The prediction of vegetation pattern using biophysical landscape factors

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Abstract

We analyzed the spatial correlation of biophysical landscape factors (absolute elevation, slope angle, position on slope, soil type, soil texture) with vegetation site types (VST) and vegetation site type groups (VSTG) in 16 key areas (5-8 km^2 each) on the western Estonian islands of Saaremaa and Muhu. The main objectives of this study were to estimate the predictability of VSTs or VSTGs on the basis of soil parameters and topographical characteristics, and to prepare the existing data layers for the compilation of the digital vegetation cover model of this area. Altogether, 57 VSTs and VSTGs, 34 soil types, 19 groups of soil texture, 7 slope angle classes, 10 classes of catenary position and 16 classes of absolute elevation (0…>30 m) were distinguished. Based on various digitalized material (rasterized cadastral land use map, 1:10000; vector-format mesoscale landscape units (mesochore) subtypes map, 1:50000; vector-format CORINE Land Cover map, 1:100000; digitalized maps of soil types and textures, 1:10000; color infrared (CIR) aerial photographs, 1:10000; digital terrain models, 1:10000; biotope maps, (1:10000), the classification of Estonian vegetation site types and type groups, and field work results, we provided map overlay analysis using the toroidal shift method and the Microsoft Visual Basic for Applications module. In general, the various wetland VSTs/VSTGs and plant communities in drier positions and with higher elevations (on the upper parts of steeper slopes) showed the strongest significant association with biophysical landscape factors. However, calcareous bedrock, Ca-rich soils, a strong influence of the successional stage due to the uplift of the area, and the long-term human influence on both islands have caused an enormous variety of biophysical factors, which creates a much more complex association/segregation of VSTs and VSTGs with landscape factors than expected.

Keywords: map overlay analysis, toroidal shift, landscape map, biophysical factors, topography, soil type, soil texture, vegetation site types.

Geo-Environment, J. F. Martin-Duque, C. A. Brebbia, A. E. Godfrey & J. R. Diaz de Teran (Editors)

1 Introduction

A large variety of information sources are available in the Earth sciences, with data originating from various measurement devices and mapping methods taken over different sampling volumes and time intervals. Despite the uncertainties and errors in all topographic data, it is possible to estimate the indicator value of different data sources and to use these data as fuzzy indicators. The predictability of the spatial pattern of vegetation is one of the primary problems in ecology [1, 2, 3, 4, 5]. Several studies consider the predictability of vegetation cover pattern based on topographical data [6, 7, 8, 9, 10, 11], soil conditions [7, 12] and (micro)climatic conditions [9, 13]. Fuzzy systems theory [9, 14, 15], patch-based spatial modeling [16], and artificial neural networks [17] have been used as novel methods for modeling the distribution of vegetation. However, only a limited number of studies consider the overlay analysis of biophysical landscape factors and vegetation site types on a detailed scale [10, 18].

We therefore decided to analyze the predictability of vegetation site types (VSTs) and vegetation site type groups (VSTGs) [19] based on the topographical (digital terrain) and soil data in some nature protection areas that lacked an actual vegetation map. Two islands in the Western Estonian archipelago, Saaremaa and Muhu, proved to be an ideal location for our studies, although they have a complex pattern of both biophysical factors and vegetation cover [20].

The objectives of this study were: (1) to estimate the predictability of VSTs or vegetation site type groups (VSTGs) on the basis of soil parameters and topographical characteristics (digital terrain model parameters), (2) to analyze possible reasons for errors and disharmony between the distinguished units of vegetation cover and soil maps and topographical data, and (3) to prepare the existing data layers for the compilation of the digital vegetation cover model for this area.

2 Materials and methods

2.1 Study area

The study area included 16 key areas from the islands of Saaremaa and Muhu, which are part of the West-Estonian Archipelago Biosphere Reserve. The formation of these islands is connected to the postglacial uplift of the earth's crust; the first parts of the island appeared in the early Holocene (9000 yrs before the present) [20]. At present, uplift continues at the 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 sedimental rocks from the Silurian era. The layer of glacial sediments (abraded till, abraded endmoraines, glacio-lacustrine clays and sands, marine, lake and palustrine sediments) is up to 40 m deep. Topography is plain or undulated, 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 age predominate on both islands. Calcareous plateaus with narrow soil cover (alvars) are typical of

Geo-Environment, J. F. Martin-Duque, C. A. Brebbia, A. E. Godfrey & J. R. Diaz de Teran (Editors)

these islands. A great variety of topographic and geological features, calcareous bedrock, calcium-rich glacial sediment and relatively mild maritime-type climatic conditions dedicate a mosaic of vegetation cover which is, on the other hand, heavily influenced by human activity (most of all by traditional agriculture). Due to 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 [21]. 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 [22]. To protect the unique and heterogeneous flora, fauna and landscapes of these islands, a dense network of protected areas and recently established Natura 2000 areas covers about 18.6 % of the terrestrial part.

The key areas selected vary by size, since 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 [23, 24, 25], we preferred the varying size according to the landscape structure and biotopes' heterogeneity.

We analyzed the correspondence of biophysical landscape factors with vegetation site types (VST) and vegetation site type groups (VSTG) in 16 key areas (5-8 km^2 each) on the islands of Saaremaa and Muhu.

3 Field studies and maps

The following materials served as the basis for the work: (1) a raster-format land use map (Estonian cadastral map; 1:10,000); (2) a vector-format mesoscale landscape unit (mesochore) subtypes map (1:50,000 [26]); (3) a vector-format CORINE Land Cover map (1:100,000) [27]; (4) digitalized maps of soil types (1:10,000); (5) color infrared (CIR) aerial photographs (1:10,000); (6) digital terrain models (1:10,000) [28]; (7) classification of Estonian vegetation site types and type groups [19]; (8) biotope maps (1:10,000) [28, 29].

