

**RELATIONSHIPS BETWEEN LANDSCAPE
FACTORS AND VEGETATION SITE TYPES:
CASE STUDY FROM SAARE COUNTY,
ESTONIA**

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ORIGINAL PUBLICATIONS

This thesis is based partly on unpublished data (by Anneli Palo, Jaak Truu, Kalle Remm, Arno Kanal, Raivo Aunap and Ülo Mander) and fully (I, II, III) on the following papers, which are included at the end of the thesis.

- I **Palo, A.** and Kikas, T. 2003. Methodological problems of compiling digital vegetation site types maps: case of Saare county, Estonia. *Journal for Nature Conservation* 11: 135–144.
- II **Palo, A.**, Remm, K., Kikas, T. and Mander, Ü. 2004. The prediction of vegetation pattern using biophysical landscape factors. In: Martin-Duque, J.F., Brebbia, C.A., Godfrey, A.E. and Diaz de Teran, J.R. (Eds.) *Geo-Environment. Monitoring, Simulation and Remediation of the Geological Environment*. WIT Press, Southampton, Boston: 315–334.
- III **Palo, A.**, Aunap, R. and Mander, Ü. 2005. Predictive vegetation mapping based on soil and topographical data: A case study from Saare County, Estonia. *Journal for Nature Conservation* 13: 197–211.

AUTHOR'S CONTRIBUTION

Publications I–III: The author is responsible for the collection and preparation for analysis of all field data (also unpublished data), for the interpretation of analyzed data, and for 70–90% of writing the manuscripts.

ABSTRACT

Palo, A. 2005. Relationships between landscape factors and vegetation site types: Case study from Saare County, Estonia.

The main objectives of this thesis are: (1) to find out the main relationships between vegetation pattern (vegetation site types — VSTs) and biophysical landscape factors; (2) to analyze how the relevant anthropogenic factors influencing the variability of vegetation site types in the study area; (3) to prepare a digital vegetation site type map (data layer) for the Saare County.

16 key areas for vegetation analysis and mapping were selected in the first work phases in 1999. Only the vegetation site types (without plot descriptions; according to Paal 1997) were determined. The determined VSTs were extrapolated to polygons defined with the help of CIR aerial photos. In 2004 and 2005 the understorey vegetation in each field plot was described according to the Braun-Blanquet method. Tree stands were divided into three classes: coniferous forest, mixed coniferous-deciduous forest, and deciduous forest. In addition, based on the author's earlier works and experience, the continuity of the natural forest was assessed. For data analysis several methods (e.g., method of random (toroidal) shifting, Canonical Correspondence Analysis) and computer software (e.g., CANOCO 4.52, Idrisi, MapInfo) were used.

We found out, that both abiotic factors and human activities play an equally important role on the diversity of Saare County's vegetation cover. For instance, dominating tree species, traditional agriculture, creating semi-natural communities such as wooded meadows, alvar meadows (pastures) and grazed forests, and forestry (especially, afforestation of abandoned agricultural lands) can be highlighted as significant factors. Among the biophysical landscape factors and absolute elevation, which correlates with the successional age of communities and geomorphological factors (accumulation and abrasion of sediments and deposits) and geographical location, (integrating all the local factors) should be mentioned. According to the paradigm of distinguishing plant communities in continuous plant cover, location and spectrum of VSTs in toposequent gradient, slope angle, aspect and other topoedaphic characteristics should be taken into account when analysing the vegetation cover. We found a remarkable variability of some VSTs, related to floristic diversity and general habit of forest stands. Sometimes, this variability exceeded the limits stated by some soil-based theoretical assumptions.

The created map of VSTs can be used as source material for more general planning decisions. The present vegetation site type classification does not reflect sufficiently plant communities important for practical nature conservation and biodiversity planning in the Saare County. For practical use, mixed typology consisting of VSTs and VST groups and some additional landscape and biotope indicators, is recommended.

INTRODUCTION

The predictability of the spatial pattern of vegetation is one of the primary problems in ecology (Odum 1959; Moore et al. 1991; Goodchild 1994; Franklin 1995; Dale 1999). Several studies consider the predictability of vegetation cover pattern based on topographical data (Davis and Goetz 1990; Bolstad et al. 1998; Brown et al. 1998; Burrough et al. 2001; Hoersch et al. 2002; Pfeffer et al. 2003), soil conditions (Bolstad et al. 1998; Shoshany 2002) and (micro) climatic conditions (Burrough et al. 2001; Dymond and Johnson 2002). Fuzzy systems theory (Roberts 1996; Burrough et al. 2001; Hall and Arnberg 2002), patch-based spatial modelling (Wu and Levin 1997), and artificial neural networks (Hilbert and Ostendorf 2001) have been used as novel methods for modelling the distribution of vegetation. However, only a limited number of studies consider the overlay analysis of landscape factors and vegetation site types (VSTs) on a detailed scale (Tappeiner et al. 1998; Hoersch et al. 2002).

In Estonia the paradigm traditionally used for vegetation mapping and classification defines vegetation site types as vegetation units with similar layer structure and plant community composition that have developed in similar abiotic conditions (Paal 1997), which leads to a working hypothesis, that it is possible to predict the occurrence of vegetation site types in a region on the basis of selected abiotic factors.

The most essential factor for vegetation is soil cover, the parameter expressing the development potential of plant communities (Lõhmus 1984; Paal 1997; Kõlli and Ellermae 2001), which already combines indicators of both general soil fertility and soil moisture. Next to natural disturbances (Angelstam and Kuuluvainen 2004; Lõhmus et al. 2004), the most important cause of variation in forests today is human activity, which may in places exceed the impact of abiotic conditions. Aspects arising from the general patterns of the relief, historical vegetation development and also from traditional agricultural activities may also have an important role (Skånes 1996; Ratas et al. 1997a; Koerner et al. 1997; Aude and Lawesson 1998; Ilomets 1999; Punning and Jõgi 1999; Verheyen et al. 1999; 2003a, 2003b; Dupouey et al. 2002; Teras 2002; Saarse et al. 2002; Zechmeister et al. 2003; Wulf 2003; Paal et al. 2004a, 2004b; Alard et al. 2005; Remm 2005; Schmitzberger et al. 2005).

In nature protection and planning the habitat or biotope level is very important. In moderately varying vegetation site types analogous structures determining the habitat preferences of species have developed due to certain factors and independently of abiotic factors (Vellak and Paal 1999; Andersson et al. 1999, 2003; Lõhmus 2003; Angelstam et al. 2003; Zechmeister et al. 2003; Lõhmus et al. 2004; Kilpeläinen et al. 2005; Leito et al. 2005; Schmitzberger et al. 2005).

In 1999, the creation of a digital vegetation map was included among the priorities of the West Estonian Archipelago Biosphere Reserve's Saaremaa

Center. Using existing digital maps and data layers and theoretical knowledge of the relations between vegetation and environmental and landscape factors, the possibility of creating a large-scale vegetation map (data layer) corresponding to the vegetation site type classification (Paal 1997), developed on the basis of earlier vegetation systematization and mapping experience, began to be researched. In nature conservation and planning practice, various existing data about vegetation — databases, maps, aerial photos, and literature — can be used in GIS-based applications. For economic reasons, there is a tendency to continuously decrease the share of fieldwork and simulate the monitoring. The abrupt change in socio-political conditions and rapidly advancing IT perspectives enabled aerial photos and formerly confidential maps to be used, and the increasing additional digital data to be synthesized and verified.

The vegetation of key areas mapped in the course of fieldwork was extrapolated using CIR (color infrared) aerial photos and the digital data layer of landscape meso-scale units (Palo 1999b; Palo and Kikas 2001, 2003). In neighboring countries, selective or overlay mapping based on aerial photos, for conservation purposes, has for years been carried out in several areas (Bierhals 1988; Lippert 1995; Skånes 1996; Kotiluoto & Toivonen 1997; Cousins and Ihse 1998). In Estonia, this was restricted by the confidential status of aerial photos, but the method was known and its potential was acknowledged briefly in several publications of that time (Laasimer 1965; Kalda 1991).

A soil-type data layer digitized on the basis of a large-scale soil map (Estonian Land Board 2001) and a relief model were employed; this enabled relations between vegetation units mapped independently of soils and soil types and selected relief parameters to be analyzed (Palo et al. 2004, 2005). Considering the lower than average forestation and high diversity of secondary agricultural forest use in Saare county during the last centuries, compared Estonia as whole (Eichvald 1934; Mathiesen 1934, Kukk and Kull 1997; Meikar 1997, 2002a, 2002b; Mander and Palang 1999; Sooväli 2004), the study focuses on the variability of forests (including treed semi-natural communities).

Main objectives of this thesis are:

- To discover main relationships between vegetation site types and biophysical landscape factors;
- To analyze anthropogenic factors in the variability of forest site types of the study area;
- To prepare a digital vegetation site type map (data layer) for Saare County.

1. VEGETATION COVER: SUCCESSION, TYPOLOGY AND MAPPING

1.1. Main factors of vegetation cover succession and landscape development in Estonia

Climate change has been the main natural factor influencing landscape and vegetation development in the Baltic Sea area during the last 15000 years. Melting of the giant glaciers of last glaciation period and the formation of large flooded areas in the late Pleistocene, and the following development of terrestrial marine ecosystems intersected with several transgressions of the Baltic Sea during the Holocene, determined the pattern of relief, vegetation and soil cover, and the whole landscape formation. A large variety of glacial, glacio-limnic, glacio-fluvial, aeolian, marine, lacustrine and palustrine deposits of various thickness cover the Palaeozoic bedrock. The latter is divided between the Ordovician/Silurian limestone and calcareous rock formations in the northern part and the Devonian sandstone bedrock formations in the southern part of the country. The quality of both the soft Quaternary sediments and the Palaeozoic bedrock determine the soil and vegetation cover pattern and hydrological features of landscapes in Estonia. As an additional natural factor, the post-glacial uplift of the earth crust, being up to 3 mm yr⁻¹ on the northwestern coast and 0 to -1 mm yr⁻¹ in the south and southeast, influences landscape development, especially in the coastal areas (Raukas, 1995).

According to Varep (1964), the upper limit of local glacial lakes in late Pleistocene divides Estonia into two parts, Lower and Upper Estonia. Lower Estonia, which has once been the bottom of the sea or some local glacial lakes, is a low plain with large bogs and forests. Upper Estonia, on the contrary, has not been overflowed by the melting water of glaciers and the large scale landscape pattern is therefore much more mosaic, with different kinds of glacial, glaciofluvial, and glaciolimnic landforms, such as drumlins, eskers, kames, etc., prevailing. Ice cover left Upper Estonia approximately 12000 years BP, while the landscape development in Lower Estonia could begin only some 7000–9000 years BP. In Holocene, the change of climatic conditions has been relatively fast. It culminated with climatic optimum during the Atlantic climate period (8000–5000 years BP) when a large-scale invasion of deciduous tree species and fast development of soil cover can be observed (Raukas 1995). Present sub-atlantic climate conditions are cooler than during the Atlantic optimum. Respectively, Estonian plant communities are classified as a part of the boreo-nemoral (hemi-boreal) zone dominated by mixed forests.

Today's climate is moderately maritime, however, there are significant differences between the more continental eastern part and more maritime western Estonia: differences between the maximum air temperatures in summer and minimum air temperatures in winter on the western coast and islands are

significantly smaller than those in the eastern part of the country. Also, the coastal areas and West-Estonian islands are significantly more windy and receive less precipitation than the areas in the continental part (Raukas 1995; Ratas et al. 1997a; Ilomets 1999; Teras 2002; Saarse et al. 2002; Arold 2005). Due to the global climate change, a significant shortening of the snow period and a thinning of snow cover can be observed overall in Estonia, being more remarkable in the western part of Estonia and islands (Jaagus 1997).

Among biophysical landscape factors determining the vegetation pattern. The hydrological regime, in both quantitative (water availability, water dynamics) and qualitative (mineral concentration) aspects, plays a crucial role (Von Asmuth et al. 2002). In climatic, geomorphic, and hydrological conditions of early Holocene, primary succession of vegetation started, being always densely connected with soil cover development (Laasimer 1965). Likewise, the further development of vegetation and soil cover until the present day can always be considered as one complex process, reflecting changes of both biophysical landscape factors (also natural disturbances) and anthropogenic influences (management practice, pollution; Reintam 2004).

In the relatively flat relief conditions of Estonia, and especially island areas, topographical features (absolute and relative height, aspect, slope angle, slope shape), as direct biophysical factors, do not play an very important role. Only in combination with soil types, may they be significant. A similarly low influence of relief factors on vegetation pattern was reported from hilly areas in Otepää and Karula Uplands in South Estonia (Punning and Jõgi 1999; Paal et al. 2004a, 2004b).

