Temporal Variability of Deadwood Volume and Quality in Boreal Old-Growth Forests

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Reference deadwood volumes from natural forests for forest management and restoration are often derived from one-time measurements or from repeated measurements over short time-scales. Such an approach often assumes an equilibrium state between tree mortality and decomposition, which is questionable in many boreal forest ecosystems due to the occurrence of allogenic disturbances. Using a simulation model based on empirical estimates of tree mortality, disturbance chronologies and models of wood decay class dynamics, this study aimed at characterizing variability in the volume and quality of deadwood for the past 200 years. The variability of deadwood volumes in old-growth forests, arising from differences in disturbance regimes and differing decay rates, was exemplified in two areas of *Picea abies*-dominated forests in northern Europe. The results imply that with stable deadwood input and slow decay rates the deadwood volume may be in an equilibrium state. On the contrary, if moderate-severity disturbances occur such a state seems improbable. Both study areas displayed continuity in deadwood availability, although temporary paucity in the early decay classes with shortest residence times was also observed. The results stress the importance of understanding the dynamic nature of deadwood in old-growth forests, instead of the traditional view of deadwood as a static ecosystem component.

1   Introduction

Reduced deadwood volume is one of the most apparent differences between the intensively managed Fennoscandian forests and natural forests. At the same time, it is one of the greatest threats to the maintenance of forest biodiversity (Siitonen 2001, Kuuluvainen 2009). The re-introduction of deadwood into managed forests is therefore considered a pre-requisite for achieving long-term ecological sustainability and biodiversity conservation goals of forest management (Kuuluvainen 2009).

When considering the re-introduction of deadwood into managed forests or targets for forest restoration, the question is how much and what kind of deadwood is enough. Currently the emphasis here is on defining these quantities from natural forests (e.g. Gauthier et al. 2009). These reference conditions can be derived from a number of studies that have focused on deadwood in natural forests (e.g., Sippola et al. 1998, Siitonen et al. 2000, Lilja et al. 2006). It is understood that deadwood abundance along stand succession follows a U-shaped pattern: deadwood is abundant following a stand-replacing disturbance, decreases in early successional stages as the legacy deadwood gradually decays, and increases again with stand maturation as the trees senesce and larger trees begin to die (Sturtevant et al. 1997, Brassard and Chen 2008). The quantities are assumed to stabilize in old-growth forests as small-scale gap dynamics become the dominant driver of forest development, maintaining the balance between tree mortality and regeneration (Janisch and Harmon 2002). This would justify treating deadwood as a static structural component of the ecosystems, and the use of values from one-time measurements as a reference.

Considering the documented fluctuations in the occurrence of disturbances that create deadwood (Fraver et al. 2008), it is unclear how well this steady-state assumption holds, and how well such data can be generalized to other stands or even to the same stands at different times (Lang 1985); the studies are commonly snapshots of the conditions that prevailed during the measurements (cf. Hofgaard 1993). Furthermore, because the deadwood quantities are also determined by the output from the ecosystem through decomposition, information on the fluctuations of tree mortality alone is not sufficient for assessing its dynamics. Decay rates, which may differ among species and regions (Mackensen et al. 2003, Yatskov et al. 2003, Mäkinen et al. 2006), eventually determine the rate of quality change and the persistence of deadwood in forest ecosystems.

Longer-term dynamics of deadwood have been assessed with simulation models. The emphasis has in many cases been on deadwood as a part of the organic matter pool in more general models of vegetation dynamics, aiming primarily at an assesment of biomass dynamics (e.g. Scheller and Mladenoff 2004, Kurz et al. 2009). Several studies have also treated deadwood more explicitly in predicting future quantities of deadwood under different scenarios. As an example, Tinker and Knight (2001) simulated the impact of different fire return intervals and forest management strategies on the amount of deadwood, and Brown et al. (2003) used the Forest Vegetation Simulator to simulate CWD as fuel for forest fires.

Despite the increasing number of studies on deadwood, we still have a limited knowledge of its dynamics in natural conditions across the boreal zone (Bradshaw et al. 2009). This applies especially to stands that have escaped stand-replacing disturbances for extended periods of time and are thus "outside" of the traditional, and better-documented U-shaped model of deadwood abundance along stand succession (Sturtevant et al. 2007, Janisch and Harmon 2002). How deadwood abundance varies after stands reach the old-growth stage (*sensu* Oliver and Larson 1996) is much less studied. The current study aimed at modeling deadwood variability in old-growth forests, by using disturbance history reconstructions and past tree mortality rates as inputs to decomposition models, in two areas of boreal forest. The purpose was to exemplify the variability in deadwood quantities in boreal old-growth forests under differing disturbance regimes and wood decay rates, and to assess the validity of the traditional view of deadwood as a static component of old-growth forest structure.

