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Successional Dynamics of Tree Composition in Mixed Boreo-Nemoral Stands from Habitat Directive Annex I Forest Types *9020, 9050, 9060, *9010

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Abstract

Without human influence, boreo-nemoral (hemi-boreal) landscapes on fertile soils would be covered with mixed deciduous-spruce-forest. At the stand level, patches with only dominant tree species (spruce or some broadleaved species) may also be present. Nowadays, human impact seldom allows such forests to reach late-successional phase.

Our study results confirmed that also Habitat Directive Annex I forest types present on mesic fertile soils in Estonia, are mostly highly human-influenced. Broadleaved forests (*9020) are very common on areas that have been wooded meadows or pastures a century ago. Depending on the soil type, they will remain as broadleaved communities, although the proportions of tree species may change, or they will change to mixed forests with a variable cover of spruce in following generations. In contrast, the current Herb rich spruce forests (9050) will develop into more diverse stands, containing many broadleaved species, especially in the understory. Preferably on Gleysols and probably more frequently on Gleyic Cambisols or Luvisols, the spruce forest belonging to the type *9050 according to spruce coverage criteria may change into Broadleaved old-growth forest type (*9020). Spruce has been highly favored on areas with evidence of management; the trend was confirmed by the analysis of deadwood parameters. The Esker forests (9060) will have a different successional path on Arenosols and Mollic Cambisols.

We suggest that increasing the area and connectivity of the fertile soil forest habitat patches will ensure the heterogeneity and availability of habitat conditions and substrates. Therefore, instead of implementing protection measures for each Natura habitat type separately to maintain their current tree composition and structure, which is result of the nineteenth and twentieth century land use practices, the entire forest area on fertile soil should be treated as one unit, within which patches are promoted to follow different trajectories.

Keywords: Habitat Directive Annex I forest habitat types *9020, 9050, 9060, *9010; changing land use; tree composition; succession; forest conservation.

Introduction

European hemi-boreal or boreo-nemoral mixed forests are growing in Estonia on relief formed by the Weichselian glaciation (Kalm et al. 2011). The mixture of spruce and nemoral deciduous trees on fertile soils is viewed as the climax stage of boreo-nemoral forests in Estonia (Laasimer 1965, Reitalu et al. 2013). Currently in Estonian landscapes, three main forest landscape complexes alternate: 1. Overgrown, historically agriculturally used sites on fertile soils with various amounts of secondary deciduous forests or traditional wooded meadows and wood-pastures; 2. Typical, mainly managed mixed forests with some historical agricultural activities on moderately fertile and sometimes drained minerotrophic peat soils; 3. Relatively large boreal coniferous (mixed) forests with birch and aspen on peaty soils around oligotrophic bogs or on sandy and limestone areas. In practice it needs to be specified whether the discussion concerns landscape or stand level. However, the mixed forests are difficult to define, study and protect as the mixture of different trees is a complex phenomenon created by soil and climatic conditions, ecological interactions and management processes that have occurred in both time and space (Barbati et al. 2006, Bravo-Oviedo et al. 2014).

In the last few thousand years, transformation of the Estonian forest tree composition has been related to the cumulative impacts of changing climate and human influences. While the first large regression of broadleaved nemoral tree species was associated with the cooling climate (5150 – 3800 cal. yr BP), the subsequent land use intensification (around 3800 – 2000 cal. yr BP) had parallel influences on the distribution of different tree species. Pedunculate oak (*Quercus robur* L.) benefitted from human made semi-open landscapes, in contrast with other nemoral deciduous tree species, which were more sensitive to climate change and especially to increasing competition with Norway spruce (*Picea abies* L.) (Diekmann 1994, Reitalu et al. 2013). As a result of fire cultivation and increasing forest felling around settlements, silver birch (*Betula pendula* Roth.*)*, grey alder (*Alnus incana* L.) and mixed spruce forests became widespread (Jääts et al. 2010, Laasimer 1965).

The latest decline of all nemoral tree species started with the preference for conifer timber in modern forestry during the eighteenth and nineteenth centuries, and culminated with the abandonment of semi-natural woodlands during the twentieth century (Etverk 2003, Etverk and Meikar 2008, Palo et al. 2013, Sammul et al. 2008). Until the middle of the twentieth century, some agricultural activities such as mowing and grazing around settlements were still common in forests on fertile soils. Nowadays there is little grazing in forests (Kull et al. 2003, Palo et al. 2008, Sammul et al. 2008). For a long time, selective cutting was widespread in private forests. In some areas (also in state forests) clear-cuts started occurring and overcutting was especially evident during the 1930-s. During the soviet regime, the large parts of these formerly over-used forests were managed with low intensity or not at all, allowing aging and recovery of the stands' natural structure (Etverk 2003). Therefore, by the 2000s, their structural quality was high enough to be considered as valuable and in need of protection. Currently, logging in strictly protected areas is prohibited in Estonia since the protection of forests in their natural state (including natural disturbances) is the primary objective of Estonian forest conservation (Lõhmus et al. 2004, Nature Conservation Act). Next to maintenance for protected species habitats, only aging and natural disturbances are considered as factors that are allowed to influence the development and successional dynamics of the stands (Lõhmus and Kraut 2010, Šorohova et al. 2009).