The mesoscale map of landscape unit subtypes was superimposed on a cadastral map, resulting in a synthesized map that served as the basis for the fieldwork. The vegetation pattern was thoroughly examined using aerial photographs prior to the fieldwork; the information obtained from cadastral maps and mesoscale landscape unit subtype maps was explored [29]. Provisional routes were designated in order to determine which locations to cover for specifying biotope structure and vegetation types in the research area. The fieldwork included the documentation of field data and photographing of biotopes. The map of biotopes was drawn on transparent plastic overlaid on the aerial photo, by interpolating the data regarding the composition of biotopes in the field study area of 5-8 km^2. A mesoscale map of landscape units subtypes was used to specify the potential borders of vegetation site types within a similar biotope (e.g. forest). The data regarding biotope structure, vegetation site types and additionally compiled information were entered in a digital database.

Previously compiled biotope maps were scanned, georeferenced and digitized in MapInfo format (version 5.0). The field work's entry numbers were used as identifiers for aerial objects.

3.1 Overlay analysis

The overlay of soil classes and parameters of the elevation model with VSTs and VSTGs was analyzed using a special module written in MicroSoft Visual Basic for Applications.

Table 1: Codes of soil types and soil texture groups that occurred in key areas [30].

Soil type code	Soil type (WRB-FAO/UNESCO)	Soil texture code	Soil texture group
T	Disturbed soils on gravel and sand quarries	**S**	clay, loam
K	Rendzic Leptosols	**LS**	sandy loam, clay-loam
Kg	Calcaric-gleyic Leptosols	**SL**	loamy sand, clayey sand
Kh	Rendzic Leptosols	**RL**	sand with limestone fragments
Khg	Gleyic Rendzic Leptosols	**RsL**	loamy sand with limestone fragments
Kk	Skeletic Leptosols	**RlS**	sandy loam with limestone fragments
Kkg	Gleyic Skeletic Leptosols	**sL/lS**	loamy sand on sandy loam
Ko	Mollic Cambisols	**sL/P**	loamy sand on calcareous regolith
Kog	Gleyic Mollic Cambisols	**lS/P**	sandy loam on calcareous regolith
Kr	Skeletic Leptosols	**L**	sand
L	(Primitive) Podzols	**V**	pebbles
Lg	Gleyic Podzols	**RS**	clay with limestone fragments
LG	Humic Gleysols	**KS**	stony clay
Lk	Leptic Podzols	**KL**	stony sand
Lkg	Gleyic Podzols	**KlS**	stony sandy loam
LkG	Dystric Gleysols	**KsL**	stony loamy sand
G	Gleysols	**T**	peat
Gh	Calcaric Gleysols	**L/p**	sand on calcareous regolith
Gk	Rendzic Gleysols	**P**	calcareous regolith
Go	Cambic Gleysols		
Gr	Calcaric Gleysols		
AG	Eutric Fluvisols		
Ar	Coastal Ridge Soils		
ArG	Marsh Soils		
AM	Flooded Histosols		
M1-3	Eutric-sapric Histosols (Fens)		
S1-3	Fibric Histosols (Mires)		
R1-3	Dystric Histosols (Bogs)		
V	Submerged (Littoral) Soils		

We used the method of random shifting of map layers called toroidal shifts, as it is similar to the rotation of one tube within another [31]. This method has been used in several ecological studies for the comparison and edge correction of point patterns [32, 33, 34, 35, 36, 37]. In each study site, 200 random shifts in the direction of both Cartesian coordinates were undertaken. The extents of overlap and the maximum possible overlaps calculated for correction from all study sites were analysed together. Overlaps are characterized as relative values (*O*) showing how much the actual extent of overlap differs from expected overlay in the case of the random distribution of patterns. The greater the value of *O*, the greater the difference in the actual extent of overlap, and the more closely the two data sets are associated. On the other hand, *O* values below 0 demonstrate the avoidance (segregating character) of two data sets, while 0-values indicate random distribution. In all cases, the level of significance was: $\alpha=0.05$. The toroidal shift helps to avoid biased estimations caused by spatial autocorrelation [38, 39, 40].

According to Paal [19] and Palo [41], 57 VSTs and VSTGs were distinguished in all of the 16 key areas. In all of the key areas, digital maps of VSTs and VSTs were superimposed with topographical and soil data layers of the following classes: **(1)** absolute elevation (16 classes in the range of 0…>30 m a.s.l.), **(2)** elevation relative to the mean elevation at 100m distance (9 classes), **(3)** elevation relative to the minimum elevation at 100m distance, (9 classes), **(4)** surface curvature along the direction of aspect (position on slope or catenary position; 10 classes divided into 3 subclasses of upper, middle and lower slope), **(5)** slope aspect as the direction of the steepest descent (4 classes), (6) slope angle in degrees derived from the maximum difference in elevation of neighboring cells (7 classes), **(7)** soil type (34 classes; Table 1), **(8)** soil texture (19 classes; Table 1).

Topographical features were extracted using the IDRISI32 TOPOSHAPE module by Clark University, US. All data layers were analyzed within the same 10x10 m^2-size pixels.

