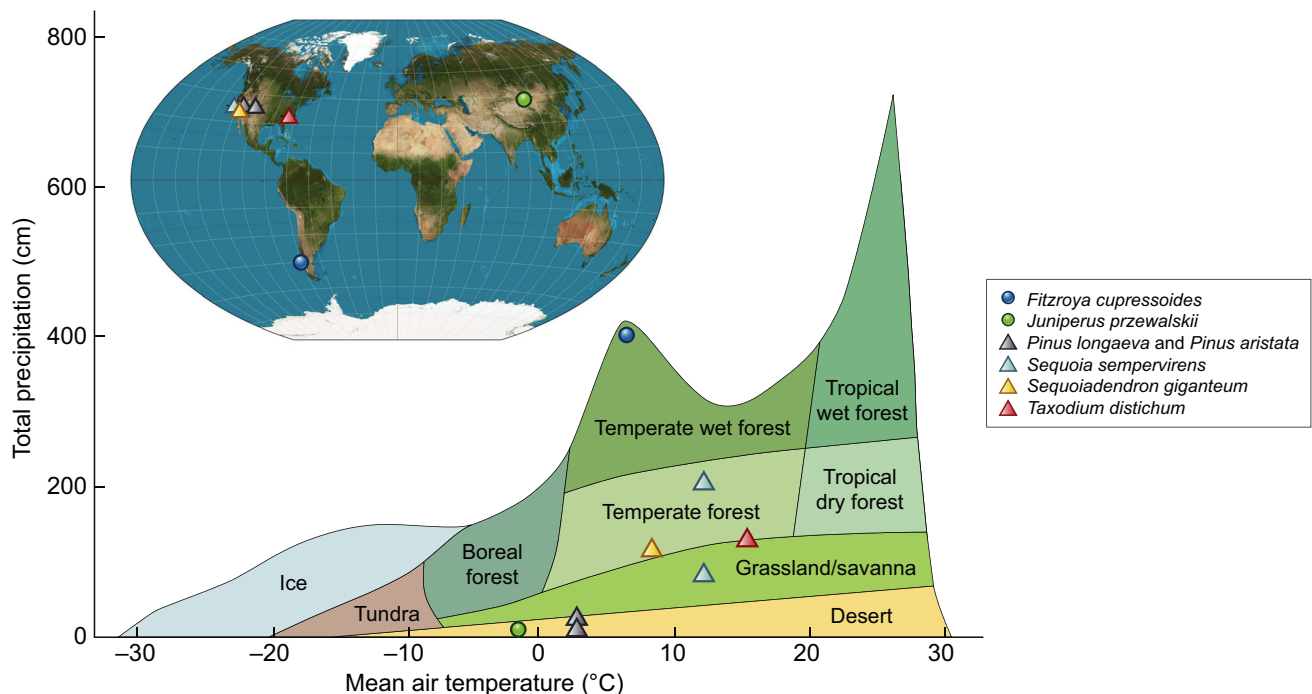
Fig. 1 Distribution of tree species with longevity > 2000 yr in relation to average annual air temperature and total annual precipitation, which were also used to draw biome boundaries (modified from Fig. 2.22 in Chapin III et al., 2011). *Fitzroya cupressoides* (blue circle); *Juniperus przewalskii* (green circle); *Pinus longaeva* and *Pinus aristata* (gray triangles); *Sequoia sempervirens* (cyan triangle); *Sequoiadendron giganteum* (orange triangle); *Taxodium disticum* (red triangle). Climatic data for the USA were obtained from the online public-domain version of the PRISM dataset (Daly *et al.*, 2008). The map inset shows tree species locations.
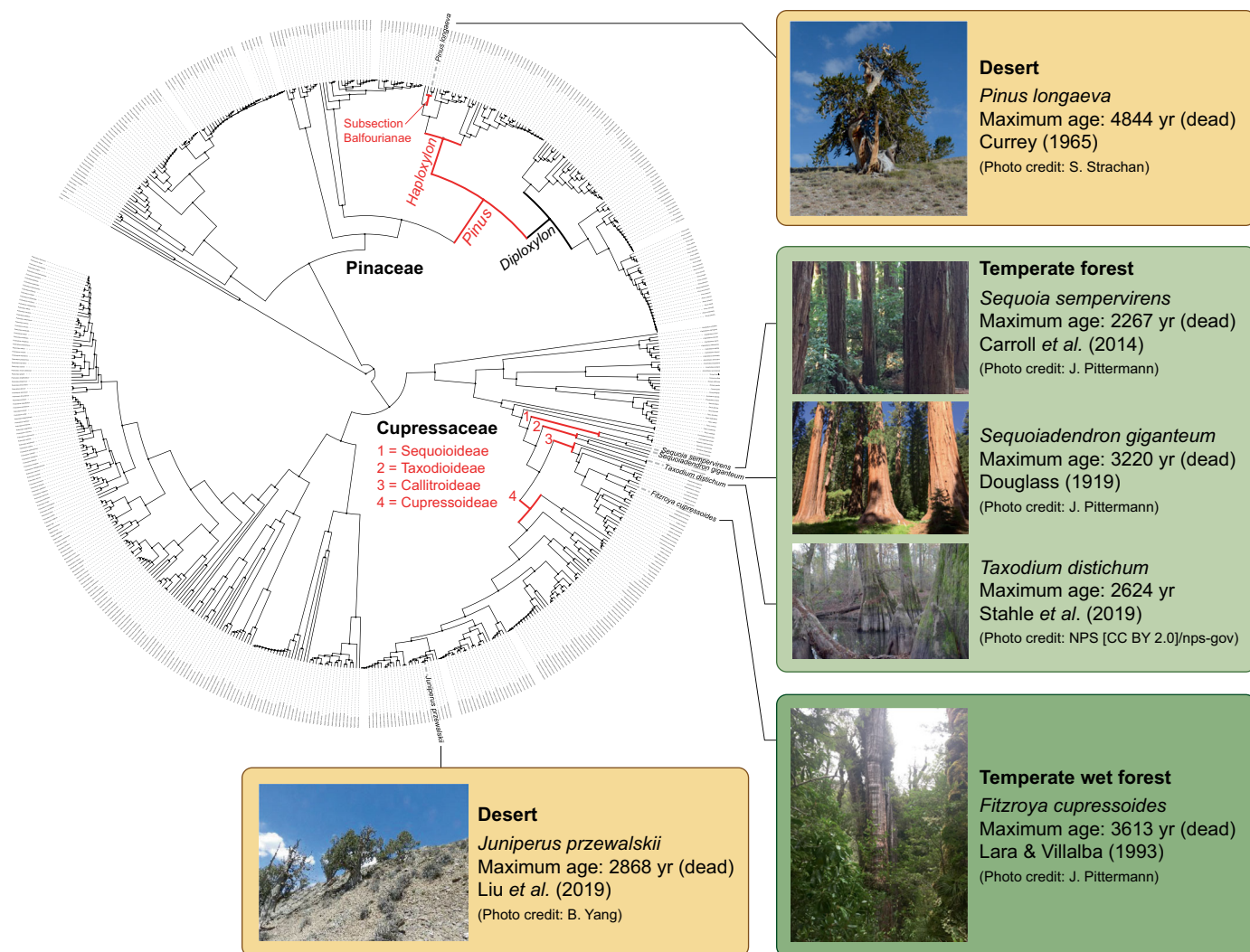
Fig. 2 Summary representation of the six conifer species that can live more than 2000 yr. The phylogenetic tree graph was obtained using the Interactive Tree Of Life online tool (Letunic & Bork, 2019); taxonomic data are from Leslie *et al*. (2018). Clades highlighted in red are mentioned in the text because they include at least one species whose longevity exceeds 2000 yr.

2020) – which is listed as *Dacrydium franklinii* with a maximal lifespan of +2200 years by Thomas (2013)) has been reported to reach 3000 yr of age in the popular press. However, peer review articles with publicly available Huon pine datasets do not include any tree-ring series longer than 1774 yr (Contributors of the International Tree-Ring Data Bank, 2020). Similarly, we cannot find any scientific confirmation for Thomas' (2013) claim of *Juniperus communis* reaching 2000 yr of age, or for 930-yr-old *Fagus sylvatica* trees, even though our own work has identified the oldest, scientifically dated, European beech (622 yr; Piovesan *et al.*, 2019a). Anecdotal reports are often useful as a starting point to stimulate further investigation, but scientific theories and ecological syntheses must be based on rigorous dating tools (Box 1).
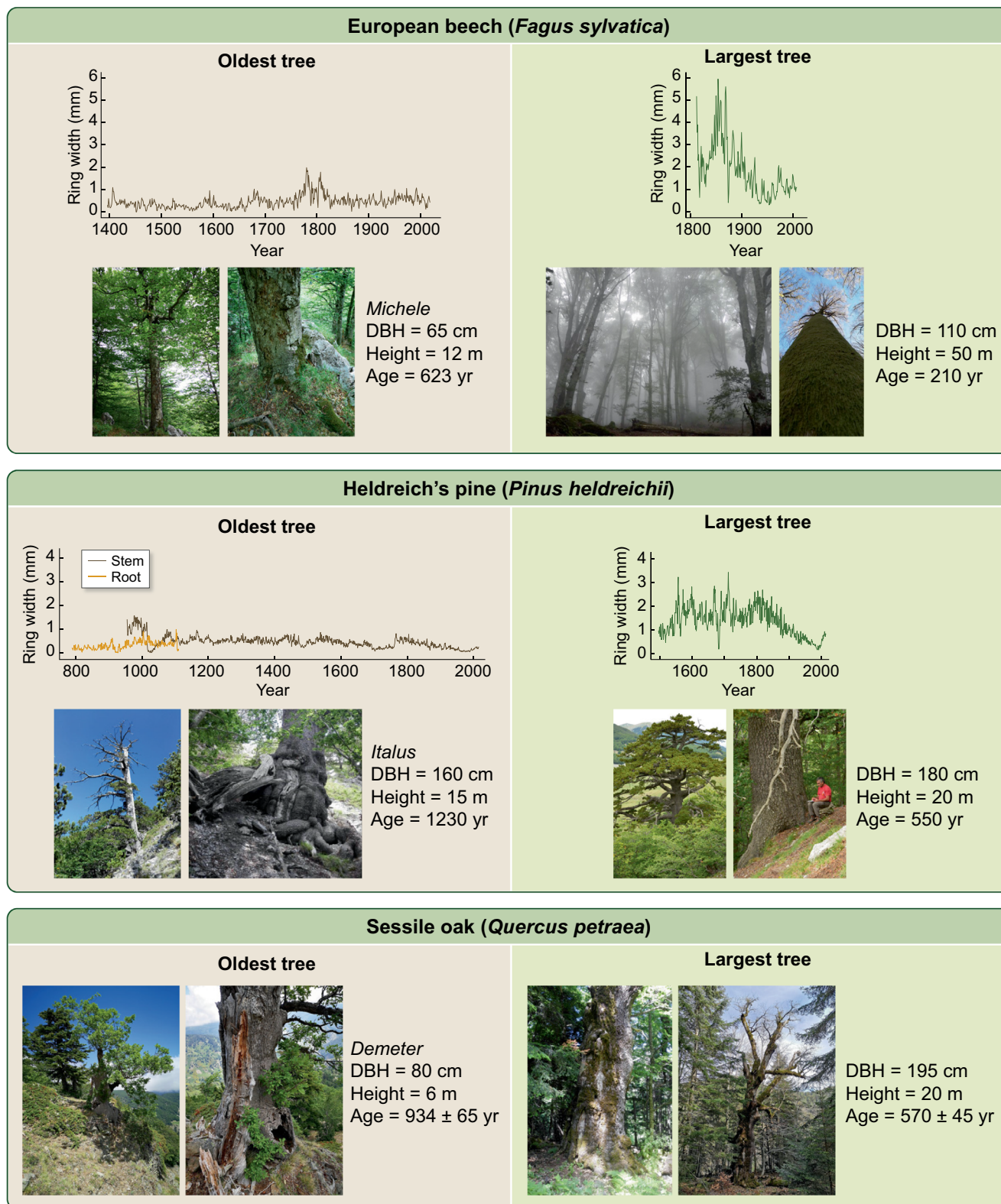
As more and more scientific information is systematically collected on tree ages within and between species under various ecological settings, it is becoming possible to evaluate how long they have withstood natural disturbances, with or without their combination with human activities. Identifying extremely old trees is therefore the groundwork not only for protecting and/or restoring entire landscapes (Lindenmayer, 2017; Chiarucci & Piovesan, 2020), but also to revisit and update classic ecological theories that shape our understanding of environmental change. A key aim of this review is to convey that, while maximum tree ages differ among species, with conifers reaching maximal lifespans an order of magnitude greater than angiosperms, there are similarities among the conditions that need to be satisfied for trees to achieve their greatest longevity. We also explicitly challenge the long-held notion that shade-tolerant, late-successional species are long-lived compared to early-successional species, as for instance claimed by Körner & Basler (2010).

