



Analysis of forest naturalness and tree mortality patterns in Estonia

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ABSTRACT

New methods for evaluating structural properties of stands and individual tree mortality within forests are needed to enhance biodiversity assessment in forest inventories. One approach is to assess the degree of naturalness in a forest. We assessed forest naturalness by examining patterns and causes of mortality and deadwood amount and spatial distribution as indicators of naturalness, or degree of anthropogenic disturbance. This study is based on 5-year interval measurement using 294 permanent samples plots from a forest growth network in Estonia. The average annual mortality was 1.3% from stem number counting 29% of Scots pine, 27% of silver and downy birch and 20% of Norway spruce. Most common reasons for the individual tree death were growth-dependent reasons (45%), fungi (23%) and wind damage (16%). Modelling showed that relative diameter of a tree in a stand is significantly related to mortality probability. Modelling the reasons of tree death showed that with increasing relative diameter there was a greater probability that mortality was caused by wind or damage from game (mostly moose (*Alces alces* L.)), insect or fungi and a lower probability that mortality was due to competition between trees. Use of structural variable such as deadwood mingling, which was based on the neighbouring trees, improved the assessment of forest naturalness and helped to distinguish recent disturbances. A comparison of deadwood mingling and nature value scores in managed and semi-natural forests showed that dead trees were more dispersed and the naturalness score was higher in semi-natural forest stands. The nature score was significantly correlated with the diversity of mortality causes indicating that mortality causes are more diverse in semi-natural stands. Mean values and distribution of the deadwood mingling index in managed and semi-natural forests were not significantly different. In middle-aged semi-natural forests, mortality is spatially more random than in managed forests, thus there is no evidence of gap formation yet.

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1. Introduction

Forests in Baltic countries are structurally diverse, often with complex structures (Nilson, 1996). Factors that have contributed to this structural diversity include infrequent management intervention, reliance on natural regeneration methods, as well as great variation in site conditions within stands, even in commercial forests (Jõgiste, 1998). New methods for evaluating structural properties of ecosystems and mortality within forests are needed to enhance biodiversity assessment in forest inventories (Lee et al., 2000). Increasingly, the importance of stand dynamics and resulting structural properties are recognized in forest management and modelling (Ozolincius et al., 2005; Kint et al., 2004; Gadov, 1993) and environmental planning (Pommerening, 2006). One approach is to assess the degree of naturalness in a forest but naturalness is difficult to objectively evaluate in routine forest

inventories and therefore is often omitted or very simplified methods are used (McElhinny et al., 2005).

Forest “naturalness” is a complex issue converging forest dynamics, disturbances at different scales, adaptation to changing environment and human influence. Stanturf et al. (2004) stated that even without anthropogenic disturbances it is difficult to specify what constitutes a natural forest in a given place and time. Sprugel (1991) explained that in some regions an equilibrium may exist in which patchy disturbance is balanced with regrowth, but in others equilibrium may be impossible. Where equilibrium does not exist, defining “natural” vegetation becomes much more challenging, because the vegetation would not be stable over long periods even without man’s influence. Ecosystems in a steady state (climax ecosystems) are still continuously dynamic and changing due to gap formation caused by the mortality of large trees. Borman and Likens (1994) defined this as a “shifting-mosaic steady state” ecosystem. In many areas it may be unrealistic to define natural vegetation for a site and often several communities could be “natural” vegetation for any given site at any given time. In regions characterized by infrequent or only fine-scale disturbance,

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naturalness can be assessed by quantifying the level of human influence to a forest ecosystem. Uotila et al. (2002) define the level of naturalness as the extent to which human influence has affected the current forest structure. Nevertheless, it is often possible to distinguish between managed and unmanaged forests for only a limited interval following a disturbance or management intervention. As managers attempt to emulate natural disturbances in their interventions by adopting principles of “ecological forestry” (Franklin et al., 2007) “continuous cover forestry” (Gadow et al., 2002) or “nature-based silviculture” (Larsen, 1995), definitions of naturalness as being the opposite of anthropogenic disturbances become even more problematic. Despite the difficulty of defining naturalness, it is an accepted concept in European forest management and nature conservation and an ability to assess forest naturalness is important for forest management and conservation decisions (Šaudyte et al., 2005).

In this study we used a random selection of commercially managed forests between 10 and 170 years of age in Estonia. We examined the usefulness of individual tree mortality and composition and structure of deadwood for evaluation of forest naturalness and biodiversity value at the stand level, with application for forest inventory methods. Our rationale was that because of the relatively undisturbed nature of forests in Estonia, mortality and deadwood were useful for operationally defining “naturalness”. Individual tree death and replacement (fine-scale disturbance) as a process guarantees vitality and dynamics of forest ecosystems. Its main features are altered forest structure and release of additional resources for the remaining trees and other organisms (Köster et al., 2005). The process of tree mortality is critical for understanding forest stand dynamics (Juknys et al., 2006; Ozolincius et al., 2005; Monserud and Sterba, 1999) and a likely indicator of naturalness (Debeljak, 2006; Rouvinen et al., 2002). Assessment of individual tree mortality permits evaluation of stand development stage and the level of human influence. Deadwood structure includes both the variety and condition of individuals such as snags and logs and their spatial arrangement. These attributes change during stand development and the amount and structure of deadwood is another indicator of the level of human disturbance, i.e., the amount of material that has been removed in harvests.