4 Results and discussion

4.1 General overlapping results

On the basis of the overlay pattern of distinguished VSTs and VSTGs with each of the selected biophysical landscape factors (absolute elevation, slope angle, position on slope, soil texture, soil type), we classified the overlapping types in the following order: A – clear avoidance (segregation; $p\leq0$ by $\alpha<0.05$), B – mixed association and avoidance (all of the p values presented), and C – clear association (possibility of overlapping extent $p>1$ by $\alpha<0.05$; see Table 2 and Fig. 1-4). The recombination of all the A-, B-, and C-types of overlapping over all of the data sets of both topographical and soil factors gives the following classes of VSTs and VSTGs: **(a)** Clear segregation and/or association (A- and C-types presented; 10 VSTs or VSTGs found), **(b)** Mixed segregation and association (both A-, B- and C-types; 28), **(c)** Association with some segregation

Geo-Environment, J. F. Martin-Duque, C. A. Brebbia, A. E. Godfrey & J. R. Diaz de Teran (Editors)

(A- and B-types; 4), and **(d)** Clear association (only C-type; 15). No clear avoidance (only A-type) was observed. For instance, the mesotrophic (mixotrophic) bog forest ST (code 30, Table 2) would not be found at certain elevation above sea level (>30m a.s.l.), in the middle segment of slopes, and in sandy or gravel soils. On the other hand, this type is strongly integrated with clayey or peat soils, peatland soil types and is found on transition bog plains or fen plains. The coastal grassland STG (code 4) is clearly associated (only C-type presented) with the middle and lower segments of slopes on clay and/or peat soils.

In general, the various wetland VSTs/VSTGs and plant communities in drier positions with higher elevations (upper segments of steeper slopes) showed the strongest significant association with biophysical landscape factors. Nevertheless, calcareous bedrock, Ca-rich soils, the strong influence of the successional stage due to the uplift of the area, and long-term human influence on both islands have generated an enormous variety of biophysical factors, which creates a much weaker association/segregation of VSTs and VSTGs with landscape factors than expected.

The following detailed analysis of the association/segregation of VSTs and VSTGs with concrete biophysical conditions will offer a clearer picture of the predictability of vegetation cover patterns.

4.2 The overlapping of VSTs with topographical features

Due to low absolute elevation and the uplift-influenced continuity of vegetation cover succession in the Holocene, many VSTs and VSTGs associate or segregate with absolute elevation values (Fig. 1 upper part). At the lowest position (0-2 m a.s.l.), shallow water VSTs (reed-beds; code 57 in Table 2), geolittoral and epilittoral grasslands (42 and 43), as well as *Calla* swamp forest VST (29, Fig. 1 upper part). At the same time, the dry alvar grassland ST (34) 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 forest VSTs (10 and 11), *Vaccinium vitis-idaea* and *Vaccinium myrtillus* boreal forest STs (12 and 13, respectively) and dry boreal heath grassland VSTs (36), and second, vegetation of raised bog complexes such as oligotrophic (ombrotrophic) bog forest VSTs (31), mixotrophic (transitional) grass mire VSTs (49) and hummock and hollow-ridge bog VSTs (52 and 53). Sandy areas at higher elevations (>30 m a.s.l.) represent dune complexes. Raised bogs that need a long time period for their development are found on higher plateaus that rose above sea level as the first parts of these islands [20]. Paludified forest VSTs are found at both lower and higher elevations. Somehigher-elevation VSTs such as *Filipendula, Polytrichum*, and *Vaccinium uliginosum* paludifying forest VSTs, forests (23, 26, and 27, respectively) are typically found in depressions between the dunes and coastal ridges.

The association of VSTs with elevation relative to the minimum elevation at 100m distance was quite similar to the association/segregation with absolute elevations. For instance, VSTs located at low absolute elevations were predominantly found relatively close to the minimum elevation at 100m distance.

Geo-Environment, J. F. Martin-Duque, C. A. Brebbia, A. E. Godfrey & J. R. Diaz de Teran (Editors)

These include freshwater and halotrophic waterbodies (5 and 56), wet floodplain grassland VSTs (41), species-rich (eutrophic) fen and minerotrophic quagmire (meso-eutrophic quaking fen) VSTs (47 and 48, respectively), mixotrophic grass mire VSTs (49), hummock bog VSTs (52), oligotrophic bog forest VSTs (31) and *Filipendula* and *Vaccinium uliginosum* paludifying forest VSTs (23 and 27, correspondingly).

Also, both littoral grasslands (42 and 43) and shallow-water VST (reed bed) VSTs (57), *Sesleria* alvar (8), *Oxalis-Vaccinium myrtillus* boreal (14), *Molinia* paludifying (24), *Polytrichum-Vaccinium myrtillus* paludifying (25), *Oxalis* drained peatland (33) and mesotrophic bog forest (30) VSTs and *Salix* floodplain shrubland (21) VSTs are located significantly close to the relative minimum elevations. They all are associated with gleyic soils, gleysoils and/or peatland soils.

In contrast to the elevation relative to the minimum elevation, the elevation relative to the mean elevation (both at 100m distance) did not bear a significant relation to the location of VSTs. Only the littoral grasslands (42, 43) and shallow water (reed-bed) VST (57) are always located significantly lower than the mean elevation (at 100 m radius). It is obvious that the *Cladina* boreal heath (10) and *Calluna* boreal heath (11) forest VSTs, as well as dry alvar (34) and dry boreal heath grassland (36) VSTs, are located higher than the mean relative elevation, although no significant association/segregation has been found. This is most likely related to the low absolute elevations and relatively plain relief of these islands. The relatively high location of the *Polytrichum* paludifying forest VST (26) is explained by their vicinity to raised bogs, which are located on the oldest (highest) parts of Saaremaa Island.