II. Ecological considerations in space and time

Trees of proven longevity tend to have similar morphologic features associated with the advanced phase of their ontogenetic development (Stahle, 1997; Evstigneev & Korotkov, 2016). Stem size varies greatly for trees of the same age, and is therefore not a reliable

European beech (*Fagus sylvatica*)

Oldest tree

Michele
DBH = 65 cm
Height = 12 m
Age = 623 yr

Largest tree

DBH = 110 cm
Height = 50 m
Age = 210 yr

Heldreich's pine (*Pinus heldreichii*)

Oldest tree

Italus
DBH = 160 cm
Height = 15 m
Age = 1230 yr

Largest tree

DBH = 180 cm
Height = 20 m
Age = 550 yr

Sessile oak (*Quercus petraea*)

Oldest tree

Demeter
DBH = 80 cm
Height = 6 m
Age = 934 ± 65 yr

Largest tree


DBH = 195 cm
Height = 20 m
Age = 570 ± 45 yr

Fig. 3 Examples of trees that have been found to be the oldest (left side) but not the largest (right side) in the Italian Apennines. When shown for the same species, the two ring-width time-series plots have identical scales. Top panel: for European beech (*Fagus sylvatica* L.), the oldest tree (*Michele*) was found in the high-mountain old-growth forest of Pollino National Park (Piovesan *et al.*, 2019a), even though a larger and much younger beech is present on Mount Cimino in central Italy (Piovesan *et al.*, 2008). Middle panel: for Heldreich's pine (*Pinus heldreichii* Christ), the oldest tree in Europe (*Italus*) was found in Pollino National Park (Piovesan *et al.*, 2018b), where a larger pine was considerably younger. Bottom panel: for sessile oak (*Quercus petraea* (Matt.) Liebl.), the oldest oak (*Demeter*) found to date is located at 1700 m elevation, compared to a larger but younger one at 1300 m elevation in Aspromonte National Park (Piovesan *et al.*, 2020). DBH, diameter at breast height.

Fig. 4 Photographs of stem cross-sections with roughly equal diameter that were taken from saplings of western larch (*Larix occidentalis* Nutt.) cut in 2014 at Snow Bowl (western Montana, USA; photo credit: S. Hood): (right) *c.* 10-yr-old tree growing in an area that had been thinned; (left) *c.* 90-yr-old tree growing in a control area. The scale of the two photographs is not exactly the same, as can be inferred from the ruler images beneath the sections.
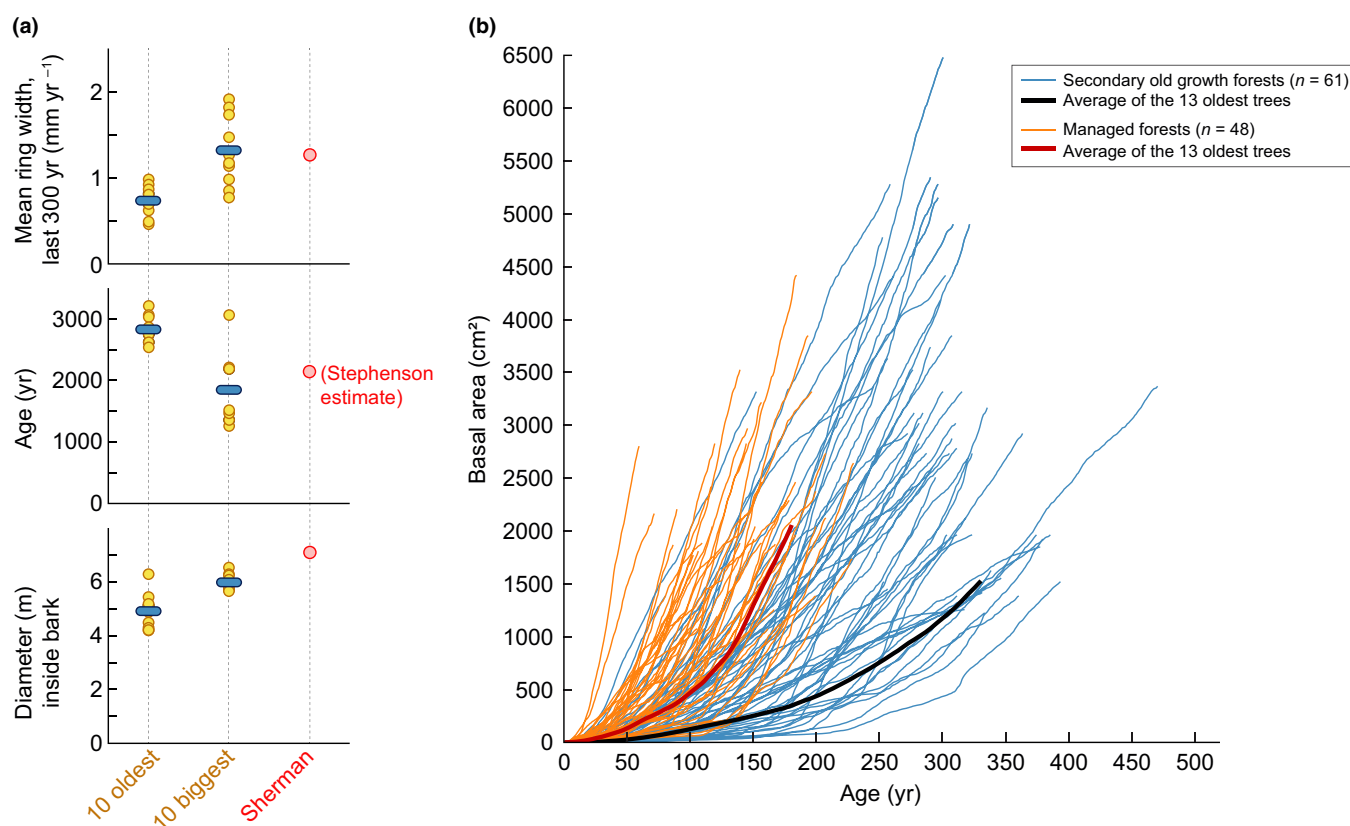
Fig. 5 Comparison of growth rates for the oldest trees and for the largest trees. (a) Stem size, age and growth rate of the ten largest and the 10 oldest giant sequoias in Huntington (1914) compared to the General Sherman Tree (courtesy of N. Stephenson; data from Stephenson & Demetry, 1995). On average (blue segments), the 10 oldest sequoias were almost 1000 yr older than the 10 largest ones, but were *c.* 1 m less in diameter because of slower growth rates (average ring widths of *c* 0.5–1 mm compared to *c* 0.8–2.0 mm). (b) Cumulative growth (basal area) trajectories of managed (orange lines) and secondary old-growth (blue lines) montane beech forests (*n* = number of trees) in Marsica (Abruzzo, Italy). The average of the 13 oldest trees (red for managed forests, black for secondary old-growth forests) highlights faster tree growth histories caused by human impacts (i.e. logging).

indicator of maximal lifespan (Stephenson & Demetry, 1995; Sillett *et al.*, 2010). As a general, practical rule, which is explained and supported by research presented in this review, 'the largest trees are not the oldest ones', especially within a species (Figs 3–5). More reliable indicators of old age can be found in crown and bark characteristics, as well as partially exposed root systems (Pederson, 2010; Brown *et al.*, 2019). Commonly accurate indicators of extreme longevity in conifer crowns are relatively large branches, with a mixture of live and dead ones, within relatively sparse foliage, possibly with epicormic shoots as well as flat or spiked tops (Van

Fig. 6 Photographs of strip-bark trees, with only a fraction of the trunk and crown still alive: (left) single-needle pinyon (*Pinus monophylla* Torr. & Frém) in the Great Basin of North America; (right) sessile oak (*Quercus petraea* (Matt.) Liebl.) in the Aspromonte Mountains of southern Italy.

Pelt & Sillett, 2008). The exterior surface of the bark in the oldest individuals is often deeply fissured, twisted or highly irregular, and missing in certain areas (Figs 3, 6), eventually culminating in the strip-bark growth forms typical of old conifers in semi-arid environments (Bunn *et al.*, 2003). Bark stripping, which occurs through partial cambial dieback, is associated with old age, as it may allow trees to persevere longer in unfavorable and heterogeneous habitats (Matthes *et al.*, 2002). Such extreme bark features can also be found in hardwoods, and are again highly indicative of extreme longevity (Figs 3, 6). While visual clues can provide approximate estimates of age, multicentury-old trees that share similar morphological features can still have originated at widely different times, and a century or more may separate their germination dates (Martin *et al.*, 2020).

Longevity hotspots (where the old trees are)

Based on the concept of biome, a Cartesian graph of average annual air temperature and total annual precipitation is sufficient to summarize where millennia-old trees have been discovered to date (Fig. 1). Climatic regimes are mostly temperate, ranging from wet to arid, and organized either by latitude or along orographic gradients. All genera that include trees older than 2000 yr are conifers located in the Americas, in temperate environments between 30° and 45°N and S (Fig. 1). A notable geographic exception is *Juniperus*, which reaches such extreme ages at those latitudes but in the Tibet region, at elevations greater than 4000 m and under extreme cold and arid climatic conditions. Despite the relatively narrow range of latitudes, forests harboring the oldest trees are environmentally and structurally quite diverse (Fig. 2), ranging from sea-level swamps dominated by *Taxodium* (Stahle *et al.*, 2019) to the subalpine and timberline zones occupied by *Pinus* in the Great Basin and Rocky Mountains (Currey, 1965; Brunstein & Yamaguchi, 1992) and by *Juniperus* in Tibet (Liu *et al.*, 2019). Somewhere in between are foggy coastal areas and mountains with a Mediterranean-type climate where one finds the

gigantic *Sequoia* and *Sequoiadendron* in the northern hemisphere (Douglass, 1919; Stephenson & Demetry, 1995; Carroll *et al.*, 2014), and the similarly majestic *Fitzroya* in the southern hemisphere (Lara & Villalba, 1993; Premoli *et al.*, 2003).

These regions have largely remained outside the permanent ice sheets that covered the northern latitudes in glacial times, providing refugia, and thus becoming a biodiversity hotspot, for conifer species (Farjon, 2018). Gymnosperms with extreme longevity evolved in the Mesozoic and Cenozoic, and since then have been progressively replaced by other species, except in restricted temperate Quaternary glacial refugia, often becoming narrow endemics (Ahuja, 2009). As will be mentioned in other sections of this review, a long lifespan still remains one of the competitive advantages of conifers with respect to hardwoods (Brodribb *et al.*, 2012).

The hypothesis that millennium-old trees are concentrated in glacial refugia is supported in the middle latitudes of North America by Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey), which during the early Tertiary was concentrated in Rocky Mountain refugia together with the other two members of *Pinus* subsection *Balfourianae*, namely *Pinus aristata* Engelm. and *Pinus balfouriana* Balf., two species that are also capable of attaining millennial lifespans (Richardson, 2000). Similar glacial refugia can be found in southern Europe with the location of *Pinus heldreichii* Christ on the Pollino (Piovesan *et al.*, 2018b) and Pindo (Konter *et al.*, 2017) mountains, for *Cupressus dupreziana* A.Camus in the Sahara desert (Abdoun *et al.*, 2005), for *Lagarostrobus colensoi* (Hook.) Quinn in New Zealand (Cook *et al.*, 2002), for *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. (Arkawa, 1960) and for *Cryptomeria japonica* (Thunb. ex L.f.) D.Don (Suzuki, 1996) in Japan. Even the Tibet region where the oldest Asian trees are found (Liu *et al.*, 2019) was not fully covered by glacial ice (Hewitt, 2000).

In the northern high latitudes, taiga conifer species do not seem to include extremely old individuals, despite a geoclimatic limitation to growth. It is possible that large-scale, severe

disturbances (e.g. wildfires, glaze storms, strong polar vortex) recurring at centennial timescales reduce the potential for extended tree lifespans in those areas (Kharuk *et al.*, 2013). In landscapes with stand-replacing disturbances, the oldest trees are in fact ecological indicators for estimating the time since the last large-scale event (Metsaranta, 2020). Indeed, disturbance phenomena, both abiotic (droughts, wildfires, hurricanes, etc.) and biotic (insect outbreaks, human impacts, etc.) represent the main causes of tree mortality, either through a direct kill or indirectly by weakening defenses against pathogens, especially for large trees (Pennisi, 2019). It is noteworthy that some disturbance processes, when occurring at low severity, may extend longevity by reducing the risk of high-severity events (e.g. crown fires) that could otherwise wipe out the oldest individuals. For open-grown conifer species, damaged stems may even develop the strip-bark habit that is conducive to greater ages compared to individuals with a fully functional root–stem–crown continuum (LaMarche, 1969; Leland *et al.*, 2018).