2　Material and Methods

2.1　Study Areas and Field Data

The study was based on a combination of tree mortality reconstructions, longer-term disturbance histories, and models for deadwood dynamics in two areas in northern Europe, published earlier (Table 1). The focal species was *Picea abies* (L.) Karst. The study areas are located in Pallas-Ylläs national park in northern Finland (67°40′N, 24°22′E), and in a large forested area between the Dvina and Pinega rivers in Arkhangelsk region, northwestern Russia (63°00′N, 44°10′E; hereafter Dvina-Pinega area).

The study areas are described in more detail in earlier studies (see Table 1 for the references). In short, the Pallas-Ylläs study area is located in the northern boreal zone, while the Dvina-Pinega area is in the climatically milder middle boreal zone (Ahti et al. 1968). Topography in the Pallas-Ylläs area is varied, with *P. abies* stands commonly found on the slopes of gently rolling hills, and growing in thin undifferentiated tills. In contrast, the Dvina-Pinega is located on flat terrain, with the forests growing in deep tills containing a high gleyic fraction (Batjes 2005). In both study landscapes, five old-growth forests were sampled, using 1.6 ha sample plots on which all trees over 10 cm diameter-at-breast-height (DBH) were mapped. Living and dead trees were sampled for dendrochronological reconstructions of past mortality, and growth-release analysis (Caron et al. 2009, Aakala et al. 2009, Aakala et al. 2011).

On average, the living tree volumes were 106 m³ha⁻¹ in Pallas-Ylläs, and 150 m³ha⁻¹ in Dvina-Pinega. The share of *P. abies* was 78% and 88% in the two areas, respectively. Both study areas had been minimally directly influenced by humans, and held practically no signs of past cuttings. The fire cycles in *P. abies* dominated forests in northern Europe are in general estimated to be long, and lie in the range of 300 years or more (Wallenius et al. 2005). Neither of the study areas showed any direct signs of forest fires:in the Dvina-Pinega area, no fire scars or macroscopic charcoal in uprooting pits were found. In the Pallas-Ylläs area pieces of charred wood were recovered, and carbon-dated to year 1045 AD (±30 years), but other, more prominent signs of forest fires were absent here as well. The oldest trees in the highly uneven aged stands in both areas were well over 300 years, which is considered as the normally attained maximum age of *P. abies*, thus also attesting to the absence of stand-replacing disturbances (including agents other than fire, see Fraver et al. 2008). Thus, all stands fit the true old-growth category of Oliver and Larson (1996).

Except for the rare occurrence of forest fires, the disturbance regimes differ between the areas. The Dvina-Pinega area is influenced by infrequent moderate-severity disturbances with droughts and subsequent bark beetle attacks as the likely causes (Aakala et al. 2011). The last such disturbance took place in 1999–2004, and was reflected in the high deadwood quantities in the stands, with an average of 115 m³ha⁻¹, measured in 2007 (Aakala 2010). Outside of those distinct disturbances, the dynamics in the Dvina-Pinega area are controlled by small-scale mortality of individual to small groups of trees. This is the dominant disturbance type also in the Pallas-Ylläs study area (Caron et al. 2009), driven by the wood-decaying fungi and winds (Lännenpää et al. 2008).

Table 1. Study area characteristics and data sources.

	Pallas-Ylläs	Dvina-Pinega
Annual average temperature	–1.1 °C	1.5 °C
July mean temperature	14.1 °C	17.2 °C
January mean temperature	–15.2 °C	–13.2 °C
Annual precipitation sum	500 mm	670 mm
% snow	37%	35%
Tree mortality data	Aakala et al. 2009	Aakala et al. 2011
Disturbance chronologies	Caron 2008	Aakala et al. 2011
Decay models	Aakala 2010	Aakala 2010

Table 2. Relationships between tree mortality rate and the decadal disturbance rates (factor), used for converting the disturbance chronologies to volume per ha, followed by expected snag and log residence times (or half-lives) to illustrate differences in decay rates.

