

Stand and landscape scale variability in the amount and diversity of coarse woody debris in primeval European boreal forests



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ABSTRACT

Factors influencing natural variability in coarse woody debris (CWD) as an indicator of ecosystem services in boreal forests need to be better defined. We analysed the CWD characteristics in 194 dynamic primeval boreal forest stands and 3 landscapes under different disturbance regimes. The volume of CWD in the spruce dominated forests linearly increased with increasing annual temperature. The CWD amount and species diversity were higher in spruce than in pine dominated stands. The CWD volume increased in relationship to the types of forest stand dynamics in the order: 'even-aged', 'cohort', 'fine-scale gap'. The CWD volumes were 52.3; 207.0 and 146.8 m³ ha⁻¹ and the dead:live wood volume ratios were 29%, 102% and 60% in the landscapes with disturbance regimes driven by periodic surface fires, cohort-replacing windthrow, and fine-scale gap dynamics, respectively. Mean dead:live wood volume ratios exceeded 100% in spruce stands with even-aged and cohort dynamics and in pine stands with even-aged and fine-scale gap dynamics. The CWD decay class diversity was higher in pine than in spruce dominated stands. The CWD volume distribution by decay class was the most even in forest stands driven by fine-scale gap dynamics in both spruce and pine dominated stands. The CWD position diversity was higher in spruce than in pine dominated forests. Fallen logs dominated among other CWD position types in the spruce dominated stands with cohort and fine-scale gap dynamics and in pine stands with cohort and even-aged dynamics. Pine forests with fine-scale gap dynamics stored the greatest volume of snags. In the spruce dominated stands, the proportion of leaning logs decreased and the proportion of snags and stumps increased among forest dynamic types in the following order: even-aged, cohort, fine-scale gap. The CWD diameter distribution had peaks in small-sized CWD in even-aged spruce stands and pine stands with fine-scale gap dynamics. Mid-sized CWD dominated in spruce stands driven by cohort and fine-scale gap dynamics and pine stands with even-aged and cohort dynamics. The large quantity of CWD that encompassed a wide range of variation in tree species, decay class, position type and size creates a diversity of CWD habitats for saproxylic organisms and ensures functional resilience in boreal forest ecosystems. Our results stress that mean annual temperatures and natural site-specific disturbance regimes should be taken into account when setting targets for CWD volumes and dead:live wood volume ratios for management and restoration of CWD in boreal forests.

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1. Introduction

Coarse woody debris (CWD) has been acknowledged as an important component for maintaining the biodiversity and function of forest ecosystems (Stokland et al., 2012). A lack of CWD is one of the most crucial factors for many threatened species of bryophytes, lichens, fungi, insects and birds (Bader et al., 1995; Ulikzka and Angelstam, 2000; Nilsson et al., 2001; Junninen et al., 2006). The total mass and decomposition rates of CWD

influence net ecosystem production status (Janisch and Harmon, 2002) and nutrient turnover (Laiho and Prescott, 2004; Palviainen et al., 2011). Recently, CWD was selected as an important indicator of forest ecosystem services (Helfenstein and Kienast, 2014).

In managed forests, different forest management practices simultaneously reduce the amount of CWD and change the quality and dynamics of CWD when compared to natural forests at the levels of both individual stands and landscapes. Typically, the volume of CWD in intensively managed boreal forests is less than 10% of comparable types of natural forests, as reviewed by Siitonen (2001). Current CWD patterns are driven by forest management history, current rotation periods, amount and extent of thinning,

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salvage logging, biofuel harvesting and other treatments (Stokland et al., 2012). In regions with a long management history, the CWD volumes are generally lower than in regions where forestry has started more recently (Fridman and Walheim, 2000; Krankina et al., 2002; Shorohova and Tetiukhin, 2004; Junninen et al., 2006; Rondeux and Sanchez, 2009). Forest management does not reduce all CWD uniformly, creating landscapes with variable spatial distribution and continuity of CWD. The heterogeneity in CWD quality found in natural forests is much lower in intensively managed forests. Large-diameter dead trees in advanced stages of decay have been reduced the most (Siitonen, 2001; Similä et al., 2003; Seidling et al., 2014).

Most of the numerous reviews on the relationship of various organisms and dead wood point to the necessity to increase the amount of CWD in managed forest stands and landscapes (Kirby et al., 1998; Ranius and Fahrig, 2006; Davies et al., 2008). The importance of evaluating the different types of CWD, i.e., tree species, decomposition stage, position and diameter for biodiversity (Similä et al., 2003; Heilmann-Clausen and Christensen, 2005; Juutilainen et al., 2014) makes the task more challenging. The CWD quality and temporal continuity of various types, each fulfilling different ecological functions, is necessary to maintain the CWD-dependent species in the long term (Albrecht, 1991; Abrego and Salcedo, 2013). Quantitative recommendations are essential as operational management goals. Without quantitative targets neither verification of progress towards sustainable forest management nor sound adaptive management is possible (Hagan and Grove, 1999). In order to set forest management or restoration targets for the amount and quality of CWD, the critical thresholds for CWD volumes and the ranges of natural variability should be known (Angelstam, 1997; Müller and Bütler, 2010).

Natural variability of CWD volume in forest ecosystems is determined by the balance between inputs (tree mortality and residual timber following harvesting) and outputs (decomposition and removal – e.g., during sanitary cuttings), both of which change during stand development. In unmanaged forests, the complexity and dynamic nature of natural tree mortality and decomposition processes influences the variability in CWD quantity and quality. Tree mortality as a result of natural tree senescence, competition and disturbances (Esseen et al., 1997; Shawn et al., 2008; Kneeshaw et al., 2011) is related to climate, site conditions, composition, structure and dynamics of forest stands and landscapes (Stokland et al., 2012). Some stand-scale case studies demonstrated that the quantity and quality of CWD in unmanaged boreal forest vary according to site productivity and disturbance history (Edman et al., 2007; Brassard and Chen, 2008; Aakala, 2010). Only limited information is available on CWD compositional diversity, i.e. its distribution by tree species, wood position type (snags, fallen and leaning logs, stumps), decay class and size distribution at stand and landscape scales in primeval forests of boreal Eurasia (Jonsson et al., 2005; Roberge et al., 2008; Stokland et al., 2012).

The productivity of forest stands and intensity of biological processes increase from northern to southern boreal vegetation zones (Hyttborn et al., 2005). Moist, productive sites with high stand volumes have more CWD than less productive, dry sites with small stand volumes (Sippola et al., 1998). However, CWD amounts related to the volume of living trees may not follow the same tendency, as wood decomposition rate also increases from north to south (Laiho and Prescott, 2004). More diverse tree species composition and more diverse disturbance regimes may lead to higher compositional diversity of CWD in southern versus northern boreal forests. Differences in tree mortality patterns between vegetation zones may influence differences in CWD types and consequently differences in CWD decomposition rates (Shorohova and Kapitsa, 2014).

Tree species composition of forest stands may affect both tree mortality and CWD decomposition patterns and consequently CWD quantity and quality. In primeval European boreal forest landscapes, Scots pine (*Pinus sylvestris* L., hereafter referred to as pine) dominates mainly on nutrient-poor wet sites or dry sites affected by repeated surface fires leading to cohort dynamics of tree stands. Under more favourable growth conditions, dark coniferous taiga species of spruce (*Picea abies* Karst., *P. fennica*, *P. obovata* Ledeb., hereafter referred to as spruce), Siberian fir (*Abies sibirica* Ledeb.), and Siberian pine (*Pinus sibirica* Du Tour or (Loudon) Mayr) form the forest stands (Shorohova et al., 2009). Thus, higher CWD volumes may be expected in more productive spruce dominated forests compared to pine dominated forests.

