Habitat Directive Forest Type Western Taiga (*9010) in Estonia – the First Description of Stand Structure According to Mapping and Monitoring Data

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Abstract

This paper provides a comparative description of the Estonian Western taiga habitat type (*9010) based on data from the national Habitat Directive Annex I forest habitat monitoring program and two regional studies. Various stand structure characteristics associated with forest representativity, continuity age, region and dominant tree species are analyzed using logistic regression and models for count data. We found that most of the studied characteristics show expressive regional differences. Many stands' traits are well associated with representativity grading and continuity age. To predict the presence of many structure characteristics, we found that it may be sufficient to know the forest's stand composition (coniferous, deciduous or mixed) instead of tree species. We conclude that the Estonian mapping and monitoring methodologies are well-suited to describing and assessing the quality of the Western taiga habitat type in Estonia.

Key words: Habitat Directive, forest habitat types, mapping, monitoring, representativity, Western taiga *9010.

Introduction

The Interpretation Manual of European Union Habitats and the Natura 2000 Standard Data Form for habitat evaluation (European Commission 1996, 2007) establishes the terminology and principles for the inventory of Habitat Directive Annex I habitat types, including their representativity and conservation status. The general overview of the status of habitats throughout the European Union is organized as 6-year interval monitoring; there is no unified mapping or monitoring methodologies for individual habitat patches (European Commission 2006, Kuris and Ruskule 2006).

The first published Estonian national interpretation manual was the general description of the habitats based on the Interpretation Manual of European Union Habitats, and was the key document for Estonian forest site type classification (Paal 1997, 2002, 2004). The habitat quality requirements (stand structure, functions, age gap of trees, etc.) were described very briefly. According to the results of an audit on the implementation of the NATURA 2000 network in Europe (ECA 2008, NAO 2008), there proved to be a clear need for a detailed mapping methodology that would also offer data to complete Natura 2000 site management plans and the grounded zoning of protected areas. The first edition of the new mapping manual was prepared in 2008 (Viilma and Palo 2008). Because of institutional and legislation changes at that time, it was edited repeatedly, and the final edition was ready for implementation in 2010 (Palo 2010a,b). The new methodology with statistically representative sample design for Habitat Directive forest habitats monitoring was completed at the same time (Liira 2009, 2010). Both projects have many comparable characteristics, describing stand's structure and land use details of valuable habitat patches. The first tests to further optimize the set of collected characteristics were also performed (Palo et al. 2010, 2011). Other countries probably have their own monitoring methodologies by now, but we didn't find any scientific publication with comparable data about structural characteristics or stand development trends of Annex I habitats yet.

In several overviews, Estonian forests are classified as belonging to the boreonemoral vegetation zone (Barbati et al. 2006, Lõhmus and Kraut 2010, Sjörs 1965), but in the Natura 2000 network they are generalized as part of the boreal biogeographical region (EEA 2002; European Commission 1996, 2006, 2007). Typical boreal forest habitat types approved in Estonia are Western taiga (*9010), Fennoscandian hemiboreal natural old broad-leaved deciduous forests rich in epiphytes (*9020), Fennoscandian herb-rich forests with *Picea abies* (9050), Coniferous forests on or connected to glaciofluvial eskers (9060), Fennoscandian wooded pastures (9070) and Fennoscandian deciduous swamp woods (*9080). A total of 10 Habitat Directive forest types and Wooded dunes (type 2180) are presented in Estonia (Paal 2002, 2004). Estonian boreal landscapes are not comparable with large intact boreal areas in Russia (Angelstam and Kuuluvainen 2004, Potapov et al. 2008,Yaroshenko et al. 2002), but at the regional level the connectivity of forests and their biota is preserved quite well (Barbati et al. 2006, Kurlavicius et al. 2004, Tammeleht et al. 2010). Estonian landscapes include several environmental gradients: climatic (from sea to mainland), base rock (limestone on North-Estonia, sandstone on South-Estonia), postglacial formation (transgressions of Baltic Sea in West-Estonia) (Liira et al. 2011, Niinemets and Saarse 2009, Paal 1997). Typical Estonian boreal forests are presented in landscapes dominated by sandy, podzolic to thin-peaty soils (Paal 1997, 2002, 2004); forest fires have been characteristic over history (Lõhmus et al. 2004), regional large wind throws and fire disturbances also appear today (Asi and Õunap 2010, Köster et al. 2009). Some of the Western taiga forest soils have been secondarily impoverished through slash-and-burn land use in early history (Etverk and Meikar 2008, Jääts et al. 2010). In recent history, timber cutting and soil drainage reduced the area of natural stands (Lõhmus et al. 2004). Studies of specific species groups point out that substratum availability may be a major problem, as is microclimate continuity and forest management itself (Lõhmus 2005; Lõhmus et al. 2005, 2007, 2010, Lõhmus and Lõhmus 2008, 2011, Remm and Lõhmus 2011, Runnel et al. 2013), and therefore ecological quality, i.e. the continual presence of old-growth stand structure elements, is a highly important factor.

The paper gives a short ecological description of the Western taiga habitat type (*9010), based on habitat monitoring data from all over Estonia and on the habitat mapping data of Northeastern and Southern Estonia. The differences at the regional level and according to representativity grade, as well as the impact of stand dominant trees and stand age, will also be discussed.