Study area	Calibration period	Factor	Expected snag residence time	Expected log residence time
Pallas-Ylläs	1980–1989	0.082	21	30
Dvina-Pinega	1980–1989	0.950	12	20

2.2 Input Data

Variability in the deadwood availability was assessed, using data on tree mortality over the past 200 years as the input to a decay model. This input data was derived from two sources (Table 2). The first source was the tree mortality estimates for the past 2–3 decades that were reconstructed using dendrochronology, by cross-dating the years of death of trees in different decay classes (Aakala et al. 2009, Aakala et al. 2011). The data from those two studies gave the number of trees killed each year per hectare. The results were therefore directly suitable as input to the simulations. The reconstructions were problematic because of short temporal coverage: with elapsing time since tree death the number of trees decayed past cross-dating possibilities increases (i.e., either eroded tree rings at the surface, or decomposed so that the tree ring structure is no longer discernible). Thus, the reconstructions were deemed reliable only for the past 2–3 decades.

The second source consisted of disturbance history reconstructions that were based on growth release analysis (Caron 2007, Aakala et al. 2011). These reconstructions express disturbances as a relative proportion of trees showing evidence of disturbances (growth releases or gap-origin trees) per decade. As the results give a relative proportion of trees per decade, they were not directly suitable as an input to the decay class dynamics model. Moreover, due to the way the growth releases were defined (abrupt growth increases that are sustained a minimum of 10 years) they could not be used for the most recent 10 years (Nowacki and Abrams 1997).

To overcome the shortcomings of both methods, i.e., the short temporal coverage of the mortality reconstructions and the lack of data directly
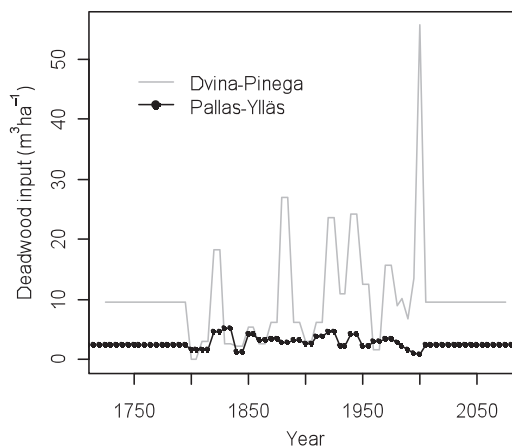

Fig. 1. Deadwood volume input into the simulation.

suitable for input into the decomposition model from the disturbance chronologies, the two data sources were combined. This was done by relating the number of trees killed per decade to the relative value in the disturbance chronology for the same decade. This relationship was established for 1980–1989, which was subjectively estimated to be reliably covered by both data types. This relationship was then used to reconstruct the number of trees killed per decade for the rest of the disturbance chronology (Table 2). The decomposition model has a 5-year time step, so the decadal input from the disturbance chronologies was divided into two equal periods, beginning from the year 1800. From 1980 onwards the tree mortality reconstructions were used as the input, ending in year 2005 for Pallas-Ylläs study area and 2007 for the Dvina-Pinega study area (the years of field sampling). The numbers of trees killed were converted to volume of deadwood entering the decomposition models, by multiply-

ing with the average intact volume of a dead tree in both study areas (0.33 m^3 in Pallas-Ylläs and 0.54 m^3 in Dvina-Pinega; Fig. 1).

The trees killed entered the decay models either as snags or logs, with snags having the possibility to fall and enter the log pool. In both study areas, background mortality produced snags and logs in the same proportion as observed in the recently killed trees (early decay class) during the field sampling. For these trees, it was possible to state with confidence whether they had been killed standing, or fell at death. The ratio of snags to logs was 9:5 in Pallas-Ylläs and 11:17 in Dvina-Pinega. Fluctuations above the background level were entered as logs in Pallas-Ylläs (as storms were considered as the primary cause for fluctuations), and snags in Dvina-Pinega (as droughts and bark beetles were considered as the primary causes for fluctuations).

2.3 Decay Models

Stage-based matrix models (Kruys et al. 2002) were used in the simulations to determine the rates at which the trees input into the model move from one decay class to another, and leave the system. The models give the probability that a dead tree in a specific decay class moves from its current decay class to the next decay class or, for snags, loses part of its volume or falls entirely, entering the corresponding log decay class (see Aakala 2010 for details). The model output is a decay class distribution after each transition, separately for snags and logs. Thus, it is possible to track the development of deadwood volume in individual decay classes through time, in addition to the total amount of deadwood present in the stands.