Tree mortality patterns can be classified according to the stand-scale dynamic types in European boreal forests related to certain site conditions, tree age and diameter distribution, dominant species, severity of disturbance, time since last disturbance, and spatial structure (Shorohova et al., 2009). Thus, natural stand dynamic types with gradations: 'even-aged dynamics' with or without tree species compositional change, 'cohort dynamics' and 'fine-scale gap dynamics' can be considered as factors influencing CWD quality and quantity in primeval forests. Tree mortality, and consequently the CWD stores are expected to be highest in the forests with even-aged dynamics after stand-replacing disturbances and lowest in the forests with fine-scale gap dynamics (Shorohova et al., 2008; Aakala, 2011). Spatial variation in disturbance severity creates diverse tree mortality patterns, and consequently diverse CWD. Thus, higher CWD compositional diversity can be expected after partial disturbances compared to stand-replacing disturbances, i.e. in the forests with stand structures reflecting cohort and fine-scale gap dynamics compared to forests with even-aged dynamics.

We examined the range of natural variability in the amounts and diversity of CWD in primeval European boreal forests to provide a baseline for CWD management and restoration in forest stands and landscapes. Our specific objectives were: (1) to analyze CWD volumes, dead:live volume ratios, and CWD distribution by tree species, decay class, position and size, as related to climatic and site conditions, dominant tree species in forest stands and type of stand dynamics; (2) to quantify CWD volumes and compositional diversity in forest landscapes with different disturbance regimes namely: the dominance of cohort dynamics after surface fires or windthrows and the dominance of fine-scale gap dynamics. We hypothesized that (1) CWD volume increases with increasing annual temperature, (2) CWD volumes and compositional diversity are higher in spruce than in pine dominated forest stands and under rich rather than poor site conditions; (3) site-specific natural disturbance regimes drive the CWD dynamics; at the stand scale, mean values and amplitude of fluctuation of the CWD volumes decrease and the compositional diversity increases in relationship to the types of inferred stand dynamics in the order: 'even-aged', 'cohort', 'fine-scale gap'; (4) at the landscape scale, the CWD volume decreases depending on the dominant type of natural dynamics in the order: 'wind induced cohort dynamics of spruce forests', 'fine-scale gap dynamics of spruce dominated forests' and 'cohort dynamics related to periodic surface fires in pine forests'.

2. Materials and methods

2.1. Study areas

The studies were performed in 1997–2011 in a subset of eight primeval old-growth forests located in north-western Russia (Fig. 1, Table 1). According to the forest vegetation zoning on the basis of the map of the natural vegetation of Europe (Bonh et al.,

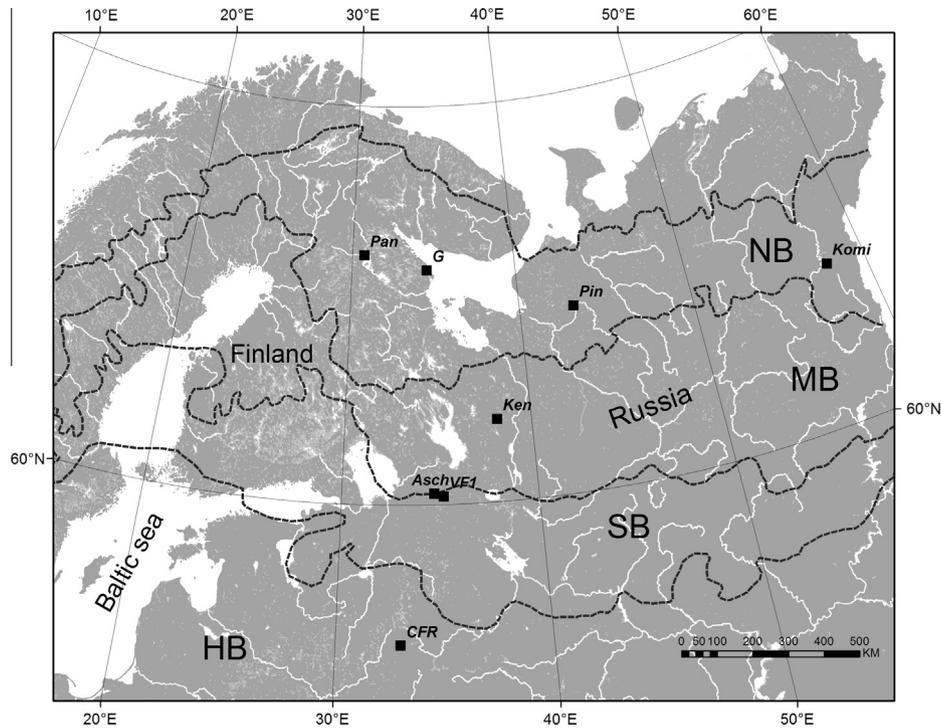


Fig. 1. Location of the study sites. VF1 – ‘Vepssky forest’ reserve of the ‘Vepssky forest’ nature park, Saint-Petersburg region, Asch – ‘Aschozersky’ reserve of the ‘Vepssky forest’ nature park, the Saint-Petersburg region, Pin – ‘Pinezhsy’ reserve, Arkhangelsk region, Ken – ‘Kenozersky’ national park, Arkhangelsk region, G – ‘Gridino’ reserve, the Republic of Karelia, Pan – the sites near ‘Paanajarvi’ national park, the Republic of Karelia, Komi – ‘Ygyd-Va’ national park, Komi Republic, CFR – Central Forest State Natural Biosphere Reserve, Tver region. NB – northern boreal zone, MB – middle boreal zone, SB – southern boreal zone, HB – hemiboreal zone.

Table 1
Characteristics of the study sites.

Site	Vegetation zone ^a	Coordinates	# of sample plots	Mean annual temperature, °C ^b	Mean annual precipitation, mm ^b	Tree species, dominating in the landscape	Recorded fires on the sample plots, years	Windthrow years ^c
VF1	MB/SB	60°14'–60°11'N, 35°09'–35°13' E	59	2.6	750	<i>Picea abies</i>	1797, 1807, 1814, 1824, 1833, 1869, 1879, 1887, 1896, 1906, 1930, 1942, 1947, 1952	1983
Asch	MB/SB	60°16'43''N 34°42'27''E	20	2.6	750	<i>Pinus sylvestris</i>	1932	–
CFR	HB	56°26'–56°31'N, 32°29'–33°29'E	36	3.6	700	<i>Picea abies</i>	1856, 1931, 1934, 1943	1939, 1987
G	NB	65°54'N, 34°37'E	3	0.1	470	<i>Pinus sylvestris</i>	1800, 1897, 1887, 1911, 1968	–
Pan	NB	66°16'N, 30°45'E	4	0	520	<i>Pinus sylvestris</i>	1692, 1765, 1777, 1940	–
Pin	NB	64°40'36'' N 43°11'57''E	14	–0.2	560	<i>Picea obovata</i>	1812, 1860, 1872, 1893, 1906, 1932, 1937, 1961	–
Ken	MB	62°4'39'' N 38°11' 39''E	25	1.5	580	<i>Picea abies</i>	1841	–
Komi	NB	63°94'N, 57°89'E	33	–3	600	<i>Picea obovata</i>	–	–

^a Vegetation zones: NB – northern boreal, MB – middle boreal, SB – southern boreal, HB – hemiboreal.

^b Mean annual temperature and precipitation are given according to the data from nearest meteorological stations during last 50 years.

^c Windthrows caused more than 10% of the living tree volume decrease in the studied landscapes.

^d Landscape-scale CWD patterns were studied on additionally established transects (see Section 2).

2000, 2000/2003) the G, Pan, Pin and Komi sites belong to the northern boreal vegetation zone, Ken belongs to the middle boreal, and CFR belongs to the hemiboreal vegetation zone. The VF1 and Asch are located on the border between middle and southern boreal zones (Fig. 1).

Geomorphologically, the VF1 and Asch sites are situated on the Russian Plain, Valdaisko-Onezhskaya ridge. The dominating relief types are lacustrine glacial and morainic plains and morainic hills.