Materials and Methods

Western taiga (9010*) habitat type and representativity grading

The Western taiga habitat type (*9010) was interpreted in accordance with the Estonian habitat interpretation manuals (Paal 2002, 2004), and representativity grading was given by an expert on the basis of the available mapping manuals (Palo 2010a,b, Viilma and Palo 2008).

In addition to the habitat description provided by Paal (2002, 2004), the forests of habitat type *9010 mainly grow on different Podzols and Albeluvisols, while special Alvar forests grow on Rendzic and Endogleyic Leptosols, Calcari-Skeletic Regosols and Calcaric Cambisols (Kõlli et al. 2004). The main natural succession in Western taiga habitats leads to the expansion of the regional climax community: mixed spruce and broad-leaved forests, while forest paludification is an alternative successional direction. Therefore habitat type has transitional stands of types 9050 (spruce forests or mixed aspen-spruce stands on more nutrient-rich soils such as various Cambisols and Luvisols), *9020 (mixtures of birch and aspen with broad-leaved trees growing on Cambisols and Luvisols), *9080 (paludifying birch or mixed birch- alder-conifer forests on thin-peaty Histosols), *91D0 (paludifying pine forests on thin-peaty Histosols), and 2180 (successional overgrowing of dyne forests) (Paal 2002, 2004, Palo 2010a,b).

In general, the forests that satisfy general habitat quality requirements are characterized as: 1. Forests with site-type-typical well developed stand structure or a stand structure that will be recovering over the next 30 years; 2. Signs of earlier natural disturbances independent of tree age; or the stand age is higher than the predefined forestry middle-aged class for stand dominant tree species; 3. The habitat patch area is larger than 0.01 ha; 4. Regular drainage areas are not allowed, but some old and stabilized or not functioning ditches may appear.

Representativity grades were used to assess the finer ecological quality of the stands: “A” – an old-growth forest typical for the predefined site type range; “B” – a near-natural mature stand, with a few small deficiencies in stand structure or a stand of premature age with high structural quality; “C” – some greater deficiencies are found, but the stand also has some relevant qualities and deficit substrates, and the stand main structure recovers over 30 years; “D” or “p” (potential) – the forest habitat has serious deficiencies but corresponds to the predefined site type range and has some important nature conservation tasks, i.e. networking, as a habitat for rare or protected species etc. For data analysis, both A and B (habitats with good representativity: AB) and D and p (habitats with low representativity: Dp) were combined in order to minimize the expert’s subjectivity when assessing representativity in the field (Palo et al. 2010, 2011).

Study area and data gathering

Three different data sources were used:

• data collected from all over Estonia in a forest habitat monitoring program performed in the years 2010-2012 (86 plots);

• data from Northeastern Estonia collected in 2008-2009 (74 plots; Palo et al. 2010, 2011);

• data from different habitat mapping projects in Southern Estonian protected areas in 2010-2012 (302 plots).

All field work data were gathered by Anneli Palo (with Dagmar Hoder in Northeastern Estonia).

Monitoring field work plots were studied around randomly generated points with a radius of 20m. Using randomization, the frequencies of the representativity grades and site types in the database of *9010 are taken into account, and the sample was statistically representative all over Estonia (Liira 2010).

In addition to mining areas, the Northeastern Estonian region also includes the most untouched and densely forested parts of Estonia (called the Alutaguse forests), where intensive cutting and drainage first began in the 19th and 20th century (Etverk and Meikar 2008, Paal et al. 2007). The data collected there were used in earlier publications (Palo et al. 2007, 2010, 2011, Palo and Hoder 2009); the field work methodology was quite comparable with the collection of the monitoring data.

Southern Estonian forest landscapes are very heterogeneous despite the relief conditions, and also because of the long history of human activity in the area (Etverk and Meikar 2008, Jääts et al. 2010, Kusmin 2011, Niinemets and Saarse 2009). In Southern Estonia the data originates from larger homogenous habitat patches, but the differences are probably not too significant, as the average size of habitats in this region is low, and the field work practice is to describe the stand by a spot that is characteristic of the entire stand. However, the influence of size may be taken into account when interpreting the results.

Characteristics and statistics

Due to differences in data sampling methodologies, the data values of the compared characteristics (listed in Table 1) are mainly reduced to binary presence/absence data. Only comparable characteristics are presented here, although in every project more characteristics were collected. The following is an explanation of the characteristics we used:

• *Tree stools/moss and herb tussocks* are higher than 30 cm from base ground;

• *Gaps in canopy* had a comparable or larger diameter than the mean tree height in the stand;

• *Supporting/exposed roots* are all kinds of supporting or exposed roots (on peaty soil, on slopes);

• *Stumps* – if there was one or more recognizable stumps of removed trees;

• *Beaver signs* are traces of beaver activity, such as fallen trees, dams and flooded areas;

• *Small depressions* are regularly wet/flooded areas with a size of > 1m² and different plant/moss cover or bare ground;

• *Lying large-size dead wood* had a diameter of > 25 cm;

• *Pendulous lichens* are mainly *Lobaria pulmonaria* exemplars and lichens from the genera *Usnea* and *Bryoria*, but in some cases *Evernia* or *Ramalina* exemplars are probably also assessed (*Alectoria* is very rare in Estonia);

• *Standing dead trees* are dead trees of the I or II tree layer range;

