



Review

Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review

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ABSTRACT

Temperate forests have been fundamentally altered by land use and other stressors globally; these have reduced the abundance of primary and old-growth forests in particular. Despite many regional studies, the literature lacks a global synthesis of temperate old-growth structural characteristics. In this study we compare literature derived data on mature and old-growth moist temperate forests with the aim of: (i) exploring global commonalities; (ii) investigating sources of variability among systems; and (iii) highlighting data gaps and research needs. We compiled a dataset of 147 records from 93 papers, and analyzed a set of structural indicators: basal area, stem density, large living trees, live aboveground biomass, quadratic mean diameter, and coarse woody debris volume. These indicators were contrasted between mature and old-growth age classes at a global level and across continents and broad forest types, testing for significance through Monte-Carlo permutation procedure. We also related structural indicators to age, climatic and geographical descriptors. Our results suggest that all structural indicators vary across systems in relation to geographical, compositional, and climatic influences. However old-growth forests showed global commonalities in structure when compared to mature forests: significantly higher densities of large living trees, higher quadratic mean diameter, and higher amounts of live aboveground biomass and coarse woody debris. Furthermore we found inconsistency in the structural variables reported by different papers; lack of studies on temperate forests in Russia, and Western and Central Asia. The findings improve our understanding of old-growth structure and function, and will help inform sustainable forest management and conservation approaches world-wide.

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Abbreviations: LLT, large living trees density; LAB, live aboveground biomass; QMD, quadratic mean diameter; CWD, coarse woody debris volume.

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1. Introduction

Temperate forests are generally more altered and reduced in extent globally than other forested biomes (Silander, 2001) due to their distribution at mid-latitudes with moderate climates, which are also some of the most heavily populated and developed regions of the world. About 35% of the world forests are considered primary (i.e. never cleared though subject to natural disturbances) but these mostly occur in tropical and boreal zones (FAO, 2010); according to one estimate less than 1% of the northern hemisphere's temperate broad-leaved forests remain in a primary condition (Silander, 2001).

Landscapes dominated by primary forests are comprised of complex patch mosaics and host a full range of stand development stages, from disturbance and cohort establishment to old-growth (Franklin et al., 2002). The latter is a late stage of stand development that typically does not occur or is rare in managed forest systems, and has been defined by many authors based on a combination of structural features, age, and sometimes human disturbance history (Wirth et al., 2009). The 'structural' approach, first developed through studies performed in the Pacific Northwest (Spies and Franklin, 1991), is useful because it can both be a good proxy of ecosystem function and is a readily measured surrogate for habitat of many taxa difficult to sample (Franklin et al., 2002; Burrascano et al., 2011).

Structural indicators, often combined with ecological and compositional information, have been proposed for temperate forests in North America (Franklin et al., 1981; Keddy and Drummond, 1996), Europe (Peterken, 1996; Nilsson et al., 2002), South America (Gutierrez et al., 2004) and China (Chen and Bradshaw, 1999). Nevertheless old-growth forests may display strong variation in their structure in different forest types (e.g. Jones, 1945; Burgman, 1996; Wells et al., 1998).

Such variation derives from the fact that the old-growth condition should be defined not only on the basis of a set of structures providing desired functions, such as habitat for late-successional biodiversity, but also of the developmental processes that produce those structures. However the lack of a global theoretical framework of temperate forest development has hindered broad application of a widely accepted process-based approach. Previous research on forest dynamics suggests considerable uncertainty in segmenting stand structural development, because many developmental processes operate continuously or episodically, often rendering discretely defined stages arbitrary (Franklin et al., 2002; Spies, 2004). Moreover, stand development may undergo several different pathways in relation to disturbance regimes and environmental controls (Donato et al., 2012). Furthermore, the age threshold to define developmental stages will differ by forest type and geographic region due to differences in stand development rates, tree longevity, disturbance regime and other factors related to these, such as climate and site conditions (Franklin et al., 1987; Motta et al., 2010). Recognizing these limitations, our review compares "mature" stands with stands classified as "old-growth". These largely age-based classes, commonly reported in the literature, are employed as surrogates for the developmental processes described in Franklin et al. (2002) and other models (e.g. Oliver and Larson, 1990). They generally correspond with the "maturation" (i.e. mature) and "vertical/horizontal diversifica-

tion and pioneer cohort loss" (i.e. old-growth) stages proposed by Franklin et al. (2002).

We focus on late-successional stands since most temperate forests are either managed for wood production or reflect the long-term influence of human activities. As a consequence, old-growth forest structural features are underrepresented in most contemporary landscapes (Bauhus et al., 2009; Rhemtulla et al., 2009) and biodiversity provisioning and other functions associated with them are frequently impaired (Siitonen, 2001; Hatanaka et al., 2011). Though some extended rotation systems may approximate old-growth structural conditions (Keeton, 2006; Bauhus et al., 2009), most silvicultural regimes narrow the range of possible developmental processes as well as the type and spatial distribution of structures, since they do not allow the stands to develop past the maturation phase or they selectively remove certain structures, like large or dead trees (Hunter, 1999).

Our prediction was that moist temperate forests globally will share distinct differences when comparing mature to old-growth conditions, because stand structural heterogeneity (vertical and horizontal) is presumed to increase as late-successional stands develop. For example, coming out of the maturation phase a marked increase in coarse woody debris (CWD) volumes can occur (Harmon et al., 1986), and re-establishment of shade-tolerant trees in the understory initiates redevelopment of stand vertical complexity (Keeton and Franklin, 2005); while horizontal heterogeneity is primarily created by the shift from density-dependent to density-independent mortality (Franklin et al., 2002). These processes drive development of many structural characteristics associated with old-growth. Our review evaluates indirectly through a focus on structural indicators – whether these are universally operative or whether there is significant variation among systems.

Comparison between mature and old-growth forests allows identification of structures that could be promoted silviculturally in managed stands. There are a number of reasons why managers might be interested in this objective. For example, old-growth forests are known to host high plant (Aude and Lawesson, 1998; Burrascano et al., 2009), fungi (Odor et al., 2006; Persiani et al., 2010) and animal diversity (Mikusinski and Angelstam, 1998; McKenny et al., 2006; Winter and Moller, 2008). Recent studies have also shown the importance of old-growth forests in storing high quantities of carbon both as aboveground biomass (Keith et al., 2009; Keeton et al., 2010) and in soils (Zhou et al., 2006) and their ability, in some cases, to maintain positive Net Primary Productivity very late into stand development (Field and Kaduk, 2004; Luysaert et al., 2008; Xu et al., 2012).

Based on the services they provide, old-growth forests represent an important reference point for evaluating human impacts on forest ecosystems, and for understanding forest development processes through observation of the temporal and spatial interactions between successional processes, disturbance events, and tree mortality (Peterken, 1996; Keeton, 2006; Rhemtulla et al., 2009; Hoover et al., 2012). Studying old-growth forests has long been considered the basis for developing natural disturbance-based (North and Keeton, 2008), 'close-to-nature' (Commarmot et al., 2005; Heiri et al., 2009) or 'natural dynamics' (von Oheimb et al., 2005) silvicultural systems able to emulate natural processes and fulfill socio-economic goals while maintaining a full range of

Table 1

Structural data and site descriptors of the stands included in the review. Age class: M – mature, OG – Old-growth. Forest types: C – conifer, DB – deciduous broadleaf, EB – evergreen broadleaf, C/DB – mixed conifer/deciduous broadleaf, EB/C – mixed evergreen broadleaf/conifer. Age values marked with asterisks represent time since last disturbance and were excluded from the analysis. LLT data marked with † were approximated from stand diameter distributions. Live Aboveground Biomass values marked with ‡ refer to stem biomass only. An asterisk (*) before the reference indicates that we averaged multiple stands data in a single record.

Continent	Region	Altitude (m a.s.l.)	Mean T (°C)	Mean P (mm)	Forest type	Dominant tree taxa	Age Class	Age	Basal Area (m ² ha ⁻¹)	Stem density (n ha ⁻¹)	Large living trees (n ha ⁻¹)	Live Aboveground Biomass (Mg ha ⁻¹)	Quadratic Mean Diameter (cm)	Coarse Woody Debris (m ³ ha ⁻¹)	Reference
Asia	Iran	1475	8.0	1800	DB	<i>Fagus orientalis</i>	M		44.5	336	70 [†]		41.1		Akhavan et al. (2012)
	Iran	1475	8.0	1800	DB	<i>Fagus orientalis</i>	OG		39.8	302	68 [†]		40.9		Akhavan et al. (2012)
	China - Changbaishan	1600			C	<i>Picea jezoensis, Abies nephrolepis</i>	OG		50.2	1316			22.0		Chen and Bradshaw (1999)
	China - Changbaishan	800	2.8	700	C/DB	<i>Pinus koraiensis, Tilia amurensis, Quercus mongolica</i>	OG	300	43.2	299	64 [†]		42.9		Hao et al. (2007)
	China - Changbaishan	1300	4.8	612	DB	<i>Quercus liaotungensis, Betula dahurica</i>	M	100	15.6	729			16.5		Hou et al. (2004)
	China - Changbaishan	740	3.3	672	C/DB	<i>Pinus koraiensis, Fraxinus mandshurica, Tilia amurensis</i>	OG	>200	46.5	515			33.9		Dai et al. (2011)
	China - Changbaishan	1680	3.3	672	C	<i>Picea jezoensis, Abies nephrolepis</i>	OG	>200	35.2	745			24.5		Dai et al. (2011)
	China - Sichuan	2930	2.3	1100	C	<i>Abies faxoniana, Picea purpurea, Sabina saltuaria</i>	OG	>250	45.2	404	83 [†]		37.7		*Taylor et al. (2006)
	Japan - Hokkaido		3.1	1652	DB	<i>Quercus mongolica</i>	OG	110		804	16 [†]				Sano (1997)
	Japan - Hokkaido	245	5.7	1043	C/DB	<i>Abies sachalinensis, Acer palmatum, Quercus mongolica</i>	OG	>300	51.2	958			26.1		Abrams et al. (1999)
	Japan - Honshu	2200	0.0	1750	C/DB	<i>Abies mariesii, A. veitchii, Picea jezoensis, Tsuga diversifolia</i>	OG	>200	69.4	496.9			42.2		*Narukawa and Yamamoto (2001)
	Japan - Honshu	1319	7.8	2500	C	<i>Chamaecyparis obtusa, C. pisifera, Thujopsis dolabrata</i>	OG	300	64.8	1618.5			22.6		Hoshino et al. (2001)
	Japan - Honshu	900	11.0	3450	DB	<i>Fagus crenata, Quercus mongolica, Betula grossa, Acer mono</i>	M	105	39.9	536			30.8		*Yamamoto and Nishimura (1999)
	Japan - Honshu	650	11.0	3450	DB	<i>Fagus crenata, Quercus mongolica, Betula grossa, Acer mono</i>	OG	140	58.4	281.3			51.4		*Yamamoto and Nishimura (1999)
	Japan - Honshu	1100	11.0	3450	DB	<i>Fagus crenata</i>	OG		34.3	541			28.4		Yamamoto et al. (1995)
	Japan - Kyushu	460	14.2	3070	EB	<i>Dystilium racemosum, Persea thunbergii, Castanopsis cuspidata</i>	OG	>100*		696		315.7			Sato (2010)
	Japan - Kyushu	490	14.9	2370	EB	<i>Dystilium racemosum, Persea thunbergii, Castanopsis cuspidata</i>	OG	>100*		564		254.3			Sato (2010)
	Japan - Tsushima	340	15.3	2140	EB	<i>Castanopsis cuspidata, Dystilium racemosum</i>	OG		63.9	4570			13.3		Manabe et al. (2000)
	Japan - Satsunan islands	550			EB	<i>Castanopsis cuspidata, Dystilium racemosum, Quercus salicina</i>	M	41-60	54.7	2805		258.0	15.8		Aiba et al. (2001)

Table 1 (continued)