The G and Pan sites are situated on the Fennoscandian Shield on the aqueoglacial and marine plains as well as denudation-tectonic with large ridge blocks relief types. The Ken sites are situated on the border between the Fennoscandian Shield and the Russian Plain with lacustrine glacial and morainic plains as the main relief types. The Pin sites are located on the Belomor–Kuloi Plateau with active karst processes and small ridge-hilly morainic relief. The Komi sites are situated on foothill

landscapes of the western slope of the northern Ural Mountains. The soils in the VF1, Asch, Ken, Pin and Komi sites are mostly coarse humus podzolic sandy loam and loam on morainic tills but peaty humus soils also occur. In the CFR, the soils are podzolic and more fertile on limestone bedrock and sod-podzolic. The soils on the G sites are podzols, and those on the Pan sites are podzolic sandy loam formed on rocks (Fedorchuk et al., 1998; Taskaev, 2001; Gromtsev et al., 2003; Torkhov, 2003).

The forested areas of VF1, Ken and CFR landscapes are dominated by Norway spruce (*Picea abies* Karst., *P. fennica*) with an admixture of birch (*Betula pubescens* Ehrh. and *Betula pendula* Roth.), aspen (*Populus tremula* L.) and, in some cases, Scots pine (*Pinus sylvestris* L.). In the CFR, the broadleaved species Norway maple (*Acer platanoides* L.) and European white elm (*Ulmus laevis* Pall.) also occur. The Asch, Pan and G sites are dominated by Scots pine mixed with Norway spruce and birch. The Pin forests are mostly mixed Norway spruce, Scots pine, Siberian larch (*Larix sibirica* Ledeb.) and birch. The Komi forests are mixed Siberian spruce (*Picea obovata* Ledeb.), Siberian fir (*Abies sibirica* Ledeb.), Siberian pine (*Pinus sibirica* Du Tour or (Loudon) Mayr) and birch. According to the information from the archives, the forests of all sampled sites have never been commercially harvested.

The main forest types in the study sites were herb-rich, *Oxalidosum*, *Equisetosum*, *Hylocomiosum-Myrtillosum*, *Myrtillosum*, *Cladinosum*, *Cladinoso – Vacciniosum*, *Ledosum*, *Polytrichoso-Myrtillosum* and *Sphagnoso-Myrtillosum* according to the classification of forest ecosystems in the North-West of Russia (Fedorchuk et al., 2005).

2.2. Site and sample plot description

The stand-scale inventories were made in 194 permanent and temporal 0.1 ha and more sample plots (Appendix A).

Based on indicator plant species and soil characteristics the study sites were classified by forest type and then grouped according to favorability of site conditions (Table 2).

Disturbance history for the study sites was reconstructed by analysing combined information from historical archives, forest inventory data, aerial images from different years and previous research (Fedorchuk et al., 1998; Smirnova and Shaposhnikov, 1999; Taskaev, 2001; Gromtsev et al., 2003; Torkhov, 2003). In the field, all signs of past disturbances were recorded (Lorimer, 1985). We cored 2–5 trees from each cohort to determine the stand

Table 2
Number of sample plots for the stand-scale inventories by tree species dominating in forest stands, type of forest stand dynamics and site conditions.

Tree species	#	Type of stand dynamics	#	Site conditions*	#
Spruce	157	Even-aged	39	Poor	5
				Moderate	26
				Favourable	8
	Cohort	65	65	Poor	21
				Moderate	22
				Favourable	22
	Fine-scale gap	50	50	Poor	33
				Moderate	3
				Favourable	14
Pine	37	Even-aged	3	Poor	1
				Moderate	2
	Cohort	27	27	Poor	22
				Moderate	4
	Fine-scale gap	7	7	Poor	6
				Moderate	1

* Favourable site conditions: herb-rich and *Oxalidosum* forest types. Moderate site conditions: *Equisetosum*, *Hylocomiosum-Myrtillosum*, *Myrtillosum* forest types. Poor site conditions: *Cladinosum*, *Cladinoso – Vacciniosum*, *Ledosum*, *Polytrichoso-Myrtillosum*, *Sphagnoso-Myrtillosum* forest types.

age structure type. The main types of age structure of a stand were differentiated by Dyrenkov (1984) as indicated below. Relative even-aged stands are characterised by the age variation of the overstorey trees not exceeding 40 years. Relative uneven-aged stands; the age distribution of the predominant tree species is continuous up to over 200 years, but 50–90 per cent of the total biomass is concentrated in one of the 40-year cohorts. The diameter and age distributions have several peaks. In the all aged (absolutely uneven-aged) stands, all 40-year groups of the predominant tree species population up to the lifespan limit are present, but none of them exceeds 50 per cent of the total biomass. The stand successional phase was determined according to visual characteristics (size and distribution of canopy gaps, presence of snags vs. uprooted and broken trees, tree regeneration, over- and understorey size structure: Fedorchuk et al., 2011). Fire scars from living trees and CWD were sampled and then cross-dated in the lab to record fire history. In cross-dating, the master chronologies were created from growth rings of living trees. A total of 37 fires were recorded in the vicinity of the sample plots (Table 1). Recent windthrow events were dated using the growth release response of suppressed trees and saplings and dating treefall scars (Dynesius and Jonsson, 1991).

In the permanent sample plots, volume of all trees with diameter at the height of 1.3 m (DBH) more than 6 cm calculated based on the measurements of DBH and height using taper functions. In the temporal sample plots, mean basal area of living trees, by species and age cohorts, was calculated from 3 relascope plot measurements. The tree age cohorts (40 years) were identified visually; 3 trees were randomly selected from each cohort and cored to estimate tree ages. Mean DBH and height of the three measured trees were calculated to represent each tree species age cohort. The volume of each cohort was calculated by multiplying basal area by mean species height (Tetioukhin et al., 2004). Finally, all the volumes were summed up. The stand growing stock varied from 0 in the gap after stand replacing windthrow in CFR to 502 m³ ha⁻¹ in over-mature mixed even-aged stand in VF1. All forest stands were uneven-aged with the tree age ranging from 1 to 460 years. The period of time since last disturbance determined by dating fire scars or uprooted trees varied from 1 to 380 years.

Finally, depending on time since disturbance, prevailing disturbance regime, site type and stand characteristics, the forest stands sampled were classified into 3 types of natural stand dynamics: (1) even-aged, (2) cohort dynamics and (3) fine-scale gap dynamics (Shorohova et al., 2009) (Table 2). Even-aged stands consisted of a successional chronosequence in gaps after windthrows or fresh burns to over-mature stands up to 200 years old. Stands undergoing cohort dynamics consisted of uneven-aged forest stands being at different stages after cohort-replacing windthrows or surface fires. Stands driven by fine-scale gap dynamics consisted of all-aged stands developed over 300 years without significant disturbances.

2.3. CWD sampling, calculations and data analysis

2.3.1. Stand scale

In total, stand-level CWD inventories were conducted in 194 forest stands. In the permanent sample plots, the heights and diameters of all stumps, standing dead trees (snags), fallen and leaning logs were measured at the stem base, at 1.3 m and at the top. Assuming a conical shape for each stump, its volume (V_{st}) in m³ was calculated as follows:

$$V_{st} = \frac{\pi h}{3} (R^2 + Rr + r^2) \quad (1)$$

where h is the height of the stump in metres; R and r are respectively the maximum and minimum radii in metres.

The log and snag volumes (V_{sn}) were calculated using the formula:

$$V_{sn} = SHF \quad (2)$$

where S is the snag basal area at breast height, m^2 , HF is the species-specific height, m (Tetioukhin et al., 2004).

In the temporal sample plots, the line intercept sampling was used in the downed wood (fallen and leaning logs) inventory (Ståhl et al., 2001). The volume of downed wood was calculated as:

$$V = \left(\frac{\pi^2}{8} \sum d_i^2 S \right) \sum L_j \quad (3)$$

where V is the volume of the downed wood of the i -th decay class, d_i is the diameter of the i -th wood unit at the point of interception of the survey line, L_j is the length of the survey line (in our case 50 m, or in some cases 100 m), and S is the area of the stand. The snags and stumps were measured on 4-m wide and 50 (100) m long transects. Their volumes were calculated using formulae (1) and (2).

