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Variability and Dynamics of Old-Growth Forests in the Circumboreal Zone: Implications for Conservation, Restoration and Management

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Due to the unprecedented loss of old-growth forests to harvesting throughout circumboreal regions an understanding of similarities and differences in old-growth dynamics is needed to design effective restoration, management and conservation efforts. This paper reviews concepts, prevalence and variability of old-growth forests across landscapes, and evaluates different stand scale dynamics at the old-growth stage across the circumboreal zone. Old-growth historically dominated many boreal forest landscapes in both Eurasia and North America. Throughout much of North America, and to some extent in western Siberia, the natural prevalence and development of old-growth forests are regulated by the occurrence of stand-replacing fires. In eastern North America and Siberia, insect outbreaks may, however, be more important. Insect outbreaks as well as recurrent non-stand replacing surface fires and windthrows, when occurring at the old-growth stage, often form stands characterized by several tree age-class cohorts. This multi age-class forest development type is common in Europe and eastern Siberia but its prevalence and importance in boreal North-America is not well documented. Similarities in successional dynamics across the circumboreal region are found in the development of mono-dominant even-aged stands, the replacement of shade intolerant tree species by shade tolerant species, as well as in all-aged stands driven by small-scale gap dynamics. The message to land managers is that the focus should not only be on setting aside remaining old-growth forests or in restoring static old-growth attributes, but also in emulating natural disturbances and successional dynamics at landscape and regional scales to maintain natural variability in old-growth attributes through time.

Keywords late-successional forest, disturbance regimes, stand dynamic types, cohort dynamics
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1 Introduction

Boreal old-growth forests of North America, Fennoscandia and Russia share many environmental and ecological characteristics, but differences exist in land use history, as well as concepts and traditions of scientific exploration. A number of studies over the past two decades have shown that the proportion of old-growth forests is rapidly decreasing across the entire boreal zone (Burton et al. 2003, Angelstam 2003, Cyr et al 2009). For example, forest landscapes in Fennoscandia in natural or near-natural conditions were dominated by old trees and uneven-aged or cohort stand structures (Axelsson et al. 2002, Pennanen 2002, Kuuluvainen 2009), while currently only a small fraction of forests can be characterized as old near-natural forests (e.g. 4.4% in Finland, Punttila and Ihalainen 2006). However, old-growth forests still dominate in unmanaged boreal regions in Europe and Siberia (Smolonogov 1990, Ohlson and Tryterud 1999, Yaroshenko et al. 2001, Wallenius et al. 2004). Old-growth forests also naturally dominated landscapes in those parts of North America where the climate is moist and fire cycles are long, such as in eastern and western maritime Canada (Foster 1983, Kneeshaw and Gauthier 2003). However, even in many regions throughout boreal Canada where fires were an important feature of the natural dynamics, old-growth forests were more abundant than following even-aged forest management (Bergeron et al. 2001, Gauthier et al. 2002, Kneeshaw and Gauthier 2003, Bergeron and Harper 2009, Cyr et al. 2009).

In many parts of Canada and Russia, where forest management is occurring, pristine old-growth forest landscapes are being logged for the first time. Wide-scale implementation of clear-cut harvesting as the most common harvesting practice makes the future of forests with old-growth features questionable, especially as sustainable management is hindered by a lack of research describing locally relevant structural, compositional and functional characteristics of old-growth forests (Hilbert and Wiensczyk 2007). In areas where old-growth forests have been reduced to a few fragmented patches, such as southern Fennoscandia, the extinction of several old-growth dependent forest species is probable unless "new" old-growth is created, i.e. old-growth structural characteristics are restored into the managed forest matrix (Hanski 2000, Lilja et al. 2005, Jönsson et al. 2009). One solution to this problem is to design forestry operations that maintain essential old-growth characteristics (Bergeron et al. 2002, Angelstam and Dönz-Breuss 2004). To facilitate such restoration, there is a need for an adequate understanding of the processes and features that characterize old-growth forests at multiple spatial and temporal scales. Developing an understanding of how these processes occur across the circumboreal forest should enable us to develop a robust comprehension and to avoid inappropriate generalities of old-growth forests.

The aim of this paper is to review and examine differences and similarities in 1) old-growth forest concepts, 2) historical and current factors limiting the amount of old-growth forest, and 3) stand dynamics at the old-growth stage across the circumboreal, i.e. in North America, Northern Europe, and in Siberia. Based on this, we discuss possible approaches for maintaining and restoring old-growth forests at stand and landscape scales.

2 The Concept of Old-Growth Forest: Issues of Dynamics and Scale

Although there is no universal definition of old-growth forest (Wirth et al. 2009) the concept has evolved from one listing static properties to one emphasizing a dynamic view of this forest stage and its associated outcomes (stand structural complexity, coarse woody debris etc.) at multiple scales (Kneeshaw and Gauthier 2003). For example, in early papers it was common to treat old-growth forests as more or less homogeneous and static entities, without paying attention to spatial and temporal variability. This was obviously a reflection of the view of old forests as climax communities following the Clementsian paradigm (Clements 1936). More recently the dynamic characteristics of old-growth forests have been documented and emphasized (Harper et al. 2003, Mosseler et al. 2003, Lilja et al. 2006, Wirth et al. 2009, Aakala et al. 2009). It has also been shown that several threatened species are connected with and favored by not only structural attributes such as old slowly growing trees, abundant and well-decomposed coarse woody debris and other stand features but also by dynamic features in late-successional stands created by periodic "secondary" disturbances (surface fire, windthrow or insect outbreak) such as charred wood or favorable mineral seedbeds (Rouvinen and Kouki 2008, Fenton and Bergeron 2008 (Table 1). It is also evident that the definitions of old-growth forest can and must vary depending on the purpose and the region (Table 1) (Wells et al. 1998). In this paper, we use a broad and pragmatic approach and define old-growth forest as a naturally regenerated forest, with low human impact and dominated by trees approaching their biological life-span or trees that have replaced the original post-disturbance cohort. Thus, our definition leaves room for human intervention (e.g. restoration, nature-based management), although our discussion mostly focuses on forests with negligible human impact.