As typical for boreal zones without significant human influence, the climax vegetation pattern of Estonia would consist of forests, fens, and bogs, whereas open areas would appear only in new areas of the coastal zone due to the post-glacial uplift (Laasimer 1965; Puurman et al. 2004; Sepp et al. 2003). Also, some natural disturbances, like fire, floods or storms, will cause temporarily open patches as secondary succession stages within forest climax (Angelstam and Kuuluvainen 2004; Lõhmus et al. 2004). Many plant and animal species typical for open areas of present landscapes have colonized such temporarily open patches. With an increasing share of open landscapes due to human activities, new plant communities and ecosystems stabilized. Most probably, prehistoric people who habited Estonia since 9000 years BP did not influence surrounding environment in a remarkable way. More intensive human activity began about 6000 years BP and only since about 4000 years BP can we could talk about significant influence of human population on landscapes. However, there are different views on this dating, depending on the definition of human influence. For instance, already the temporary dwelling sites of Neolithic people changed their surroundings by fire, openness (change in carbon and nitrogen budgets, invasion of new species), whereas, according to another view, only the beginning of regular agricultural activities meant the begin of principal changes in landscapes (Laasimer 1965, 1981; Kriiska 2004; Veski and Poska 2004;

Veski et al. 2005). Signs of earlier traditional agricultural practices (slash and burn systems, grazing, mowing) can be found in the plant cover of forest ecosystems even after a millennium (Koerner et al. 1997; Dupouey et al. 2002), whereas in soils, this influence can be recognizable much longer (Reintam, 2004). A large variety of coniferous forests of less productive site types are grown on former slash and burn or grazed areas of degraded soils (Laasimer 1965; Meikar and Uri 2000; Kriiska 2004).

Human activity can influence the local variability of vegetation site types and the biodiversity at the same level with biophysical factors and even more intensively (Skånes 1996; Aude and Lawesson 1998; Verheyen et al. 1999; 2003a, 2003b; Wulf 2003; Zechmeister et al. 2003; Schmitzberger et al. 2005). In terms of meadows, this is obvious, because long-term monotonic management practice equalizes plant cover of large areas, even if the biophysical factors differ significantly (Krall et al. 1980; Paal 1997; Kukk 2004). After dropping of grazing or mowing, the open areas will turn back to forests, whereas the landscape heterogeneity increases: trees colonize most optimal sites first and areas with lower productivity (dry and nutrient-poor sites) remain open. In terms of postglacial uplift areas of coasts and islands, it means that the most stable plant communities of former agriculturally used meadows can be found in concave moist alvars, which are less well suited for afforestation (Pärtel et al. 1999a,b).

In forests growing on former agricultural areas, changes in plant cover, as well as dominating tree species, can be observed. Accordingly, light conditions on the forest floor and radiation balance can be changed. Forest cuttings mostly influence the last two factors, and today managed forests cover significantly larger areas than forests influenced by only natural disturbance regime (Økland 2003; Lõhmus et al. 2004). On the other hand, both artificial regulation of light regime and domination of only coniferous or deciduous trees in forest stands cause significant change in plant cover structure (in the same biophysical conditions), regardless of the origin of the disturbance (cuttings, agricultural activities, natural disturbances; Laasimer 1965; Lõhmus 1984, 2004; Huber 1992; Zobel et al 1993; Pärtel 1999b; Etverk 2000; Meikar and Uri 2000; North et al. 2002; Prescott 2002; Frey 2004; Paal et al. 2004b; Parrest 2005).

1.2. Classification and mapping of vegetation cover

In hierarchical classification of ecosystems, leading biophysical factors should be taken into account, whereas at higher (more generalized) levels, general (synthetic) factors play the most important role (Bailey 1985, 1987; Masing 1992). In the flat relief conditions of Estonia, with relatively similar climatic conditions in various parts of the country (maritime climate, hemiboreal mixed forest zone), main variability of vegetation is caused by soil, hydrologic, and

geomorphic conditions in combination with anthropogenic influences (Raukas 1995; Arold 2004). A classification of landscape mesochores (*paigastikud* in Estonian): landscape units with relatively homogeneous geomorphic conditions (one mesorelief form), has been worked out (Arold 1991, 2001, 2005). This system is similar to the landscape mesochore classification in Germany (Bastian and Schreiber 1999). Mesochores of the same type have similar regular pattern of vegetation and soil cover and similar pattern of other landscape biophysical factors (hydrological regime, microclimate, geomorphology).

In Estonia, a paradigm, which combines (rather binds) abiotic environmental factors and vegetation cover, has been used for vegetation classification since the 1930s. It has a complex political-historical background which will not be discussed in this thesis (see Masing et al. 1995). However, one can briefly mention that a reason for the broad usefulness of this system was the pragmatic orientation of nature studies during the Soviet period. For instance, many vegetation classification systems from 1950s and 1960s are directly targeted to dramatic changes in vegetation cover (e.g., drainage, fertilization, afforestation etc.).

The vegetation site type classification used in Estonia is an applied-typological list where the basic unit is vegetation site ("*kasvukoht*" in Estonian) — a relatively stable complex of environmental factors, such as topography, soil and climate conditions, and water regime. Similar vegetation sites are combined into vegetation site types (VST); these are combined into vegetation site type groups (VSTG); type groups belong to type classes, and the most general units are habitat types such as Forests, Grasslands, Mires, Vegetation of outcrops, Vegetation of dunes and sandy plains, Vegetation of waterbodies, Ruderal vegetation, Cultivated vegetation (Paal 1997). The current classification of Estonian vegetation site types (Paal 1997, revised and enlarged 8.11.2001) generally follows earlier traditions and data (Kalda 1970; Krall et al. 1980; Rebasoo 1975; Masing 1969a, 1975; Trass 1955; Zobel 1987) also partly the typological classification of Estonian forests (Lõhmus 1984). Names of site types are created on the basis of dominating plant species. This system follows the traditions of Nordic countries.

The forest vegetation of Estonia has been classified mainly according to Cajander's site type system and later using Sukachev's approach. A new approach was introduced by Lõhmus (1974, 1984; Annex 5, Figure 1; Annex 6, Figure 1 and Table 1), who ordinated forest stands, representing all the site types of Karu & Muiste (1958), by means of Wisconsin polar ordination. The latest version of this (Lõhmus 1984) also included detailed characteristics of both plant communities and soil conditions of each site type (Masing et al. 1995; Masing 1998; Jõgiste 2002). An updated and adequately illustrated version of this classification was published in 2004 (Lõhmus 2004). Despite similar names, the classification of forest site types worked out by biologists for nature conservation purposes (Paal 1997) is not equal to the classification worked out by forest specialists for forest management purpose (Lõhmus 1974,

1984, 2004). The first one has new classification units that are important from the point of view of biodiversity (e.g., floodplain forest site type group and hillock forest site type group). On the other hand, some earlier site types that were not clearly recognizable in the field have been united with more common ones (Masing 1969a; Kalda 1970; Marvet 1970; Lõhmus 1974, 1984). In forest management the Lõhmus' system is still in use.

Practical use of forest site type classification has several problems: (1) unclear description of vegetation site types, (2) missing of clear indicatory species, which is, however, typical for relatively species-poor hemi-boreal forests, (3) disturbing influence by human activities (grazing, cutting), (4) unclear presentation or even understanding of forest successions (Laasimer 1965; Marvet 1968; Lõhmus 1984; Masing 1969a, 1991, 1994, 1998; Kalda 1991; Frey 2004; Kukk 2004). There are not many concrete examples on the differences in interpretation of forest site types in the field, but investigations in the Kihelkonna area forests (Saare County) show that there are large differences in forest site type maps created by various specialists of forest management authorities for the same area. However, a concrete prescription of edaphic factor (soil features) should lead to relatively similar classification (Annex 6, Figure 1 and Table 1). Thus, soil classification also has applicability problems, at least on the calcareous soils of Saaremaa. As a result of these classification problems, forest management can result in a management plan that is unsuited to local conditions (Etverk 2000; Frey 2004).

The first detailed description of regional vegetation, including the compiling of a vegetation map, was made by T. Lippmaa for the southwestern part of Estonia (1931). In 1934 he organized countrywide vegetation mapping in 1:42000, however, his activities were cut short by World War II. This work was continued (using a modified methodology) by L. Laasimer, who lead Estonian vegetation analysis team. A map of scale 1:600 000, made on the basis of this material, was published in 1965 (Laasimer 1969; Masing et al. 1995). Detailed vegetation cover maps of nature protection areas on scale of 1:5000 to 1:25000 were created for forest management and conservation purposes. However, due to Soviet security requirements, all the maps had falsified projection (Laasimer 1969; Örd et al. 1981, 1985, 1986, Masing 1991; Kalda 1991; Roosaluuste 1993).

Since the 1980s, remote sensing methods (satellite images and aerial photographs) have been used for vegetation mapping. Again, due to security reasons, use of aerial photographs in the Soviet period was very much limited (Aaviksoo et al. 1984; Aaviksoo 1986, 1993). Therefore, even attempts to more widely use aerial photographs in nature conservation were limited to only some selected key areas (Palo 1997, 1998a, 1998b, 1998c, 1998d, 1999a, 1999b). Satellite images are in intensive use since the 1990s: in addition to land cover mapping (Meiner 1999) and forest inventarisation (Nilson et al. 1999; Peterson 1993), satellite images are used in various areas related to vegetation cover or landscape analysis such as landscape monitoring (Aaviksoo et al. 1997, 2000;

Sepp 1999; Meiner and Aaviksoo 2001; Eluslooduse seire...) and vegetation cover analysis (Kuusk et al. 2004). For Otepää Nature Park, a GIS-based vegetation cover model will be created using the most innovative machine-learning modeling system (Remm 2002, 2004).

Soil types of both agricultural and forest land have been mapped throughout Estonia for natural resources planning purposes. Large-scale soil cover mapping (M 1:10 000 and 1:5000) was started in 1954. In the beginning, only agricultural lands were mapped. Soils in state forest lands (100% of forests in the Soviet period) were mapped from 1976 to 1989. In comparison with agricultural areas, the forest soils were mapped according to a unified methodology (e.g., a lot of attention was paid to detailed classification of acid sandy soils typical for forested areas). Number of soil determination pits depended on the heterogeneity of the soil cover: if there were less than 3 soil types in a 1 km transect, 1 pit per 2 ha in forests and 1 pit per 1 ha in agricultural lands was made. The soil map can be also used for provisory vegetation type classification thanks to its relative independence from vegetation data. Due to the method used, water regime and the calcium content of the soil were indirectly estimated using indicator plants, but not using any valid vegetation classification (Kokk et al. 1973; Kalda 1991).

Soil mapping was based on aerial photographs (Vabariigi... 2001). In 2001 digitized soil map was completed; the available maps at a scale of 1: 5000 were reduced and generalized to correspond to a scale of 1: 10 000 (Kõlli and Ellermäe 2001). Similarly to forest site type classification, the soil classification has also been changed: complex soils were divided into smaller types and less recognizable soils were united into complex ones (Kask 1997, 1999; Paal et al. 2004a).

Nowadays, when there are sophisticated technical possibilities for the mapping of any biophysical factors, and also vegetation in various scales, the expert-knowledge-based classification methods for both soil and vegetation site types seem like anachronisms. However, it is not clear which methods are better for practical implementation. For any case, taking into account several biophysical landscape factors in a holistic way (instead of only limited characteristics of soil cover) may allow us to get a more adequate vegetation site type classification (see Masing 1969b, 1998). New digital techniques also allow us to avoiding mistakes and difficulties in data management and image operation, often appearing in hand-made-methods (Marvet 1968; Kalda 1991; Masing 1991). Etverk (2000) pointed out the practical need in forest site type classification to take into account easily quantifiable biophysical parameters determining tree growth, rather than the fuzzy site types and site types groups. On the other hand, the widely used site types system allows easy understanding between the forest management specialists (Lõhmus 2004). Therefore, most probably, this traditional system will continue to be used.

Likewise, the EU nature protection strategy assumes all-European biotope classification. However, this is rather general and does not accord to Estonian classification (Natura 2000; Paal 2000, 2004; Palo 2004). A more detailed classification has been created for rare and endangered plant communities (Paal 1998a, 1998b) and valuable forest biotopes (Andersson et al. 1999, 2003; Palo and Klvik 2001), but these classifications also do not cover the full spectrum of biodiversity. For instance, the problem of plant community classification for the Red Data Book of habitats in Estonia still needs to be solved (Palo and Klvik 2003; Palo et al. 2003). Also, a general biotope and habitat classification is missing. Traditional habitat names like reedbed, juniper bush, hazelnut bush, wooded meadow, sedge stand etc., which are used in nature conservation practice, often do not cover enough information on species requirements. Studies on species' habitat preferences use the system of biotopes, biotope elements, and/or biotope complexes, which are systematically improved in field studies (Vellak and Paal 1999; Andersson et al. 1999, 2003; Lhmus 2003; Angelstam et al. 2003; Lhmus et al. 2004; Leito et al. 2004, 2005). Nevertheless, a comprehensive classification covering all the biodiversity scales is still missing in this field.

Most probably, the solution depends on the development of remote sensing and GIS techniques. Another benefit of the automatic system is easily manageable databases open for new data entry and additional modeling (Petersen and Stering 2003; Gourmelon 2005). However, the complex character of landscape ecological factors and the large number of relationships between different systems in landscapes needs more detailed analyses, also regarding the classification schemes (Roberts 1996; Tappeiner et al. 1998; Hilbert and Ostendorf 2001).