There are different ways to categorize causes of tree death. One possibility is to distinguish between abiotic and biotic factors (Franklin et al., 1987; Rouvinen et al., 2002). Abiotic factors are fire, wind, flooding, snow breakage etc. Biotic causes of tree mortality are diseases, insects, mechanical imbalance, old age etc. Another possibility is to group tree mortality into density-dependent

(Greenwood and Weisberg, 2008) and density-independent factors (Franklin et al., 2002; Ozolincius et al., 2005). Density-dependent tree mortality is due to competition among individuals (self-thinning mortality) and density-independent mortality is due to other agents.

Our specific hypotheses were that (a) multiple causes (processes) for individual tree mortality are a good indicator of naturalness in a forest stand; (b) the spatial distribution of dead trees within a stand is a good indicator of naturalness, specifically in middle-aged semi-natural forests, dead trees are not clumped together as they would be in a managed forest; (c) deadwood properties (distribution by size, spectrum of mortality causes, species composition) may be used to detect recent forest disturbances in a stand; and (d) trees with smaller relative diameter are more likely than larger trees to have died because of tree competition.

2. Material and methods

2.1. Estonian forest growth network

Estonia is situated in the hemiboreal vegetation zone (Ahti et al., 1968) and covers a broad range of biogeographical conditions. The climate varies from maritime to continental. Average annual precipitation increases from west to east within a range of 600–700 mm. Mean temperature of the warmest month (July) ranges from 16.3 to 17.4 °C; and the coldest month (February) from –2.0 to –7.4 °C.

We used 5-year interval measurement data provided by the Estonian forest growth network permanent research plots. This network was established during the period 1995–2004 and covers all of Estonia (Kiviste et al., 2003). Since 1999, the network of forest research plots has been extended using the sample grid of the ICP Forest level I monitoring plots (Karoles et al., 2000) to place the centers of plot groups. The plot locations in the field were selected randomly on a map and represent the most common forest types and age groups in Estonia. The method of establishing the plots is mainly based on the experience of the Finnish Forest Research Institute (Gustavsen et al., 1988). Data on 98,106 trees from 680 sample plots had been recorded in the database until 2008.

Generally the permanent sample plots were circular with a radius of 15, 20, 25 or 30 m. The size depended on the forest density and age, and as a rule every plot had at least 100 trees in the upper-storey. On each plot the azimuth and distance from plot centre to each tree was recorded along with its diameter at breast height (DBH) and defects. For every fifth tree and also for dominant

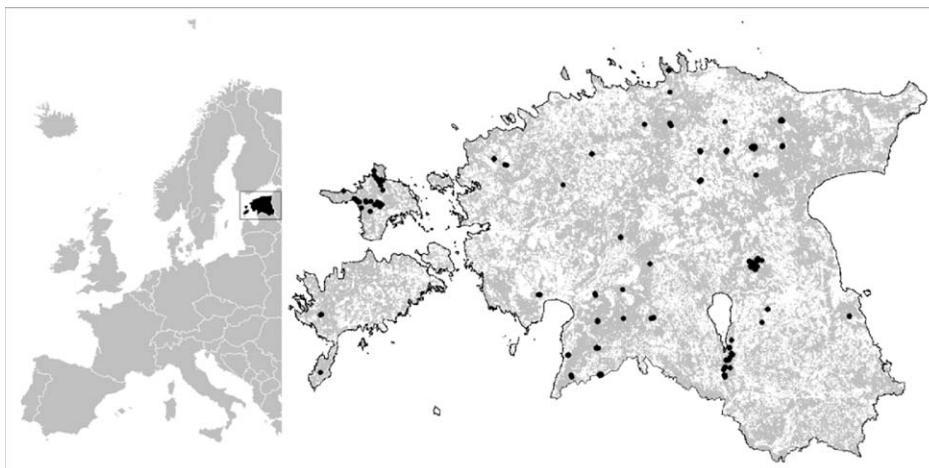


Fig. 1. Geographic location of study areas (black dots). Grey area indicates forests in Estonia.

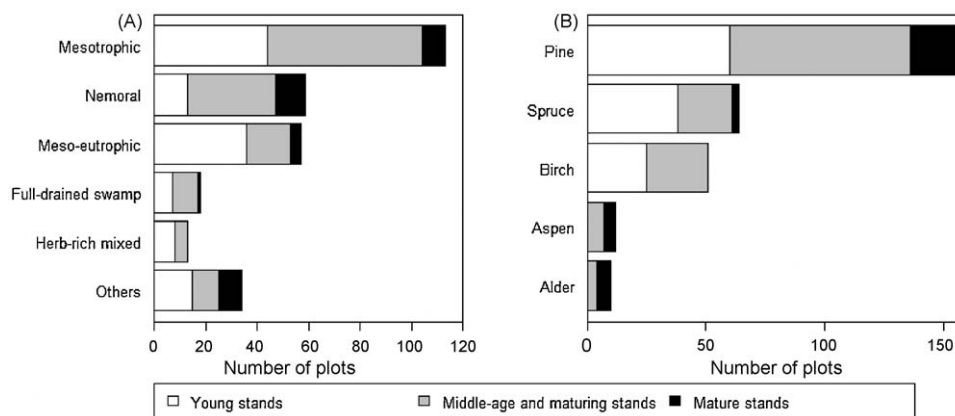


Fig. 2. Distribution of plots by groups of forest site types (A) and main tree species (B). The site type “others” includes alvar, bog moss, heath, paludified and fen forests. Age classes are appropriate to the dominant species (e.g., mature pine stands are considerably older than mature alder stands).