3 Controls and Status of Old-Growth Forests in the Circumboreal

The importance of old-growth forest in a given landscape or region for maintaining native biodiversity depends on the natural or historical extent and characteristics of this habitat type. The proportion of old-growth in a given landscape was naturally determined by the occurrence and return interval of stand-replacing disturbances, such as severe fires, wind storms or insect outbreaks (Johnson 1992, Furyaev 1996, Gromtsev 2002).

In the North American boreal forest, the area burned is controlled by large scale climatic patterns. Thus, in North-America, the cycle and severity of fires are mostly under a top-down climatic control (Cyr et al. 2007, Mansuy et al. 2010, Fauria and Johnson 2008). Both stand- and landscape-scale forest dynamics strongly depend on the fire regime. When fires are stand-replacing the rule is: the longer the fire cycle, the more old forest there is in the landscape, and vice versa (Lesica 1996). Under unmanaged conditions, the frequency and extent of fires generally decrease from south to north because the fire season becomes shorter and the availability of continuous fuels decreases (Larjavaara et al. 2004, Kneeshaw et al. 2011). Low-density 'open taiga' forests generally have longer fire cycles and smaller fires than closed boreal forests (Payette et al. 1989).

In boreal North-America, the documented average fire cycle for different ecozones is highly variable, ranging from 50 years in the western boreal shield to 800 years in the Hudson plain ecozone (the ecozone extending from the western coast of Quebec to the coast of Manitoba) (Bergeron and Harper 2009). In Canada, 3% of the fires, which are the ones uncontrolled by fire suppression activities, are responsible for 97% of area burned (Stocks et al 2003). These fires occur during very dry conditions (Fauria and Johnson 2008, Girardin et al. 2009) which makes suppression difficult. Therefore fire frequency estimates made over one to several centuries are thought to be only minimally affected by fire suppression activities (Johnson et al. 2001, Lefort et al. 2003). Differences among regions in fire frequency are mainly due to a drier climate in the west since the dominant tree cover is relatively similar across the Canadian boreal biome (Bergeron and Harper 2009, Kneeshaw et al. 2011). Within the Boreal Cordillera (the ecozone that covers southern Yukon and half of northern British Columbia) the fire frequency is extremely variable (50–300+ years) but generally moderate on a region-wide basis because of the lack of large areas of homogenous terrain. East of the Cordillera, the natural fire frequency is high <50–100 year average fire cycle in Alberta and Saskatchewan and old-growth forests are thus infrequent over much of the Boreal Plains and Western Shield (Larsen 1997, Weir et al. 1999). However, the fire cycle lengthens as one continues east to 100–300 years in eastern Ontario and Quebec (Cogbill 1985, Bergeron 1991, Cyr et al. 2007, Bouchard et al. 2008) to 500 years or more in humid Labrador (Foster 1983). Thus the proportion of old-growth forests tends to increase as one proceeds east from the Rocky Mountains.

The natural fire regimes in the Eurasian boreal forest can be characterized as mixed-severity fire regimes where fire severity ranges from stand replacing crown fires to very light surface fires (Sofronov and Volokitina 1990, Furyaev 1996,

Table 1. Present views on old-growth forests in North America, Fennoscandia and Russia.

	North America	Fennoscandia	Russia
Commonly used terms for unmanaged forests with high conservation value	Old-growth	Old-growth, natural	Pristine, primeval, virgin
Definitions in use for old-growth	Ecological definitions are divided into 3 categories: conceptual *functional* (climax, net annual growth close to zero, final stage of stand development etc., Kneeshaw and Burton 1998), or functional and successional (Wirth et al. 2009); conceptual *structural* (dominant trees are at the age of physiological maturity, large trees, decaying wood of all stages, pits and mounds, snags, multi-aged, multi-layered canopy etc., Duchesne 1994, Johnson et al 1995, Kneeshaw and Burton 1998) and *quantitative working* (cohort basal area proportion; Kneeshaw and Gauthier 2003) (Hilbert and Wiensczyk 2007); the old-growth concept has evolved *a from static to a dynamic approach* (Kneeshaw and Gauthier 2003)	'The forest that is essentially *unmanaged* and in forestry terms *over-aged*, often including abundant large living and dead trees' (Wallenius et al. 2004), 'a forest of greater than 129 years old, without or with few cut stumps' (Siitonen et al. 2000), '*undisturbed*' (Svenson and Jelgum 2001); spatio-temporal scales of 'naturalness' are important Rouvinen and Kouki 2008)	'Naturally regenerated *over-mature* forest, developed without direct human impact including felling and recreation during the life of the older cohort.' (Maslov 1999)
Scale focus	Stand and landscape	Stand	Landscape (forest tract)
Fire regime controlling abundance of old-growth	Mainly crown fire – the main factor impeding formation of old-growth	In the European boreal forest and Eastern Siberia, mainly ground-, low- and medium-severity fire – inherent part of dynamics of the old-growth Scots pine and larch stands. In Western Siberia, crown fire can preclude old-growth formation	
Main disturbances at the old-growth stage	Spruce budworm (*Choristoneura fumiferana* Clem.), tent caterpillar (*Malacosoma disstria* Hübner), hemlock looper (*Lambidina fiscellaria* Guen.), windthrow to some extent	Surface fire, windthrow, bark beetles (*Ips typographus* (L.)), Siberian silk moth (*Dendrolimus sibiricus* (Tschetverikov))	
Tree species composition of stands	Both early-successional and late-successional species can dominate	Late-successional species (Norway and Siberian spruce, fir, Siberian pine, on some site conditions Scots pine) dominate with a mixture of pioneer species (birch, aspen)	

	North America	Fennoscandia	Russia
Examples of old-growth “anomalies” from the perspective of the other regions	Stands dominated by a few post-fire cohort individuals of birch and/or aspen with an understory of spruce and fir	Pure even-aged mature coniferous stand	A few ha windthrow gap in a pristine forest landscape
Past policy	‘Old-growth forests should be harvested before they rot and have no value’ (Sloan 1956, cited in Hilbert and Wiensczyk 2007)	Over-mature non-productive forest that should be clear-cut and regenerated (Tasanen 2004)	
Recent	Landscape ecological planning, variable retention felling, maintaining old-growth attributes in managed landscapes (Arsenault 2003, Kimmins 2003), but also harvesting	Landscape scale ecological planning, variable retention felling, conservation of remaining old-growth fragments (Fries et al. 1997)	No uniform policy, debates between NGOs and forest companies. Sustainable management is slowed down due to politic and economic pressures. (Aksenov et al. 1999)
Future	Uneven-aged management or no management	Sustainable forestry. Conservation of all old-growth fragments, restoration, creation of “new old-growth” (Vanha-Majamaa et al. 2007, Gustafsson et al. 2010)	Transition: either sustainable or rotation forestry; either exploitation or protection of remaining old-growth. (Aksenov et al. 1999)

Gromtsev 1996, 2002, Valendik and Ivanova 2001, Buryak et al. 2003, Wallenius et al. 2010). However, unlike the boreal forest in North America, in Finland and Sweden, efficient fire suppression has almost totally eliminated fires as natural drivers of stand dynamics.