Hardwood species often experience heart rot in large and old trees, making it necessary to combine tree-ring analysis with radiocarbon dating. Based on that evidence, a hardwood species that exceeds 1000 yr of age is the baobab (*Adansonia digitata* L.), with maximum longevity up to 2000 yr in the savannah regions of tropical Africa between 16°N and 26°S (Patrut *et al.*, 2018). Reports of other tropical species that include millennium-old individuals have been based on radiocarbon dating alone (e.g. see Kurokawa *et al.*, 2003), and may require additional confirmation from tree-ring analysis (Box 1). Old hardwood trees normally do not exceed 300 yr of age, with a few genera that include individuals older than 500 yr (Di Filippo *et al.*, 2015; Worbes & Schöngart, 2019). Large olive trees (*Olea europea* L.) are considered capable of living for millennia, but to date the oldest radiocarbon-dated olive stems have maximum ages approaching, albeit not reaching, a millennium (Bernabei, 2015).

Climatic regimes experienced by the oldest hardwoods outside the tropics range from Mediterranean for blue oaks (*Quercus douglasii* Hook. & Arn.) in California (553 yr; Stahle *et al.*, 2013) to the temperate–boreal transition for pedunculate oaks (*Quercus robur* L.) in Scandinavia (*c.* 583 yr; Drobyshev & Niklasson, 2010), with intermediate bioclimatic cases linked to elevation, such as the high-mountain beech forests of the Italian Apennines (622 yr; Piovesan *et al.*, 2019a). Recent wood samples obtained from a metapopulation of sessile oaks (*Quercus petraea* (Matt.) Liebl.) in the high-mountain vegetation zone of Aspromonte National Park in southern Italy have uncovered maximum tree ages ranging from *c.* 500 to *c.* 1000 yr, according to radiocarbon dating (Fig. 3; Piovesan *et al.*, 2020).

The ecology of maximal tree lifespans

Local edaphic and physiographic factors determine the ecological niche of maximal stem age, which is typically different from the optimum combination for growth. For instance, it is well established that unproductive sites tend to yield the oldest trees of any given species (Schulman, 1954). Vertical cliffs harbor millennia-old individuals for conifer species that elsewhere remain alive over a few centuries at most. This phenomenon, first reported in North America and Europe mainly for the genera *Thuja* and *Juniperus* (Larson *et al.*, 1999, 2000), has also been reported in Mediterranean environments (Mathaux *et al.*, 2016). Similarly, in floodplains the oldest trees of a species are often found in nutrient-poor sites, as for instance shown by the Amazonian *Macrolobium acaciifolium* (Benth.) Benth (Brienen *et al.*, 2016). For species with wide biogeographic ranges, the oldest trees are located at or near the highest elevations (Di Filippo *et al.*, 2012; Rötheli *et al.*, 2012), where growth rates are most limited by climatic and soil conditions. Nutrient limitations do not necessarily correspond to increased longevity, as shown by prostrate scrubs and 'pygmy' forest
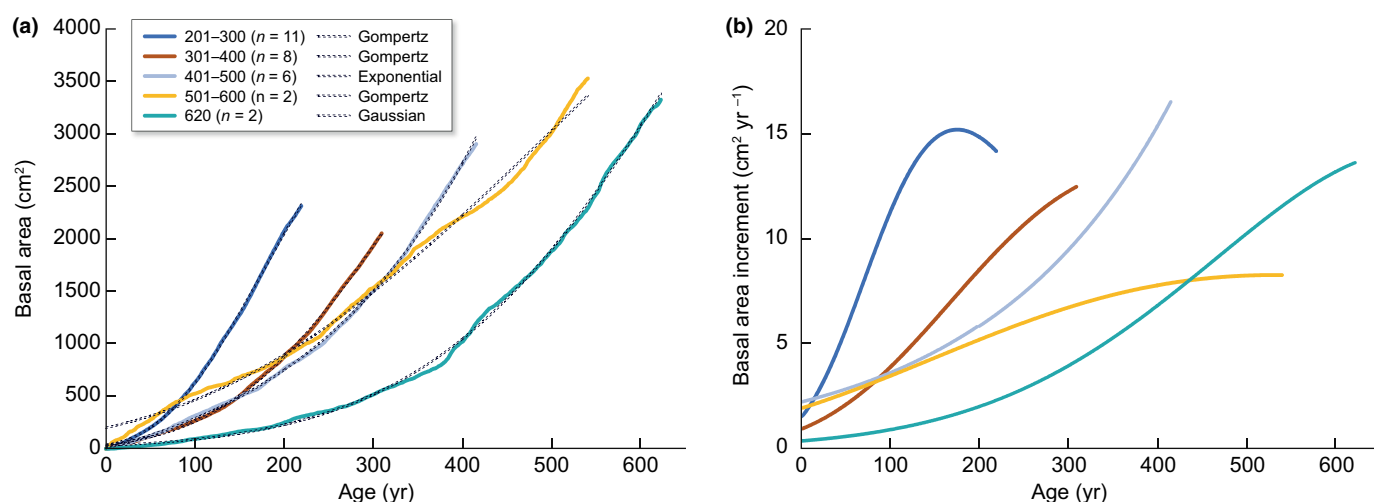
Fig. 7 Cumulative growth curves (a) constructed using basal area increments (b) of beech trees calculated from increment cores containing the stem pith collected from an old-growth stand in the Mediterranean high-mountain environment (Piovesan *et al.*, 2019a). Tree growth was averaged using five age classes (*n* = number of trees). In (a), empirical curves (solid lines in various colors) were overlaid with theoretical nonlinear models (dashed black lines) selected according to the Akaike Information Criterion (Akaike, 1974). In (b), basal area increment follows an increasing trend but with different rates depending on tree age class.

populations with stunted and multistemmed growth forms. An example is found in California sites dominated by shrub-like redwoods (*Sequoia sempervirens* (D.Don) Endl.) of greatly reduced size and age compared to nearby populations on fertile soils (Cary & Pittermann, 2018; Russell *et al.*, 2019).

In closed-canopy forests, multiple processes can reduce growth rates during early life stages, thereby allowing for increased longevity in shade-tolerant tree species (e.g. Woods, 2008). Beech and fir communities impacted by gap dynamics and their associated growth oscillations from suppression to release can harbor much older trees than areas where competition for resources is less intense, as is the case in large clearings or in managed stands (Fig. 5; Di Filippo *et al.*, 2017). Clonal regenerations (Sillett *et al.*, 2020) and mycorrhizal networks, formed predominantly in the root systems of canopy trees, can favor survival of juveniles in the understory, thereby facilitating tree establishment as well as sustain survival of suppressed trees during their initial life (Simard, 2018). In vertically complex tropical forests, stem ages of understory trees can then be comparable to those of dominant individuals (Hubau *et al.*, 2019).

A widespread tree species that is characterized by substantial variability in maximum stem ages depending on environmental conditions is the European beech (*Fagus sylvatica* L.). An overall inverse relationship exists between growth rates and longevity along an elevation gradient, so that at low elevations in fertile soils beech trees exceed 1 m in diameter and 50 m in height, reaching a maximum lifespan of about three centuries, whereas much smaller individuals (60–70 cm diameter at breast height, 12–20 m height) can live twice as long (six centuries) at high elevations (Fig. 3; Di Filippo *et al.*, 2012; Piovesan *et al.*, 2019a). The oldest trees, even within the high-mountain zone, are never the largest ones, and instead they typically have smaller, broken-up crowns (Fig. 3), probably derived from abiotic disturbance such as snow and wind damage. In old-growth stands, the correlation between stem diameter and age of dominant beeches is low to absent, as trees with the same stem size may have experienced widely different growth histories, leading to widely diverse lifespans. The oldest individuals are those that remain suppressed in the understory during their initial development, thereby accumulating smaller increments and slower growth histories (Figs 5, 7). Reduced growth rates, starting from the earliest ontogenetic stages, can then be viewed as a necessary condition for attaining maximum tree longevity, not just for trees (Bigler & Veblen, 2009) but also for lianas (Roeder *et al.*, 2019).

An alternative explanation of factors leading to maximal tree lifespans was proposed by Stephenson *et al.* (2011). In that context, environments that cause slow tree growth also inhibit plant enemies that otherwise would kill more trees and thus reduce tree longevity. In fact, there may be no universal way to determine if harsh environments directly favor tree attributes that increase resistance to biotic and abiotic disturbances or if harsh environments inhibit the action of such disturbances, thereby indirectly leading to greater tree longevity. For instance, while insect performance and fitness may be reduced at higher elevations (Dahlhoff *et al.*, 2019), plant defenses also decrease along elevational gradients (Ferrenberg *et al.*, 2017), ultimately leaving unresolved the question of why tree mortality caused by biotic agents is reduced at the highest elevations (Das *et al.*, 2016).

The latitudinal herbivory-defense hypothesis, which predicts an increase in both herbivory and plant defenses against herbivores toward tropical regions and lower elevations, is still a subject of some controversy (Anstett *et al.*, 2016). Moreover, disentangling genetic and plastic responses of plant defenses inevitably requires accounting for intraspecific trait variation (Siefert *et al.*, 2015; Hahn & Maron, 2016) – see also 'Trade-off theory and phenotypic plasticity' below. As an example, faster growth at an early stem age may increase the risk of herbivory later in life (Ruel & Whitham, 2002). On the other hand, when considering a large tree-ring width dataset from boreal, temperate and Mediterranean sites in North America and Europe, no universal trade-off was found between early growth and mortality (Cailleret *et al.*, 2017). Regardless of environmental controls, trees of great age are a unique attribute of old-growth stands (Fig. 7), and the slowest growing individuals provide a distinctive metric for assessing forest naturalness. The age difference between the mean of the three youngest and of the three oldest trees when growth trajectories reach canopy accession was therefore proposed as a functional metric for assessing old-growth forest naturalness (Di Filippo *et al.*, 2017).

Succession and longevity

Species with the longest lifespans (Cupressaceae and Pinaceae) do not fit well within classic ecological theories related to forest succession (e.g. Whittaker, 1953). The extremely long-lived pines of subsection *Balfourianae*, for instance, inhabit areas where there is no replacement of one dominant species by another as the stand develops through an internal, continuous stochastic process (Lienard *et al.*, 2015). On the contrary, these extremely long-lived, slow-growing species are capable of regenerating in open-canopy stands where they also dominate the vegetation, either alone or together with other species (LaMarche, 1969; Brown & Schoettle, 2008). The relative lack of competition for light, compared to the scarcity of water, does not allow any other species to replace the shade-intolerant pines, which cannot then be called 'early-successional' because forest succession simply has not happened in these ecosystems for thousands of years (LaMarche & Mooney, 1972; Millar *et al.*, 2018). A recent, high-profile example of analyzing and discussing conifer xylogenesis using the dichotomous successional categories of 'early' and 'late' can be found in Huang *et al.* (2020), where juniper and pine species that can live more than 2000 yr (Fig. 2) were placed into the 'early-successional' bin.

Approximate determination of stem ages could have affected long-standing ecological paradigms. Process-based forest gap models, such as FORCLIM, which are used for addressing basic and applied questions in forest ecology (Chauvet *et al.*, 2017), are built on the assumption that late-successional species have traits that lead to slow growth, a long lifespan and a high shade tolerance, whereas early-successional species have opposite traits (Bugmann, 2020). However, once accurate methods were used to determine the establishment date of both shade-tolerant and shade-intolerant species after fire in boreal forests, no significant age differences could be found between tree species classified as early, mid- or late

successional (Gutsell & Johnson, 2002). Within closed-canopy forests dominated by shade-tolerant taxa, trees of shade-intolerant species can achieve comparable maximal ages, as shown for example by a 501-yr-old *Acer pseudoplatanus* L. in beech stands of the Italian Apennines (Biondi, 1992) and by a 509-yr-old *Liriodendron tulipifera* L. in the deciduous forests of the eastern USA (Pederson, 2010). Additional examples have recently been uncovered in southern Italy, including a 570-yr-old *Quercus petraea* in mixed beech–fir forests (Piovesan *et al.*, 2020), and > 550-yr-old *Pinus heldreichii* trees within beech stands (Piovesan *et al.*, 2019b).

Disturbance processes, such as those related to wildfire regime and insect outbreaks, are critical factors for shaping ecosystems, including those where the longest lived species are found (Swetnam, 1993; Campbell *et al.*, 2011; Kilpatrick & Biondi, 2020). Severe disturbances limit longevity, but repeated low-severity events, such as low-intensity wildfires, allow for the regeneration – and hence fitness – of redwoods (Sillett *et al.*, 2019) and giant sequoias (Stephenson, 1999). As the connection between disturbance and succession has kept ecologists busy for decades, tree species assigned to different successional stages have been found to differ in a set of traits related to growth rate, stress tolerance, dispersal, longevity and response to disturbance (e.g. Morin & Chuine, 2006). More recently, global-scale re-analysis of plant traits have been used to propose the fast–slow continuum theory of plant performance, which postulates differences in resource allocation at interspecific and intraspecific levels (Reich, 2014). Ecological inquiry is now focused on further refining the links between traits dimensions and demographic tradeoffs (see also section 'Trade-off theory and phenotypic plasticity'), as shown by the addition of a stature–recruitment axis orthogonal to the growth–survival one when considering closed-canopy tropical forests (Rüger *et al.*, 2018, 2020). Such a demographic model helps explain compositional forest dynamics by separating short-lived high-breeders from fast-growing long-lived pioneers, the latter being capable of occupying a predominant condition in old-growth forests as seed sources for several centuries. However, to date, only a minority of traits has been found to match the early-to-late successional axis of temperate tree species, with no clear pattern for stem longevity (Leuschner & Meier, 2018).