The decay classes in the current study included four classes for snags and logs (early, early-intermediate, intermediate, and intermediate-advanced; Table 3). The decay class models were parameterized with dendrochronological methods, which in practice excluded the most advanced stages of decay from the model, because wood in those stages could not be accurately dated. This imposed limitations for modeling carbon or necromass dynamics, because trees in the last decay class still retained a considerable share of their original density, and thus still maintained a considerable carbon pool whose fate could not be assessed with the models (Aakala 2010). Therefore, this simulation exercise was better suited for assessing habitat dynamics, and the simulations were done with deadwood volumes and quality. The model also produced uncertainty limits, using a bootstrapping algorithm. These reflect the variability in the material used for parameterizing the model, but it should be noted that they do not include any uncertainty estimates in the input data, which are lacking from the disturbance chronologies.

The models were parameterized separately for both study areas (Aakala 2010; transition matrices in Table 4), as in the climatically more favorable Dvina-Pinega area decay rates were considerably faster. As an illustration of these differences, the expected residence times (time since tree death after which it has a 50% chance of having decomposed past the last decay class included in the model) were 21 and 30 years for Pallas-Ylläs snags and logs, and 12 and 20 years for Dvina-Pinega snags and logs, respectively (Table 2).

In running the simulations, an annual background mortality rate (Aakala et al. 2009, Aakala et al. 2011) was used to run the model for 150 years to

Table 3. Decay classes used in the simulations (Aakala 2010).

Class	Type	Description
1. Early	Snag or log	Small branches with at least some foliage still attached
2. Early-intermediate	Snag or log	Foliage absent, small twigs still present
3. Intermediate	Snag or log	Smallest twigs absent, Most of the largest branches still present
4. Intermediate-advanced	Snag	Only a few of the largest branches possible present, snapped
	Log	Only a few of the largest branches possible present, log shape still round

Table 4a. Transition matrices for the Pallas-Ylläs study area.

	From class							
To class	Snag 1	Snag 2	Snag 3	Snag 4	Log 1	Log 2	Log 3	Log 4
Snag 1	0.028	-	-	-	-	-	-	-
Snag 2	0.806	0.726	-	-	-	-	-	-
Snag 3	0.145	0.153	0.390	-	-	-	-	-
Snag 4	-	0.104	0.159	0.003	-	-	-	-
Log 1	0.022	-	-	-	0.031	-	-	-
Log 2	-	0.017	-	-	0.755	0.670	-	-
Log 3	-	-	0.053	-	0.214	0.259	0.555	-
Log 4	-	-	-	0.376	-	0.071	0.347	0.555
out	0.000	0.000	0.398	0.621	0.000	0.000	0.098	0.445

Table 4b. Transition matrices for the Dvina-Pinega.

	From class							
To class	Snag 1	Snag 2	Snag 3	Snag 4	Log 1	Log 2	Log 3	Log 4
Snag 1	0.126	-	-	-	-	-	-	-
Snag 2	0.364	0.048	-	-	-	-	-	-
Snag 3	0.501	0.153	0.004	-	-	-	-	-
Snag 4	-	0.617	0.370	0.479	-	-	-	-
Log 1	0.008	-	-	-	0.237	-	-	-
Log 2	-	0.182	-	-	0.206	0.031	-	-
Log 3	-	-	0.347	-	0.557	0.673	0.555	-
Log 4	-	-	-	0.065	-	0.295	0.306	0.402
out	0.000	0.000	0.279	0.456	0.000	0.000	0.139	0.598

reach a steady state (i.e., an input of a fixed deadwood volume until the simulation results stabilize). At year 1800 the deadwood volume determined from the disturbance chronology was then used as the input, until 2005 (for Pallas-Ylläs) and 2007 (for Dvina-Pinega). These were followed again by the same background mortality for 50 years, to observe how fast the deadwood volumes again stabilize. Models were run in R (version 2.13.0; R Development Core Team 2011)

3 Results

Deadwood volumes in the Dvina-Pinega study area ranged widely in the simulation period from 1800 to 2007 (Fig. 2a). Mean volume was 46.2 $m^3 ha^{-1}$, with a wide range of 16.7 $m^3 ha^{-1}$ in the year 1815 and 93.6 $m^3 ha^{-1}$ in the year 2000. In the Pallas-Ylläs study area the fluctuations were much smaller (Fig. 2c), ranging from 25.8 $m^3 ha^{-1}$ in the year 1925 and 14.2 $m^3 ha^{-1}$ in the year 1815, with a mean of 21.5 $m^3 ha^{-1}$.