It has been estimated that the mean occurrence of fires in Russia's European boreal forests varies from 1–2 per century to 1–2 per millennium (Gromtsev 2002). According to Melekhov (1947), surface fires comprised 76–84%, crown fires 16–24% and underground fires 0.1% of the total number of fires in the European Russian boreal forest. Crown fires in the European boreal forest are exceptionally rare (1–2 per thousand years in most landscape types, Gromtsev 1999) and usually do not spread to cover large territories. High-severity crown fires therefore were historically not a factor limiting the proportion of old-growth throughout Fennoscandia and only to a limited extent in Russia.

In western Siberia, infrequent high severity fires characteristic of moist 'dark coniferous' forests dominated by Siberian spruce (*Picea obovata* Ledeb.), Siberian fir (*Abies sibirica* Ledeb.) and Siberian pine (*Pinus sibirica* Du Tour or (Loudon) Mayr) limit the proportion of old-growth forests. In contrast, the high flammability of low-mountain 'light coniferous' forests dominated by Scots pine (*Pinus sylvestris* L.) and Siberian larch (*Larix sibirica* Ledeb.) in Eastern Siberia leads to more frequent non-stand-replacing fires. Of the total number of fires in Siberia, most (83%) occur in Eastern Siberia and the Far East, whereas only 17% occur in Western Siberia (Valendik and Ivanova 2001).

The variation in fire regimes is a main ecological difference between regions affecting the proportion of old-growth forests in circumboreal forest landscapes. Prevalent crown fires throughout North America and also in parts of Russia limit old-growth formation, while the natural dominance of surface fires in Fennoscandia and the European part of Russia are an integral part of old-growth forest dynamics (Pennanen 2002, Kuuluvainen 2009). Under an infrequent fire cycle, insect herbivory (Bergeron and Leduc 1998, Vaschuk and Shvidenko 2006), wind storms (Skvortsova et al. 1983, Ulanova 2000), and weather-induced decline (Zhigunov et al. 2007, Aakala et al. 2009) can also cause severe and widespread destruction, thus affecting the dominance of old forests throughout the circumboreal region. The biogeographic causes of these patterns are further explored in Kneeshaw et al. (2011).

Insect outbreaks as disturbance factors re-initiating succession play an important role mostly in eastern North America and Siberia. In North America, the eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) is the dominant insect causing mortality of fir and spruces primarily in the eastern part of the boreal forest. Outbreaks occur approximately every 30–40 years and affect millions of hectares synchronously. Other insects, such as the forest tent caterpillar (*Malacosoma disstria* Hübner), jack pine budworm (Choristoneura pinus Freeman*)* and hemlock looper (*Lambdina fiscellaria* (Guenee)) also outbreak in boreal forests although they do not cause as widespread mortality as the spruce budworm. As with many other insects the spruce budworm is species specific causing most damage in balsam fir (*Abies balsamea* (L. Mill.) stands and much less mortality in spruce stands. This insect also causes more mortality in mature stands than in immature younger stands (Hennigar et al. 2008). Mortality can vary from large tracts of 100's ha to small patches less than a hectare in size (D'Aoust et al. 2004, Kneeshaw et al. 2009). Subsequent stand dynamics and old-growth forest structure are determined by the area affected, the forest species composition (i.e. host species or non-hosts) and the insect disturbance itself. Spruce budworm, for example, in severe outbreak years can return large monocultures of balsam fir forests to an early development stage or it can increase deadwood and modify composition in old-growth mixed species forests.

In Europe, the main outbreaking insects are the spruce bark beetle (*Ips typograhus* L.) and autumnal moth (*Epirrita autumnata* (Borkhausen)) in mountain birch forests, which however only affect a small proportion of the forest in the boreal part of Western Europe (Gromtsev 2002). In Siberia, the Siberian silk moth (*Dendrolimus sibiricus* (Tschetverikov)) is the most aggressive insect (Vaschuk and Shvidenko 2006). The main host for this insect is Siberian pine, and, to a lesser extent, larch, fir, spruce and Scots pine. The impact of these outbreaks is most severe when followed by