Current boreo-nemoral stands in Estonia include Norway spruce and nemoral deciduous tree species such as pedunculate oak, small-leaved lime (*Tilia cordata* Mill.), Norway maple (*Acer platanoides* L.), common ash (*Fraxinus excelsior* L.), Scots elm (*Ulmus glabra* Huds.). In the understory, hazel (*Corylus avellana* L.) has a high cover. In early- or mid-succession phases, Scots pine (*Pinus sylvestris* L.), grey alder and black alder (*Alnus glutinosa* L.), silver birch and moor birch (*Betula pubescens* Ehrh.), and common aspen (*Populus tremula* L.) may occur (Diekmann 1994; Paal 1997). Corresponding Estonian boreo-nemoral forest site types in *sensu stricto* are *Antennaria dioica, Fragaria vesca, Corylus, Hepatica nobilis* and *Aegopodium podagraria* site types. In addition some stands from dry alvar forest *Calamagrostis arundinaceus* type and nutrient rich paludified *Dryopteris spp., Filipendula ulmaria* and *Molinia caerulea* forest site types may occur (Paal 1997, 2002, 2004). According to the Nordic vegetation type list, these forests belong to *Ulmus glabra* type, *Fraxinus excelsior* type, *Tilia cordata* type, *Quercus robur-Ulmus glabra-Tilia cordata*-type, *Picea abies-Oxalis acetosella-Melica nutans* type, *Picea abies-Dryopteris spp.* type, *Picea abies-Geranium sylvaticum-Aconitum lycoctonum* type, *Pinus sylvestris-Fragaria vesca* variant and *Pinus sylvestris-Lathyrus spp.-Rubus saxatilis* type (Påhlsson 1994, following Paal 2004).

In our previous paper (Palo and Gimbutas 2013) we demonstrated that according to dominance and frequency of tree species in different forest strata, large changes are to be expected in the canopy composition of the habitat types in the next generation. This would also mean some alterations in their proportional coverage in Estonia, which then needs to be explained in terms of the Habitats Directive Boreal region level (European Commission 2006). We offered the hypothesis, that the land use practices and intensity in the nineteenth and twentieth centuries have widely influenced the current stands' tree composition (Palo and Gimbutas 2014 a, b). Therefore, the current monitoring results of protected forest habitats are describing the ongoing succession (including natural disturbances), which means the results must be interpreted from their ecological point of view.

The aim of the current research is: 1. To specify the soil and management factors affecting stand development on fertile soils in habitat types *9010, *9020, 9050, and 9060; 2. To predict the most important changes of stands' tree composition in the near future, if natural succession prevails; 3. To discuss the present habitat mapping and conservation policy in the light of predicted changes.

Material and Methods

Identifying of habitats

The most typical Estonian lowlands boreo-nemoral mixed forests on non-alluvial fertile soils Lõhmus 1984; Paal 1997, 2002, 2004) belong to forest habitat types herb-rich spruce forest (9050) or Broadleaved forest (*9020), in terms of European Habitat Directive (92/43/EEC). Patches of Western taiga (*9010) and fire-influenced species-rich Esker forests (9060) may also exist on these soils.

The habitat types were identified in the field according to characteristic species composition (trees, shrubs, herb and moss layer) and qualifiers (Paal 2002, 2004, Palo 2010). In addition to the forest site type criteria, the 'habitat type' refers to dominant tree species in the canopy and understory: Herb-rich spruce forest (9050) must be a spruce-dominated (mixed) stand; Broadleaved forest (*9020) tree composition contains >50% of species such as lime, ash, oak, maple or elm; Esker forests (9060) are defined as pine or mixed coniferous forests with xeric and/or calciphilous herbs, typically these forests are present on positive relief forms; Western taiga (*9010) is uncommon on fertile soils but possible if the above mentioned sites types are dominated by *Betula* sp., *Populus tremula* or *Pinus sylvestris*. In Estonia, the Habitat Directive Annex I forest habitats are mapped and monitored at a scale of 1:10 000, which means a very high resolution in stands' tree composition estimates. All habitats need to contain enough old-growth stand structural features; normally managed commercial forests are not presented (Palo 2010).