Simulation results implied constant availability of snags in both study areas (Fig. 2b and 2d). In Dvina-Pinega, the average volume of snags was 20.5 $m^3 ha^{-1}$, and in Pallas-Ylläs 4.9 $m^3 ha^{-1}$. The ranges were very different, from 3.5 to 62.0 $m^3 ha^{-1}$ in Dvina-Pinega and from 4.4 to 5.0 $m^3 ha^{-1}$ in Pallas-Ylläs. Log volumes fluctuated less in Dvina-Pinega compared to snag volumes. Average log volumes were 25.7 $m^3 ha^{-1}$ with a range from 13.3 $m^3 ha^{-1}$ to 43.4 $m^3 ha^{-1}$ in the Dvina-Pinega. In Pallas-Ylläs fluctuations in log volumes were higher than in snag volumes. Average log volume was 16.6 $m^3 ha^{-1}$, with a range from 9.2 $m^3 ha^{-1}$ to 20.8 $m^3 ha^{-1}$.

The simulation results correspond with the average volumes measured in the field (Fig. 2). However, it should be noted that this is not a proper test of model validity, because the field measurements were used in calculating the input data in trees per hectare.
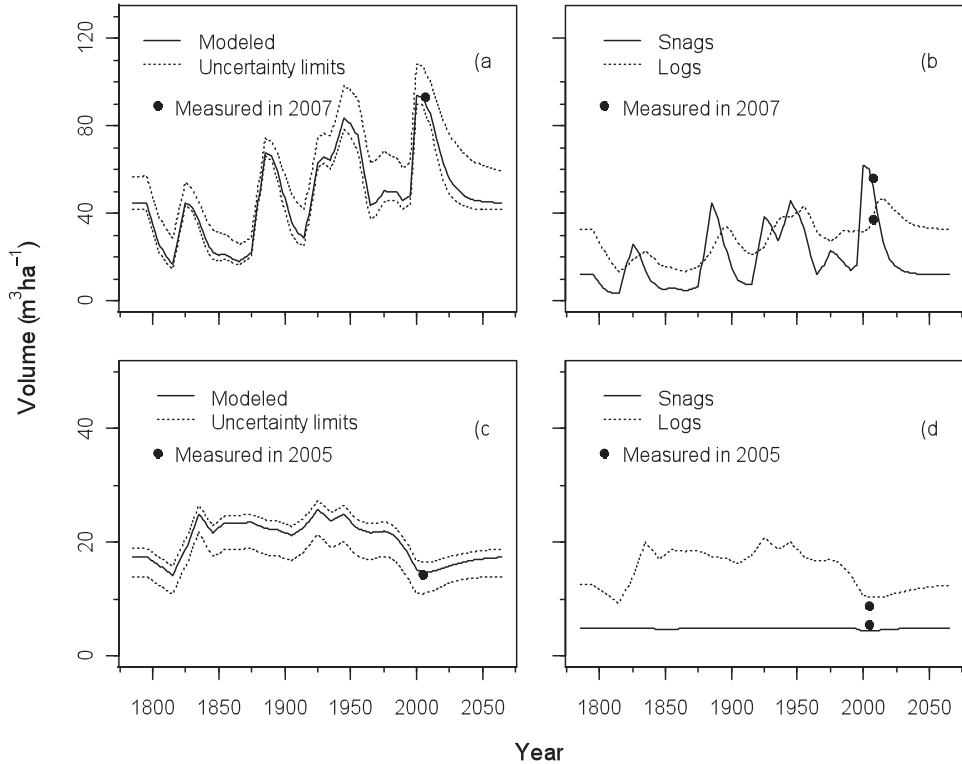
Fig. 2. Total volume of deadwood in the Dvina-Pinega (a–b) and Pallas-Ylläs (c–d), and separated into snag and log volumes. The uncertainty limits that are derived from the decay class dynamics model are shown only for the total deadwood graph, for clarity of presentation. The volumes measured in the field during the sampling year are marked with points.

