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Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient

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We aimed to quantify the effects of anthropogenic disturbances on forest structure and diversity in deciduous and mixed boreo-nemoral stands, conditioned on potential confounding factors. Based on these results, we created a statistically-supported indicator list of stand "naturalness". We surveyed 50 quantitative and qualitative characteristics of a stand, the understorey and forest floor, and several widely accepted biodiversity indicators in 171 forests in Estonia. Multi-factorial GLM and GLIM analyses showed that many forest structural characteristics were confounded by forest site-type specificity, stand age and/or biogeography. Near-natural old-growth forests had higher proportions of deciduous trees, a larger amount of coarse woody debris, a higher frequency of logs in each decay class, a denser understorey, and were more homogeneous in the horizontal pattern of each layer than mature managed forests. By improving light conditions, forest management indirectly increased herb layer richness and coverage and the proportion of graminoids. The critical easy-to-apply set of indicators to assess forest ecosystem quality includes the amount and type of dead wood, the canopy closure of a stand and the presence of specially-shaped trees, specific epiphytic indicator lichens, mosses and wood-dwelling insects, and forest site-type specific herb layer species.

Key words: anthropogenic disturbance, biodiversity indicators, dead wood, ecosystem quality, forest management, indicator species, stand structure

Introduction

During the last century, global biodiversity had been changing at an unprecedented rate in response to human-induced changes in the environment (Vitousek *et al*. 1997, Foley *et al*. 2005). The exploitation of forests in recent centuries has left only a few remnants of virgin forest habitats in Europe (Scheller *et al*. 2008). Forest land area has actually increased in recent decades (FAO 2007), particularly in Estonia (from 30% to 52% during the last century; Meikar & Etverk 2000, Adermann 2008). Most forest land has been covered by secondary forests or intensively managed mono-species stands (Valk & Eilart 1974, Linder & Östlund 1998, Bengtsson *et al*. 2000, Larsen & Nielsen 2007, Adermann 2008). A contemporary forest stand has undergone homogenisation, simplification and fragmentation (Axelsson & Östlund 2001, Jantunen *et al*. 2002, Weibull &

Rydin 2005, Brown & Cook 2006). Silvicultural practices have reduced species populations that are adapted to natural forests and diminished the amount of services provided by forest ecosystems (Nilsson & Ericson 1997, Gustafsson 2002, Balmford *et al.* 2003, Pykälä 2004, Weibull & Rydin 2005).

In the temperate and boreal vegetation zones, numerous studies have shown the sensitivity of various taxonomic or ecological groups to forest management intensity (Berg *et al.* 1994, Martikainen *et al.* 2000, Bergstedt & Milberg 2001, Buckley *et al.* 2003, Jansson & Andren 2003, Meier *et al.* 2005, Nelson & Halpern 2005). Many of these negative effects of management on biodiversity are indirect and confounded with other ecological processes. For example, understorey vegetation, epiphytic lichen and insect diversity are not a direct object of management, but management effects are mediated via changes in the tree and shrub layers, host tree availability and old-growth legacies, as well as stand age and historical continuity (Zobel 1989, Foster *et al.* 1996, Lawesson *et al.* 1998, Bergstedt & Milberg 2001, Kuuluvainen 2002, Marozas *et al.* 2005). Old-growth forest specialist species are shown to be sensitive to the availability of particular forest structural aspects, such as the amount of coarse woody debris, multi-species stand, burnt trees or multi-aged stand structure (Berg *et al.* 1994, Jonsell *et al.* 1998, Gustafsson 2002, Similä *et al.* 2003).

In recent decades, issues of forest biodiversity and sustainable forestry have received increasing attention (Noss 1990, Foster *et al.* 1996, Norton 1996, Trass *et al.* 1999, Bengtsson *et al.* 2000, Kuuluvainen 2002, Larsen & Nielsen 2007). Endorsed or certified silvicultural practices are expected to use more sustainable and diversity-centred methods (Lähde *et al.* 1999, Larsen & Nielsen 2007). This has provided grounds for the development of a concept of the "naturalness" or "ecosystem quality" of a forest community (Arler 2000, Ejrnaes *et al.* 2002, Gamborg & Rune 2004, Liira *et al.* 2008). The concept of habitat quality combines information about biodiversity and the complexity of ecosystem functions (e.g. Kohv & Liira 2005). The sustainable management of forests tends to mimic small- and large-scale natural processes in forests, extend the rotation period and create structural components resembling natural forest structures, e.g. retaining dead standing and lying trees, or creating additional coarse woody debris (Peterken 1999, Lilja *et al.* 2005, Jonsson *et al.* 2006). It has also been recognized that biodiversity stored in fragmented patches of protected old-growth forests needs the additional support of older conventionally-managed stands, in which natural disturbances have been mimicked (Franklin & Forman 1987, Gustafsson 2002, Kuuluvainen 2002, Vanha-Majamaa *et al.* 2007). Forest monitoring and the evaluation of near-natural stands are often limited by financial considerations (Ejrnaes *et al.* 2002, Jonsson *et al.* 2006). Therefore, forest evaluation and monitoring agencies urgently need optimal methods for objective and easily applied assessment indicators to estimate the naturalness, quality or conservational value of a habitat (Smith & Theberge 1987, Norton 1996, Nilsson & Ericson 1997, Ejrnaes *et al.* 2008). An efficient set of indicators should consist of surrogate traits correlated with both biodiversity and management activities, they should be easy to detect and evaluate, and they should be informative over a wide range of environmental conditions, forest types and geographical regions (Lindenmayer 1999, Brooks & Kennedy 2004).

In forest conservation, many management-sensitive structural legacies and species have been listed as distinctive indicators of a forest's near-natural state (Smith & Theberge 1987, Trass *et al.* 1999, Kuuluvainen 2002). Those structural characteristics and their threshold values are, however, often specific to particular forest types (Vanha-Majamaa *et al.* 2007). Their threshold values depend on soil moisture and productivity, species composition and natural disturbance regimes (Linder *et al.* 1997, Jonsson & Jonsell 1999, Meier *et al.* 2005, Liira *et al.* 2007). Consequently, there is a need for a critical set of indicators of forest ecosystem health or habitat quality that has been subjected to rigorous testing across a range of stand management and disturbance intensities (Smith & Theberge 1987, Dale & Beyeler 2001, Kohv & Liira 2005).

The complexity of different parallel factors and processes influencing forest vegetation, such as habitat quality, the history of a stand and the structure of the surrounding landscape, can easily produce biased relationships or conceal causal ones (Flinn & Vellend 2005). There are only a few studies in which all possible confounding factors have been measured and analysed simultaneously (e.g. Jacquemyn *et al.* 2003, Kohv & Liira 2005, Liira *et al.* 2007, Aparicio *et al.* 2008), which means that knowledge of this topic is too scarce to produce widely accepted generalizations.

We hypothesize that anthropogenic disturbances have a combined effect on forest structure, but this is confounded with other factors such as forest type, forest age and geographic location. The latter is itself frequently a factor variable combining climatic differences, local geology and region-specific management traditions. These factors can blur the detection of the "true" effect of anthropogenic disturbances and obstruct the creation of indicators for the monitoring of the habitat quality of forests. Large-scale multi-sample inventories would provide more objective information about the statistics of forest structural characteristics than small-scale regional studies (Elofsson & Gustafsson 2000, Fridman & Walheim 2000, Liira *et al.* 2007). Therefore, (i) to have the power to make a broader geographical extrapolation of the conclusions, the whole distribution area of these forest site-types should be covered with sampling locations; (ii) to avoid clearly trivial successional effects, one should limit the sample to stands at least 75 years old; (iii) to detect true management effects, the full range of forest stands with various anthropogenic disturbance intensities should be sampled in each sub-region; and (iv) all of these effects should be tested simultaneously in multi-factorial models.

In this study, we first define forest structural characteristics of old-growth and mature managed stands that are sensitive to forest management practices. Second, we aimed to produce a statistically-supported set of indicators for the evaluation of forest "naturalness".

Material and methods

Studied communities

Estonia is situated in the transitional area between boreal and broad-leaved forests, the so-called hemi-boreal vegetation zone (Ahti *et al.* 1968), and covers a broad range of biogeographical conditions in a small geographical range (Lippmaa 1935, Laasimer 1965). The climate varies from maritime to continental. Average annual precipitation increases from west to east within a range of 600 to 700 mm. Average temperatures in July and February along this west–east gradient range from 16.3 to 17.4 °C and –2 to –7.4 °C, respectively (Aunap *et al.* 2004). The Baltic region, including Estonia, can also be considered to be a transitional zone between intensively managed western Europe and old-growth forest rich northwestern Russia (Angelstam *et al.* 1995, Carlsson & Lazdinis 2004). According to the Statistical Forest Inventory in Estonia, 48% of the stands are mixed stands, 14% of the stands are mature or over-mature, only 2%–3% of the forests are near-natural (*sensu* Kohv & Liira 2005), while ca. 30% of the forest land has some kind of restrictions in management and 28% of the forests are affected by the edge effect (Adermann 2008).