and rare tree species, tree height and height to crown base were measured. (Kiviste and Hordo, 2003).

Relative tree diameters were calculated for each measured tree, where relative diameter is defined as the ratio of an individual tree's diameter to the mean diameter of the stand (Eid and Tuhus, 2001). A relative tree diameter value <1.0 indicates a tree smaller than the stand average tree. Measurement records were available for living trees (upper-, mid-, under-storey and shrub layer trees), dead trees (standing, downed, and broken trees) and fresh stumps.

This study was based on 294 sample plots (Fig. 1) and the data from 43,848 trees. Species composition of the sampled trees was 42% Scots pine (*Pinus sylvestris* L.), 25% Norway spruce (*Picea abies* (L.) Karst.), 21% birch (*Betula pendula* Roth. and *Betula pubescens* Ehrh.) and 12% of several deciduous species. Fig. 2 presents distributions of permanent sample plots analyzed in this study by forest site types, dominant species and stand development classes. Distribution of plots by stand age and dominant species is presented in Table 1.

2.2. Analysis of patterns of individual tree mortality

For each sampling period, mortality rate was calculated as the number of trees that died, expressed as a percent of the number of trees living at the beginning of the period. Annual mortality is the number of dead trees in an interval divided by the number of years in the period.

The cause of the mortality (CM) of each dead tree was categorized into density-dependent and density-independent factors. One of the most important density-dependent effects is competition among individual trees including unspecified causes

Table 1
Distribution of sample plots by main species and age classes.

Age	Alder	Aspen	Birch	Pine	Spruce
5–14	1				1
15–24			10	18	12
25–34	7	1	18	28	26
35–44	1	4	12	12	14
45–54	1	7	11	26	5
55–64				18	1
65–74				16	2
75–84				16	2
85–94				6	1
95–104				10	
105–114				2	
115–124				3	
135–144				1	
165–174				1	

of mortality for suppressed trees. Density-independent mortality was identified more precisely:

- Wind damage, including wind throw and stem breakage;
- Game damage, mainly by moose peeling the bark from spruce and pine leading to death of trees;
- Insect attacks, mainly bark beetle (*Ips sp.*) as primary or secondary causes;
- Fungi and disease, mainly root rot, heart rot, canker and other pathogens as primary or secondary causes;
- Other, including flooding, frost or unknown reasons.

The logistic function (Eq 1) (Freund and Littell, 2000) was used to model mortality of individual trees due to the causes considered with each dead tree being an observation, as

$$\text{logit}(p) = \ln \frac{p}{1-p} \quad (1)$$

where p is probability of CM (e.g., wind).

The logit-transformation rendered CM into a dependent variable with a normal distribution, which can be analyzed with methods of regression and variance analysis:

$$\text{Logit}(p) = f(x) \quad (2)$$

where $f(x)$ is a linear function of the vector x of measurement variables.

Goodness of model fit was determined by examining percent concordant values which indicate overall model quality through the association of predicted probabilities and observed responses. The higher the predicted event probability of the larger response variable, the greater the percent concordant value will be.

Diversity index of mortality reasons (CMDI) was adopted from Shannon (1948) H' index for the estimation of diversity in an ecosystem. CMDI can be calculated by the formula:

$$\text{CMDI} = -\sum_{i=1}^S p_i \ln(p_i) \quad (3)$$

S = number of CM; p_i = proportion of the CM ($p_i = N_i/N$); N_i = number of dead trees because of CM_{*i*}; N = total number of dead trees.

2.3. Deadwood mingling

The spatial distribution of deadwood in a stand can be evaluated by the pattern of mingling of dead and live stems. Deadwood mingling is defined as the proportion of the n nearest

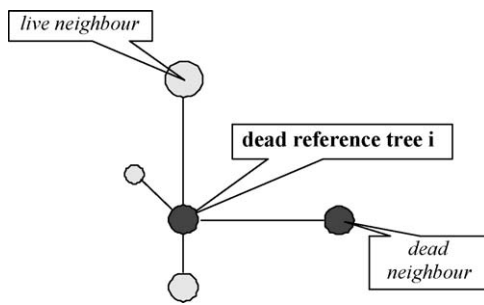


Fig. 3. Structure variable—deadwood mingling for reference tree and four of its nearest neighbours. The mingling index value DM_i is 0.25 in this example.