Continent	Region	Altitude (m a.s.l.)	Mean T (°C)	Mean P (mm)	Forest type	Dominant tree taxa	Age Class	Age	Basal Area (m ² ha ⁻¹)	Stem density (n ha ⁻¹)	Large living trees (n ha ⁻¹)	Live Aboveground Biomass (Mg ha ⁻¹)	Quadratic Mean Diameter (cm)	Coarse Woody Debris (m ³ ha ⁻¹)	Reference
	Japan - Satsunan islands	550			EB	<i>Castanopsis cuspidata</i> , <i>Dystilium racemosum</i> , <i>Quercus salicina</i>	OG	>150*	61.5	1795		279.0	20.9		Aiba et al. (2001)
Australia	Australia (Eastern)	850		2000	EB	<i>Nothofagus moorei</i> , <i>Eucalyptus</i> sp.pl.	OG		69.2						Bale et al. (1998)
	New Zealand	100	10.9	4500	EB/C	<i>Nothofagus menziesii</i> , <i>Weinmannia racemosa</i> , <i>Dacrydium cupressinum</i>	OG	>800*	55.9	445	55 [†]		40.0		Lusk and Smith (1998)
	New Zealand	550	11.0	2000	EB/C	<i>Dacrydium cupressinum</i> , <i>Weinmannia racemosa</i>	M	252	144.5	6015			17.5		Smale et al. (1997)
	New Zealand	50	11.3	3400	EB/C	<i>Dacrydium cupressinum</i> , <i>Weinmannia racemosa</i>	M	197	61.0	1660			21.6		Walcroft et al. (2005)
	New Zealand	1136	8.0	1447	EB	<i>Nothofagus solandri</i>	M	>150	68.2	1216		240.4	26.7		Davis et al. (2003)
Europe	Czech Republic	1220	4.0	1400	C	<i>Picea abies</i>	OG	300	32.0	131	80 [†]		55.8	311	Svoboda and Pouska (2008)
	Czech Republic	780	4.3	875	C/DB	<i>Fagus sylvatica</i> , <i>Picea abies</i> , <i>Abies alba</i>	OG	169*	40.6	205	76		50.3	201.9	Král et al. (2010)
	Czech Republic	765	5.4	1144	C/DB	<i>Fagus sylvatica</i> , <i>Picea abies</i> , <i>Abies alba</i>	OG	57*	38.5	306	68		40.0	149.8	Král et al. (2010)
	Czech Republic	770	6.1	740	C/DB	<i>Fagus sylvatica</i> , <i>Picea abies</i> , <i>Abies alba</i>	OG	66*	26.5	124	47		52.2	300.8	Král et al. (2010)
	France - Alps	1425	5.8	1138	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	M	109	42.2	748			26.8		Marage and Lemperiere (2005)
	France - Alps	1425	5.8	1138	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	OG	141	27.1	558			24.9		Marage and Lemperiere (2005)
	France - Fontainebleau	140	10.2	897	DB	<i>Fagus sylvatica</i> , <i>Quercus petraea</i>	OG	100-300	24.4	445			26.4	214.2	Wijdeven (2004)
	France - Vosges	200		850	DB	<i>Fagus sylvatica</i> , <i>Quercus petraea</i>	M	100-150	54.0	320			46.4	91.4	Schnitzler and Borlea (1998)
	Germany (NE)	100	7.8	593	DB	<i>Fagus sylvatica</i>	OG	200-230	32.7	263	75.1		39.8	94	Von Oheimb et al. (2005)
	Poland - Bialowietza				C/DB	<i>Picea abies</i> , <i>Carpinus betulus</i> , <i>Tilia cordata</i>	OG		36.3	665			26.4		Bernadzki et al. (1998)
	Poland - Carpathians	1300	3.0	1635	C	<i>Picea abies</i>	OG		41.2 [†]	314	69 [†]		40.9	192	Zielonka (2006)
	Poland - Carpathians	900	4.5	1050	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	OG		36.3		73 [†]			383	Paluch (2007)
	Slovakia	890	5.0	1000	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i> , <i>Picea abies</i>	OG		41.9	255	81 [†]		45.8	306	Holeksa et al. (2009)
	Slovakia	1350	2.8	1105	C	<i>Picea abies</i>	OG		41.0	290			42.4	144	Holeksa et al. (2007)
	Slovakia	878	6.0	975	DB	<i>Fagus sylvatica</i>	OG		37.4	303			39.6	469	Kucbel et al. (2012)
	Switzerland	470	8.9	976	DB	<i>Fagus sylvatica</i>	M	70*	39.0	422	15.5 [†]		34.3		Heiri et al. (2009)
	Switzerland	500	8.9	910	DB	<i>Fagus sylvatica</i> , <i>Quercus robur</i>	M	70*	40.8	400	24.2 [†]		36.1		Heiri et al. (2009)
	Switzerland	650	7.5	1250	DB	<i>Fagus sylvatica</i>	M	150	30.7	259	83 [†]		38.9	8	Commarmot et al. (2005)
	Ukraine -	750	7.0	950	DB	<i>Fagus sylvatica</i>	OG		38.5	219	81 [†]		47.3	111	Commarmot et al.

Table 1 (continued)

Continent	Region	Altitude (m a.s.l.)	Mean T (°C)	Mean P (mm)	Forest type	Dominant tree taxa	Age Class	Age	Basal Area (m ² ha ⁻¹)	Stem density (n ha ⁻¹)	Large living trees (n ha ⁻¹)	Live Aboveground Biomass (Mg ha ⁻¹)	Quadratic Mean Diameter (cm)	Coarse Woody Debris (m ³ ha ⁻¹)	Reference
	Carpathians Ukraine - Carpathians	1035	7.0	790	C	<i>Picea abies</i> , <i>Abies alba</i>	M	100-150	45.3	1541	4.2	181.3	19.3	77	(2005) Keeton et al. (2010)
	Ukraine - Carpathians	1035	7.0	790	C	<i>Picea abies</i> , <i>Abies alba</i>	OG	250	47.7	725	59.8	255.5	31.9	176	Keeton et al. (2010)
	Ukraine - Carpathians	1035	7.0	790	C	<i>Picea abies</i> , <i>Abies alba</i>	OG	250	54.0	339	93.1	303.0	38.3	157	Keeton et al. (2010)
	Romania	1250	4.9	755	C	<i>Picea abies</i>	OG		42.1	348			39.2		Lamedica et al. (2011)
	Romania	485	8.5	838	DB	<i>Fagus sylvatica</i>	OG		37.3	499	72.2 [†]		30.9	75	Petritan et al. (2012)
	Romania	485	8.5	838	DB	<i>Fagus sylvatica</i> , <i>Quercus petraea</i>	OG		38.3	487	80.6 [†]		31.6	135	Petritan et al. (2012)
	Romania	485	8.5	838	DB	<i>Quercus petraea</i>	OG		39.5	713	120.4 [†]		26.6	134	Petritan et al. (2012)
	Bosnia- Herzegovina	1386	7.8	1600	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i> , <i>Picea abies</i>	OG		47.1	489	117.0		35.0	327	Motta et al. (2011)
	Bosnia- Herzegovina	1150	5.9	1837	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	OG		56.8	466			39.4		*Nagel et al. (2010)
	Italy - Apennines	1725	10.6	1035	DB	<i>Fagus sylvatica</i>	M		39.9	2182	22.0		15.3	12	Burrascano et al. (2008)
	Italy - Apennines	1725	10.6	1035	DB	<i>Fagus sylvatica</i>	OG		30.7	1835	71.0		14.6	45	Burrascano et al. (2008)
	Italy - Apennines	975	9	1750	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	OG	>140	57.4	177	122 [†]		64.3	65.2	Travaglini et al. (2012)
	Italy - Alps	1695			C	<i>Picea abies</i>	M	200	63.3	466			41.6	28	Motta et al. (2010)
	Italy - Alps	1815			C	<i>Picea abies</i>	M	220	69.2	513			41.5	80	Motta et al. (2010)
	Slovenia	900	8.2	1400	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	OG		41.6	341	119 [†]		39.4		Nagel et al. (2006)
	Slovenia	905	8.3	1500	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	OG			265				138	Boncina (2000)
	Slovenia	905	8.3	1500	C/DB	<i>Fagus sylvatica</i> , <i>Abies alba</i>	M			393				10	Boncina (2000)
	Spain (NW)	140	14.0	1200	DB	<i>Fagus sylvatica</i> , <i>Quercus robur</i>	OG	220	31.9	1112	36.5 [†]		19.1		*Rozas (2003)
	Spain (NW)	780	9.8	1600	DB	<i>Fagus sylvatica</i>	OG		48.0	569	54 [†]	410.0	32.8		Merino et al. (2007)
North America	US - Michigan				C/DB	<i>Acer saccharum</i> , <i>Betula allegghaniensis</i> , <i>Tsuga canadensis</i>	OG	200-300	33.0	1130	60 [†]	262.0	19.3		Fisk et al. (2002)
	US - Michigan				C/DB	<i>Acer saccharum</i> , <i>Betula allegghaniensis</i> , <i>Tsuga canadensis</i>	M	60-80	31.0	970	10 [†]	230.0	20.2		Fisk et al. (2002)
	US - Michigan	390	5.5	935	C/DB	<i>Acer saccharum</i> , <i>Betula allegghaniensis</i> , <i>Tsuga canadensis</i>	OG		45.6				30.4		*Dahir and Lorimer (1996)
	US - Michigan	390	5.5	935	C/DB	<i>Acer saccharum</i> , <i>Betula allegghaniensis</i> , <i>Tsuga canadensis</i>	M	100-175	49.4				35.2		*Dahir and Lorimer (1996)
	US - Michigan	525	3.2	850	DB	<i>Acer saccharum</i>	M	65-75	32.3	828			22.3	39	Goodburn and Lorimer (1998)
	US - Michigan	525	3.2	850	C/DB	<i>Acer saccharum</i> , <i>Betula allegghaniensis</i> , <i>Tsuga</i>	M		28.0	469			27.6	61	Goodburn and Lorimer (1998)

Table 1 (continued)