The boreo-nemoral forests (by Paal 1997, Natura 2000 codes 9020, 9050, 9060 and 9180 according to Paal 2007), belong to the group of the most productive forest types in Estonia, which can reach a stand volume of up to 600–700 $m^3 ha^{-1}$. The humus layer of these forests is commonly 15–30 cm thick and has humus content of 3%–13% (Lõhmus 2004). Eutrophic boreo-nemoral forests in Estonia consist of two major forest site-types: *Aegopodium* type and *Hepatica* type. *Aegopodium* type forests mostly grow on Gleyic Cambisols and Luvisols and are more often found in central and eastern Estonia, comprising 10.4% of the Estonian forest land (Fig. 1) (Adermann 2008). The *Hepatica* type is common on deep Rendzinas, Calcaric Cambisols and Luvisols of moraine-rich areas, particularly hillocks, and represents 9.5% of the Estonian forest land (Fig. 1) (Adermann 2008). In the *Aegopodium* site-type, ground water is available continuously, while soils of the *Hepatica* site-type can be periodically dry. As compared with those of the *Aegopodium* site-type, soils in the *Hepatica* site-type tend to be more alkaline (pH around 4.7–6.5 and 5.5–7, respectively) (Lõhmus 2004).

Tree species composition is one feature where there is a remarkable difference between the

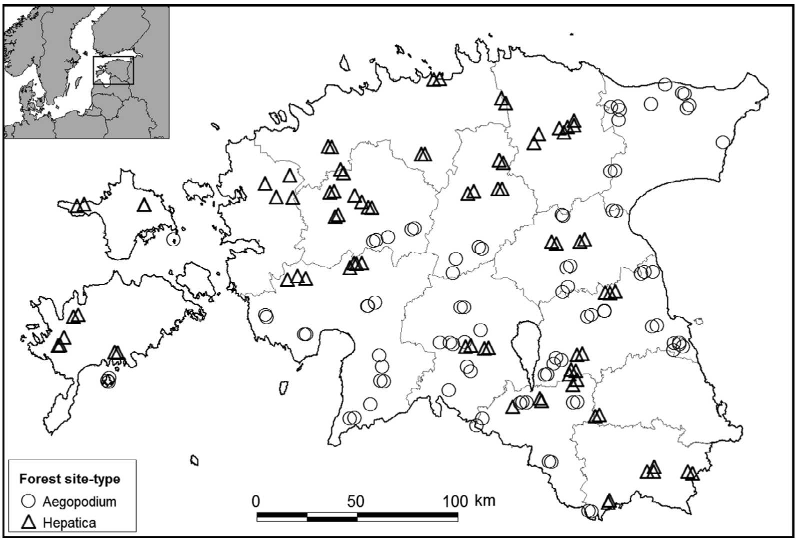

Fig. 1. Location of the forest study sites.

two site-types. The Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) mostly dominate over deciduous trees in the *Hepatica* type, but the situation is reversed in the *Aegopodium* type. In the *Aegopodium* type, over half of the stands are dominated by silver birch (*Betula pendula*), followed by spruce and aspen (*Populus tremula*). The boreo-nemoral forests, especially the *Aegopodium* type, constitute the highest proportion of "noble" broadleaved trees/ash (*Fraxinus excelsior*), elm (*Ulmus glabra*), lime (*Tilia cordata*) and oak (*Quercus robur*). Common understorey species in the shrub layer of the Estonian fresh boreo-nemoral forest are *Corylus avellana, Sorbus aucuparia* and *Lonicera xylosteum*. The herb layer is species-rich, whereas the *Aegopodium* type is characterized by a greater abundance of nemoral species, such as *Aegopodium podagraria*, *Galeobdolon luteum* and *Mercurialis perennis*. Typical plant species for the *Hepatica* type forest floor are *Hepatica nobilis*, *Oxalis acetosella*, *Rubus saxatilis* and *Anemone nemorosa* (Paal 1997). The moss cover is patchy and species-rich, and more continuous in the *Hepatica* type.

The common management cycle of a productive Estonian forest involves planting, sowing or natural regeneration with soil preparation, two or three thinnings at approximately 20-year intervals and clear-cutting at the age of about 60–120 years.

Sampling methods

We selected a methodological scheme for forest sampling that would maximise the estimation of management effect and minimize the confounding effects of large-scale heterogeneity in environment and biogeography. This is particularly important in designing a wide-scale monitoring system. We used stratified sampling, locating contrasting pairs of study sites more or less evenly over the entire distribution area of both site-types in Estonia (Kohv & Liira 2005, Liira *et al*. 2007). In detail, this was done by using the following algorithm. As the first step, we used the Estonian State Forest Management Centre database and a forest map to select areas with an abundant presence of these forest types. We targeted forest sub-compartments with an area of more than 1 ha and an average stand age of more than 75 years. These criteria were used to exclude the effects of forest edges, fragmentation and successional stages (Zobel *et al*. 1993, Liira *et al*. 2008, Aavik *et al*. 2009). Finally, based on the forest management information gathered over the last 10–20 years in the State Forest Management Centre database and the information of the Forest Key-habitat Network (Andersson *et al*. 2003), we selected pairs of forest sub-compartments at a distance of no more than 5 km. In a pair of stands, one of these had to be as pristine or old-growth as possible (e.g. forests in Poruni, Vinni, Nigula, Abrouka, Järvselja or northern escarpment), and anther one as intensively-managed a sub-compartment as possible in that neighbourhood. By such sample-site selection algorithm, we expected to minimize regional variations and maximize options to reveal pure stand level relationships.

Data were collected during four summers (late June, July and early August of 2003–2006). In total, forest structure and biodiversity were described at 171 sites: 88 sites of the *Aegopodium* type and 83 of the *Hepatica* type (Fig. 1). A few study sites were recorded without a matched pair site, as management alternatives were not found within an acceptable distance.

At each forest study site, we recorded a large set of forest structural and species composition features (50 characteristics; most of which are presented in Tables 1 and 2) using the questionnaire developed by Kohv and Liira (2005). The methodology and trait measurements were set to be as robust as possible and as informative as allowed, to minimize random error fluctuations for what ever reason (observer, season, year or region). The robustness of trait estimates should allow us to compare statistically more adequately these traits among forest types and regions, and to implement them into practical use or monitoring.

In a radius of 30 m from a site centre, we recorded the basal area of each tree species in diameter size classes 8–40 cm, 40–80 cm and > 80 cm at a height of 1.3 m, using the Bitterlich relascope. In the same area, we also visually measured the vertical structure of the canopy by estimating the cover of three canopy layers (1–4 m, 4–10 m, 10–25 m; separately for conifers and deciduous species) and the total cover of the tree layer. We characterized stem diameter diversity as the number of trunk diameter classes (DBH 0–2, 2–8, 8–20, 20–40, 40–80, and more than 80 cm) in a study area of $r = 30$ m that were represented with two or more stems.

We measured the quantity of standing dead wood and large snags (DBH > 8 cm and height > 1.3 m) using the Bitterlich relascope and separately for trees with DBH < 40 cm and DBH > 40 cm. We estimated the basal area of lying dead trees (as a surrogate indicator for the amount of lying dead wood) using a methodological analogy of the relascope — counting lying logs longer than 1.3 m with a diameter greater than 8 cm, 15 cm and 40 cm in concentric circles around the central observation point with a radius of 0–5 m, 5–10 m and 10–30 m respectively. Such a zone-diameter system imitates the increasing threshold of tree diameter with distance based on viewing angle through a Bitterlich relascope and provides a sufficiently good and quick estimate of the basal area of lying dead wood in conditions of dense understorey (K. Kohr unpubl. data). We recorded the presence of various stand indicators, such as windthrown or wind-broken trees, specially-shaped (crooked, forked or damaged trees, or trees with wide crowns or cavities), three different classes of decay, and the number of cut stumps within a radius of 30 m. Decay classes of coarse woody debris (CWD) were defined as early, medium or late decay (Kohv & Liira 2005), shown to be sufficient in large-scale surveys (Ekbom *et al*. 2006).

We estimated understorey shrub and tree sapling layer composition in a circle with a radius of 5.6 m (100 m^2). We described shrub species in percentages of coverage and tree species regeneration by counting all of the specimens (DBH < 8 cm and height between 1.3 m and 25% of stand height) of each species.

Within a 30 m radius, we used 10 randomly located 2 × 2 m plots to characterize the composition and coverage of herb layer vegetation and moss layer coverage. We applied the index of relative richness, calculated as the average proportion of the number of herb layer species in 2 × 2 m plots within the total number of species in a stand (Zobel & Liira 1997) to describe the homogeneity of the herb layer — values close to 0 express high heterogeneity of the herb layer, and values close to 1 express high spatial homogeneity within a stand. Tree and shrub layer canopy closure was additionally estimated above each herb layer plot.