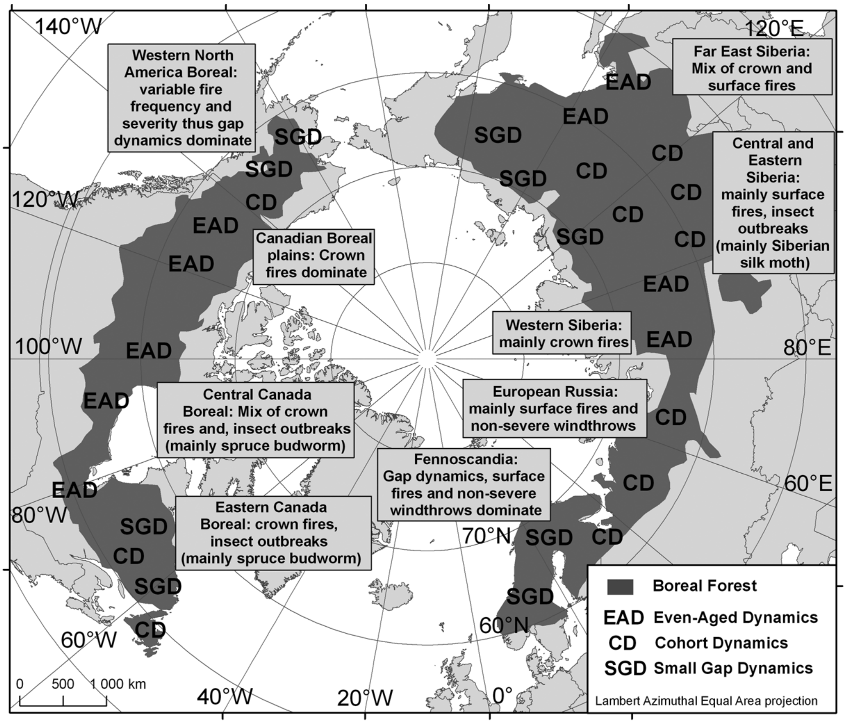

Fig. 1. An approximate illustration of the circumboreal variability and distribution of naturally occurring dominant forest dynamic types. In general, areas characterized by stand-replacing disturbances and even-aged dynamics (EAD) have a low proportion of old-growth (e.g. the boreal plains due to short crown fire intervals), whereas regions void of severe disturbances and driven by small-scale gap dynamics (SGD) have the highest old-growth proportions (e.g. eastern Canada and western Fennoscandia with moist maritime climates). Regions characterized by variable-severity disturbances and cohort dynamics (CD) are intermediate between these two extreme types. It is important to note that in most regions, all of these types are present in varying proportions depending on the variability associated with the disturbance regimes. In many regions forest management has significantly altered forest structure and dynamics, the naturally occurring types of forest dynamics represent an important reference point for the management and conservation of old-growth forests.

fire (Furyaev 1970), because of high fuel loads of standing dead wood (Verkhunov 1970). Thus these insect outbreaks modify old-growth forests without eliminating them unless they interact with other disturbances.

Windthrow also occurs and shapes stand dynamics in North America and Eurasia. In North America, wind causes both partial and total mortality of trees in stands in maritime regions due to strong winds from oceans and in central, continental sites primarily due to downbursts associated with thunderstorm activity (Frelich 2002). Return intervals for these disturbances are generally quite long (in excess of a thousand years vs. between fifty and a few hundred years for fires) and so their effect is often observed locally but not across a large region. Thus, on a regional basis, wind disturbance although affecting from a few hectares to hundreds of square kilometres is too infrequent and too localised to appear as a dominant disturbance type although locally it may have a large influence on forest dynamics at a given point in time (Fig. 1). In other words, although some stands may be returned to an earlier developmental state, wind usually only modifies the structure of old-growth forests across a landscape. In Eurasia, wind caused mortality is a more significant driver of forest dynamics. The sizes of gaps formed after low- or moderate-severity windthrows can vary from 0.01 to 1 ha (Skvortsova et al. 1983). The reported stand-replacement windthrow return intervals in boreal coniferous forests vary from 50 to 200 and more years (Skvortsova et al. 1983, Fedorchuk et al. 1998). In Eurasia, old-growth dynamics are thus under a potentially larger influence of wind activity than in North America.

Although we lack rigorous quantitative comparisons it seems apparent that Eurasian boreal forest landscapes are characterized by a more complex and fine-grained mosaic structure compared to North American forests as the disturbance size distribution in the European boreal forest is more determined by site conditions (bottom up, site-specific disturbance regime) compared to North American boreal forest (top-down, climate driven disturbance regime). In North America, fire cycles influence the amount of old-growth across the landscape and also its spatial distribution. In Western Canada, where the fire cycle is relatively short, old-growth forests are usually small patches, preserved from fire by surrounding younger forests (Johnson et al 1998). On the other hand, in eastern Canada old-growth naturally occurs in large tracks of forest that have not burned for a long time (Lefort et al. 2003, Bergeron et al. 2004) but that are affected by different partial disturbances which create a diversity of structure and composition within those large tracks of old-growth.

4 Tree Species' Life-History Traits and Old-Growth Forests

The ecological traits of the main boreal tree species and their adaptations to the regionally occurring natural disturbance regimes directly determine the type of old-growth forests found in different regions (summarized in Table 2). For example, trees with short longevities will be replaced more quickly than trees with long longevities and thus transitions to all-aged old-growth stands will occur more rapidly in such forests. In general, species in Eurasia have greater longevities than the North American species (Nikolov and Helmisaari 1992).

The North American pioneer tree species, trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.) and jack pine (*Pinus banksiana* Lamb.) or Lodgepole pine (*Pinus contorta* Douglas ex Loudon), are well adapted to recurring fires by vegetative reproduction, wind-distributed seeds and serotinous cones (Table 2). Even late-successional species such as black spruce (*Picea mariana* (Mill.) B.S.P.) have semi-serotinous cones and may thus re-establish following fire. On the other hand, late-successional shade tolerant species such as balsam fir, white spruce (*Picea glauca* (Moench) Voss.) and northern white cedar (*Thuja occidentalis* L.) are poorly adapted to fire; and must colonize burned areas from unburned refugia. Pollen records show that their abundance increases in periods with few fires (Liu 1990). Most of these species are relatively short-lived (100–150 yrs) with the exception of cedar and the spruces.

Tree species diversity is lower in boreal forests of northwestern Europe compared to those in North America. Scots pine (*Pinus sylvestris* L.) has the widest ecological amplitude in terms of moisture and nutrient requirements, and is fire-tolerant because of its thick heat-insulating bark (Nikolov and Helmisaari 1992). However, in the absence of fire pine is displaced (except from the driest sites) by shade tolerant but fire-intolerant Norway spruce (*Picea abies* L. (H.) Karst.), which subsequently reduces wildfire activity further due to the moister environments that they create (Ohlson et al. 2011). Norway spruce, which invaded Europe in the late Holocene, typically forms old-growth stands on well drained productive sites. Scots pine dominates on poor dry sites forming uneven-aged or cohort structure stands driven by recurrent surface fires and/or gap and patch dynamics. This is because large Scots pines often survive surface fires, due to their thick insulating bark, and provide seeds for regeneration after fire. Similarly, Siberian larch (*Larix sibirica* Ledeb.) and Dahurian larch (*Larix gmelinii* (Rupr.) Rupr.), found in North-Eastern Europe and Siberia, are fire-resistant and

Table 2. Ecological traits and occurrence of tree species associated with old-growth (Burns and Honkala 1990, Nikolov and Helmisaari 1992, Harvey et al. 2002, Hytteborn et al. 2005, Kneeshaw et al. 2006).