neighbours that are also dead trees (Fig. 3). We developed a deadwood mingling index (DM_i) using the species mingling formula proposed by Gadov (1993) for a group with four nearest neighbours of a dead reference tree i :

$$DM_i = \frac{1}{4} \sum_{j=1}^4 v_j$$

with

$$v_j = \begin{cases} 1, & \text{when the neighbour } j \text{ is dead tree} \\ 0, & \text{when the neighbour } j \text{ is living tree} \end{cases} \quad (4)$$

With four neighbours, DM_i can assume five different values: 0, 0.25, 0.50, 0.75 and 1. The mingling index value of 1 indicates that all neighbouring trees of a dead tree are also dead trees; conversely a mingling value of 0 indicates that all neighbouring trees are alive. The distribution of all reference trees or average DM_i can be used as a surrogate for deadwood clumping in a stand. We calculated the DM_i for each plot and tested for homogeneity of variances in deadwood mingling of each category of forest using the Fligner–Killeen test implemented with the R statistical software.

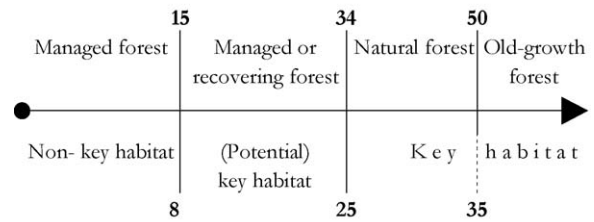
Edge effects should be considered in calculating the mingling index. One way is to consider a buffer zone around the edge of the plot, with a buffer width equal to the distance to the fourth nearest neighbour. This method has been shown to reduce bias effectively in a comparison of several edge correction techniques (Pommerening and Stoyan, 2006). In the case of deadwood mingling, edge effects cannot be effectively adjusted afterwards because there are usually just few dead trees on a plot.

2.4. Nature value assessment

Nature value assessment has been included in sample plot measurements since 2006 using a method that incorporates both quantitative and qualitative scoring (Korjus, 2002). The method is based on evaluating specific stand and landscape attributes to arrive at a score that is compared to a scoreboard (Fig. 4).

Naturalness was measured as different levels of anthropogenic influence in a forest stand. Forests were classified as old-growth, natural, recovering, or commercial forests, depending on the signs of management activities. As most forests in Estonia have been managed or influenced by humans to some degree, by “old-growth” we meant that the remnants have not been managed for at least 200 years. According to the special full-scale inventory of present and possible forest conservation areas (Viilma et al., 2001) there are several hundred hectares of such “old-growth” still existing in Estonia. Natural forest included uneven-aged forests of natural origin with a composition characteristic of the site. Natural forest can bear traces of earlier cuttings but these must have no effect on the present structure of the stand. There is also some downed dead wood in different stages of decomposition in such stands. Recovering forest has come into existence as a result of

FERTILE FOREST SITES



POOR FOREST SITES

Fig. 4. The scale for evaluating forest naturalness by the method of nature value assessment (Korjus, 2002). Numbers represent total scores of nature value for distinguishing different levels of naturalness and key habitats. For example, on poor forest sites the margin between natural forests and recovering forests is 25 points; on fertile sites the margin between non-key habitats and potential key habitats is 15 points.

human activities, bears numerous traces of earlier cuttings but their effect on the present structure of the stand is insignificant such that the stand would develop into a natural forest in 20–30 years if left untouched. Standing and downed dead wood is present in various amounts in a recovering forest. Compared to a classification for Lithuania (Šaudyte et al., 2005), our recovering forests match their semi-natural forests and the natural forests are the same for both classifications. Managed forests have evidence of cuttings with a strong effect on the species composition and structure of the stand; there is very little or no downed dead wood.

For our sample plots, all old-growth forests, natural forests and recovering forests were regarded as semi-natural forests in the analysis. Of the sample plots, 32 were classified as semi-natural and 262 as managed forests. Large-scale disturbances (at least 15% of trees died within last 5-year) were present on 13 sample plots, all in managed forests.

3. Results

A total of 2493 trees died during the study period from 2001 to 2007. Of the dead trees, 29% were pine, 27% birch, and 20% spruce. The average annual tree mortality rate was 1.3% based on the initial stem numbers. Grey alder (*Alnus incana* (L.) Moench) had the highest mortality rate (4.3%) and pine and spruce had the lowest (0.9%) (Table 2).

Data analysis showed that the main CM was competition (45%) between trees. Scots pine, birch and aspen (*Populus tremula* L.), were the most influenced by tree competition and spruce was the least (Fig. 5). Fungi and diseases was the second commonest CM, accounting for 30% of grey and black alder (*Alnus glutinosa* (L.) Gaertn.) mortality. Wind (wind throw and storm breakage) was the third commonest CM (19%). Spruce was the most influenced (more than 40% of dead trees) and pine the least influenced (10%).

Table 2

Annual mortality rates (% from stem number per year) by tree species and stand development class.