Data sampling and statistical analysis

The field data was collected from throughout Estonia during the Habitat Directive Annex I forest habitat type monitoring program (2010-2012 and 2014-2015; 204 plots). Whole sampling was completed according to Liira (2009) based on habitats' actual area in so called Annex I habitat types' database managed by Estonian Ministry of the Environment. The center coordinates for sample plots with radius of 20 m were randomly generated. The plots' forest structure was described in detail in the field. From the long list of monitored parameters, factors relevant for this study were selected

The soil type and past land use type of plots were manually identified from the maps of the Estonian Land Board Web Map Server using public WMS-service (MapInfo 11.5). On the basis of 1:42 000 scale topographical map from the beginning of the twentieth century two parameters were recorded: 1. Main land use type in the radius of 100 m around monitoring plot center point (wooded meadows/pastures, continuous forest, open meadow/crop); 2. Main land use type in the radius of 300 m around the monitoring plot center point (continuous forest, mixed land use). The soil types (Table 1) of the monitored plots were taken from 1:20 000 scale soil type map. Some soil subtypes were merged and there are many reasons, why these soil data must be treated and interpreted on a generalized scale (Kõlli and Kanal 2010, Reintam et al. 2005). There was no field sampling of soil in the plot except for estimation of the depth of organic horizon.

The distribution of soil types among forest types, characteristic of dry or mesic fertile forests, was revised as a first step. Plots growing on Endogleyi-Calcaric Cambisols were removed from the data, since only Broadleaved forest type (*9020) occurred on these, 70% of which are former wooded meadows, as described by Palo et al. (2013) (compare also with the data from Table 2). Esker forest (9060) was absent form Gleysols/Gleyic soils and in addition the type Herb-rich spruce forest (9050) was never found on Calcari-Skeletic Cambisols.

Data analysis was performed in R (R Core Team 2015) and STATISTICA. The influence of soil type and past land use type on contemporary forest habitat type was analyzed by multiple multinomial logistic regression. The results are supported by frequency tables (Tables 1, 2 and 3). The influence of soil type and past land use on various forest stand parameters was analyzed with one-way ANOVA (Table 4).

Results

Relationships between main factors

The Western taiga (*9010) stands grow mainly on Calcari-Skeletic Cambisols and Arenosols (comparing frequency with other habitat types $p < 0.05$, Table 1). The latter is also common on Esker forest (9060) plots. The other common soil type under Esker forests was Mollic Cambisols, where also many Broadleaved forests (*9020) grow. Broadleaved forests prefer Gleyic Cambisols ($p < 0.05$) and also Endogleyi-Calcaric Cambisols, as was mentioned before. Herb-rich spruce forests (9050) existed on a wide range of soils. However, on Calcari-Skeletic Cambisols and

Table 1. Distribution (%) of forest habitats on fertile soils. Theoretically typical combinations (Paal 1997, 2002) are in ***italic-bold***. Soil type abbreviations according Estonian soil map and classification: Kr – Calcari-Skeletic Regosols or Cambisols (Pebble-rich rendzinas); $L_{(k)}I$ – Podzol (Arenosols; Sod-podzolic soils); Lp – Stagnic Luvisols (Pseudopodzolic soils); K – Calcaric Cambisols (Pebble rendzinas); Ko – Mollic Cambisols (Leached or typical brown soils); KI –Luvisols (Eluviated brown soils); G – (Gleysols *s.l.,* combined Mollic, Dystric, Histic Gleysols); Kog – Gleyic Cambisols (Gleyed typical brown soils); KIg – Gleyic Luvisols (Gleyed eluvial soils) (soil names by Kõlli and Kanal 2010; Kõlli et al. 2004, World Reference Base for Soil Resources (WRB))

	Type	Kr	$L_{(k)}I$	Lp	K	Ko	KI	G	Kog	KIg	%	Count
Habitat types distribution on soils (%)	*9010	57.2	45.2	33.4	9.5	13.9	5.9	11.1	9.1	21.4		
	*9020	19.0	3.2	20.8	23.8	27.8	17.6	33.3	50.0	14.3		
	9050	0.0	9.7	25.0	33.4	22.2	35.3	55.6	40.9	64.3		
	9060	23.8	41.9	20.8	33.3	36.1	41.2	0.0	0.0	0.0		
		Kr	$L_{(k)}I$	Lp	K	Ko	KI	G	Kog	KIg		
Soil distribution within habitat types (%)	*9010	***24.5***	***28.6***	***16.3***	4.1	10.2	2.0	4.1	4.1	6.1		
	*9020	8.5	2.1	***10.6***	***10.6***	21.3	6.4	***12.8***	***23.4***	***4.3***		
	9050	0.0	5.2	***10.3***	***12.2***	***13.8***	***10.3***	***17.2***	***15.5***	***15.5***		
	9060	10.0	26.0	10.0	***14.0***	***26.0***	***14.0***	0.0	0.0	0.0		
		Kr	$L_{(k)}I$	Lp	K	Ko	KI	G	Kog	KIg	%	Count
Total (%)	*9010	5.9	6.9	3.9	1.0	2.5	0.5	1.0	1.0	1.5	23.0	47
	*9020	2.0	0.5	2.5	2.5	4.9	1.5	2.9	5.4	1.0	24.0	49
	9050	0.0	1.5	2.9	3.4	3.9	2.9	4.9	4.4	4.4	24.5	50
	9060	2.5	6.4	2.5	3.4	6.4	3.4	0.0	0.0	0.0	28.4	58
	%	10.3	15.2	11.8	10.3	17.6	8.3	8.8	10.8	6.9	100.0	
	Count	21	31	24	21	36	17	18	22	14		204

Endogleyi-Calcaric Cambisols spruce rarely dominates in canopy but usually appears in the understory and regrowth.