Region	Characteristics			
Moisture regime				
	Dry sites	*Moist, well drained sites*	*Moist, paludified sites*	
NA	Black spruce, Jack pine, Lodgepole pine, Eastern white cedar	Balsam fir, Black spruce, Jack pine, Lodgepole pine, Trembling aspen, White birch, Eastern white cedar, White spruce	Black spruce, Tamarack, Eastern white cedar	
WE	Scots pine	Aspen, Downy birch, Norway spruce, Scots pine, Silver birch	Downy birch, Scots pine, Silver birch	
EE, Siberia	Scots pine, Siberian larch, Dahurian larch	Downy birch, Dahurian larch, Scots pine, Siberian fir, Siberian larch, Siberian spruce, Silver birch	Dahurian larch, Scots pine, Siberian pine, Siberian larch	
Soil parent material				
	Sandy	*Till*	*Clay*	
NA	Black spruce, Jack pine, Lodgepole pine	Balsam fir, Jack pine, White spruce, White birch, Eastern white cedar	All species	
WE	Scots pine	Aspen, Downy birch, Norway spruce, Scots pine, Silver birch	Aspen, Downy birch, Norway spruce, Silver birch	
EE, Siberia	Scots pine	Aspen, Downy birch, Dahurian larch, Siberian pine, Siberian fir, Siberian spruce, Siberian larch, Silver birch	Aspen, Downy birch, Dahurian larch, Siberian pine, Siberian fir, Siberian larch, Siberian spruce, Silver birch	
Shade tolerance				
	Very intolerant	*Intolerant*	*Tolerant*	*Very tolerant*
NA	Jack pine, Lodgepole pine, Trembling aspen	White birch	Black spruce, White spruce	Balsam fir, Eastern white cedar
WE	Scots pine	Aspen, Downy birch, Silver birch		Norway spruce
EE, Siberia	Dahurian larch, Scots pine, Siberian larch	Aspen, Downy birch, Silver birch	Siberian pine	Siberian fir, Siberian spruce
Reproductive mode				
	Suckers	*Stump sprouts*	*Layering*	*Seeding*
NA	Trembling aspen	White birch	Black spruce, Eastern white cedar	Balsam fir, Jack and Lodgepole pines (from serotinous cones), Trembling aspen, White birch, Eastern white cedar, White spruce
WE	Aspen	Downy birch, Silver birch		Aspen, Downy birch, Norway spruce, Silver birch
EE, Siberia	Aspen	Downy birch, Silver birch	Siberian fir, Siberian larch, Dahurian larch	Dahurian larch, Siberian pine (obligatory needs animals and birds for seed distribution, mainly the Spotted Nutcracker), Siberian fir, Siberian larch, Siberian spruce

Table 2 continued.

Region	Characteristics		
Regeneration time after fire			
	Rapid	*Gradual*	*Late*
NA	Black spruce, Jack pine, Lodgepole pine, Trembling aspen, White birch	Balsam fir, White spruce	Eastern white cedar
WE	Aspen, Downy birch, Scots pine, Silver birch	Norway spruce	
EE, Siberia	Aspen, Dahurian larch, Downy birch, Scots pine, Siberian larch, Silver birch	Siberian fir, Siberian spruce	Siberian pine

Fire tolerance / resistance					
	None	*Vegetative reproduction*	*Serotinous cones*	*Semi-serotinous cones*	*Thick bark*
NA	Balsam fir, Eastern white cedar	Trembling aspen, White birch	Jack pine, Lodgepole pine	Black spruce	
WE	Norway spruce	Aspen, Downy birch, Silver birch			Scots pine
EE, Siberia	Siberian pine, Siberian fir, Siberian spruce	Aspen, Downy birch, Silver birch			Dahurian larch, Scots pine, Siberian larch

Old-growth stage disturbance factors				
	Main fungi	*Main insects*	*Windthrow*	*Surface fire*
NA		Spruce budworm (Balsam fir, Black spruce, White spruce), Jack pine budworm (Jack pine), tent caterpillar (Trembling aspen)	Balsam fir, Black spruce, Trembling aspen	
WE	Biaterella cancer (Scots pine) Hardwood trunk rot (Trembling aspen), heart rot and annosus root rot (Norway spruce), white pocket rot (Norway spruce, Scots pine)	Spruce bark beetle (Norway spruce)	Norway spruce	Scots pine
EE, Siberia	Hardwood trunk rot (Trembling aspen), white pocket rot, Golden Spreading Polypore (Siberian spruce, Siberian fir, Siberian pine, (Scots pine)	Siberian silk moth (Siberian pine, Siberian fir, Siberian larch, Siberian spruce)	Siberian pine, Siberian spruce	Dahurian larch, Scots pine, Siberian larch

Table 2 continued.

Region	Characteristics		
Natural longevity in a stand			
	Short (< 100 years)	*Medium (100–200 years)*	*Long (200+ years)*
NA	Balsam fir, Trembling aspen	Black spruce, Jack pine, Lodgepole pine, White birch	Eastern white cedar, White spruce
WE		Aspen, Downy birch, Silver birch	Scots pine, Norway spruce
EE, Siberia		Aspen, Downy birch, Silver birch, Siberian fir	Dahurian larch, Scots pine Siberian pine, Siberian larch, Siberian spruce
Successional role			
	Early	*Late*	
NA	Black spruce, Jack pine, Lodgepole pine, Trembling aspen, White birch	Balsam fir, Black spruce, Eastern white cedar	
WE	Downy birch, Scots pine, Silver birch	Norway spruce, Scots pine	
EE, Siberia	Downy birch, Scots pine, Silver birch	Dahurian larch, Scots pine, Siberian pine, Siberian fir, Siberian larch, Siberian spruce	