In the study area of $r = 30$ m, we recorded the presence of well-known and easily recognizable forest biodiversity or historical indicators such as the epiphytic lichens *Usnea* spp., *Bryoria* spp. and *Lobaria pulmonaria*, epiphytic moss *Neckera pennata*, ground lichen *Peltigera* spp., macrofungi on live and dead wood, large insect

Table 1. Average values of characteristics of forest structure and composition in two site-types. According to GLM analysis results, significant differences among forest site-types are given, with homogeneity group classes indicated by the superscript labels. Test results and parameter sign estimation of the general linear model of forest structure are presented for forest site-type, geographical coordinates, management intensity (MI) index and stand age. In the models of forest floor structure, additional predictor variable – canopy closure of a stand have been tested. Multiple determination coefficient and model significance values are presented. Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Stand trait	Transform.	Model adj. R^2%	Model P	Mean value in site-types		Beta estimate of slope and significance of continuous factors				
				Aegop.	*Hepatica*	MI	Stand age	Long.	Lat.	Closure
Basal area (BA) (m^2 ha^{-1})	log	6.798	0.0051	26.86	25.30	–0.075	–0.177*	0.043	–0.222**	
BA: DBH < 40 cm	log	10.251	0.0003	21.01	19.64	–0.042	–0.318***	–0.034	–0.156*	
BA: DBH > 40 cm	log	9.491	0.0006	5.85	5.66	–0.091	0.294***	0.190*	–0.079	
BA: Conifers	log	23.516	0.0001	10.70	18.99***	0.056	–0.290***	0.075	–0.026	
BA: Deciduous	log	40.959	0.0001	16.15	6.31***	–0.210***	0.205**	0.122*	–0.128*	
Dominant tree (%)	arcsine-sqrt	5.575	0.0126	55.81	63.98**	0.124	–0.017	–0.100	–0.050	
Conifers (%)	arcsine-sqrt	38.006	0.0001	39.62	73.89***	0.155*	–0.269***	–0.044	0.070	
Tree sp. richness	log	4.092	0.0358	5.09	4.47**	–0.005	0.108	0.100	0.026	
No diameter classes	log	13.849	0.0001	3.80	3.53	–0.399***	–0.034	–0.012	–0.073	
BA: Dead wood, standing (m^2 ha^{-1})	log	26.603	0.0001	1.93	1.84	–0.475***	0.131	0.168*	0.025	
BA: Dead wood, lying (m^2 ha^{-1})	log	28.986	0.0001	6.53	4.46	–0.477***	–0.150*	0.196**	–0.042	
Tree canopy closure (0, …, 1)	log	13.106	0.0001	0.67	0.70	–0.354***	0.095	–0.028	–0.046	
CV(Closure) (%)	arcsine-sqrt	8.698	0.0012	18.77	17.11	0.278***	–0.031	–0.041	0.184*	
Conif. foliage layer 10–25 m (%)	log	13.049	0.0001	20.11	33.57***	0.015	–0.241**	0.008	0.055	
Decid. foliage layer 10–25 m (%)	log	25.328	0.0001	34.74	16.93***	–0.174*	0.140	0.078	0.027	
Conif. foliage layer 4–10 m (%)	log	12.091	0.0001	15.32	22.14***	–0.152*	–0.259**	0.136	–0.087	
Decid. foliage layer 4–10 m (%)	log	9.646	0.0006	16.34	22.52	–0.179*	0.274***	0.083	–0.001	
Conif. foliage layer 1–4 m (%)	log	10.869	0.0002	6.53	11.38*	–0.252***	–0.118	–0.164*	–0.059	
Decid. foliage layer 1–4 m (%)	log	14.975	0.0001	23.08	39.29**	–0.206**	0.147	0.035	0.051	
Shrub coverage (%)	log	18.482	0.0001	16.05	37.86***	–0.188**	0.131	–0.027	0.124	
Shrub sp. richness (in 100 m^2)	log	2.505	0.1016	5.32	6.16*	–0.048	–0.013	–0.036	0.088	
Sapling count (in 100 m^2)	log	15.216	0.0001	15.10	5.81***	–0.110	–0.017	–0.009	–0.073	
Sapling sp. richness (in 100 m^2)	log	15.393	0.0001	2.89	1.70***	–0.055	0.055	0.031	–0.128	
Herb coverage	log	25.494	0.0001	50.95	41.59***	–0.140	–0.055	0.084	0.342***	–0.262***
Moss coverage (%)	log	18.790	0.0001	23.96	45.69***	–0.072	–0.102	–0.037	0.165*	–0.261***
Herb sp. richness	log	23.408	0.0001	38.25	38.30	0.062	–0.033	–0.186**	0.140*	–0.435***
Herb layer relative richness (%)	arcsine-sqrt	10.829	0.0003	36.37	33.70**	–0.157*	–0.050	0.001	–0.186*	0.025
Graminoid (%)	arcsine-sqrt	21.883	0.0001	12.09	11.24	0.014	–0.063	–0.266***	–0.093	–0.407***

holes (separately diameter classes 5–10 mm and more than 10 mm) and any signs of woodpecker activities. Some of the registered indicators appeared very infrequently at the study sites (e.g. ant nests), hence they were considered to be uninformative, and thus were not used in the analyses.

Management intensity index

We estimated the intensity of the anthropogenic disturbances of the stand from inventories, based on the presence or absence of anthropogenic disturbance indicators within two distance classes with a radius of 30 m and 30–60 m and using an original management intensity index (so called because the dominant feature of anthropogenic disturbances is forest management) (Liira *et al*. 2007). At each study site we recorded visible signs of anthropogenic activities (e.g., cut stumps, forest tracks, neighbouring clear-cut areas, trampling, ditches, trash, etc.). Each indicator of anthropogenic activities has a score (1 or 2) that describes its proportional effect. The management intensity index (MI) is the sum of scores of indicators of anthropogenic disturbances, weighted by the distance class from the centroid of the study site. The observation of any sign within a radius of 0–30 m doubled the effect score compared to the score within a radius of 30–60 m. The management intensity index is equal to zero if none of the anthropogenic activity indications were present within a radius of 60 m. The maximum value of the MI index for the forestland fraction can reach the value of 50 in the case of a forest clear-cut area with soil damage, trash pollution, intersecting ditches and roads, and surrounded by neighbouring arable fields or buildings.

Table 2. The average presence/absence probabilities of forest structure indicators in two forest site-types. According to GLIM analysis (Binomial error distribution, logit-link) results, significant differences among forest site-types are given. Test results and estimated slope of the generalized linear model are presented for forest site-type, geographical coordinates, management intensity (MI) index and stand age. Model significance values are presented. Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Indicator variable	Model *P*	Probability in a site-type		Parameter estimate and significance			
(0 = absent; 1 = present)		Aegop.	Hepatica	MI	Stand age	Long.	Lat.
Diam cl > 2 cm	0.0072	0.636	0.578	–0.117***	–0.002	0.005	–0.300
Diam cl 2–8 cm	0.0002	0.670	0.578	–0.141***	–0.006	–0.190	–0.393
Diam cl 8–20 cm	0.0035	0.830	0.723	–0.094**	–0.022**	–0.208	–0.213
Diam cl 40–80 cm	0.0030	0.659	0.651	–0.035	0.032**	0.182	0.073
Early decayed	0.0238	0.898	0.843	–0.138**	0.002	–0.005	–0.857
Medium decayed	0.0001	0.818	0.831	–0.236***	–0.016	0.164	–0.701
Late decayed	0.0001	0.716	0.735	–0.225***	–0.010	0.421**	–0.527
Specially shaped trees	0.0386	0.773	0.735	–0.070*	0.004	0.130	–1.082*
Abundant wind throw/break[a]	0.0003	0.455	0.446	–0.104**	0.002	0.471***	0.036
Wind throw (at least one obs.)	0.1790	0.705	0.723	–0.037	–0.012	0.253	0.328
Windbreak (at least one obs.)	0.0001	0.670	0.783	–0.145***	0.014	0.337*	–0.144
Fungi on dead wood	0.0135	0.795	0.771	–0.112**	–0.003	0.262	–0.086
Fungi on living wood	0.0001	0.568	0.145***	–0.031	–0.001	0.145	–0.080
Woodpecker	0.0029	0.739	0.711	–0.135***	–0.010	–0.033	0.041
Insect holes 5–10 mm	0.0001	0.523	0.687	–0.126***	0.008	–0.244	–0.020
Insect holes >10 mm	0.4230	0.125	0.217	–0.030	0.002	–0.031	–0.591
Neckera spp.	0.0001	0.477	0.036***	–0.123**	–0.007	0.343	0.290
Lobaria pulmonaria	0.0539	0.057	0.048	–0.225	0.011	–0.367	1.141
Peltigera spp.	0.0001	0.352	0.096***	–0.137**	0.001	0.369*	0.548
Bryoria spp.	0.0190	0.023	0.133*	0.024	–0.001	0.195	1.482*
Usnea spp.	0.0004	0.045	0.205**	–0.080	–0.006	0.525*	0.961

[a] More than one observation of either windthrow or windbreak in a plot with radius 30 m.