When the specific decay classes were followed through time, Dvina-Pinega simulation results illustrated the results of episodic disturbances in the deadwood volumes (Fig. 3a, intermediate stage not shown for clarity). The early decay class, in which the residence time was short the combined result of the peaks in input and short residence times resulted in peaked behavior. As could be expected, the fluctuations in the subsequent decay classes followed the fluctuations in the previous class with a slight delay.

In Pallas-Ylläs the fluctuations in the early decay class were less pronounced, compared to Dvina-Pinega. Similar to the total deadwood, the availability of deadwood in different decay classes was relatively stable. The early-intermediate decay class was the most abundant, which was contrary to what was observed in the Dvina-Pinega. The advanced-intermediate class showed very little variability.

The influence of the differing decay rates on the variability of deadwood volumes was evident when the variability in input and the amount of deadwood were compared (Fig. 4). The two systems show different patterns: Dvina-Pinega, with fast decay rates has higher variability in deadwood volumes than in the input, despite the episodic nature of tree mortality. In the Pallas-Ylläs study area the opposite was observed: the variability in input is higher than in the deadwood volumes, showing the stabilizing influence of slow decay rates on the availability of deadwood.
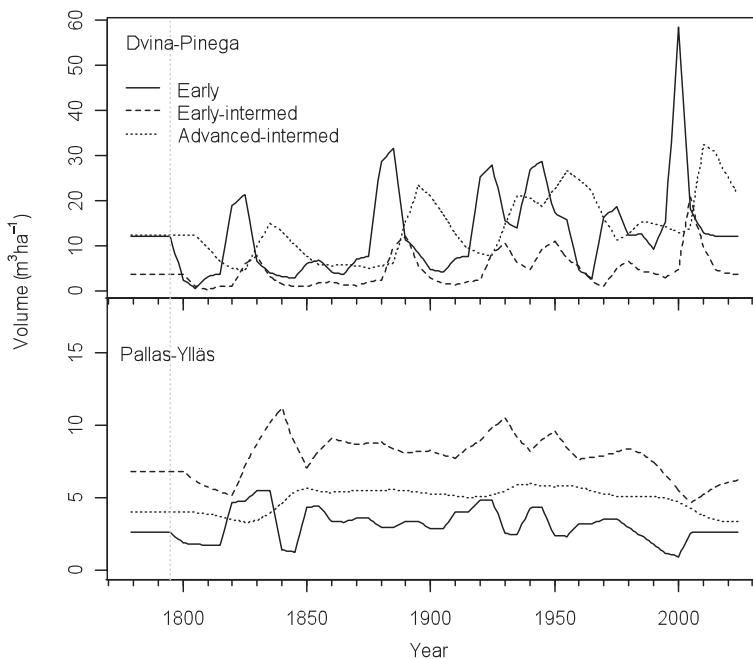
Fig. 3. Deadwood volumes through time in early, early-intermediate and the inter-mediate-advanced decay classes. The intermediate decay class is omitted for clarity.
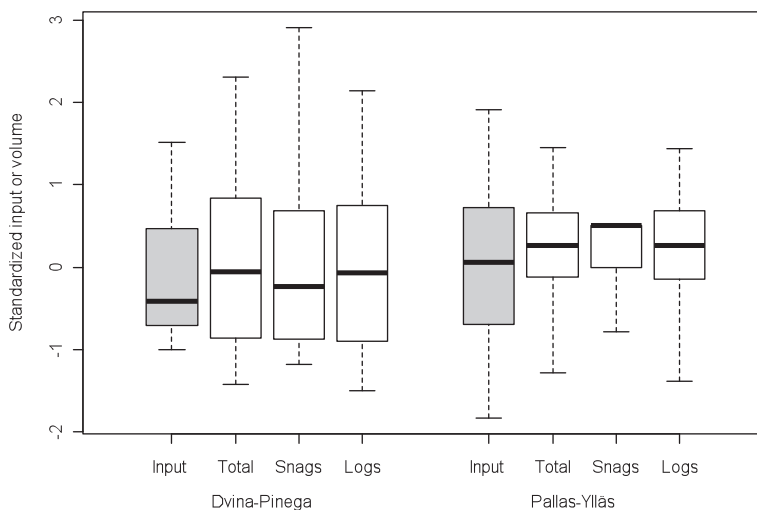

Fig. 4. Boxplots of standardized input (i.e. tree mortality) and deadwood volumes (total, snags and logs) for both study areas. Values are standardized to zero mean and unit standard deviation. The boxplots show the median values, quartiles, as well as the minimum and maximum values.