Abbreviations: NA – North America, WE – western Europe (including Fennoscandia), EE – eastern Europe. Tree species: Aspen – *Populus tremula* L., Balsam fir – *Abies balsamea* (L.) Mill., Black spruce – *Picea mariana* (Mill.) B.S.P., Dahurian larch – *Larix gmélinii* (Rupr.) Rupr.; syn. *Larix dahurica*), Downy birch – *Betula pubescens* Ehrh., Jack pine – *Pinus banksiana* Lamb., Lodgepole pine – *Pinus contorta* Douglas ex Loudon, Northern White cedar – *Thuja occidentalis* L., Norway spruce – *Picea abies* L. (H.) Karst., Scots pine – *Pinus sylvestris* L., Siberian fir – *Abies sibirica* Ledeb., Siberian larch – *Larix sibirica* Ledeb., Siberian pine – *Pinus sibirica* Du Tour or (Loudon) Mayr, Siberian spruce – *Picea obovata* Ledeb., Silver birch.– *Betula pendula* Roth, Tamarack – *Larix laricina* (Du Roi) K. Koch., Trembling aspen – *Populus tremuloides* Michx., White birch – *Betula papyrifera* Marsh., White spruce – *Picea glauca* (Moench) Voss. Insect species: *Jack pine budworm* – Choristoneura pinus Freeman, Siberian silk moth – *Dendrolimus sibiricus* (Tschetverikov), spruce bark beetle – *Ips typograhus* (L.), spruce budworm – *Choristoneura fumiferana* Clem., tent caterpillar – *Malacosoma disstria* Hübner. Fungi: annosus root rot – *Fomes annosus* Fr Chc., Biaterella cancer – *Biatorella difformis* (Fr.) Vain., Hardwood trunk rot – *Phellinus igniarius* (L.) Quél., heart rot – *Onnia leporina* (Fr.) H. Jahn., white pocket rot (red heart of pine, Golden Spreading Polypore) – *Phellinus pini* (Thore) Fr., *Phellinus chrysoloma* (Fr.) Donk. Spotted Nutcracker – *Nucifraga caryocatactes* L.

can, when recurrent surface fires occur, form pure old-growth stands and mixed stands with Siberian pine (*Pinus sibirica* Du Tour), Norway spruce, Siberian spruce (*Picea obovata* Ledeb.) and Scots pine. The difference between these species and those in North American boreal forests is in their fire adaptation: North-American species are regeneration adapted to fire (serotiny), while Eurasian species are resistance adapted (no serotiny, but characteristics such as thick bark permit them to survive fire).

In boreal Europe, when fire is absent for prolonged periods, Norway spruce dominates late successional stands on mesic sites. Similarly in Siberia, Siberian pine, Siberian spruce and Siberian fir form mixed 'dark coniferous' old-growth forests in fire refugia. Deciduous tree species Downy birch (*Betula pubescens* Ehrh.), Silver birch (*Betula pendula* Roth.), aspen (*Populus tremula* L.), Goat willow (*Salix caprea* L.) and European rowan (*Sorbus aucuparia* L.) usually occur as mixtures in old-growth forests as a legacy from earlier successional stages . Deciduous trees often dominate the early successional stage, and because some deciduous tree species have a maximum-life span (up to 100+ years), e.g white birch and trembling aspen in North America and (200 yrs) Silver birch and common aspen in Eurasia, some intolerant deciduous species can remain as a component of old-growth stands as well. Deciduous trees can also regenerate in treefall gaps and remain a component old-growth forest even when the forest escapes severe disturbance for many centuries (Kuuluvainen 1994, Kneeshaw and Bergeron 1998). The life-history characteristics of the different species are thus critical in determining the different stand developmental pathways of old-growth forests in the different regions of the boreal.

5 Old-Growth Stand Dynamics Types

Depending on their severity and occurrence, disturbances may maintain or destroy old-growth forest. Although much variability in post-disturbance-successional dynamics has been recognized, Eurasian forest stands have been characterized into three main dynamic types (Shorohova et al. 2009): 1) even-aged, a) with compositional change dynamics or b) with mono-dominant dynamics, 2) cohort dynamics and 3) small-scale gap dynamics. Using information on disturbance interval and disturbance severity, we suggest that these types can also be used to characterize the prevalence and dynamics of the old-growth stage for all cirumboreal forests. Fig. 1 attempts to provide a broad illustration of the distribution these forest dynamic types in the circumboreal forest (see also Table 3).

Even-aged old-growth dynamics (types 1a and 1b) dominate when the return interval of stand-replacing disturbances such as high-severity fires, windthrows and insect outbreaks approaches the life-span of the dominant tree species but is not long enough for recruitment of new cohorts to take place (Aakala et al. 2009). In western European forests, type 1a dynamics dominate the more nutrient-rich sites with a more pronounced dominant role of deciduous tree species (birch, aspen) as compared to type 1b. In North America, when the fire interval is short old-growth black spruce forests are characterized by even-aged type 1b mono-dominant dynamics (Payette et al. 1989, Jasinski and Payette 2005). Mixed-wood North American boreal forests dominated by both shade intolerant hardwoods (trembling aspen and paper birch) and shade tolerant conifers correspond to the type 1a even-aged compositional change dynamics in fire-prone landscapes. Aspen or jack pine forests as an ‘initial old-growth’ represent the type 1b stage of even-aged mono-dominant dynamics. On occasion multiple partial disturbances can also lead to unimodal age class structures (Szewczyk et al. 2011). In the continued absence of major disturbances and with senescence of the trees from the initial cohort, canopy gaps are gradually formed, leading to a patchy recruitment of new trees and the stand shifts first to type 2 dynamics if partial disturbances synchronize mortality and recruitment within patches in the stand and then gradually, if void of major disturbances over lengthy periods, towards type 3 dynamics characterized by all-aged old-growth forest.

Old-growth forests characterized by cohort dynamics (type 2) prevail when recurring partial disturbances stimulate cyclical tree death and regeneration processes and lead to a multimodal stand age structure. In cases, where a site experiences punctual moderate severity disturbances (Reyes et al. 2010) there will be a deviation of tree diameter and age distributions from the ‘inverse J-shaped’ structure. The more pronounced the

Table 3. Disturbance regimes and dynamic types at the old-growth stage.