For the CWD inventory we used the decay class system described in Shorohova and Shorohov (2001). Briefly, these five decay classes can be characterised as:

- (1) Volume of decomposed wood is 0–10%; the remaining wood is sound. Bark may be present or absent due to bark beetle activity, sporocarps of wood decay fungi are absent. Only epiphytic lichens may be present.
- (2) Slightly decomposed wood accounts for 10–100%, the remaining wood is sound. Sporocarps of wood decay fungi and epixylic mosses may be present.
- (3) Decayed wood (soft rot) accounts for 10–100%, remaining wood is slightly decayed or sound. Inclusions of mycelium, small pits and cracks occur. Wood may be crumbled or broken. Sporocarps of wood decay fungi occur. Coverage of mosses, lichens and higher plants can be up to 100%. Tree seedlings may be present.
- (4) All wood is well decayed. Wood samples of white rot are fragmented into separate fibres. Humification processes are beginning in the brown rot wood. Some pieces of wood have been lost via fragmentation and complete decomposition. Other features are the same as in decay class 3.
- (5) Types and borders of rot are difficult to distinguish. Pieces of CWD have significantly changed shape. Humification is continuing. Sporocarps of wood decay fungi are absent or very old. Vegetation on the trunk is similar to the ground vegetation, but with a higher number of tree seedlings and undergrowth.

The Shannon index (H) of CWD compositional diversity was calculated as:

$$H = - \sum_{i=1}^n p_i \log_2 p_i \quad (4)$$

where p_i is the volume proportion of the i -th tree species, decay class, position (according to the following four categories: fallen logs, leaning logs, snags, and stumps) in total CWD volume and/or number.

Distribution of the variables CWD volume, dead:live wood volume ratio, CWD species, decay class, position and diameter as well as the Shannon indexes were checked for normality and log-transformed if necessary. The effect of mean annual temperature on the CWD volume was tested using linear regression analysis. The effects of site conditions (poor, moderate, favourable), dominating tree species (spruce vs. pine) and type of forest stand dynamics (even-aged, cohort and fine-scale gap dynamics) and their interrelation were tested for on the above variables. We used

analysis of variance (one-way ANOVA or factorial ANOVA, with type III sum of squares for unbalanced design when the number of observations for different groups were unequal) and Duncan's post hoc tests. Based on the post hoc tests the groups were pooled together if the differences between means were not statistically significant.

2.3.2. Landscape-scale

Landscape-scale CWD patterns were studied only for the spruce dominated forests of Vepssky Forest and Kenozersky National Park and the Scots pine dominated forest of Aschozersky Reserve. Forest types in the study area of the Vepssky Forest were *Myrtillosum*, *Polytrichoso-Myrtillosum* and *Sphagnoso-Myrtillosum*. Forest types in the study area in Kenozersky National Park were herb rich, *Oxalidosum*, *Equisetosum*, *Myrtillosum*, *Ledosum*, *Polytrichoso-Myrtillosum* and *Sphagnoso-Myrtillosum*. Forest types in the study area in the Aschozersky Reserve were *Cladinosum* and *Cladinoso – Vacciniosum*. The disturbance regimes in the research areas can be characterised as follows: cohort-replacing windthrows in the Vepssky Forest; surface fires inducing cohort dynamics in the Aschozersky landscape; and primarily fine-scale gap dynamics in the Kenozersky landscape.

The stand and CWD characteristics were inventoried on 20 m wide transects in south-north and west-east directions with the total length 10,975, 1,250 and 1,550 m, in the Vepssky, Aschozersky, and Kenozersky landscapes, respectively. The methods for CWD inventory included line intercept sampling for fallen and leaning logs combined with transect sampling for snags and stumps. Calculations were made using formulae (1)–(4).

3. Results

3.1. The amounts of CWD in forest stands

Volumes of CWD varied greatly among the plots, ranging from 2 to 1267 $m^3 ha^{-1}$. The greatest CWD values were found after stand-replacing windthrows in highly productive forests in CFR.

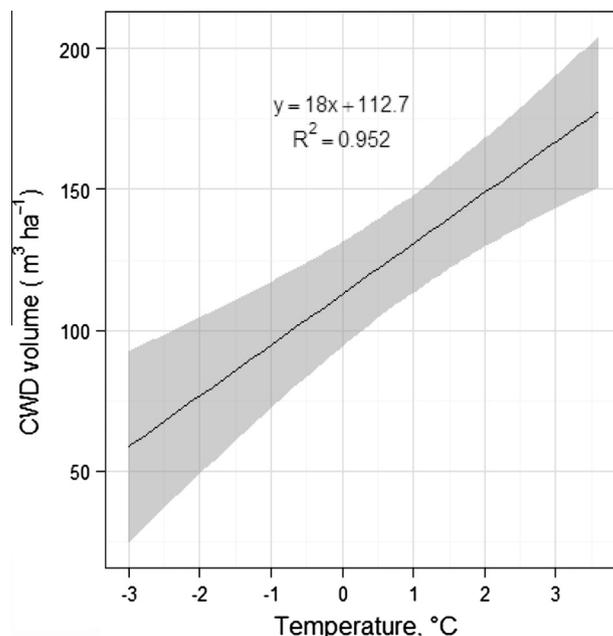


Fig. 2. CWD volumes in the spruce dominated stands including successional stages with the dominance of birch and aspen and mixed coniferous stands with admixture of Siberian pine, fir and Siberian larch averaged by study sites depending on the annual temperature.

The CWD volume in spruce dominated stands linearly increased with increasing mean annual temperature (Fig. 2). In pine dominated stands, the CWD volume did not depend on the annual temperature within the studied range (-0.2 ± 2.6 °C).

The variation in CWD volume and dead:live wood volume ratio depended on the interrelated characteristics of forest stands (Table 3). The amount of CWD was greater in spruce than in pine dominated stands and under moderate and favourable than under poor site conditions (Tables 4 and 5). The greatest CWD volumes were found in even-aged spruce dominated stands, and the lowest volumes were found in pine dominated stands driven by cohort and fine-scale gap dynamics (Table 4). Variation in CWD volumes was greater in pine than in spruce stands. It decreased, depending on the type of forest stand dynamics in the order: even-aged – cohort dynamics – fine-scale gap dynamics (Table 4).

The pattern was different for dead:live wood volume ratios. In spruce dominated stands, the ratios were the lowest in the stands with fine-scale gap dynamics. CWD volumes were greater than volumes of living trees in the spruce stands with even-aged and cohort dynamics (Table 4). Pine dominated stands with cohort dynamics were characterised by lower CWD volumes compared to the volume of living trees. In pine stands with even-aged and fine-scale gap dynamics, CWD volume exceeded the volume of living trees (Table 4). Variation in dead:live wood volume ratio was greater in pine than in spruce dominated stands (Table 4) and in the stands driven by even-aged and gap dynamics compared to stands driven by cohort dynamics (Table 4).

3.2. Compositional diversity of CWD in forest stands

The compositional diversity of CWD varied greatly as well. Shannon index values ranged from 0 to 2.03, 2.27 and 1.98 for CWD distribution by tree species, decay classes and position, respectively.

The CWD species diversity depended on the site conditions, type of forest stand dynamics and the interrelationship between site conditions, stand composition and type of forest stand dynamics (Table 3). Similar to the amount of CWD, the CWD species diversity increased with the site quality and was higher in spruce than in pine dominated stands (Tables 4 and 5). The lowest CWD species diversity was recorded in pine dominated stands driven by cohort dynamics. In spruce stands, CWD species diversity did not depend on the type of forest stand dynamics (Table 3). Variation in CWD species diversity was higher in spruce compared to pine dominated stands, and in even-aged forest stands compared to forest stands with cohort and fine-scale gap dynamics.