2. STUDY AREA AND METHODS

2.1. Description of study area: Estonian West-Coast Islands, Saaremaa and Muhu

The formation of these islands is connected with the postglacial uplift of the earth's crust; the first parts of the islands appeared in the early Holocene (~10 000 yrs ago). At present, uplift continues at a rate of 1–3 mm per year. Due to this process, the highest areas (up to 50 m a.s.l.) of these islands are the oldest. Bedrock is formed by a variety of calcareous sediment rocks from the Silurian era. The layer of glacial sediments (abraded till, abraded end moraines, glacio-lacustrine clays and sands, marine, lake and palustrine sediments) is up to 40 m deep. The topography is plain or undulating, with rare hilly areas in the oldest parts of western Saaremaa Island. Among relief forms, coastal formations (coastal ridges, dunes, coastal plains, former lagoons) of various ages predominate on both islands. Calcareous plateaus with thin soil cover (alvars) are typical of these islands. A great variety of topographic and geological features, calcareous bedrock, calcium-rich glacial sediment and relatively mild maritime-type climatic conditions (Luha and Tammekann 1934; Frisch 1934; Kaar 1959; Mardiste 1990; Raukas 1995; Ratas et al. 1997a; Saarse et al. 2002; Eltermann and Raukas 2002; Raudsepp and Jaagus 2002; Arold 2005) give rise to a mosaic of vegetation cover that is heavily influenced by human activity (most of all by traditional agriculture). As little as 200 years ago there were very few areas that we would nowadays classify as forests (Ellermaa 1980; Kalda 1990; Meikar and Uri 2000; Meikar 1997, 2002a,b). For political and economic reasons, the proportion of areas occupied by agriculture, especially meadow formations, has fallen drastically: from about 80% in 1913 to <40% at the end of the 1990s (17% in 2001) (Mander and Palang 1999; Sooväli 2004). Therefore, some semi-natural vegetation formations, like alvar meadows and wooded meadows, which are typical to the islands and support a great variety of species of flora and fauna, are threatened by spontaneous bush encroachment and forestation (Kukk and Kull 1997).

The soils on Saaremaa and Muhu have developed on surface substrate washed through by the sea or directly on the compact limestone layer. As a result of the continuing land uplift, young soils are being formed in coastal areas. Low-lying areas rising from the sea are characterized by subaqueous soils that are similar to coastal soils. Flooding is seasonal and varies from year to year. Coarse underlying substrate, the proximity of limestone, and the large number of karst areas result in a large variation in soil water regime. Soils saturated in spring may dry out in summer. Indeed, Gleysols (37%) and gleyic soils (19%) are the most widespread soils on Saaremaa; automorphic soils constitute 28% and peat soils 15% of the soils (Teras 2002).

Saaremaa and Muhu islands have been very popular research sites for botanists. The islands are characterized by exceptional floristic diversity (ca. 1150 species, or 2/3 of Estonia's known vascular plant species). Later research has also focused on semi-natural communities and the landscape as a whole (Eichvald 1934, 1964; Reitalu and Roosalu 1990, 2002; Ratas et al. 1997a, 1997b; Sooväli 2004). There are vegetation units on Saaremaa that differ from common vegetation units in mainland Estonia; there is also a greater than average proportion of human-impacted forests and valuable animal habitats.

2.2. Materials and methods

2.2.1. Field observations

The 16 key areas selected for vegetation analysis and mapping in the first work phases in 1999 vary in size due to the fact that the research area was delimited with roads or natural borders of land use (large fields, ditches etc.). Densely populated areas were avoided, and the focus was on areas with natural or semi-natural vegetation. Instead of using fixed size sample plots, which is the common method in landscape ecological research (Bunce and Heal 1984; Brandt et al. 1994; Ihse 1996), varying size plots, according to the landscape structure and the heterogeneity of the biotopes, were preferred. In later field observations, key areas were no longer delimited. In 2004 and 2005 the locations of plant cover plots were recorded using GPS (Magellan SporTrak Map).

In 1999, only the vegetation site type (classification Paal 1997) was determined at the studied locations (key areas); they were used for extrapolating to polygons defined with the help of CIR aerial photos. A detailed description of vegetation was not carried out. In 2004 and 2005 the understorey vegetation in every study location was also described according to the Braun-Blanquet method. The tree layer was divided into three classes: coniferous forest, mixed coniferous-deciduous forest, deciduous forest; and, based on the author's earlier works and experience, the continuity of the forest was assessed (Andersson et al. 1999, 2003; Lõhmus et al. 2004; Palo and Külvik 2001). Forest management status was determined according to direct evidence of such activity: the presence/absence of a recognizable planted tree species and stock fencing, old roadways, stone walls, etc. characteristic of semi-natural communities. If signs of neither forest planting nor semi-natural communities were observed, the forest was categorized as natural forest. Therefore, this category also contains felled forests with natural or near natural regrowth. Vegetation cover analyses were never carried out in clearings. All understorey vegetation plot analyses in forest samples originated from areas, covered with trees.

In the 2005 fieldwork, soil pits down to the bedrock were carried out at the sampling plots and the soil type was determined. The existence of soil carbonates in soil profiles was determined with 10% hydrochloric acid reaction.

2.2.2. Maps and databases

The following materials and digital databases served as a basis for the work:

- (1) Raster-format land use type map, or so-called cadastral map, (1:10000; Land-Board) and Estonian Basic Map (1:10000 vector map; Land-Board);
- (2) Vector map outlining the borders of the mesoscale landscape units' (landscape mesochore) subtypes (1:50000; Arold 2001);
- (3) CORINE Land Cover vector map (1:100 000; Meiner 1999);
- (4) Printed soil maps (1:10000; 1:20000; West Estonian Archipelago Biosphere Reserve) and digitalized maps of soil types (1:10000; Land-Board);
- (5) Colour infrared (CIR) aerial photos (1:10000; Forestry Board);
- (6) Digital terrain model (1:10000; data from Tambet Kikas);
- (7) Saaremaa state forest survey database (data from 2004; 1:10000; Forestry Board);
- (8) Viidumäe Nature Reserve vegetation map (1:10000; Viidumäe Nature Reserve);
- (9) Digital biotope map, created by 1999 mapped data (1:10000; West Estonian Archipelago Biosphere Reserve).

2.2.3. Statistical analysis and calculations

The first statistical overlay analysis of soil classes and parameters of the elevation model with VSTs and VSTGs was carried out using a special module written in Microsoft Visual Basic for Applications (Kalle Remm, University of Tartu). The method of random shifting of map layers was used; this is called toroidal shifts, as it is similar to the rotation of one tube within another (Palo et al. 2004). Level of significance $\alpha = 0.05$ was accepted in all cases.

The Kappa Index of Agreement (KIA) was used to assess the strengths of the relations in the verification of the map layers used to study the predictability of vegetation site types (Palo et al. 2005). The hard classification, allowing only correct (one-to-one) accordance, produces a low value of the KIA (Lillesand and Kiefer 1994): in our investigations the KIA was lower than 0.3. However, considering communities on an environmental gradient (the same or similar soil and water regime), transitional units (permitted relations) were also accepted, which significantly improved the results. The initial pivot tables were re-organized on the basis of the ordination of vegetation site types and their soil relations (Lõhmus 1984; Paal 1997; Kölli and Lemetti 1999; Palo et al. 2005).

Canonical Correspondence Analysis (CANOCO 4.52) was used to evaluate the role of selected landscape parameters (location coordinates, slope angle, and elevation a.s.l.), dominating tree species and forest continuity in the determination of forest site types. This method was preferred after performing Detrended Correspondence Analysis (DCA; CANOCO 4.52), which showed that all gradients in data fields were higher than 2. These relatively high gradient values indicated that the analysed forest site types consisted of a low number of common plant species. Likewise, low eigenvalues of DCA axes suggested that various additional (environmental) factors influence the species structure of site types (unpublished data by Palo, Truu, Kanal, Aunap and Mander).

2.2.4. Map analysis and verification

The vegetation site-type data layer (Palo and Kikas 2003) of the 1999 fieldwork-based biotope database was used to study the dependency on soil type. In the case of the toroidal shift technique, all data layers were analysed within the 10x10 m²-size pixels (see 2.2.3; Palo et al. 2004).

For creating a predictive vegetation map, raster data analysis was chosen and all source data were converted from vector to raster format. Idrisi32 and, in some instances, ArcGIS were used to perform the analysis. Considering the relatively large study area, (100 x 90 km) the optimum raster resolution was found to be 20 m. Very simple, so-called hard classification was used, i.e. mainly Boolean logical operations (Chang 2003) in the form of an overlay of the supplementary criterion layers defined in the table and in the soil and basic map synthesis layer (Palo et al. 2005).

Three digital vegetation site type databases were used to verify the data layer:

- 1) Saaremaa state forest survey database (data from 2004; 1: 10000; 169.35 km²);
- 2) Viidumäe Nature Reserve vegetation map (1: 10000; 1842.4 km²);
- 3) Our fieldwork point data (706 points).

During verification the numbers of corresponding pixels in all classes were counted (Palo et al. 2005).

3. RESULTS AND DISCUSSION

3.1. Vegetation analysis of landscape mesochores

The landscape mesochores' definition (meso-scale landscape units; Bastian and Sreiber 1999) of Estonia includes the spectrum of the vegetation site types characteristic to certain mesochore (sub)types (Arold 1993, 2001, 2005). However, there are several subtypes where it is difficult to specify the dominating vegetation site types since the soil and humidity conditions probably vary greatly (unpublished material by Palo, Remm, Kikas, Mander).

Till plains with calcareous cover (2.1, now and later see of code explanations in Table 1) is the most common landscape mesochore subtype on Saaremaa, and it is here that most of the oldest settlements and arable lands are located. The fresh boreo-nemoral forests of *Aegopodium* and *Hepatica* site types (FST), which are particularly characteristic of this mesochore subtype, have been used as wooded meadows or meadows (today overgrown).

The forest site types most probably characteristic of lacustrine plains with non-calcareous cover (4.3) are *Molinia*, *Oxalis-Vaccinium myrtillus* and *Vaccinium myrtillus*, although, in theory, dry boreal and boreal heath forests should be most common in dryer site types (Arold 2005). Since these appear on aerial photos as structurally uniform coniferous forests, this may also be the result of an interpretation error in the course of extrapolation. Most of the mapped area was covered by forest and mire (>99 %; Palo 1999b; Palo and Kikas 2003).

The relations between the forest site types on marine plains and the calcareousness of the sedimentary cover are in good accordance with theory. Marine plains with calcareous cover (6.1) are characterized by *Arctostaphylos* FST and rich paludified grasslands. The negative relation of dry alvar grasslands to this mesochore type needs further study, because they exist instead of *Arctostaphylos* FST on the agricultural areas. Marine plains with non-calcareous cover (6.3) are likely to include paludified forests, dry and fresh boreal forests and coastal meadows. During mapping, this mesochore type was characterized by extreme heterogeneity of the vegetation: the occurrence of 31 vegetation site types was reported (Palo 1999b).

Paludified and drained site types are characteristic of mire plains (10). Some dry calcareous forest and meadow site types clearly avoid these mesochore types.

The vegetation of dune mesochore type (16) is predictable, although area-wise there is a significant occurrence of paludified forests in dune hollows with a site type that is difficult to classify, which have probably been influenced by calcareous water; these have been classified as belonging to *Molinia* FST in fieldwork, but in theory they should be *Vaccinium uliginosum* FST, transitional bog forest or swamp forest VST (Arold 2005).

Coastal ridge mesochore types (17) are a mosaic of regularly recurring vegetation types or plant communities, each normally with a small area, so that vegetation types are difficult to map even on a scale of 1:10 000. Coastal ridges with calcareous cover (17.1) have a particularly large variety of sediments (and hence also vegetation), and they often include sandy as well as clayey less well-drained areas. The vegetation of coastal ridges covered with low-calcareous material (17.3) is more homogenous.

The conditional probability of a vegetation site type (on the condition that the mesochore type is known; unpublished material by Palo, Remm, Kikas, Mander) characterizes its indicative value regarding mesochore type. There are few vegetation site types that are strongly associated with a landscape mesochore type (mesochore subtype; Table 1). By definition, associations between fresh water and lake localities (lacustrine plains) and hummock bogs and peat milling fields (9.4) are an exception. There is about a 70% probability to find wet floodplain meadows even in the present-day wetlands on Saaremaa's glaciofluvial plains (8.2, 8.4). The probability of the occurrence of other vegetation site types in a certain mesochore type remains below 45%.

Table 1. Probability (%) of association between vegetation site types and landscape mesochore sub-types if the mesochore type is known ($p < 0.05$; unpublished data by Palo, Remm, Kikas, Mander).