The plain topography of the Saaremaa and Muhu islands clearly influences the relations between the distribution of VSTs with their catenary position, slope angle and slope aspect. Typical VSTs on plain areas (slope angle $<3^o$) are wet and paludified forests like the *Salix* floodplain shrubland VST (21), *Molinia* paludifying (24), *Polytrichum-Vaccinium myrtillus* paludifying (25), mesotrophic bog (30), oligotrophic bog (31), *Vaccinium myrtillus* and *Oxalis* drained (32 and 33) peatland forest VST-s. As is to be expected, all mire-sites and waterbodies are on plain areas. On the other hand, *Cladina* boreal heath (10), *Calluna* boreal heath (11), *Vaccinium vitis-idaea* boreal (12), *Corylus* boreo-nemoral hillock (18) and *Polytrichum* paludifying forest (26), and dry alvar grassland VSTs (34) prefer steep slopes. However, all of these can also be found on less steep slopes (Fig. 1 lower part). The *Vaccinium vitis-idaea* boreal (12) and *Corylus* boreo-nemoral hillock (18) forest VST prefer south-facing slopes; while gray coastal dune VSTs (54) predominantly face northward.

According to classical knowledge in this field (Lõhmus, 1984), the *Calamagrostis* alvar forest VST (7), the *Hepatica* (19) and *Aegopodium* boreo-nemoral (20) forest VSTs, and the *Vaccinium myrtillus* boreal (13), *Oxalis-Vaccinium myrtillus* boreal (14), *Oxalis* boreal forest (15) VSTs should be presented on non-paludified plains with low slopes. However, none of these VSTs and VSTGs gave statistically significant relations with slope angle.

Table 2: Ordination of vegetation site types (ST) and site type groups (STG) in accordance to the overlapping character of their patches with selected biophysical landscape factors (AE–absolute elevation, Sa –slope angle, PoS–position on slope: U–upper, M–middle (stable), L–lower, STex–soil texture: C&P–clay (loam) and peat, S&G–sand and gravel; SType–soil type: Am–automorphic soils, G–glayic soils, Gs–gleysoils, P–peatland soils). Overlapping types with biophysical factors: A–clear avoidance (segregation), B–mixed association and avoidance, C–clear association. Only statistically significant (α<0.05) overlay extents are given. Example: the mesotrophic (mixotrophic) bog forest VST is never located at a certain height above sea level (>30m a.s.l.), in the middle section of slopes, and in sandy or gravel soils. This type is strongly integrated with clayey or peat soils, peatland soil types, and is found on transition bog plains or fen plains.

Vegetation site types and site type groups	**Code**	**AE**	**Sa**	**PoS**			**STex**		**SType**				**Score**
				U	**M**	**L**	**C&P**	**S&G**	**Am**	**G**	**Gs**	**P**	
Clear segregation and/or association													
Mesotrophic (mixotrophic) bog forest ST	**30**	A			A		C	A				C	3A+2C
Mixotrophic (transitional) grass mire ST	**49**	A	C			A					A	C	3A+2C
Paludifying eutrophic grassland ST	**45**							A	A	C	C		2A+2C
Fresh floodplain grassland ST	**40**	A	C			A					C		2A+2C
Halotrophic lake ST	**56**					A		A	C		C		2A+2C
Eutrophic boreo-nemoral forest STG	**9**		C		C		A	C		C	C		A+5C
Oxalis boreal forest ST	**15**	C						C		C		A	A+3C
Vaccinium myrtillus drained peatland forest ST	**32**		C			A						C	A+2C
Paludifying mesotrophic/oligo-mesotrophic grassland ST	**44**						C				C		A+2C
(Wooded) hollow-ridge bog site type	**53**	C	C			A						C	A+2C
Mixed segregation and association													
Eutrophic fen ST	**47**	B	C	A	B	A	C	A	A	A	C	C	5A+2B+4C
Dry alvar grassland ST	**34**	A	B	C	B	C	B	B	C	A	A	A	4A+4B+3C
Type class of vegetation of fresh waterbodies	**5**	B		A	B		A	A	B	A	C	B	4A+4B+C

Dry boreo-nemoral grassland ST	**38**	A			B	C	B	B	C	A	A	A	4A+3B+2C
Vaccinium vitis-idaea boreal forest ST	**12**	B	B	C	A	C	A		C		A	A	4A+2B+2C
Geolittoral grassland (marsh) ST	**42**	B	B		B	C	A	B	A	A	B	C	3A+5B+2C
(Wooded) hummock bog ST	**52**	C		A	B	A	C	A				B	3A+2B+2C
Epilittoral grassland ST	**43**	B	C		A	C	C	C	A	A	B		3A+2B+4C
Wet floodplain grassland ST	**41**	A	B				C			A	A		3A+1B+C
Calamagrostis-alvar forest/shrubland ST	**7**	B	B	C	B		B	A	C		A		2A+4B+2C
Molinia paludifying forest ST	**24**	A	B				B		A	C	B	B	2A+4B+C
Filipendula paludifying forest ST	**23**	B		C	B	A	B		A		C	C	2A+3B+3C
Vaccinium myrtillus boreal forest ST	**13**	B			A		A		C	C	B		2A+2B+2C
Cladina boreal heath forest ST	**10**	B	B	C	A	C		C	C		A		2A+2B+4C
Calluna boreal heath forest ST	**11**	C	B	C	A	C			C		A		2A+B+4C
Oxalis-Vaccinium myrtillus boreal forest ST	**14**				C	A	A	C	B	C			2A+B+3C
Sesleria-alvar forest/shrubland ST	**8**		B				C	A		C	C	A	2A+B+3C
Meso-eutrophic quaking fen subtype	**48**	A	B		A			C					2A+B+C
Hepatica boreo-nemoral forest ST	**19**		B	C	C		B	C	B	B	B	A	A+5B+3C
Shallow water ST	**57**	B				C	C		B	A	B	C	A+3B+3C
Aegopodium boreo-nemoral forest ST	**20**	B					B	B	C	C	A		A+3B+2C
Polytrichum-Vaccinium myrtillus paludifying forest ST	**25**	C	B				A			B	C	C	A+2B+3C
Dry boreal heath grassland ST	**36**	B	B	C	A	C							A+2B+2C
Oxalis drained peatland forest ST	**33**		B		C	A						B	A+2B+C
Polytrichum paludifying forest ST	**26**	C	B	A		C		C		C		C	A+B+5C
Vaccinium uliginosum paludifying forest ST	**27**	C		A	B		C			C		C	A+B+4C
Meso-eutrophic fen ST	**46**		B		C				A		C	C	A+B+3C
Corylus boreo-nemoral forest ST	**18**	C		C			A	B					A+B+2C