Table 3

ANOVA results for the effects of ecosystem attributes on CWD characteristics. Factors significant at the $p < 0.05$ level are denoted by bold font.

Variable	Site conditions			Site conditions * Type of stand dynamics			Tree species			Type of stand dynamics			Tree species * Type of stand dynamics		
	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df
CWD volume	4.6^a	0.011	2	1.9	0.116	8	6.6	0.011	1	6.0	0.003	2	9.0	<0.001	4
dead:live wood volume ratio	0.6	0.513	2	3.3^b	0.012	8	0.8	0.361	1	5.8	0.004	2	19.9	<0.001	4
Shannon index for species	5.0	0.007	2	8.6	<0.001	8	<0.001	0.984	1	4.1	0.019	2	8.1	<0.001	4
Shannon index for decay classes	0.1	0.904	2	1.1	0.369	8	3.9	0.050	1	2.4	0.010	2	1.4	0.247	4
Shannon index for position	0.4	0.674	2	0.5	0.712	8	27.1	<0.001	1	1.8	0.163	2	3.2	0.042	4
CWD distribution by tree species	3.4	0.033	2	–	–	–	37.8	<0.001	1	1.7	0.183	2	–	–	–
CWD decay class distribution	<0.001	0.999	2	–	–	–	14.2	<0.001	1	10.1	<0.001	2	–	–	–
CWD distribution by position type	0.003	0.997	2	–	–	–	46.7	<0.001	1	34.8	<0.001	2	–	–	–
CWD DBH distribution	30.9	<0.001	2	–	–	–	13.0	<0.001	1	42.5	<0.001	2	–	–	–

– The analysis is too complicated to be performed.

^a Only the difference between groups: 'poor' and 'favourable and moderate' site conditions was significant at $p < 0.05$.

^b Only the differences between groups: 'favourable site conditions, cohort dynamics' and 'poor site conditions, cohort dynamics'; 'favourable site conditions, cohort dynamics' and 'poor site conditions, even-aged dynamics'; 'favourable site conditions, cohort dynamics' and 'poor site conditions, fine-scale gap dynamics'; 'favourable site conditions, fine-scale gap dynamics' and 'poor site conditions, cohort dynamics' and were significant at $p < 0.05$.

Table 4

CWD mean and (SE) characteristics in stands with different tree species composition and dynamics.

Variable	Even-aged	Cohort	Fine-scale gap	Mean
CWD volume ($m^3 ha^{-1}$)	199.5 (30.3)	139.2 (10.3)	73.0 (5.5)	132.1 (8.97)
Spruce dominated stands	210.5 (36.0)	128.4 (8.1) ^a	–	147.7 (10.8)
Pine dominated stands	152.1 (32.6)	68.0 (13.5) ^a	–	74.4 (13.1)
dead:live wood volume ratio (%)	134.9 (21.2)	78.5 (9.2) ^a	–	90.6 (8.65)
Spruce dominated stands	115.3 (10.8) ^a	39.1 (4.3)	–	89.6 (7.86)
Pine dominated stands	178.8 (51.3) ^a	34.1 (5.6)	178.8 (51.3) ^a	73.2 (17.58)
Shannon index for species	0.76 (0.08)	0.52 (0.04) ^a	–	0.56 (0.04)
Spruce dominated stands	0.61 (0.04) ^a	–	–	0.61 (0.04)
Pine dominated stands	0.73 (0.14) ^a	0.19 (0.10)	0.73 (0.14) ^a	0.34 (0.09)
Shannon index for decay classes	1.71 (0.03) ^a	–	–	1.71 (0.03)
Spruce dominated stands	1.43 (0.10) ^a	–	–	1.43 (0.10)
Pine dominated stands	1.78 (0.03) ^a	–	–	1.78 (0.03)
Shannon index for position	1.47 (0.03) ^a	–	–	1.47 (0.03)
Spruce dominated stands	1.54 (0.03) ^a	–	–	1.54 (0.03)
Pine dominated stands	1.16 (0.09) ^a	1.28 (0.09)	1.16 (0.09) ^a	1.25 (0.07)
Mean CWD diameter at 1.3 m (cm)	12.5 (0.5)	17.4 (0.3)	14.2 (0.3)	15.6 (0.2)
Spruce dominated stands	12.0 (0.5)	19.6 (0.3)	16.2 (0.3)	15.9 (0.2)
Pine dominated stands	24.0 (1.2)	15.2 (0.6)	12.7 (0.8)	14.3 (0.5)

^a No statistically significant differences between the stands with different dynamics at $p < 0.05$.

Table 5

CWD mean and (SE) characteristics in stands with different site conditions.

Variable	Poor	Moderate	Favourable
CWD volume ($m^3 ha^{-1}$)	82.0 (6.6)	174.0 (14.3) [^]	–
Shannon index for species	0.39(0.05)	0.62 (0.07)	0.81 (0.07)
Mean CWD diameter at 1.3 m (cm)	15.2 (0.3)	20.5 (0.5)	16.9 (0.3)

[^] No statistically significant differences between the stands under moderate and favourable site conditions at $p < 0.05$.

CWD species distributions depended mainly on dominant tree species in the forest stands (Table 3, Fig. 3). Mainly coniferous CWD was found in the forest stands studied (Fig. 3).

The CWD decay class diversity was higher in pine than in spruce dominated stands (Table 4), independent of site conditions and type of forest stand dynamics (Table 3). Variation in CWD decay class diversity was higher in pine compared to spruce dominated stands, and in the stands driven by even-aged and gap dynamics compared to the forest stands driven by cohort dynamics. CWD volume distribution by decay class varied depending on species composition and type of dynamics of the forest stands (Table 3). It was most even in the forest stands driven by fine-scale gap dynamics in both spruce and pine dominated stands (Fig. 4). Even-aged and cohort dynamics resulted in different CWD decay class distributions in the spruce and pine dominated stands. In these forest stands, CWD distribution by decay class in spruce stands was much more even compared to pine stands. In pine stands with even-aged dynamics, CWD volume gradually increased from the 1st to the 5th decay classes. In pine stands with cohort dynamics, the tendency was the opposite – the greatest amount of CWD was recorded in the 1st decay class.

The CWD position diversity depended on the species composition in forest stands and the type of stand dynamics (Table 3). It was higher in spruce than in pine dominated forests (Table 4). In pine stands, position diversity was higher after cohort replacing disturbances than during even-aged and fine-scale gap dynamics. In spruce stands, it did not depend on the type of forest stand dynamics (Table 4). The variation in CWD position diversity was in pine than in spruce dominated stands (Table 4). CWD distribution by position type depended on the same factors as the CWD decay class distribution, namely species composition and forest stand dynamics type (Table 3). Fallen logs dominated among other CWD position types in the spruce dominated stands with cohort and fine-scale gap dynamics and in pine stands with cohort and even-aged dynamics. In the spruce dominated stands, the proportion of leaning logs decreased and the proportion of snags and stumps increased from even-aged to cohort to fine-scale gap forest

types. Pine forests with fine-scale gap dynamics stored more CWD volumes as snags compared to other CWD position types (Fig. 4).

The diameter distribution of CWD pieces depended on all studied factors (Table 3). There were peaks in small-sized CWD in even-aged spruce stands and pine stands with fine-scale gap dynamics. Mid-sized CWD dominated in the spruce stands driven by cohort and fine-scale gap dynamics and in pine stands with even-aged and cohort dynamics (Fig. 4). In spruce dominated forest stands, the greatest mean diameter of CWD was recorded for the stands with cohort dynamics. In pine stands, the greatest mean bole diameter was recorded in stands with even-aged dynamics (Table 4).

3.3. Landscape scale patterns

The CWD volumes and dead:live wood volume ratios decreased from 'wind induced cohort dynamics of spruce forests' to 'cohort dynamics related to periodic surface fires in pine forests' to 'fine-scale gap dynamics of spruce dominated forests', i.e., from the Vepsky, to the Aschozersky, and Kenozersky landscapes, respectively (Table 6). The greatest CWD species, decay class and position diversity as well as the greatest CWD mean diameter were found in the Kenozersky landscape (Table 6, Fig. 5).