Continent	Region	Altitude (m a.s.l.)	Mean T (°C)	Mean P (mm)	Forest type	Dominant tree taxa	Age Class	Age	Basal Area (m ² ha ⁻¹)	Stem density (n ha ⁻¹)	Large living trees (n ha ⁻¹)	Live Aboveground Biomass (Mg ha ⁻¹)	Quadratic Mean Diameter (cm)	Coarse Woody Debris (m ³ ha ⁻¹)	Reference
	US - Michigan/ Wisconsin	525	3.2	850	DB	<i>canadensis</i> <i>Acer saccharum</i>	M		25.5	446			27.0	74	Goodburn and Lorimer (1998)
	US - Michigan/ Wisconsin	525	3.2	850	DB	<i>Acer saccharum</i>	OG	~350	34.4	313			37.4	127	Goodburn and Lorimer (1998)
	US - Michigan/ Wisconsin	525	3.2	850	C/DB	<i>Acer saccharum</i> , <i>Betula alleghaniensis</i> , <i>Tsuga canadensis</i>	OG	~350	37.5	388			35.1	151	Goodburn and Lorimer (1998)
	US - Michigan/ Wisconsin	1940		1100	C	<i>Abies magnifica</i> , <i>Abies concolor</i>	OG	>200	85.2	825	125		22.1		*Taylor and Halpern (1991)
	US - Michigan/ Wisconsin				C/DB	<i>Tsuga canadensis</i> , <i>Betula alleghaniensis</i> , <i>Acer saccharum</i>	OG	185	48.6		2.5			84.5	*Tyrrell and Crow (1994a,b)
	US - Michigan/ Wisconsin				C/DB	<i>Tsuga canadensis</i> , <i>Betula alleghaniensis</i> , <i>Acer saccharum</i>	OG	231	49.9		16.2			104.2	*Tyrrell and Crow (1994a,b)
	US - Michigan/ Wisconsin				C/DB	<i>Tsuga canadensis</i> , <i>Betula alleghaniensis</i> , <i>Acer saccharum</i>	OG	261	46.7		35.5			121.3	*Tyrrell and Crow (1994a,b)
	US - Michigan/ Wisconsin				C/DB	<i>Tsuga canadensis</i> , <i>Betula alleghaniensis</i> , <i>Acer saccharum</i>	OG	336	43.3		45			151.3	*Tyrrell and Crow (1994a,b)
	US- Indiana	295			DB	<i>Quercus rubra</i> , <i>Fraxinus americana</i> , <i>Q. alba</i> , <i>Q. macrocarpa</i>	OG	>350	31	321	199		35.1		Parker et al. (1985)
	Canada - Quebec		6.1	1102	DB	<i>Acer saccharum</i> , <i>Fagus grandifolia</i>	OG	>300*	29.9	382			31.6		Beaudet et al. (2007)
	US - Massachussets	466		1120	DB	<i>Fagus grandifolia</i> , <i>Quercus rubra</i> , <i>Acer sp.pl.</i>	OG	>250	35.0	509	41†		29.6		*Orwig et al. (2001)
	US - Massachussets	473			C/DB	<i>Tsuga canadensis</i> , <i>Fagus grandifolia</i> , <i>Betula sp.pl.</i>	OG	177-246	44.8	531	58†		32.8	156.4	*D'Amato et al. (2008)
	US - Massachussets	473			C/DB	<i>Tsuga canadensis</i> , <i>Fagus grandifolia</i> , <i>Betula sp.pl.</i>	M	108-136	41.2	1000	20†		22.9	43.90	*D'Amato et al. (2008)
	US - New York				C/DB	<i>Betula alleghaniensis</i> , <i>Fagus grandifolia</i> , <i>Picea rubens</i> , <i>Tsuga canadensis</i>	OG	319	33.0	1005	37	221.0	20.5	206.8	*Keeton et al. (2007)
	US - New York				C/DB	<i>Betula alleghaniensis</i> , <i>Fagus grandifolia</i> , <i>Picea rubens</i> , <i>Tsuga canadensis</i>	M	118	26.0	981	12	148.0	18.4	177.8	*Keeton et al. (2007)
	US - New York				C/DB	<i>Betula alleghaniensis</i> , <i>Fagus grandifolia</i> , <i>Picea rubens</i> , <i>Tsuga canadensis</i>	M	119	24.0	777	11	144.0	19.8	110.4	*Keeton et al. (2007)
	US - New York	595			DB	<i>Acer saccharum</i> , <i>Fagus grandifolia</i>	OG	149-259	33.7	392	65†		33.1		McGee et al. (1999)
	US - New York	630			DB	<i>Acer saccharum</i> , <i>Fagus grandifolia</i>	M	90-100	29.1	508	17†		27.0		McGee et al. (1999)
	US - Vermont	481	7.6	993	DB	<i>Acer saccharum</i> , <i>Fraxinus americana</i>	OG	150-400	34.5	97		278	28.7		*Hoover et al. (2012)
	US - Vermont	464	7.6	993	C	<i>Tsuga canadensis</i> , <i>Picea</i>	OG	150-400	35.7	103		222	22.4		*Hoover et al.

(continued on next page)

Table 1 (continued)

Continent	Region	Altitude (m a.s.l.)	Mean T (°C)	Mean P (mm)	Forest type	Dominant tree taxa	Age Class	Age	Basal Area (m ² ha ⁻¹)	Stem density (n ha ⁻¹)	Large living trees (n ha ⁻¹)	Live Aboveground Biomass (Mg ha ⁻¹)	Quadratic Mean Diameter (cm)	Coarse Woody Debris (m ³ ha ⁻¹)	Reference
	US - Maine/New Hampshire	534	6.5	1194	DB	sp., <i>Abies</i> sp. <i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Betula</i> sp.pl.	OG	150-400	28.7	111		208	19.0		(2012) *Hoover et al. (2012)
	US - Maine/New Hampshire	534	6.1	1194	C	<i>Tsuga canadensis</i> , <i>Picea</i> sp., <i>Abies</i> sp.	OG	150-400	47.7	162		263	15.7		*Hoover et al. (2012)
	US - Ohio	1300	10.7	1012	DB	<i>Quercus alba</i> , <i>Fagus grandifolia</i> , <i>Acer saccharum</i>	OG	300-350	32.9	234			42.3		*McCarthy et al. (2001)
	US - Ohio	260	10.5	980	DB	<i>Quercus alba</i> , <i>Acer saccharum</i> , <i>Quercus velutina</i> , <i>Acer rubrum</i>	OG	>150	30.8	365	33 [†]		32.8	48.3	Goebel and Hix (1996)
	US - Ohio	240	10.5	980	DB	<i>Quercus alba</i> , <i>Acer saccharum</i> , <i>Quercus velutina</i> , <i>Acer rubrum</i>	M	130-149	26.4	265	15 [†]		35.6	5.3	Goebel and Hix (1996)
	US - Ohio	265	12.6	10019	DB	<i>Quercus alba</i> , <i>Acer saccharum</i> , <i>Liriodendron tulipifera</i> , <i>Q. prinus</i>	OG		29.6	371.4			31.9		McCarthy et al. (1987)
	US - Pennsylvania	350	18.9	1000	C/DB	<i>Tsuga canadensis</i>	OG		39.1	218			47.8		Williams and Cook (2010)
	US - Pennsylvania	350	18.9	1000	C/DB	<i>Pinus strobus</i> , <i>Tsuga canadensis</i> , <i>Betula lenta</i>	M	70	27.1	266			36		Williams and Cook (2010)
	US - Pennsylvania	530	6.0	1090	C/DB	<i>Tsuga canadensis</i> , <i>Fagus grandifolia</i> , <i>Acer rubrum</i>	OG	~300	48.8	414	82 [†]		38.7		*Ruffner and Abrams (2003)
	US - Pennsylvania	470	8.0	1170	C	<i>Pinus strobus</i> , <i>Tsuga canadensis</i>	OG	250-300	78.6	347	179 [†]		53.7		Abrams and Orwig (1996)
	US - Tennessee	930			C/DB	<i>Tsuga canadensis</i> , <i>Fagus grandifolia</i> , <i>Acer saccharum</i>	OG		47.6	802		398.0	26.9		*Busing (1998)
	US - Tennessee		16.2	1320	DB	<i>Quercus</i> sp.pl., <i>Carya</i> sp.pl., <i>Acer saccharum</i> , <i>Fagus grandifolia</i>	OG		39.2	363	26		37.1		Kupfer and Kirsch (1998)
	US - Tennessee	1049			C/DB	<i>Tsuga canadensis</i> , <i>Halesia carolina</i> , <i>Fagus grandifolia</i> , <i>Acer saccharum</i>	OG		52.4	877		440.0	27.6		Busing and White (1993)
	US - Virginia	195			DB	<i>Liriodendron tulipifera</i> , <i>Quercus prinus</i>	OG		43.1	1720		379.1	17.8		*Druckenbrod et al. (2005)
	US - Virginia	1066.5	14.0	1070	DB	<i>Quercus rubra</i> , <i>Betula lenta</i> , <i>Prunus serotina</i>	OG	300	43.9	433	83 [†]		35.9		Abrams et al. (1997)
	US - Virginia	884	14.0	1070	DB	<i>Quercus prinus</i> , <i>Q. rubra</i> , <i>Acer rubrum</i>	OG	300	35.8	288	73 [†]		39.8		Abrams et al. (1997)
	US - West Virginia	994	8.8	1320	DB	<i>Acer saccharum</i> , <i>Tilia americana</i> , <i>Quercus rubra</i>	OG	~150	40.9	444	87 [†]				Abrams et al. (1998)
	US - West Virginia	1155	8.1	1340	C	<i>Picea rubens</i>	OG	164-201	37.9	475	26.2		31.9		*Adams and Stephenson (1989)
	US - Washington				C	<i>Abies procera</i>	OG	400	147.0			1562 [†]			Waring and Franklin (1979)
	US - Washington				C	<i>Sequoia sempervirens</i>	OG		247.0			3200.0			Waring and Franklin (1979)
	US - Washington	355			C	<i>Tsuga heterophylla</i> ,	OG	450	94.0	520	129 [†]		48.0		North et al. (2004)

Table 1 (continued)

Continent	Region	Altitude (m a.s.l.)	Mean T (°C)	Mean P (mm)	Forest type	Dominant tree taxa	Age Class	Age	Basal Area (m ² ha ⁻¹)	Stem density (n ha ⁻¹)	Large living trees (n ha ⁻¹)	Live Aboveground Biomass (Mg ha ⁻¹)	Quadratic Mean Diameter (cm)	Coarse Woody Debris (m ³ ha ⁻¹)	Reference
	US - Washington-Oregon			1900	C	<i>Pseudotsuga menziesii</i> <i>Pseudotsuga menziesii</i>	OG	>195	69.0	448			44.3	425	Spies and Franklin (1991)
	US - Washington-Oregon			1900	C	<i>Pseudotsuga menziesii</i>	M	80-195	59.0	452			40.8	209	Spies and Franklin (1991)
	US - Oregon				C	<i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i>	OG	>400	127.0			1590 [†]			Waring and Franklin (1979)
	US - Oregon				C	<i>Sequoia sempervirens</i>	OG	>1000	338.0			3461 [†]			Waring and Franklin (1979)
	US - California	56		1792	C	<i>Sequoia sempervirens</i>	OG		379.0	164		4277.0	171.6		Sillett and Van Pelt (2007)
	US - California	75			C	<i>Sequoia sempervirens</i>	OG	>1000	330.0	380		4248.0		797	Busing and Fujimori (2005)
	US - California	2000		1250	C	<i>Abies concolor</i> , <i>Pinus lambertiana</i> , <i>Calocedrus decurrens</i>	OG		68.0	537	91 [†]		40.2		North et al. (2004)
	US - Colorado	192		1200	C	<i>Picea engelmanni</i> , <i>Pinus contorta</i>	OG	200-450	63.0	1140	111 [†]	253.0	26.5		Binkley et al. (2003)
South America	Chile - Andes	395		3100	EB	<i>Aextoxicon punctatum</i> , <i>Laureliopsis philippiana</i>	OG	380-645	242.8	1865			40.7		*Pollmann and Veblen (2004)
	Chile - Andes	890		3100	EB	<i>Nothofagus dombeyi</i> , <i>Laureliopsis philippiana</i>	OG	570-785	224.7	1321			46.5		*Pollmann and Veblen (2004)
	Chile - Andes	1110		6800	EB	<i>Nothofagus dombeyi</i> , <i>Nothofagus pumilio</i>	OG	430-590	126.1	1185			36.8		*Pollmann and Veblen (2004)
	Chile - Andes	1320		6800	DB	<i>Nothofagus betuloides</i>	OG	410-560	98.3	1893			25.7		*Pollmann and Veblen (2004)
	Chile - Andes	775			EB/C	<i>Nothofagus dombeyi</i> , <i>Laureliopsis philippiana</i> , <i>Saxegothaea conspicua</i>	OG	>300	125.6	502		877.3	57.3	88.8	Schlegel and Donoso (2008)
	Chile - Andes	775			EB/C	<i>Laureliopsis philippiana</i> , <i>Saxegothaea conspicua</i> , <i>Dasyphyllum diacanthoides</i>	OG	>300	109.4	652		664.5	48.2	59.6	Schlegel and Donoso (2008)
	Chile (S-Central)	800		5000	EB/C	<i>Nothofagus dombeyi</i> , <i>Laureliopsis philippiana</i> , <i>Saxegothaea conspicua</i>	OG		126.0	501	127 [†]		56.6		Donoso and Lusk (2007)
	Chile (S-Central)	480	11.5		EB	<i>Eucryphia cordifolia</i> , <i>Weinmannia trichosperma</i>	OG		81.0	719			37.9		*Donoso and Nyland (2005)
	Chile (S-Central)	376			EB	<i>Aextoxicon punctatum</i>	OG	260-460	95.1	661	206 [†]		42.8		Salas et al. (2006)
	Chile (S-Central)	400			DB	<i>Nothofagus obliqua</i> , <i>N. alpina</i> , <i>N. dombeyi</i>	M	86	55.0	1006			26.4		Salas and Garcia (2006)
	Chile - Chiloe island	170	9.1	2157.8	EB/C	<i>Podocarpus nubigena</i> , <i>Saxegothaea conspicua</i> , <i>Nothofagus nitida</i>	M	112-134	97.9						*Gutierrez et al. (2009)
	Chile - Chiloe island	310	9.1	2157.8	EB/C	<i>Podocarpus nubigena</i> , <i>Saxegothaea conspicua</i> , <i>Nothofagus nitida</i>	OG	173-309	104.0	1513	177 [†]		29.6		Gutierrez et al. (2009)
	Chile - Chiloe island	350	11.0	2516	EB	<i>Amomyrtus luma</i> , <i>Laureliopsis philippiana</i>	OG		78.4	1326			27.4		Armesto and Figueroa (1987)
	Chile - Chiloe	50	11.0	2516	EB	<i>Aextoxicon punctatum</i> ,	OG		32.2	1436			1639		Armesto and

(continued on next page)

Table 1 (continued)

Continent	Region	Altitude (m a.s.l.)	Mean T (°C)	Mean P (mm)	Forest type	Dominant tree taxa	Age Class	Age	Basal Area (m ² ha ⁻¹)	Stem density (n ha ⁻¹)	Large living trees (n ha ⁻¹)	Live Aboveground Biomass (Mg ha ⁻¹)	Quadratic Mean Diameter (cm)	Coarse Woody Debris (m ³ ha ⁻¹)	Reference
	island					<i>Luma apiculata</i>									Figueroa (1987)
	Chile - Chiloe	150	11.0	2516	EB	<i>Drimys winteri</i>	OG		43.6	750			27.2		Arnesto and Figueroa (1987)
	island														
	Chile - Chiloe	30	11.0	2516	EB	<i>Drimys winteri</i> , <i>Amomyrtus luma</i> , <i>Nothofagus dombeyi</i>	OG		61.2	949			28.7		Arnesto and Figueroa, 1987
	island														
	Chile - Chiloe	680	6.0	4500	EB/C	<i>Fitzroya cupressoides</i> , <i>Pilgerodendron</i> <i>uviferum</i> , <i>Nothofagus</i> <i>nitida</i>	OG	400-425	138.2	9680	36 [†]	576.0	13.5		Battles et al. (2002)
	island														
	Chile - Chiloe	75			EB/C	<i>Nothofagus nitida</i> , <i>Drimys winteri</i> , <i>Podocarpus nubigena</i>	M	97-112	47.4	3600			13.0	215	*Carmona et al. (2002)
	island														
	Chile - Chiloe	75			EB/C	<i>Nothofagus nitida</i> , <i>Drimys winteri</i> , <i>Podocarpus nubigena</i>	OG	133	75.7	2400			20	219	*Carmona et al. (2002)
	island														
	Chile - Chiloe	550	9.5		EB/C	<i>Nothofagus nitida</i> , <i>Drimys winteri</i> , <i>Podocarpus nubigena</i> , <i>Laureliopsis philippiana</i>	OG	191	89.2	3114			19.1	782	*Carmona et al. (2002)
	island														
	Chile (Southern)	30			EB/C	<i>Nothofagus nitida</i> , <i>Podocarpus nubigena</i>	M		94.1	688			41.8		Innes (1992)
	Chile (Southern)	220	4.3	690	DB	<i>Nothofagus pumilio</i>	M	180	80.0	360		492.5	41.7		Barrera et al. (2000)
	Chile (Southern)	440	3.1	954	DB	<i>Nothofagus pumilio</i>	M	158	67.0	780		349.8	31.7		Barrera et al. (2000)
	Chile (Southern)	1200		2750	DB	<i>Nothofagus alpina</i> , <i>Nothofagus dombeyi</i>	OG	137	89.5	451	150 [†]		50.3		Pollmann (2003)
	Chile (Southern)	1500		1800	DB	<i>Nothofagus pumilio</i>	OG		68.0	499			52.2		Fajardo and de Graaf (2004)
	Chile (Southern)	900		1350	DB	<i>Nothofagus pumilio</i>	OG		61.9	782			33.8		Fajardo and de Graaf (2004)
	Argentina				DB	<i>Nothofagus pumilio</i>	OG	125-250	69.2	584			38.9		*Martínez Pastur et al. (2000)
	Argentina	150		850	EB	<i>Nothofagus betuloides</i> , <i>Drimys winteri</i>	OG	150-161	104.0	1906	25 [†]		26.4		*Rebertus and Veblen (1993)
	Argentina	350			DB	<i>Nothofagus pumilio</i>	OG	100	95.0	717	32 [†]		41.1		Rebertus and Veblen (1993)

late-successional ecosystem services (Franklin et al., 2002; Bauhus et al., 2009). However, the direct contributions from the study of old-growth forests to sustainable silvicultural systems has been partially hampered by context-dependent results from studies focused on individual forest types and by the scarcity of late-successional forest remnants for many forest types (Oliver and Larson, 1990; Brang, 2005).

Even if the interest in old-growth forests arose long ago (Jones, 1945) and these systems have been studied in many temperate regions of the world, only recently have researchers begun to work on assessments of old-growth ecosystem structure and functions at the global scale (Luyssaert et al., 2008; Keith et al., 2009). Yet there is still much to learn from old-growth forest remnants. In particular, identifying the degree to which structural characteristics co-vary among temperate old-growth forests would provide an indication of how a range of ecosystem services could respond to choices societies make about how to manage or conserve forests in the temperate zone. With old-growth forests rapidly disappearing and under pressure in many regions (e.g. Gutierrez et al., 2009; Knorn et al., *in press*), there is a compelling need to aggregate available information on old-growth structure. In this study we review the existing literature reporting data on structural attributes of moist temperate old-growth forests with a special focus on their distinctive features when compared to mature forests. Our research objectives are to (i) identify shared attributes among old-growth stands across different continents and forest types, (ii) investigate variability among these, and (iii) explore gaps in the data globally in order to inform future research.

2. Methods

2.1. Literature search

We assembled a dataset from a literature search performed in December 2011, in which we looked for studies reporting the structural attributes of old-growth temperate forests. Studies comparing data between old-growth and mature forest sites were particularly valued. Relevant publications were identified by searching the online database of Web of Science using the following search words: 'old-growth and structur* AND (volume or biomass)'. An additional search for data on mature sites was performed for those continents (Asia, Australia and South America) where age comparison studies were scarce. For these we used the additional search words: '(mature OR managed) AND forest* AND structur*'. The initial search was then further refined within the ISI website. We retained a paper in the dataset when it was associated with one or more categories of interest. These included subject area (forestry, ecology, environmental sciences, plant sciences, biodiversity conservation), and document type (article, proceeding paper, review). We considered only data published in English language and peer reviewed journals. We included data from any sites defined in their respective papers as 'temperate'. Where no direct reference to biome occurred we followed the geographic boundaries reported for the temperate forest biomes (Olson et al., 2001). We focused only on moist temperate forests, i.e. those systems where climate seasonal variation is determined more by temperature than by precipitation. The search did not include forests prone to high to moderate frequency ground-fire in regions with low precipitation during the growing season due to fundamentally different structural development processes in these systems. The Web of Science search missed several papers reporting data on old-growth forests because terms other than 'old-growth' were used in the title and abstract. Terms like 'virgin', 'ancient', 'primeval', 'near-natural', and 'untouched' were often used interchangeably with the concept of 'old-growth', sometimes without

clear distinction of whether the reference was to an old-growth condition or a primary (never cleared) forest. Therefore to achieve a comprehensive dataset, we added studies cited in other papers included in our dataset, or based on the authors' knowledge of the field, or suggested by the reviewers. Each paper was checked to confirm that data were reported for late-successional/old-growth stands, rather than early to mid-successional (natural disturbance originated) stands existing within a primary forest matrix.

This process produced a robust dataset that, nevertheless, is not meant to be a full representation of all papers ever published on this topic. Indeed, during the selection process we evaluated the return in terms of information provided by each additional paper, taking into account regional gaps, and discontinued the research when there was sufficient representation of major forest types for each region.

2.2. Data extraction

The full set of papers identified by our search was filtered to remove those not reporting values for biometrics of direct relevance to our analysis. We excluded those papers not reporting at least three of the stand structural or compositional variables included in a preliminary list comprising: basal area, stem density, large living tree density, live aboveground biomass, mean stand and quadratic mean diameter, volumes of different components of coarse woody debris, canopy height and closure, gap metrics, vertical heterogeneity indices, and tree species richness. Furthermore, in cases where more than one paper reported data for the same site(s), we selected the study reporting the largest number of variables. Since several papers reported data from numerous different stands, these structural data were averaged only if those stands were similar in terms of geographic location, canopy composition and age classes.

The final dataset consisted of 147 records derived from 93 papers (Table 1) describing late-successional/old-growth temperate forests from many different regions and forest types around the world, all continents having temperate zones were represented (Fig. 1). Each record was classified in terms of age class and broad forest type.

Age classes (e.g. mature vs. old-growth) were assigned as reported in the original paper, and not from the analysis of age or structural attributes. The criteria employed in the original papers resulted in wide age ranges, both for mature and old-growth age classes, accounting for intrinsic variability across regions and forest types. In two cases (Wijdeven, 2004; Merino et al., 2007) stands described as near-natural were included in the old-growth group. A stand attributed to the 'degradation phase' was included in the old-growth group (Marage and Lemperiere, 2005) while stands attributed to the 'optimal' and 'decay' stages were included respectively in the mature and old-growth group (Akhavan et al., 2012; Heiri et al., 2009). In few comparative studies, stands defined by authors as 'secondary' or 'second growth' (Aiba et al., 2001; Fisk et al., 2002) or in 'biostatic phase' (Marage and Lemperiere, 2005), were classified in our analysis as 'mature'.

On the basis of the main traits of dominant species we defined five broad forest types: C – conifers; C/DB – mixed conifer/deciduous broadleaf; DB – deciduous broadleaf; EB – evergreen broadleaf; and EB/C mixed evergreen broadleaf/conifer. Since very few examples of mixed evergreen/deciduous broadleaf forests occurred in our dataset (see Pollmann and Veblen, 2004; Salas and Garcia, 2006), these stands were included either in the EB or DB type according to the dominant species. In the final table, we maintained only those structural variables reported for at least 25% of the records. These were: basal area, stem density, large living tree density (LLT – i.e. trees with DBH > 50 cm per hectare), live aboveground biomass (LAB), quadratic mean diameter (QMD) and coarse woody debris volume (CWD).

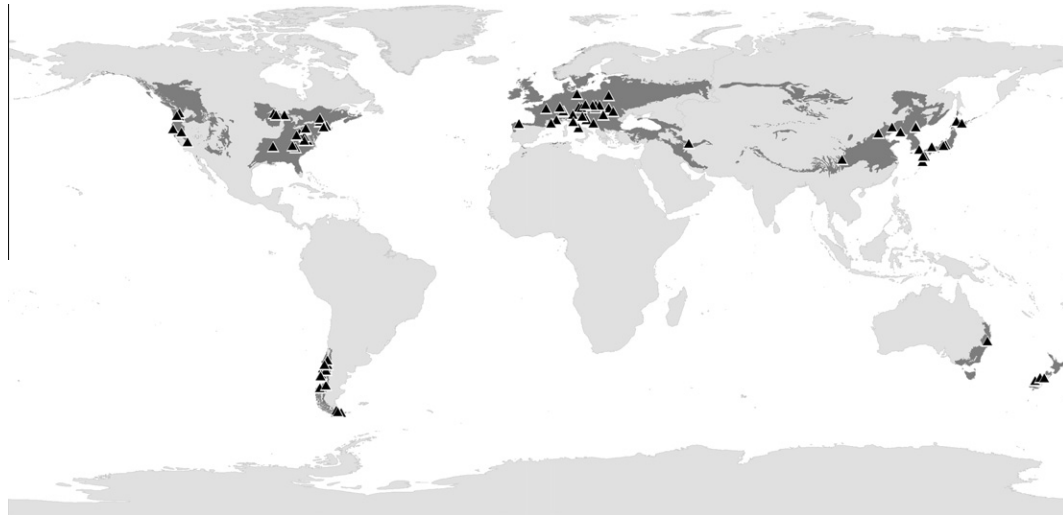


Fig. 1. World distribution of temperate forests (dark grey) within the temperate latitudinal zone according to Olson et al. (2001), and location of stands (triangles) included in the review for which detailed geographic information was available.

Inevitably structural attributes were derived from field measurements that followed different sampling designs. Only in a minority of papers, plots were randomly or systematically located. Most of the studies, instead, located plots on the basis of either subjective or qualitative assessment (closeness to the core area, no sign of alteration, etc.), also in relation to the small extent of old-growth remnants. Plot sizes and layouts varied greatly; indeed two different approaches were generally used: (i) one or few big plots (~1 ha), or (ii) several relatively small plots (100–400 m²). However the sampling of old-growth spatial heterogeneity was generally ensured by a trade-off between plot size and number.

We also found some discrepancies among structural data collection and reporting protocols in different studies, such as minimum live tree and CWD size thresholds, and LAB estimation methods. Before the analysis, we tested for significance the difference in live tree DBH thresholds between age classes (Kruskall–Wallis: $H = 1.655$, $p = 0.198$), since a systematic difference could have biased our results. Live trees and CWD thresholds were reported in Appendix B, Table B1. The lack of LAB data reported for Europe is noteworthy and is linked to the tradition of focusing on wood volumes more than aboveground biomass. Volume data was available only for 27 European records (Appendix A, Table A1, Fig. A1). For a thorough description of the variables considered in this paper and on the way the other discrepancies were taken into account see Appendix B.

Beside these structural indicators, we recorded also data to be used as site descriptors, such as stand age and environmental variables, namely geographic location (latitude and longitude), altitude, and climate (mean annual temperature and annual precipitation). In particular, stand age in multi-aged forests was assessed in several different ways in the papers included in our review. We reported as age the value given in the original papers. Most authors used the mean age of the overstorey trees. In some studies these estimates were derived from partial observations, such as the mean age of the dominant species (Sano, 1997), or the age of the illegally cut stumps at the periphery of the area (Keeton et al., 2010) or of fallen individuals (Parker et al., 1985). In other cases (Battles et al., 2002; Pollmann, 2003) we derived age from the most common class of the age histogram. Finally, in 10 stands (Lusk and Smith, 1998; Aiba et al., 2001; Beaudet et al., 2007; Heiri et al., 2009; Král et al., 2010; Sato, 2010) we reported the time since last disturbance given by the authors; however we did not use these data as age in the analysis because they were re-

ported only in a small percentage of papers and had a range substantially different from the other age values.

2.3. Statistical analysis

Age and structural variables were compared between mature and old-growth stands, globally and across different continents and broad forest types. For each contrast Monte-Carlo simulations were used to test whether the median of each variable was significantly different between age classes: we randomly reassigned each record 4999 times to an age class (mature or old-growth), while maintaining the sample size of each group. The actual difference between medians was considered significant when it was not within the range encompassing the 2.5–97.5 percentiles of the distribution of the permuted differences. When the sample size was not large enough to allow at least 4999 different combinations, we compared the actual difference to the complete distribution of the permuted differences, based on each possible combination of reassignments.

To explore sources of variability within the dataset, non-parametric correlation coefficients (Spearman's ρ) were calculated for structural variables in relation to site descriptors (latitude, altitude, mean annual temperature and precipitation, stand age), the significance level was set at $\alpha = 0.05$. All the statistical calculations were performed using R 2.12.0 (R Development Core Team, 2010).

3. Results

3.1. Data distribution across continents, forest types and age classes

North America had the largest number of records (37%), reporting data predominantly from the Midwest (13%), and U.S. Northeast (12%), although a great body of research on late-successional forest dynamics (e.g. disturbance regimes, development processes, etc.) came from the Pacific Northwest region. Europe and South America were well represented (26% and 20% of records respectively). Asia and Australia accounted only for 14% and 3% of the records respectively (Fig. 2), also in relation to the lower representation of temperate biome in these continents. The literature spanned a wealth of forest types. The majority of the papers investigated deciduous broadleaf (33%), mixed conifer/deciduous broadleaf

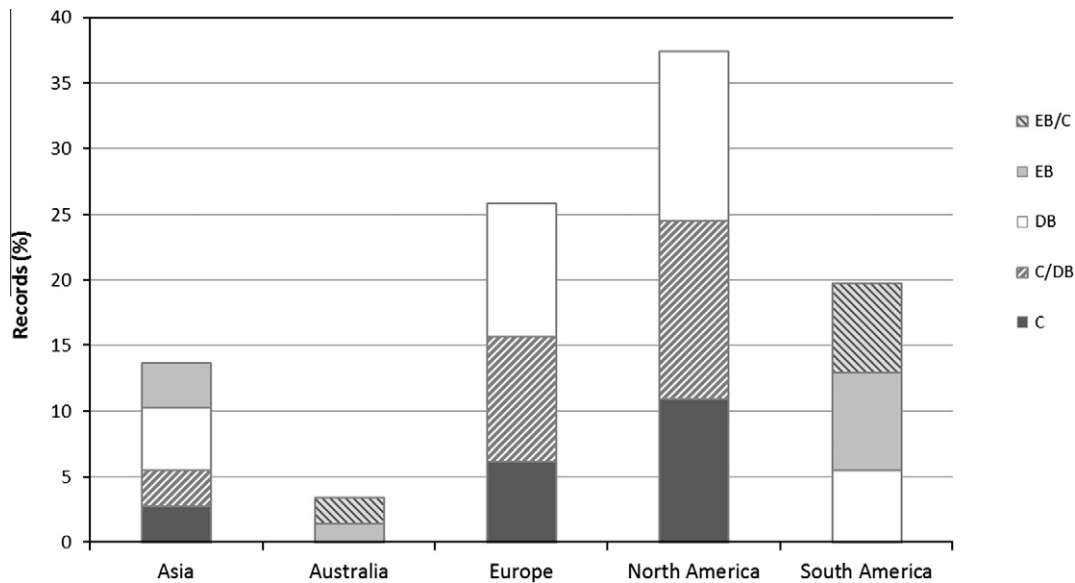


Fig. 2. Distribution of forest types across continents. C – conifer; DB – deciduous broadleaf; EB – evergreen broadleaf; C/DB – mixed conifer/deciduous broadleaf; EB/C – mixed evergreen broadleaf/conifer.

(26%), and conifer forests (20%). Less numerous were papers describing evergreen broadleaf forests (12%) and mixed evergreen broadleaf/conifer forests (9%).

Papers on late-successional stands by forest type were unevenly distributed among continents. In Europe and North America three forest types were represented (C, C/DB, DB) with very similar proportion of mixed conifer/deciduous broadleaf and deciduous broadleaf forests, which accounted respectively for 36% and 34% of the records in North America, and 37% and 39% in Europe (Fig. 2). The most common systems in our dataset were northern hardwood (*Acer saccharum*, *Fagus grandifolia*, *Tsuga canadensis*, *Betula* sp.) in North-America, and European beech-Norway spruce-silver fir (*Fagus sylvatica*, *Picea abies* and *Abies alba*) in Europe (Table 1).

At the global level median age values differed significantly between age classes (250 years for old-growth and 125 for mature stands, $p < 0.001$). When single contrasts were considered all continents displayed significant differences but Australia, for which no sufficient data were available; all forest types but deciduous broadleaf and mixed evergreen broadleaf/conifer forests significantly differed in age values (Fig. 3). The analysis of age ranges (51–252 years for mature stands and 100–1000 for old-growth) further confirms the great variability in stand development rates across forest types and geographic regions.

3.2. Comparison between mature and old-growth forests

The comparison between mature and old-growth stands identified common patterns for most of the structural attributes, but also a certain degree of variability related to management history, dominant species traits, and site characteristics. In the global dataset, old-growth forests showed higher basal area values than mature forests although the difference was not significant neither at the global level ($p = 0.207$), nor for single forest types. The only significant differences we found were for North and South America ($p = 0.028$ and 0.007 respectively). An opposite non-significant result was observed in Europe and Australia (Fig. 4; Table 2) and in deciduous broadleaf forests globally (Fig. 5; Table 3).

Stem density values recorded globally were slightly lower for old-growth forests when compared to mature stands (Table 2). This result was consistent across all continents and forest types. The data for LLT showed distinct differences between age classes,

with significantly higher densities reported for old-growth (median $72.6 \text{ trees ha}^{-1}$) compared to mature stands ($16.3 \text{ trees ha}^{-1}$; $p < 0.001$). However, we only had data to contrast LLT for Europe and North America, and for the forest types surveyed in these continents. For North America the difference between the two age classes was significant ($p = 0.031$), with mature forests having far lower LLT densities ($10\text{--}20 \text{ trees ha}^{-1}$) than old-growth ($2.5\text{--}199 \text{ trees ha}^{-1}$, Table 2). For Europe, the density of LLT ranged from 36.5 to $122 \text{ trees ha}^{-1}$ in the old-growth stands and from 4.2 to 83 trees ha^{-1} in mature stands ($p = 0.031$).

LAB data were available only for few studies ($n = 33$) and this allowed us to contrast age classes only for a subset of regions, limiting our ability to discern age related trends. At the global level we observed significantly higher LAB in old-growth than in mature stands (medians equal 379.1 and 235.2 Mg ha^{-1} respectively, $p = 0.011$, Table 2). The only individual contrast giving a significant result was North America, ($p = 0.008$). This result may have been influenced by the lack of data for mature stands dominated by *Sequoia sempervirens* and *Pseudotsuga menziesii*, that are species characterized by very high LAB values, although also excluding these stands the result did not change (not shown).

Our data demonstrated slightly higher QMD values in old-growth forests when compared to mature stands in all continents and forest types but this difference was significant only at the global level ($p = 0.026$).

CWD volumes exhibited consistent age class contrasts for all the continents and forest types. The median value calculated on the global dataset was significantly different, with $67.8 \text{ m}^3 \text{ ha}^{-1}$ for mature and $151.4 \text{ m}^3 \text{ ha}^{-1}$ for old-growth stands ($p = 0.002$). While the difference between median values was high, CWD was highly variable and the range overlapped considerably among age classes (Table 2). The only contrasts giving significant results were Europe, ($p = 0.002$), and conifer forests ($p = 0.036$). No contrasts were possible for Asia and Australia, and for evergreen broadleaf stands due to scant availability of data on CWD.

3.3. Correlation between structural attributes and site characteristics

Many site descriptors showed significant correlations with structural variables at global scale (Table 4). With regards to

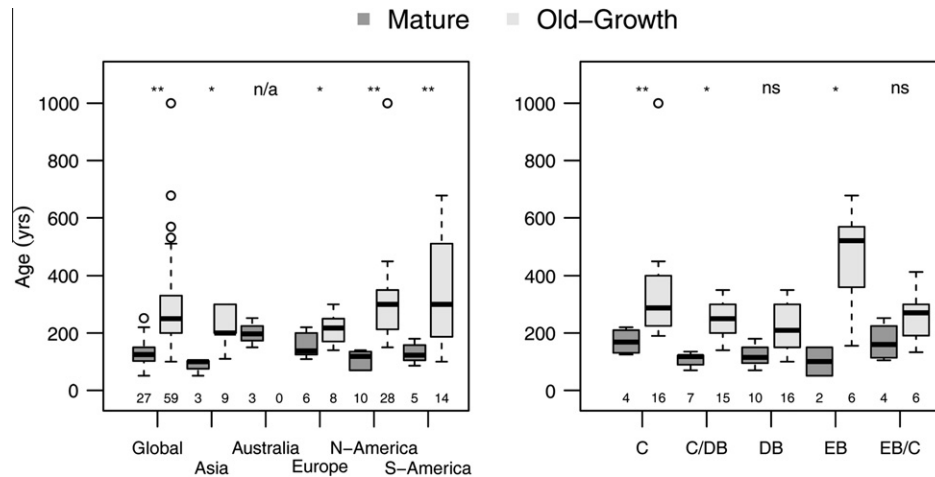


Fig. 3. Boxplots of the age data distribution for the global dataset and for each continent and forest type. The median, first and third quartiles, and whiskers (corresponding to 1.5 times the inter-quartile distance) are reported. Empty circles represent outliers. Sample size is reported at the bottom of each box. Monte-Carlo two-sided significance levels are at the top (n/a: no test was possible; ns: not significant; * $0.05 < p < 0.01$; ** $p < 0.01$).

climatic and geographic variables, basal area and stem density were positively correlated with mean annual precipitation and negatively correlated with latitude. CWD displayed a negative association with mean annual temperature, and LLT was positively correlated with precipitation. Among the site descriptors, forest age was positively and significantly correlated with the highest number of structural indicators, including basal area, LLT, LAB and QMD.

4. Discussion

With some exceptions, old-growth forests show many structural similarities at the global scale.

Contrasts against mature stands hold true across different continents and forest types despite the variability in age ranges used to differentiate between mature and old-growth stands in different regions. Indeed old-growth are characterized globally by significantly higher LLT densities, higher QMD, and greater LAB and CWD volume. We also observed somewhat higher basal areas and lower stem densities in comparison to mature stands, although these differences were not statistically significant due to substantial variability among forest types.

4.1. Global commonalities

Our review showed old-growth forests to host significantly higher amounts of biomass than mature forests, stored both in LAB and in CWD pools. Furthermore, the global data showed a significant positive correlation between LAB and stand age. This is consistent with recent models describing carbon dynamics in boreal and temperate forests, supporting the hypothesis of a potential for continued carbon accumulation late into stand development (Keeton et al., 2011), both in broadleaf and conifer stands (Luyssaert et al., 2008), often mediated by variation in climate, ecoregion and forest type (Keith et al., 2009; Hudiburg et al., 2009; Stegen et al., 2011). The analysis of trends in aboveground biomass in late-successional systems is of primary importance because it correlates also with carbon allocation to belowground biomass (Cheng et al., 2007) and to total ecosystem carbon (Houghton, 2005; Hoover et al., 2012) that is often difficult to quantify. LAB is the quickest pool to recover after disturbance, and likely a full accounting of all pools, especially C stored in soil, would reveal stronger

differences between old-growth and mature forests than comparing LAB alone (Zhou et al., 2006; Rhemtulla et al., 2009).

Higher LAB and associated carbon storage values in old-growth forests relate to structural attributes typical of this developmental stage. Living biomass reaches very high levels because of: (i) the vertically continuous and multispecies canopy typically associated with old-growth forests (Keith et al., 2009; Wirth et al., 2009), allowing for efficient allocation of growing space within three-dimensions and across trees of different age, size and shade tolerances; and (ii) the possibility of LLT to maintain net positive growth and accumulate biomass for centuries (Xu et al., 2012). Indeed the literature reports significantly a general trend of higher LLT densities in old-growth when compared to mature forests, and despite variability attributed to species composition, region, disturbance history and site productivity, our results suggest a significant correlation between stand age and LLT at global scale.

Our results at the global scale were consistent with previous studies showing LLT to be a strong predictor of late-successional structure at regional scales (e.g. Whitman and Hagan, 2007). A minimum LLT density of 30 trees with DBH > 70 cm per hectare was reported for European old-growth forests (Nilsson et al., 2002). Such a threshold seems too high and not characteristic of old-growth systems at global level; it would exclude several old-growth stands in our dataset. Indeed about 90% of the old-growth stands in our dataset contained more than 30 LLT per ha, therefore, we believe a more inclusive minimum density of 30 trees with DBH > 50 cm per hectare may be useful both at global and at European level. LLT density is directly related to CWD recruitment, particularly for the largest size classes, and contributes to the pool of long-lasting deadwood, as deadwood residence time is strongly influenced, together with wood density and decay resistance, by tree size at the time of death (Mackensen et al., 2003; Cornwell et al., 2009).

Our review showed significantly higher CWD quantities in old-growth than in mature forests and confirmed the importance of CWD as an indicator of old-growth condition (Peterken, 1996; Bobiec, 2002), at least for those continents for which we had sufficient data. Despite the significant differences between medians at the global level, ranges in CWD widely overlapped across most continents and forest types, probably due to a strong variability among and within systems that may be related to two main factors. First, our results clearly showed a climatic influence, with the warmest regions characterized by the lowest volumes of deadwood. Accordingly, the lowest values for the old-growth stands were recorded in

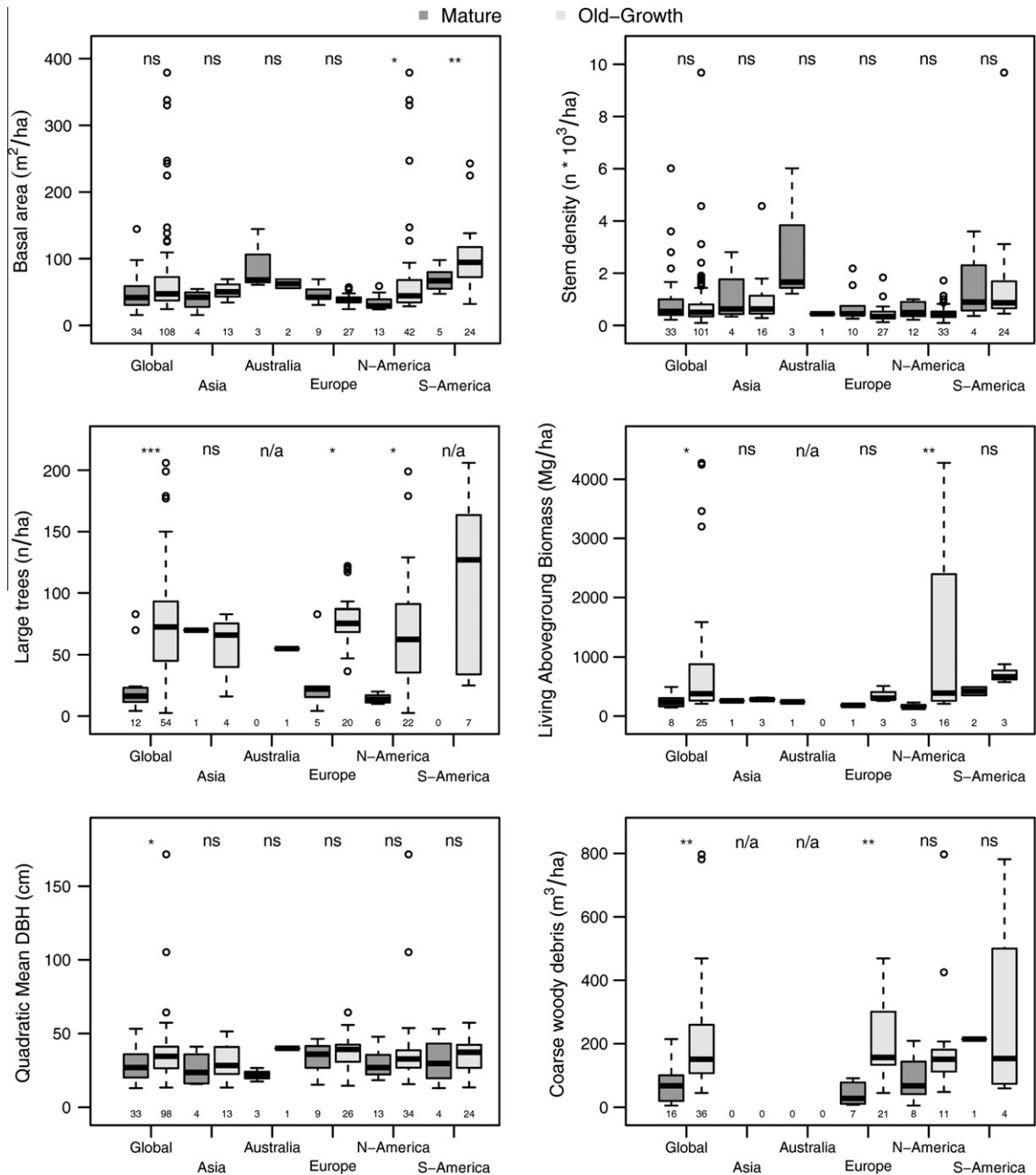


Fig. 4. Boxplots of the data distribution for the global dataset and for each continent. The median, first and third quartiles, and whiskers (corresponding to 1.5 times the interquartile distance) are reported. Empty circles represent outliers. Sample size is reported at the bottom of each box. Monte-Carlo two-sided significance levels are at the top (n/a: no test was possible; ns: not significant; * $0.05 < p < 0.01$; ** $p < 0.01$, *** $p < 0.001$).

a mixed oak forest in southern Ohio ($48.3 \text{ m}^3 \text{ ha}^{-1}$, Goebel and Hix, 1996); in Italy ($45 \text{ m}^3 \text{ ha}^{-1}$, Burrascano et al., 2008; and $65.2 \text{ m}^3 \text{ ha}^{-1}$, Travaglini et al., 2012); and in the northern-most Chilean old-growth stands ($59.6 \text{ m}^3 \text{ ha}^{-1}$, Schlegel and Donoso, 2008). The correlation we observed between CWD and temperature gradient at the global level are consistent with the results of a global analysis that highlighted mean annual temperature as a main driver of CWD decay rates (Mackensen et al., 2003). Second, the high degree of variability in CWD is also related to differences in plant traits. Especially wood decomposition rates are species-specific (Zell et al., 2009), and are far slower in gymnosperms than angiosperms due to a higher C:N ratio, higher lignin and resin content,

and fine-scale anatomical traits that slow the spread of fungi (Cornwell et al., 2009).

Understanding the sources of variability in CWD volume has important consequences for quantifying the carbon stored in deadwood, given that CWD is estimated to contain 3.3 billion tons of carbon in temperate forests globally corresponding to about 7% of total living carbon (Pan et al., 2011). Focusing on CWD/live wood ratios allows us to eliminate productivity related differences between forest types (Wirth et al., 2009). CWD/live wood volume ratios in the literature ranges from 13% to 37% in European beech forest reserves (Christensen et al., 2005), and between 6% and 23% in old-growth broadleaved forests of North America (Peterken,

Table 2
Median and range of age and structural variables, calculated for the whole dataset and for each continent. When only one value was available the median alone was reported. Bold values represent significantly different contrasts ($p < 0.05$).

	Global		Asia		Australia		Europe		North America		South America	
	M	OG	M	OG	M	OG	M	OG	M	OG	M	OG
<i>Age (yrs)</i>												
Min.	51	100	51	110	150	–	109	140	70	150	105	100
Median	125	250	100	200	197	–	137.5	217.5	118.5	300	123	300
Max.	252	1000	105	300	252	–	220	300	140	1000	180	678
<i>BA (m² ha⁻¹)</i>												
Min.	15.6	24.4	15.6	34.3	61	55.9	30.7	24.4	24	28.7	47.4	32.2
Median	41.7	47.3	42.2	50.2	68.2	62.6	42.2	38.5	29.1	44.4	67	94.6
Max.	144.5	379	54.7	69.4	144.5	69.2	69.2	57.4	59	379	97.9	242.8
<i>Stem density (n ha⁻¹)</i>												
Min.	217.5	96.7	336	281.3	1216	–	259	124	217.5	96.7	360	451
Median	536	501	632.5	630	1660	444.7	444	341	488.5	392	893	865.5
Max.	6015	9680	2805	4570	6015	–	2182	1835	1000	1720	3600	9680
<i>LLT (n ha⁻¹)</i>												
Min.	4.2	2.5	–	70	–	–	4.2	36.5	10	2.5	–	25
Median	16.3	72.6	70	66	–	55	22	75.5	13.5	62.5	–	127
Max.	83	206	–	83	–	–	83	122	20	199	–	206
<i>LAB (n ha⁻¹)</i>												
Min.	144	208	–	254.3	–	–	–	255.5	144	208	349.8	576
Median	235.2	379.1	258	279	240.4	–	181.2	303	148	388.6	421.2	664.5
Max.	492.5	4277	–	315.7	–	–	–	510	230	4277	492.5	877.3
<i>QMD (cm)</i>												
Min.	13	13.4	15.8	13.4	17.5	–	15.3	14.6	18.4	15.7	13	13.5
Median	27	34.6	23.7	28.4	21.6	40	36.1	39.3	27	32.8	29.8	37.4
Max.	53.2	171.6	41.1	51.4	26.7	–	46.4	64.3	47.8	171.6	53.2	57.3
<i>CWD (m³ ha⁻¹)</i>												
Min.	5.3	45	–	–	–	–	8	45	5.3	48.3	–	59.6
Median	67.8	151.4	–	–	–	–	28	157.3	67.8	151.3	214.5	153.6
Max.	214.5	797	–	–	–	–	91.4	469	209	797	–	781.5

1996). The ratios based on our data on CWD and live wood volume in Europe ranged from 6% to 89% in old-growth and from 2% to 9% in mature forests (see Table A1). Indeed, Europe was the only contrast returning significant differences between CWD volumes in mature and old-growth stands. Very low CWD values in European mature forests may be due to the long history of forest exploitation that probably limited the ability of European studies to find or assess unmanaged mature reference stands (Commarmot et al., 2005; Merino et al., 2007; Burrascano et al., 2008; Motta et al., 2010). It may relate also to higher amounts of deadwood collected for fuel by local populations in mature forests, which are usually more accessible than old-growth remnants located in reserves or in remote areas and high altitudes.

In conclusion, these results showed ratios for late successional forests to be much higher than the global average of temperate forests, suggesting that the CWD carbon pool is currently understocked in secondary and managed temperate forests, especially in Europe. The CWD pool, though transient, can represent an important net C sink as long as input rates (mortality) equal or exceed outputs (decomposition), and thus should be carefully accounted for in terrestrial carbon models (Stephenson et al., 2011). Management practices aimed at maintaining, or recreating, old-growth forest attributes (Keeton, 2006; Bauhus et al., 2009; Rhemtulla et al., 2009) may increase the amount of carbon stocked in temperate forests, both in live biomass and CWD (Keeton, 2006; Bauhus et al., 2009; Rhemtulla et al., 2009). This is especially relevant given the growing interest in extending mechanisms like REDD (Reduced Emissions from Deforestation and Degradation) to temperate regions, to maintain terrestrial carbon sinks.

Furthermore high CWD volumes and LLT densities in old-growth forests, which were evident in our data, also influence the provision of habitat for late-successional biodiversity. CWD is a key ecosystem feature supporting high levels of biodiversity,

for instance by providing diverse microhabitats for numerous specialized and saproxylic organisms (Grove, 2002; Odor et al., 2006; Mckenny et al., 2006). The long-term availability of deadwood may be related to the persistence of many saproxylic organisms (Lassauce et al., 2011) with low dispersal capabilities that may be driven to local or regional extinction in the absence of a temporal continuity in the deadwood substrate, due to intensive management (Siitonen, 2001). For this reason, besides being a robust indicator of old-growth condition (Whitman and Hagan, 2007), CWD has become one of the primary indicators of sustainable forest management in Europe (MCPFE, 2003; Lassauce et al., 2011) and a structural indicator in the context of Biodiversity Evaluation Tools (Larsson, 2001) and international certification systems (Foster et al., 2008).

Also LLT, besides storing a large amount of carbon, provide habitat functions for a number of threatened or ecologically important temperate forest species, ranging from fungi to lichens, saproxylic beetles, birds and bats (Mikusinski and Angelstam, 1998; Ruffell et al., 2007; Persiani et al., 2010; Hatanaka et al., 2011). These functions relate to the great variety of microhabitats large trees offer, including rough bark, trunk hollows, exposed deadwood, sapflows, dead branches, and dead tops (Nilsson et al., 2002; Winter and Moller, 2008).

4.2. Sources of variability

Although our review found distinct commonality in old-growth structure, several attributes showed a high degree of variation precluding overly simplistic generalizations at the global scale. Indeed basal area and stem density did not show statistically significant differences between age classes in our dataset, but instead were more strongly related to geographic location, species composition, and climatic influences. QMD on the other hand, showed a signifi-

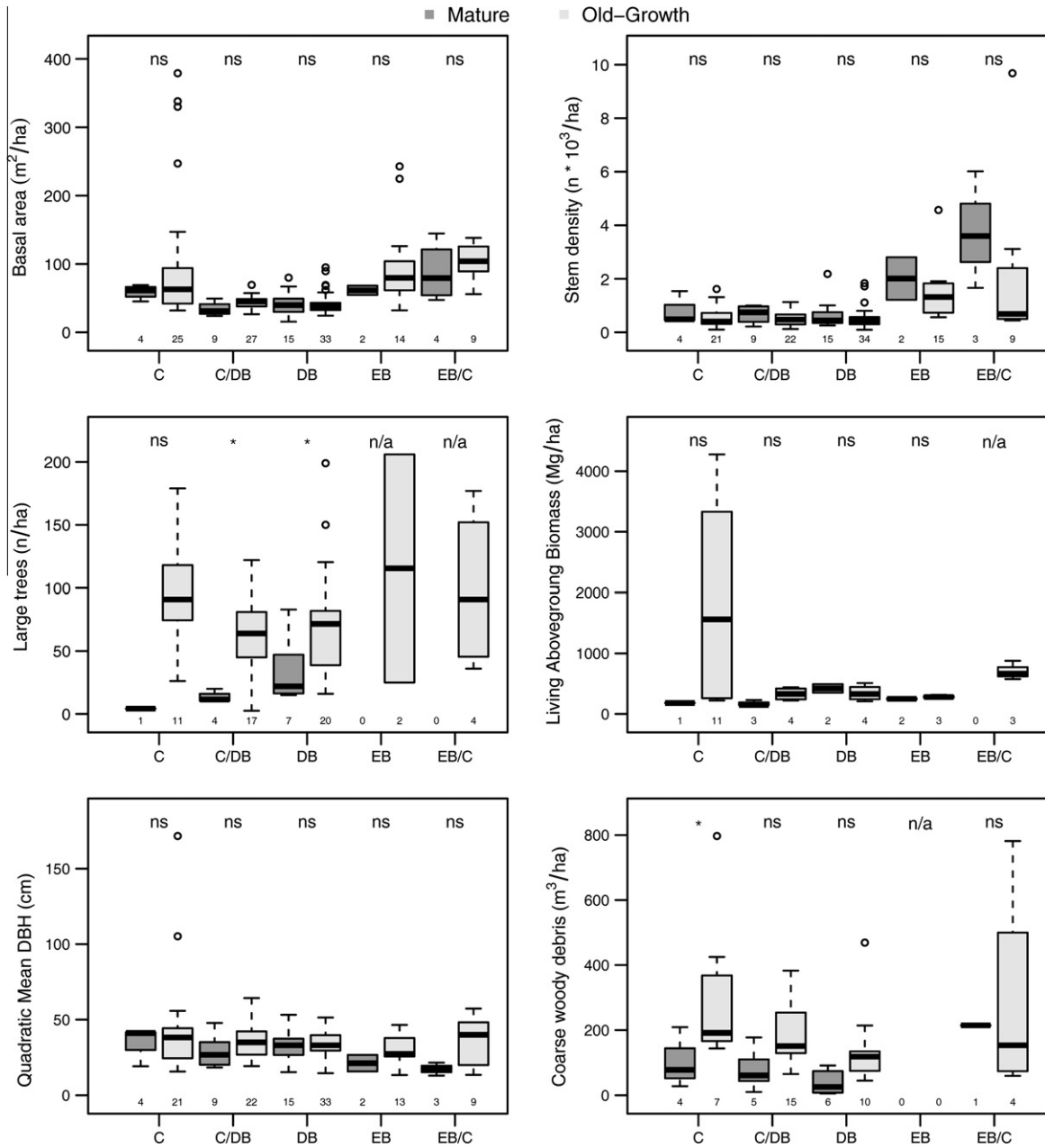


Fig. 5. Boxplots of data distribution for forest types (C – conifer, DB – deciduous broadleaf, EB – evergreen broadleaf, C/DB – mixed conifer/deciduous broadleaf, EB/C – mixed evergreen broadleaf/conifer). The median, first and third quartiles, and whiskers (corresponding to 1.5 times the inter-quartile distance) are reported. Empty circles represent outliers. Sample size is reported at the bottom of each box. Monte-Carlo two-sided significance levels are at the top (n/a: no test was possible; ns: not significant; *0.05 < p < 0.01; **p < 0.01, ***p < 0.001).

cant difference between age classes only at the global level with slight, non-significant differences in the other contrasts.

Variation like this raises interesting questions regarding differences among forest systems, for instance related to environmental controls, disturbance regimes, and management history. Previous researchers have found old-growth to generally have higher basal areas compared to mature forests (Keddy and Drummond, 1996; Gutierrez et al., 2009). Nevertheless, despite the significant positive correlation between basal area and age, our contrasts highlighted a large amount of variation between forest types and continents: old-growth showed significantly higher values in North and South America and non-significantly lower basal area in Australia and Europe when compared to mature stands. For

Australia, very few basal area data were available and the high value reported for mature stands may derive from a single mature site with a relatively high age (252 years) (Smale et al., 1997). In Europe old-growth showed lower basal area values than mature stands, either depending on the confusion in terminology for late-successional stands, especially pervasive in the European literature, or because the old-growth remnants spared from exploitation are mostly located in remote, unproductive areas at relatively high altitude, where a lower basal area is naturally expected to occur (Nagel et al., 2006; Burrascano et al., 2008; Svoboda and Pouska, 2008; Holeksa et al., 2009). In some cases, anthropogenic influence may explain the high basal area values observed in European mature stands. Indeed timber production

Table 3
Median and range of age and structural variables calculated for each forest type. When only one value was available the median alone was reported. Bold values represent significantly different contrasts ($p < 0.05$).

	Conifer		Mixed conifer/ deciduous broadleaf		Deciduous broadleaf		Evergreen broadleaf		Mixed conifer/ evergreen broadleaf	
	M	OG	M	OG	M	OG	M	OG	M	OG
<i>Age (yrs)</i>										
Min.	125	190	70	140	70	100	51	155.5	105	133
Median	168.5	287.5	118	250	115	209.5	100.5	520.5	160	270.5
Max.	220	1000	135	350	180	350	150	678	252	413
<i>BA (m² ha⁻¹)</i>										
Min.	45.3	32	24	26.5	15.6	24.4	54.7	32.2	47.4	55.9
Median	61.2	63	31	44.8	39.9	37.3	61.5	79.7	79.45	104
Max.	69.2	379	49.4	69.4	80	95	68.2	242.8	144.5	138.2
<i>Stem density (n ha⁻¹)</i>										
Min.	452	103	217.5	124	259	96.7	1216	564	1660	444.7
Median	489.5	404	748	477.5	446	438.2	2010	1321	3600	687.5
Max.	1541	1618	1000	1130	2182	1835	2805	4570	6015	9680
<i>LLT (n ha⁻¹)</i>										
Min.	–	26.2	10	2.5	15	16	–	25	–	36
Median	4.2	91	11.5	64	22	71.6	–	115.5	–	91
Max.	–	179	20	122	83	199	–	206	–	177
<i>LAB (n ha⁻¹)</i>										
Min.	–	222	144	221	349.8	208	240.4	254.3	–	576
Median	181.2	1562	148	330	421.2	328.6	249.2	279	–	664.5
Max.	–	4277	230	440	492.5	510	258	315.7	–	877.3
<i>QMD (cm)</i>										
Min.	19.2	15.7	18.4	19.3	15.3	14.6	15.8	13.4	13	13.5
Median	41.2	38.3	26.8	35.1	33.1	33.1	21.3	27.4	17.5	40
Max.	41.6	171.6	47.8	64.3	53.2	51.4	26.7	46.5	21.6	57.3
<i>CWD (m³ ha⁻¹)</i>										
Min.	28	144	10	65.2	5.3	45	–	–	–	59.6
Median	78.4	191.5	61.1	151.4	25.6	119	–	–	214.5	153.6
Max.	209	797	177.8	383	91.4	469	–	–	–	781.5

Table 4
Spearman correlation coefficients (ρ), significance and sample size (n) for each pair of structural/explanatory variables. Bold values represent significant correlations ($p < 0.05$).

	Latitude		Altitude		Temperature		Precipitation		Age	
	ρ	n	ρ	n	ρ	n	ρ	n	ρ	n
Basal area	-0.25**	120	-0.04	121	0.08	81	0.52***	105	0.39***	83
Stem density	-0.25**	120	-0.08	120	0.19	82	0.33***	105	-0.07	75
Large trees	-0.26	52	0.14	53	-0.17	38	0.29*	46	0.60***	40
LAB	-0.27	23	-0.20	22	-0.07	11	0.43	15	0.74***	18
QMD	0.10	117	0.12	118	-0.18	79	0.04	102	0.33**	75
CWD	0.25	38	-0.05	41	-0.39*	30	0.18	38	0.25	31

* $0.01 < p < 0.05$.

** $0.001 < p < 0.01$.

*** $p < 0.001$.

management both controls species composition towards more productive species and efficiently allocates growing space, and results in optimized tree production and high stand basal area.

The global variability among continents and forest types in the relationship between basal area and age class, may also relate to differences in the density of shade-tolerant species and productivity-related climatic controls. Indeed in a comprehensive study of old-growth forests on Chiloe island (Chile) the density of shade-tolerant stems was positively correlated with basal area, vertical heterogeneity and age, with high variability in relation to changes in temperature and in distance to coastline (Gutierrez et al., 2009). At the global scale our results showed precipitation to have a significant positive relation with basal area. We recommend further research on the relationships among these variables to assess the consistency of high basal area as a characteristic of old-growth conditions.

The relative abundance of shade-tolerant and intolerant species, together with differences in gap dynamics and pattern, and the

rapidity of the self-thinning process, may also influence variation in stem densities observed among late-successional systems globally. Although stem density was generally lower in old-growth than in mature forests across most forest types, this difference was not statistically significant, nor did we find any significant correlation between stem density and age. This is consistent with the forest development model proposed by Franklin et al. (2002), wherein tree mortality in late-successional forests becomes increasingly influenced by density-independent factors (Das et al., 2011), such as natural disturbances, which can be highly variable across regions and forest types (Franklin et al., 1987; Allen et al., 2010). The death of overstory dominants allows more light to reach the forest floor, encouraging re-establishment of the understory community, depending on previous stand density dynamics. Other causes of variability in stem density from the mature to the old-growth condition may be environmental conditions (e.g. precipitation) together with factors affecting seed germination and establishment, such as availability of seed

sources, presence of suitable seed beds, and competition with herbaceous shrubs (Franklin et al., 1987; Donato et al., 2012).

In the comparative studies included in our review, stem density was generally lower in old-growth stands. Nevertheless, an increase in stem density with age was found in two comparative studies performed in U.S. Northeast forests dominated by *T. canadensis* and *Betula alleghaniensis* (Fisk et al., 2002; Keeton et al., 2007). These exceptions may be attributed to dense regeneration of intermediate to shade tolerant species within canopy gaps, at gap edges, or in the suppressed layers.

Variability in stem density was also related to latitudinal and precipitation gradients. Indeed, the stands with the highest stem density, with values up to four times greater than the other forest types, were evergreen broadleaf and mixed conifer/evergreen broadleaf stands that were located at lowest latitudes and displayed the highest precipitation values. Accordingly, at lower latitudes the more vertical sun angles may allow the evolution of vertically complex canopies with emerging large trees, and shade-tolerant trees in both the upper and lower canopy layers and thus very high stem densities (Armesto and Figueroa, 1987; Stephenson et al., 2011).

The slightly higher QMD values reported for old-growth when compared to mature stands were consistent with the results reported for basal area and stem density. At the global level the general higher basal areas and lower stem densities in the old-growth stands when compared to mature ones result in a significant higher QMD, that is by nature correlated with the variables from which it is derived. However QMD helps elucidate how basal area is distributed across sizes classes, in this case indicating an allocation weighted more heavily towards larger trees in old-growth.

4.3. Comparison against structural variability in fire-prone late-successional forests

Our review was restricted to moist temperate forest ecosystems and therefore excluded forest types classified as temperate, but characterized by lower growing season precipitation, warmer temperatures and, most significantly, high to moderate frequency ground-fire regimes. These systems share some structural characteristics common in moist temperate old-growth, such as abundant large living and dead trees (Covington et al., 1997; Mitchell et al., 2009). However, low to moderate severity fire disturbances result in fundamentally different vertical development, spatial patterning, and CWD accumulation processes (North et al., 2004; Larson and Churchill, 2012).

For example, fire maintained old-growth Ponderosa pine forests (*Pinus ponderosa*) historically had low vertical complexity and open canopies, and widely spaced over-stories (Cooper, 1960). Moderate severity mixed-conifer forests, for example in the Sierra Nevada mountains of California have complex spatial structure (i.e. patchiness) driven by variable burn intensity and associated understory mortality effects (North et al., 2007). This produces a mosaic of both multi- and single-layered patch structures (Kane et al., 2013). As another example, variable vertical structure and multi-aged demographics in *Eucalyptus regnans* forests of southeastern Australia have been attributed to fire effects (Lindenmayer et al., 2000). Clearly an expansion of scope to include all temperate forests, particularly drier systems prone to fire, would substantially increase the range of variability in old-growth structure and development described in this review.

4.4. Incomplete data and research needs

Through our literature review we identified gaps in knowledge both in terms of seldom reported relevant structural attributes and of poorly investigated regions. Indeed papers focused on old-

growth forests often do not report a comprehensive set of structural attributes, including those deemed particularly useful for understanding old-growth forest dynamics and structure. These include, for example, volume of deadwood components, such as logs and snags, vertical and horizontal heterogeneity indices, gap metrics, and tree species diversity indices (Nilsson et al., 2002; Keith et al., 2009; Wirth et al., 2009).

Data on these old-growth indicators are often available in studies focused on a single specific attribute (e.g. deadwood, vertical structure, gaps, etc.), that often do not provide a holistic sense of structure or dynamics (Woldendorp et al., 2004; Zenner, 2004; Schliemann and Bockheim, 2011). We recommend that future studies of old-growth forests provide as wide set of meaningful structural attributes as is possible in order to contribute to a thorough description of these ecosystems.

Through our review we also identified a considerable unevenness of research studies among geographic regions. Old-growth ecosystems in some regions, in particular, seem to be poorly investigated. For instance, though Russian temperate forests are widespread (Silander, 2001), to the best of our knowledge data on old-growth forests are almost completely lacking in English language peer-reviewed journals. Furthermore, in our search we found no or scarce data concerning old-growth temperate forests in Western Asia (Anatolian, Colchic and Hyrcanic region) and for Central Asia in general (e.g. Altai-Sayan and Himalayan regions). We have no data on the occurrence of old-growth remnants in these regions, however, even if few old-growth forests remain, it is important to identify and study forests that are in the most advanced developmental condition, regardless of the successional status of species, and to use them as long-term monitoring areas. We also observed a scarcity of studies comparing age classes in Asia, Australia, and South America that provide a comprehensive characterization of old-growth forest ecosystems. For example, temperate forests in Australia have been extensively investigated (see, for example, Keith et al., 2009, and references therein), yet published structural data were difficult to find. Several studies are rather focused on more specific issues, such as spatial structure, explored extensively in Asia for example (Chen and Bradshaw, 1999; Manabe et al., 2000; Hou et al., 2004; Salas et al., 2006; Hao et al., 2007); regeneration, studied especially in South America (Pollmann and Veblen, 2004; Donoso and Nyland, 2005); deadwood (Schlegel and Donoso, 2008); and forest response to topographical factors (Bale et al., 1998; Barrera et al., 2000).

Based on these gaps in knowledge, future research on old-growth systems needs, above all, to integrate analyses of different ecosystem components and processes. For example, interdisciplinary investigations could better relate old-growth forest structural and compositional dynamics to their carbon storage capacity and biodiversity (e.g. Hatanaka et al., 2011). While a comprehensive body of knowledge is available for some systems, such as *P. menziesii* forests of Pacific Northwest (Franklin et al., 2002; Field and Kaduk, 2004) and northern hardwood forest in U.S. Northeast (Keeton et al., 2007; D'Amato et al., 2008, 2009), it is noticeably incomplete for others.

5. Conclusions

Based on the existing data, our review identified a number of stand structure attributes strongly associated with temperate old-growth forest globally. The published data support a contention that some stand development processes, such as LLT, LAB, and CWD accumulation, have the potential to continue very late into stand development.

Given the commonality in structure among late-successional temperate systems, a consistent set of indicators can be used to describe, map, and understand old-growth globally. However, this set

must recognize that structural indicators can be highly dynamic, reflecting varied disturbance processes and successional pathways, as well as climatic and edaphic differences among sites and regions. Consequently, a context-specific analysis, for instance employing a comparative approach involving multiple age classes, is necessary to accommodate the high levels of variability we observed globally.

5.1. Management implications

Our review suggests that temperate old-growth forests globally share characteristics associated with a range of important ecosystem services. As a consequence, conservation of the world's remaining old-growth forests and, where appropriate, management to restore old-growth to landscapes where they are poorly represented, are required to maintain provisioning of these unique services. Management for 'old-growthedness' (Bauhus et al., 2009) can be incorporated into a variety of forest management scenarios, both commercial and restorative (Keeton, 2006; Gronewold et al., 2010). However, to operationalize this objective, forest managers will need quantitative, regional targets for many of the structural attributes identified in this review. Our review highlighted a minimum LLT density threshold of at least 30 trees with DBH > 50 cm per hectare. This threshold should be employed as a minimum target for promotion by disturbance-based or 'close-to-nature' silviculture in managed forests. It would not be appropriate as a fixed level to be maintained in stands already displaying old-growth structural attributes, and therefore capable of recruiting higher LLT densities. Crown release is an example of a silvicultural technique that can be used to increase large tree densities (Singer and Lorimer, 1997).

Another key attribute of old-growth forests, both in terms of long-residence carbon accumulation and habitat provisioning, is the amount of CWD. The latter could be increased through silvicultural techniques, such as girdling of selected medium to large sized, low vigor trees, felling or pulling over and leaving some dead or dying trees, where microhabitat requirements related to LLT are already met. These techniques can be employed to varying degrees and in different combinations depending on stand conditions and management objectives. This approach would allow forest managers to build some degree of old-growth associated structure into actively managed stands, while maintaining timber management flexibility (Choi et al., 2007).

Our results contribute to a growing understanding of old-growth temperate forests structure across continents and systems. This is critical to enhance forestry practices that maintain both biodiversity associated with structural complexity (e.g. management for microhabitats), and overall favorable conditions for increasing carbon stocks in forest pools, such as large living trees, CWD and soils. Our results will also help inform discussions of the importance of conserving forests with large carbon stocks and providing late-successional habitats.

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Appendix A and B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2012.11.020>.

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