Reconstructing the growth history of old trees: is the sigmoidal model appropriate?

Tree-ring chronologies, especially in combination with forest inventories, can reveal growth trends of entire forest stands (Biondi, 1999; Biondi & Qeadan, 2008; Evans *et al.*, 2017) and tree populations at continental scales (Babst *et al.*, 2018). The focus of this review is, however, on growth histories of the oldest trees, rather than the whole stand where they are found. For this application, a sigmoidal curve is often used to describe tree size as a function of cambial age, for instance when evaluating global change impacts on tree longevity (Büntgen *et al.*, 2019). Life-history studies of tree growth have shown that diameter increment, basal area increment and volume increment follow different trajectories with age, with the one-dimensional radial increment (ring width) peaking at younger ages than either the two- (ring area) or three-dimensional

(ring volume) stem increments (Sillett *et al.*, 2010; Bowman *et al.*, 2013). Using the sigmoidal growth model, one can assume that reduced growth marks the entry into a senescent phase in terms of whole biomass (Thomas, 2013), and in fact lower stem increments often precede tree death (Das *et al.*, 2016; Cailleret *et al.*, 2017).

For modular organisms such as trees, the sigmoidal model may yet not be appropriate, or at least may not be applicable to all of its components (Watkinson *et al.*, 1986). Individual growth curves derived from beech chronologies of basal area increment do not follow the complete sigmoidal curve (Fig. 7). A similar mismatch with the sigmoidal model has been found for other temperate (Black *et al.*, 2008; Granda *et al.*, 2017) and tropical (Worbes & Schöngart, 2019) species. Climatic conditions are the main cause for temporary deviations from smooth growth curves, either by negatively impacting growth (Piovesan *et al.*, 2008) or by favoring it (Salzer *et al.*, 2009). Climatic changes can therefore be responsible, depending on their interactions with tree and site conditions, for either sustained or reduced growth of old veterans (see section 'Old Trees in a Changing World'). Further complications ensue when one considers the difference between whole-bark and strip-bark individuals, and how the latter can have greater ring widths (Leland *et al.*, 2018) even while reaching greater stem ages (Kelly *et al.*, 1992) than the former.

Dendrochronologically reconstructed growth histories support the hypothesis that the oldest trees, both in hardwoods and in conifers, reach extreme longevity when their basal area increments tend to increase over most of their life (Fig. 7; Piovesan *et al.*, 2019a, 2019b). This necessary, albeit not sufficient, condition for longevity was also suggested in a new model for estimating the age of ancient oaks (Moller, 2018). When large trees of more than 400 different species were considered, their mass growth rate was characterized by a constantly increasing trend (Stephenson *et al.*, 2014). High levels of stem growth have been observed in extremely old redwoods and sequoias (Sillett *et al.*, 2015); particularly for giant sequoia (*Sequoiadendron giganteum* (Lindl.) J.Buchholz), some of the world's largest trees may also be the world's fastest growing (Weatherspoon, 1986). A potential explanation for the connection between sustained growth and extreme longevity is the need to support larger leaf areas by maintaining flow of resources from the roots to the crown (Sillett *et al.*, 2010).

Other examples of prolonged tree life linked to greater stature and growth rates are found in species that normally have relatively low longevity of *c.* 100 yr, such as sub-arctic birch (*Betula pubescens* var. *pumila* (L.) Govaerts) (Jónsson, 2004) and aspen (*Populus tremuloides* Michx.) (Ireland *et al.*, 2014). Poplars (*Populus* spp.), whose lifespan does not normally exceed two centuries, can reach greater ages either by achieving large sizes through rapid growth under favorable conditions (Patrut *et al.*, 2013) or by surviving in dry areas (*Populus euphratica* Oliv.) (Dong *et al.*, 2019) where wood is likely to be less susceptible to internal rot. Chestnuts (*Castanea sativa* Mill.) of large sizes, with stem circumference > 10 m, may have record-setting ages of 400–600 yr (Krebs *et al.*, 2019). According to Loehle (1988), angiosperms with relatively short lifespans such as poplars, whose wood is subject to decay and poor ability to compartmentalize injuries and/or attacks from insects and pathogens, can reach greater longevity in sites that allow for higher

growth rates. On the other hand, the tallest trees of a given species may be at greater risk of dying during droughts if they had become locally reliant on high soil water availability (Stovall *et al.*, 2019). Again, however, it needs to be clarified that placing the emphasis on tree size, without knowing stem age, may lead to misconceptions. For instance, forest inventories, even when collected over entire countries and multiple decades, cannot properly describe the abundance of old trees if only stem size is measured (Henttonen *et al.*, 2019).

III. Evolutionary features and trade-off theories

Phylogeny and modularity

Longevity is a key trait in plant life history (Salguero-Gómez, 2017). Genetically controlled traits that are common among long-lived species are vegetative vigor (sprouting, epicormic and reiteration branches), long reproductive period, resistance to stress, such as long droughts, and to pests, including insects, bacteria, viruses and fungi (Major, 1967; Lanner, 2002; Munné-Bosch, 2018). Trees reaching maximal lifespans have to date been found within only two families of gymnosperms, Pinaceae and Cupressaceae (Fig. 2). In mesic to hydric Cupressaceae, extreme longevity appears as an outdated Mesozoic evolutionary character (Pittermann *et al.*, 2012), which is also suggested by the relic status of temperate-adapted *Sequoia*, *Sequoiadendron*, *Fitzroya* and *Taxodium* (Leslie *et al.*, 2018). In all of these genera, extreme stem ages are linked with gigantism, as was mentioned in previous sections. In Pinaceae, especially *Pinus* subsection *Balfourianae*, as well as in *Juniperus*, an extremely long lifespan appeared in a more recent geologic era, the Cenozoic, in cold and arid, mostly high-elevation continental environments with very short growing seasons (Keeley, 2012), open canopies, and lack of successional and/or gap-dynamics processes. These independent evolutionary processes that led to extreme tree longevity are also reflected in the phylogenetic distance of the taxa (Fig. 2).

The connections between tree longevity and fire regime extend into evolutionary processes. Since the late Cretaceous, competition with the emerging angiosperms together with changing fire regimes pushed the *Haploxylon* fire-avoider pines into subalpine and desert environments (Keeley, 2012), which then allowed for extreme longevity. *Diploxylon* pines, by contrast, became adapted to fire-prone landscapes with Mediterranean and subtropical climates (Badik *et al.*, 2018), where they could achieve longevity mostly similar to that of coexisting hardwoods (e.g. *c.* 300 yr). Trees older than 1000 yr have, however, been recently discovered for *Pinus heldreichii*, a *Diploxylon* Mediterranean pine that evolved during the early Tertiary and is now found in high-elevation environments, which limit growth and also represent Quaternary refugia (Schirone *et al.*, 1991).

Among Cupressaceae, early diverging species (*Sequoia*, *Sequoiadendron*, *Fitzroya*, *Taxodium*) achieved extreme longevity by means of their superior sizes, which allowed outcompeting hardwoods in closed-canopy, temperate-moist habitats. In the drier climates of the Oligocene, *Juniperus* and *Cupressus* developed drought-resistant xylem (e.g. tracheids with small lumen area) and foliage (e.g. small leaves that are pressed closely to the stem and overlap each other) at the expense of reduced hydraulic efficiency and lower rates of photosynthesis (Pittermann *et al.*, 2012). Wood anatomy of Cupressaceae does not include resin ducts, except for trauma-induced canals (Román-Jordán *et al.*, 2017), but it is typically characterized by durability and resistance to pathogens, which are common among tree species with long lifespans. Combining comparative studies of xylem form and function with phylogenetic analyses is one of the most promising areas of research to uncover the mechanisms behind tree longevity (Sperry *et al.*, 2006; Brodribb *et al.*, 2012; Roskilly *et al.*, 2019). Another open question with regard to the genetic control of longevity is the role of polyploidy, which only occurs in 5% of 685 gymnosperm taxa (Rastogi & Ohri, 2020) but is present in *Sequoia*, *Fitzroya* and *Juniperus*, that is in the majority of Cupressaceae taxa that include trees older than 2000 yr.

Trees have complex crown architectures where the axillary meristems, which form in the axils of leaves and grow out to form branches, are set aside earlier to prevent the accumulation of deleterious DNA replication errors known as Muller's ratchet, thereby extending tree lifespan (Burian *et al.*, 2016). Thanks to their modular architecture, trees may have the ability to compartmentalize deleterious somatic mutations, and escape senescence if the negative consequences are restricted to that module (Bernard *et al.*, 2020). Plants of great longevity are characterized by a greater degree of modularity, which is apparent in root-to-shoot connections (Larson *et al.*, 1993), bark stripping, and defense systems that compartmentalize injuries and biotic attackers (Morris *et al.*, 2019). Tree longevity would therefore rely on vegetative vigor and disease resistance together with plastic crown branching and root readjustments (Lanner, 2002).

Trade-off theory and phenotypic plasticity

The evolution of life history traits is expected to maximize survival and reproduction, and thus fitness. Because of finite resources in a changing environment, a number of trade-offs have emerged as a consequence of natural selection forces that shape organism traits and investments in survival, growth and reproduction (Fabian & Flatt, 2012). In the absence of extreme disturbance events that cause widespread mortality, trees that invest resources in defenses from insects and/or drought resistance (e.g. the 'fight trees' mentioned by Lauder *et al.*, 2019) would achieve a prolonged lifespan and the associated reproductive output (Dani & Kodandaramaiah, 2019). Species capable of extreme longevity are not only characterized by multiple reproductive cycles over their lifetime but also by the production of viable seeds regardless of age (Lanner & Connor, 2001; Alejano *et al.*, 2019). Because only past survival, but not past reproductive effort, can be reconstructed over centuries and millennia, it remains impossible to clearly distinguish how fitness evolved with regard to those two adaptation strategies.

All tree organs are likely to face physiological, structural and defensive trade-offs, and wood tissue allocation plays a central role in these complex interactions (Chave *et al.*, 2009). Reduced stem growth may be more easily obtained by conifers due to their simpler wood anatomy compared to hardwoods (Fig. 8), especially those with ring-porous structures, which do not seem to

Fig. 8 Schematic representation of factors that can influence tree longevity. In the photographs of ring widths, time is progressing from left to right, and a black bar is used for scale to represent 1 cm in length.

allow the locally absent rings that are often found in long-lived conifers (Baillie & Pilcher, 1973; Carroll *et al.*, 2014). Another trade-off worth considering involves hydraulic efficiency and safety of vessels in stems (Gleason *et al.*, 2016). In ponderosa pine (*Pinus ponderosa* Douglas ex C.Lawson) a single xylem trait – pit morphology – may determine tree longevity, because slower lifelong growth rates in the oldest trees are determined by functional constraints for hydraulic safety at the expense of growth efficiency (Roskilly *et al.*, 2019). Older trees have a greater torus/opening ratio that leads to reduced transport efficiency, and hence lower growth when water is available, but also to greater protection from embolism, and hence lower mortality during drought episodes.

Xylem traits and plasticity, together with decay resistance, especially in the heartwood (Taylor *et al.*, 2002), influence

longevity. Dark-colored heartwoods, rich in secondary compounds, are more resistant to wood decay (Chave *et al.*, 2009). Disease-resistant genes abound in the genome of long-lived hardwoods, such as oaks (Plomion *et al.*, 2018). The total energy, both chemical and structural, allocated by a tree to wood structure and composition can be measured as volumetric heat of combustion ($J cm^{-3}$), which is positively correlated with longevity in angiosperms (Loehle, 1988). Greater wood density in tropical species is associated with lower mortality, especially during early life stages (Osazuwa-Peters *et al.*, 2017).

In conifers, the presence or absence of resin ducts is genetically controlled, and therefore used for wood species identification (e.g. Wu & Hu, 1997). Producing chemical compounds in resin-based defenses that protect conifers from biological agents of mortality, such as bark beetles (Kane & Kolb, 2010), comes at the expense of

Fig. 9 'Dolmen in the Snow', by Caspar David Friedrich, about 1807 CE. (This image is in the public domain (see https://commons.wikimedia.org/wiki/File:Huenengrab_im_Schnee_(C_D_Friedrich).jpg) and was reproduced under a Creative Commons Attribution 4.0 License.)

growth and reproduction (Loehle, 1988). Long-lived bristlecone (*Pinus longaeva*) and foxtail (*Pinus balfouriana*) pines are characterized by defense traits, including constitutive monoterpenes, resin ducts and wood density, that make them less vulnerable to mountain pine beetle compared with limber pine (*Pinus flexilis* E.James) (Bentz *et al.*, 2017). However, peer-reviewed articles to date indicate longer maximal lifespan for limber (1575 yr; Millar *et al.*, 2018) than foxtail pine (1183 yr; Scuderi, 1993). One could then speculate that population size, which is much lower for foxtail than limber pine, influences stochastic mortality, thereby reducing realized longevity of foxtail pine. It is difficult to ascertain if a lack of widespread interest in scientifically determining tree maximum ages or an inability to capture all published scientific information is also contributing to these differences.