Statistical analyses

General Linear Model (GLM) analysis for metric forest structural characteristics was performed using a statistical package Statistica ver. 7.1 to test for the significance of effects of anthropogenic disturbances, stand age and biogeography and environment. We used the factor "forest site-type" as a surrogate variable that summarizes the complex of environmental conditions (mainly soil conditions) and management type. An additional variable, the canopy closure of the tree layer, was also included in the models of herb and moss layer characteristics. Where necessary, the log-transformation of measurement variables or the arcsine of square-root transformation for proportion variables were applied to attain the normal distribution of residuals. Standardized parameter estimates were used to estimate the descriptive power of factors. We applied Generalized Linear Model (GLIM, binomial error distribution and logit-link) analysis on binomial structural features (described at the scale of presence/absence) with similar independent variable settings in the model. The Wald χ^2 statistic was used to estimate the importance rank of the factor.

We used another GLIM analysis to select a critical and statistically confirmed list of indicators to estimate the degree of "naturalness" of a forest. For that purpose, we classified stands into two groups (near-natural stands and anthropogenetically disturbed stands) according to MI-index values, using the threshold value of 3.5. A stepwise selection of variables was applied, using traits revealing a response to management in previous GLM and GLIM analyses.

Results

The significance of anthropogenic disturbances of the forest was tested taking into account the effect of confounding factors: forest site-type, geographical location and stand age. Exploiting the multi-factorial design in the General and Generalized Linear Models, the resulting parameter estimation statistics indicate the relative importance of these driving forces for the forest structural characteristics (Tables 1 and 2). Counting the models where a factor had the greatest descriptive power (the largest standardized parameter value or parameter test statistic within a model) reveals that the forest site-type and the intensity of anthropogenic disturbances are the main leading factors, both being the most dominant factor in about 1/3 of the models. Other factors lead in only few models out of 49. These counts of leading factor indicate the importance of environmental aspects in the analysis of management effect. Therefore, before concentrating on anthropogenic effects, we will first summarise the environmental effects revealed in models.

Forest structure in the three site-types and biogeographic trends

The geographical location and particularly the forest type of a stand significantly affect many aspects of forest structure (Table 1). The basal area measurements of a stand reflect nearly equally high productivity of both site types (26.9 and 25.3 m^2 ha^{-1}); deciduous trees dominate in the *Aegopodium* site-type and conifers in the *Hepatica* site-type. The basal area of smaller trees (DBH < 40 cm) increases from north to south and that of large trees (DBH > 40 cm) from west to east (Table 1). The basal area of deciduous trees increases in a south-easterly direction. As a combined result, the higher abundance of deciduous trees and the smaller dominance of a single tree species can also explain the significantly higher tree species richness in the *Aegopodium* site-type. Specially shaped trees are more common in southern regions (Table 2).

Canopy closure of the tree layer is not correlated with the forest site-type or geographical region. In detailed analysis one can see that the understorey foliage strata (1–4 m and 4–10 m) are generally denser in the *Hepatica* site-type (Table 1). Within a stratum, the dominance of deciduous trees is observed in the *Aegopodium* site-type for the lowest (1–4 m) and the upper (above 10 m) strata, but not in the intermediate stratum of the height range 4–10 m. While the cover and species richness of shrubs is greater in the *Hepatica* site-type, the number of individuals and species richness of tree saplings is higher in the *Aegopodium* site-type.

The forest floor in the *Aegopodium* site-type is slightly more densely covered with vascular plants (51% *vs*. 42%), while the *Hepatica* site-type forest has twice as extensive moss cover (46% *vs*. 24%) (Table 1). The cover of both layers increases in the direction of northern forests. The large-scale herb layer species richness of both site-types is similarly high (ca. 38 species per forest patch), and it increases in the direction of limestone-rich soils, towards the north-west. The herb layer is more homogeneous in the *Aegopodium* site-type and in southern forests, as relative richness tends to be higher in these stands (Table 1). The proportion of graminoids in the herb layer tends to increase toward western regions.

Windbreaks are more common in eastern forests, while no statistically significant tendencies were found in the frequency of occurrence of wind throws (Table 2). In eastern forests, logs and snags are more abundant (Table 1), and the probability of the presence of more decayed wood is greater (Table 2).

Indicators of forest biodiversity such as macrofungi on living trees and *Peltigera* lichens were found more than three times as often in the *Aegopodium* site-type than in the *Hepatica* site-type (Table 2). *Usnea* and *Bryoria* prefer more coniferous-abundant *Hepatica* type forests. *Peltigera* and *Usnea* were more common in eastern forests, and *Bryoria* in northern forests. The indicator moss *Neckera pennata* is common in *Aegopodium* site-type forests, which is probably partly because of the frequent presence of its host-tree species (deciduous trees) in that forest type. At the very least this could be a good explanation of why it is rare in the *Hepatica* site-type. The presence of woodpeckers appears to be independent of forest site-type and geographical location.

Effects of management and stand age on forest structure

Management and stand age effects were analyzed after taking into consideration the variability explained by geographical location and forest site-type. We did not detect any remarkable effect of management intensity on total basal area in a stand nor on the basal area within tree diameter classes (Table 1). The significant effects of anthropogenic disturbance, however, can be seen in more detailed stand characteristics. Forest management has a significant negative effect on the basal area of deciduous trees in a stand (Fig. 2), and a positive effect on the percentage of conifers. The models also reveal the negative effect of silvicultural activities on the number of diameter classes (Table 1 and Fig. 2), by reducing the presence probability of diameter classes of 20 cm or less (Table 2 and Fig. 2).

In addition to the demonstrated effects of management, increasing stand age predicts a higher frequency and basal area of large trees (DBH > 40 cm) and deciduous tree species in total (Table 1 and 2). Older stands have a smaller basal area of trees with DBH < 40 cm, a smaller share of conifers (Table 1), and a reduced probability of the presence of trees with diameter class DBH 8–20 cm (Table 2).

Management is the main factor that reduces stand canopy closure in the studied mature forests (Fig. 2). Anthropogenic disturbances also increase the horizontal heterogeneity of a tree canopy and shrub layer (Fig. 2), i.e. the variation coefficient of canopy closure (Table 1 and Fig. 2) and shrub layer cover (studied only in the *Aegopodium* site-type; GLM: $P = 0.004$ and not presented in Table 1) tends to increase toward disturbed forests. Analyzing the vertical structure of old forests, the increasing intensity of anthropogenic disturbances reduces the abundance of each stratum in a stand, including shrubs, except for conifers in the upper (10–25 m) tree layer. Cover by conifers in the upper layer decreases with increasing stand age (Table 1).

Management intensity is also the prevailing factor that determines the amount of dead wood, snags and logs (Fig. 3). Additionally, there is a tendency for the amount of logs to decline toward older or over-mature forests. We found that intensive anthropogenic disturbance results in a reduced probability of finding various components of coarse woody debris (decay classes and wind breaks) (Table 2 and Fig. 3), but we did detected no statistically significant relationships among management and the probability of finding wind throws (Fig. 3).

After removing differences specific to forest site-types, we found no indications of the effect