Association with some segregation													
Gray coastal dune ST	**54**		C	C	B	C		C	C				B+5C
Stagnant water swamp forest ST	**28**				B	C		C		C		C	B+4C
Brown coastal dune ST	**55**		B		C			C	C				B+3C
Salix floodplain shrubland ST	**21**	B	C									C	B+2C
Clear association													
Arctostaphylos-alvar forest/shrubland ST	**6**												(C)*
Eutrophic alvar forest and shrubland STG	**1**								C				C
Moist alvar grassland ST	**35**							C					C
Heath moor ST	**51**	C											C
Oligo - mesotrophic boreal forest STG	**2**											C	C
Spring fen ST	**50**						C						C
Antennaria boreo-nemoral hillock forest ST	**16**	C							C				2C
Fragaria boreo-nemoral hillock forest ST	**17**	C							C				2C
Dryopteris paludifying forest ST	**22**						C					C	2C
Coastal grassland STG	**4**				C	C	C						3C
Calla swamp forest ST	**29**	C									C	C	3C
Eutrophic paludifying forest STG	**3**	C									C	C	3C
Oligotrophic (ombrotrophic) bog forest ST	**31**	C	C									C	3C
Moist boreo-nemoral grassland ST	**39**						C	C	C		C		4C
Dry boreal grassland ST	**37**		C	C		C		C		C			5C

* - associating only with mesochore type data set which is not considered in this study

Geo-Environment, J. F. Martin-Duque, C. A. Brebbia, A. E. Godfrey & J. R. Diaz de Teran (Editors)

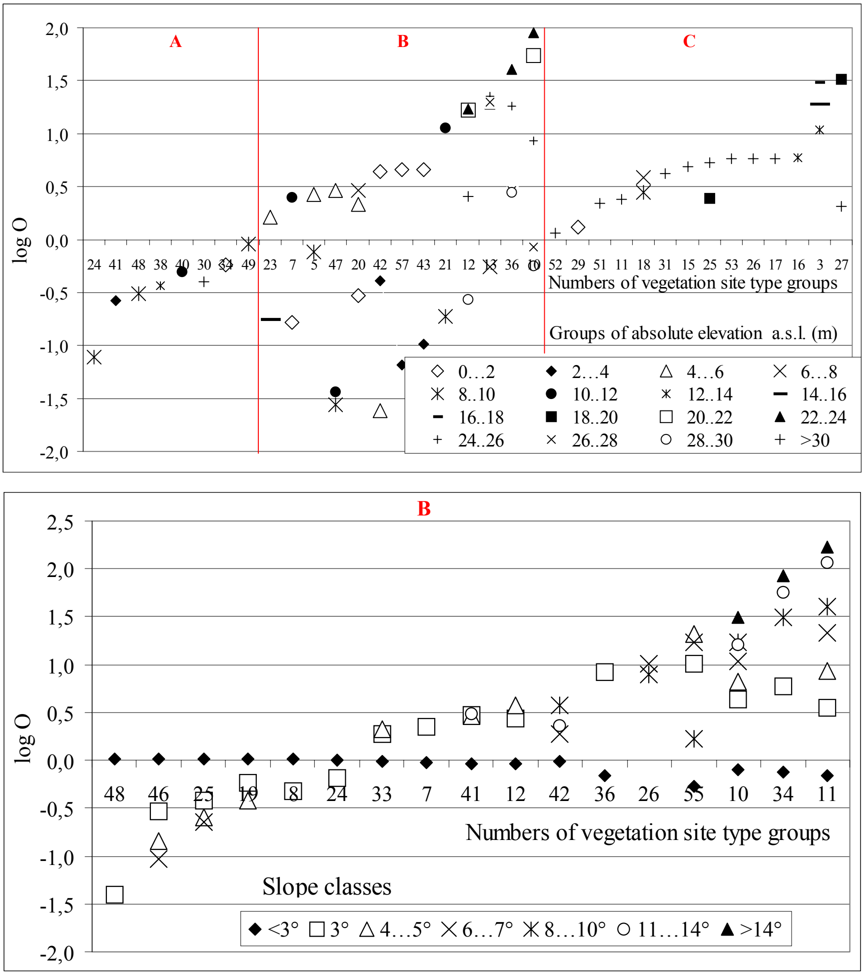

Figure 1: Ordination of vegetation site types and site type groups (see codes in Table 1) according to the logarithm values of overlapping extents (*O*) with absolute elevations (above) and slope angle classes (below). A–clear overlapping (association), B–mixed overlapping and avoidance, C–clear avoidance (segregation). Only statistically significant ($p<0.05$) overlay extents are given.

The dry boreal heath, dry grassland and dry alvar grassland VSTs (36, 37 and 34), *Cladina* boreal heath (10), *Calluna* boreal heath (11), and *Calamagrostis* alvar (7), *Corylus* boreo-nemoral hillock (18) forest VST, as well as gray coastal dune VSTs (54) are typically found on the upper segments of slopes (Fig. 2 upper part). At the same time, *Polytrichum* paludifying forest VST (26), geolittoral (marsh) and epilittoral grasslands (42 and 43, respectively), and shallow water VST (reed bed) VST (57) 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.