Tree species	Stand development class		
	Young stands	Middle-aged and maturing stands	Mature stands
Scots pine	1.21	0.55	0.48
Norway spruce	1.05	0.97	0.84
Black alder	1.52	1.80	1.43
Birch	1.54	2.05	1.28
Aspen	0.95	2.90	–
Grey alder	–	3.74	5.06

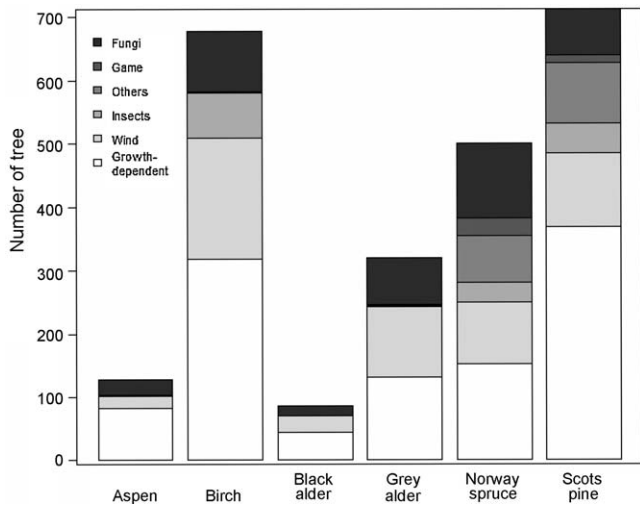


Fig. 5. Distribution of dead trees by causes of mortality (CM) and tree species.

The best relationship between CM and tree size was with relative tree diameter. Growth-dependent causes, wind and insects are showing different behavior related to relative diameter in semi-natural and managed forests (Fig. 6). Growth-dependent causes and wind were relatively less important reasons and insects a more important reason for individual tree mortality in semi-natural stands (Fig. 7). Logistic regression modelling (Table 3) showed that trees with lower relative diameters were more likely to die because of tree competition. Larger relative diameter trees were more likely to die because of wind damage and from game (mostly moose) and insect damage. However there seemed to be no relationship between relative diameter and mortality caused by fungi and diseases. The relationships between causes of mortality and relative diameter differed among species. We found significant relationships between relative diameter and mortality probability for all CM for Scots pine (p -value < 0.001); fungi (p -value < 0.001) and growth-dependent (p -value < 0.001) CM for Norway spruce; and fungi (p -value < 0.001), growth-dependent (p -value < 0.001) and wind (p -value < 0.001) CM for birch trees.

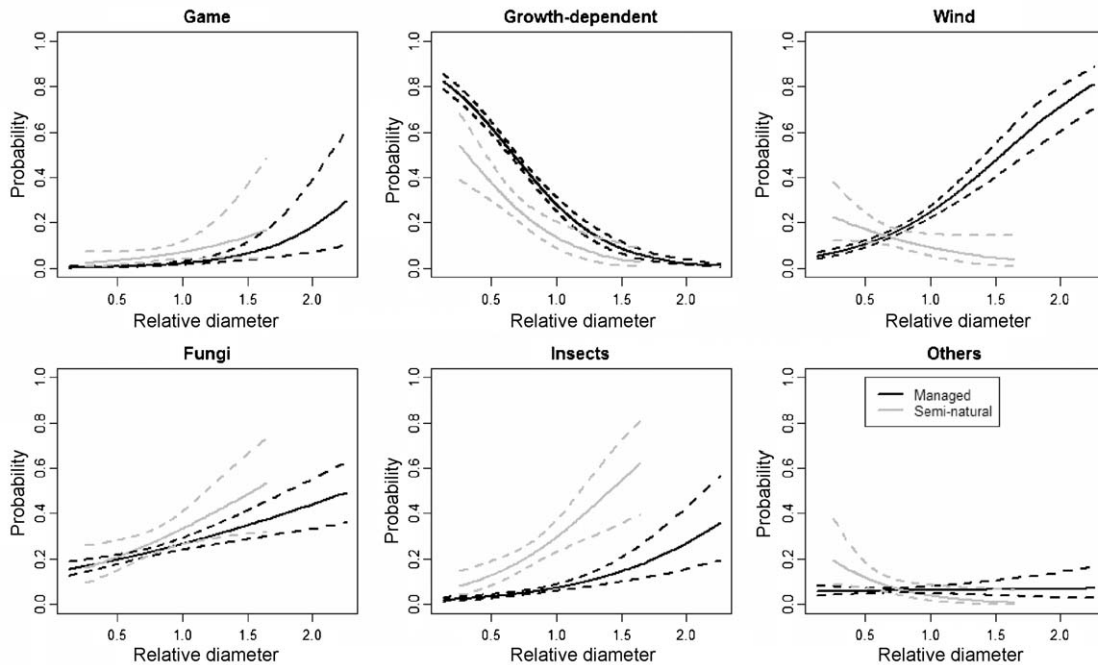


Fig. 6. Predicted probability (%) of different CM (solid line) with 95% confidence limits (dashed lines) depending on relative diameter in managed and semi-natural stands.