4 Discussion

4.1 Deadwood Variability

The simulation results for the Pallas-Ylläs study area displayed very small fluctuations in the amount of deadwood for the past 200 years, in sharp contrast to the Dvina-Pinega study area. These differences between the areas reflect differences in the disturbance regime. However, the integration of both output and input produced different patterns of variability compared to what could be expected from the temporal variability in the input alone. This was exemplified in the early decay class volume in Dvina-Pinega, where even short periods of minimal deadwood input led to short-term paucity of the fastest decaying class (the early decay class).

The low variability in deadwood availability in Pallas-Ylläs study area conforms to the idea of a relatively stable deadwood availability that is often assumed for old-growth forests (Janisch and Harmon 2002). This assumption relies on the existence of the theoretical quasi-equilibrium state (Bormann and Likens 1979), where tree mortality and regeneration in a forest stand are balanced. The findings in the current study are thus in line with those suggested solely based on the disturbance reconstructions by Caron et al. (2009) for this study area, showing only minor fluctuations in the disturbance chronology during the past 200 years. Although the simulation results from Pallas-Ylläs imply that such a stage is attainable, it is likely that it takes centuries of stand development in the absence of larger disturbances to reach such a stage. This is due to the long-lasting influence moderate- and high-severity disturbances have on the tree age distributions, composition and structure, that alter patterns of tree mortality (Aakala et al. 2009, Shorohova et al. 2009).

In the Dvina-Pinega study area attaining an equilibrium state in deadwood quantities seems unlikely, and the variability seen in the modeling results contrasts with the idea of an equilibrium state in deadwood dynamics (Janisch and Harmon 2002). Deadwood volumes peaked following disturbances, which led to rapid drop due to the relatively fast decay rates (compared to Pallas-Ylläs). However, it is noteworthy that at no point did the deadwood volume reach zero. From the simulation results it is evident that measuring deadwood at any point in time during the past 200 years would have produced results that cannot be readily considered representative of the deadwood volumes in these forests.

Snag volumes in Pallas-Ylläs were very stable in the simulation results. The reason for this was the simplifying assumption in the simulations that tree deaths above the background level were due to storms and thus deadwood input was in logs. During the calibration period 1980–1989 tree mortality was lower than during most of the reconstruction period (see Caron 2007), which resulted in limited variability in snag volumes. However, judged from the stable availability of total deadwood, and the availability of logs, it seems evident that adjusting the mode of tree death would not have changed the interpretation of the results. Even with the limitation in snag recruitment their availability was continuous. Similar limitation is not obvious in the Dvina-Pinega area, because there the mode of death (i.e., standing or fallen) during the episodes has, according to historical records, been standing death (Nevolin et al. 2005). Standing dead trees later become logs, which is evident also in that the fluctuations in log volumes are slightly out of phase compared to snag availability. This contrasting pattern between the two study areas illustrates the role the mode of tree death plays in stand structural dynamics (Hennon and McClellan 2003): ecosystems where standing tree deaths dominate produce higher structural variability than systems where trees fall at death.

The abundance among decay classes varied between the study areas. A potential reason for this is in the differences of the decomposition pathways. In the Dvina-Pinega, most of the trees had *Fomitopsis pinicola* fruit bodies and wood material decayed by the white-rotting fungi over the entire cross-section (Aakala et al. 2011), whereas in the Pallas-Ylläs study area the most common cause of death was brown rotting fungi, which had caused substantial heart-rot prior to the death of the tree (Lännenpää et al. 2008). These differences could lead to differences in how the decay proceeds, as the decaying fungi are known to show succession in the decomposer community (Niemelä et al. 1995), leading to differences in decomposition pathways and in class residence times.