• *Holes in trunks* are larger than approximately 2cm, which means they are clear signs of woodpeckers and cavities suitable as nesting places for birds and other animals;

• *Lying dead wood in many decay stages* was assessed if more than three different decaying stages of dead wood were found;

• *Bracket fungi* fruiting bodies were assessed;

• *Varying aged stand* was assessed if there were differences of over 20-30 years in I layer tree age;

• *Signs of forest fire* are all detected signs of earlier fires on trees bark, stumps etc.;

• *Old Hazel clumps/trunks* (> 70cm diameter) were presented;

• *Over-mature-aged trees* must be at least 20 years older than the mature edge of that tree species used in forest management (approximately by pine > 110; spruce > 100; birch > 90; aspen > 60); in the plot it was estimated if there were trees with clear signs of aging;

• *Number of structure characteristics* is the sum of all previous indicators;

• *Number of I layer tree species* – how many tree species were detected in I tree layer of plot;

• *Number of regrowth/shrub species* – how many tree regrowth and shrub species were on the plot;

• *Continuity age* was the expert assessed age of the oldest tree on the plot, which is not always the age of the dominant tree species, and therefore the continuity age may be substantially higher than the mean age of the stand as a whole.

Regression models were developed to describe regional differences of the above-mentioned stand characteristics, accounting for the representativity grade of the forest and also its stand composition and continuity age (Table 1). All data analysis was conducted in R (R Core Team 2013). The considered predictors were region (as a factor with levels Northeastern Estonia, Southern Estonia and monitoring data, the latter being the reference level), representativity grade (as a factor with levels AB, Dp and C, the latter being the reference level), stand composition (as a factor with levels deciduous forest, coniferous forest and mixed forest, i.e. forest with deciduous or coniferous component in I tree layer >30%, the latter being the reference level) and stand continuity age (as a continuous variable). An additional linear model was also estimated for stand continuity age, in order to shed light on the associations between that and other predictors. Residuals were plotted against predictions in order to check normality and constant variance, and R^2 was calculated for the model. The general method for model selection was backwards selection, manually removing insignificant terms one-by-one (based on Wald chi-squared statistics, starting from terms with the largest p-values), beginning from a model with all of the main effects and two-way interactions. Region was always retained in the model, even if it was not significant. Since predictors were correlated, we proposed a few plausible alternatives for each backwards selected model. The effect of replacing representativity grade by continuity age (or *vice-versa*) was always checked. Final models were chosen based on AIC. If a final model included interaction terms, then continuity age was centred by subtracting the sample mean (113.68 years), and the model was refitted in order to enhance the interpretability of the main effects. All final models were significantly better than the corresponding null models (likelihood ratio tests $p<0.0001$, except for the model for tree stools/moss and herb tussocks, which had $p=0.007$). We also estimated models in which three-levelled stand composition was replaced by a finer grading, dominant tree species (pine, spruce, birch, aspen or mixed), to see if it allowed for a better model (in the sense of AIC).

For all characteristics except the number of I layer tree species, the number of regrowth/shrub species and the number of structure characteristics present, binary logistic regression models were fitted (Harrell 2013). If separation or quasi-separation was detected in the final model (extensive estimated variance of an estimated effect), then the corresponding Firth's penalized-likelihood binary logistic regression model was fitted instead (Heinze et al. 2013). That was the case with models for signs of forest fire, old Hazel clumps/trunks and over-mature-aged trees (sample prevalence respectively 12%, 2% and 64%). The discriminating ability of binary logistic regression models was described by the c-index (concordance statistic). The c-index varies from 0.5 to 1, with larger values indicating a better model. The goodness of fit of ordinary binary logistic regression models was tested by le Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares tests (Harrell 2013), the goodness of fit of Firth's penalized-likelihood logistic regression models was tested using the Hosmer-Lemeshow test (Kohl 2013).

Count data were modelled using logistic regression (number of structure characteristics) (R Core Team 2013), zero-truncated Poisson regression (number of I layer tree species) (Yee 2013) and negative binomial regression (number of regrowth/shrub species) (Venables and Ripley 2002). The goodness of fit of the final selected models was tested using Pearson chi-square tests.

Model predictions were calculated for each combination of discrete predictor variables (using the mean continuity age of each separate group as a predictor, where relevant) and reported in Tables 2 and 3. Bootstrap percentile 95% confidence intervals were obtained for all predictions (Canty and Ripley 2013), based on 100 000 bootstrap samples. These confidence intervals are not strictly symmetrical, so we report the distance between the prediction and the farther confidence limit in tables.

Results

Representativity grading

As methodologically expected, the majority of characteristics had different frequencies and counts, when one compares habitats with different representativity grades (regional aspect, continuity age and stand composition taken into account; Table 1).

The only negative characteristic toward high representativity (AB-grade) was the presence of stumps (parameter estimate β = -0.98, Wald Z = -3.48, p = 0.0005). Varying aged stand structure, described as a very important characteristic of Western taiga (Paal 2002), had no significant relation to representativity grading in this study (Wald chi-square χ^2 = 0.03, df = 2, p > 0.9). Excluding stand continuity age from the model indeed makes representativity grade a factor that is significantly associated with the varying age stand structure (χ^2 = 2.63, df = 2, p < 0.0001), but the overall performance of the model will be diminished (model with continuity age and without representativity: AIC = 356, c-index C = 0.89, model without continuity age and with representativity: AIC = 511, C = 0.70).