Looking at the distribution of today's forest habitat types on past land use units (Table 2), the former wooded meadows and pastures are now, in half of the cases, covered by Broadleaved forests (*9020, different from other habitat types, $p < 0.05$). Monitoring plots on past wooded meadows/pastures also showed more signs of management (75%; signs of management are mainly stumps, but also fences, traces of vehicles etc.) compared to forests on past meadows/crops (41%, $p < 0.05$). 73% of monitored areas that were meadows or crops about 100 years ago have nowadays developed into Herb-rich spruce forests or Esker forests.

Table 2. Distribution (%) of monitored forest habitats with different land use history

	Type	*9010	*9020	9050	9060
Habitat types distribution in land use types (%)	Wooded meadow/pasture (W)	10.2	36.2	10.3	8.0
	Forest (F)	83.7	57.4	75.9	76.0
	Open meadow/crop/pasture (M)	6.1	6.4	13.8	16
		***9010**	***9020**	**9050**	**9060**
Land use types distribution in habitat types (%)	Wooded meadow/pasture (W)	15.6	53.1	18.8	12.5
	Forest (F)	27.3	18.0	29.3	25.3
	Open meadow/crop/pasture (M)	13.6	13.6	36.4	36.4
		***9010**	***9020**	**9050**	**9060**
Total (%)	Wooded meadow/pasture (W)	2.5	8.3	2.9	2.0
	Forest (F)	20.1	13.2	21.6	18.6
	Open meadow/crop/pasture (M)	1.5	1.5	3.9	3.9

Past agriculturally used areas have existed on most soil types (Table 3). Only on Gleysols, no meadows were found in the beginning of the twentieth century, but it is probably not a rule: solitary trees and shrubs were common on most wet meadows. The symbols used for these kind of meadows on the topographical maps were the same for typical wet wooded meadows. Meadows and crops were quite evenly found on Stagnic and Gleyic Luvisols, Mollic and Calcari-Skeletic Cambisols. Wooded meadows were most common on Gleyic and Mollic Cambisols ($p < 0.05$). Historically continuous forests were found on every soil type. As for the most agriculturally used soils (Gleyic Cambisols and Luvisols), only about 54-57% of monitoring areas were regular forests about 100 years ago. Management signs were least often found on Gleysols (22.2%), on other soils the signs of management were found on 45.8% (Stagnic Luvisols) – 81% (Calcaric Cambisols) of the monitoring plots, (the difference between Gleysols and Calcaric Cambisols was statistically significant).

Influence of main factors on the forest stand parameters

The organic horizon in the forests was thickest on Gleysols (15.7cm) ($p < 0.05$), on other soils the mean thickness was 1.6-3.4 cm less. The depth clearly depends on land use type since all kinds of agricultural and forestry signs had statistically significant decreasing effect ($p < 0.05$, one-way ANOVA, Table 4 for now on).

Compared to other soil types, the number of tree species on Calcari-Skeletic Cambisols was among the lowest in all forest strata (canopy, sub canopy and regrowth). Similarly, the tree species number on Mollic Cambisols Gleyic Luvisols and Gleysols was among the highest in all forest strata. On the other hand, some soil types have relatively more species in one of these layers, but less species in other layers (f.e. Stagnic Luvisols and Calcaric Cambisols); some soils always have modest values (f.e. Gleyic Cambisols).

Canopy layer species number was higher for historical wooded meadows or pastures ($p < 0.05$). In forests with management signs, the canopy layer species number may be somewhat lower ($p < 0.08$). Significant relationships between signs of management or appearance of stumps and the forest regrowth layer species number indicate that natural forests have a higher number of species in the regrowth layer ($p < 0.05$).

The coverage of Scots pine in the canopy layer was dependent ($p < 0.05$) on soil type as well as on management. Pine prefers dry soils, which were avoided by spruce ($p < 0.09$). There was always a higher coverage of pine in

Table 3. Distribution (%) of past land use types on different soils. Soil abbreviations see in Table 1 and land use type abbreviations in Table 2