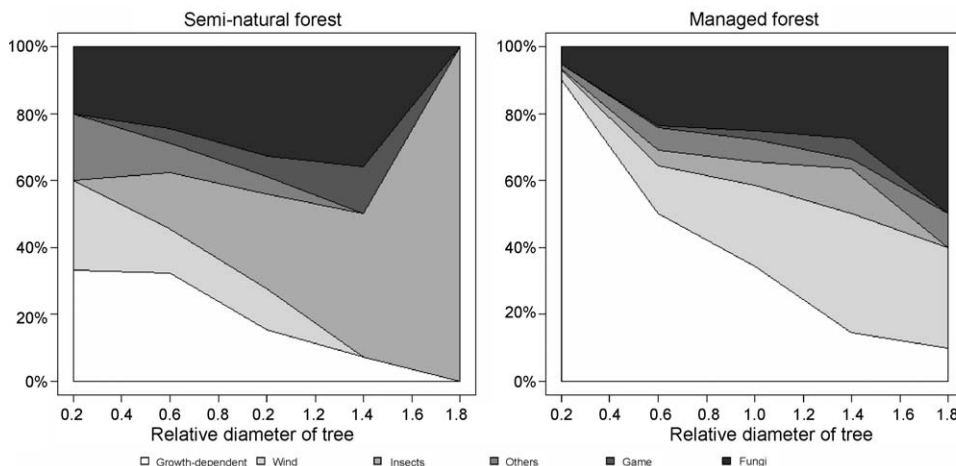


Fig. 7. Probability (%) of CM for individual trees depending from relative tree diameter in semi-natural and managed forests.

Table 3
Results of logistic regression for probability of individual tree mortality on relative diameter of tree (Dr) by different reasons.

Reason for individual tree mortality	Parameter	Estimate	Standard error	Pr > Chi-Square	Percent concordant
Fungi	Intercept	-1.8179	0.1327	<.0001	56.3
	Dr	0.8435	0.1654	<.0001	
Game	Intercept	-5.7174	0.4048	<.0001	69.1
	Dr	2.1289	0.4081	<.0001	
Insects	Intercept	-3.9417	0.2201	<.0001	65.1
	Dr	1.7507	0.2439	<.0001	
Wind	Intercept	-2.9240	0.1579	<.0001	64.6
	Dr	1.6984	0.1854	<.0001	
Growth-dependent	Intercept	1.8309	0.1331	<.0001	69.0
	Dr	-2.8806	0.1855	<.0001	

The average recent deadwood volume (RDV5) for the last 5-year period for all stands was 6.1 m³ ha⁻¹. The highest average RDV5 was found in aspen stands (15.3 m³ ha⁻¹), the lowest in black alder stands (1.0 m³ ha⁻¹) (Fig. 8). The average RDV5 was significantly lower (*p*-value < 0.001) in managed forests (5.4 m³ ha⁻¹) than in semi-natural forests (12.3 m³ ha⁻¹) (Fig. 9). RDV5 is correlated to the number of mortality causes and deadwood mingling (Table 4).

A comparison of deadwood mingling and nature value scores in managed and semi-natural forests showed that dead trees were more dispersed (Fligner–Killeen test, *p*-value < 0.001) and the naturalness score was higher in semi-natural forest stands (*t*-test, *p*-value < 0.001) (Fig. 10). The nature score was significantly correlated with the diversity index of mortality causes (CMDI), indicating that CM are more diverse in semi-natural stands

(Table 4). Mean values and distribution of the deadwood mingling index (DM_i) in managed and semi-natural forests (Table 5) were not significantly different. In middle-aged semi-natural forests, mortality is spatially more random than in managed forests, thus there is no evidence of gap formation. Gap formation, however, should be more characteristic of older stands.

4. Discussion

There are many different definitions of forest naturalness (Lee et al., 2000). A true “natural” forest can be defined as an idealized virgin forest condition that is not influenced by large-scale, systematic human activity (Bradshaw, 2005). Accumulation of large standing and downed deadwood and complex structural properties are often important indicators in these definitions (Kneeshaw and Burton, 1998). However, most definitions of “old-growth” include the premise that recent large-scale forest disturbances are absent (Rubin et al., 2006), which is challenged by some authors (e.g., Oliver and O’Hara, 2005). As recent disturbances are almost always present at the landscape level, we expected a variety of tree mortality patterns even on landscapes dominated by old-forests. Managed forests usually have an even distribution of stands in different developmental stages (age classes) except that old over-mature forests are generally lacking in managed landscapes. Often a mosaic of stands in different stages of forest development is desirable for biodiversity considerations, which also can be characteristic of unmanaged forests.

In the real world “naturalness” is almost impossible to define quantitatively. A bare landscape destroyed by natural large-scale

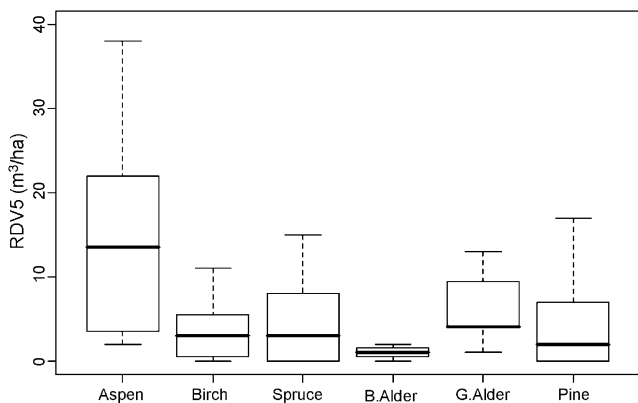


Fig. 8. Amount of recent deadwood volume (RDV5) in stands dominated by different species.