Disturbance severity	Types of old-growth		
High	No old-growth	Even-aged old-growth	Even-aged old-growth ↔ Cohort dynamics ↔ Small-scale gap dynamics
Medium	Cohort dynamics	Cohort dynamics	Cohort dynamics ↔ Small-scale gap dynamics
Low	Small-scale gap dynamics	Small-scale gap dynamics	Small-scale gap dynamics
	<100	100–250	>250
	Disturbance interval, years		

cohort dynamics and discrete regeneration process the greater is the deviation from the inverse-J type diameter distribution. Forest stands situated on slopes, subject to periodic windthrow disturbances provide such an example (Shorohova et al. 2008). Another example can be found in some fire driven forests when the small-scale variation in past fire frequencies are concordant with the existing small-scale variation in site moisture and vegetation characteristics in the area (Kuuluvainen et al. 2002, Wallenius et al. 2004). In cohort dynamics, different phases and dynamic oscillations can be distinguished: a mortality/regeneration phase, a phase of growing stock increment (young cohorts predominate), stabilization and growing stock decline (old cohorts dominate) (Fedorchuk et al. 1998). The oscillation of these phases, and thus the proportion of old-growth, is dependent on the disturbance frequency and severity that influences regeneration conditions: from decades in the case of recurrent mid-severity windthrow or surface fires to centuries in the case of stand decline due to insect attack, e.g., by the Siberian silk moth or infrequent wind events.

In North America's boreal forest, cohort dynamics (type 2) have rarely been described. However, the role of moderate-severity disturbances leading to cohort dynamics is probably underestimated (Seymour et al. 2002) and relatively little studied as compared to the two extreme ends of the disturbance spectrum, i.e. catastrophic disturbances and small-scale gap dynamics (Hanson and Lorimer 2007, McCarthy and Weetman 2007). This being said the 'bimodal' and 'bistaged' black spruce-balsam fir stand structural types distinguished by McCarthy and Weetman (2007) could be interpreted as cohort dynamics. Furthermore, the difference in the identified proportions of the cohort stand development type may also at least partially be an artifact due to the terminology used. For example, the spatial structure of old-growth balsam-fir stands in Gaspésie, eastern Quebec is characterized by a mean opening size following spruce budworm outbreaks of 13.4 ha with a variation from 1 to 45 ha (Kneeshaw et al. 2009). In European boreal forest, stands, i.e. relatively homogenous units of forest successional development, are small, averaging only a few hectares to some tens of hectares. If stand canopy openings, or area in gaps exceed 0.1 ha, the stand dynamic type is classified as either even-aged or multi-cohort. Spruce budworm outbreaks may thus create the conditions for multi-cohort dynamics as stands are disturbed at fairly frequent intervals permitting small even-aged cohorts to recruit to the canopy (Morin 1994, Rossi and Morin 2011).

The third type of old-growth forest dynamics leads to an uneven-age and -size distribution of trees. In Eurasia, homogenous site conditions are a prerequisite for the formation of all-aged structures of Norway spruce dominated forests (Volkov 2003). Fedorchuk et al. (1998) showed that when a stand has escaped exogenous disturbances for lengthy periods, the pronounced oscillations in tree mortality and regeneration are dampened, and stand dynamics become characterized by a fine-scale mosaic of mortality and regeneration processes. These old-growth stands are often dominated by one or two shade tolerant species (Pham et al. 2004, Cyr et al 2009) but they are not obligatorily mono-specific. In Eastern Europe and Siberia, they consist of spruce, fir and Siberian pine whereas in boreal North America these forests are dominated by black spruce and balsam fir. Usually the percentage of the deciduous tree mixture increases with an increase in site productivity and is more present in Type 1 or Type 2 dynamics (Pugachevsky 1992). Old-growth black spruce forests are characterized by small-scale gap dynamics in the absence of fire or when the fire cycle is long (Pham et al. 2004, Gauthier et al. 2010). In forests with long fire intervals, small-scale gap dynamics characterize the mixed-wood type (Kneeshaw and Bergeron 1998, McCarthy 2001).

In North America, as compared to the Eurasian boreal, the small-scale gap dynamics stage arrives earlier since tree species' longevity is shorter (Kneeshaw and Gauthier 2003). The transition from the first to the third types of old-growth forest dynamics can last for centuries depending on species longevities and this is one of the major differences between North America and Eurasia. Based on chronosequences of Norway spruce dominated forests Kazimirov (1971) in the Russian Karelia in middle boreal zone and Pugachevsky (1992) in the Tver region (Central Biosphere Forest Reserve, southern boreal zone), concluded that the formation of all-aged old-growth stands after a stand-replacing disturbance could take 600–700 years

Table 4. Examples of proportions (in %) of different dynamic types in old-growth Eurasian boreal forest landscapes. Interpreted based on the proportion of stands of different age structure types: even-aged, uneven-aged and all-aged and tree species composition in even-aged stands

Region, area name, tree species dominants, main disturbances	Types of stand-scale dynamics at the old-growth stage				Reference
	Even-aged, mono-dominant Type 1a	Even-aged, compositional change Type 1b	Cohort Type 2	Gap Type 3	
WE, Karelia, whole northern boreal part, surface and stand-replacement fires. Landscape types:					Gromtsev 2008 [1,b)]
1) Glaciofluvial highly paludified spruce dominated plains	6	-	8	92	
2) Glaciofluvial hilly-ridge moderately paludified pine-dominated landscapes	19	-	79	15	
3) Denudation-tectonic hilly-ridge with low mountains moderately paludified spruce dominated landscapes	51	-	-	81	
4) Denudation-tectonic with glacial complexes hilly-ridge moderately paludified pine-dominated landscapes	-	-	9	40	
5) Rocky moderately paludified pine-dominated landscapes	-	-	55	45	
WE, middle boreal zone; ‘Vepssky Les” reserve (1975 ha); Norway spruce, Scots pine, Silver and Downy birch, aspen; windthrows and, to a smaller extent, fires	10	16	60	14	Fedorchuk et al. 1998 [1,a)]
WE, middle boreal zone; Karelia, Vodlozersky national park (120 000 ha), Norway spruce dominated; only Norway spruce stands are analyzed	36	-	44	20	Ananyev and Raevsky 2010 [1,a)]
EU, southern boreal zone; Srednee Prikam’e, (2490 ha); Siberian spruce, Siberian fir	7	-	45	48	Dyrenkov 1984 [1,a)]
EU, southern boreal zone (6935 ha); Siberian spruce, Siberian fir	18	-	63	10	Dyrenkov 1984 [1,a)]
Siberia, Magadansky region; Dahurian larch, surface fires	26	.	65	9	Tetioukhin 1987 [2,a)]

WE – western Europe, EE – eastern Europe. Species: Aspen – *Populus tremula* L., Dahurian larch – *Larix gmélinii* (Rupr.) Rupr.; syn. *Larix dahurica*), Downy birch – *Betula pubescens* Ehrh., Norway spruce – *Picea abies* L. (H.) Karst., Scots pine – *Pinus sylvestris* L., Siberian fir – *Abies sibirica* Ledeb., Siberian spruce – *Picea obovata* Ledeb., Silver birch.– *Betula pendula* Roth

[1)] Based on area proportion

[2)] Based on number of the stands sampled

[a)] Direct estimate

[b)] Based on estimates of forest type proportions and main age structure types by forest type depending on site conditions. Interpreted from this model, 'even-aged old-growth' could occur after 180–200 years of post-fire succession and 'cohort dynamics old-growth' after 280–300 years. Zyabchenko (1986) calculated a similar temporal horizon of development of Scots pine dominated stands in Russian Karelia.