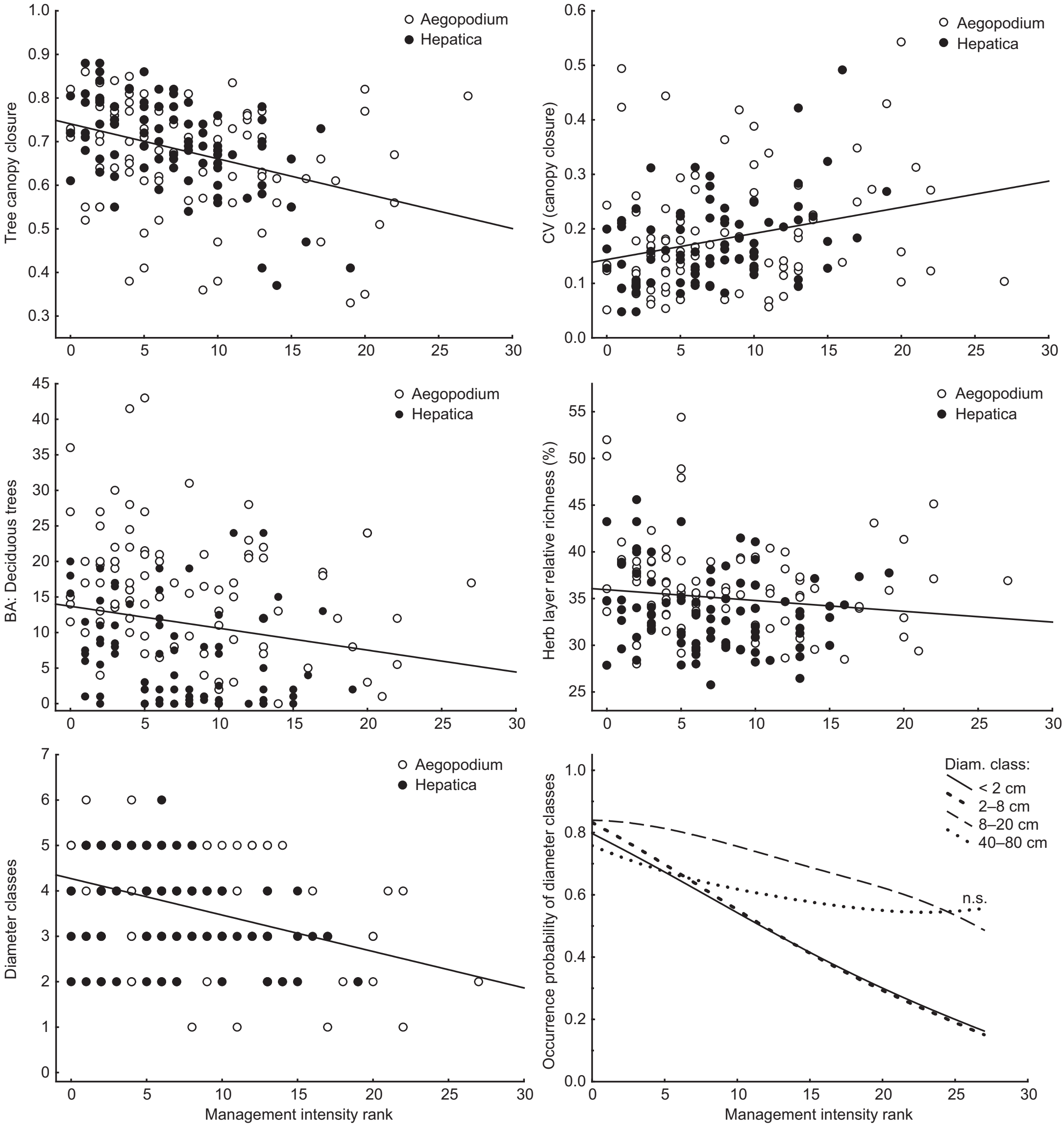

Fig. 2. Relationships between management intensity and stand structural characteristics. For the binomial indicator variable (the presence of diameter classes) the logistic regression trend-lines are shown for each diameter class.

of management on the diversity of tree saplings, shrubs or the herb layer. The relative richness of the herb layer is the only forest floor characteristic that shows a direct correlation with management activities (Fig 2). A negative relationship points to a more heterogeneous forest floor in managed forests, i.e. in each 2 × 2 m sampling plot in a managed forest, there are proportionally less species present from an actual species pool than in old-growth forests (Table 1). However, stand closure is a significant factor for most of the characteristics of forest floor structure. Light availability as the primary limiting factor of ground layer communities is enhanced by forest management in mature stands (Table 1), and therefore management has an indirect effect on herb and moss coverage on the forest floor, the species richness of the herb layer and the proportion of graminoids (Table 1 and Fig. 4). It is remarkable to note that in contrast to the charac-

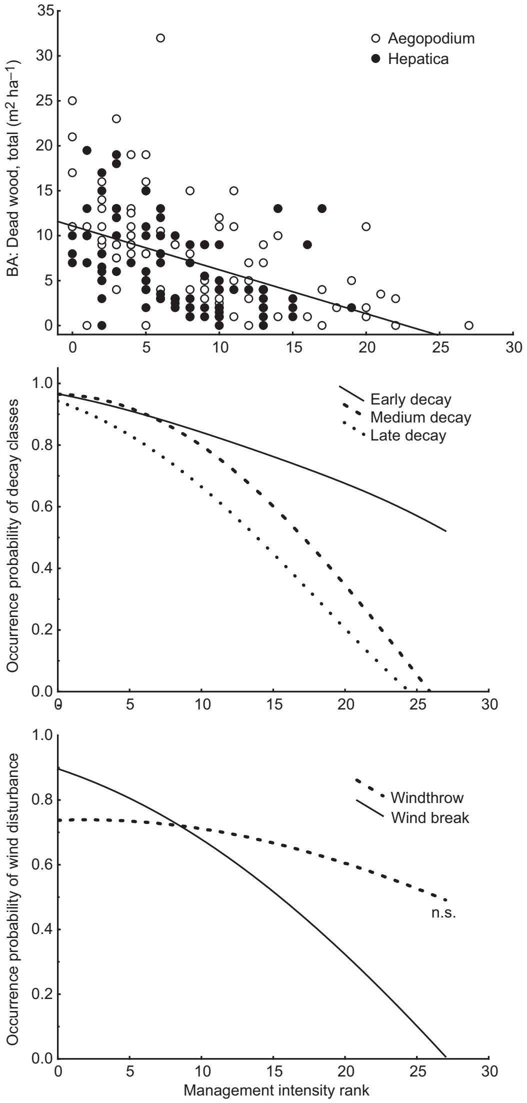

Fig. 3. Relationships between management intensity and the amount of dead wood, the presence of decay classes and wind disturbances. For the binomial indicator variables (the presence/absence of decay classes and wind disturbance type) the logistic regression trend-lines are shown for each class.

teristics of the upper layers, the characteristics of the forest floor are not dependent on stand age.

In the group of biodiversity indicators, the probability of woodpecker activity, insect holes of 5–10 mm diameter in trunks, epiphytic moss *Neckera pennata* and *Peltigera* lichen are negatively correlated with management intensity (Table 2 and Fig. 5). After the removal of forest site-type and bio-geographic effects, other selected indicators of old-growth forest or ecosystem quality, *Lobaria*, *Usnea* or *Bryoria* lichens, fungi on living wood or insect holes with a diameter greater than 10 mm show no significant correlations with either the intensity of anthropogenic disturbance (Fig. 5) or stand age, some of them because their frequency in stands was too low.

Critical set of forest ecosystem quality indicators

We classified all forest stands into two natural status groups: (1) 48 out of 171 sites (27%–29% within a site-type) fell into the group of near-natural old-growth forest with low management intensity (MI < 3.5); and (2) conventionally managed mature stands (MI > 3.5). After the stepwise selection of forest traits and indicator species in GLIM analysis, the final set of indicators correctly classified 64.6% of near-natural forest stands and 88.6% of stands with anthropogenic disturbances (Table 3).

Compared with the extended list of forest structural characteristics studied, only a few characteristics turned out to be critically useful for the classification of forests. None of these was in itself a single sufficient predictor of a forest in natural status. Indicators of the natural quality of a forest ecosystem are the amount of standing dead wood (threshold value basal area 3.75; Fig. 6), canopy closure (threshold value 0.85; Fig. 6), the presence of more than one lying dead tree (wind throw and windbreak), the presence of specially shaped trees and indicator epiphytic lichens and mosses (Table 3) in a plot with the radius of 30 m. A stand has higher rate of anthropogenic perturbation if the forest herb-layer plant *Veronica officinalis* is present (Table 3), i.e. it is a "negative" indicator of stand natural quality or a "positive" indicator of a disturbed forest.

Discussion

Near-natural old-growth *vs.* conventionally managed mature forest

As generally shown in the boreal and hemi-boreal vegetation zone, silvicultural practices cause stands to become more homogeneous in structure, with uniformly sized trees dominated by conifers, having an optimized canopy density in the upper or subordinate tree layer, a less dense shrub layer, and containing a smaller amount of dead wood (Fridman & Walheim, 2000, Maltamo *et al*. 2000, Siitonen *et al*. 2000, Uotila *et al*. 2002, Köster *et al*. 2005). We found similar trends in the studied productive forests along the management intensity gradient. At the same time, management does not cause remarkable changes in the growing stock of stands described as basal area, shown also for other less productive forest types (Liira *et al*. 2007). However, in contrast to statistics describing average values, the variability of some characteristics — the heterogeneity of the canopy, shrub and herb layer — increased with the intensification of anthropogenic disturbance, suggesting that forest management can generate small-scale heterogeneity more effectively than natural disturbance processes, at least in a short time range. If to bear in mind the future of these managed stands, then forestry still have to put more effort in the increase of stand heterogeneity, tree and

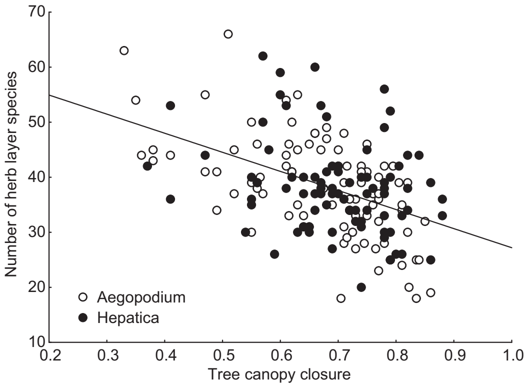

Fig. 4. Relationship between tree canopy closure and community species richness.

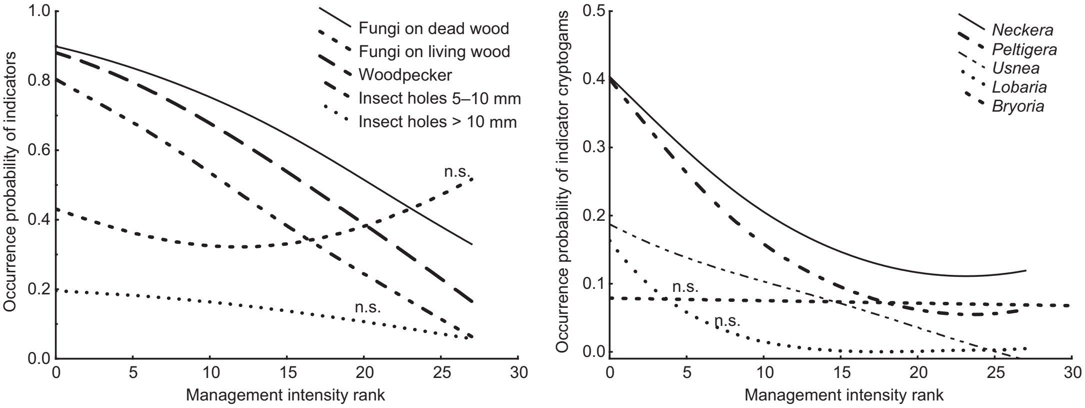

Fig. 5. Relationships between forest management intensity and commonly used indicators of forest naturalness.