The presence of old Hazel clumps/trunks, signs of forest fires and gaps in the canopy (Table 1) were also not significantly associated with representativity grading (respectively χ^2 = 3.59, df = 2, p > 0.1; χ^2 = 1.32, df = 2, p > 0.5; χ^2 = 3.63, df = 2, p > 0.1). Fires are altogether rare in whole contemporary landscapes (Lõhmus et al. 2004), and Hazels are more common in

Table 1. Models for stand characteristics. Each row represents the final selected model for a particular stand characteristic. Parameter estimates for levels of factors afford to compare the stand characteristic (its occurrence probability or mean) in the level and respective reference level. Factors are region, representativity grade and stand composition; their reference levels are monitoring data, habitats with average representativity grade and mixed forests, respectively. Positive parameter estimate indicates larger mean than that of reference level and negative estimate indicates smaller mean. Asterisks next to parameter estimates indicate whether the parameter is significantly different from zero (for factors: is the level different from the reference level) (*** p<0.001, ** 0.001≤p<0.01, * 0.01≤p<0.05). "***Bold italic***" levels are significantly different from each other. N.S. denotes predictors not included in the final model (see Chapter 2.3 for model selection; note that region was always retained). For all models containing interactions, stand continuity age is centered by subtracting the sample mean (113.68 years). Other signs and abbreviations: AB – habitats with high representativity grade; Dp – habitats with low representativity grade; NE – Northeastern Estonia; S – Southern Estonia; Dec – deciduous trees; Con – coniferous trees; ContA – stand continuity age; C-H-C-H p – le Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares tests p-value; H-L p – Hosmer-Lemeshow tests p-value; Pearson p – Pearson chi-squared goodness-of-fit tests p-values. For the latter three tests, p<0.05 indicates that the model does not fit the data

Binary logistic regression models		Region		Repr. grades		Stand composition		ContA			
	Intercept	NE	S	AB	Dp	Dec	Con	ContA	Interactions	C-H-C-H p	c statistic
Tree stools/moss and herb tussocks	-2.15***	0.99*	0.26	0.56	-0.32	N.S.		N.S.		0.36	0.63
Gaps in canopy	-1.09*	0.29	-0.74**	N.S.		-0.21	-0.75**	0.0186***		0.93	0.67
Supporting/exposed roots	-0.25	-0.97*	-1.16***	***0.59****	***-0.95****	-0.22	-0.72*	N.S.		0.21	0.69
Stumps	-1.28*	***-1.52******	***0.04***	***-0.98******	***0.38***	-0.31	0.42	0.0216***		0.58	0.75
Beaver trees/flood	-4.95***	0.94	2.19*	1.05*	-1.46	N.S.		N.S.		0.35	0.75
Small depressions	-2.04***	1.16*	0.43	0.48	-0.6	0.76*	-1.43***	N.S.		0.36	0.77
Lying large-size dead wood	2.30**	1.30*	1.40***	***0.74***	***-1.16*****	-0.35	-1.12	N.S.		0.48	0.78
Pendulous lichens	-1.80***	***-0.48***	***1.75******	***1.20******	***-0.6***	-1.33***	-0.12	N.S.		0.34	0.80
Standing dead trees	1.06*	***-0.31***	***1.40******	***1.21*****	***-0.49***	N.S.		-0.0418**	ContA*NE 0.0369* ContA*S 0.0131 ContA*AB 0.0423** ContA*Dp 0.0263*	0.63	0.80
Holes in trunks	-1.20	-0.2	1.13***	0.37	-0.90**	***0.66***	***-1.56******	0.0234***		0.67	0.81
Lying dead wood in many decay stages	0.9	***0.37***	***2.18******	***1.60******	***-1.06*****	-0.09	-1.26**	N.S.		0.05	0.85
Bracket fungi	1.50**	***-1.38*****	***1.80******	***0.82****	***-0.61***	***1.86****	***-2.01******	N.S.		0.71	0.86
Varying aged stand	-8.35***	***1.60******	***-1.34******	N.S.		N.S.		0.0668***		0.69	0.89
Signs of forest fire	-4.50***	1.68***	-0.11	N.S.		-1.19		2.77***	N.S.	0.99	0.78
Old Hazel clumps/trunks	-3.43***	-2.31	0.34	N.S.		1.87*	-1.65	0.0713*	ContA*Con -0.0737 ContA*Dec 0.0132	0.67	0.89

boreonemoral or nemoral forest habitats (Paal 1997, 2002). Representativity significantly predicts gaps in the canopy if continuity age is left unobserved (χ^2 = 14.67, df = 2, p = 0.0007, but C=0.64 < 0.67 and AIC = 620 > 608).

All stand structure qualities (except stumps) are components of the general indicator "number of structure characteristic" which in coniferous forests makes it possible to distinguish all three representativity classes from each other, and in mixed or deciduous forests makes a clear difference between AB and Dp grade forests (Table 1, 2). As in an earlier study (Palo et al. 2011), this secondary characteristic provides summarized information about habitat type stands complexity and may also provide information about changes therein during the monitoring process. We did not find a significant effect of representativity grade on the number of stands I layer tree species and the number of regrowth/shrub species (respectively $\div^2$ = 1.72, df = 2, p > 0.4; χ^2 = 2.87, df = 2, p > 0.2), suggesting that even studied low-quality Dp-grade forests were in a near-natural stage, as the habitat-specific number of woody species may generally be reduced through intensive management. The number of understories species may also be affected by light conditions and microhabitat density, and therefore somewhat useful for direct boreal forest stand quality assessment (Liira et al. 2007, 2011).