	Type	Kr	$L_{(k)}l$	Lp	K	Ko	Kl	G	Kog	Klg	%	Count
Soil type distribution in land use types (%)	**W**	4.8	9.7	8.3	19.0	22.2	5.9	11.1	40.9	14.3		
	F	76.2	87.1	70.8	76.2	66.7	82.4	88.9	54.5	57.1		
	M	19.0	3.2	20.8	4.8	11.1	11.8	0.0	4.5	28.6		
		Kr	**$L_{(k)}l$**	**Lp**	**K**	**Ko**	**Kl**	**G**	**Kog**	**Klg**		
Land use types distribution in soil types (%)	**W**	3.1	9.4	6.3	12.5	25.0	3.1	6.3	28.1	6.3		
	F	10.7	18.0	11.3	10.7	16.0	9.3	10.7	8.0	5.3		
	M	18.2	4.5	22.7	4.5	18.2	9.1	0.0	4.5	18.2		
		Kr	**$L_{(k)}l$**	**Lp**	**K**	**Ko**	**Kl**	**G**	**Kog**	**Klg**	**%**	**Count**
Total (%)	**W**	0.5	1.5	1.0	2.0	3.9	0.5	1.0	4.4	1.0	15.7	32
	F	7.8	13.2	8.3	7.8	11.8	6.9	7.8	5.9	3.9	73.5	150
	M	2.0	0.5	2.5	0.5	2.0	1.0	0.0	0.5	2.0	10.8	22

plots with historically continuous forests (as opposed to forests grown on former wooded meadows/pastures or meadows/crops) and management signs also increased the coverage of pine. Management signs ($p < 0.06$) and occurrence of stumps ($p < 0.08$) was also related to higher coverage of spruce, which may refer to its former high coverage, too.

Birch preferred mesic soils, with a higher coverage in forests without management signs ($p < 0.05$). Aspen also

Table 4. Influence of historical land use factors and soil type on forest stand parameters. Based on one-way ANOVA, levels of factors are grouped according to results of Duncan's multiple range tests. If *p*-value is not noted, it is less than 0.05. For continuous variables, minimal and maximal least squares means are reported in brackets

Parameter	Soil type	Land use type (abbr. in tabel B)	Land use type (abbr. in „Data sampling“)	Managed (M)-nonmanaged (N)	Stumps found (S)/not found (N)
Organic horizon (cm)	(1.6 cm) K,Kog,Klg,Lp,Ko,L$_{(k)}$l,Kl,Kr (3.4cm) <G (15.7cm)	(1.8cm) W(M)<F (4.3cm)	(3.0cm) MIX<F (5.5cm)	(3.2cm) M<N (4.7cm)	(3.2cm) S<N (4.7cm)
Canopy layer species number	(2.1 species) Kr[Lp,L$_{(k)}$l]<Kl,K,Ko,Klg<[G]Kog (3.1 species)	(2.6 species) M(F)<W (3.5 species)		*p < 0.08*; (3 species) M<N (3.3 species)	
Subcanopy layer species number	(1.9 species) Kr[K]<[Ko,Kl,Lp,Kog,L$_{(k)}$l]Klg,G (3.8 species)				
Regrowth layer species number	(2.3 species) Kr,K,Ko[L$_{(k)}$l,Kl]<[Lp,Klg,Kog]G (4.6 species)			(3.1 species) M<N (3.6 species)	(3 species) S<N (3.7 species)
Presence/density of subcanopy layer (0,1,2)	Kr,K,Kog,Ko,[Klg,Kl,G,L$_{(k)}$l]<Lp		MIX<F		
Presence/density of regrowth layer (0,1,2)	Ko[L$_{(k)}$l]<[Kog,K,Kl,Lp,Kr,Klg]<G				
Presence/density of shrub layer (0,1,2)	L$_{(k)}$l[Kog,G,Kr]<[Lp,Ko,Klg,Kl]K		F<MIX		
Coverage of *Pinus sylvestris*	(2%) Klg,G,Kog,K,Lp,Kl,Ko<L$_{(k)}$l,Kr (52%)	(6%) W(M)<F (24%)	(18%) MIX<F (29%)	(15%) N<M (25%)	
Coverage of *Picea abies*	*p<0.09*; (23%) Kr,L$_{(k)}$l[Kog,Lp,Ko,G,Klg,Kl]<K (50%)			*p < 0.06*; (29%) N<M (37%)	*p < 0.08*; (29%) N<S (37%)
Coverage of *Betula pendula*	(5%) Kr,Kl,L$_{(k)}$l,K,Ko,Kog[G]<[Klg]Lp (34%)			(13%) M<N (21%)	(14%) S<N (21%)
Coverage of *Populus tremula*				*p < 0.07*; (8%) M<N (14%)	(8%) S<N (14%)
Coverage of *Quercus robur*	(3%) G,L$_{(k)}$l,K,Klg,Lp,Kl,Kr[Ko]<Kog (26%)	(3%) M,F<W (28%)	(4%) F<MIX (12%)		
Presence of large semi-open woodland-trees	Klg[Lp,G,K,Kl]<[L$_{(k)}$l,Ko,Kog]<Kr	M,F<W	F<MIX		
Standing recently dead trees	Klg,Ko,Kl,L$_{(k)}$l,K,Lp[Kog,Kr]<G			M<N	S<N
Snags	Kl[Kr,Ko,Klg,Kog,L$_{(k)}$l][Lp,K]<G			M<N	S<N
Deadwood from first decay classes with d=10-25cm	Kl[Kr,Ko,Kog,L$_{(k)}$l,Klg][K,Lp]<G			M<N	S<N
Deadwood from latest decay classes with d=10-25cm	Kr[L$_{(k)}$l,Kl][Kog,Ko,Klg,K,Lp]<G			M<N	S<N
Deadwood from first decay classes with d>25cm	Kog,Kr[Kl,L$_{(k)}$l,Ko,K,Klg]<Lp,G			M<N	S<N
Deadwood from latest decay classes with d>25cm	Kr[Kog,L$_{(k)}$l,Ko,Kl,Lp,Klg,K]<G			M<N	S<N
Diameter of greatest lying deadwood stump	(28 cm) Kr[L$_{(k)}$l,Kog,Ko,Kl,K,Klg,G]<Lp (45 cm)			M<N	S<N
Mean diameter of 3 greatest living trees	(41 cm) Kr[K,G,Kog,Klg,Kl,Ko,Lp]<L$_{(k)}$l (52 cm)				

showed a tendency for higher coverage in unmanaged forests ($p < 0.07$). The cover of oak was linked to a higher historical wooded meadows/pastures percentage ($p < 0.05$) and this relationship was in concordance with the soils since the Gleyic and Mollic Cambisols had the highest percentage of historical wooded meadows/pastures ($p < 0.05$, Table 3). The coverage of shadow tolerant nemoral broadleaves (elm, ash, maple, and lime) had no significant relationship with the studied factors.

The presence of large semi-open woodland trees was connected with the dryer soil types, historically covered with wooded meadows/pastures ($p < 0.05$) because the tree species, which have a large canopy in lighter conditions are mainly pine and oak, which are widespread on these soils.

All deadwood parameters also reflect the soil properties and have quite similar trends as tree species numbers on different layers. At the same time, the presence of deadwood was highly dependent on management signs and stumps found in stands. In natural stage forests, deadwood appeared significantly more frequently.

The soil type order by average diameter of three largest living trees probably reflects some mixture of all studied factors, as it may depend on tree species, tree age, soil properties as well as management type and intensity. Also, the breast diameter of the largest living tree were analyzed, but did not have significant relationships with land use and soil type.

Discussion

Most habitat types were found on soils, where the respective forest site types (Kõlli and Kanal 2010, Paal 1997, 2002, 2004) were expected to occur. There are some exceptions, which we will discuss in depth.

Inspection of the raw data reveals that the presence of Western taiga plots on Mollic Cambisols (10.2%, Table 1) is explained by higher coverage of successional tree species (birch and aspen) in these stands. Alternatively these stands are spruce forests with species poor regrowth and shrub layer. Therefore these forests do not fit the definition of Herb-rich spruce forests or Esker forests which typically occur on this soil type (Paal 2004, Palo 2010). It was not possible to identify the main driving factor for the changes in composition, but it can be related to the historical land use and management intensity. Most of these plots showed signs of management or they were located on past private ownership land with mixed land use, where selective felling and grazing in forests was common a century ago.

Also, an exceptionally high percentage of Broadleaved forests was present on Mollic Cambisols (21.3% of total *9020, Table 1); which is clearly related with the historical land use, since 22.2% of monitoring plots on these soils incurred on past wooded meadows/pastures (Table 3) and altogether from earlier wooded meadows/pastures 25% (Table 3, $p < 0.05$) was located on Mollic Cambisols. The semi-natural origin of these forests could refer to possible changes in the future because of changes in land use practice (Kull et al. 2003, Palo and Gimbutas 2014a,b, Palo et al. 2008, Sammul et al. 2008). Since typical Herb-rich spruce-forests and Esker forests were also common on Mollic Cambisols, the question to be posed is: will the forests on past semi-natural plots develop into coniferous stands in the future? Contrary to this, several researchers hold the opinion that coniferous forests on mesic fertile soils are secondarily impoverished and that the natural forest could consist of nemoral deciduous species with different proportions of spruce in time and space (Jääts et al. 2010, Laasimer 1965, Reintam 1995, Reitalu et al. 2013). This subject is discussed thoroughly by Lõhmus and Kraut (2010). Also, the results in Table 4 show that pine and spruce cover is higher in stands with management signs as opposed to birch and aspen cover. Based on a comparison with the raw monitoring data, we support the idea that the unmanaged pine-forests (Esker-forests 9060) on this soil will develop into spruce forests (9050) and all current Herb-rich spruce forests will be replaced with spruce-broadleaved tree mixtures in time (with about 200 years or two new spruce generations). If hazel shrub rich stands are included to natural forest types as well, then it will probably take only 50-100 years to develop such mixed or broadleaved forests.

By raw monitoring data we noticed the tendency, that *9020 on the Mollic Cambisols, which have been forests all the time, do not change very much: maple, elm and spruce stay as common species but there will probably be more lime and ash and all other currently growing tree species may also occur with a lower percentage. Broadleaved stands with management signs and which have grown on earlier wooded meadows are species-poorer and there are more pioneer tree species, but their subcanopy and regrowth layer contained more nemoral broadleaved tree species than their canopy layer. Therefore broadleaved trees percentage will probably increase in future (generally presented in Table 4 – earlier wooded meadows' canopy layer was species-richer as in continuous forests, but the clear management signs had a decreasing effect on the species number).

The pines from Esker forests growing on Mollic Cambisols will totally disappear in next generations and these stands are expected to develop into mixed broadleaved forests, since the subcanopy and regrowth layer are very species-rich and contained many nemoral broadleaved tree species. We find 9060 type forests on Mollic Cambisols today probably only because of earlier land use methods, management intensity and disturbance (pasturing, fire, cutting) effects, which have changed the soil properties in upper horizon and thus supported the high coverage of pines (Paal et al. 2004a, b, Bizzari et al. 2015). Nowadays spruce-forests (9050) on Mollic Cambisols are probably more resistant to changes in the canopy layer; however the spruce will have lower coverage in the future. This trend in raw data was probably supported due to higher percentage of spruce on managed areas (Table 4). The possible changes in forests growing on Mollic Cambisols confirm our general results in Palo and Gimbutas (2013), where stands' composition of the monitoring plots were analyzed without considering the past land use effects. There we also found that in type *9020, oak, birch and aspen frequency will decrease in the future and there will be an increase in the frequency spruce and nemoral broadleaves in the next generations. The type 9060 will lose pine and the canopy composition will change in the direction of current 9050; however, the current 9050 tree composition in the next generation will have much more similarities with current old-growth *9020 type canopy layer.

Another atypical soil seems to be Podzols in Esker forests (9060) (Lõhmus 2004, Paal 2002, 2004). The later studies within these soil type areas have described special Arenosols - sandy soils without diagnostic horizons, which are particularly typical for South-Estonian Esker forests (Paal et al. 2004a, b, 2011). According to sediments' geographical location and origin (in Estonia mostly glacio-fluvial or coastal sediments; the base rock consists of limestone and sandstone) the sand may have different calcareous/clay content. In Estonia, the habitat type Esker forest (9060) was defined as coniferous species-rich esker, drumlin or hillock forest (Paal 2002, Paal et al. 2004a, b, species-poor coniferous forests on sandy soils are, for example, dune forests from type 2180), since very few of these landforms consist of nutrient-poor sand and silicate boulders, in contrast to Finland (Heikkinen 1991, Karukäpp 2005). Esker forests in Latvia and Sweden are quite similar to the Estonian descriptions (Laiviņš 2014, Åsbarrskog 2012). We inspected the raw data to see if present or future differences are to be expected in 9060 forest type tree composition growing on Mollic Cambisols or Arenosols. The current canopy layer had similar tree species frequencies and coverages on both soil types, however in following generations the succession on both soils may differ. Pine will not disappear on Arenosols and the frequency of oak will also be much higher than on Mollic Cambisols. Spruce will remain as the dominant species, but birch and aspen will become more common, as well as maple, lime and elm. Hazel is common on both soils, but in addition, on Arenosols, juniper (*Juniperus communis* L.) and rowan (*Sorbus aucuparia* L.) may appear more frequently and with a higher cover. The results of this comparison agree well with earlier results from South-Estonia (Paal et al. 2011), since these authors did not find major differences between tree composition in Esker forests that had been used differently historically. If looking at the places, where Esker forests on Arenosols were monitored, then all of them were located on South-Estonian hillocks or on the island Saaremaa (Ancylus Lake seashore terrace on Viidumäe Reserve). Comparable forest communities are also described in a neighboring country, Latvia (Ikaniece et al. 2012, Laiviņš 2014). The majority of Esker forests growing on Mollic Cambisols were located in North-Estonian Pandivere Upland and only very few examples were present in South-Estonia, most of which had developed on past meadows or wooded pastures.

A large part of Arenosols are currently covered with Western taiga stands (*9010). How will these stands change in the future, compared to Esker forests on the same soil? Most of these forests are located on continuously forested land and despite the management signs, the comparison of different tree layers indicated the likely future disappearance of pine, a slight rise in spruce frequency, relative stability of birch and aspen, but also a great increase in broadleaved tree species frequency, especially oak. There was also hazel present in about 70% of the plots. The current pine-dominated or pine-spruce Western taiga forests will, without any management or burning, develop into spruce-deciduous mixed forests with a much species-richer canopy and sub-canopy layers containing oak, lime, elm, both alders, maple, together with shrubs such as hazel and rowan. The growth of broadleaved saplings depends on many factors and interactions between the structural layers of the different forests. Light availability will be an important factor, especially for oak (Brumelis et al. 2011, Götmark et al. 2005, Ikauniece et al. 2012, Liira et al. 2011, Sims et al. 2014). Many saplings, present in regeneration layer, are unlikely to ever reach higher layers, but their presence in forests still retains that potential.

Another interesting forest succession path will be the Herb-rich spruce forests (9050) development on fertile gleyic soils. As mentioned before, on Endogleyi-Calcaric Cambisols soils they were absent but on Gleysols and Gleyic Cambisols or Luvisols such forests are dominant in conjunction with Broadleaved forests (*9020). If on Endogleyi-Calcaric Cambisols, the main reason for low cover of spruce was past land use (there are many broadleaved forests from earlier wooded meadows), then low spruce cover in the canopy layer may be also be a result of fungal disease, especially on human-influenced fertile soils. Root rot, especially *Heterobasidion* spp., is a problem in forests managed today with maintenance logging, as well as in stands growing on afforested historical agricultural land (Hanso and Hanso 1999a,b, Piri and Korhonen 2008). Gleysol forests are mostly historically continuous forests; in contrast to Gleyic Cambisols or Luvisols, which have a high percentage of former wooded meadows, meadows and crops (Table 3). 30% of the spruce forests were also located on past agricultural land (within radius of 100 m from monitoring plot) and about 70% were on areas with mixed land use (within radius of 300 m from monitoring plot). The type 9050 on Gleysols have species-richest canopy layer (Table 4: all these 3 soils have the highest tree species richness). There was no difference in the frequency of pine, spruce, birch and aspen, but on Gleysols, both alder species and other nemoral broadleaved tree species were more frequently found. These differences will probably also persist in the following generations. However, spruce will always appear on about 50% of the areas where birch and/or aspen are now found. Also both alder species, ash, lime and oak will be frequent in such stands. The old-growth forests on Gleysols will probably become mixed deciduous-spruce forests. Comparing the Gleyic Cambisols with Gleyic Luvisols, the last one will probably become a little bit species-richer and have more frequent shade-preferring broadleaved species such as lime, maple and elm. At the same time, forests on Gleyic Cambisols will have more ash, grey alder and other woody species, mostly occurring in lower layers (rowan, bird cherry (*Prunus padus* L.) etc.). In spruce forests growing on earlier agricultural land, grey alder and some tall willows (*Salix* sp.) or rowan are especially common. Therefore these spruce forests may develop into broadleaved forests in the future. On the other hand, the majority of monitored *9020 forests on Gleyic Cambisols were located on former agricultural land and their subcanopy as well as regrowth contained dominantly spruce. Therefore *9020 on Gleyic Cambisols and Luvisols will very likely have higher spruce cover in future. In contrast, in current 9050 forests on these soils, spruce will have a somewhat lower cover: pine will totally disappear from these unmanaged forests and there will be many more deciduous species present with higher cover.

In the future, we will see stands with very different and diverse tree composition instead of the current clearly distinguishable structural layers with dominant tree species in the upper canopy. Main reasons are the competition for light between different tree species and the local environmental conditions, as well as other stand level natural disturbances (Brumelis et al. 2011, Götmark et al. 2005, Ikauniece et al. 2012, Liira et al. 2011, Lõhmus and Kraut 2010, Sims et al. 2014). In the light of successional changes, there is no need for maintenance thinning to preserve the current composition of habitat patches. Rather it will be more effective to connect these areas with each other, in a similar way to the boreal forests growing on soils with lower fertility (Lõhmus et al. 2004, Šorohova et al. 2009). Considering the habitat preferences of species, the continual availability of different substrates and microhabitats must be ensured through maintaining a sufficient patch size of forests that have developed naturally. The exact composition of the tree layers will be mostly temporary and will vary from patches containing only spruce to those dominated only by broadleaves.

Conclusions

Our study results confirmed that current Habitat Directive Annex I forest types related to the mesic fertile soils are in Estonia mostly highly human-influenced. Broadleaved forests (*9020) are very common on areas that have been wooded meadows or pastures a century ago. Depending on the soil type, they remain broadleaved communities (the composition of tree species may change) or there will change to mixed forests with varying coverage of spruces in the next generations. In contrary, the current Herb rich spruce forests (9050) will develop into much more diverse stands, containing many broadleaved species in their canopy and especially in the subcanopy layer. Instead of Herb-rich spruce forests now growing on Gleysols, Gleyic Cambisols or Luvisols, typical broadleaved old-growth forests belonging to the type *9020 according to tree species coverage criteria may occur. The spruce is highly favoured on areas with management signs, the trend is confirmed with the response of deadwood parameters. The Esker forests (9060) will have a different successional path on Arenosols and Mollic Cambisols.

We suggest to consider the protection of habitat types on fertile soils (*9020, 9050, 9060) together, since in natural conditions they will form a continuum of stands with temporarily prevailing tree species. To ensure the availability of habitat conditions and substrates for all species found in these habitat types, the naturally developing areas must be large enough to hold different patches in the entire forest landscape.

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