Table 3. Characteristics of the GLIM model (Binomial distribution, logit-link) predicting the ecosystem quality within each forest site-type. Model parameters, significance of factors, the relative effect of a single factor on probability are provided. The starting value of quality probability is given for categorical factor.

Indicator trait	Parameter	*P*	Single factor effect	Starting value
Intercept	–11.19	0.0001		
BA: Dead wood, standing (m² ha⁻¹)	0.39	0.0040	0.114	0.5
Specially shaped trees (0,1)	1.79	0.0135	0.278	
Tree canopy closure (0–1)	8.56	0.0007	0.100	0.35
Veronica officinalis (0,1)	–2.07	0.0015	0.250	
Insect holes > 5 mm (0,1)	1.68	0.0017	0.249	
Indicator epiphytes (0,1)	0.98	0.0284	0.259	
Abundant wind throw/break (0,1)	1.10	0.0142	0.269	

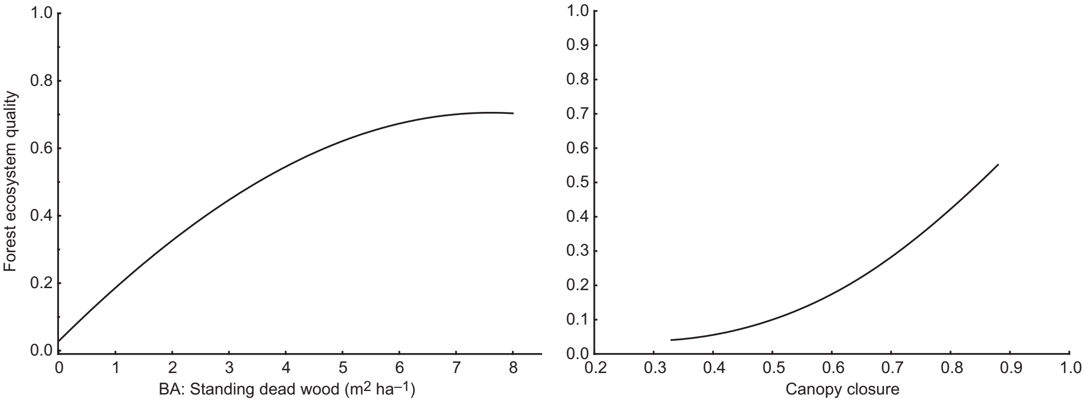

Fig. 6. Prediction trend lines of the probability of ecosystem to be high natural quality, presented for selected forest biodiversity indicators according to the results of stepwise GLIM. More detailed information is presented in Table 3.

understorey species diversity, that would generate true natural heterogeneity and consequently the stability with less management effort needed.

Forest floor vegetation has a high resilience to stand disturbances. The most common reaction of forest floor vegetation to modest disturbances is to change the relative abundances of compositional species (Bailey & Tappeiner 1998, Bergstedt & Milberg 2001, Liira *et al.* 2002, Kohv & Liira 2005), and only intensive felling changes small-scale diversity or the heterogeneity of forest floor diversity (Griffis *et al.* 2001, Jalonen & Vanha-Majamaa 2001, Götmark *et al.* 2005, Meier *et al.* 2005, Moora *et al.* 2007). The effects of anthropogenic disturbances on the forest floor are complex and should therefore be classified into direct and indirect effects. The direct effects of management can be observed only in the form of decreased shrub cover and facilitated mosaic of the herb layer. As an indirect effect of management, selective cutting of the overstorey and understorey creates numerous canopy openings and increases average light availability, which induces advanced regeneration and induces a denser understorey with changed composition (Zobel 1989, Zobel *et al.* 1993, Bailey & Tappeiner 1998, Griffis *et al.* 2001, Götmark *et al.* 2005, Halpern *et al.* 2005). In our study, enhanced light availability (decreased canopy closure) increased moss- and herb-layer coverage and the proportion of graminoids, and increased the species richness of the herb layer.

Time-scale of anthropogenic disturbances

It has been shown that mature stands have features created by mid-term (decades) and long-term (centuries) forest management practices (Ohlson *et al.* 1997, Linder & Östlund 1998). Traits created by mid-term management effects are those that have been created by management in the last thinning, selective cutting, and other silvicultural practices. The resulting structural aspects are frequently correlated to stand age, most commonly the amount of CWD (Sturtevant *et al.* 1997, Lõhmus *et al.* 2005, Ekbom *et al.* 2006). We also found correlations between stand age and basal area, the conifer/deciduous tree ratio, the volume of deciduous trees and the amount of CWD. As analyses revealed, in mature forests stand age can have significant effects, but only as a secondary effect on the amount of dead wood in addition to the effects of mid-term management history (Siitonen *et al.* 2000, Jantunen *et al.* 2002, Kohv & Liira 2005, Liira *et al.* 2007).

The long-term continuity and management history (centuries) of a stand are the factors influencing biodiversity and the presence of specific features in a stand (Zobel 1989, Linder *et al.* 1997, Ohlson *et al.* 1997, Jantunen *et al.* 2002, Flinn & Vellend 2005). For example, we found only a few stands where trees had DBH > 80 cm or several other biodiversity indicators were present. This finding suggests that forests have historically been intensively managed, and the forest stand's spatiotemporal continuity has been interrupted, causing the loss of commonly accepted old-growth forest indicators. Therefore large-sized old-growth trees and large-diameter CWD can be considered as random features in the structure of contemporary stands, and in many cases cannot be used as broad-scale indicators to assess the naturalness of mature stands (Linder & Östlund 1998, Nilsson *et al*. 2002), even if they are vital elements required to support biodiversity (Berg *et al*. 1994, Summers 2004).

Indicators and their usefulness

The assessment of habitat natural quality takes a different approach to the estimation of the effects of management. In practice, the difference between these two courses of action implies that not all forest characteristics shown to depend on silvicultural management or other anthropogenic disturbances are effective indicators of forests with high conservation value. We found that only a few forest structural characteristics and biodiversity indicators proved to be informative indicators of forest ecosystem quality, and none of them was a sufficient single predictor.

Some stands' structural traits or specific species groups can be correlated to the diversity of other species groups (Jansson & Andren 2003, Meier *et al*. 2005), but most are not applicable as generalizing indicators (Ohlson *et al* 1997, Jonsson & Jonsell 1999, Juutinen *et al*. 2006). For instance, only within a single forest site-type where the same herb layer species pool is involved, can researchers find indicator species even for past modest intensity disturbances (Ohlson *et al*. 1997, Halpern *et al*. 2005, Kohv & Liira 2005, Liira *et al*. 2007), or the volume of dead wood can be a good indicator of diversity of saproxylic species, but not for all species groups (Juutinen *et al*. 2006).

Our study showed that very different structural aspects of forest and indicator species are important traits in recognizing the naturalness of a forest — standing dead wood, canopy closure, specially shaped trees, wood-dwelling insects, specific epiphytic lichens and mosses and herb layer species. It is particularly interesting to point out the 'negative' indicator of *Veronica* species in the herb layer as the indicator of highly disturbed forest, open canopies or disturbed ground.

The most common feature used as an indicator of forest ecosystem quality is the presence or amount of dead wood and wind damage, which has been pointed out by numerous earlier studies (Ohlson *et al*. 1997, Gustafsson 2002, Ekbom *et al*. 2006) and also confirmed by us. However, we showed that additional traits still have to be considered before reaching the satisfactory generalized predictive result for the indication of the natural quality of a stand.

We conclude that any individual indicator can be sufficient for the evaluation of forest community status, as its indicative power and threshold level depend on soil properties, forest productivity, composition and historical aspects (Jonsson & Jonsell 1999, Lindenmayer 1999, Siitonen *et al*. 2000, Norden & Appelqvist 2001, Liira *et al*. 2007). Using such a complex of rough indicators, one can cost-effectively implement them into a large-scale survey to obtain a fast and easy estimation of forest stands in near-natural status (e.g. as done by Adermann 2008).

Conclusions

In studying the effects of specific driving forces on ecosystem quality, the collinearity between factors should always be kept in mind and included in the sampling methodology.

Adequate determination of the intensity of anthropogenic disturbances and its true effects (considering other factors) is crucial in selecting areas of high conservation value and planning the maintenance of forest biodiversity. Nature conservation efforts have concentrated too much attention on characterizing the status of a habitat in conditions of present-day disturbances, while insufficient interest has been sown on processes in or around it, particularly concerning wide time frame. But processes in larger scale, both space and time, have affected the habitat status in the past and will continue to do so. This is a weakness, because many conservation efforts can fail or have already failed.

We defined a long list of structural and compositional characteristics which status in the forest depends on management and other anthropogenic disturbances. Many of them have been used in monitoring systems. However, the statistically supported set of indicators used to estimate forest ecosystem quality turned out to be much shorter. The resulting set of indicators consists of easily recognizable traits of various structural aspects of a forest, which can be easily implemented in forest monitoring systems or used by a forest manager to improve their forest management design toward sustainability *in situ*.

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References

Aavik, T., Püssa, K., Roosaluste, E. & Moora, M. 2009: Vegetation change in boreonemoral forest during succession — trends in species composition, richness and differentiation diversity. — *Annales Botanici Fennici* 46: 326–335.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Annales Botanici Fennici* 5: 169–211.

Adermann, V. 2008: *Estonian forests 2007. The estimation of forest sources by statistical sampling methodology*. — Ketsakaitse- ja Metsauuenduskeskus, Tallinn. [In Estonian with English summary].

Andersson, L., Martverk, R, Külvik, M., Palo, A. & Varblane, A. 2003: *Woodland key habitat inventory in Estonia 1999–2002*. — Regio Publishing, Tartu.

Angelstam, P., Majewski, P. & Bondrupnielsen, S. 1995: West-East cooperation in Europe for sustainable boreal forests. — *Water Air and Soil Pollution* 82: 3–11.

Aparicio, A., Albaladejo, R. G., Olalla-Tarraga, M. A., Carrillo, L. F. & Rodriguez, M. A. 2008: Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes. — *Forest Ecology and Management* 255: 2894–2906.

Arler, F. 2000: Aspects of landscape or nature quality. — *Landscape Ecology* 15: 291–302.

Aunap, R., Ainsaar, L., Rattas, M., Mardiste, H., Jaagus, J., Kull, A., Ahas, R., Aasa, A., Järvet, A., Rooma, I., Tarre, A., Kuusk, V., Arold, I., Remm, K., Tikk, U., Tammaru, T., Kask, I., Pae, T., Liiber, Ü., Rõivas, T., Thomson, H., Vessin, U. & Kurs, O. 2004: *Eesti atlas* [*Atlas of Estonia*], 2. — Avita, Tartu. [In Estonian with English summary].

Axelsson, A. L. & Östlund, L. 2001: Retrospective gap analysis in a Swedish boreal forest landscape using historical data. — *Forest Ecology and Management* 147: 109–122.

Bailey, J. D. & Tappeiner, J. C. 1998: Effects of thinning on structural development in 40- to 100-year-old Douglas-fir stands in western Oregon. — *Forest Ecology and Management* 108: 99–113.

Balmford, A., Green, R. E. & Jenkins, M. 2003: Measuring the changing state of nature. — *Trends in Ecology & Evolution* 18: 326–330.

Bengtsson, J., Nilsson, S. G., Franc, A. & Menozzi, P. 2000: Biodiversity, disturbances, ecosystem function and management of European forests. — *Forest Ecology and Management* 132: 39–50.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M. & Weslien, J. 1994: Threatened plant, animal, and fungus species in Swedish forests: Distribution and habitat associations. — *Conservation Biology* 8: 718–731.

Bergstedt, J. & Milberg, P. 2001: The impact of logging intensity on field-layer vegetation in Swedish boreal forests. — *Forest Ecology and Management* 154: 105–115.

Brooks, T. & Kennedy, E. 2004: Conservation biology: Biodiversity barometers. — *Nature* 431: 1046–1047.

Brown, P. M. & Cook, B. 2006: Early settlement forest structure in Black Hills ponderosa pine forests. — *Forest Ecology and Management* 1–3: 284–290.

Buckley, D. S., Crow, T. R., Nauertz, E. A. & Schulz, K. E. 2003: Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in Upper Michigan, USA. — *Forest Ecology and Management* 175: 509–520.

Carlsson, L. & Lazdinis, M. 2004: Institutional frameworks for sustainability? A comparative analysis of the forest sectors of Russia and the Baltic States. — *Ambio* 33: 366–370.

Dale, V. H. & Beyeler, S. C. 2001: Challenges in the development and use of ecological indicators. — *Ecological Indicators* 1: 3–10.

Ejrnaes, R., Aude, E., Nygaard, B. & Münier, B. 2002: Prediction of habitat quality using ordination and neural networks. — *Ecological Applications* 12: 1180–1187.

Ejrnaes, R., Liira, J., Poulsen, R. S. & Nygaard, B. 2008: When has an abandoned field become a semi-natural grassland or heathland? — *Ecological Applications* 42: 707–716.

Ekbom, B., Schroeder, L. M. & Larsson, S. 2006: Stand specific occurrence of coarse woody debris in a managed boreal forest landscape in central Sweden. — *Forest Ecology and Management* 221: 2–12.

Elofsson, M. & Gustafsson, L. 2000: Uncommon vascular plant species in an east-central Swedish forest area — a comparison between young and old stands. — *Nordic Journal of Botany* 20: 51–60.

FAO 2007: *State of the World's forests 2007*. — Food and Agriculture Organization of the United Nations.

Flinn, K. M. & Vellend, M. 2005: Recovery of forest plant communities in post-agricultural landscapes. — *Fron-*

tiers in Ecology and the Environment 3: 243–250.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. 2005: Global consequences of land use. — *Science* 309: 570–574.

Foster, D. R., Orwig, D. A. & McLachlan, J. S. 1996: Ecological and conservation insights from reconstructive studies of temperate old-growth forests. — *Trends in Ecology & Evolution* 11: 419–424.

Franklin, J. F. & Forman, R. T. T. 1987: Creating landscape patterns by forest cutting: Ecological consequences and principles. — *Landscape Ecology* 1: 5–18.

Fridman, J. & Walheim, M. 2000: Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131: 23–36.

Gamborg, C. & Rune, F. 2004: Economic and ecological approaches to assessing forest value in managed forests: Ethical perspectives. — *Society & Natural Resources* 17: 799–815.

Götmark, F., Paltto, H., Norden, B. & Götmark, E. 2005: Evaluating partial cutting in broadleaved temperate forest under strong experimental control: short-term effects on herbaceous plants. — *Forest Ecology and Management* 214: 124–141.

Griffis, K. L., Crawford, J. A., Wagner, M. R. & Moir, W. H. 2001: Understory response to management treatments in northern Arizona ponderosa pine forests. — *Forest Ecology and Management* 146: 239–245.

Gustafsson, L. 2002: Presence and abundance of red-listed plant species in Swedish forests. — *Conservation Biology* 16: 377–388.

Halpern, C. B., McKenzie, D., Evans, S. A. & Maguire, D. A. 2005: Initial responses of forest understories to varying levels and patterns of green-tree retention. — *Ecological Applications* 15: 175–195.

Jalonen, J. & Vanha-Majamaa, I. 2001: Immediate effects of four different felling methods on mature boreal spruce forest understorey vegetation in southern Finland. — *Forest Ecology and Management* 146: 25–34.

Jansson, G. & Andren, H. 2003. Habitat composition and bird diversity in managed boreal forests. — *Scandinavian Journal of Forest Research* 18: 225–236.

Jantunen, J., Saarinen, K., Saarnio, S. & Marttila, O. 2002: Stand structure in pine, spruce and deciduous forests: A comparison between Finnish and Russian Karelia. — *Scandinavian Journal of Forest Research* 17: 53–61.

Jacquemyn, H., Butaye, J. & Hermy, M. 2003: Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. — *Ecography* 26: 768-776.

Jonsell, M., Weslien, J. & Ehnström, B. 1998: Substrate requirements of red-listed saproxylic invertebrates in Sweden. — *Biodiversity and Conservation* 7: 749–764.

Jonsson, B. G. & Jonsell, M. 1999: Exploring potential biodiversity indicators in boreal forests. — *Biodiversity and Conservation* 8: 1417–1433.

Jonsson, M., Ranius, T., Ekvall, H., Bostedt, G., Dahlberg, A., Ehnstrom, B., Norden, B. & Stokland, J. N. 2006: Cost-effectiveness of silvicultural measures to increase substrate availability for red-listed wood-living organisms in Norway spruce forests. — *Biological Conservation* 127: 443–462.

Juutinen, A., Mönkkönen, M. & Sipploa, A.-L. 2006: Cost-efficiency of decaying wood as a surrogate for overall species richness in boreal forests. — *Conservation Biology* 20: 74–84.

Kohv, K. & Liira, J. 2005: Anthropogenic effects on vegetation structure of the boreal forest in Estonia. — *Scandinavian Journal of Forest Research* 20(Suppl. 6): 122–134.

Kuuluvainen, T. 2002: Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. — *Silva Fennica* 36: 97–125.

Köster, K., Jõgiste, K., Tukia, H., Niklasson, M. & Möls, T. 2005: Variation and ecological characteristics of coarse woody debris in Lahemaa and Karula National Parks, Estonia. — *Scandinavian Journal of Forest Research* 20(Suppl. 6): 102–111.