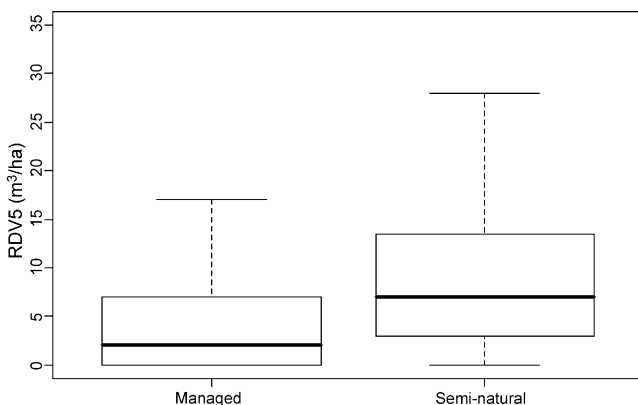


Fig. 9. Comparison of the volume of recent deadwood (RDV5) in managed and semi-natural stands.

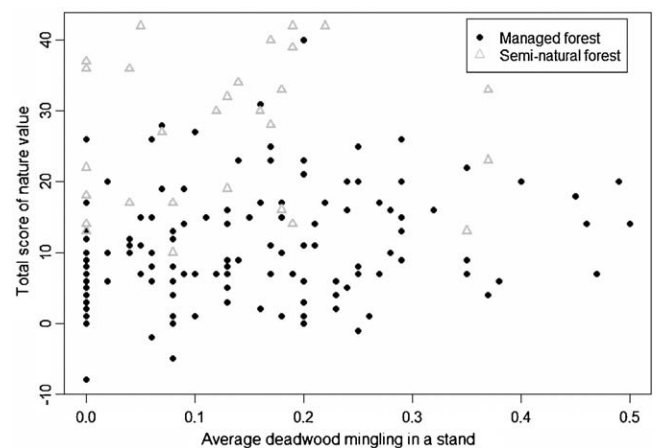


Fig. 10. Deadwood mingling and score of nature value in managed and semi-natural stands.

Table 4

Spearman correlation matrix of mean deadwood mingling index (DMi), nature value score, diversity index of mortality causes (CMDI), number of mortality causes (CM) and recent deadwood volume (RDV5) on sample plot data (values in bold are significantly different from zero).

	Mean DMi	Nature score	CMDI	Number of CM	RDV5
Mean DMi	1.000				
Nature score	0.182	1.000			
CMDI	0.194	0.471	1.000		
Number of CM	0.331	0.423	0.914	1.000	
RDV5	0.630	0.291	0.469	0.661	1.000

Table 5

Mean values and distribution of the deadwood mingling index (DMi) in managed and semi-natural forests.

Forest class	Mean value of DMi	Percent of trees with corresponding DMi value				
		0.00	0.25	0.50	0.75	1.00
Managed forests	0.220	44.23	31.55	17.32	5.91	1.00
Without large disturbance	0.196	48.28	30.78	15.63	4.77	0.54
With large disturbance	0.291	31.86	33.89	22.47	9.39	2.39
Semi-natural forests	0.199	49.82	30.26	13.28	3.69	2.95

disturbance may be more natural than a beautiful planted forest with high biodiversity value. We can only use surrogates to define a degree of naturalness. We hypothesized that multiple causes of tree mortality indicated naturalness of a stand. Our analysis results showed that the number of reasons for mortality was not directly connected to the number of processes leading to tree death. Our experience was that determining with certainty the reason or reasons a tree dies is often difficult. Visible or detectable evidence for a cause of mortality was present for some trees but also several trees died without any indication of the cause. Tree death is

generally the result of complex interactions among multiple factors (Franklin et al., 1987; Manion, 1981). In future studies, better results may be obtained by not constraining mortality to be caused by a single reason but rather to use a process-based multiple-reason method (Fig. 11).

Modelling the CM showed that with increasing relative diameter there was a higher probability for tree mortality to be caused by wind, insect or fungi damage and a lower probability for tree mortality to be due to growth-dependent causes. The survival probability of a tree was dependent on its relative diameter in the stand (Laarmann, 2007). Usually forest growth and yield models use data representing past forest dynamics. The applications of these models in simulating the future growth and development of a stand assume that future conditions will be similar to the past (García-Gonzalo, 2007). Because changing growth conditions that influence the resilience of trees may lead to increased mortality, therefore the actual changes in forest growth conditions can bias judgments made about the nature value of a forest.