The simulation models contain several assumptions, due to which the results should be considered indicative of the variability and the differences between the regions, but are not suitable for quantitative inferences. First, a constant relationship is assumed between the number of trees killed and the longer-term estimates, which was derived from the relatively short calibration period of 1980–1989. In reality, the strength of the response can be expected to be dependent on the size of the trees killed and released, as well as their spatial distribution (Nowacki and Abrams 1997), which has likely fluctuated during the 200-year simulation period. A second assumption is that the decay class dynamics models assume constant transition rates between successive classes over the modeling period. Third, the relationship between standing and fallen deaths was assumed constant, although it is largely dependent on the characteristics of the tree-killing disturbances. Regarding the development of the simulation approach, the first assumption would probably the most important one to focus on in future studies. This is because it currently produces an unknown amount of uncertainty in the results, which could be quantified with a careful calibration of a spatially explicit disturbance chronology (linking the area of canopy disturbed each decade to volume of trees, instead of number of trees as was done here; see Frelich and Reich 1991). Proper calibration of the growth release analysis would open up possibilities for assessing the uncertainty in the simulation results. An important future application would be then to assess any trends in the deadwood volumes over the past centuries. It is tempting to make interpretations of the apparent trend of increasing deadwood volumes in the Dvina-Pinega area (Fig. 2a), but the lack of information on the uncertainty precludes such interpretations; the trend might simply be a methodological artifact. Quantitatively reliable simulations would also facilitate estimates of carbon storage, as even the simple appearance-based decay classes are connected to remaining wood density and carbon content (Aakala 2010).

Despite these uncertainties, the results are nevertheless indicative of the wide range of natural variability among boreal forests. The simulation results demonstrated the dynamic nature of deadwood as a structural component, being dependent both on the temporal patterns of input and rates of output, and producing structural complexity that can greatly vary through time. The approach implemented here differs from earlier studies in that it combines longer-term empirical data on deadwood inputs with models that facilitate assessing the dynamics in various quality classes of deadwood. The first one is essential, given that our understanding of forest dynamics in natural conditions has undergone considerable changes recently (Fraver et al. 2008, Kuuluvainen 2009), and that determining input scenarios from earlier models of stand development (such as the U-shaped pattern followed by a steady-state) impose unrealistic restrictions to deadwood input, as would have been the case in the Dvina-Pinega area (see for instance Tinker and Knight 2001). More general models of forest dynamics incorporate variabililty in disturbances (e.g. Scheller and Mladenoff 2004), but they are usually not developed for tracking the availability of different types of deadwood, which would be essential for modeling habitat availability for saproxylics. In practice, the proposed approach has potential for increasing our understanding of deadwood dynamics, given that disturbance history reconstructions and decomposition models are increasingly available for many regions.

4.2 Implications

It seems evident that any attempts to create guidelines and recommendations for deadwood management in managed forests or restoration areas based on observations from natural forests require understanding of forest dynamics. Using simple guidelines over the whole variety of different forest types is theoretically ill-justified, due to the heterogeneity of the processes driving forest development.

Although total deadwood, snags and logs as a whole were consistently available in both study areas for the past 200 years, there were some differences when further divided into different decay classes. For the early decay classes (right after tree death), where the changes in the suitability of the deadwood are most rapid due to drying of the phloem, paucity may occur. It has been argued that bark beetles and other species specialized in

such short-residence substrate have developed good dispersal capabilities, and are thus not necessarily threatened by small-scale paucity in the availability of specific classes (e.g., Jonsson et al. 2005). However, the lack of available habitat may prove more problematic for organisms adapted into using resources with much more stable availability. If we assume that our appearance-based decay classification reflects the suitability of the deadwood material for different organisms, the more advanced decay classes in the current study areas would appear to be a critical element in this respect.

Thus, implications for forest management aiming at mimicking natural structures would entail ensuring stand-level availability of well-decayed material with longer-residence times, which was common for both study areas. The early classes with shorter residence times are more problematic. Creating a nearly continuous supply of recently dead wood at the stand scale is not a feasible management target, but given the potentially higher capacity for dispersal for those organisms, this availability could be produced at the landscape-level by including areas outside of management that would have the potential to produce recently killed trees. In addition, more studies would be needed to understand what the role of episodic tree mortality and the subsequent fluctuations of deadwood is on the maintenance of biodiversity in areas such as Dvina-Pinega.

Although the meaningfulness of documenting past changes for future use can be challenged based on the predicted changes in climatic conditions, such information on past variability does provide important baseline information against which to assess future changes. This is especially apparent with deadwood, because both of the processes controlling its dynamics, mortality and decomposition, are linked to climatic variability (Mackensen et al. 2003, Van Mantgem et al. 2009). Solid knowledge on the variability and its drivers provides a baseline for comparing future changes, as well as a meaningful target for comparing management alternatives and restoration efforts to natural conditions, stressing the importance of the dynamic nature of deadwood as an ecosystem component.

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