On AB-C-Dp representativity levels, many characteristics had a remarkably different range of percentages in regional grading when continuity age and stand composition were taken into account. The most frequent characteristics in all regions with excellent representativity habitats (AB) were standing dead trees, lying dead wood in many stages of decay and lying large-sized dead wood. We expect to find these indicators in 78-99% of habitats throughout Estonia. Holes in trunks and bracket fungi were also often found in deciduous and mixed forests (Table 3).

Table 2. Predictions of models of count data. These figures indicate the mean number of structure characteristics or species in stands of various representativity, composition and region. Bootstrap percentile 95% confidence interval of the predicted mean is contained in the indicated interval. See continuity ages from Table 2 and other abbreviations from Table 1

		Coniferous			Deciduous			Mixed		
Characteristic	**Repr. grade**	**NE**	**S**	**M**	**NE**	**S**	**M**	**NE**	**S**	**M**
Number of structure characteristics	AB	7.4±0.6	8.1±0.3	6.0±0.7	7.4±0.9	7.7±0.4	7.4±0.9	9.3±0.8	8.4±0.4	7.2±0.9
	C	5.7±0.6	6.5±0.3	4.4±0.6	5.9±0.8	6.3±0.5	6.1±0.9	7.0±0.9	6.7±0.5	5.5±0.8
	Dp	4.5±0.6	5.1±0.4	3.6±0.6	4.6±0.8	5.0±0.5	4.8±0.9	6.2±1.0	5.5±0.5	4.8±0.8
Number of I layer tree species	AB, C, Dp	2.2±0.2	2.6±0.1	2.3±0.2	2.9±0.4	3.5±0.3	3.1±0.4	3.1±0.4	3.8±0.2	3.3±0.3
Number of regrowth/shrub species	AB	4.2±0.3	4.2±0.3	4.2±0.3	6.3±0.6	6.4±0.6	6.3±0.6	6.4±0.9	5.5±0.6	5.3±0.6
	C	4.2±0.3	4.1±0.3	4.1±0.4	6.3±0.6	6.3±0.6	6.3±0.6	4.5±0.6	4.7±0.6	4.4±0.7
	Dp	4.1±0.3	4.1±0.4	4.1±0.4	6.2±0.9	6.3±0.7	6.2±0.8	5.0±0.6	4.4±0.7	4.8±0.6

Table 3. Binary logistic regression model predictions of proportions (as percentages). These figures indicate the occurrence probabilities of studied stand characteristics in stands of various representativity, composition and region. The first line of each of the three sub-tables lists the sample mean continuity age of the specified group of forests (abbreviated as ContA). The accuracy of predictions is represented by asterisks (*** 95% bootstrap percentile confidence interval is contained in ± 5, ** ± 10, * ± 15). For other signs and abbreviations, see Table 1

		Coniferous			Deciduous			Mixed		
Repr. grade	**Characteristic**	**NE**	**S**	**M**	**NE**	**S**	**M**	**NE**	**S**	**M**
AB	**ContA (years)**	**144**	**135**	**126**	**96**	**99**	**91**	**139**	**117**	**113**
	Stumps	44	75**	71*	12**	40*	36	32	58*	54
	Varying aged stand	95**	33**	51	42*	4***	10**	93**	14***	30*
	Gaps in canopy	76*	48**	62*	69*	45*	60*	86*	59*	73*
	Lying dead wood in many decay stages	83*	97***	78*	94**	99***	92**	95**	99***	92**
	Bracket fungi	26*	89**	58	94**	100***	98***	72	98***	91*
	Supporting/exposed roots	21*	18**	41*	30	26*	53	35	31*	58
	Holes in trunks	69	87**	63*	87*	96***	88*	90**	96***	86*
	Lying large-sized dead wood	96**	97***	87*	98***	98***	94**	99***	99***	95**
	Standing dead trees	96**	98***	91**	79	97***	91*	95**	98***	91**
	Small depressions	14**	7***	5***	59	41	31	40	24*	17
	Tree stools/moss and herb tussocks	35*	21**	17**	35*	21**	17**	35*	21**	17**
	Pendulous lichens	23*	74**	33*	8*	45	13*	25	76*	35
	Beaver trees/flood	5**	15**	2***	5**	15**	2***	5**	15**	2***
	Signs of forest fire	49*	14***	15**	2***	0***	0***	6**	1***	1***
	Over-mature-aged trees	100***	99***	49	100**	75	36	100***	96**	60
	Old Hazel clumps/trunks	0***	0***	0***	0***	10**	4**	1***	6**	3**
C	**ContA (years)**	**120**	**119**	**98**	**83**	**91**	**87**	**90**	**95**	**88**
	Stumps	55	85**	78*	21*	60*	57	30	69*	65
	Varying aged stand	78*	15***	14**	23*	3***	7**	32*	3***	8**
	Gaps in canopy	67*	41**	50*	63*	42*	58*	71	48*	63
	Lying dead wood in many decay stages	50	86**	41	76	95**	69	78	96**	71
	Bracket fungi	13*	78**	37	88*	99***	97***	53	96***	82
	Supporting/exposed roots	13*	11**	28*	19*	16*	38	23	20*	44
	Holes in trunks	46	76**	38	77	94**	82*	67	90**	70
	Lying large-sized dead wood	92*	93***	76	96**	97**	88*	97**	98***	91*
	Standing dead trees	67	91***	85*	71	96***	90*	70	95***	89*
	Small depressions	9**	5***	3***	47	30	22	29	17*	12*
	Tree stools/moss and herb tussocks	24*	13**	10**	24*	13**	10**	24*	13**	10**
	Pendulous lichens	8**	46*	13**	3***	20*	4**	9**	49	14*
	Beaver trees/flood	2***	6**	1***	2***	6**	1***	2***	6**	1***