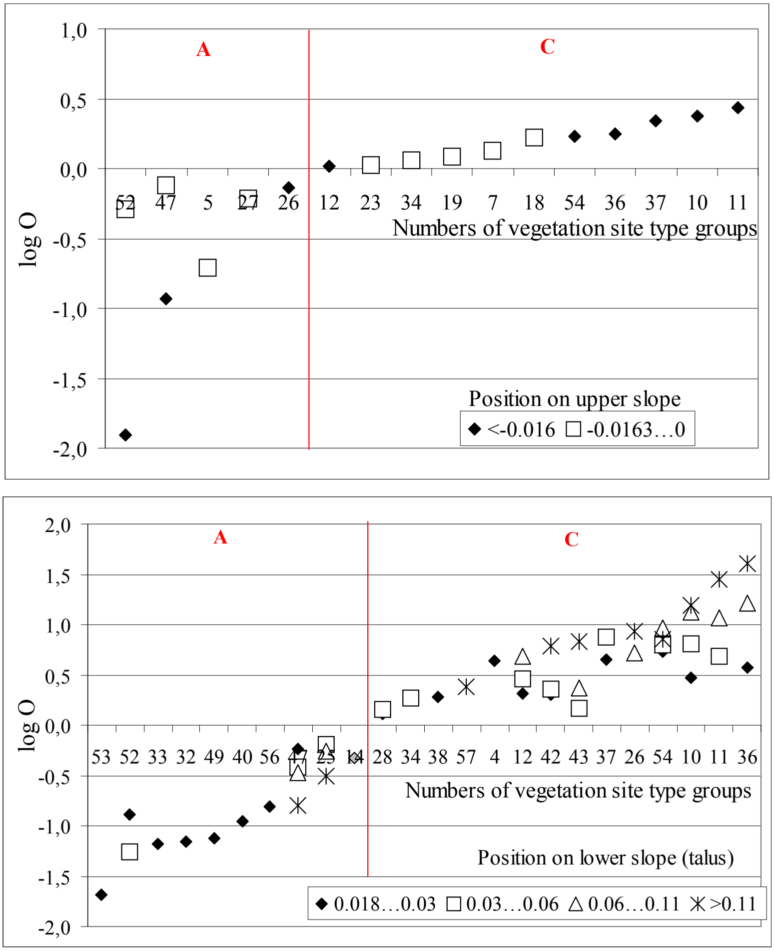

Figure 2: Ordination of vegetation site types and site type groups (see codes in Table 2) according to the logarithm values of overlapping extents (*O*) with different positions on slope. For explanation see Fig. 1.

4.3 Overlap of VSTs with soil characteristics

The nutrient-rich soils (K, Kr, Ko, Kh, Kg, Kk, Khg, Kkg, Kog; see Table 1) bear few significant correlations with VSTs. A better relationship has been found with VSTs that avoid these soil types (Fig. 3, 4). In contrast, less nutrient-rich soils (L, Lg, LG, Lk, Lkg, LkG) or peatland soils (M1-3, S1-3, R1-3) are more significantly associated than segregating with VSTs. Soil texture classes are significantly correlated with VSTs that prefer carbonaceous soils (see Lõhmus [41]). An unexpectedly low number of significant overlaps was found with forest VSTs that prefer peatland soils, such as *Calla* swamp (code 29, Table 2), mesotrophic bog (30), oligotrophic bog (31), *Vaccinium-* (32) and *Oxalis* drained (33) peatland forest VSTs. This is probably due to the influence of the carbonaceous bedrock of these two islands, which equalizes the acid peat conditions.

The most typical soil types in our key areas were the Skeletic Leptosols (10.5% of the area) and Rendzic Leptosols of various depths (8.7%). According to different classifications [19, 30, 42], dry alvar- and boreo-nemoral hillock forest VSTGs (16, 17) and some boreo-nemoral forest VSTGs (18, 19) are expected on these soils.On the islands of Saaremaa and Muhu, however, we only found a few significant overlaps between these soils and VSTs. On Rendzic Gleysols (Gk, 7%), *Molinia* paludifying forest VST (24) is expected [42], and this is supported with a significant overlap value. In addition, the correlation between the soil texture classes (rlS, see Table 1) and the *Molinia* paludifying forest VST is expectedly significant. In addition, the species-rich paludifying grassland VSTs (45) and species-rich fen VSTs (46) are expected on Gk soils [19], although on Saaremaa the most significant overlapping values have been found with Gleyic Skeletic Leptosols (Fig. 4). The species rich fens can also be found on various gleysoils and peatland soils.

Cambic Gleysols (9.4%) are represented by a great variety of both species-rich and species-poor VSTs, but all prefer wet conditions.

The Mollic Cambisols (7%) are, as expected, covered by the *Antennaria* boreo-nemoral hillock, *Fragaria* boreo-nemoral hillock (16) and the *Hepatica* boreo-nemoral forest (17) VSTs. Some of these forest are probably “hidden” in the *Vaccinium vitis-idaea* boreal forest VST (12) because the ground-layer plant species composition is sometimes similar in these forest VSTs. Again, the calcareous-rich conditions may be a reason for this coincidence. On the other hand, some overcoming VSTs between the *Vaccinium vitis-idaea* and *Antennaria-* and *Fragaria* boreo-nemoral hillock forest VSTs are foreseen in earlier classifications [42].

Very thin Rendzic Leptosols on calcareous plateaus are most typically covered by dry alvar grasslands (34). This VST is associated with soil texture classes of rsL, lS/P and V (see Table 1). On Gleyic Rendzic Leptosols of lS/P texture class, the *Sesleria* alvar forest VST (8) is predominant. In addition, this forest VST is significantly associated with Calcaric Gleysols. The moist alvar grassland VST (35) is expected on Gleyic Rendzic Leptosols [19], although no significant correlation has been found. The species-rich paludifying grassland VST (45) and the species rich fen VST (47) are typically found on these soils. The most closely associated texture classes of these VSTs are the V, rS and T classes (Table 1, Fig. 3).