In the Eurasian boreal forest, the prevalence of different stand dynamic types is landscape- and site-specific, because of the important regulating role of bottom-up factors, i.e. characteristics of the landscape mosaic (Shorohova et al. 2009). In North America, landscape structure and site conditions may be less important due to climate driven top-down fire-induced disturbance dynamics. However, work by Cyr (2010), Bridge and Johnson (2000), Gavin et al. (2006) has also shown that local and regional site conditions modify fire regimes and vegetation dynamics in North America.

The pristine European taiga contains mosaics of forest communities at different successional stages from fresh burns and windthrow gaps to all-aged old-growth forests (Gromtsev et al. 2010). Studies demonstrate that in pristine Eurasian boreal forests the landscape-scale proportion of different dynamic types is highly variable (Table 4). Most studies have, however, demonstrated the prevalence of cohort dynamics caused by low-severity fires, windthrows, insect outbreaks or drought-induced decline. Even-aged dynamics with compositional change occurs only rarely in the case of replacement of post-fire cohorts of Scots pine, birch and aspen by Norway spruce (Fedorchuk et al. 1998). In North America, such a classification has rarely been done precluding a precise portrait of the situation (but see McCarthy and Weetman 2007).

6 Implications for Conservation and/or Management of Old-Growth

Given the complexity of old-growth forest dynamics, shortcomings in scientific understanding and uncertainties about management impacts, simplistic approaches to managing and restoring old-growth forests to a static endpoint should be avoided. Instead an adequate understanding of the natural extent and variability of old-growth, its structures and processes is required (Angelstam and Pettersson 1997, Fries et al. 1997, O'Hara 2002, Kuuluvainen 2009). The conservation value or management possibilities of old-growth forest depends on the current state of the forest, which is affected both by recent management practices, past decisions on forest protection and overall forest and land use history. Finally, the socio-economic context (e.g. the presence of resource dependent communities, etc.) is essential for determining future possibilities for both old-growth management and conservation. An inspection of areas of old-growth forest at different scales suggests that relevant policy and management of old-growth needs to be tailored to local conditions (Spies 2004).

Stand-scale management for old-growth attributes can be based on the three identified types of stand dynamics (Table 5). As suggested development pathways may be more complex in Eurasia where all three of the previously described types are common due to the greater prevalence of moderate disturbances. In North America stand development to the old-growth stage occurs more frequently along a continuum linked to time since fire. Possible silvicultural treatments can be used to maintain current structure or accelerate succession. Equally important will thus be to understand the transitions between types and their relative proportions in the landscape. Favoring transitions/ fluxes between different cohorts (Harvey et al. 2002) could be used to maintain ecological processes associated with succession (Kimmins 1997).

Determining the proportion of areas that should be set aside in a landscape suggests three basic approaches 1) permanent protection areas 2) shifting mosaics in the matrix (Burton et al. 1999, Bengtson et al. 2003), and 3) the combinations of the two approaches, i.e. combinations of protection (reserves) and "managed old-growth". For example, old forest patches could be maintained with fire suppression, whereas where old-growth is more abundant, silvicultural practices such as partial logging could be used to maintain the structure of managed stands surrounding conservation patches. In managed forests, variable retention felling is another potential solution for maintaining structure and hastening the return of

Table 5. From characteristics of the stand-scale disturbance dynamics to management treatments.

	Types of stand-scale dynamics at the old-growth stage			
	Even-aged (1)		Cohort (2)	Gap (3)
	Compositional change (1b)	Mono-dominant (1a)		
	Possible management treatments			
To maintain current dynamic type	Retention felling		Uneven-aged management (selection felling with single tree or group selection, gap felling)	Gap felling, Selection felling, Dauerwald
To facilitate successional development (shift to another dynamic type)	Shelterwood felling	Selection felling, gap felling		

old-growth structural elements (Rosenwald and Löhmus 2008, Gustafson et al. 2010). Plantations on the other hand would require active management in the form of old-growth restoration if they are to serve a contributing role in the matrix.

Regional old-growth management strategies are necessarily highly dependent on the management history of the area – they will be different for countries with vast areas of natural forests compared to regions that have been previously intensively managed. In North America, forest management models have been developed based on natural disturbance regimes (Burton et al. 2003, Perera et al. 2004, Gauthier et al. 2009) and there is now a push for greater uneven-age and continuous forest cover management as well as conservation of old-growth. This is also true in Fennoscandia, where suggested approaches to sustainable forest management have emphasized mimicking natural processes at stand scales to restore system complexity (Vanha-Majamaa et al. 2007, Kuuluvainen 2009) , as well as conserving remaining old-growth remnants. In Russia, socioeconomic difficulties such as a lack of developed infrastructure especially forest roads, have lead to a de-facto maintenance of old-growth in remote regions while the advent of new technologies and socio-economic pressures in other regions threatens remaining old-growth forests. Thus, information from countries with intensively managed forests that are experiencing threats to biodiversity can be exported to countries where natural forests still occur. Similarly information about natural structures and natural dynamics can be exported from countries with abundant old-growth to those with few remaining natural forests, if we understand the stand development similarities between regions. In Eurasia, developmental pathways are more site specific and old-growth management will need to be tailored to site-specific conditions (e.g. species composition, prevalence of different disturbance factors). In contrast, the proportion of old-growth in North America would naturally have been determined in many regions by the fire cycle. In terms of conserving old-growth, options for alternative forest management may either be disappearing quickly or be constrained by the legacy of past management decisions.

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