4. Discussion

4.1. The variability in the amounts of CWD in natural boreal forest stands and landscapes

The stand-scale volumes of CWD and the dead:live wood volume ratios exceed the ranges reported for other boreal old-growth forest stands in Fennoscandia and the Russian Plain (Siitonen, 2001; Hahn and Christensen, 2004; Junninen et al., 2006; Storozhenko, 2011; Aakala, 2010, 2011). In agreement with the results acquired by Merganičová and Merganič (2010), we found CWD volumes of more than $400 \text{ m}^3 \text{ ha}^{-1}$ in the post-disturbance forest stands at the 'breakdown' successional stage. Greater CWD volumes and greater proportion of snags in Russian old-growth boreal forest stands compared to European old-growth boreal forest stands can be explained by the differences in the landscape matrix. Russian sites represent primeval forest landscapes with diverse natural disturbance regimes. European, especially Western European sites, are mainly 'islands' in fragmented landscapes with intensively managed forests and rare severe disturbances. The CWD characteristics acquired in our study are close to those for boreal coniferous and mixed old-growth forests in North America (Hély et al., 2000; Pedlar et al., 2002; Harper et al., 2003).

The landscape scale CWD volume and the dead:live wood volume ratio estimates in our pure Scots pine forest landscape are similar to those earlier reported for comparable Scots pine dominated landscape in Russian Karelia (Karjalainen and Kuuluvainen, 2002). The CWD volume in our spruce dominated forest landscape in the Arkhangelsk region, where fine-scale gap dynamics prevail, is somewhat greater than average CWD volumes reported for a spruce forest landscape dominated by fine-scale gap dynamics in Komi Republic (Kuuluvainen et al., 2001).

We hypothesized that the CWD volume increases with increasing annual temperature. This was confirmed for spruce dominated stands. In the temperature range from -3 to $+3$ °C, the difference in mean CWD volume can reach 30%. The absence of temperature effect on the CWD volumes in pine dominated stands can be explained by possible consumption of CWD by fire as well as by too narrow temperature range and insufficient sample size.

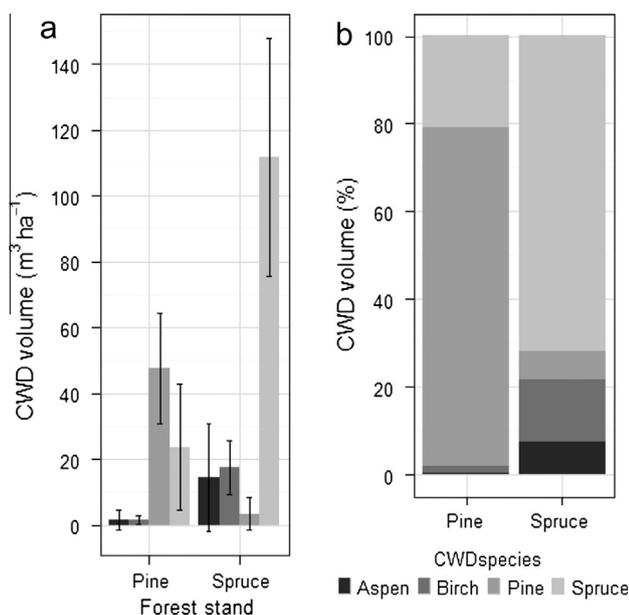


Fig. 3. Distribution of (a) CWD volume by tree species and (b) percent of CWD tree species in total CWD volume in the pine dominated stands and spruce dominated stands, including successional stages with the dominance of birch and aspen and mixed coniferous stands with admixture of Siberian pine, fir and Siberian larch. Error bars are SE.

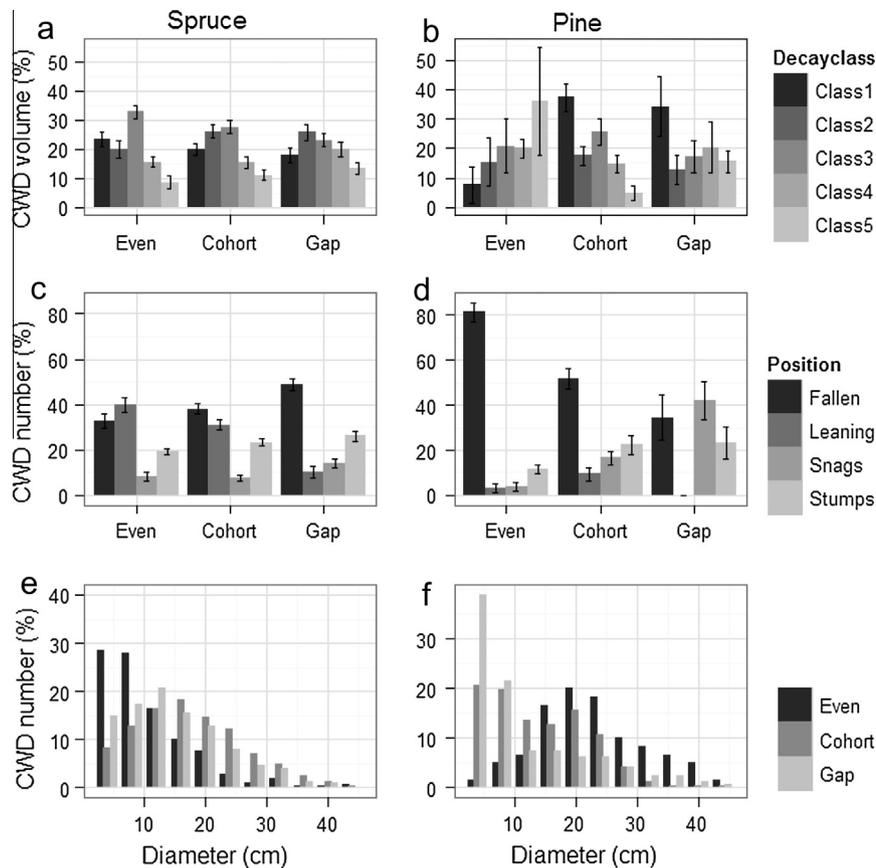


Fig. 4. Stand-scale CWD patterns. Distributions of CWD volume by decay classes (a and b) and CWD number by position (c and d) and diameter (e and f) in the spruce dominated stands, including successional stages with the dominance of birch and aspen and mixed coniferous stands with admixture of Siberian pine, fir and Siberian larch and the pine dominated stands with different types of dynamics. Error bars are SE.

Table 6

The CWD characteristics in studied forest landscapes. Asch – cohort dynamics related to periodic surface fires in pine forests, VF – wind induced cohort dynamics of spruce dominated forests and Ken – fine-scale gap dynamics of spruce dominated forests.

Variable	Asch	VF	Ken
CWD volume ($\text{m}^3 \text{ha}^{-1}$)	52.3	207	146.8
Dead:live volume ratio (%)	29	102	60
Shannon index for species	0	0.46	0.52
Shannon index for decay classes	1.73	2.17	2.3
Shannon index for position	1.7	1.82	1.91
Mean diameter at 1.3 m (cm)	14.4	17.6	19.7

Our hypothesis that the dominant tree species in the forest stands would influence the CWD volume was only partly supported by our results. Our hypothesis that dead:live wood volume ratio would be greater in pine than in spruce dominated forest stands was not supported at all. In boreal Europe, mean CWD volumes in spruce and pine forests did not differ either (Siitonen, 2001; Hahn and Christensen, 2004). In contrast, in North American boreal forest, tree species composition of forest stands significantly influences the CWD volumes (Pedlar et al., 2002).

The difference between CWD volumes in the forest stands growing under ‘poor’ and ‘favourable and moderate’ site conditions was independent of the tree species dominating in the forest stands. Site moisture and productivity positively influenced CWD volumes, which is in agreement with the results acquired for other boreal forests, e.g. Scots pine dominated forests in Karelia (Karjalainen and Kuuluvainen, 2002), black spruce forests in Quebec and Ontario (Harper et al., 2003).