Skeletic Leptosols, with their high water permeability (texture class V dominates), are typically covered by dry alvar grasslands (34). Here, the sandy soil texture classes with limestone fragments (rsL, rL, L/P) dominate (Fig. 3). The *Arctostaphylos* alvar forest VST (6), which is supposed to be the most typical VST on these soils [42], does not offer any significant overlaps. Significant occurrence of species-rich paludifying grasslands (45) was found on Gleyic Skeletic Leptosols, as expected [19].

Among nutrient-poor soils, various Podzols are represented (Fig. 4). The Primitive Podzols are typically covered by *Cladina* boreal heath (10) and *Calluna* boreal heath forest (11) VSTs. Surprisingly, no significant correlation was found with soil texture class. On these soils the *Vaccinium vitis-idaea* boreal (12) and *Vaccinium myrtillus* boreal (13) forest VSTs can also occur, although these VSTs are most typically associated with Leptic Podzols and Gleyic Podzols. In addition, the *Oxalis-Vaccinium myrtillus* boreal forest VST (14), the *Oxalis* boreal forest VST (15) and the *Filipendula* paludifying (23) and stagnant water swamp forest VSTs (28) have been found on these soils, although for two last VSTs these soil types are non-typical.

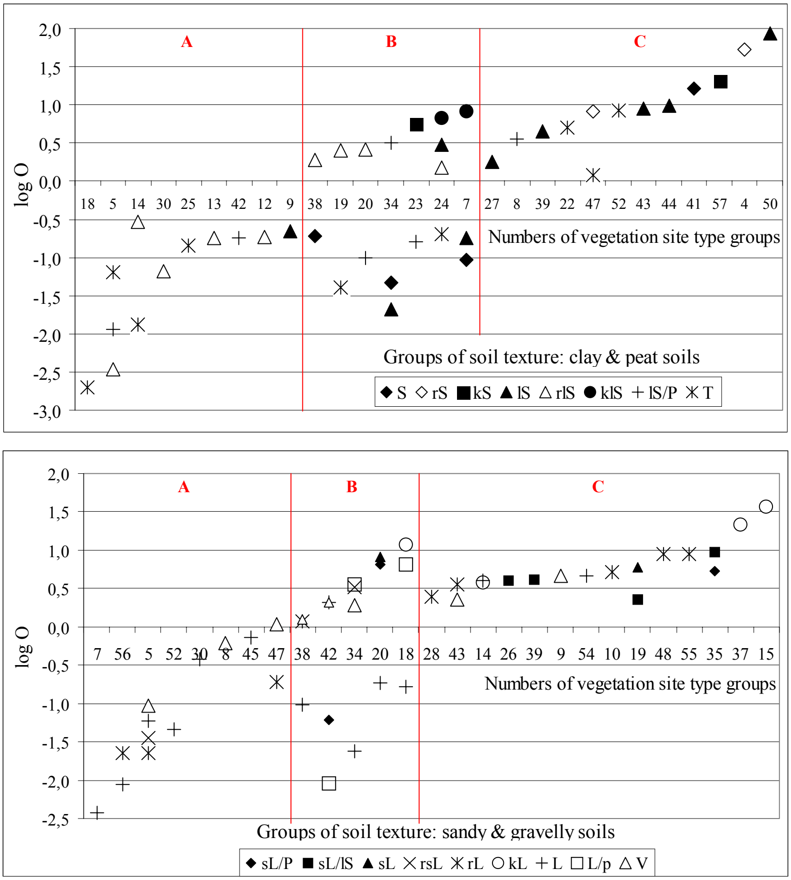

Figure 3: Ordination of vegetation site types and site type groups (see codes in Table 2) according to the logarithm values of overlapping extents (O) with soil texture groups (see codes in Table 2). For explanation see Fig. 1.