Budgetary compromises between fast-growing, short-lived plant species at one end of the spectrum and slow-growing, long-lived species at the other are consistent with the notion that tree longevity is mediated by the interaction between genotype and expressed traits under environmental influences (Rüger *et al.*, 2020). A greater allocation of resources to resin-based defenses with respect to growth was recently reported in whitebark pines (*Pinus albicaulis* Engelm.) that survived mountain pine beetle outbreaks (Kichas *et al.*, 2020). Outbreaks also reduced survival of fast-growing ponderosa pine compared to slow-growing ones, suggesting a host-based life history trade-off that favors the maintenance of genetic diversity on growth rates (de la Mata *et al.*, 2017). In previous sections, we noted how both the environment (e.g. elevation) and tree properties such as age, growth rate and size influence tree defenses (Ferrenberg *et al.*, 2017).

The resource availability hypothesis (Endara & Coley, 2011) may include trade-offs between growth and defenses. Under limited nutrient availability, conifers show an increased investment in chemical and anatomical defenses (Moreira *et al.*, 2015), which favor longevity. Stronger defenses in infertile soils should then be the best strategy for tree survival because under adverse environmental conditions trees are expected to have greater difficulties in replacing tissues removed by herbivory pressure (Fine *et al.*, 2006). Ultimately, these considerations lead to an evolutionary choice between 'to grow or to defend' (Herms & Mattson, 1992). In the same vein, the widespread occurrence of center-rot and/or hollow stems in many tree species could be a balance between, on the one hand, mortality from reduced structural integrity, and, on the other, the metabolic costs required to protect the central part of the trunk (Ruxton, 2014). An opposite strategy consists of withstanding stem breakage, for example from strong winds in hurricane-prone areas, as in the case of *Taxodium distichum* (L.) Rich. (Middleton, 2009).

IV. Old trees in a changing world

Uncovering bioecological processes that regulate tree longevity has taken on a renewed emphasis in the age of global change. Longevity is complementary to mortality (Stephenson *et al.*, 2011), and both depend on evolutionary history, environmental conditions, biotic interactions and disturbance regimes. The value of old trees as archives of environmental variability and abrupt events, which has long been recognized for temperate and high-latitude areas, has recently been extended to tropical forests (Caetano-Andrade *et al.*, 2020). At the same time, the distribution of old-growth forests has been reduced greatly by human impacts (e.g. Bonnicksen, 2000). There is therefore a possibility that our view of processes governing tree longevity

suffers from a survivor bias, whereby an emphasis is placed on remote mountain locations because those have been least affected by human impacts.

Environmental shifts or megadisturbances (droughts, wildfires, pests; Millar & Stephenson, 2015) and direct human impacts, such as land use changes (Fig. 5), can substantially modify tree lifespans. Responses are complex and not clearly predictable, with taxonomic differences between conifers and angiosperms related to resilience and resistance (DeSoto *et al.*, 2020). While old trees are capable of increased growth when environmental conditions become more favorable (Phillips *et al.*, 2008), higher increments, especially during the early phase of a tree's life history, have been linked with decreased longevity (Bigler, 2016; Brienen *et al.*, 2020). A warming trend may favor fungal activity, which in turn would speed up wood decay, decrease stem resistance and heighten the chance of snapping (Oberle *et al.*, 2018).

Mountains, which are hotspots of terrestrial biodiversity (Rahbek *et al.*, 2019), harbor most of the oldest trees, but instrumental observing networks located along ecological gradients have only recently become operational (Hopkin, 2006). No modeling effort, as sophisticated as it may be, can replace the value of obtaining *in situ*, subhourly measurements of ecophysiological responses for species with extreme longevity, such as *Pinus longaeva* and *Pinus flexilis* (e.g. Liu & Biondi, 2020). After all, old trees in growth-limiting environments, with their stunted form and relatively small size, are likely to be more resistant to a changing climate than large, monumental trees (Fajardo *et al.*, 2019).

Understanding how complex human–climate interactions shape forest dynamics and impact tree longevity has a fundamental role in science-based forest management and conservation (Sangüesa-Barreda *et al.*, 2020). Tree longevity, when properly determined (Box 1), can be considered a fundamental feature of forest ecosystems, even becoming a super-trait that defines the health and integrity of ecological processes. In fact, extremely old trees are silent witnesses not only of natural landscapes but also of the societies that live on them. In areas where dendroecological studies have been combined with palynological ones, it has been possible to distinguish long-term changes due to human sociopolitical and demographic transformation from those linked to climate change. As an example, historical landscape changes in central Italy caused by human impacts have driven the modern location of old-growth forests in remote areas (Mensing *et al.*, 2020). Similarly, it has been possible to establish a direct link between the abundance of multicentury-old *Pinus heldreichii* trees and the disappearance of anthropogenic impacts in southern European mountains during the late medieval plagues (Piovesan *et al.*, 2019b; Sangüesa-Barreda *et al.*, 2020).

Defining tree longevity has direct forest management implications when identifying old-growth stands. In particular, two of the currently accepted criteria for old-growth status are: the average age of dominant species equaling about half their maximum longevity; and the presence of old trees approaching the maximum longevity for the species (Mosseler *et al.*, 2003), which in closed-canopy forests is generally considered to be > 300 yr (Wirth et al., 2009). Proper application of these guidelines requires in-depth knowledge of longevity not only by species but also, for the same tree species,

under different environmental conditions and historical legacies. As a case in point, the US Forest Service old-growth definition in the Northern Region changes by forest type, and is based partly on the age of large trees and on stand basal area by species (Green *et al.*, 1992).

Stem age is also a key variable for understanding, and properly modeling, carbon residence and turnover times, which in turn define the role of old-growth forests as a benchmark for maximum carbon stocks, and of recovering forests as carbon sinks (Körner, 2017; Requena Suarez *et al.*, 2019; Brienen *et al.*, 2020). While single large and/or old trees are capable of accumulating carbon at surprising rates (Sillett *et al.*, 2020), the role of old-growth forests in biogeochemical cycles remains an area of active research (e.g. Anderegg *et al.*, 2020). It is worth mentioning that large uncertainties still exist with regard to sinks and fluxes in soils, vegetation and the associated boundary layer (e.g. Rayback *et al.*, 2020).

Large old trees are themselves habitat to several species that would be equally damaged from tree mortality (Lindenmayer & Laurance, 2017). So-called veteran trees (Fay, 2002) also deserve protection, because they occur within rural and urban landscapes, where they offer tangible reminders of past economic, cultural, and social practices and landscapes that may disappear when left to natural processes. While the growth patterns and history of such monumental trees typically differ from those of individuals of the same species located in forest sites, they can still reach extremely old ages, especially for hardwoods (Drobyshev & Niklasson, 2010). Yet, the lack of natural landscapes located next to areas where veteran trees are located may hamper the assessment of agrarian practices, such as pollarding, litter removal, livestock grazing, slash-and-burn or other forms of fire use, etc., on the longevity of such trees.

It may be worth noting that the peculiar features of extremely old trees have attracted the attention of artists, with notable examples during the European romantic period of the early 19th century (Fig. 9). During that historical period, and in the same geographic region, a growing conservationist movement began to recognize the fundamental role of large old trees in natural landscapes for sociocultural and aesthetic reasons (Mölder *et al.*, 2020). An appreciation of the long time required for trees to reach their maximum lifespan, and of the ups and downs that are recorded in their growth history, may inspire and remind people of the need to maintain natural dynamics and habitats over a substantial portion of our planet.

V. Last words

A preponderance of evidence has suggested that trees do not die because of genetically programmed senescence in their meristems (Mencuccini *et al.*, 2014), and rather are killed by an external agent, either biotic or abiotic. It is beyond the scope of our review to further investigate the complexity of tree growth, which for instance relies heavily on programmed cellular death, or apoptosis, both in xylem and in heartwood formation (Kampe & Magel, 2013). We are also aware of alternative hypotheses, such as the rate of living theory of aging, which considers tree longevity to be a result of low

metabolic rates in the stem compared to organs capable of photosynthesis (Issartel & Coiffard, 2011). Here we argue that long tree lifespans are allowed by specific combinations of life-history traits within realized niches that support resistance to, or avoidance of, extrinsic mortality (Stephenson *et al.*, 2011; Fig. 8). Furthermore, trees can achieve their maximum longevity through sustained growth over extended periods of time or at least by retaining the capacity to increase their growth rates when conditions allow it. The growth plasticity and modularity of trees can then be viewed as an evolutionary advantage that allows them to survive for centuries and millennia.

The two main life-history strategies we have outlined in connection with tree longevity mimic two essential trade-offs, one between growth and survival and the other between stature and recruitment. The first strategy includes low radial growth rates, often associated with strip-bark stems, in extreme environments where climate (arid and/or cold) and soil (rocky and/or nutrient-poor) are particularly limiting for tree growth. Isolated and stunted trees are relatively free from competition, rarely subject to high-severity wildfires, and well adapted to resist other environmental and biotic hazards. The second strategy involves sustained growth rates that lead to large sizes in environments that favor tree growth, under temperate or tropical climates. While tree density can be high and disturbance events can be frequent, these gigantic trees are able to escape competition and resist perturbations thanks to their resistance and resilience. Even under this strategy, however, the oldest trees are usually those that have relatively lower growth rates, thereby suggesting a universal role for the growth–survival tradeoff.

It cannot be emphasized enough that understanding tree longevity requires accurate, replicable dating methods, which were outlined at the start of this review (Box 1). While dendrochronologists are often mired in climate reconstructions of increasing numerical complexity, the importance of tree-ring data for evaluating and understanding the biology of secondary plant growth is undisputable, and provides yet another motive for collecting such data. As more and more scientific information is systematically collected on tree ages and other plant traits within and between species under various ecological settings, it becomes feasible to incorporate tree lifespan as a key ecological dimension in global syntheses of life history strategies (Ottaviani *et al.*, 2017), especially in connection with disturbance regimes and their possible future modifications.

ORCID

Franco Biondi (iD) https://orcid.org/0000-0003-0651-104X
Gianluca Piovesan (iD) https://orcid.org/0000-0002-3214-0839

References

Abdoun F, Jull AJT, Guibal F, Thinon M. 2005. Radial growth of the Sahara's oldest trees: *Cupressus dupreziana* A. Camus. *Trees - Structure and Function* **19**: 661–670.

Ahuja MR. 2009. Genetic constitution and diversity in four narrow endemic redwoods from the family Cupressaceae. *Euphytica* **165**: 5–19.

Akaike H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control AC-19: 716–723.

Alejano R, Domínguez-Delmás M, García-González I, Wazny T, Vázquez-Piqué J, Fernández-Martínez M. 2019. The age of black pine (*Pinus nigra* Arn. ssp. *salzmannii* (Dunal) Franco) mother trees has no effect on seed germination and on offspring seedling performance. *Annals of Forest Science* **76**: 15.

Anderegg WRL, Trugman AT, Badgley G, Anderson CM, Bartuska A, Ciais P, Cullenward D, Field CB, Freeman J, Goetz SJ et al. 2020. Climate-driven risks to the climate mitigation potential of forests. *Science* **368**: eaaz7005.

Andreu-Hayles L, Santos GM, Herrera-Ramírez DA, Martin-Fernández J, Ruiz-Carrascal D, Boza-Espinoza TE, Fuentes AF, Jørgensen PM. 2015. Matching dendrochronological dates with the southern hemisphere ^{14}C bomb curve to confirm annual tree rings in *Pseudolmedia rigida* from Bolivia. *Radiocarbon* **57**: 1–13.

Anstett DN, Nunes KA, Baskett C, Kotanen PM. 2016. Sources of controversy surrounding latitudinal patterns in herbivory and defense. *Trends in Ecology & Evolution* **31**: 789–802.

Antos JA, Guest HJ, Parish R. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *Journal of Ecology* **93**: 536–543.

Arkawa H. 1960. Japanese tree-ring analyses. *Archiv für Meteorologie, Geophysik und Bioklimatologie, Serie B* **10**: 210–212.

Babst F, Bodesheim P, Charney N, Friend AD, Girardin M-P, Klesse S, Moore DJP, Seftigen K, Björklund J, Bouriaud O et al. 2018. When tree rings go global: challenges and opportunities for retro- and prospective insight. *Quaternary Science Reviews* **197**: 1–20.

Badik KJ, Jahner JP, Wilson JS. 2018. A biogeographic perspective on the evolution of fire syndromes in pine trees (*Pinus*: Pinaceae). *Royal Society Open Science* **5**: 172412.

Baillie MGL, Pilcher JR. 1973. A simple cross-dating program for tree-ring research. *Tree-Ring Bulletin* **33**: 7–14.

Bentz BJ, Hood SM, Hansen EM, Vandygriff JC, Mock KE. 2017. Defense traits in the long-lived Great Basin bristlecone pine and resistance to the native herbivore mountain pine beetle. *New Phytologist* **213**: 611–624.

Bernabei M. 2015. The age of the olive trees in the Garden of Gethsemane. *Journal of Archaeological Science* **53**: 43–48.

Bernard C, Compagnoni A, Salguero-Gómez R. 2020. Testing Finch's hypothesis: the role of organismal modularity on the escape from actuarial senescence. *Functional Ecology* **34**: 88–106.

Bigler C, Veblen TT. 2009. Increased early growth rates decrease longevities of conifers in subalpine forests. *Oikos* **118**: 1130–1138.

Bigler C. 2016. Trade-offs between growth rate, tree size and lifespan of mountain pine (*Pinus montana*) in the Swiss National Park. *PLoS ONE* **11**: e0150402.

Biondi F. 1992. Development of a tree-ring network for the Italian peninsula. *Tree-Ring Bulletin* **52**: 15–29.

Biondi F. 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecological Applications* **9**: 216–227.

Biondi F, Fessenden JE. 1999. Radiocarbon analysis of *Pinus lagunae* tree rings: implications for tropical dendrochronology. *Radiocarbon* **41**: 241–249.

Biondi F, Qeadan F. 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research* **64**: 81–96.

Biondi F, Bradley M. 2013. Long-term survivorship of single-needle pinyon (*Pinus monophylla*) in mixed-conifer ecosystems of the Great Basin. *USA. Ecosphere* **4**: 120.

Biondi F. 2020. From dendrochronology to allometry. *Forests* **11**: art. 146.

Black BA, Colbert JJ, Pederson N. 2008. Relationships between radial growth rates and lifespan within North American tree species. *Ecoscience* **15**: 349–357.

Bonnicksen TM. 2000. *America's ancient forests.* New York, NY, USA: John Wiley & Sons.

Bowman DMJS, Brienen RJW, Gloor E, Phillips OL, Prior LD. 2013. Detecting trends in tree growth: not so simple. *Trends in Plant Science* **18**: 11–17.

Brienen RJW, Schöngart J, Zuidema PA. 2016. Tree rings in the tropics: Insights into the ecology and climate sensitivity of tropical trees. In: Goldstein G, Santiago LS, eds. *Tropical tree physiology: adaptations and responses in a changing environment.* Cham, Switzerland: Springer International, 439–461.

Brienen RJW, Caldwell L, Duchesne L, Voelker S, Barichivich J, Baliva M, Ceccantini G, Di Filippo A, Helama S, Locosselli GM *et al.* 2020. Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nature Communications* **11**: art. 4241.

Brodribb TJ, Pittermann J, Coomes DA. 2012. Elegance versus speed: examining the competition between conifer and angiosperm trees. *International Journal of Plant Sciences* **173**: 673–694.

Brown PM. 2007. A modified increment borer handle for coring in locations with obstructions. *Tree-Ring Research* **63**: 61–62.

Brown PM, Schoettle AW. 2008. Fire and stand history in two limber pine (*Pinus flexilis*) and Rocky Mountain bristlecone pine (*Pinus aristata*) stands in Colorado. *International Journal of Wildland Fire* **17**: 339–347.

Brown PM, Gannon B, Battaglia MA, Fornwalt PJ, Huckaby LS, Cheng AS, Baggett LS. 2019. Identifying old trees to inform ecological restoration in montane forests of the central Rocky Mountains, USA. *Tree-Ring Research* **75**: 34–48.

Brunstein FC, Yamaguchi DK. 1992. The oldest known Rocky Mountain bristlecone pines (*Pinus aristata* Engelm.). *Arctic and Alpine Research* **24**: 253–256.

Bugmann H. 2020. Tree diversity reduced to the bare essentials. *Science* **368**: 128–129.

Bunn AG, Lawrence RL, Bellante GJ, Waggoner LA, Graumlich LJ. 2003. Spatial variation in distribution and growth patterns of old growth strip-bark pines. *Arctic, Antarctic, and Alpine Research* **35**: 323–330.

Büntgen U, Krusic PJ, Piermattei A, Coomes DA, Esper J, Myglan VS, Kirdyanov AV, Camarero JJ, Crivellaro A, Körner C. 2019. Limited capacity of tree growth to mitigate the global greenhouse effect under predicted warming. *Nature Communications* **10**: 2171.

Burian A, Barbier de Reuille P, Kuhlemeier C. 2016. Patterns of stem cell divisions contribute to plant longevity. *Current Biology* **26**: 1385–1394.

Caetano-Andrade VL, Clement CR, Weigel D, Trumbore S, Boivin N, Schöngart J, Roberts P. 2020. Tropical trees as time capsules of anthropogenic activity. *Trends in Plant Science* **25**: 369–380.

Cailleret M, Jansen S, Robert EMR, Desoto L, Aakala T, Antos JA, Beikircher B, Bigler C, Bugmann H, Caccianiga M *et al.* 2017. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* **23**: 1675–1690.

Campbell EM, Keane RE, Larson ER, Murray MP, Schoettle AW, Wong C. 2011. Disturbance ecology of high-elevation five-needle pine ecosystems in western North America. In: Keane RE, Tomback DF, Murray MP, Smith CM, eds. *The future of high-elevation, five-needle white pines in Western North America: Proceedings of the High Five Symposium.* Fort Collins, CO, USA: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, 154–164.

Carroll AL, Sillett SC, Kramer RD. 2014. Millennium-scale crossdating and inter-annual climate sensitivities of standing California redwoods. *PLoS ONE* **9**: e102545.

Cary KL, Pittermann J. 2018. Small trees, big problems: comparative leaf function under extreme edaphic stress. *American Journal of Botany* **105**: 50–59.

Chambers JQ, Higuchi N, Schimel JP. 1998. Ancient trees in Amazonia. *Nature* **391**: 135–136.

Chapin FS III, Matson PA, Vitousek PM. 2011. *Principles of terrestrial ecosystem ecology.* New York, NY, USA: Springer.

Chauvet M, Kunstler G, Roy J, Morin X. 2017. Using a forest dynamics model to link community assembly processes and traits structure. *Functional Ecology* **31**: 1452–1461.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**: 351–366.

Chiarucci A, Piovesan G. 2020. Need for a global map of forest naturalness for a sustainable future. *Conservation Biology* **34**: 368–372.

Contributors of the International Tree-Ring Data Bank. 2020. *International Tree-Ring Data Bank (ITRDB).* [WWW document] URL http://www.ngdc.noaa.gov/paleo/treering.html.

Cook ER, Palmer JG, Cook BI, Hogg A, D'Arrigo RD. 2002. A multi-millennial palaeoclimatic resource from *Lagarostrobos colensoi* tree-rings at Oroko Swamp, New Zealand. *Global and Planetary Change* **33**: 209–220.

Currey DR. 1965. An ancient bristlecone pine stand in eastern Nevada. *Ecology* **46**: 564–566.

Dahlhoff EP, Dahlhoff VC, Grainger CA, Zavala NA, Otepola-Bello D, Sargent BA, Roberts KT, Heidl SJ, Smiley JT, Rank NE. 2019. Getting chased up the mountain: high elevation may limit performance and fitness characters in a montane insect. *Functional Ecology* **33**: 809–818.

Daly C, Halbleib M, Smith JI, Gibson WP, Doggett MK, Taylor GH, Curtis J, Pasteris PP. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology* **28**: 2031–2064.

Dani KGS, Kodandaramaiah U. 2019. Ageing in trees: role of body size optimization in demographic senescence. *Perspectives in Plant Ecology, Evolution and Systematics* **36**: 41–51.

Das AJ, Stephenson NL, Davis KP. 2016. Why do trees die? Characterizing the drivers of background tree mortality. *Ecology* **97**: 2616–2627.

DeSoto L, Cailleret M, Sterck F, Jansen S, Kramer K, Robert EMR, Aakala T, Amoroso MM, Bigler C, Camarero JJ *et al.* 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nature Communications* **11**: 545.

DesRochers A, Gagnon R. 1997. Is ring count at ground level a good estimation of black spruce age? *Canadian Journal of Forest Research* **27**: 1263–1267.

Di Filippo A, Biondi F, Maugeri M, Schirone B, Piovesan G. 2012. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. *Global Change Biology* **18**: 960–972.

Di Filippo A, Pederson N, Baliva M, Brunetti M, Dinella A, Kitamura K, Knapp HD, Schirone B, Piovesan G. 2015. The longevity of broadleaf deciduous trees in Northern Hemisphere temperate forests: insights from tree-ring series. *Frontiers in Ecology and Evolution* **3**: 46.

Di Filippo A, Biondi F, Piovesan G, Ziaco E. 2017. Tree ring-based metrics for assessing old-growth forest naturalness. *Journal of Applied Ecology* **54**: 737–749.

Doi Y, Mori AS, Takeda H. 2008. Adventitious root formation of two *Abies* species on log and soil in an old-growth subalpine forest in central Japan. *Journal of Forest Research* **13**: 190.

Dong Q, Friedman J, Zhou H. 2019. An old tree and its many-shaped leaves. *Frontiers in Ecology and the Environment* **17**: 15.

Douglass AE. 1919. *Climatic cycles and tree-growth.* Washington, DC, USA: Carnegie Institution.

Drobyshev I, Niklasson M. 2010. How old are the largest southern Swedish oaks? A dendrochronological analysis. *Ecological Bulletins no. 53* (Broadleaved Forests in southern Sweden: management for multiple goals), 155–164.

Endara M-J, Coley PD. 2011. The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology* **25**: 389–398.

Evans MEK, Falk DA, Arizpe A, Swetnam TL, Babst F, Holsinger KE. 2017. Fusing tree-ring and forest inventory data to infer influences on tree growth. *Ecosphere* **8**: e01889.

Evstigneev O, Korotkov V. 2016. Ontogenetic stages of trees: an overview. *Russian Journal of Ecosystem Ecology* **2**.

Fabian D, Flatt T. 2012. Life history evolution. *Nature Education Knowledge* **3**: 24.

Faison EK. 2014. Large old tree declines at broad scales: a more complicated story. *Conservation Letters* **7**: 70–71.

Fajardo A, McIntire EJB, Olson ME. 2019. When short stature is an asset in trees. *Trends in Ecology & Evolution* 34: 193–199.

Farjon A. 2018. The Kew review: conifers of the world. *Kew Bulletin* 73: 8.

Fay N. 2002. Environmental arboriculture, tree ecology and veteran tree management. *Arboricultural Journal* 26: 213–238.

Ferrenberg S, Langenhan JM, Loskot SA, Rozal LM, Mitton JB. 2017. Resin monoterpene defenses decline within three widespread species of pine (*Pinus*) along a 1530-m elevational gradient. *Ecosphere* 8: e01975.

Fine PVA, Miller ZJ, Mesones I, Irazuzta S, Appel HM, Stevens MHH, Sääksjärvi I, Schultz JC, Coley PD. 2006. The growth–defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87: S150–S162.

Friedrich M, Remmele S, Kromer B, Hofmann J, Spurk M, Kaiser KF, Orcel C, Küppers M. 2004. The 12,460-year Hohenheim oak and pine tree-ring chronology from central Europe: a unique annual record for radiocarbon calibration and paleoenvironment reconstructions. *Radiocarbon* 46: 1111–1122.

Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, Bhaskar R, Brodribb TJ, Bucci SJ, Cao K-F *et al.* 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist* 209: 123–136.

Granda E, Camarero JJ, Galván JD, Sangüesa-Barreda G, Alla AQ, Gutierrez E, Dorado-Liñán I, Andreu-Hayles L, Labuhn I, Grudd H *et al.* 2017. Aged but withstanding: maintenance of growth rates in old pines is not related to enhanced water-use efficiency. *Agricultural and Forest Meteorology* 243: 43–54.

Green P, Joy J, Sirucek D, Hann W, Zack A, Naumann B. 1992. *Old-growth forest types of the northern region. Report R-1 SES 4/92*. Missoula, MN, USA: USDA Forest Service.

Gutsell SL, Johnson EA. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. *Journal of Ecology* 90: 153–166.

Hahn PG, Maron JL. 2016. A framework for predicting intraspecific variation in plant defense. *Trends in Ecology & Evolution* 31: 646–656.

Henttonen HM, Nöjd P, Suvanto S, Heikkinen J, Mäkinen H. 2019. Large trees have increased greatly in Finland during 1921–2013, but recent observations on old trees tell a different story. *Ecological Indicators* 99: 118–129.

Herms DA, Mattson WJ. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* 67: 283–335.

Hewitt G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405: 907–913.

Hopkin M. 2006. Spying on nature. *Nature* 444: 420–421.

Huang J-G, Ma Q, Rossi S, Biondi F, Deslauriers A, Fonti P, Liang E, Mäkinen H, Oberhuber W, Rathgeber CBK *et al.* 2020. Photoperiod and temperature as dominant environmental drivers triggering secondary growth resumption in Northern Hemisphere conifers. *Proceedings of the National Academy of Sciences, USA* 117: 20645–20652.

Hubau W, De Mil T, Van den Bulcke J, Phillips OL, Angoboy Ilondea B, Van Acker J, Sullivan MJP, Nsenga L, Toirambe B, Couralet C *et al.* 2019. The persistence of carbon in the African forest understory. *Nature Plants* 5: 133–140.

Huntington E. 1914. *The climatic factor as illustrated in arid America*. Washington, DC, USA: Carnegie Institution of Washington.

Ireland KB, Moore MM, Fulé PZ, Zegler TJ, Keane RE. 2014. Slow lifelong growth predisposes *Populus tremuloides* trees to mortality. *Oecologia* 175: 847–859.

Issartel J, Coiffard C. 2011. Extreme longevity in trees: live slow, die old? *Oecologia* 165: 1–5.

Jónsson TH. 2004. Stature of sub-arctic birch in relation to growth rate, lifespan and tree form. *Annals of Botany* 94: 753–762.

Kampe A, Magel E. 2013. New insights into heartwood and heartwood formation. In: Fromm J, ed. *Cellular aspects of wood formation*. Berlin, Germany: Springer, 71–95.

Kane JM, Kolb TE. 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia* 164: 601–609.

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M *et al.* 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* 26: 119–188.

Keeley JE. 2012. Ecology and evolution of pine life histories. *Annals of Forest Science* 69: 445–453.

Kelly PE, Cook ER, Larson DW. 1992. Constrained growth, cambial mortality, and dendrochronology of ancient *Thuja occidentalis* on cliffs of the Niagara Escarpment: an eastern version of bristlecone pine? *International Journal of Plant Sciences* 153: 117–127.

Kharuk VI, Ranson KJ, Im ST, Oskorbin PA, Dvinskaya ML, Ovchinnikov DV. 2013. Tree-line structure and dynamics at the northern limit of the larch forest: Anabar Plateau, Siberia, Russia. *Arctic, Antarctic, and Alpine Research* 45: 526–537.

Kichas NE, Hood SM, Pederson GT, Everett RG, McWethy DB. 2020. Whitebark pine (*Pinus albicaulis*) growth and defense in response to mountain pine beetle outbreaks. *Forest Ecology and Management* 457: 117736.

Kilpatrick M, Biondi F. 2020. Post-wildfire regeneration in a sky-island mixed-conifer ecosystem of the north American Great Basin. *Forests* 11: 900.

Konter O, Krusic PJ, Trouet V, Esper J. 2017. Meet Adonis, Europe's oldest dendrochronologically dated tree. *Dendrochronologia* 42: 12.

Körner C, Basler D. 2010. Phenology under global warming. *Science* 327: 1461–1462.

Körner C. 2017. A matter of tree longevity. *Science* 355: 130–131.

Krebs P, Poli A, Conedera M. 2019. I castagni monumentali dell'Alpe di Brusino (Cantone Ticino, Svizzera): indicazioni per chi volesse azzardarne l'età. *Bollettino della Società Ticinese di Scienze Naturali* 107: 41–53.

Kurokawa H, Yoshida T, Nakamura T, Lai J, Nakashizuka T. 2003. The age of tropical rain-forest canopy species, Borneo ironwood (*Eusideroxylon zwageri*), determined by ¹⁴C dating. *Journal of Tropical Ecology* 19: 1–7.

LaMarche VC Jr. 1969. Environment in relation to age of bristlecone pines. *Ecology* 50: 54–59.

LaMarche VC Jr, Mooney HA. 1972. Recent climatic change and development of the bristlecone pine (*P. longaeva* Bailey) Krummholz Zone, Mt. Washington, Nevada. *Arctic and Alpine Research* 4: 61–72.

Lanner RM, Connor KF. 2001. Does bristlecone pine senesce? *Experimental Gerontology* 36: 675–685.

Lanner RM. 2002. Why do trees live so long? *Ageing Research Reviews* 1: 653–671.

Lara A, Villalba R. 1993. A 3620-year temperature record from *Fitzroya cupressoides* tree rings in southern South America. *Science* 260: 1104–1106.

Larson DW, Matthes-Sears U, Kelly PE. 1993. Cambial dieback and partial shoot mortality in cliff-face *Thuja occidentalis*: evidence for sectored radial architecture. *International Journal of Plant Sciences* 154: 496–505.

Larson DW, Matthes U, Gerrath JA, Gerrath JM, Nekola JC, Walker GL, Porembski S, Charlton A, Larson NWK. 1999. Ancient stunted trees on cliffs. *Nature* 398: 382–383.

Larson DW, Matthes U, Gerrath JA, Larson NWK, Gerrath JM, Nekola JC, Walker GL, Porembski S, Charlton A. 2000. Evidence for the widespread occurrence of ancient forests on cliffs. *Journal of Biogeography* 27: 319–331.

Lauder JD, Moran EV, Hart SC. 2019. Fight or flight? Potential tradeoffs between drought defense and reproduction in conifers. *Tree Physiology* 39: 1071–1085.

League K, Veblen T. 2006. Climatic variability and episodic *Pinus ponderosa* establishment along the forest–grassland ecotones of Colorado. *Forest Ecology and Management* 228: 98–107.

Leland C, Cook ER, Andreu-Hayles L, Pederson N, Hessl A, Anchukaitis KJ, Byambasuren O, Nachin B, Davi N, D'Arrigo RD *et al.* 2018. Strip-bark morphology and radial growth trends in ancient *Pinus sibirica* trees from central Mongolia. *Journal of Geophysical Research: Biogeosciences* 123: 945–959.

Leslie AB, Beaulieu J, Holman G, Campbell CS, Mei W, Raubeson LR, Mathews S. 2018. An overview of extant conifer evolution from the perspective of the fossil record. *American Journal of Botany* 105: 1531–1544.

Letunic I, Bork P. 2019. Interactive Tree Of Life (iTOL) v4: recent updates and new developments. *Nucleic Acids Research* 47: W256–W259.

Leuschner C, Meier IC. 2018. The ecology of Central European tree species: trait spectra, functional trade-offs, and ecological classification of adult trees. *Perspectives in Plant Ecology, Evolution and Systematics* 33: 89–103.

Lienard J, Florescu I, Strigul N. 2015. An appraisal of the classic forest succession paradigm with the shade tolerance index. *PLoS ONE* 10: e0117138.

Lindenmayer DB, Laurance WF, Franklin JF. 2012. Global decline in large old trees. *Science* 338: 1305–1306.

Lindenmayer DB. 2017. Conserving large old trees as small natural features. *Biological Conservation* 211: 51–59.

Lindenmayer DB, Laurance WF. 2017. The ecology, distribution, conservation and management of large old trees. *Biological Reviews* 92: 1434–1458.

Liu J, Yang B, Lindenmayer DB. 2019. The oldest trees in China and where to find them. *Frontiers in Ecology and the Environment* 17: 319–322.

Liu X, Biondi F. 2020. Transpiration drivers of high-elevation five-needle pines (*Pinus longaeva* and *Pinus flexilis*) in sky-island ecosystems of the North American Great Basin. *Science of the Total Environment* 739: 139861.

Loehle C. 1988. Tree life history strategies: the role of defenses. *Canadian Journal of Forest Research* 18: 209–222.

Major RT. 1967. The ginkgo, the most ancient living tree. *Science* 157: 1270–1273.

Martin M, Krause C, Fenton NJ, Morin H. 2020. Unveiling the diversity of tree growth patterns in boreal old-growth forests reveals the richness of their dynamics. *Forests* 11: 252.

de la Mata R, Hood S, Sala A. 2017. Insect outbreak shifts the direction of selection from fast to slow growth rates in the long-lived conifer *Pinus ponderosa*. *Proceedings of the National Academy of Sciences, USA* 114: 7391–7396.

Mathaux C, Mandin J-P, Oberlin C, Edouard J-L, Gauquelin T, Guibal F. 2016. Ancient juniper trees growing on cliffs: toward a long Mediterranean tree-ring chronology. *Dendrochronologia* 37: 79–88.

Matthes U, Kelly PE, Ryan CE, Larson DW. 2002. The formation and possible ecological function of stem-strips in *Thuja occidentalis*. *International Journal of Plant Sciences* 163: 949–958.

Mencuccini M, Oñate M, Peñuelas J, Rico L, Munné-Bosch S. 2014. No signs of meristem senescence in old Scots pine. *Journal of Ecology* 102: 555–565.

Mensing S, Schoolman EM, Palli J, Piovesan G. 2020. A consilience-driven approach to land use history in relation to reconstructing forest land use legacies. *Landscape Ecology* 35: 2645–2658.

Metsaranta JM. 2020. Dendrochronological procedures improve the precision and accuracy of tree and stand age estimates in the western Canadian boreal forest. *Forest Ecology and Management* 457: 117657.

Middleton BA. 2009. Effects of Hurricane Katrina on the forest structure of *Taxodium distichum* swamps of the Gulf Coast, USA. *Wetlands* 29: 80–87.

Millar CI, Stephenson NL. 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349: 823–826.

Millar CI, Charlet DA, Delany DL, King JC, Westfall RD. 2018. Shifts of demography and growth in limber pine forests of the Great Basin, USA, across 4000 yr of climate variability. *Quaternary Research* 91: 691–704.

Mölder A, Schmidt M, Plieninger T, Meyer P. 2020. Habitat-tree protection concepts over 200 years. *Conservation Biology* 34: 1444–1451.

Moller TH. 2018. Estimating the age of ancient oaks. *Landscapes* 19: 91–110.

Moreira X, Zas R, Solla A, Sampedro L. 2015. Differentiation of persistent anatomical defensive structures is costly and determined by nutrient availability and genetic growth-defence constraints. *Tree Physiology* 35: 112–123.

Morin X, Chuine I. 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters* 9: 185–195.

Morris H, Hietala AM, Jansen S, Ribera J, Rosner S, Salmeia KA, Schwarze FWMR. 2019. Using the CODIT model to explain secondary metabolites of xylem in defence systems of temperate trees against decay fungi. *Annals of Botany* 125: 701–720.

Mosseler A, Thompson I, Pendrel BA. 2003. Overview of old-growth forests in Canada from a science perspective. *Environmental Reviews* 11: S1–S7.

Munné-Bosch S. 2018. Limits to tree growth and longevity. *Trends in Plant Science* 23: 985–993.

Oberle B, Ogle K, Zanne AE, Woodall CW. 2018. When a tree falls: controls on wood decay predict standing dead tree fall and new risks in changing forests. *PLoS ONE* 13: e0196712.

Ogden J. 1981. Dendrochronological studies and the determination of tree ages in the Australian tropics. *Journal of Biogeography* 8: 405–420.

Osazuwa-Peters OL, Wright SJ, Zanne AE. 2017. Linking wood traits to vital rates in tropical rainforest trees: Insights from comparing sapling and adult wood. *American Journal of Botany* 104: 1464–1473.

Ottaviani G, Martínková J, Herben T, Pausas JG, Klimešová J. 2017. On plant modularity traits: functions and challenges. *Trends in Plant Science* 22: 648–651.

Parent S, Morin H, Messier C. 2002. Missing growth rings at the trunk base in suppressed balsam fir saplings. *Canadian Journal of Forest Research* 32: 1776–1783.

Patrut A, Von Reden KF, Lowy DA, Alberts AH, Pohlman JW, Wittmann R, Gerlach D, Xu L, Mitchell CS. 2007. Radiocarbon dating of a very large African baobab. *Tree Physiology* 27: 1569–1574.

Patrut A, von Reden KF, Lowy DA, Patrut RT, Lucian Vaida D, Margineanu D. 2013. Old ages of two historical Romanian trees assessed by AMS radiocarbon dating. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms* 294: 616–621.

Patrut A, Woodborne S, Patrut RT, Rakosy L, Lowy DA, Hall G, von Reden KF. 2018. The demise of the largest and oldest African baobabs. *Nature Plants* 4: 423–426.

Pederson N. 2010. External characteristics of old trees in the eastern deciduous forest. *Natural Areas Journal* 30: 396–407.

Pennisi E. 2019. Forest giants are the trees most at risk. *Science* 365: 962–963.

Peñuelas J, Munné-Bosch S. 2010. Potentially immortal? *New Phytologist* 187: 564–567.

Phillips NG, Buckley TN, Tissue DT. 2008. Capacity of old trees to respond to environmental change. *Journal of Integrative Plant Biology* 50: 1355–1364.

Piovesan G, Biondi F, Di Filippo A, Alessandrini A, Maugeri M. 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology* 14: 1265–1281.

Piovesan G, Biondi F, Baliva M, Calcagnile L, Quarta G, Di Filippo A. 2018a. Dating old hollow trees by applying a multistep tree-ring and radiocarbon procedure to trunk and exposed roots. *MethodsX* 5: 495–502.

Piovesan G, Biondi F, Baliva M, Presutti Saba E, Calcagnile L, Quarta G, D'Elia M, De Vivo G, Schettino A, Di Filippo A. 2018b. The oldest dated tree of Europe lives in the wild Pollino massif: *Italus*, a strip-bark Heldreich's pine. *Ecology* 99: 1682–1684.

Piovesan G, Biondi F, Baliva M, De Vivo G, Marchianò V, Schettino A, Di Filippo A. 2019a. Lessons from the wild: slow but increasing long-term growth allows for maximum longevity in European beech. *Ecology* 100: e02737.

Piovesan G, Biondi F, Baliva M, Dinella A, Di Fiore L, Marchianò V, Presutti Saba E, De Vivo G, Schettino A, Di Filippo A. 2019b. Tree growth patterns associated with extreme longevity: Implications for the ecology and conservation of primeval trees in Mediterranean mountains. *Anthropocene* 26: 100199.

Piovesan G, Baliva M, Calcagnile L, D'Elia M, Dorado-Liñán I, Palli J, Siclari A, Quarta G. 2020. Radiocarbon dating of Aspromonte sessile oaks reveals the oldest dated temperate flowering tree in the world. *Ecology* 101: e03179.

Pittermann J, Stuart SA, Dawson TE, Moreau A. 2012. Cenozoic climate change shaped the evolutionary ecophysiology of the Cupressaceae conifers. *Proceedings of the National Academy of Sciences, USA* 109: 9647–9652.

Plomion C, Aury J-M, Amselem J, Leroy T, Murat F, Duplessis S, Faye S, Francillonne N, Labadie K, Le Provost G et al. 2018. Oak genome reveals facets of long lifespan. *Nature Plants* 4: 440–452.

Premoli AC, Vergara R, Souto CP, Lara A, Newton AC. 2003. Lowland valleys shelter the ancient conifer *Fitzroya cupressoides* in the Central Depression of southern Chile. *Journal of the Royal Society of New Zealand* 33: 623–631.

Rahbek C, Borregaard MK, Colwell RK, Dalsgaard B, Holt BG, Morueta-Holme N, Nogues-Bravo D, Whittaker RJ, Fjeldså J. 2019. Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* 365: 1108–1113.

Rastogi S, Ohri D. 2020. Chromosome numbers in gymnosperms – an update. *Silvae Genetica* 69: 13.

Rayback SA, Belmecheri S, Gagen MH, Lini A, Gregory R, Jenkins C. 2020. North American temperate conifer (*Tsuga canadensis*) reveals a complex physiological response to climatic and anthropogenic stressors. *New Phytologist* 228: 1781–1795.

Reich PB. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* 102: 275–301.

Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Cheng H, Edwards RL, Friedrich M et al. 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55: 1869–1887.

Requena Suarez D, Rozendaal DMA, De Sy V, Phillips OL, Alvarez-Dávila E, Anderson-Teixeira K, Araujo-Murakami A, Arroyo L, Baker TR, Bongers F et al. 2019. Estimating aboveground net biomass change for tropical and subtropical forests: refinement of IPCC default rates using forest plot data. *Global Change Biology* 25: 3609–3624.

Richardson DM. 2000. *Ecology and biogeography of* Pinus. New York, NY, USA: Cambridge University Press.

Roeder M, Liu J, Pasion B, Yasuda M, Slik JWF, Tomlinson KW. 2019. Wood density, growth and mortality relationships of lianas on environmental gradients in fragmented forests of montane landscapes. *Journal of Vegetation Science* 30: 1143–1152.

Román-Jordán E, Esteban LG, de Palacios P, Fernández FG. 2017. Comparative wood anatomy of the Cupressaceae and correspondence with phylogeny, with special reference to the monotypic taxa. *Plant Systematics and Evolution* 303: 203–219.

Roskilly B, Keeling E, Hood S, Giuggiola A, Sala A. 2019. Conflicting functional effects of xylem pit structure relate to the growth-longevity trade-off in a conifer species. *Proceedings of the National Academy of Sciences, USA* 116: 15282–15287.

Rötheli E, Heiri C, Bigler C. 2012. Effects of growth rates, tree morphology and site conditions on longevity of Norway spruce in the northern Swiss Alps. *European Journal of Forest Research* 131: 1117–1125.

Rozas V. 2003. Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. *Plant Ecology* 167: 193–212.

Ruel J, Whitham TG. 2002. Fast-growing juvenile pinyons suffer greater herbivory when mature. *Ecology* 83: 2691–2699.

Rüger N, Comita LS, Condit R, Purves D, Rosenbaum B, Visser MD, Wright SJ, Wirth C. 2018. Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree community. *Ecology Letters* 21: 1075–1084.

Rüger N, Condit R, Dent DH, DeWalt SJ, Hubbell SP, Lichstein JW, Lopez OR, Wirth C, Farrior CE. 2020. Demographic trade-offs predict tropical forest dynamics. *Science* 368: 165–168.

Russell W, Lambert Z, Woolhouse S. 2019. Old-growth characteristics on a coast redwood (*Sequoia sempervirens* (D. Don) Endl.) pygmy forest ecotone. *Madroño* 66: 14–23.

Ruxton GD. 2014. Why are so many trees hollow? *Biology Letters* 10: art. 20140555.

Salguero-Gómez R. 2017. Applications of the fast–slow continuum and reproductive strategy framework of plant life histories. *New Phytologist* 213: 1618–1624.

Salzer MW, Hughes MK, Bunn AG, Kipfmueller KF. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences, USA* 106: 20348–20353.

Sangüesa-Barreda G, Esper J, Büntgen U, Camarero JJ, Di Filippo A, Baliva M, Piovesan G. 2020. Climate–human interactions contributed to historical forest recruitment dynamics in Mediterranean subalpine ecosystems. *Global Change Biology* 26: 4988–4997.

Schirone B, Piovesan G, Bellarosa R, Pelosi C. 1991. A taxonomic analysis of seed proteins in *Pinus* spp. (Pinaceae). *Plant Systematics and Evolution* 178: 43–53.

Schulman E. 1954. Longevity under adversity in conifers. *Science* 119: 396–399.

Scuderi LA. 1993. A 2000-year tree ring record of annual temperatures in the Sierra Nevada mountains. *Science* 259: 1433–1436.

Sedmák R, Sedmáková D, Bošeľa M, Marušák R, Ježík M, Murgaš V, Blaženec M. 2014. Age estimation of Norway spruce using incomplete increment cores: testing new and improved methods. *Dendrochronologia* 32: 327–335.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18: 1406–1419.

Sillett SC, Van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM. 2010. Increasing wood production through old age in tall trees. *Forest Ecology and Management* 259: 976–994.

Sillett SC, Van Pelt R, Carroll AL, Kramer RD, Ambrose AR, Trask DA. 2015. How do tree structure and old age affect growth potential of California redwoods? *Ecological Monographs* 85: 181–212.

Sillett SC, Van Pelt R, Carroll AL, Campbell-Spickler J, Antoine ME. 2019. Structure and dynamics of forests dominated by *Sequoiadendron giganteum*. *Forest Ecology and Management* 448: 218–239.

Sillett SC, Van Pelt R, Carroll AL, Campbell-Spickler J, Antoine ME. 2020. Aboveground biomass dynamics and growth efficiency of *Sequoia sempervirens* forests. *Forest Ecology and Management* 458: 117740.

Simard SW. 2018. Mycorrhizal networks facilitate tree communication, learning, and memory. In: Baluska F, Gagliano M, Witzany G, eds. *Memory and learning in plants*. Cham, Switzerland: Springer International Publishing, 191–213.

Speer JH. 2010. *Fundamentals of tree-ring research*. Tuscon, AZ, USA: University of Arizona Press.

Sperry JS, Hacke UG, Pittermann J. 2006. Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany* 93: 1490–1500.

Spicer R, Groover A. 2010. Evolution of development of vascular cambia and secondary growth. *New Phytologist* 186: 577–592.

Stahle DW. 1997. Tree rings and ancient forest relics. *Arnoldia* 56: 2–10.

Stahle DW, Griffin RD, Meko DM, Therrell MD, Edmondson JR, Cleaveland MK, Stahle LN, Burnette DJ, Abatzoglou JT, Redmond KT *et al.* 2013. The ancient blue oak woodlands of California: longevity and hydroclimatic history. *Earth Interactions* 17: 1–23.

Stahle DW, Edmondson JR, Howard IM, Robbins CR, Griffin RD, Carl A, Hall CB, Stahle DK, Torbenson MCA. 2019. Longevity, climate sensitivity, and conservation status of wetland trees at Black River, North Carolina. *Environmental Research Communications* 1: 41002.

Stephenson NL, Demetry A. 1995. Estimating ages of giant sequoias. *Canadian Journal of Forest Research* 25: 223–233.

Stephenson NL. 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. *Ecological Applications* 9: 1253–1265.

Stephenson NL, van Mantgem PJ, Bunn AG, Bruner H, Harmon ME, O'Connell KB, Urban DL, Franklin JF. 2011. Causes and implications of the correlation between forest productivity and tree mortality rates. *Ecological Monographs* 81: 527–555.

Stephenson NL, Das AJ, Condit R, Russo SE, Baker PJ, Beckman NG, Coomes DA, Lines ER, Morris WK, Ruger N *et al.* 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507: 90–93.

Stokes MA, Smiley TL. 1996. *An introduction to tree-ring dating*. Tucson, AZ, USA: University of Arizona Press.

Stovall AEL, Shugart H, Yang X. 2019. Tree height explains mortality risk during an intense drought. *Nature Communications* 10: 4385.

Suzuki E. 1996. The dynamics of old *Cryptomeria japonica* forest on Yakushima Island. *Tropics* 6: 421–428.

Swetnam TW. 1993. Fire history and climate change in giant sequoia groves. *Science* 262: 885–889.

Taylor AM, Gartner BL, Morrell JJ. 2002. Heartwood formation and natural durability—a review. *Wood and Fiber Science* 34: 587–611.

Telewski FW. 1993. Determining the germination date of woody plants: a proposed method for locating the root/shoot interface. *Tree-Ring Bulletin* 53: 13–16.

Thomas H. 2013. Senescence, ageing and death of the whole plant. *New Phytologist* 197: 696–711.

Van Pelt R, Sillett SC. 2008. Crown development of coastal *Pseudotsuga menziesii*, including a conceptual model for tall conifers. *Ecological Monographs* 78: 283–311.

Wang L, Cui J, Jin B, Zhao J, Xu H, Lu Z, Li W, Li X, Li L, Liang E *et al.* 2020. Multifeature analyses of vascular cambial cells reveal longevity mechanisms in old *Ginkgo biloba* trees. *Proceedings of the National Academy of Sciences, USA* 117: 2201–2210.

Watkinson AR, White J, Harper JL, Rosen BR, White J. 1986. Some life-history consequences of modular construction in plants. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 313: 31–51.

Weatherspoon CP. 1986. Silvics of giant sequoia. In: Weatherspoon CP, Iwamoto YR, Piirto DD (technical coordinators), eds. *Proceedings of the Workshop on Management of Giant Sequoia*. Berkeley, CA, USA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, 4–10.

WFO. 2020. *World flora online*. [WWW document] URL http://www.worldflora online.org.

Whittaker RH. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs* 23: 41–78.

Wirth C, Messier C, Bergeron Y, Frank D, Fankhänel A. 2009. Old-growth forest definitions: a pragmatic view. In: Wirth C, Gleixner G, Heimann M, eds. *Old-growth forests: function, fate and value*. Berlin, Germany: Springer, 11–33.

de Witte LC, Stöcklin J. 2010. Longevity of clonal plants: why it matters and how to measure it. *Annals of Botany* 106: 859–870.

Woods KD. 2008. Living long by staying small: stem layering as an adaptive life–history trait in shade-tolerant tree seedlings. *Canadian Journal of Forest Research* **38**: 480–487.

Worbes M, Schöngart J. 2019. Measures for sustainable forest management in the tropics – a tree-ring based case study on tree growth and forest dynamics in a Central Amazonian lowland moist forest. *PLoS ONE* **14**: e0219770.

Wu H, Hu Z-h. 1997. Comparative anatomy of resin ducts of the Pinaceae. *Trees – Structure and Function* **11**: 135–143.

Zaitsev GA, Kulagin AY, Davydychev AN. 2018. The particularities of the growth of Siberian fir (*Abies sibirica* Ledeb.) in the first stages of ontogeny in conifer forests (Ufa plateau, Pre-Ural). *Trees – Structure and Function* **32**: 511–518.

About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Foundation, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews and Tansley insights.

- Regular papers, Letters, Viewpoints, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <26 days. There are **no page or colour charges** and a PDF version will be provided for each article.

- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.

- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)

- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**