Several studies (e.g. Neumann and Starlinger, 2001) have found that forest naturalness is not correlated with tree species composition or stand diversity. It can be true also in relation to the amount and distribution of deadwood. Debeljak (2006) found that there is a considerable difference in deadwood quantity between managed and virgin forests in European temperate forests. Several studies (Liira et al., 2007; Kohv and Liira, 2005; Jonsson and Jonsell, 1999; Ohlson et al., 1997) found that the amount of deadwood is an important indicator of forest ecosystem quality in boreal and hemiboreal zone. Individual tree mortality in natural forests of a *Pinus*-dominated landscape in a wilderness area in Fennoscandia was characterized by a continuous flow of local-scale autogenic mortality of individual trees or small groups of trees (Rouvinen et al., 2002). Rouvinen et al. (2002) found deadwood accumulation levels of $1.8 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ in the old-growth forest in Eastern Fennoscandia. In our study, deadwood accumulated twice as quickly in forests that were left for natural development (semi-natural forests; $2.5 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) than in

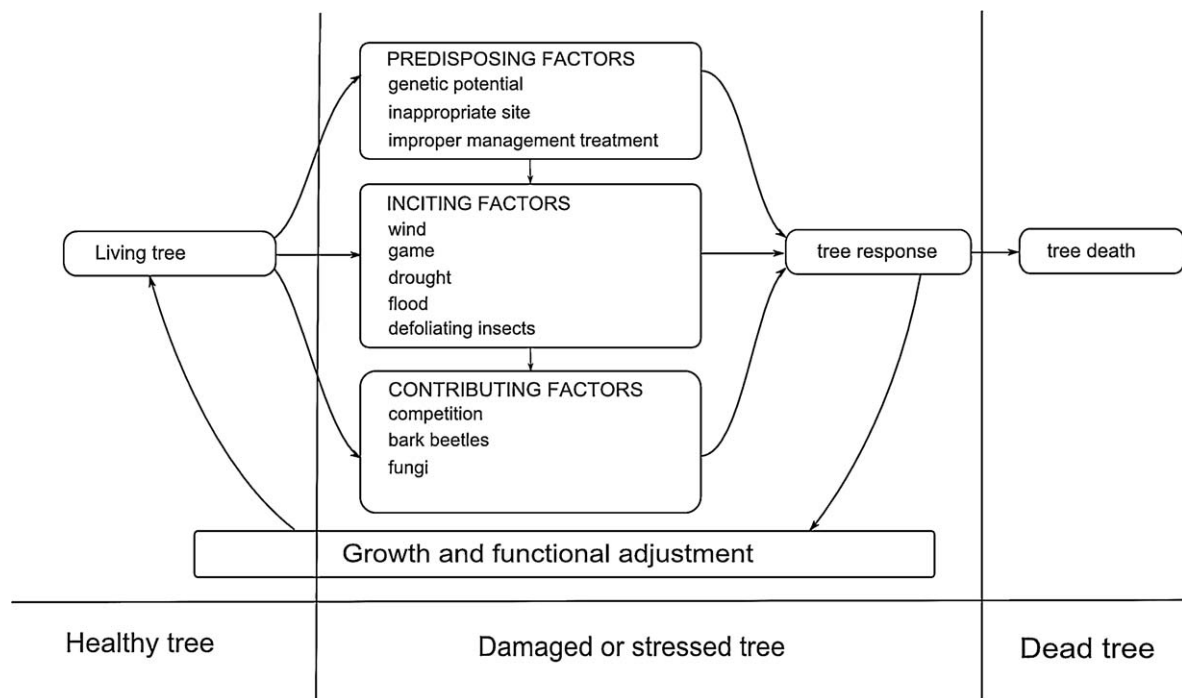


Fig. 11. Principal scheme of a process-based method for determining multiple causes for individual tree mortality; revised from Franklin et al. (1987); terminology after Manion (1981). Predisposing factors are generally static or non-changing factors. Inciting factors are short in duration and may be physical or biological in nature; these generally produce a drastic damage. The contributing factors produce noticeable symptoms and sign on the weakened tree.

managed forests ($1.1 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$). This difference may indicate that deadwood accumulation is more intensive in semi-natural forests than in old-growth climax forests.

Our results indicate that forest naturalness cannot be explained only by the amount of dead trees or by tree survival rates in a stand. Laarmann (2007) estimated that approximately 40% of forest stand naturalness in Estonia can be described with structural and qualitative properties of dead trees (how and where trees died). Therefore deadwood quantity itself is not a good indicator of forest naturalness. Better indicators are deadwood spatial and size distributions and the variety of CM.

Kint et al. (2003) compared nearest neighbour indices with other method and concluded that these indices are suitable for quantifying forest structure characteristics. Kint (2005) showed that the clustered spatial pattern that followed large disturbances will develop to a regular spatial point pattern in young Scots pine stands because of self-thinning and competition with other species. The deadwood mingling variable we used was acceptable for distinguishing the clumping of dead trees that indicated recent disturbances and for characterizing deadwood spatial pattern. Patches of clumped dead trees in a stand often indicate recent forest disturbance and, in this case, the quantity of deadwood may not indicate forest naturalness. Our study showed that variation of deadwood mingling is characteristic of both managed and semi-natural forests in the Baltic countries. However, higher values of deadwood mingling indicate recent disturbances in forest stands.

The current study showed that assessment of forest naturalness can be improved with analysis of tree mortality patterns. Deadwood quantity and spatial distribution, recent mortality rate and causes of mortality together are good indicators of forest naturalness and should be useful in assessing and conserving biodiversity. Assessment and analysis of causes for individual tree mortality remains a challenge for applications in forest inventory and conservation planning.

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