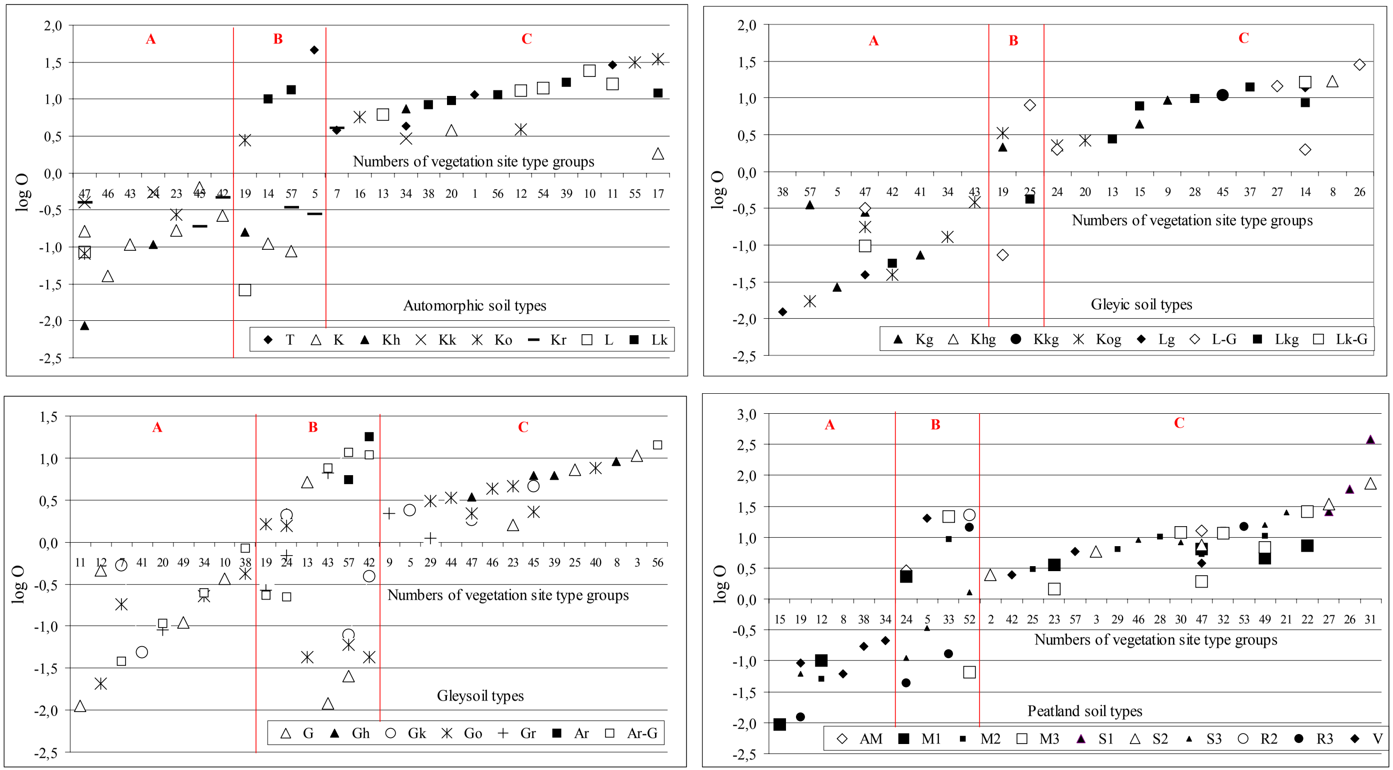

Figure 4: Ordination of vegetation site types and site type groups (see codes in Table 2) according to the logarithm values of overlapping extents (*O*) with soil types (see codes in Table 1). Explanation see Fig. 1.

The *Oxalis-Vaccinium myrtillus* boreal (14) and *Oxalis* boreal forest (15) VSTs, as well as the *Corylus* boreo-nemoral hillock forest VST (18) prefer sandy soils. Surprisingly, the *Corylus* boreo-nemoral hillock forests, which are supposed to be correlated with Rendzic Leptosols and Mollic Cambisols [19, 42] are typically found on Leptic Podzols (Fig. 4). The similarity of ground-level plant cover with that of the *Oxalis-Vaccinium myrtillus* boreal and *Oxalis* boreal forest VSTs may be the reason for complications in determining VSTs in the field.

The dry boreal heath- and dry boreal grassland VSTs (36 and 37) can typically be found on various Podzols, but they are only presented in small patches (0.1% of key areas). The same is true of the gray and brown coastal dune VSTs (54 and 55), which also cover about 0.1% of the total area. The brown coastal dunes are partly formed on very dry Mollic Cambisols of sandy texture in very plain areas, which is an unexpected result [19], although more detailed investigations in the field are required in this area.

The most typical VSTs growing on Dystric Gleysols are the *Oxalis* boreal and *Oxalis-Vaccinium myrtillus* boreal forest VSTs (15 and 16). The Humic Gleysols are typically covered by the *Oxalis-Vaccinium myrtillus* boreal (15), *Polytrichum-Vaccinium myrtillus* paludifying (25), *Polytrichum* paludifying (26), and *Vaccinium uliginosum* paludifying forest (27) VSTs. All of these communities prefer sandy loams and loamy sands on sandy loams. The *Molinia* paludifying forest VST (24) can occur as a transitional VST of these soils.

Various coastal and littoral/alluvial soils (AG, AM, Ar, ArG, Gr, V; Table 1) are very typical for both islands. As expected, geolittoral and epilittoral grasslands (42 and 43) are typical VSTs on these soils. The geolittoral grassland VST also occurs on submerged soils, and both grassland types are typical on Coastal Ridge Soils and Marsh Soils. On the latter, significant occurrence of halotrophic waterbodies (56) and shallow water VST (reed beds; 57) was observed. Submerged soils are expectedly represented by freshwater bodies (5), shallow water VSTs (57), geolittoral grassland VST (42) and the species rich (eutrophic) fen VST (47). Variety of soil texture reaches from sandy and stony to the clay and regolith classes (Fig. 3). In addition to the predominant epilittoral grasslands (43), the forests of boreo-nemoral VSTG and *Calla* swamp forest VST (29) can occur on coastal Calcaric Gleysols (Gr).

Alluvial soils (AM; Table 1) are less often presented, and the most typical VSTs on these soils are the *Molinia* paludifying forest (24) and the species-rich fens (47).

Peatland soils are normally the most representative, as concerns VSTs [19, 42]. However, in our key areas the VSTs typical for gysils or even gleyic soils grow on peatlands: the *Salix* floodplain shrubland VST (21), *Dryopteris* paludifying (22), *Filipendula* paludifying (23), *Molinia* paludifying (24), *Polytrichum-Vaccinium myrtillus* paludifying (25), *Polytrichum* paludifying (269, and *Vaccinium uliginosum* paludifying forest (279 VSTs. On the other hand, some communities that are typical for peatland communities, for instance the stagnant water swamp (28), *Calla* swamp forest (29) VST, and the *Vaccinium myrtillus* drained peatland forest VST (13), may occur on gleysoils. In addition, the overlap analysis of soil texture classes and VSTs yields some atypical results (e.g., the *Dryopteris* paludifying forest VST on peat). Although there are some atypical results, the typical peatland VSTs such as raised bog communities (52, 53) and transitional grass mires (49) occur significantly on various peatland soils (R, S; