Tree-ring based metrics for assessing the functional naturalness of old-growth beech forests

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Summary

1. Old-growth studies commonly emphasize structural and age conditions, selecting proxy indicators of long-term ecological processes. Transition dynamics from mature to old-growth status reveal how natural legacies are progressively accumulated in forests after major disturbances, including human ones. In late-successional, multi-aged forests, the chronosequential ranking of developmental stages is a difficult task, as stand age provides little information, and time since last stand-replacing disturbance cannot be easily determined.

2. Canopy age features, disturbance/suppression history, and growth trajectories were reconstructed from ring-width series of canopy trees in a network of 19 old-growth and managed European beech forests in the eastern Alps and central Apennines. A set of tree-ring metrics able to describe the intensity and time distribution of biological and ecological processes (e.g. understory suppression, canopy accession age), was used to describe the advancement of old-growth status, and compared to established metrics of forest structure.

3. Tree-ring metrics were site dependent, as biogeoclimate affects turnover rates and

constrains the onset and recovery rate of old-growth attributes. Under the same environmental conditions (high-mountain, limestone-bedrock beech forests), values of the best indicators (number/duration of growth suppression phases; synchronicity of first release; maximum and range of canopy tree age; canopy accession age of the slowest-growing trees) increased monotonically (2 to 5 times) from managed to secondary and primary old-growth forests. Trees in well-conserved primary old-growth forests experienced several and long suppressions, showing the highest complexity in recruitment history, canopy accession, and growth trajectories. The best tree-ring metrics, condensed in a Naturalness Score to provide a synthetic functional ranking of forests, varied coherently with structural complexity, which represented stand dynamics more closely than biomass-related metrics.

4. *Synthesis and applications*. We proposed a synthetic ranking of forest functional naturalness based on the ecological processes experienced by trees, which helps overcoming the limitations associated to the use of arbitrary size- or age-related thresholds of old-growth status and may provide a more consistent approach for establishing chronosequences in ecological studies. The connection between tree-ring inferred functional complexity and structural metrics allows exploring how forest patterns and processes develop with increasing naturalness, and how stand development affects the provision of ecosystem services, such as biodiversity conservation or carbon storage. Protecting relict primary forests and describing their unique functional naturalness is therefore key to comprehend the impacts of forest management and establishing reference values for ecological restoration and biodiversity conservation.

Key-words: naturalness; old-growth; forest pattern and process; tree-rings; structural complexity; chronosequence; suppression and release; Gini coefficient; *Fagus sylvatica*.

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INTRODUCTION

Studying the long-term recovery of human-impacted forest ecosystems towards natural structure and function requires a practical and ubiquitous approach for quantifying naturalness. Peterken (1996) identified naturalness as a property of ecosystems whose attributes and dynamics are strictly derived from natural factors alone (climate, hydrology, geology, disturbance). The degree of forest naturalness can be difficult to measure in practice (Winter 2012), being a continuous variable from artificial (plantations) to pristine ecosystems (Peterken 1996). Forests with a continuous history of natural disturbance and regeneration can be defined as “primary” or “natural heritage” forests (Frelich & Reich 2003). In forest recovering from past harvesting, the old-growth concept has been used as a surrogate for naturalness. After the abandonment of silviculture, the transition to old-growth status leads to increasingly natural conditions as natural legacies accumulate and progressively replace human-induced ones (Frelich & Reich 2003). Recognizing structural and compositional patterns, together with ecological processes associated with natural development helps with understanding forest self-organization dynamics, and could serve as a reference model for close-to-nature silviculture (Brang 2005) or conservation measures/restoration programs of rare/threatened species (Moning & Müller 2009; Moravcık *et al*. 2010).

Original European landscapes have been deeply transformed into cultural ones, making it difficult to determine the natural reference state of ecosystems (Schultze *et al*. 2014). We still lack a comprehensive, quantitative understanding of old-growth developmental dynamics in different environments, to describe how natural legacies accumulate once silviculture ceases. The scarcity of long-term forest monitoring programs, invaluable for understanding the temporal structural dynamics of forest ecosystems (Wolkovich *et al*. 2014), has made chronosequences crucial for studying old-growth dynamics. Chronosequential forest ordering generally relies on mean/maximum tree age, mean age of the 5-10 oldest trees, and time since the last stand-replacing disturbance (Bradford *et al.* 2008; Gutiérrez *et al.* 2009; Lichstein *et al*. 2009). Because measuring the age of uneven-aged forests is an "inexact process" (Pan *et al.* 2011), ranking old-growth stages chronologically is difficult (Gerzon *et al.* 2011), and a structural approach is often preferred (Lorimer & Halpin 2014). Old-growth chronosequences can be affected by additional limitations: the rarity of such ecosystems in historically exploited territories; frequent heart rot in old broadleaf trees, implying large sampling efforts, and restricting confidence on age structure reconstruction.

Forest naturalness has been described by means of structural, compositional, and process-based indicators (e.g. Liira & Kohv 2010; Brumelis *et al*. 2011; Maes *et al.* 2011). Field studies emphasize thresholds in structural indicators, e.g. density/biomass of living/dead trees (Keddy & Drummond 1996), as proxies of natural ecological processes, useful to assess the conservation of rare species (Heilmann-Clausen *et al*. 2014; Stachura-Skierczyńska & Kosiński 2016). However, the informative power of structural/compositional indicators to assess forest naturalness still needs to be fully explored (Gao *et al*. 2015), and may be affected by various limitations. Firstly, structural attributes may show non-linear trends during the naturalization process (Kucbel *et al*. 2012): if the selected attributes (e.g. large trees density, deadmass) don't increase monotonically with stand development, or naturalness is described through species relying on their abundance (e.g. woodpeckers), this may lead to more emphasis on intermediate than advanced old-growth stages. In addition, old-growth stands with similar overstory species can differ widely in structure: tree growth rates and maximum stem size, for instance, largely depend on site bioclimatic and soil conditions (Ziaco *et al.* 2012a; Lorimer & Halpin 2014). Site conditions affect the pace of ecological processes during the recovery of natural attributes, via their control over tree lifespan and turnover rates (Di Filippo *et al.* 2015), a fact that hampers the use of age or structural metrics to compare forests from different environments (Ziaco *et al.* 2012b), unless adjustments have been made for site differences (Lorimer & Halpin 2014).

A more precise way to quantify the naturalness of an ecosystem should be based on its functional dynamics (Schultze *et al*. 2014), i.e. the several ecological processes controlling the acquisition of natural attributes throughout stand structural development (Bormann & Likens 1979). Late-successional temperate forests, composed mainly of long-lived shade-tolerant trees, are subject to frequent small-gap openings combined with rare severe disturbances (Runkle 2000). Functionally, attainment of old-growth status can be identified by the passage from even- to uneven-aged conditions (Lorimer & Halpin 2014), when new cohorts establish because of natural large tree dieback and mortality. The onset of dominant tree mortality is a discrete ecological event that, besides tree age or size thresholds, links quantitative structural changes to the local environment via a disturbance regime (Di Filippo *et al.* 2012). As the dominant tree cohort gradually fades away, deadwood accumulates and new cohorts establish in the canopy (Lorimer & Halpin 2014), leading to descending monotonic curves in stem size distributions typical of all-aged stands (e.g. rotated sigmoid; Alessandrini *et al.* 2011). New cohorts can permanently access the canopy after a severe canopy breakdown, or experience a variable number of release/suppression phases (multi-gap episodes; Runkle 2000). Long suppression periods are typical of natural forests (Brang 2005). Increased uneven-agedness is the result of a myriad of growth histories originating from repeated, stochastic disturbances of small-to-intermediate severity, including the legacies of rare, exceptionally intense events (Piovesan *et al.* 2005b).

Tree-rings integrate plant and ecosystem dynamics, allowing us to date and quantify the duration and intensity of ecological processes experienced by tree communities throughout old-growth development (e.g. Biondi 1999). Growth histories can also connect tree age, productivity, and forest structure (Piovesan *et al.* 2005b). Tracking growth suppressions and releases can describe disturbance history (Lorimer & Frelich 1989; Ziaco *et al.* 2012a). However, specific growth thresholds need to be defined for different bioclimatic contexts, both for release detection (Ziaco *et al.* 2012a) and for suppression (Di Filippo *et al.* 2012).

No systematic analysis exists on how age (mean/maximum) and functional (suppression, release, recruitment, growth history) indicators change across a complete series (early to advanced) of old-growth developmental stages. We developed a set of tree-ring metrics to describe the intensity and time distribution of ecological processes in forests, therefore called chrono-functional indicators. Our research was aimed at (i) quantitatively describing and monitoring forest naturalness, (ii) testing environmental influences on chrono-functional indicators, (iii) developing synthetic metrics for measuring the ecological distance between forests, (iv) comparing our chrono-functional framework with widely used structural indicators. We analyzed a network of managed and old-growth European beech (*Fagus sylvatica* L.) forests along a latitudinal (Mediterranean to Alpine climate) and altitudinal (low-elevation to high-mountain) gradient in central-southern Europe (Italy and Austria).

MATERIALS AND METHODS

Study sites

We analyzed 19 beech-dominated forests, 11 in the Apennines and 8 in the Eastern Italian/Austrian Alps (Fig. 1; Table 1). In both areas, stands were arranged along elevation gradients and organized into three orographic belts: high-mountain, mountain, low-elevation (Piovesan *et al.* 2005a; Di Filippo *et al.* 2007). Each belt, identified through dendroclimatic techniques, has its distinct climatic signal controlling tree-ring variability, which incorporates bioclimatic (also floristic; Filibeck *et al*. 2015) differences among sites. Old-growth forests covered all three belts in the Apennines, but missed the low–elevation belt in the Alps. Most sites had sedimentary bedrock, with the exception of low-elevation forests in central Italy (volcanic bedrock; Table 1).

Each belt included at least two old-growth (OG) and one managed forest (Table 1). OG stands have dead dominant trees, and new cohorts establishing in gaps and entering the canopy (Di Filippo *et al.* 2012). OG were catalogued as primary or "natural heritage" forests (OG1) if they had a continuous history of natural disturbance and regeneration, while secondary forests (OG2) were logged in the past (Frelich & Reich 2003). The OG1-OG2 distinction was based on evidence of past human interference (presence/absence of logging stumps, completeness of the deadwood decomposition process) together with historical information (past forest plans, aerial photographs; Table S1). Managed forests were mature stands not heavily logged, i.e. with many large trees remaining in the canopy and bimodal to uneven-aged DBH distribution.

Field sampling

Living and dead tree structures for the selected forests were already available (Ziaco *et al.* 2012b; Table 1). Sample plots covered an increasing area proportional to stand structure complexity (from bimodal to rotated-sigmoid DBH frequency distribution), hence meeting a minimum area requirement (up to ~1 ha in complex forests; Table 1; Alessandrini *et al.* 2011). The number of increment cores per site (20 to 50+; Table 1) also varied according to structural complexity. Many study sites fell within protected areas, and sampling was restricted to one core (at 1.3 m above ground) from canopy trees covering all forest area (Table 1). We focused on trees with DBH ≥ 37.5 cm, as the 5-cm DBH class centred on 40 cm identifies canopy trees in beech forests (Peters 1997). Since heart rot is a common problem in old beech trees, hampering the direct calculation of stem age (Di Filippo *et al.* 2012), a standard protocol was designed to estimate age from cores that did not include the pith (Appendix S1).

Chrono-Functional Indicators

Tree age and ring-width data were used to develop 39 indicators (Table 2), subdivided into three categories: Age Indicators, Growth History Indicators, Disturbance and Suppression Indicators. Metrics related to the same naturalness attribute (e.g. suppression length) were aggregated into subgroups (Table 2). Different metrics were developed to account for the central tendency, the variability, the extreme values, the range of selected attributes. In calculations, we used the following approach: (a) indicators measuring the variability of an attribute (e.g. canopy age variability) were based on adimensional indices such as skewness, kurtosis, Gini, Shannon, (inverse) Simpson; (b) extremes derived from averaging the highest or lowest 3-5 values, rather than a single extreme and, similarly, (c) the range was calculated from the mean of the three lowest and highest observations.

Age Indicators (AI). Most age statistics came from the literature: *MEAN*, *MEDIAN*, *MAX*, *AGE5* (Ziaco *et al.* 2012b), *AGE10* (Gutierrez *et al.* 2009). We added *AGE3* to measure maximum tree age, and a number of canopy age complexity metrics: the age range; skewness; kurtosis; age diversity/equitability (quantified by indices as Gini, Simpson, Shannon; Table 2).

Disturbance and Suppression Indicators (DSI). Boundary Line criteria available for the study forests were used to detect moderate release events on decadal growth changes (Ziaco *et al.* 2012a). Disturbance events were grouped in sequential, non-overlapping 20-yr intervals. Late successional beech old-growth forests generally have a mixed disturbance regime with prevailing infrequent events (Piovesan *et al*. 2005b). Thus, the synchronicity in the year of the first/last release in trees of a forests, or in the their age of first release, was used as a descriptor of a simplified artificial disturbance regime. Metrics were based on the Shannon and Simpson indices, skewness, kurtosis, the maximum event frequency per time interval.

With regard to understory growth suppression, an important feature of natural late-successional forests (Brang 2005), we developed a method to account for different growth thresholds within each belt (Appendix S2). The mean/maximum number of suppressions phases, the length of single phases, and their overall length in each tree were pooled into stand-level metrics (Table 2).

Growth History Indicators (GHI). The variability of canopy tree growth trajectories over time was represented by reconstructing stem DBH as a function of age (Fig. S1). Age variability at canopy accession (DBH ≥ 37.5; Table 2) informed on the uniformity/complexity of processes acting in forests, i.e. the range between canopy accession age *(TrajRANGE3*), or the highest canopy accession age needed by the 3 slowest-growing trees (*TrajSLOW3*, *TrajSLOW3mean*, *TrajSLOW3median*), an important feature in old-growth beech forests (Di Filippo *et al.* 2012).

We referred to the overall set of 39 metrics as "chrono-functional indicators", each contributing to describe the intensity (e.g. number/length of suppression phases, maximum number of years needed to reach the canopy) and time distribution of ecological processes in forests (e.g. synchronization of recruitment dynamics or disturbance events), resulting in specific structural features (e.g. canopy age variability, maximum age, growth trajectories variability).

For GHI and DSI, where the entire tree growth history was required, the use of ring-width data was restricted to increment cores including the pith.

Exploring the chrono-functional metrics

Since tree longevity is linked to bioclimate (Di Filippo *et al.* 2012), many chrono-functional indicators are not comparable among altitudinal belts. The 10 Alps and Apennines high-mountain stands were merged, considering their similar maximum tree age (560 and 520 years) and environmental conditions (cold-limited forests on limestone bedrock). These forests, including the only primary old-growth forests (Table 1), were used for evaluating the indicators; observed patterns were then compared with results from other belts.

The 39 indicators for the 10 high-mountain forests were combined in a Principal Component Analysis (PCA). Only the first principal component (PC1) was significant according to Parallel Analysis (Franklin *et al.* 1995). Metrics with PC1 loading ≥ 90% of the maximum value were retained. The best indicators were selected among those with highest loading within each subgroup (Table 2). Site scores on PC1 were used as a Naturalness Score (NS), i.e. a linear combination of the best indicators expressing stand differences. A Redundancy Analysis (RDA; Ter Braak & Prentice 1988) was performed to check whether process metrics (DSI and GHI, predictors) were related to canopy age ones (AI, predictands).

The NS of each site was compared to Structural Indicators (SI) and Structural Complexity Indices (SCI) from old-growth literature (e.g. Ziaco *et al.* 2012b; Zenner *et al.* 2015). SI were related to living tree density/volume, established regeneration density, large tree density/volume, deadwood volume, snags density. SCI computations considered either the relative frequencies of stems or their relative basal area in 5-cm DBH classes. Measures of structural complexity included: the DBH mean, standard deviation, coefficient of variation; Shannon and (inverse) Simpson indices, De Camino homogeneity index, Gini coefficient, Lorenz asymmetry coefficient (Valbuena *et al.* 2012), and the DBH distribution skewness (Wright *et al.* 2003). No structural data were available for the Austrian sites (ZWI, GEI, KHO; Table 1). Statistical analyses were performed using R software (R Core Team 2014).

RESULTS

Naturalness described by classical age indicators

Mean and maximum tree age in old-growth forests (OG) increased with elevation (Table 1, Fig. 2). Not all high-mountain OG clearly exceeded the old-growth age threshold (Cogbill 1996; Fig. 2). Under similar environmental conditions, i.e. for Apennines and Alps high-mountain forests, OG1 is clearly distinguished from OG2 when using maximum age (Fig. 2b), whereas mean age is not always an accurate indicator (Fig. 2a).

In the Alps, OG2 and managed forests were clearly separated by mean/maximum age indicators (Fig. 2), since the latter have been cut regularly at length (Fig. S1). In the mountain and low-elevation belts of the Apennines, OG2 and managed forests had comparable age statistics (Fig. 2). Here, managed forests (FOG and MOR; Table S1) retain old legacy trees, being old-growth forests not uniformly logged in recent decades.

Select chrono-functional indicators

The first principal component (PC1) explained 55% of variance for the 10 high-mountain forests (Table S2). Out of the 39 metrics, 16 were retained. 7 of them had the highest loadings among each subgroup (Table S2, Fig. 3a):

- Age Indicators (AI): mean age (*MEAN*), mean age of the three oldest trees (*AGE3*), age range (*RANGE3*) of canopy trees.
- Growth History Indicators (GHI): age needed by the 3 slowest-growing trees to reach the canopy (*TrajSLOW3*).
- Disturbance-Suppression Indicators (DSI): maximum number (*SupN.5*) of single suppression phases; maximum duration (*SupL.5*) of overall suppression; synchronization of the first release's year (measured by the inverse Simpson's index, *Rel1Yr.D*).

Forests were aligned along the PC1 axis according to their naturalness degree: managed forests and OG1 at the extremes, OG2 in the middle (Fig. 3). The selected Age Indicators accounted for different aspects of canopy tree age (Table S2): the age of the 3 oldest trees *(AGE3)* had the highest loading, but similar to metrics using the 1, 5, 10 oldest trees (respectively *MAX*, *AGE5*, *AGE10*). Canopy age range (RANGE3) was lower, but significant. The only significant Disturbance Indicator was the synchronization of the first release (*Rel1Yr.D*): metrics related to the first release age and the last release date were discarded (Table S2). The most important suppression metrics were the maximum number of suppression phases (*SupN.5*) and the highest duration of overall suppression (*SupL.5*) per tree (both measured by averaging the 5 highest values per stand). The best growth history metric was related to slow-growing trees (*TrajSLOW3*), but even the difference in canopy accession age between the fastest- and slowest-growing trees (*TrajRANGE3*) showed high PC1 loading. A PCA restricted to trees with observed pith (discarding those with reconstructed pith) gave the same results (Fig. S2). The selected process indicators, i.e. related to growth history (*TrajSLOW3)* and disturbance/suppression (*SupN.5*, *SupL.5*, *Rel1Yr.D*), explained 84% of Age Indicators variance on the first redundancy axis (Fig. 3b). The Naturalness Score (NS) of each forest (PC1 scores using the best 7 metrics) was ~4 in OG1, ~1 in OG2, and < -4 in managed forests. Most OG2 had similar PC1 scores; sites SCA and COP had respectively the highest and the lowest. Stands with higher NS had older trees and more variable canopy age, several long suppression phases, and slower canopy accession (Table S3).

Chrono-functional vs. structural metrics

Structural Indicators (SI) didn't correlate significantly with NS (Table S4). Biomass-related variables often showed an increase from managed stands to OG, but in general failed to match the NS values (Fig. S3a). Living/dead tree volume, and large tree/snag density/volume varied largely within OG2 and did not necessarily linearly followed the transition to the most natural forests (OG1, Fig. S3a). Structural Complexity Indices (SCI) described better OG development (Table 3; Fig. S3b), especially the Gini coefficient based on basal area distribution (*Gini*), followed by the DBH coefficient of variation calculated using stem frequencies (*CV*). *Skewness* and *Simpson* were mainly linked to structural changes distinguishing managed from OG (Table 3). *Gini* increased linearly with NS in OG, along with increasing maximum age (Fig. 4). In managed forests, *Gini* varied depending on even- (lowest *Gini*) or uneven-aged (medium *Gini*) structure.

Gini was most correlated to maximum age, the canopy accession age range (*TrajRANGE3)*, and the maximum number of suppressions per tree (*Sup.N5*) among age, growth history and disturbance-suppression indicators, respectively (Table S5, Fig. S4). High-mountain

OG1 had *Gini* >70 and maximum age >500 yr. *TrajRANGE3* was ~300 years in OG1, but < 200 years in OG2 (Fig. 6; Table 4). Also, the most natural forests had more suppression events (*SupN.5* ≥4 in OG1; Table 4, Fig. S4). Surprisingly, the maximum suppression length (*SupL.5*) was less connected to structural complexity, but showed high predictive capacity in explaining the transition from managed to OG stands (especially when regressing with *skewness*; Fig. S4). The most extreme suppression experienced by single trees within our network was: 6 distinct suppression phases, 105 years for a single suppression, and 155 years for the overall duration of suppression.

In relation to *Gini*, the canopy accession age range (*TrajRANGE3)* underlines how processes allowing the existence of very old, slow-growing trees, and the establishment of fast-growing cohorts in large gaps denote the most natural old-growth forests. Growth trajectories of the slowest growing trees are almost straight lines in OG2, but are more curved in OG1 (Fig. 5). The range covered by growth trajectories varied considerably among different belts (Fig. 6). Canopy accession age of the slowest growing trees (*TrajSLOW3*) increased with elevation (Fig. 6). As bioclimate controls growth rates and maximum longevity, time needed to reach 37.5-cm DBH decreases at lower elevation; less than 100 years at low-elevation and 300+ years in high-mountain OG2. Accordingly, the value of selected chrono-functional indicators increased with elevation (Table 4), so that their use for assessing naturalness must be confined within the same bioclimatic context.

DISCUSSION

Chrono-functional metrics and forest naturalness

Forests with different levels of naturalness were ordered according to the properties of tree growth history. The selected metrics described how ecological processes evolve through old-growth development. Primary forests had long, recurrent suppression phases (Brang 2005): often more than four phases lasting over 70 years. Interestingly, many repeated suppression cycles were associated with higher naturalness more than the overall duration of suppression: protracted life in the understory may be mitigated by repeated small gap openings, and even nearby branch falls, typical of late-successional temperate old-growth stands (Runkle 2000). Canopy accession was asynchronous in multi-aged OG forests, and synchronized in managed ones. Widely different suppression and canopy accession histories generate complex growth trajectories and age structures (Piovesan *et al.* 2005b).

Trees in late-successional old-growth European beech forests feature a mixed-severity disturbance regime, made up of frequent small gaps combined with severe rare disturbances (Trotsiuk *et al.* 2012; Ziaco *et al.* 2012a), leading to widely diverging growth trajectories. Slow-growing trees originating in the understory take centuries to establish into the canopy (Peters 1997; Hobi *et al.* 2014), and coexist with fast-growing trees established after storm blowdowns. Slow growth is a life-history trait tightly connected with long and repeated suppressions, leading to delayed canopy accession and predisposing trees to longevity (Di Filippo *et al.* 2012). Exceptionally slow-growing trees are most representative of OG1, while growth trajectories for fast-growing trees overlap between OG1 and OG2 (Figs. 5-6). In managed forests, silviculture synchronizes recruitment and canopy accession, simplifying structure and tree competition, and only a restricted range of growth histories is found: canopy accession age between slow- and fast-growing trees (*TrajRANGE3*) is about 50 years in managed forest, 100-200 years in OG2, and approaches 300 years in OG1. Growth trajectories integrate the complexity/intensity of recruitment dynamics, suppression phases, and disturbance events throughout forest development.

The limits of tree age indicators

Canopy tree age indicators are easily obtainable, thus have practical value to describe forest naturalness. Age structure can contribute to defining naturalness (Wirth & Lichstein 2009), so that old-growth status in temperate forests is supposedly reached when mean canopy age is at least half the maximum lifespan of the dominant tree species (Cogbill 1996). We demonstrated that mean age in old multi-cohort stands with a mixed disturbance history is a biased indicator of developmental stages, especially when time since stand-initiating disturbance exceeds the mean lifespan of the dominant species (Garet *et al*. 2012). Maximum age (Manusch *et al.* 2012), the mean age of the 3-5 oldest trees (Ziaco *et al.* 2012b), and the canopy age range were better age indicators for describing the advancement of old-growth status, tightly connected to suppression (Di Filippo *et al.* 2012), recruitment and disturbance regime. Maximum age can overestimate time since disturbance in young stands, if scattered legacy trees are present, or underestimate it in old forests, when the return time of stand-replacing disturbances is longer than the longevity of canopy trees (Bradford *et al.* 2008). Advanced old-growth forests have multiple cohorts and wide variability in stem age for a given DBH. Also unevenly-aged managed sites can show complex structures, but selective cutting prevents growth trajectories as complex as old-growth forests (e.g. site FOG in Fig. S1). Furthermore, in the absence of intense, protracted competition for light, maximum lifespans cannot be realized (Di Filippo *et al.* 2012).

Environmental conditions affect chrono-functional metrics

Bioclimate and soil conditions control tree growth rates and maximum size, thus stand productivity and structural attributes (Di Filippo *et al.* 2012; Lorimer & Halpin 2014). Site productivity, together with compositional and habitat type, influences the development of old-growth attributes (Halpin & Lorimer 2016), controlling tree lifespan (Di Filippo *et al.* 2012, 2015) and turnover rates (Stephenson & Van Mantgem 2005). Stands at low-elevation in warmer sites develop faster than in high-mountain ones, where trees reach higher lifespans and display lower growth release potential (Ziaco *et al.* 2012a). Stands featuring longer lifespans can host more complex canopies. In conclusion, no universal age/size threshold can be established to identify the achievement of old-growth status, and age or structural metrics can’t be directly used to compare forests from different sites unless adjustments have been made for ecological differences.

Chrono-functional vs. structural metrics

Chrono-functional and structural complexity indicators increased coherently from managed to primary old-growth forests. Stand structural complexity reflects ecological processes active throughout old-growth development (Zenner *et al.* 2015). The Gini coefficient in particular followed the naturalness level obtained combining chrono-functional indicators (or even single ones; Fig. S4). Primary old-growth beech forests are characterized by monotonically descending diameter distributions, resulting in a higher structural complexity (*Gini* > 70; Table 4). In OG2, *Gini* values were 55-65, suggesting less developed uneven-sized structures (Duduman 2011).

Stand-scale biomass and deadwood are not accurate indicators of naturalness in old-growth forests, because of their dependence on site fertility (Ziaco *et al.* 2012a) and the wide variability during the breakup phase (Lorimer & Halpin 2014): early stage OG may possess more living and/or dead biomass than advanced OG (Halpin & Lorimer 2016). Beech forests do not necessarily show significant biomass increases once they reach old-growth status (Kucbel *et al.* 2012), in line with classic models of biomass accumulation during forest development (Bormann & Likens 1979) and other recent studies in tropical (Poorte et al. 2016) and temperate biomes (Halpin & Lorimer 2016). However, recent studies reported biomass accumulation increases in advanced OG stages (Lichstein *et al.* 2009; Keeton *et al.* 2011), and further research is needed on this topic.

Conclusions: chrono-functional metrics and forest chronosequences

Given the rarity of long-term monitoring datasets, constructing habitat-specific chronosequences represents an obligate step for understanding forest dynamics. Forest chronosequences play a central role in setting reference conditions in ecological restoration programs or in large-scale assessments of old-growth stand contribution to the carbon cycle (Lichstein *et al.* 2009). The space-for-time approach requires ecosystems that infrequently experience severe disturbances, follow convergent pathways, and develop at similar rates (Walker *et al.* 2010). Thus, a preliminary biogeoclimatic assessment and the reconstruction of disturbance regime are needed to test for similar developmental dynamics among ecosystems in a chronosequence. Although biomass- and age-related measures can help distinguishing forest changes throughout old-growth development, their nonlinear behavior in time and limited ability to account for fertility and specific disturbance factors make them incomplete descriptors of forest naturalness. Finally, the use of canopy age to establish chronosequences becomes increasingly doubtful as time since last stand replacing disturbance increases and the age structure diversifies (Gerzon *et al.* 2014).

An effective natural resource management needs to rely on scientifically validated proxy indicators to establish reference conditions and assess ecosystem service provision under different environmental conditions (Stephens *et al.* 2015). Synthetic metrics such as the Naturalness Score provide a functional ranking of forests based on measuring the ecological distance between managed, early, and advanced old-growth forests. The increasing intensity and complexity of processes experienced by trees along the naturalness gradient constitutes a further aspect of forest biodiversity. Interactions in unmanaged forests can be more complex than generally assumed (Fichtner *et al*. 2015), and patterns and processes may even develop with nonlinear dynamics in ecosystems affected by stochastic effects, like gap opening (Walker *et al.* 2010). Indeed, primary forests contain unique features that makes them irreplaceable for nature conservation, but more consistent methods are still required for quantifying the naturalness value of forests (Barlow *et al*. 2007). The selected tree-ring indicators represent functional traits that may be quantified as processes (e.g. understory suppression, canopy accession, growth trajectories, canopy tree age structure) occurring in a wider range of environments, succession stages, and disturbance regimes from boreal to tropical forests, wherever tree-ring crossdating is possible. Quantifying those functional traits, together with structural and biodiversity ones (Moning & Muller 2009), that are more tightly related to forest naturalness provides ecological benchmarks for monitoring and assessing the sustainability of silvicultural practices (Moravčík *et al.* 2010). Diversity in old-growth functional attributes should become a tool to prescribe targets for conservation purposes, or to evaluate the functional effectiveness of restoration programs.

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Table 1. Summary information on the study forests. Elevation belts are high-mountain (H), mountain (M), low-elevation (L).

	Site	Code	Belt	Bedrock	Status	Latitude (°N)	Longitude (°E)	Elevation (m asl)	Sampled Area (ha)	N (stem/ha)	St (m)	BA (m^2/ha)	LTV (m^3/ha)	DWV (m^3/ha)	Total cores	Used cores	Maximum Age (y)
Central Apennines	Valle Cervara	VCH	H	Lim	OG1	41.829	13.7326	1725 (1600-1850)	1.01	818	33	38	545	59	53	32	559
	Coppo del Morto	COM	H	Lim	OG1	41.863	13.8453	1850 (1800-1900)	0.87	1431	23	47	480	64	50	24	548
	Scangive	SCA	H	Lim	OG2	42.4850	13.0022	1792 (1765-1820)	0.75	750	25	39	413	52	47	32	453
	Coppo del	COP	H	Lim	OG2	41.788	13.7381	1625 (1500-1750)	0.88	296	32	44	715	91	28	19	376
	Collelongo	COL	H	Lim	MAN	41.8491	13.5878	1536 (1528-1550)	0.44	1189	28	40	490	1	20	12	126
	Monte Cimino	CIM	M	Vol	OG2	42.408	12.2033	1000 (950-1050)	3.14	197	46	48	707	19	56	22	192
	Fonte Regna	REG	M	Lim	OG2	42.325	12.7194	954 (880-1010)	0.47	317	32	42	540	42	23	20	233
	Morino	MOR	M	Lim	MAN	41.833	13.4085	1200 (1150-1250)	0.35	752	35	40	627	1	47	33	287
	Monte Venere	VEN	L	Vol	OG2	42.344	12.1840	800 (700-840)	0.87	242	41	52	927	26	54	26	136
	Oriolo Romano	ORI	L	Vol	OG2	42.1732	12.1581	542 (505-565)	0.97	221	39	36	632	29	49	22	115
	Monte Fogliano	FOG	L	Vol	MAN	42.325	12.1344	782 (635-870)	0.60	241	39	47	899	9	27	25	206
Eastern Alps	Lateis	LAT	H	Lim	OG2	46.459	12.7489	1450 (1370-1530)	0.75	878	30	40	533	18	45	35	380
	Timau	TIM	H	Lim	OG2	46.582	13.005	1160 (1000-1500)	0.88	568	33	40	647	na	36	16	348
	Zwielauf	ZWI	H	Lim	OG2	47.7959	14.3337	1275 (1205-1340)	na	na	na	na	na	na	26	14	424
	Geisslucke	GEI	H	Lim	OG2	47.7941	14.4284	1257 (1190-1340)	na	na	na	na	na	na	21	14	520
	Colle dei Galli	GAL	H	Lim	MAN	46.4216	13.0719	1200 (1190-1225)	0.38	453	29	42	584	20	23	10	161
	Gracco	GRA	M	Lim	OG2	46.551	12.8519	825 (750-900)	mp	336	21	34	302	na	20	21	351
	Kholersgraben	KHO	M	Lim	OG2	47.8148	14.4446	902 (805-995)	na	na	na	na	na	na	20	14	316
	Pian della Gatta	GAT	M	Lim	MAN	46.4597	13.0904	856 (815-925)	mp	230	28	21	260	na	24	14	157

Bedrock: Lim, Limestone; Vol, Volcanic. **Elevation:** mean (range). **Sampled Area:** structural data were obtained by sampling plots (data reported correspond to cumulated plot area), or by the management plan (**mp**) or not available (**na**). **Total cores:** number of sampled canopy trees. **Used cores:** number of cores used after the age estimation process. **Status:** OG1 and OG2 are primary and secondary old-growth forests, MAN are managed ones.

Table 2. Description of the chrono-functional indicators. Grey shading: loading ≥ 90% of the maximum on the first principal component axis. Bold: metrics used to calculate the Naturalness Score.

AI	***MEAN***	***yr***	**Mean canopy age**	1	+
	MEDIAN	*yr*	Median canopy age	1	+
	RANGE3	*yr*	**Range between the mean of the 3 youngest and the 3 oldest ages measured in canopy trees**	**2**	**+**
	GINI	-	Canopy age Gini coefficient	2	+
	H	-	Canopy age Shannon index	2	+
	D	-	Canopy age (inverse) Simpson index	2	+
	SKEW	-	Canopy age Gini coefficient	2	+
	KURT	-	Canopy age Shannon index	2	+
	AGE3	***yr***	**Mean age of the 3 oldest trees**	**3**	**+**
	AGE5	*yr*	Mean age of the 5 oldest trees	3	+
	AGE10	*yr*	Mean age of the 10 oldest trees	3	+
	MAX	*yr*	Age of the oldest tree	3	+
GHI	*TrajRANGE3*	*yr*	Range between the mean of the 3 youngest and the 3 oldest ages when growth trajectories reach DBH=37.5 cm (canopy accession)	4	+
	TrajSLOW3	***yr***	**Mean of the 3 oldest ages when growth trajectories reach DBH = 37.5 cm (i.e. in the slowest-growing trees)**	**4**	**+**
	TrajSLOW3mean	*yr*	*TrajSLOW3* minus mean age of growth trajectories at DBH=37.5 cm	4	+
	TrajSLOW3median	*yr*	*TrajSLOW3* minus median age of growth trajectories at DBH=37.5 cm	4	+
DSI	*SupN.avg*	*n*	Average number of suppression phases experienced by trees	5	+
	SupN.5	***n***	**Average of the 5 highest number of suppressions per tree in each forest**	**5**	**+**
	SupL.avg	*yr*	Average length of total suppression (all phases) experienced by trees	6	+
	SupL.5	***yr***	**Average length of the 5 longest total suppressions experienced by trees**	**6**	**+**
	SupL.max	*yr*	Maximum length of total suppression experienced by a tree in the forest	6	+
	MaxSupL.avg	*yr*	Average length of the longest single suppression phase per tree	6	+
	MaxSupL.5	*yr*	Average length of the 5 longest single suppression phases experienced by trees	6	+
	MaxSupL.max	*yr*	Maximum length of the single suppression phase experienced by a tree in the forest	6	+
	Rel1Yr.H	-	Shannon index of each tree's first release year	7	+
	Rel1Yr.D	**-**	**Inverse Simpson index of each tree's first release year**	**7**	**+**
	Rel1Yr.Peak	*%*	Highest relative frequency of each tree's first release year	7	-
	Rel1Yr.SK	-	Skewness of each tree's first release year	7	-
	Rel1Yr.KU	-	Kurtosis of each tree's first release year	7	-
	Rel1Age.H	-	Same as *Rel1Yr.H* but using last release age	8	+
	Rel1Age.D	-	Same as *Rel1Yr.D* but using last release age	8	+
	Rel1Age.Peak	*%*	Same as *Rel1Yr.Peak* but using last release age	8	-
	Rel1Age.SK	-	Same as *Rel1Yr.SK* but using last release age	8	-
	Rel1Age.KU	-	Same as *Rel1Yr.KU* but using last release age	8	-
	LastRelYr.H	-	Same as *Rel1Yr.H* but using last release year	9	+
	LastRelYr.D	-	Same as *Rel1Yr.D* but using last release year	9	+
	LastRelYr.Peak	*%*	Same as *Rel1Yr.Peak* but using last release year	9	-
	LastRelYr.SK	-	Same as *Rel1Yr.SK* but using last release year	9	-
	LastRelYr.KU	-	Same as *Rel1Yr.KU* but using last release year	9	-

Subgroup: Variables with the same number represent metrics related to the same indicators. **Effect:** Expected relationship with forest naturalness degree. **AI**: Age Indicators; **GHI:** Growth history Indicators; **DSI**: Disturbance-Suppression Indicators.

Table 3. Correlation of the Naturalness Score (NS) with Structural Complexity Indices in the high-mountain belt. Statistics computed for all forests or for old-growth forests only (OG). Italics, bold-italics, bold refer to correlations with *P* below 0.05, 0.01 or 0.001.

Metric	**Prop**	**All**	**OG**
Mean DBH	Freq	-0.37	-0.72
Standard Deviation	Freq	0.68	0.10
Coefficient of Variation	Freq	0.82	***0.97***
Coefficient of Variation	BA	-0.86	-0.50
Gini Coefficient	BA	0.83	**0.99**
Lorenz Asymmetry Coefficient	BA	0.05	0.23
De Camino Homogeneity Index	BA	-0.85	-0.43
Simpson Index	BA	*0.91*	0.59
Shannon Index	BA	0.85	0.5
Skewness	Freq	*0.89*	0.84

Prop: variable used to compute the proportion of trees in DBH classes (Freq: stem frequency; BA: basal area).

Table 4. Range of the best chrono-functional indicators for primary (OG1) and secondary (OG2) old-growth forests within the three bioclimatic belts of the Eastern Alps and Apennines. Metrics explained in Table 2.

	Metric	Unit	High-mountain		Mountain	Low-elevation
			OG1	OG2	OG2	OG2
SCI	***Gini Coefficient***	-	74-80	56-65	39-58	37-42
AI	***MEAN***	years	312-385	216-308	136-284	83-110
	RANGE3	years	322-371	105-257	74-199	49-57
	AGE3	years	514-528	342-435	185-320	114-132
	MAX	years	548-559	348-520	220-351	115-136
GHI	***TrajRANGE3***	years	266-268	110-185	70-95	46-74
	TrajSLOW3	years	360-397	242-309	100-243	66-106
DSI	***Rel1Yr.D***	-	82-90	83-90	53-79	68-73
	SupN.5	n	4.0-5.2	3.0-4.4	1.2-3.0	1.4-1.6
	SupL.5	years	70-117	49-77	14-36	10-21

SCI: Structural Complexity Indices. **AI, GHI, DSI:** Age, Growth History, Disturbance-Suppression Indicators.

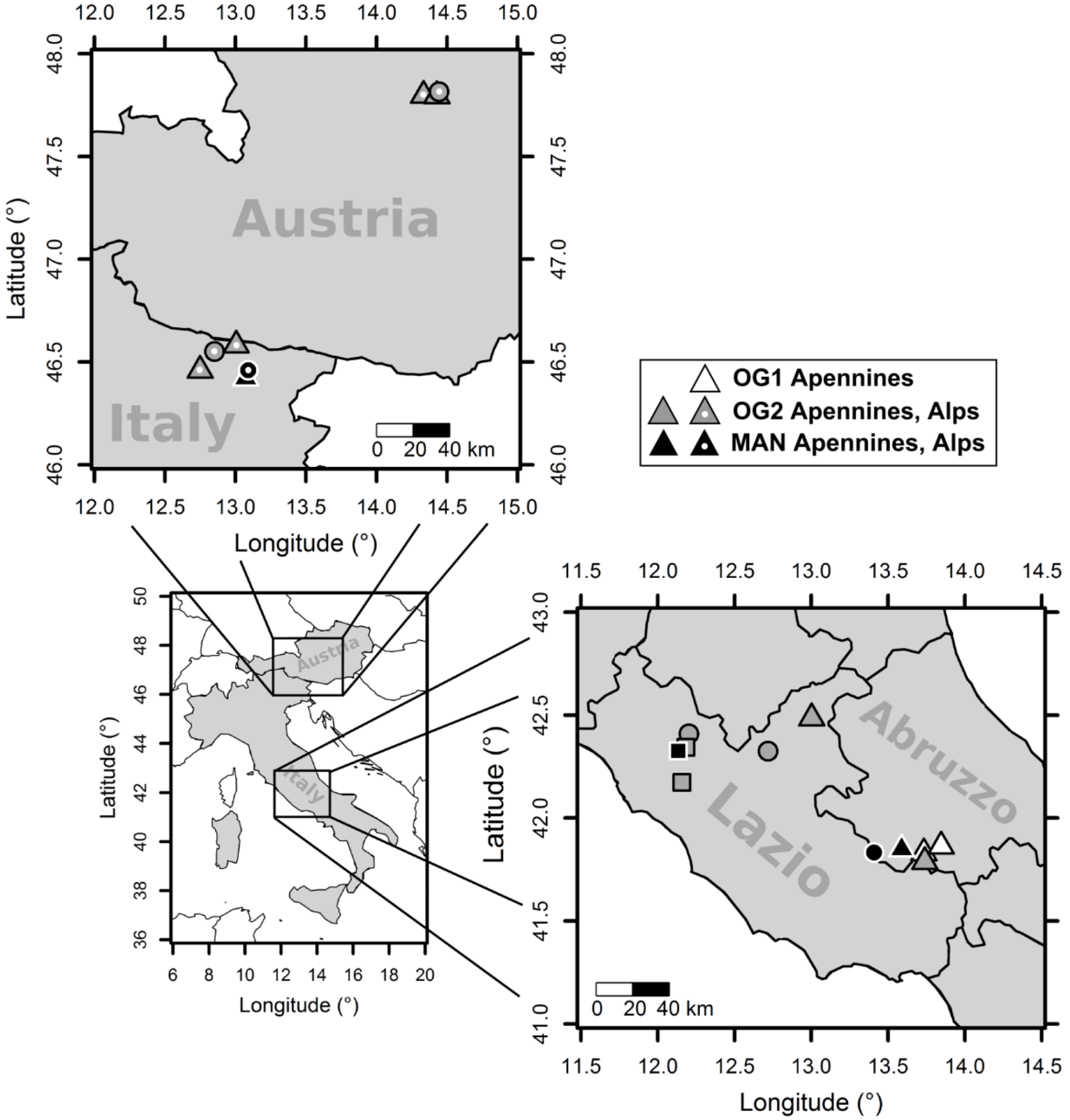

Figure 1. Map of the study sites. Details in Table 1.

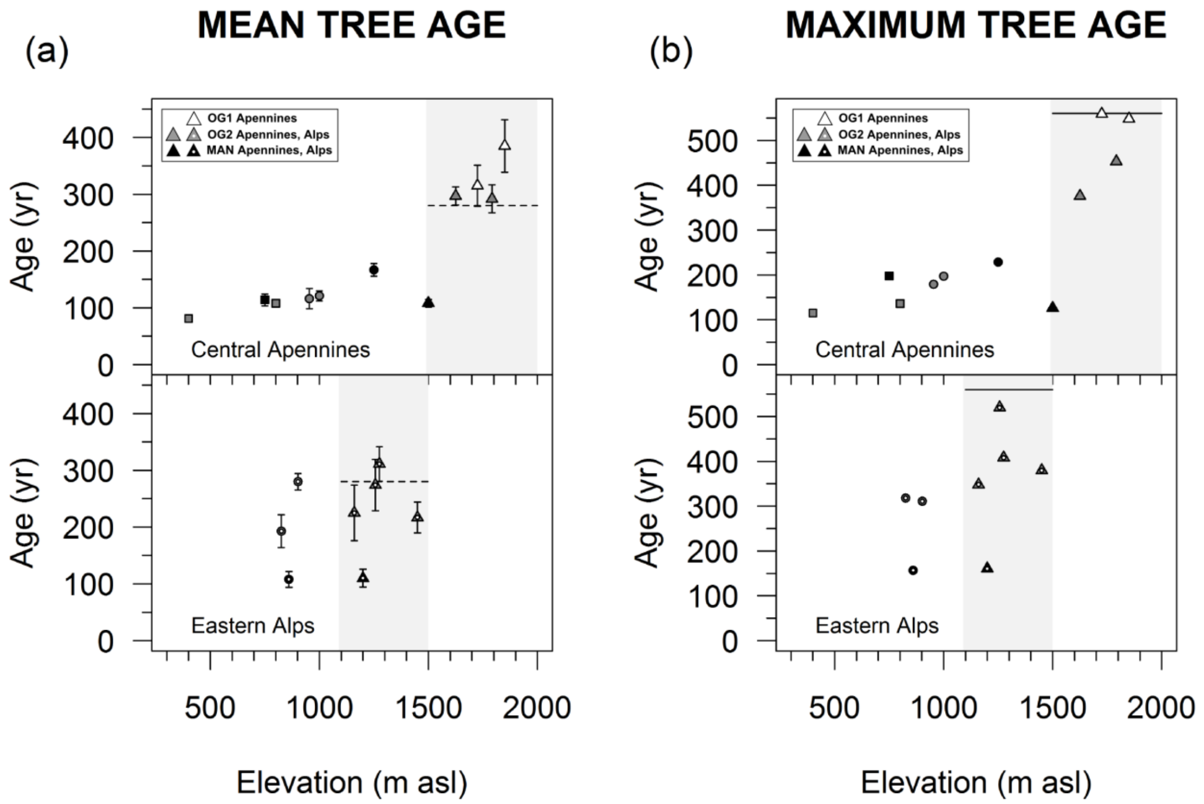

Figure 2. Elevation changes in (a) mean (± 2 SE) and (b) maximum tree age in the Apennines and the Eastern Alps. The continuous line represents the maximum lifespan detected within the high-mountain belt of the Alps and Apennines (grey area), the dotted line represents half of the maximum lifespan (Table 1).

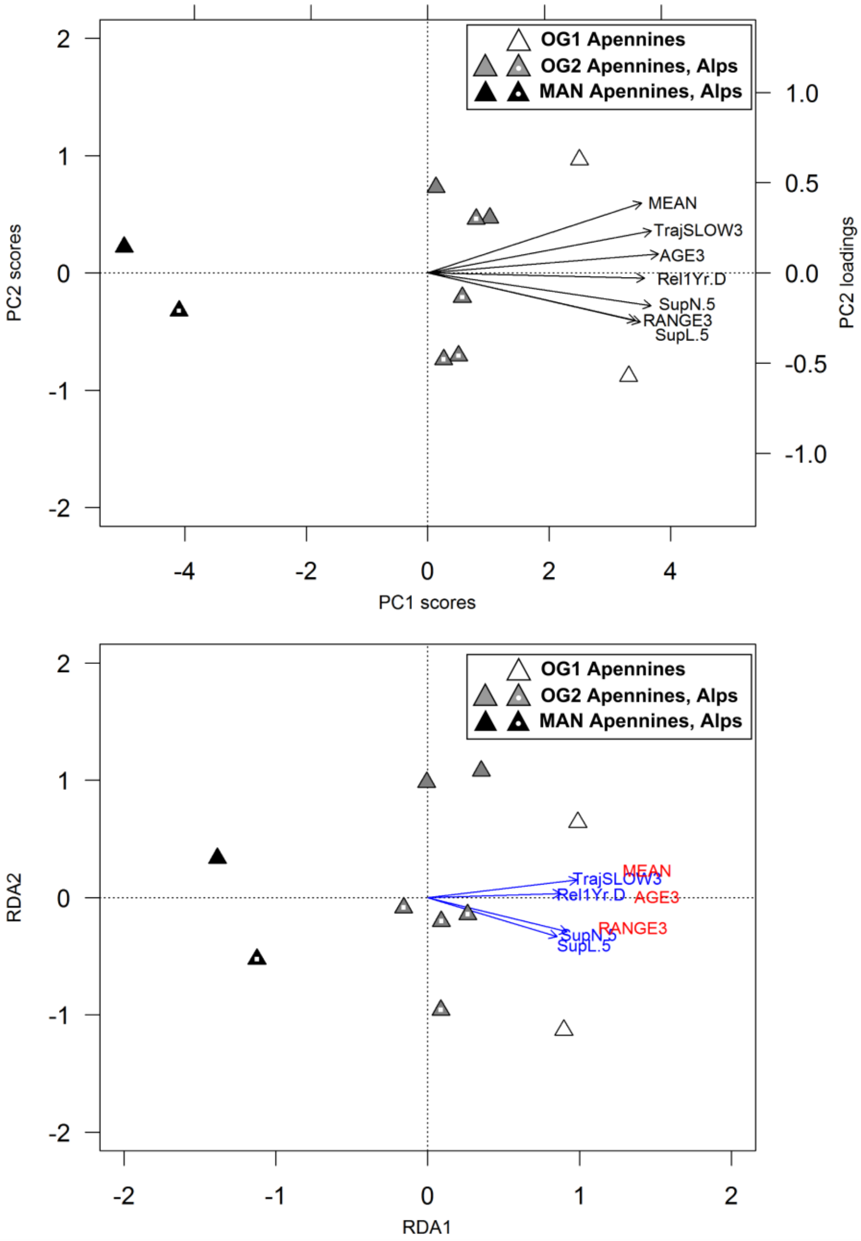

Figure 3. Principal component analysis (PCA, above) and redundancy analysis (RDA, below) of the best chrono-functional indicators for high-mountain forests (OG1, OG2, MAN: primary old growth, secondary old growth, managed forests, respectively). Only the first axis is significant in both analyses. In RDA, predictands are represented in blue and predictors in red ($R^2 = 0.84$, $P = 0.002$).

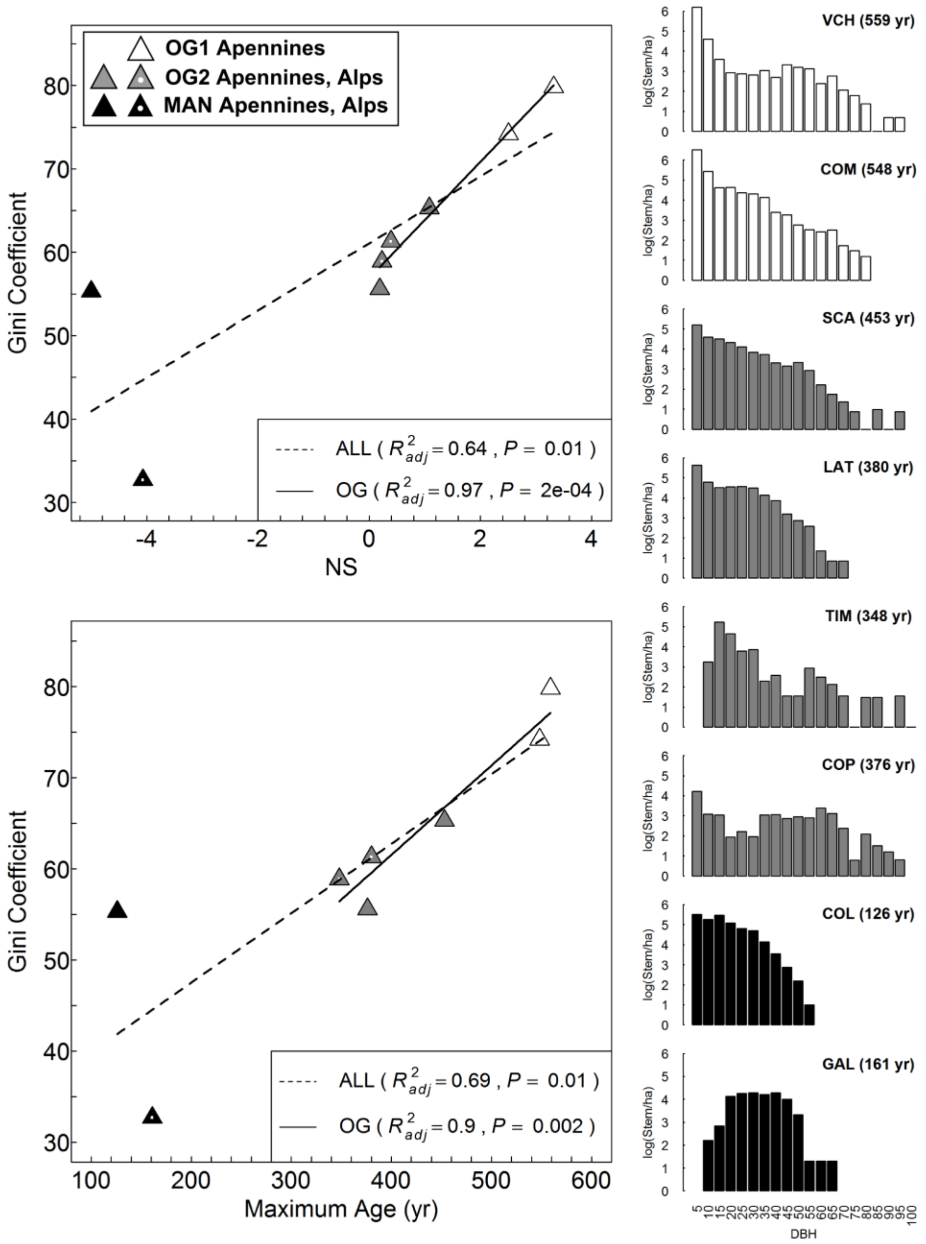

Figure 4. (Left) Relationship between the *Gini* coefficient (of basal area distribution) with the Naturalness Score (*NS*, top) or maximum age (bottom) in high-mountain sites of the central Apennines and Eastern Alps. Regression lines relate to all sites (ALL) or only to old-growth forests (OG). (Right) DBH distribution (logarithm of stem frequency) for sampled sites, arranged top-to-bottom in order of decreasing *Gini* (maximum age within parentheses). Bars colour indicates primary old-growth (white), secondary old-growth (grey) and managed (black) forests.

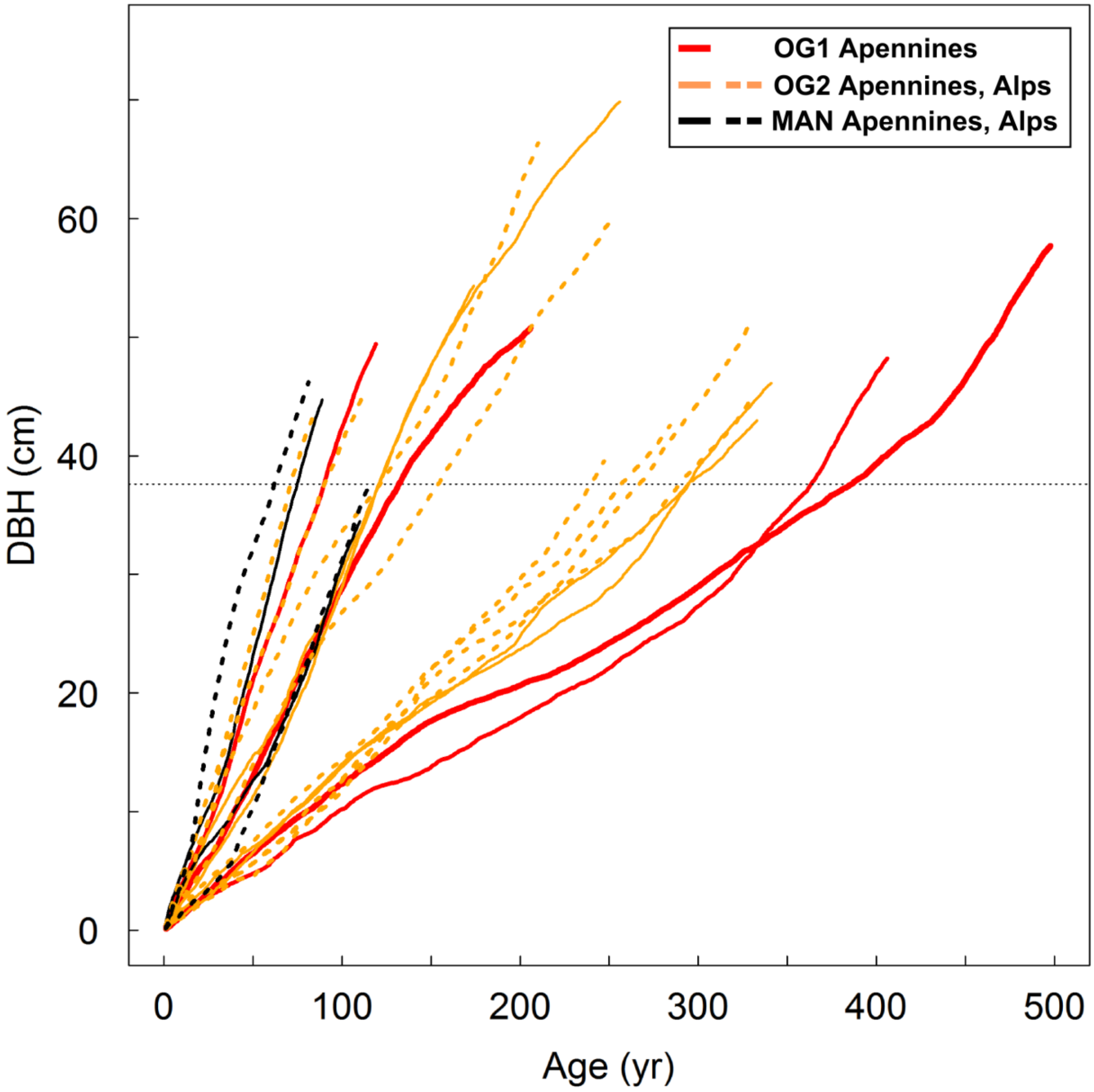

Figure 5. Average growth trajectories of the three slowest and three fastest trees in reaching DBH=37.5 cm within the high-mountain stands of the Alps and Apennines. Only the fully replicated portion of curves is shown. OG1, OG2, MAN: primary old-growth, secondary old-growth, managed forests.

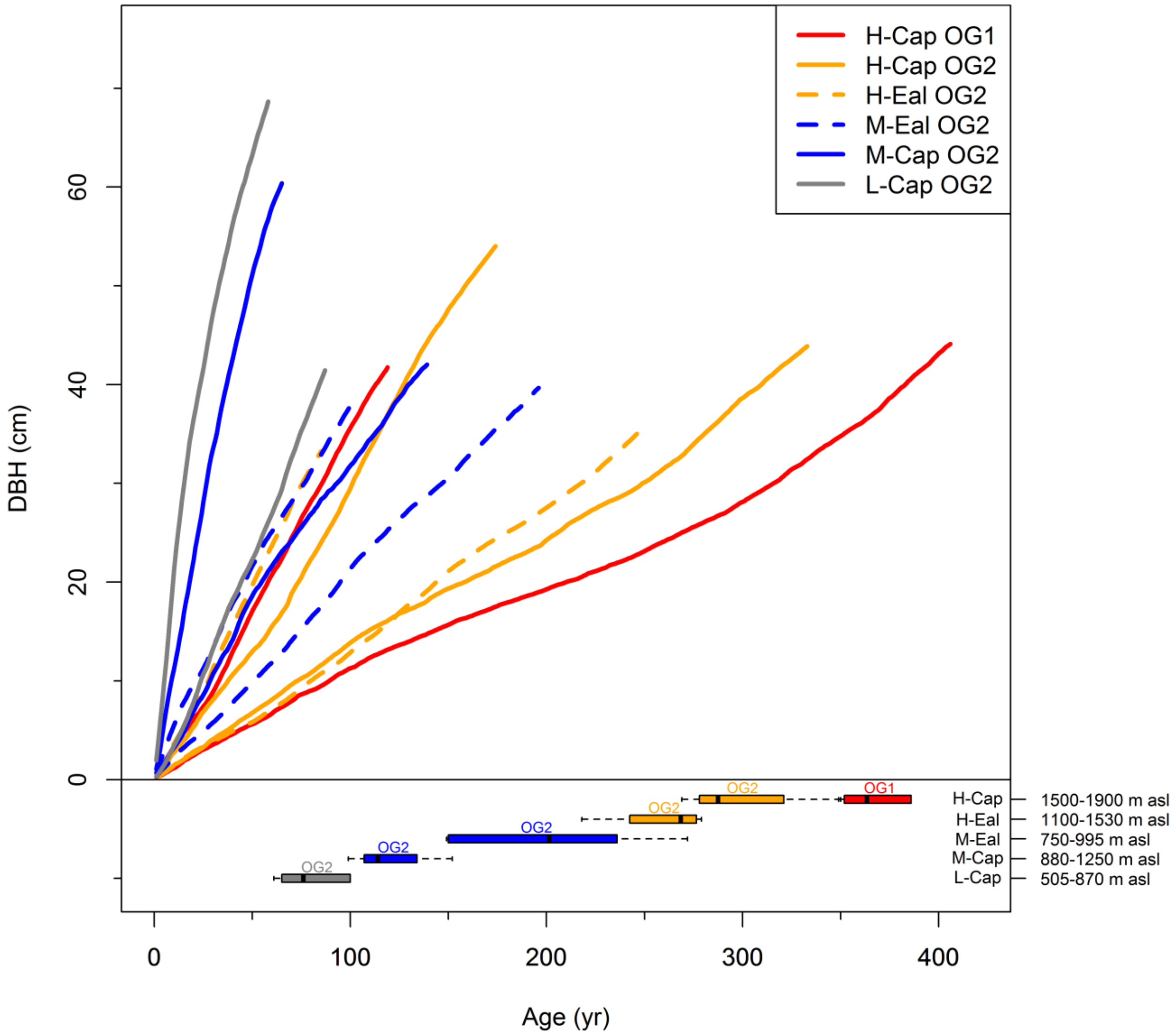

Figure 6. Average growth trajectories of the three slowest and three fastest trees in reaching DBH=37.5 cm by naturalness level (OG1 and OG2) and elevation belt (Cap, central Apennines; Eal, eastern Alps; H, high-mountain; M, mountain; L, low-elevation). Only the fully replicated portion of curves is shown.

Bottom panel: boxplots of the age when slow-growing trees reached DBH=37.5 cm within each belt (stands arranged from top to bottom according to increasing mean annual temperature). The elevation range covered by each BU is shown on the right.