Vegetation site type	Landscape mesochore types	%
Freshwater	Lake	78
<i>Arctostaphylos</i> forest ST	6.1 Marine plains with calcareous cover	71
<i>Calamagrostis</i> FST	2.1 Till plains with calcareous cover	25
<i>Vaccinium vitis-idaea</i> FST	16 Dune localities	32
<i>Vaccinium myrtillus</i> FST	4.3 Lacustrine plains with non-calcareous cover	30
<i>Hepatica</i> FST	2.1 Till plains of calcareous cover	35
<i>Molinia</i> FST	4.2 Lacustrine plains with slightly calcareous cover	27
	1.1 Limestone plain with a very thin cover	29
	1.3 Limestone plain with sand cover (30–100 cm)	30
Dry alvar grassland ST	17.1 Coastal ridges with calcareous cover	27
Dry boreo-nemoral GST	2.1 Till plains with calcareous cover	45
	8.2 Alluvial plain with slightly calcareous cover	66
Wet floodplain GST	8.4 Alluvial plain with peaty cover	69
Hollow ridge bog VST	9.4 Technogenous plain with peaty cover, peat milling field	100

Analysis did not reveal typical vegetation spectra for landscape mesochore types, and the extent of the test areas and the number of plots needed to achieve this would, in practice, be too great. Of course there are relations between mesochore types and the vegetation growing there, but these can be inferred from the geomorphologic and soil characteristics of a particular mesochore type, or, in effect from the definition of the mesochore type (Arold 1991, 2001, 2005; Eltermann and Raukas 2002). The result refers to significant landscape-, and thus vegetation-shaping tendencies: (1) human impact diversifies the actual vegetation in most mesochore types to such an extent that, in the case of a detailed typology and analysis methodology, it is possible to reveal strong relations only in mesochore types little affected by human impact and with homogenous vegetation cover (e.g. mire mesochore types); (2) the development of vegetation is influenced by narrower biophysical landscape parameters than those used to define landscape mesochore types, also, they may occur, at least partly, independently of the mesorelief, or may recur in developmentally different localities (soil types, water movement peculiarities, the calcareousness of the groundwater, the exposition of slopes, etc.).

3.2. Relationship between vegetation cover and relief parameters

Relationships between the vegetation site types and selected relief characteristics were analysed based on a comparison of different map layers using the toroidal shift technique and Canonical Correspondence Analysis (CCA).

At the lowest position (0–2 m a.s.l.), shallow water VSTs (reed-beds), geolittoral and epilittoral grasslands, as well as *Calla* swamp forest VST dominated. At the same time, the dry alvar grassland VST avoids the lowest locations. At the highest positions, two associating groups of VSTs can be distinguished: — first, xerophile vegetation of sandy areas such as *Cladina* and *Calluna* boreal heath FSTs, *Vaccinium vitis-idaea* and *Vaccinium myrtillus* boreal FSTs and dry boreal heath grassland VSTs, and second, vegetation of raised bog and transitional bog complexes such as oligotrophic (ombrotrophic) bog forest site types, hummock and hollow-ridge bog site types, and mixotrophic (transitional) grass mire site types. Sandy areas at higher elevations (>30 m a.s.l.) represent dune complexes or the highest and respectively oldest areas of Saaremaa island. Paludified forest site types are found at both lower and higher elevations. Some higher-elevation VSTs, such as *Polytrichum*, *Polytrichum-Vaccinium myrtillus* and bog FSTs are typically found in depressions between the dunes and sandy coastal ridges or on the borders of bogs (Luha and Tammekann 1934; Eltermann and Raukas 2002; Palo et al. 2004).

Likewise, the CCA results indicate that the oldest successional stages of forests and typical forest soils in Saaremaa are related to absolute height above the sea level (a.s.l.; Figure 1). A group of characteristic plant species for dry and sandy podzolic soils (*Calluna vulgaris*, *Calamagrostis arundinacea*, *Deschampsia flexuosa*, *Melampyrum pratense*, *Pteridium aquilinum*, *Solidago virgaurea* and *Vaccinium myrtillus*), related to elevation factor, can be distinguished in Figure 1. These species typically colonize sandy soils (Haplic Podzols or Leptic Podzols). In Saaremaa, these soils can be found in the former coastal zone and on inland dunes far from the actual shoreline, or on old glacio-limnic and marine plains covered with deposits of low carbonate content (Arold 2005). One of the interesting findings of the CCA is that it clearly shows that two rare relic plant species *Trifolium alpinum* and *Vicia cassubica* (Annex 1, Photo 4) are found in the highest (resp. oldest) locations of Saaremaa. The CCA also indicates the concentration of continuous natural forests and coniferous forests (characterised by plant species such as *Festuca ovina*, *Briza media*, *Asperula tinctoria*, *Epipactis atrorubens*) in northern and western part of the island (Figure 1). This can be related to somewhat intensive uplift in the northwest and domination of young and low productivity soils in the western and northern parts of Saaremaa. Conversely, broadleaved forests and seminatural agricultural communities (e.g. wooded meadows; most frequently found and significantly related plant species: *Dactylorhiza fuchsii*, *Poa nemoralis*, *Melampyrum nemorosa*, *Carex vaginata*, *Aegopodium podagraria*, *Mercurialis perennis*, *Lathyrus vernus*, *Paris quadrifolia*, *Carex nigra*, *Filipendula ulmaria*, *Anemone nemorosa*, *Convallaria majalis*, *Geum rivale*) can often be found in the southern and western parts. Traditional (semi-natural) plant communities such as young coniferous forests on relatively lately abandoned alvar pastures (significantly associated plant species: *Rubus caesius*, *Dactylis glomerata*, *Fragaria vesca*, *Filipendula vulgaris*, *Ranunculus acris*, *Galium verum*, *Sesleria caerulea*, *Briza media*, *Centaurea jacea*, *Campanula rotundifolia*, *Asperula tinctoria*) are related to Eastern and lower (younger) locations (unpublished data by Palo, Truu, Kanal, Aunap and Mander).

Significance of geographical location as an important factor in determining species diversity and its variability has been pointed out in several studies (Pärtel et al 1996, 19991, 1999b; Myklestad and Sætersdal 2003; Otsus 2004; Parrest 2005). This is due to the interaction of several abiotic and human-influenced landscape factors. In the case of Saaremaa, the following factor groups are integrated: age of communities and microclimatic characteristics (both along the gradient from coastal zone to inland parts) in combination with character and extent of anthropogenic influence within the plant communities (successional gradient: seminatural community — afforested seminatural community — continuous forest).

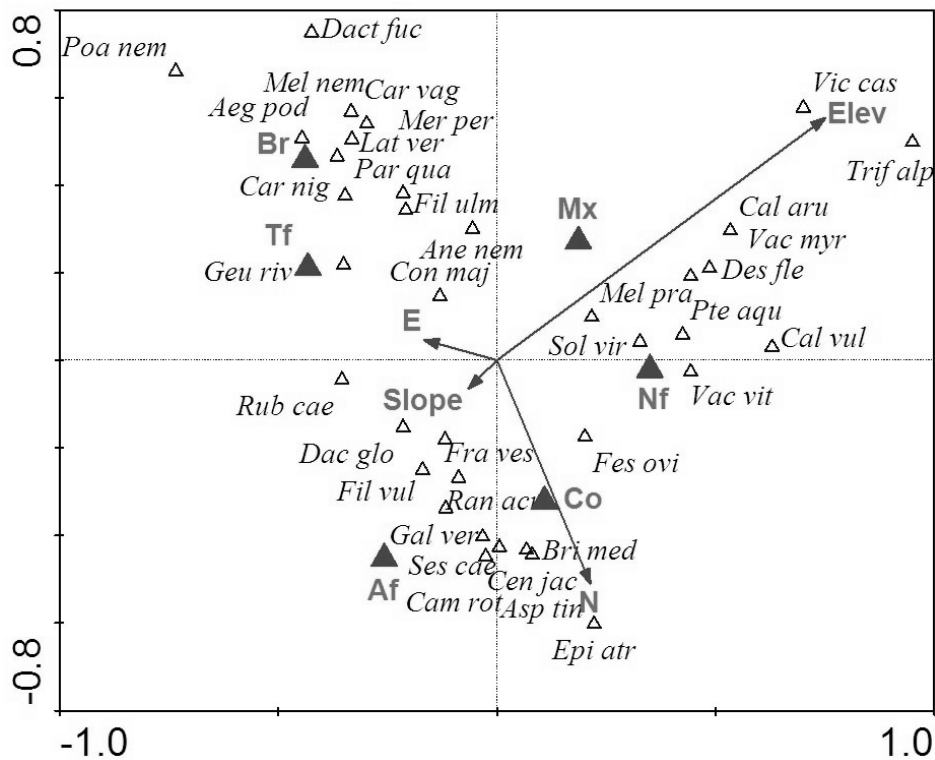


Figure 1. Ordination of plant species, based on Canonical Correspondence Analysis displaying 4.3% of the inertia in the abundances and 57.8% of the variance in the weighted averages of species with respect to the environmental variables. The eigenvalues of axis 1 (horizontal) and axis 2 (vertical) are 0.23 and 0.21, respectively. Arrows indicate quantitative environmental variables. The class variables are indicated by the triangles.

Abbreviations of variables: Elev — absolute elevation; Slope — slope angle; E — geographical coordinate East (Eastern longitude); N — geographical coordinate North (Northern latitude); Br — broadleaved forest; Co — coniferous forest; Mx — mixed forest; Af — afforested semi-natural or traditional agricultural forest vegetation; Tf — semi-natural or traditional agricultural forest vegetation; Nf — natural continuous forest.

The association of VSTs with elevation relative to the minimum elevation within 100 m radiuses was quite similar to the association/segregation with absolute elevations. In contrast to the elevation relative to the minimum elevation, the elevation relative to the mean elevation (both within 100 m radius) did not have a significant relation with the location of VSTs. Only the littoral grasslands and shallow water (reed-bed) VST are always located significantly lower than the mean elevation (at 100 m radius; Palo et al. 2004).

The plain topography of Saaremaa and Muhu islands clearly influences the relations between the distribution of VSTs and their catenary's position, slope angle and slope aspect. Typical VSTs on plain areas (slope angle $<3^{\circ}$) are wet and paludified forests like the *Salix* floodplain shrubland VST, *Molinia* paludifying, *Polytrichum-Vaccinium myrtillus* paludifying, mesotrophic bog, oligotrophic bog, *Vaccinium myrtillus* and *Oxalis* drained peatland FST-s. As is to be expected, all mire-sites and waterbodies are on plain areas. On the other hand, *Cladina* boreal heath, *Calluna* boreal heath, *Vaccinium vitis-idaea* boreal, *Corylus* boreo-nemoral hillock and *Polytrichum* paludifying forest, and dry alvar grassland VSTs prefer steep slopes. However, all of these can also be found on less steep slopes. The *Vaccinium vitis-idaea* boreal and *Corylus* boreo-nemoral hillock FSTs prefer south-facing slopes; while gray coastal dune VSTs predominantly face northward. The dry boreal heath, dry grassland and dry alvar grassland VSTs, *Cladina* boreal heath, *Calluna* boreal heath, and *Calamagrostis* alvar, *Corylus* boreo-nemoral hillock FSTs, as well as gray coastal dune VSTs are typically found on the upper segments of slopes. At the same time, *Polytrichum* paludifying FST, geolittoral (marsh) and epilittoral grasslands, and shallow water VST (redbeed) are found on lower sections of the topographical curvature. However, some VSTs that are typical of higher positions (e.g., *Cladina* and *Calluna* heath forest) can also be located on the talus (Palo et al. 2004).

According to the CCA, slope angle did not have significant influence on VSTs plant species distribution (Figure 1), however, it may distinguish some differences on the understory vegetation structure of some VSTs, such as *Aegopodium* VST (Figure 2) (Paal et al. 2004a, b).

3.3. Relationship of floristic variability in vegetation site types in relation to former land use and forest stands character

The majority of forests in Saare County are heavily influenced by human activities. Slash-and-burn technique and grazing in forests were common until the beginning of 20th century. Typical land use forms were wooded meadows: mowed park-like deciduous forests with sparse tree cover (Eichvald 1934; Mathiesen 1934; Tuiskvere 1938a, 1938b; Vester 1938; Maimre 1944; Kukk and Kull 1997; Troska 2004). At present, the majority of forests in Saare County (67%) are in private own. In comparison with state owned forests, the collection of management statistics in private forests is weakly organised. Therefore, there is no adequate statistical overview about a large part of Saare County's forests (Aastaraamat. Mets 2004).

CCA showed that both dominating tree species in forest stand as well as forest management have significant influence on forest ground species diversity (Figure 1). Based on floristic diversity, semi-natural plant communities of

traditional agricultural practice (e.g., wooded meadows) and natural forest stands were classified as the most differing communities, whereas the afforested areas on earlier alvar meadows or wooded meadows are more similar to natural forests than to initial semi-natural communities. For instance, most of formerly grazed alvar communities are turning to coniferous forests. This is well illustrated by characteristic plant species such as *Rubus caesius*, *Dactylis glomerata*, *Fragaria vesca*, *Filipendula vulgaris*, *Ranunculus acris*, *Galium verum*, *Sesleria caerulea*, *Briza media*, *Centaurea jacea*, *Campanula rotundifolia*, *Asperula tinctoria*. Earlier land-use areas of traditional land use (semi-natural communities), that were not afforested, are predominately now represented by deciduous forests. These are typical wooded meadows, both formerly and presently used, characterized by species such as *Dactylorhiza fuchsii*, *Poa nemoralis*, *Melampyrum nemorosa*, *Carex vaginata*, *Aegopodium podagraria*, *Mercurialis perennis*, *Lathyrus vernus*, *Paris quadrifolia*, *Carex nigra*, *Filipendula ulmaria*, *Anemone nemorosa*, *Convallaria majalis*, *Geum rivale*.

Typically, understorey species of deciduous and coniferous forests differ significantly, whereas floristic structure of mixed forests is more similar to coniferous than to deciduous forests, but it may depend on FST (Figures 1 and 2).

3.4. Relation of vegetation site types with soil types

An analysis using the toroidal shift method indicated the existence of relations between vegetation types and soils that differ from current theory. The nutrient-rich soils (K, Kr, Ko, Kh, Kg, Kk, Khg, Kkg, Kog; Annex 6, Figure 1 and Table 1) have few significant correlations with VSTs. In contrast, less nutrient-rich soils (L, Lg, LG, Lk, Lkg, LkG; Annex 6, Figure 1 and Table 1) are more significantly associated than segregating with VSTs (Palo et al 2004).

Correlation was defined as low in Histosol forest site types (Palo et al. 2004). The variability of Saaremaa's drained peatland forest soil data is partly caused by their definition according to the vegetation site type classification as forests arising from the draining of deep Histosols (Paal 1997); deep Histosols are, however, relatively rare on Saaremaa. Drained forests are classified as paludified forests in regard to their bonity and understorey vegetation (Lõhmus 1981, 1982; Paal 1997; Kalda 1991; Reitalu and Trass 2002), particularly if the peat has decomposed over a long period of time. According to vegetation and stand descriptions, stands similar to the *Filipendula* FST are formed as a result of the draining of *Calla*-swamp FST and the shallow peat stagnant swamp FST, while the drainage of the more oligotrophic *Calla*-swamp FST, *Dryopteris* FST, and *Filipendula* FST result in the formation of *Oxalis-Vaccinium myrtillus* FST stands (Pikk 1997). Similarity in the ground vegetation composition of forest communities on Gleysols and Histosols may also be caused by seasonally highly variable groundwater levels and surface water quantities and the constant

high carbonate content of the water (Teras 2002; Perens 2002). Close to $\frac{3}{4}$ of Saaremaa's soils are temporarily or permanently waterlogged (Teras 2002). Soils have been extensively dried for decades (Loigu and Hansen 2002), and therefore it cannot be said that Saaremaa has few drained forests (Reitalu and Trass 2002; Lõhmus 2004).

The analysis carried out pointed to soil texture as an essential soil parameter determining the distribution of vegetation types. Soil texture classes are significantly correlated with VSTs that prefer carbonaceous soils. An unexpectedly low number of significant overlaps were found with forest site types that prefer peatland soils or podzols (Palo et al. 2004). Soil texture is very variable in most landscapes on Saaremaa. Since even the soil types are often combined polygons (see 3.1), the defined texture sample point frequency is too small, and vegetation models must take into account that the texture associated with the soil polygon on the map may vary widely in nature (see 1.3.2).

Data concerning the relations between forest site types and soils and additional theoretical input was used to interpret the data layer created by combining the soil map and basic map, as a result of which, a map of probable vegetation site types in the area was produced (Palo et al. 2005; see Annex 1, Map 1).

The inclusion of several soil sub-types in the database (spring-influenced soils and Fibric Histosols of quaking mires) enabled the locations of spring fen forest site type, spring fen site type and quagmire VSTs to be queried. Spring-influenced treeless Gleysols were treated together with spring fens, and treed areas together with spring fen forests. Despite the theoretical consideration (Paal, 1997) that does not permit forests on Salic Fluvisols (Av), Coastal Ridge Soils (Ar), Submerged (Littoral) Soils (Arv) and Endo-Hyposalic Gleysol (Gr), the Basic Map showed forests in these areas. Those FSTs are united in a complex unit 1100 (coastal forests). Other new VSTs, such as littoral and epilittoral reed stands, fen reed stands, and mixotrophic mire reed stands, were distinguished (Palo et al. 2005).

The correlation of the new data layer with actual vegetation was verified with independently compiled site type data layers originating from the national forest survey database and from Viidumäe Nature Reserve; also, the data from the vegetation descriptions in the field and the vegetation site types of the new data layer were compared. Depending on the data layer used, 25–38% of the forests correlated with the expected areas; 46–57% correlated with related site types. We therefore succeeded in querying 77–88% of forests with suitable abiotic conditions (a small number of neighbouring mire, grassland and sandy plain communities) on the map. The largest correlation for forests was achieved on the basis of the forest survey database. Since sandy plains, meadows and mires were not represented in the forest survey database, their high correlation with so-called permitted vegetation types was expected. A correlation of over 95% with permitted types was achieved for Viidumäe grasslands and mires. The area of grasslands is relatively low and the theoretical error is high, but the relation structure is nevertheless good. Viidumäe is renowned for its species-

rich spring fens; their percentage correlation in correct overlapping — 40%, is also remarkable. We checked errors by analysing the VST data of all the databases used for verification, with the soil data. It appears that in the verification databases, there are a large number of VSTs assigned to soils on which they should not occur (Palo et al. 2005).

In 2005, in addition to the vegetation cover descriptions, the soil type was also determined at the sample sites. The assessment of soil type and carbonate content did not give sufficient data about the root nutrition conditions in the soil, because there was an apparent contradiction between the soil and vegetation types described (Table 2). The most contradictory results were found for *Vaccinium myrtillus* FST, *Hepatica* FST and *Molinia* FST; variable soils were also found in *Calamagrostis*-alvar FST, *Sesleria*-alvar FST, *Aegopodium* FST and *Filipendula* FST. Meso-eutrophic boreo-nemoral hillock forest STG (not divided into sub-types), *Arctostaphylos*-alvar FST, *Vaccinium vitis-idaea* FST, *Oxalis-Vaccinium myrtillus* FST, *Calla* swamp FST and drained peatland FST were more easily recognisable and associated with a relatively narrow soil spectrum (unpublished data by Palo, Truu, Kanal, Aunap, Mander).

Table 2. Soil types determined in the soil pits during field work in 2005. Unexpected soil types are remarked with **bold** text.

FST	Soil type
<i>Arctostaphylos</i>	5 Skeletic Leptosols (Kk)
<i>Calamagrostis</i>	6 Skeletic Leptosols (Kk), 3 Leptic Podzols (Lk), 2 Rendzic Leptosols (Kh), 1 Rendzic Leptosols (K), 1 Skeletic Leptosols (Kr), 1 Calcari-gleyic Leptosols (Kg), 1 Gleyi-Skeletic Leptosols (Kkg)
<i>Sesleria</i>	3 Rendzic Gleysols (Gk), 2 Rendzic Gleysols (Gkr), 2 Gleyi-Hyposalic Fluvisols (ArG), 1 Calcari-gleyic Regosols (Krg), 1 Rendzic Leptosols (Kh)
<i>Vaccinium vitis-idaea</i>	3 Haplic Podzols (1 L, 1 Ls, 1 Lo)
<i>Vaccinium myrtillus</i>	2 Cambic Gleysols (Go)
<i>Oxalis-Vaccinium myrtillus</i>	2 Gleyic Albeluvisols (Lkg)
Dry boreo-nemoral hillock forests	7 Mollic Cambisols (Ko), 2 Molli-Skeletic Cambisols (Kor), 2 Skeletic Leptosols (Kr), 2 Leptic Podzols (Lk or Arenosol), 1 Gleyi-Mollic Cambisols (Kog)
<i>Hepatica</i>	3 Skeletic Leptosols (Kr), 3 Molli-Skeletic Cambisols (Kor), 3 Mollic Cambisols (Ko), 2 Calcari-gleyic Regosols (Krg), 2 Calcari-gleyic Leptosols (Kg), 2 Rendzic Gleysols (Gk), 1 Rendzic Leptosols (K), 1 Mollic Cambisols (Ko), 1 Gleyi-Skeletic Leptosols (Kkg), 1 Gleyi-Mollic Cambisols (Kog), 1 Cambic Gleysols (Go)

FST	Soil type
<i>Aegopodium</i>	5 Mollic Cambisols (Ko), 4 Gleyi-Mollic Cambisols (Kog), 3 Skeletic Leptosols (Kr), 3 Rendzic Gleysols (Gk), 2 Calcari-gleyic Leptosols (Kg), 1 Rendzic Leptosols (K)
<i>Filipendula</i>	8 Cambic Gleysols (Go), 4 Rendzic Gleysols (Gk), 1 Coastal Gleysols (Gr)
<i>Molinia</i>	2 Rendzic Gleysols (Gk), 2 Cambic Gleysols (Go), 1 Coastal Gleysols (Gr), 1 Gleyi- Rendzic Leptosols (Khg), 1 Rendzic Gleysols (Gkr), 1 Gleyi-Hyposalic Fluvisols (ArG)
Swamp forests	1 Rendzic Gleysols (Gk), 1 Cambic Gleysols (Go), 1 Eutri-Sapric Histosols (M)

Some extremely unusual sites were also found; for instance, on a soil that was on the soil map defined as a Haplic Podzol (L), which on pit proved to be a uniform silicate gravel (no carbonate reaction with 10% hydrochloric acid up to a depth of 30 cm; described as Lk), grew a community that, according to the floristic composition of the ground vegetation, corresponded to *Calamagrostis-alvar* (or meso-eutrophic boreo-nemoral hillock forest) (abundant *Geranium sanguineum*, *Calamagrostis arundinacea* etc.; Annex 2, Photo 1).

A soil defined as a Gleyic Albeluvisol (Lkg) on the soil map (in addition the respective positive relief feature was partially missing on the map, and thus the Gleysol soil type distribution area), on pit, was found to be a Podzol with no gleyic properties and with an almost undifferentiated soil profile (Annex 1, Map 1), which had oak growing on it with encroaching spruce. Typically for the meso-eutrophic boreo-nemoral hillock forest site type, the ground vegetation contained, for instance, coexisting *Vaccinium vitis-idaea*, *Pteridium aquilinum*, *Hepatica nobilis*, *Melampyrum nemorosum*, *Asperula tinctoria*, *Galium boreale*, *Calamagrostis arundinacea* etc. (Annex 1, Photos 1, 2). The occurrence of the meso-eutrophic boreo-nemoral hillock forest STG on (LP) Planasols and more productive Leptic Podzols (so called Arenosols) is typical on the hilly landscape of southeastern Estonia (Paal et al. 2004a). The study of North Estonian coastal sandy forest soils has revealed that their chemical composition is locally very variable, which also results in large variances in forest bonity (Kokk 1988). Hence sandy soils may be of differing chemical productivity in Estonia, which means that the classification of sandy soils according to water regime or chemistry into acidic, leptic and non-acidic nutrient rich sandy soils, may not reflect the characteristics of forest site types.

The occurrence of forest types on soil types theoretically representing the respective site type conditions (Paal 1997; Lõhmus 1984, 2004) was found to be less clearly defined than expected in the study area. By compiling digital data layer of forest site types for certain soils, rather than trying to find one single main FST, it may be better to permit several FSTs existing in the same biophysical conditions. At the moment there are no digital data sets containing

parameters that would allow such VSTs to be distinguished within a soil region. Some VSTs need to be combined in this stage of the work in order to increase the rate of predictability. Such cases include fens (excluding fens with reed stands), where existing parameters do not permit their calcareous status to be ascertained, and species-poor grasslands and sandy areas (GST 2121, 2122, 2131, 2132, VST 5112, 5121), where the area of each type is very small and which often are situated contiguously in the landscape.

3.5. Exceptional and characteristic vegetation site types on Saaremaa and Muhu

Special characteristics of Saare county forests, related to soil, relief or landuse conditions have been referred to already in earlier reviews (Eichvald 1934; Mathiesen 1934), yet contemporary studies still find that a big part of this peculiarity does not fit into the typology (Reitalu and Trass 2002). The same paper contains one of the few Saaremaa-oriented typological lists, which differs in details from forest typology (Lõhmus 1984, 2004) and the extended vegetation site type classification (Paal 1997). Several characteristic features (Eichvald 1934; mainly based on Linkola 1929), are present also in the results of this study, based on contemporary vegetation site type classification (Paal 1997).

In heath pine forest have varying understorey vegetation; there can be other dominant species besides the lichens, mainly *Arctostaphylos uva-ursi* and to a lesser extent other species, e.g. *Deschampsia flexuosa*. During the data verification it emerged that the forest surveyors often define calcareous forest site types (*Arctostaphylos*-alvar and less often *Calamagrostis*-alvar) on non-calcareous Haplic Podzols (L), which are main site types for heath forests. Also during the fieldwork, communities similar to *Calamagrostis*-alvar site type were found on fine silica gravel (see chapter 3.5; Annex 2, Photo 1). Forest communities characteristic to calcium poor soils (*Calluna*, *Vaccinium vitis-idaea*, *Oxalis-Vaccinium myrtillus* site types) were also defined on calcium rich soils (Rendzic Leptosols, Calcari-gleyic Leptosols, Mollic Cambisols) (Palo et al. 2005).

Some studies have focused on dry pine forest communities with spruce and oak regrowth on moraine-based sandy soils, which are common on the Saaremaa Central Upland, but not so typical in other areas (Eichvald 1934; Eilart 1963; Örd 1981; Meikar 1990). In forest typology, besides the obvious mistakes (dry, according to the soil map on Gleyic Albeluvisols growing oak forest with abundant growth of *Pteridium aquilinum*, *Calamagrostis arundinacea* and *Melampyrum nemorosum* in understorey are defined by forest surveyor as (humid) *Dryopteris* site type) (Annex 1, Photo 2) these forests are also designated as alvar, dry boreal, meso-eutrophic boreo-nemoral hillock, fresh

boreal and fresh boreo-nemoral forest site type groups (Annex 1, Photos 3, 4; Annex 2, Photo 1). Similar communities, defined by understorey vegetation usually as meso-eutrophic boreo-nemoral hillock site type group, have also been described on sandy soils in South-Eastern Estonian uplands. To describe these soils, a special soil type “Arenosol” (Annex 1, Photo 1) has been distinguished (Paal 2004a). Factors influencing the development of this site type need further studies because abundant regrowth of oak, as well as other broadleaved trees, makes it reasonable to assume that forests on these site types have high species diversity and nature conservation value.

Some coastal forests in western Saaremaa on clayey soils and forests growing next to them, which in principle belong under alvar forests, are mentioned (Eichvald 1934). It was difficult to define them site type during the fieldwork, because they are characterized by a peculiar understorey vegetation community that differs from classical descriptions, and changes in the composition of the understorey vegetation do not follow the distribution of soil types. Most common species everywhere were *Sesleria caerulea* and *Molinia caerulea* and this made it difficult to separate between *Sesleria* and *Molinia* site type.

Also several communities defined according to the understorey as close to *Hepatica* site type were located on Gleysols (Palo et al. 2004, 2005; Annex 3, Photo 1). CCA analyses did not give reliable results for these site types, if the obvious relationships between absolute height and geographical coordinates are not taken into account. Probably understorey vegetation, which mainly uses resources located in upper soil layers, can resemble vegetation of dryer site types because of local microclimatic conditions. Water content of Saaremaa’s soils may seasonally strongly vary and coastal forests are characterised by summer drought. As a rule there is less precipitation compared to inland areas and more solar radiation together with stronger winds, which are accelerating total transpiration (Kaar 1959; Lillema 1964; Ratas et al. 1997a; Raudsepp and Jaagus 2002). The lower soil layers are gleyic, but dry microclimate in summer and specific coastal conditions are creating a vegetation composition that is more xerophilous. Studies about species richness on coastal alvar grasslands (Otsus 2004) outline the critical importance of precipitation for the establishment of seedlings for some species, and therefore their abundance in communities.

Slightly halophytic species (*Tetragonolobus maritimus* etc.) can be found in inshore (temporally) moist forests (on the Gleyic and Gleysols) hundreds of meters away from the current coastline. There also exist sparse primary forests on coastal soil, where they should not exist according to the literature (Paal 1997; Lõhmus 2004). Salinity does not have to affect tree growth (Paal and Rooma 2001), but its effect on the biological diversity of understorey vegetation on coastal soils is recognizable. Designation of Saaremaa’s coastal primary forests based on their species composition, structure and landscape characteristics may give additional information for predicting and monitoring the

development of nature in areas subject to land uplift (Ratas et al. 1997b). Environmental features in coastal forests affect also other life forms (strong winds affect the composition of flying insect community; Talvi 2004). Landscape characteristics are also included in the definition of alluvial forest and meso-eutrophic boreo-nemoral hillock forests (Masing 1969a; Marvet 1970; Paal 1997; Rannik 2005).

In Eichvald's text (1934) there is a reference to moist swamp deciduous forests. During the field works several deciduous forest stands with vegetation-free patches and high root stumps were also found, which were growing on soils not characteristic to classical swamp forest (Go, Gk, Gr, LG, Lkg, Kg; Annex 6, Figure 1 and Table 1) (Palo et al. 2004, 2005; unpublished data by Palo, Truu, Kanal, Aunap, Mander). If the presence of swamp forests on Calcari-gleyic Leptosols and Gleyic Albeluvisols needs further research, then the presence of alluvial forests on Gleysols in Saaremaa is common (Table 2) and related to seasonally high groundwater on clayey or limestone layers (Luha and Tammekann 1934; Perens 2002). In the above situation the correct site type should be *Filipendula* (sometimes also *Dryopteris* or *Molinia* FST) (Paal 1997; Lõhmus 2004), but that does not reflect the vegetation heterogeneity and/or understory species characteristic to those site types.

Deciduous and mixed forests are considered more similar than mixed and coniferous forests, it is also noted that deciduous forests are closely related with wooded meadows and typical wooded pastures (Eichvald 1934). The same tendencies occurred when contemporary vegetation was analyzed with CCA (Figure 1). In Saaremaa's environmental conditions it is questionable whether the distribution of *Aegopodium* site type can be related with soil type. *Aegopodium* site type is more frequently defined in deciduous forest stands, which can be former wooded meadows and wooded pastures, partially even former fields; therefore this forest site type can in Saaremaa be found, besides the typical Calcari-Gleyic Leptosols and Gleyi-Mollic Cambisols, also on dryer Rendzic Leptosols and Skeletic Leptosols (alvar nemoral forests) and on Rendzic Gleysols or Cambic Gleysols (Table 2). At the same time the part of *Hepatica* site type (usually coniferous- deciduous mixed forests) is defined on soils that are more suitable for *Aegopodium* site type (Table 2; Annex 3, Photo 1). CCA showed that *Paris quadrifolia* and *Melica nutans* probably grow in mixed forests of both site types. These shade tolerant species may indicate problems related to defining site types in closed mixed forest stands with almost missing understory vegetation. CCA on *Aegopodium* forest site type (Figure 2) suggests that the absence of *Aegopodium podagraria* is caused by a high proportion of coniferous trees in primary forests on the north and west coasts and in formerly grazed forests or in former semi-natural communities afforested by coniferous tree species, which is accompanied by a higher frequency of species tolerating more acid forest litter (Hédli 2004). This is mainly caused by changes in upper soil layer, because the effect of acid needle litter on whole soil development depends strongly on the calcium content of bedrock and on climate (Alfredsson et al. 1998; Augusto et al.

2002). Understorey vegetation species depend mainly on the chemical characteristics of the upper soil horizon, which however do not have to correlate unambiguously with the factors influencing the growth of trees, nor with the soil type (Kukk 1967; Rebane 1967; Masing 1998; Frey 2004).

North latitude, coniferous forests and afforestation are associated mainly (Figure 2) with *Mycelis muralis*, *Hypericum maculatum*, *Galium album*, *Rubus idaeus*; west longitude, and, to a lesser extent, slope angle are associated with *Maianthemum bifolium*, *Melampyrum sylvestris*, *Anemone nemorosa*, *Brachypodium sylvaticum*, *Poa compressa*, *Hedera helix*, *Neottia nidus-avis*, *Scorzonera humilis*, *Geranium sanguineum*. Absolute altitude on the other hand is associated with *Sanicula europaea*, *Anthriscus sylvestris*, *Geum urbanum* etc. In the eastern longitude there are considerably more species typical to site types (Figure 2), such as *Aegopodium podagraria*, *Poa nemoralis*, *Milium effusum*, *Lathyrus vernus*, *Campanula trachelium*, *Polygonatum odoratum* etc.). The occurrence of the natural *Aegopodium* site type forest is associated with the absolute altitude of the area (see also Figure 1) and it is more likely to be a mixed forest. Species grouping clearly indicate the transitional site types *Aegopodium-Filipendula* and *Aegopodium-Molinia* (*Filipendula ulmaria*, *Deschampsia caespitosa*, *Carex flacca*, *Carex sylvatica*, *Platanthera bifolia*, *Crepis paludosa*, *Potentilla erecta*, *Molinia caerulea*, *Agrostis capillaris*, *Carex nigra*, *Rubus caesius*, *Dactylorhiza fuchsii* etc.).

The diversity of the meadows is only briefly overviewed in this study. During the last century there have been vast changes in land use (Kukk and Kull 1997; Mander and Palang 1999; Pärtel et al. 1999a,b; Sooväli 2004;), which have induced continuous successional transitions in the few remaining areas used as pasture and mown up to virtually afforested areas or shrubs (relatively permanent tight juniper thickets and hazel groves with few trees). During fieldworks it was observed, that the soil type areas on the map often do not correspond with conditional borders of contemporary transitional phases of succession, meaning that there were different meadow successions from not overgrown up to afforested areas, in polygons simultaneously abandoned and hawing the same soils based on the soil map. They were also characterized by considerable differences in the hydrophilous character of vegetation patches. Contrary examples, where the heterogeneity of vegetation turned out to be smaller than the heterogeneity of polygons on the soil map, were found mostly in coastal meadows and mires overgrown by reed.

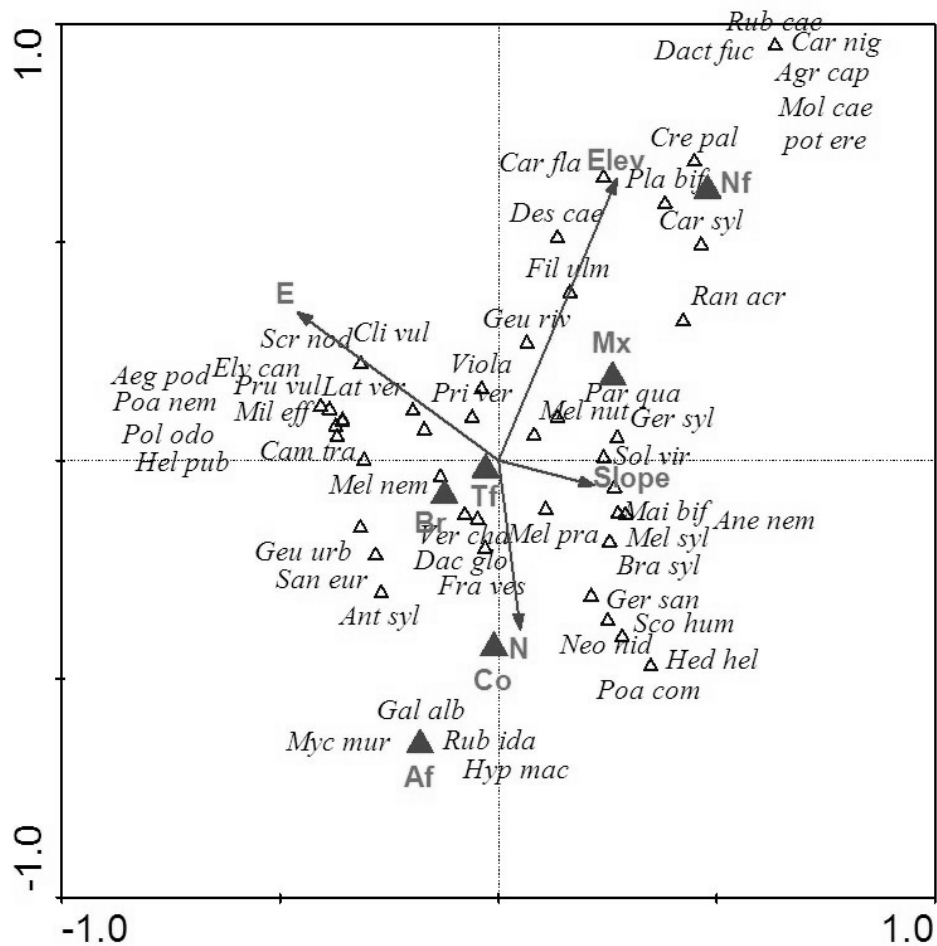


Figure 2. Ordination of *Aegopodium* site type plant species, based on Canonical Correspondence Analysis displaying 14.3% of the inertia in the abundances and 36.4% of the variance in the weighted averages of species with respect to the environmental variables. The eigenvalues of axis 1 (horizontally) and axis 2 (vertically) are 0.23 and 0.19, respectively. Arrows indicate quantitative environmental variables. The class variables are indicated by the triangles.

Abbreviations of variables: Elev — absolute elevation; Slope — slope angle; E — geographical coordinate East (Eastern longitude); N — geographical coordinate North (Northern latitude); Br — broadleaved forest; Co — coniferous forest; Mx — mixed forest; Af — afforested semi-natural or traditional agricultural forest vegetation; Tf — semi-natural or traditional agricultural forest vegetation; Nf — natural continuous forest.

The most diverse vegetation can be found in landscape concaves where the soil type defined by the soil map (Salic Fluvisols, different gleyic and Gleysols,

Eutri-sapric Histosols) gives us insufficient information about potential plant communities/site types (Palo et al. 2004) (Annex 4, Photos 1–6). Although during the fieldworks the soil type in these areas was not defined, *Cladium mariscus* “fens” (only on the Histosols according Paal 1997) could for example grow besides the Eutri-Sapric Histosols also on different Gleysols and on Salic Fluvisols, cemented and cleaved in dry summers. The vegetation covering the concaves could be extremely varied (there are communities, where prevailing species are either *Molinia caerulea*, *Potentilla anserina*, annual species, some *Carex* species, *Schoenus ferrugineus*, *Cladium mariscus* etc.). As plant communities, they belong mainly under the subtype of alvars such as concave alvars and plate alvars (Zobel 1987), which, in vegetation site type classification, is categorized usually under fresh and dry grassland site type, in case of thicker soils, also under fresh boreo-nemoral grasslands, paludified grasslands or even under fens (Paal 1997).

The study of Saaremaa and Muhu vegetation systematically indicated many cases, where the development of vegetation is affected more by human activity or other landscape parameters (absolute altitude, microclimate, probably also the flowing direction of (calcium-rich) waters etc.) than by soil. Thereby, on detailed scale maps, Saaremaa vegetation types can not be very precisely predicted only by soils, however, the additional data about tree layer composition and historical management allow the site type to be predicted with greater probability. Several vegetation types may need separately described subtypes (in some cases introduction of types described earlier and generalised in recent typologies), whereas the island’s inland and coastal area *versus* historically diversely managed areas may have subtypes differing by understorey vegetation as well as by stand parameters. Differences between islands and mainland are of course even greater.

3.6. Choice and accuracy of data layers

During the course of the study, the choice of available maps and digital data layers free of confidentiality or ownership restrictions increased steadily; as too did technological possibilities. The accuracy of determining fieldwork plots has improved considerably due to the use of GPS equipment, but this has also helped reveal errors in the data layers used for analyses. No systematic data layer checks have been performed, but when comparing different data layers in the sampling sites by hand, it became apparent that the discrepancy between today’s basic map and the Soviet era cadastral (land use) map, on which the digital soil map is based, could result in object displacements of up to 50 metres (unpublished data by Palo, Truu, Kanal, Aunap and Mander). The vegetation map compiled by combining different data layers (Palo et al. 2005), which used a pixel side length of 20m, highlighted 1–10 pixel-wide areas mainly along the

borders of polygons, in which the ground cover class and soil type were incompatible (e.g., mires on automorphic soils, automorphic soil forest types in mires) (Annex 1, Map 1, white areas excepting PpG).

Some errors have also occurred in the compilation of the soil map, where very clearly distinguishable positive relief features (therefore also automorphic soil instead of (semi)hydromorphic) are not represented on the map (Annex 1, Map 1), and data entry errors, where a map polygon delineated area actually exists in nature, but has been assigned the wrong soil code. The first type of errors are verifiable with the help of an accurate elevation model; the second type of errors can be pinpointed by analysing discrepancies between the elevation model, surface layer (bedrock) map, or some other data layers. Both methods are time consuming and unfeasible in the framework of the current research project.

As the spatial accuracy of fieldwork data increased, the question of scale also arose. In the coastal ridge and dune systems and also in the plains that have recently risen from beneath the sea, locations with different soil genesis conditions may alternate over distances of less than 20 m, while 15 m is the average legibly representable contour diameter on a 1:10000 scale map. The alternation of 3–5 m-wide strips of distinctly different vegetation site types was also observed in the field, which means that these soils must unavoidably be combined together into the soil type chosen by the mapper, and do not thus necessarily correspond to the soil as described at a vegetation description point. For such very mosaic areas or on relatively homogeneous forest and meadow areas, generalisations gave rise to soil combined polygons on the soil map, which were interpreted in data analysis according to the soil first mentioned. This may result in related vegetation site types being associated with each other's optimum soil. All the sources of the above errors reduce the reliability of the analysed relations.

Despite increased knowledge about the relations between Saaremaa's vegetation and soil cover and the use of modern soft- and hardware, it is still difficult to construct vegetation maps or models that reflect our current knowledge, since the mechanical (spatial) error of the data layers used is in places (still) too great. As a result the created map can either be used in generalised form, in which case the specific information about Saaremaa is lost, or relatively, as a so-called space pattern, in which case one can be relatively certain about the occurrence of a particular vegetation and soil combination within an area, but without field observations it is impossible (at the moment) to ascertain the exact location and actual extent of each community.

CONCLUSIONS

The development of vegetation is influenced by narrower biophysical landscape parameters than those used to define landscape mesochore types, also, they may occur, at least partly, independently of the mesorelief, or may recur in developmentally different localities.

In the formation of the vegetation cover of Saare County, both abiotic factors (e.g., post-glacial uplift, calcareous bedrock, soil type and texture and related productivity, hydrological regime, microclimate, relief factors) and human activities play an equally important role. For instance, traditional agriculture, forming semi-natural communities such as wooded meadows, alvar meadows (pastures) and grazed forests and forestry (especially, afforestation of abandoned agricultural lands) can be highlighted as significant activities.

Among the biophysical landscape factors absolute elevation, which correlates with the age of communities and geomorphological factors (accumulation and abrasion of sediments and deposits) and geographical location, integrating all the local factors) should be mentioned. According to the paradigm of distinguishing plant communities in continuous plant cover, location and spectrum of VSTs in toposequent gradient, slope, aspect and other topoedaphic characteristics should be taken into account when analysing the vegetation cover. However, due to the plain topography of the whole Saare County, their importance in prediction of VSTs remains low.

Additional biophysical landscape factors such as microclimatic features (along the gradient coastal zone — inland parts) and seasonal water regime dynamics along the topoedaphic gradient (seasonal interception of lateral carbonate water flow, severe drying up of the soil toplayer in vegetation period after being flooded in spring), which were not considered in this thesis, can play a significant role in terms of some VSTs.

The created map of VSTs can be used as source material for more general planning decisions, since the main vegetation complexes — characteristic forest, meadow, and mire types and type groups, are delineated. However, the created map of VSTs indicates the potential vegetation cover rather than the actual one because the latter is influenced by all the natural and anthropogenic factors which make it much more complex than the potential vegetation cover.

The present classification does not reflect enough plant communities that are important for practical nature conservation and biodiversity planning and their possible succession. For practical use, a kind of mixed typology, consisting of VSTs and VST groups and some additional landscape and biotope indicators, is recommended.

The main context of this particular case study was botanical and nature conservation oriented. Based on this character and related goals, several problems in the present classification of VSTs were highlighted. First of all, a large variety of small-scale biophysical landscape factors, as well as anthro-

pogenic factors, and their relationship on a spatio-temporal scale make the spatially explicit prediction of VSTs difficult. Another group of factors are several mistakes, from differences in interpretation to the incorrectness of (former) cartographic material used. VST-s classification as a expert-knowledge-based system is not flexible for the prediction of habitat preferences of organisms at higher trophical levels (e.g., bird, mammal and amphibian species).

Further GIS-based analysis of both biophysical and anthropogenic landscape factors, more detailed analysis of biotope quality indicators, and increasing topographic exactness of digital data would help in development of flexible and comprehensive classification of VSTs, biotopes, and habitats, for implementation in environmental management and nature protection.

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SUMMARY IN ESTONIAN

Maastikutegurite ning taimkatte kasvukohatüüpide vahelised seosed Saaremaa ja Muhu saare näitel

Eestis taimkatte kaardistamisel ning klassifitseerimisel traditsiooniliselt kasutatav paradigma määratleb taimkatte kasvukohatüübid kui ühtsetes abiootilistes tingimustes väljakujunenud sarnase rindelise struktuuri ja taimekooslusega üksused (Paal 1997), millest tuleneb ka tööhüpotees — valitud abiootiliste faktorite põhjal on võimalik prognoosida taimkatte kasvukohatüüpide esinemist piirkonnas. Taimkatte väljakujunemist suunavad tegurid ning muutusi ennustavad mudelid on juba aastaid olnud üheks ökoloogia uurimisteenaks. Olenevalt uurimisala asukohast võivad juhttegurid erineda, näiteks puudub Eestis vajadus arvestada vertikaalse tsonaalsusega, kuid isostaatilise maakerke tulemusena on meil rannikualade näol olemas looduslik katseala taimkatte tänapäevaste arengutegurite dokumenteerimiseks. Sadade ja kümnete aastatuhandetega mõõdetavatele looduslikele mõjutegureile nagu kliima ja geomorfoloogilised protsessid on viimaste aastatuhandete jooksul lisandunud inimtegevus. Ka Eestis on inimtekkelised maastikumuutused kohati ületanud abiootilistest faktoritest tingitud mitmekesisuse. Metsade kliimaatilised taastumistingimused on Eestis võrdlemisi head, mistõttu võib maastikul sedastada keerukat suksessioonilist taimkattemustrit. Taimkatte dünaamika ja struktuur määrab paljude spetsiifiliste kohastumustega liikide eluvõimalused maastikul.

1999. a. toimus Lääne-Eesti Biosfäärikaitseala finantseerimisel projekt, mille käigus uuriti digitaalse taimkattekaardi koostamise võimalusi. Teisenenud sotsiaal-poliitilised olud võimaldasid kasutada varem piiratud kättesaadavusega kaardimaterjale ja aerofotosid ning arenev infotehnoloogiline riist- ning tarkvara järjest lisanduvate digitaalkujul andmete sünteesimist ning verifitseerimist. Hilisemas uurimuses analüüsiti mõnede maastikuliste juhttegurite (absoluutne kõrgus, asend reljefil, mullatüüp ja mullalõimimine) seoseid taimkatte kasvukohatüüpidega. Uuriti ka traditsioonilise maakasutuse ja selle lõppemise, metsa puurinde koosseisu, paiga absoluutse kõrguse, reljefi kaldenurga ning uurimispunkti asukoha (geograafiliste koordinaatide) mõju kasvukohatüüpide floristilisele koosseisule.

Uurimisalana keskenduti Saaremaa ning Muhu saarele kui tervikule. Valitud piirkond on pärast mandrijää raskuse alt vabanemist olnud maakerkeala, mille maastikku on otseselt või kaudselt (rannikulüestikud jmt) kujundanud Läänemere transgressioonid ning hilisemal ajal ka pidev ekstensiivne põllumajanduslik kasutamine. Ligikaudu 200 aastat tagasi leidis vaid üksikuid tänases mõistes metsana majandatavaid alasid, kuid teisenenud majanduslikes oludes on olukord mõnedes piirkondades kujunenud vastupidiseks. Ulatuslikud sajandite vältel niitmiseks või karjatamiseks kasutatud poollooduslikud kooslused on maha jäetud ning nende suksessioonilisus loob ühelt poolt

ülihuvitava taimkattemosaigi, kuid teiselt poolt tõstatab küsimuse nii pärandmaastike loodusväärtuste kaardistamisest ja hooldamisest kui elutingimuste teisenemisest maastikul ning selle tagajärgedest liikidele.

Töös on kasutatud autori 1999, 2004 ja 2005.a. välitöödel kogutud taimkattekirjeldusi ning mullaandmeid, samuti mitmeid digitaalseid andmekihte, millest olulisemad on mullatüüpide andmestik (digitaalselt mullakaardilt), Eesti põhikaardi taimkatteareaalid, digitaalne kõrgusmudel, CORINE maakatteandmed ja paigasetüüpide vektorandmekiht. Andmete analüüsimisel ja kaardiloomel tehti koostööd mitmete kolleegidega.

Leiti, et Saare maakonna taimkatte kasvukohatüüpide tänapäevast levikupilti on põhiliste abiootiliste faktorite kõrval (milleks on mullatüüp, mulla lõimis ja mullatüübist sõltuv veerežiim/troofsus) mõjutanud inimtegevus ja suunanud muud maastikulised parameetrid. Maastikufaktoritest mõjutavad Saare maakonna taimkatet maismaa pärastjääaegse vanusega korreleeruv absoluutne kõrgus ning geograafiline asukoht. Selgus, et looduslikud metsad leetmuldadel ning rabad ja rabastuvad metsad paiknevad absoluutselt kõrgematel aladel. Leetmuldade ja sügavate turvasmuldade esinemine kõrgematel aladel seletub nende kujunemisega aastatuhandete jooksul ning pideva maakerke mõjuga, mistõttu rannikualad on sageli madalamad ja seal levinud mullad primitiivsemad. Samuti korreleerus absoluutselt kõrgeimate (vanimate) aladega kahe relikitse haruldase taimeliigi (*Vicia cassubica*, *Trifolium alpinum*) esinemine metsades. Seosed geograafilise asukohaga on kasvukohatüübi-spetsiifilised, mis viitab erinevaid kasvukohatüüpe kujundanud (säilitanud) põhimõjurite erinevusele piirkonniti. Olulisematest seostest võib välja tuua näiteks naadi kasvukohatüübi floristilise koosseisu erinevused, kusjuures tüüpilisi naadi kasvukoha tüüpi metsi (sageli pärandkoosluseid) leiab Saaremaa idaosast ja Muhumaalt; Saaremaa põhjaosas ja absoluutselt kõrgematel aladel esinevad looduslikud naadi-angervaksa ja naadi-sinihelmika üleminekutunnustega metsad, läänerranniku naadimetsade floristiline koosseis viitab aga loo-salu üleminekutüübile.

Mõnede metsakasvukohatüüpide varieeruvus alustaimestiku ja üldise puistuilme põhjal on väga suur ja ületab tunduvalt teoreetiliselt seatud abiootiliste kasvukohatingimuste piire (nn valed mullatüübid väljas määratud taimkatte kasvukohatüübi piires). Alustaimestu liigilisele koosseisule avaldavad tugevat diferentseerivat mõju puurinde koosseis ning metsa kasutusviis (põline metsamaa *versus* pärandkooslused), samuti ülalkirjeldatud asend reljeefil. Kogu kasvukohatüüpide sisest varieeruvust töös uuritud tegurid siiski ei seleta. Muudest biofüüsikalistest faktoritest võivad taimkatte arengut ja liigilist koosseisu mõjutada alade mikrokliima (gradiendil rannik-sisemaa) ja sesoonsed (karbonaatse) mullavee liikumise iseärasused reljeefil, samuti lähtekivimi iseärasused.

Uurimuse käigus loodud taimkatte kasvukohatüüpide kaart sobib üldisemate planeeringute alusmaterjaliks, sest joonistuvad välja põhilised taimkattekompleksid — iseloomulikud metsa-, niidu- ja sootüübid või -tüübirühmad.

Loodud kaardikiht väljendab pigem tänase Saaremaa potentsiaalset taimkatet, sest aktuaalse taimkatte väljakujunemist on mõjutanud kõik eelmainitud faktorid ja tegelik taimkate maastikul on seetõttu tunduvalt mitmekesisem.

Praegune taimkatte kasvukohatüüpide klassifikatsioon ei peegelda Saare maakonna kontekstis botaanikuile ja looduskaitajaile piisava objektiivsusega looduses olemasolevaid (kaitseväärilisi) taimkatteüksusi. Rakendusliku tulemuse parandamiseks tuleks kasutada n.ö. segatüpoloogiat, kus keskkonnamitingimustest üheselt sõltuvad kasvukohatüübid määratletakse klassifikatsioonis sisalduva tüübi või alltüübi täpsusega, teiste puhul kasutatakse lisatunnuseid maastikuliste eripärade kajastamiseks.

Saare maakonnas läbiviidud uurimuste kontekst oli botaanilis-looduskaitsealine, seda eesmärki silmas pidades tõusid selgelt esile mitmed praeguse taimkatte kasvukohatüüpide klassifikatsiooni (Paal 1997) alusel aktuaalse taimkatte määratlemist ja rühmitamist raskendavad aspektid, milleks on tegelike taimkatet kujundanud maastikufaktorite suur hulk ja raskestiennustatav koostõju konkreetses kohas, inimtegevuse erinevad vormid ning ka eristatud üksuste mitmetimõistetavus olenevalt lähtealusest (kasutatud klassifikatsioon — mulla-või taimkattetunnuste eelistamine) ja välitöötraditsioonist. Järgal etteantud kasvukohatingimuste klassifitseerimisel põhinevad lahendused ei ole ka piisavad enamuse organismirühmade elupaikade leviku ja kvaliteedi prognoosimisel. Omaette analüüsi ja mahukat tehnilist tööd vajab antud juhul veel digitaalsete ruumiandmebaaside topograafilise täpsuse tõstmine.

ANNEX 2



Photo 1. Three different field study points, where meso-eutrophic boreo-nemoral hillock forest STG (or *Calamagrostis-alvar* FST) grows on the Haplic Podzols (L; according to the soil map). In the soil profile (>10 cm) fine silica gravel was found. Soil did not consist carbonates: material from soil profile did not give any reaction with 10% hydrochloric acid.

ANNEX 3



Calcari-gleyic Leptosols (Kg).



Endo-Hyposalic Gleysol (Gr).



Rendzic Gleysols (Gk).

Photo 1. The coastal forests with non-typical underground vegetation on the gleyic and Gleysols. Our field work allowed to classify all sites as *Hepatica* FST.

ANNEX 4. Successional stages of plate and concave alvars.



Photo 1. Katre — Rendzi-Lithic Leptosols, Salic Fluvisols (Kh, Av) (*Herniaria glabra*).



Photo 2. Katre — Salic Fluvisols (Av) (*Molinia caerulea*, *Lysimachia vulgaris*).



Photo 3. Kuusnõmme — Salic Fluvisols (Av) (*Molinia caerulea*, *Cladium mariscus*).



Photo 4. Undva — Salic Fluvisols (Av) (*Cladium mariscus*).



Photo 5. Koorunõmme — Gleyic Rendzic Leptosols, Calcaric Gleysols (Khg, Gh) (*Molinia caerulea*, *Cladium mariscus*).



Photo 6. Undva — Calcaric Gleysols (Gh) (*Lysimachia vulgaris*, *Carex sp.*).

ANNEX 5

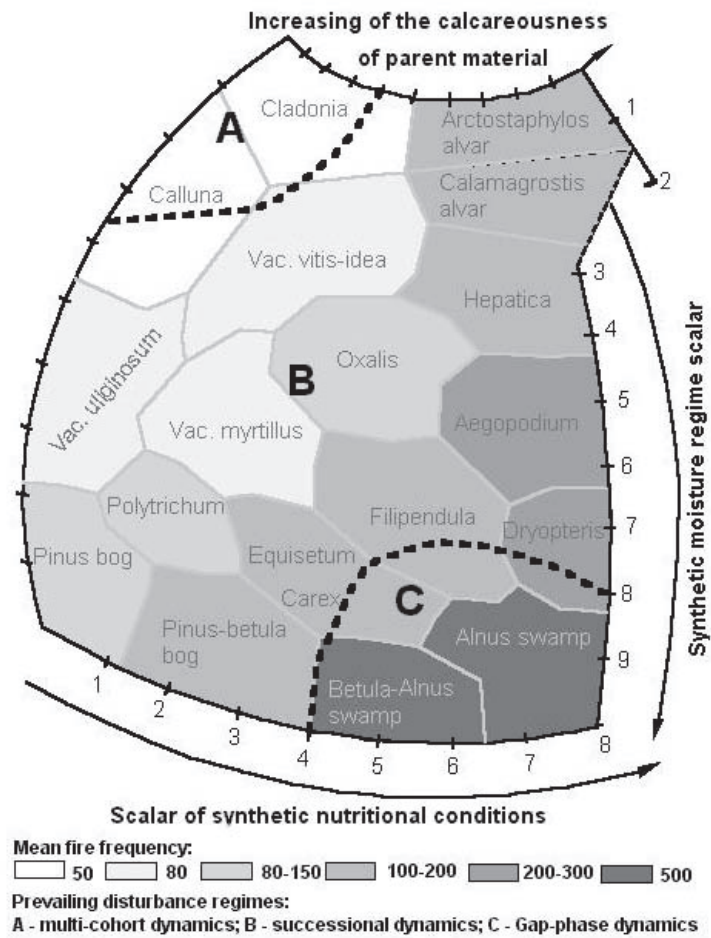


Figure 1. Estonian forest site types in the ordination plane of growing conditions (according to Lõhmus, 1984, modified), also describing natural fire frequencies and disturbance regimes in Estonian forest site types (Lõhmus et al. 2004). *Equisetum-Carex* (Lõhmus 1984) ~ *Molinia* (Paal 1997).

ANNEX 6

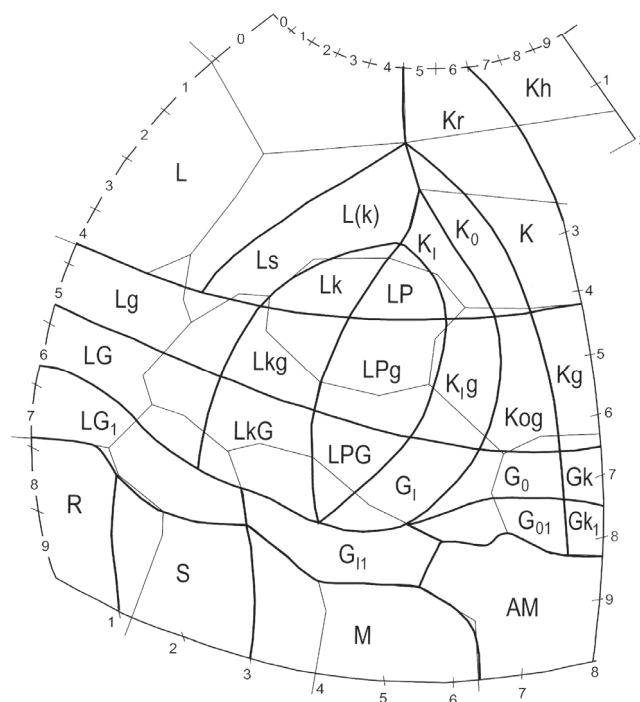


Figure 1. Estonian forest site types in the ordination plane of growing conditions (according to Lõhmus 1984, modified), also describing most distributed soil types (Lõhmus 2004, according to Asi, E., Kõlli, R., Laas, E. 2004).

Table 1. The codes explanation of Figure 1:

Code		Code	
K	Rendzic Leptosols	LP	Eutric Planosols
Kg	Calcari-gleyic Leptosols	LPg	Eutri-Gleyic Planosols
Kh	Rendzic Leptosols	LPG	Eutri-Stagnic Gleysols
Khg	Gleyi-Rendzic Leptosols		
Kk	Skeletal Leptosols	G1	Mollic Gleysols
Kkg	Gleyi-Skeletal Leptosols	G11	Molli-Histic Gleysols
Ko	Endocalcaric Cambisols	Gh	Calcari Gleysols
Kl	Endocalcaric Luvisols	Gk	Rendzic Gleysols
Kog	Endocalcari-Gleyic Cambisols	Go	Cambic Gleysols
Klg	Endocalcari-Gleyic Luvisols		
Kr	Skeletal Leptosols	AM	Flooded Sapric Histosols
L, Ls	Haplic Podzols	M	Eutri-sapric Histosols (Fens)
Lg	Gleyic Podzols	S	Fibric Histosols (Mires)
LG	Humic Gleysols	R	Dystric Histosols (Bogs)
LG1	Dystri-Histic Gleysols		
Lk, L(k)	Albeluvisols Leptic Podzols		
Lkg	Gleyic Albeluvisols		
LkG	Dystric Gleysols		

PUBLICATIONS

CURRICULUM VITAE

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Education

1985–1991 University of Tartu, Institute of Botany and Ecology
1996–1999 University of Tartu, Institute of Geography, MSc student
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Professional experience

1991–1993 Ministry of Environment Nature Conservation
Department, specialist
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1996–31.12.2004 Environmental Protection Institute of the EAU
01.04.2005–present Environmental and agricultural institute of the EAU
01.09.2005–present Institute of Sustainable Technology at TUT

Scientific activities

Participation in grant funded projects
Research on rare and endangered plant and animal species
in Estonia, the dynamics, conditions and factors influencing
of their populations and communities (2001–2005).

Participation in projects:

BioHab (A framework for the coordination of Biodiversity and
Habitats, EU Concerted Action under FP5)
IPA (Important plant Areas, Project of Planta Europa)
Forest key biotops (Östra Götaland, Sweden, County Forestry Board)
HELCOM (working group — Red List of Marine and Coastal
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Professional membership:

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Scientific interest:

Vegetation typology and relations to the landscape, vegetation conservation,
vegetation monitoring, ancient forests, rare vascular plant species.

PUBLICATIONS

- Külvik, M., **Palo, A.**, Kukk, Ü., Hurt, E., Kull, T., Parmasto, E., Vellak, K., Roosaluuste, E., Jüriado, I., Saar, I. 2005. IPA-s in Estonia. In: Anderson, S., Kušík, T., & Radford, E. (Eds), Important Plant Areas in Central and Eastern Europe. *Plantlife International*: 43–46.
- Palo, A.**, Aunap, R., Mander, Ü. 2005. Predictive vegetation mapping based on soil and topographical data: A case study from Saare County, Estonia. *Journal for Nature Conservation* 13: 197–211.
- Leito, A., Ojaste, I. Truu, J. & **Palo, A.** 2005. Nest site selection of the Eurasian Crane *Grus grus* in Estonia: an analysis of nest record cards. *Ornis Fennica*, 82(2): 44–54.
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- Leito, A. Ojaste, I., Truu, J., Kesksaik, J. **Palo, A.** 2004. Sookure pesitsemine Eestis. *ELUS Aastaraamat*, 82: 157–189.
- Lõhmus, A., Kohv, K., **Palo, A.** and Viilma, K. 2004. Loss of old-growth, and the minimum need for strictly protected forests in Estonia. In: *Ecological Bulletins* 51: 401–411.
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Haridus

1985–1991 Tartu Ülikool, bioloogia osakond
1996–1999 Tartu Ülikool, geograafia osakond, magistriõpe
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Teenistuskäik

1991–1993 Eesti Keskkonnaministeeriumi Tartu looduskaitseosakonna spetsialist;
1993–1996 Eesti Metsainstituudi looduskaitse uurimiskeskuse spetsialist;
1996–31.12.2004 EPMÜ Keskkonnakaitse Instituudi looduskaitse uurimiskeskuse spetsialist (teadur alates 1999);
01.04.2005– EPMÜ põllumajandus- ja keskkonnainstituudi teadur;
01.09.2005– TTÜ säästva tehnoloogia instituudi teadur.

Teadusorganisatsiooniline ja -administratiivne tegevus

Põhitäitja Eesti Teadusfondi grantides:

Haruldaste, ohustatud ja probleemsete liikide ning koosluste, elupaikade ja maastike struktuur, seisund ja dünaamika ning looduskaitsevalikud (2001–2005)

Osalemine projektides:

BioHab (A framework for the coordination of Biodiversity and Habitats, EU Concerted Action under FP5)
IPA (Important plant Areas, Planta Europa project — Tähtsad taimealad)
Forest key biotops (Östra Götaland, Sweden, County Forestry Board — metsa võtmebiotoobid ehk metsa vääriselupaigad)
HELCOM (töögrupp — Red List of Marine and Coastal Biotopes and Biotope Complexes of the Baltic Sea, Belt Sea and Kattegat)

Erialaliitude liige:

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OLULISEMAD PUBLIKATSIOONID

Külvik, M., **Palo, A.**, Kukk, Ü., Hurt, E., Kull, T., Parmasto, E., Vellak, K., Roosaluuste, E., Jüriado, I., Saar, I. 2005. IPA-s in Estonia. In: Anderson, S., Kušík, T., & Radford, E. (Eds), Important Plant Areas in Central and Eastern Europe. *Plantlife International*: 43-46.

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