Table 3. (Continued)

	Signs of forest fire	49*	14***	15**	2***	0***	0***	6**	1***	1***
	Over-mature-aged trees	99***	91**	3**	12	53	6*	33	60	5
	Old Hazel clumps/trunks	0***	0***	0***	0***	6**	3***	0***	2***	1***
Dp	**ContA (years)**	**109**	**102**	**102**	**70**	**78**	**73**	**103**	**87**	**100**
	Stumps	59	85**	85**	23	62	59	45	73*	78
	Varying aged stand	63*	5***	17**	11**	1***	3***	54*	2***	16**
	Gaps in canopy	62*	34**	52*	57	36*	52	76*	45*	69*
	Lying dead wood in many decay stages	26	68*	19*	53	87*	44	55	88*	46
	Bracket fungi	8**	66*	24	80	99***	94**	38	94**	71
	Supporting/exposed roots	5**	4***	13*	8**	7**	19	10*	9**	23
	Holes in trunks	22*	47*	22*	50	82*	57	53	75	56
	Lying large-sized dead wood	79	80*	50	89*	90*	69	92*	93*	76
	Standing dead trees	54	88**	68	34	89**	77	51	88**	69
	Small depressions	5**	3***	2***	33	19	13	19	10**	7**
	Tree stools/moss and herb tussocks	19*	10**	8**	19*	10**	8**	19*	10**	8**
	Pendulous lichens	5***	32*	7**	1***	12*	2***	5**	34	8**
	Beaver trees/flood	0***	1***	0***	0***	1***	0***	0***	1***	0***
	Signs of forest fire	49*	14***	15**	2***	0***	0***	6**	1***	1***
	Over-mature-aged trees	95**	53	26	1***	18	22	94**	36	51
	Old Hazel clumps/trunks	0***	0***	0***	0***	3***	1***	0***	1***	1***

Regional differences

Regions differ in terms of almost all characteristics, accounting for habitats' representativity grade, continuity age and stand composition. As the monitored Western taiga data probably describes the general representative range of these habitat type in Estonia (Liira 2009, 2010), in comparison with them the habitats in Northeastern Estonia as well in Southern Estonia had a higher stand continuity age ($\beta > 7$, $t > 2.99$, $p < 0.009$); lying large-size dead wood was found more frequently ($\beta > 1.3$, $Z > 2.45$, $p < 0.02$); supporting/exposed roots were less frequently presented ($\beta < -0.96$, $Z < -2.43$, $p < 0.02$). The region had no significant effect on the number of regrowth/shrub species and old Hazel clumps/trunks (respectively $\chi^2 = 3.02$, $df = 2$, $p>0.2$; $\chi^2 = 3.59$, $df = 2$, $p > 0.1$). Number of I layer tree species did not differ between forests of different representativity grades ($\beta_{AB} = -0.10$, standard error SE_{AB}=0.11, approximate 95% confidence interval (-0.33, 0.12); β_{Dp}=0.14, SE_{Dp}=0.09, (-0.03, 0.30)).

In Northeastern Estonia, we found a lower frequency of stumps and bracket fungi compared with the Western taiga habitats in the monitoring sample (respectively $\beta = -1.52$, $Z = -4.13$, $p < 0.0001$; $\beta = 1.38$, $Z = -3.19$, $p = 0.0014$). In addition, Northeastern Estonian stands tended to have more small depressions ($\beta = 1.16$, Z = 2.33, $p = 0.020$), tree stools/moss and herb tussocks ($\beta = 0.99$, $Z = 2.34$, $p = 0.019$), varying age ($\beta = 1.60$, $Z = 3.59$, $p = 0.0003$) and signs of forest fire ($\beta = 1.68$, $Z = 3.52$, $p = 0.0004$) than similar forests generally found in Estonia. The number of stand structure characteristics was also greater than in the monitoring sample ($\beta = 0.40$, Z=2.01, p=0.045). In Southern Estonia, higher frequencies of pendulous lichens ($\beta = 1.75$, $Z = 5.44$, $p < 0.0001$), bracket fungi ($\beta = 1.80$, $Z = 5.56$, $p < 0.0001$), beaver trees/floods ($\beta = 2.19$, $Z = 2.13$, $p = 0.034$) (see also Andersson et al. 2003), holes in trunks ($\beta = 1.13$, $Z = 3.78$, $p = 0.0002$), lying dead wood in many stages of decay ($\beta = 2.18$, $Z = 6.28$, $p < 0.0001$) and standing dead trees ($\beta = 1.40$, $Z = 3.34$, $p = 0.0008$) were detected, compared with Western taiga forests of similar representativity, stand composition and continuity age in Estonia as a whole. Gaps in the canopy and stands of varying age were less frequent in Southern Estonia than in otherwise similar forests in Estonia (respectively $\beta = -0.74$, $Z = -2.84$, $p = 0.0044$; $\beta = -1.34$, $Z = -3.53$, $p = 0.0003$).