4.2. Are ‘real’ CWD volumes in equilibrium?

Although annual tree mortality may vary widely, equilibrium volumes of CWD can be modelled simply by combining information on average input rates and decomposition rates (Siitonen, 2001; Ranius et al., 2003). The forest stands driven by fine-scale gap dynamics may be assumed to be in a state of equilibrium.

Mean annual tree mortality rate for VF1 Norway spruce dominated stands with all-aged structure, driven by fine-scale gap dynamics, is $3 \text{ m}^3 \text{ha}^{-1}$ (Shorohova et al., 2008). Mean decomposition rate for spruce fallen logs in the same forests is 0.032 yr^{-1} (Shorohova and Kapitsa, 2014). According to the model of equilibrium (Siitonen, 2001), CWD volumes of $94 \text{ m}^3 \text{ha}^{-1}$ can be expected. That volume is greater than the mean CWD volume found in the VF1 Norway spruce forests with fine-scale gap dynamics ($68 \text{ m}^3 \text{ha}^{-1}$, range $42\text{--}123 \text{ m}^3 \text{ha}^{-1}$) and less than the mean for Norway spruce dominated forest stands driven by fine-scale gap dynamics from all study sites ($128 \text{ m}^3 \text{ha}^{-1}$, range $11\text{--}196 \text{ m}^3 \text{ha}^{-1}$).

Mean mortality rate for northern boreal Scots pine forests in Grid sites under poor site conditions is $0.1 \text{ m}^3 \text{ha}^{-1}$, and the mean decomposition rate is 0.011 yr^{-1} (Shorohova, unpubl.). According to Siitonen (2001), the equilibrium CWD volume is $9 \text{ m}^3 \text{ha}^{-1}$. In this study, the CWD volumes in Scots pine stands in Grid sites under poor site conditions averaged $76 \text{ m}^3 \text{ha}^{-1}$, varying from 47 to $112 \text{ m}^3 \text{ha}^{-1}$.

Such differences between the modelled and empirical figures support the conclusion made by Ranius et al. (2003) that modelled equilibrium CWD volumes could be used to predict averages for larger unmanaged forest landscapes unaffected by large

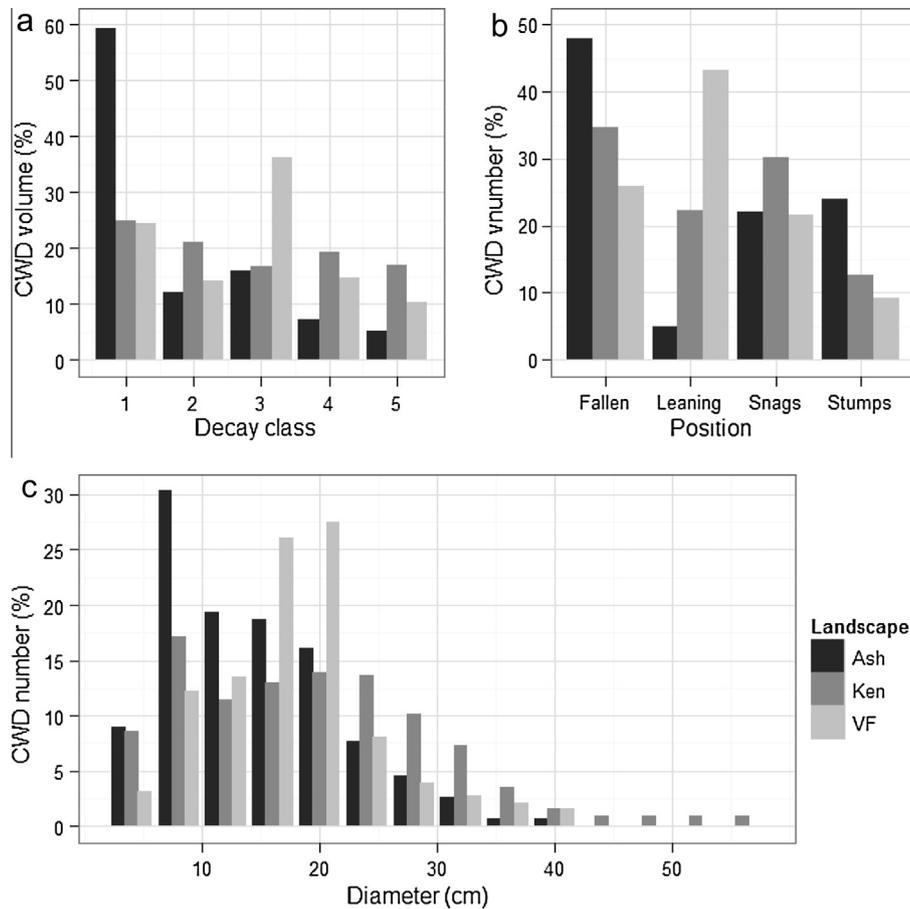


Fig. 5. Landscape-scale CWD patterns. Distributions of CWD volume by a) decay classes and CWD number by b) position and c) diameter in the landscapes characterised as 'cohort dynamics related to periodic surface fires in pine forests', 'wind induced cohort dynamics of spruce forests', and 'fine-scale gap dynamics of spruce dominated forests', i.e. in Aschozersky (Ash), Vepscky (VF), and Kenozersky (Ken) landscapes, respectively.

disturbances, while no model can predict the amount of CWD at the individual plot level.

4.3. Diversity of CWD

We hypothesized that the compositional diversity of CWD be higher in spruce than in pine dominated forest stands and under rich rather than poor site conditions. Shannon index values portraying the diversity of CWD tree species, decay class, position and size distributions confirmed this only partly.

Our hypotheses about higher CWD species diversity and variation in spruce than in pine dominated stands and under rich than poor site conditions were confirmed. Primeval boreal 'dark coniferous' forest stands are more diverse in terms of tree species composition as compared to 'light coniferous' ones (Shorohova et al., 2009). For example, the Aschozersky Scots pine forest landscape had only pine CWD. CWD species distributions follow the same trend. Highly productive forest stands have more diverse tree species and consequently more diverse CWD species compared to the forest stands with low productivity. The relatively low proportion of deciduous CWD may be explained by a generally low proportion of deciduous tree species in primeval boreal forest stands (Kneeshaw et al., 2011).

In agreement with other studies (Storozhenko, 2011), the CWD decay class diversity in our forest stands did not depend on site conditions. Refuting our hypothesis, the CWD decay class diversity and its variation were higher in pine than in spruce dominated forest stands. These results can be explained by high temporal continuity and variation of tree mortality processes in

primeval forests. High variability in proportions of earlier vs. later decay classes of CWD in natural old-growth European boreal forests was reported by Sippola et al. (1998), Kuuluvainen et al. (2001), Karjalainen and Kuuluvainen (2002), Rouvinen and Kouki (2002), Storozhenko (2011) and Aakala (2010). Modelled CWD decay class distribution, based on constant tree mortality and wood decomposition rates, has an uneven shape (Ranius et al., 2003). In our study, the variable shape of CWD distribution curves by decay classes reflects variable disturbance history (and consequently mortality rates) in forest stands, and different rates of decomposition for CWD of different tree species and positions.

In our study, the mean proportion of snags varied from 0% to 72% at the stand scale and from 21% to 30% at the landscape scale, which is in agreement with the mean proportion of snags previously reported in boreal old-growth forests (Sturtevant et al., 1997; Siitonen, 2001; Nilsson et al., 2002; Karjalainen and Kuuluvainen, 2002; Pedlar et al., 2002; Harper et al., 2003). The high diversity tree of mortality modes in all study sites explains the independence of CWD position diversity on site conditions. Spruce trees show more variable mortality modes (stem breakage, uprooting, and decline) compared to pine trees that mostly die standing and form long-lasting snags (Liu and Hytteborn, 1991). A greater proportion of snags in pine than in spruce dominated forests driven by cohort and fine-scale gap dynamics is also in agreement with the previous results for boreal Fennoscandia (Siitonen, 2001; Karjalainen and Kuuluvainen, 2002). These results could be explained by the differences in prevailing tree mortality modes for spruce and pine.