Laasimer, L. 1965: *Eesti NSV taimkate* [V*egetation of the Estonian S.S.R*.]. — Valgus, Tallinn. [In Estonian with English summary].

Larsen, J. B. & Nielsen, A. B. 2007: Nature-based forest management — Where are we going? Elaborating forest development types in and with practice. — *Forest Ecology and Management* 238: 107–117.

Lawesson, J. E., De Blust, G., Grashof, C., Firbank, L., Honnay, O., Hermy, M., Hobitz, P. & Jensen, L. M. 1998: Species diversity and area relationships in Danish beech forests. — *Forest Ecology and Management* 106: 235–245.

Liira, J., Zobel, K., Mägi, R. & Molenberghs, G. 2002: Vertical structure of herbaceous canopies: the importance of plant growth-form and species-specific traits. — *Plant Ecology* 163: 123–134.

Liira, J., Sepp, T. & Parrest, O. 2007: The forest structure and ecosystem quality in conditions of anthropogenic disturbance along productivity gradient. — *Forest Ecology and Management* 250: 34–46.

Liira, J., Schmidt, T., Aavik, T., Arens, P., Augenstein, I., Bailey, D., Billeter, R., Bukacek, R., Burel, F., De Blust, G., De Cock, R., Dirksen, J., Edwards, P. J., Hamersky, R., Herzog, F., Klotz, S., Kühn, I., Le Coeur, D., Miklova, P., Roubalova, M., Schweiger, O., Smulders, M. J. M., van Wingerden, W. K. R. E., Bugter, R. & Zobel, M. 2008: Plant functional group composition and large-scale species richness in the agricultural landscapes of Europe. — *Journal of Vegetation Science* 19: 3–14.

Lilja, S., De Chantal, M., Kuuluvainen, T., Puttonen, P. & Vanha-Majamaa, I. 2005: Restoring natural characteristics in managed Norway spruce [*Picea abies* (L.) Karst.] stands with partial cutting, dead wood creation and fire: Immediate treatment effects. — *Scandinavian Journal of Forest Research* 20(Suppl. 6): 68–78.

Lindenmayer, D. B. 1999: Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. — *Forest Ecology and Management* 115: 277–287.

Linder, P., Elfving, B. & Zackrisson, O. 1997: Stand structure and successional trends in virgin boreal forest reserves in Sweden. — *Forest Ecology and Management* 98: 17–33.

Linder, P. & Östlund, L. 1998: Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. — *Biological Conservation* 85: 9–19.

Lippmaa, T. 1935: *Eesti geobotaanika põhijooni* [*The main features of Estonian geobotany*]. — K. Mattiesen, Tartu. [In Estonian with English summary].

Lõhmus, A., Lõhmus, P., Remm, J. & Vellak, K. 2005: Old-growth structural elements in a strict reserve and commercial forest landscape in Estonia. — *Forest Ecology and Management* 216: 201–215.

Lõhmus, E. 2004: *Eesti metsakasvukohatüübid* [*Estonian forest site-types*], 2. — Eesti Loodusfoto, Tartu. [in Estonian with English summary].

Lähde, E., Laiho, O. & Norokorpi, Y. 1999: Diversity-oriented silviculture in the boreal zone of Europe. — *Forest Ecology and Management* 118: 223–243.

Maltamo, M., Kangas, A., Uuttera, J., Torniainen, T. & Saramäki, J. 2000: Comparison of percentile based prediction methods and the Weibull distribution in describing the diameter distribution of heterogeneous Scots pine stands. — *Forest Ecology and Management* 133: 263–274.

Marozas, V., Grigaitis, V. & Brazaitis, G. 2005: Edge effect on ground vegetation in clear-cut edges of pine-dominated forests. — *Scandinavian Journal of Forest Research* 20(Suppl. 6): 43–48.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. 2000: Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. — *Biological Conservation* 94: 199–209.

Meier, E., Paal, J., Liira, J. & Jüriado, I. 2005: Influence of tree stand age and management on the species diversity in Estonian eutrophic alvar and boreo-nemoral *Pinus sylvestris* forests. — *Scandinavian Journal of Forest Research* 20(Suppl. 6): 135–144.

Meikar, T. & Etverk, I. 2000: Forest ownership in Estonia. — *Forest Studies* 32: 8–18. [In Estonian with English summary].

Moora, M., Daniell, T., Kalle, H., Liira, J., Püssa, K., Roosaluste, E., Öpik, M., Wheatley, R. & Zobel, M. 2007: Spatial pattern and species richness of boreonemoral forest understorey and its determinants — a comparison of differently managed forests. — *Forest Ecology and Management* 250: 64–70.

Nelson, C. R. & Halpern, C. B. 2005: Short-term effects of timber harvest and forest edges on ground-layer mosses and liverworts. — *Canadian Journal of Botany* 83: 610–620.

Nilsson, S. G. & Ericson, L. 1997: Conservation of plant and animal populations in theory and practice. — *Ecological Bulletins* 46: 117–139.

Nilsson, S. G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J. M., Linder, P., Ljungberg, H., Mikusinski, G. & Ranius, T. 2002: Densities of large living and dead trees in old-growth temperate and boreal forests. — *Forest Ecology and Management* 161: 189–204.

Norden, B. & Appelqvist, T. 2001: Conceptual problems of ecological continuity and its bioindicators. — *Biodiversity and Conservation* 10: 779–791.

Norton, T. W. 1996: Conservation of biological diversity in temperate and boreal forest ecosystems. — *Forest Ecology and Management* 85: 1–7.

Noss, R. F. 1990: Indicators for monitoring biodiversity: a hierarchical approach. — *Conservation Biology* 4: 355–364.

Ohlson, M., Söderstrom, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997: Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. — *Biological Conservation* 81: 221–231.

Paal, J. 1997: *Classification of Estonian vegetation site types*. — Keskkonnaministeeriumi Info- ja Tehnokeskus, Tallinn. [In Estonian with English summary].

Paal, J. 2007: *Loodusdirektiivi elupaigatüüpide käsiraamat*. [*The handbook of Natura 2000 habitat types according to habitat directive*]. — Eesti Keskkonnaministeerium, Tallinn. [In Estonian with English summary].

Peterken, G. F. 1999: Applying natural forestry concepts in an intensively managed landscape. — *Global Ecology and Biogeography* 8: 321–328.

Pykälä, J. 2004: Effects of new forestry practices on rare epiphytic macrolichens. — *Conservation Biology* 18: 831–838.

Scheller, R. M., Van Tuyl, S., Clark, K., Hayden, N. G., Hom, J. & Mladenoff, D. J. 2008: Simulation of forest change in the New Jersey Pine Barrens under current and pre-colonial conditions. — *Forest Ecology and Management* 255: 1489–1500.

Siitonen, J., Martikainen, P., Punttila, P. & Rauh, J. 2000: Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. — *Forest Ecology and Management* 128: 211–225.

Similä, M., Kouki, J. & Martikainen, P. 2003: Saproxylic beetles in managed and seminatural Scots pine forests: quality of dead wood matters. — *Forest Ecology and Management* 174: 365–381.

Smith, P. G. R. & Theberge, J. B. 1987: Evaluating natural areas using multiple criteria: theory and practice. — *Environmental Management* 11: 447–460.

Sturtevant, B. R., Bissonette, J. A., Long, J. N. & Roberts, D. W. 1997: Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. — *Ecological Applications* 7: 702–712.

Summers, R. 2004: Use of pine snags by birds in different stand types of Scots pine *Pinus sylvestris*: capsule hole-nesting birds tended to breed in the largest pine snags (standing dead trees) predominating in ancient native pinewood and scarce in plantations. — *Bird Study* 51: 212–221.

Zobel, K., Zobel, M. & Peet, R. 1993: Change in pattern diversity during secondary succession in Estonian forests. — *Journal of Vegetation Science* 4: 489–498.

Zobel, K. & Liira, J. 1997: A scale-independent approach to the richness *vs*. biomass relationship in ground-layer plant communities. — *Oikos* 80: 325–332.

Zobel, M. 1989: Secondary forest succession in Jarvselja, southeastern Estonia: changes in field layer vegetation. — *Annales Botanici Fennici* 26: 171–182.

Trass, H., Vellak, K. & Ingerpuu, N. 1999: Floristical and ecological properties for identifying of primeval forests in Estonia. — *Annales Botanicy Fennici* 31: 67–80.

Uotila, A., Kouki, J., Kontkanen, H. & Pulkkinen, P. 2002: Assessing the naturalness of boreal forests in eastern Fennoscandia. — *Forest Ecology and Management* 161: 257–277.

Valk, U. & Eilart, J. 1974: *Eesti metsad* [*Estonian forests*]. — Valgus, Tallinn. [In Estonian with English summary].

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J. S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T. & Kuuluvainen, T. 2007: Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. — *Forest Ecology and Management* 250: 77–88.

Vitousek, P. M. & Mooney, H. A. 1997: Human domination of Earth's ecosystems. — *Science* 277: 494–500.

Weibull, H. & Rydin, H. 2005: Bryophyte species richness on boulders: relationship to area, habitat diversity and canopy tree species. — *Biological Conservation* 122: 71–79.