The detected regional differences are in close accordance with experts' empirical picture of habitats in these areas: based on the analyses, Northeast Estonian forest habitats are more continual, of different ages, exhibit rich stand structure and are probably less managed (with a lower frequency of plots with stumps). Southern Estonian forests are managed at the same level as monitored habitats, and have a more homogenous structure than Northeast-Estonian forests (a lower frequency of plots with gaps in canopy and different-aged stands). The higher likelihood of the presence of standing dead wood, lying large-size dead wood and dead wood in many stages of decay, as well as holes in trunks, pendulous lichens and bracket fungi in Southern Estonia (Table 1) may initially at least partly refer to the methodological differences in data sampling. However, the occurrence of genera *Usnea* and *Bryoria* is truly much more frequent in Southern Estonia than in Northeastern Estonia (Andersson et al. 2003, E-biodiversity; Marmor et al. 2010, Tõrra and Randlane 2007), although epiphytic lichens are theoretically more characteristic of continuous forests (Marmor et al. 2011, Paal et al. 2007), and some of our other results confirmed that forest habitats in Northeastern Estonia were more continuous than in Southern Estonia, which is also confirmed by the literature (Jääts et al. 2010, Niinemets and Saarse 2009, Paal et al. 2007; Palo et al 2007). If representativity grade were excluded from the model, our results would also imply that continual forests are more likely to have epiphytic lichens, although representativity seems to capture this association more effectively (model with continuity age and without representativity: AIC = 540, c-index C = 0.75, model without continuity age and with representativity: AIC = 508, C = 0.80).

The explanation of the somewhat unexpected differences in the frequencies of lying large-size dead wood and dead wood in many stages of decay may also lie in the partially different forest management practice in recent history. In historical Southern Estonian farm landscapes (later on Soviet collective farms), the cutting of individual trees or little forest patches was a more common management tool than in large state forest areas in Northeastern Estonia, where forests were managed more intensively (Etverk and Meikar 2008). Therefore in the Southern Estonian habitats one can find many patches that have long been managed using low-intensity tools and have enough heterogeneous stand structure to fulfil methodological requirements of the Western taiga habitat description, while in Northeastern Estonia only forests that have truly not been managed for a long time may fulfil them. Whether these forests in both regions indeed possess the same habitat quality for late-succession stage species should be investigated in greater detail. In some Northeastern Estonian old-growth forests, high species biodiversity is observed (Saar et al. 2007, Timm and Kiristaja 2002, Trass et al. 1999, Tõrra and Randlane 2007, Vellak and Leis 2007), but the other reason for high biodiversity besides the continuity of microclimatic conditions may be that there are enough main basic substrates left (Lõhmus et al. 2007, 2010, Lõhmus and Lõhmus 2008, 2011, Parmasto 2004, Perhans et al. 2009, Runnel et al. 2013, Vellak and Ingerpuu 2005). We do not have as much comparable biodiversity data from the more fragmented and smaller nature conservation areas of Southern Estonia, but for some old-growth species, the stand structural qualities are there (Andersson et al. 2003; Marmor et al. 2010; Tõrra and Randlane 2007) as well as for many endangered species like *Pandion haliaetus, Aquila pomarina, Osmoderma eremita* etc (E-biodiversity).

Through detected regional differences we consider that direct comparison of data between countries is hardly possible due to differences of environmental factors, land use techniques and of some interpretation variation (Kuris and Ruskule 2006) of habitat type's definitions. On the same reason we do not suggest developing of quantitative assessment of characteristics; the more qualitative index (based on presence-absence data) may occur more comparative as also presented in Palo et al. 2011.

Continuity age

The continuity age of living trees on habitat patches is an important factor to determine the number of stand structural characteristics (χ^2 = 38.18, df = 1, p < 0.0001) and also the presence of varying-aged stand (χ^2=99.54, df = 1, p < 0.0001), holes in trunks (χ^2 =20.52, df = 1, p < 0.0001), gaps in the canopy (χ^2 = 22.69, df = 1, p < 0.0001) and over-mature-aged trees (χ^2 = 23.34, df = 3, p < 0.0001) (the last one especially in Northeastern and Southern Estonia), even if other factors are taken into account. Stands with higher continuity age also had a higher probability of contain stumps (β = 0.0216, Z = 4.35, p < 0.0001) and old Hazels (β = 0.0713, Z = 2.31, p = 0.021).

Continuity age had no additional effect on the stands' lying dead wood occurrence compared to representativity grade (dead wood in many decay stages: χ^2 = 3.44, df = 1, p = 0.064; large-sized dead wood: χ^2 = 0.32, df = 1, p > 0.5), although the exclusion of representativity grade from the model makes continuity age a significant factor predicting the presence of lying large-sized dead wood (χ^2 = 5.68, df = 1, p = 0.017, but AIC = 271>256, C = 0.73 < 0.78). As old trees and large-sized dead-wood are deficient substrates for many old-growth species (Lõhmus et al. 2005, 2007; Lõhmus and Kraut 2010; Lõhmus and Lõhmus 2008, 2011; Perhans et al. 2009), they count by stands representativity assessment, although on the basis of methodology the age of stand or tree trunk is not always the most important factor predicting the high representativity of the forest patch (Palo 2010a). Continuity age was negatively correlated with the frequency of standing dead trees in monitoring forests of C-representativity (main effect β = -0.0418, Z = -2.78, p = 0.0055), while at the same time there are positive interactions with the Northeastern (β = 0.0369, Z = 2.42, p = 0.015) and Southern Estonian (β = 0.0131, Z = 0.89, p > 0.3) regions, as well as with representativity grades AB (β = 0.0423, Z = 2.64, p = 0.0083) and Dp (β = 0.0263, Z = 2.08, p = 0.038). There are probably many historical stand management and development scenarios, and thus regional differences or tree species effects may also be more persistent.

Stand tree composition

Stand tree composition has a clear impact on the frequencies and counts of characteristics (Table 1) from the point of view of ecological conditions or forest management practices. Models were also fitted using finer grading of stand composition (birch, aspen, pine, spruce or mixed) instead of differentiating coniferous, deciduous and mixed forests. However, the results suggested that the limited differences between species do not add much information. The trends were generally the same as in the case of combined groups, and the finer differentiation of stand composition tended to increase models' AIC: finer grading of stand composition allowed for a smaller AIC value only in models for gaps in canopy, supporting/exposed roots, pendulous lichens, signs of forest fire, over-mature-aged trees and number of I layer tree species.

In general, mixed forests have more similarities with deciduous forests, which had remarkably lower stand continuity age and frequency of pendulous lichens (respectively $\beta = -17$, t = -4.38, $p < 0.0001$; $\beta = -1.33$, $Z = -3.31$, $p = 0.0009$). Coniferous stands have higher frequency of forest fires and stand continuity age (respectively $\beta = 2.77$, $Z = 3.24$, $p = 0.001$; $\beta = 15$, $t = 4.9$, $p < 0.0001$), but the different dead-wood characteristics and some other diversity indicators are presented with lower frequencies, and therefore the number of stand structure characteristics is also lower (main effect $\beta = -0.41$, $Z = -2.52$, $p = .012$). It must be pointed out that in comparing the structural diversity of stands (Palo et al. 2011), coniferous stands may appear poorer if all other factors (stand continuity age etc) are the same, because of coniferous tree species' long lifetime (especially pine) and slower decay. Of course the meaning of structural diversity and stand tree composition for old-growth species is much more complicated because of the importance of large-scale landscape and microclimatic continuity.

Continuity age interaction with stand composition in the case of regrowth/shrub species ($\chi^2 = 8.93$, $df = 2$, $p = 0.012$) probably describes the natural succession (Lõhmus and Kraut 2010), and therefore the number of species may grow on forest climax succession (rich soil mixed aspen-birch-spruce forests from *9010 developing into a mixed spruce-broadleaved forest of type 9050) (main effect of continuity age $\bar{a} = 0.00786$, $Z = 3.42$, $p = 0.0006$), but never grows on acidic paludification succession (Liira et al. 2011) (from a *9010 forest to the poorer *91D0 type and raised bog) (in deciduous forests, interaction $\beta = -0.00762$, $Z = -2.00$, $p = 0.046$; in coniferous forests, interaction $\bar{a} = -0.00750$, $Z = -2.95$, $p = 0.003$).

Conclusions

Most characteristics expected differences in the frequencies and counts comparing habitats with different representativity grades (regional aspect, continuity age and stand composition taken into account), which confirms the objectivity of the newly implemented methodologies we used. Some important traits from the point of view of biodiversity occur too rarely and occasionally, and therefore all stand structure characteristics are counted as components of the general indicator "number of structure characteristics", which provides summarized information about habitat type stands' complexity and change therein. It's weakly sensitive to the regional aspect and makes habitat patches comparable with each other over all Estonia.

Regions differ in terms of almost all characteristics, accounting for habitat representativity grade, continuity age and stand composition. The characteristics generally had the lowest values in the monitoring data sample. Some underestimation of the presence of all stand characteristics may be the result of monitoring sample point selection methodology, where the earlier not very precise habitat data layer was used to generate the monitoring plots. Thus we suppose, based on our Northeastern Estonian and Southern Estonian mapping data, that the Estonian Western taiga habitats may actually have a higher structural heterogeneity and better representativity than that revealed by the monitoring data.

Although the age of trees or stands is only one possible stand characteristic among others, it turns out to be a very important one, as it determines the frequencies/counts of other characteristics, especially when expert assessed representativity grading is not taken into account. Many of the structural characteristics of old forest stands depend on tree age, but the historical intensity and frequency of timber management must also be carefully evaluated. The higher probability of the occurrence of stumps in more continual forests is likely to be an artefact, since one expects to see stumps more frequently in forests that have been exposed to longer human activity (i.e. where a stand's oldest tree is older than the whole stand). If forest management were to cease, this association would probably disappear.

We conclude that Estonia's Habitat Directive forest mapping and monitoring methodologies allow the description of the structural heterogeneity of Western taiga stands on the same level of accuracy, and they will be an objective tool to study and monitor the status of Habitat Directive type *9010 in Estonia. Since regional aspect was very important, the international comparisons of Western taiga qualities require further study.

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