All the forest stands and landscapes studied were characterised by the high availability of CWD in all size groups. However, the CWD size distribution varied greatly depending on all factors examined, deviated from the pattern of negative exponential curve observed for old-growth European boreal forests (Nilsson et al., 2002) or predicted for equilibrium state (Ranius et al., 2003). Irregular CWD diameter distributions were found also in different European old-growth forests (Karjalainen and Kuuluvainen, 2002; Rouvinen and Kouki, 2002).

4.4. CWD in natural disturbance dynamics

As we hypothesized, the site-specific natural disturbance regimes drove the CWD dynamics at the stand scale. The mean values and amplitude of fluctuation of the CWD volumes and dead:live wood volume ratios decreased in connection with the types of stand dynamics from 'even-aged' to 'cohort' to 'fine-scale gap'. However, CWD volumes did not differ between spruce and pine dominated forests driven by cohort and fine-scale gap dynamics. This result suggests that, in terms of CWD volumes, in the stands with the same tree species composition, the factor 'disturbance' may have only two gradations: 'stand replacing' and 'partial'.

Regarding the role of disturbance history in CWD abundance, the dead:live wood volume ratio is a more meaningful measure than absolute volume, due to differences in stand productivity. The stand-scale patterns for dead:live wood volume ratios differed for those for CWD volumes. The high ratio of 137% in spruce dominated stands with even-aged and cohort dynamics can be explained by high wind-induced mortality in the productive spruce stands. In pine dominated stands with cohort dynamics, where the ratio is only 34%, much CWD was most likely destroyed by fires. In pine stands with even-aged and fine-scale gap dynamics, the ratio of 179% is most likely related to CWD accumulation resulting from the slow decomposition rates of pine CWD compared to CWD of other tree species.

In general, the interrelationship between CWD patterns and disturbance regimes in boreal forests is not clear. We did not find any interrelationships between the time since last windthrow or fire and volumes of CWD. Karjalainen and Kuuluvainen (2002) did not find a relationship between the calculated fire history parameters, time since last fire and mean fire return interval and CWD volume in a natural Scots pine forest in Karelia. In contrast, in North America, time since fire is one of the most important predictor of CWD accumulation (Hély et al., 2000; Harper et al., 2003). Old-growth European boreal forests are characterised by more complex disturbance regimes with the prevalence of patchy disturbances compared to North American boreal forests with the dominance of either fine-scale gap dynamics or stand-replacing disturbances (Kneeshaw et al., 2011; Shorohova et al., 2011).

On the landscape scale, we hypothesized that the CWD volume would decrease depending on the dominating type of dynamics from 'wind induced cohort dynamics of spruce forests' to 'fine-scale gap dynamics of spruce dominated forests' to 'cohort dynamics related to periodic surface fires in pine forests'. This was confirmed for both CWD volume and dead:live wood volume ratio. In natural European boreal forests, spruce dominated stands with wind induced dynamics are more productive compared to the stands with fine-scale gap dynamics. In the richer biotopes of Norway spruce dominated stands, site productivity increases windthrow risk because spruce has a shallow root system, its wood density is lower and its crown is wider compared to its growth in poorer biotopes (Skvortsova et al., 1983). The relatively low CWD amounts in the Scots pine fire-driven ecosystems can be explained by both the low productivity of these forests and fire effects.

The diversity of CWD species and their variation were higher in even-aged forest stands compared to the forest stands with cohort

and fine-scale gap dynamics because of fewer deciduous tree species in the spruce and pine dominated forest stands driven by fine-scale gap dynamics compared to the stands with cohort or even-aged dynamics.

The Shannon index for decay classes did not depend on the type of forest stand dynamics. However, the CWD distribution by decay class reflected the effects of past disturbances. In the Aschozersky landscape, the peak in the first decay class reflects the effects of a forest fire that took place 71 year ago. The peak in the 3rd decay class in the Vepssky landscape reflects the effect of gradual windthrow after strong wind storms in 1983–84. The CWD distribution by decay class in the Kenozersky landscape was relatively even, reflecting balanced processes of tree stand recruitment and mortality.

The character of the interrelationship between CWD position diversity and the type of forest stand dynamics was contingent upon the forest stand species composition. Higher CWD position diversity in pine stands after cohort replacing disturbances compared to those during even-aged and fine-scale gap dynamics can be explained by more heterogeneous tree mortality patterns in the first case compared to the second one. In spruce stands, equally diverse tree mortality modes independent of the type of forest stand dynamics create equally high diversity of CWD position types. The CWD position diversity reflected equal representation of all tree mortality modes during fine-scale gap dynamics in spruce forests, compared to a dominance of tree uprooting during wind-induced cohort-replacing disturbances and gradual decline of pine forests, which has resulted in long-lasting snags.

The character of CWD DBH distributions depended on the dynamics of forest stands. The peaks in small-sized CWD in even-aged spruce stands and pine stands with fine-scale gap dynamics reflect natural self-thinning processes of forest stands. The dominance of mid-sized CWD in the spruce stands driven by cohort and fine-scale gap dynamics reflects wind and pathogen induced mortality of mid-sized trees and tree patches. The dominance of mid-sized CWD in pine stands with even-aged and cohort dynamics reflects possible short- and long-term effects of fires. Mid-sized and big trees survive during fire but most of them gradually die due to damaged root systems.

5. Conclusions

The large quantity of CWD in the studied primeval European boreal forest stands and landscapes encompassed a wide range of variation in tree species, decay class, position type and size of CWD. The natural disturbance regimes related to certain site conditions and tree species composition of forest stands determined the ranges of natural variability in the volumes of CWD, dead:live wood ratios and compositional diversity of CWD. Altogether this variation creates a large diversity of CWD habitats for saproxylic organisms and ensures a functional resilience of boreal forest ecosystems.

The revealed patterns of CWD amounts and diversity in primeval European boreal forests can be used as a baseline for CWD management and restoration in boreal forest stands and landscapes. When defining volume targets for CWD in spruce dominated forests, regional mean annual temperatures need to be taken into account. Given the dynamic nature of CWD, not only the volume targets, but also the dead:live wood volume ratio targets need to be set in guidelines for CWD management. In spruce dominated forests, these targets can be higher for forest types naturally subjected to windthrow disturbances compared to forest types with natural fine-scale gap dynamics. In pine dominated stands, these targets can be higher for the stands driven by even-aged and fine-scale gap dynamics than for the stands driven by fire-induced cohort dynamics. In managed forests, creating high

compositional diversity of CWD typical to primeval boreal forests requires development of special multi-interventional CWD management systems.

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Appendix A

History of the sample plot establishment

Study site	Permanent plot #	Size (ha)	Established		Temporal plot #	Size (ha)	Established	
			When	By whom			When	By whom
VF1	11	0.18–0.55	1973–1985	S. Dyrenkov, V. Fedorchuk	35	0.1	2000	A. Shorohov, E. Shorohova
	13	0.1	1991	S. Dyrenkov, S. Savitsky				
Asch	3	0.15	2003	V. Gorshkov, N. Stavrova, E. Shorohova, A. Shorohov	17	0.1	2003	V. Gorshkov, N. Stavrova, E. Shorohova, A. Shorohov
CFR	4	0.2–0.6	1972–1992	V. Karpov, E. Shaposhnikov, V. Storozhenko	32	0.1	2004–2005	E. Shorohova
G	3	1.1	2006	E. Shorohova, E. Kapitsa				
Pan					4	0.2	2007	E. Shorohova
Pin					14	0.1	2011	E. Shorohova, E. Kapitsa
Ken					25	0.1	2005	E. Shorohova
Komi					33	0.1	2010	E. Kapitsa

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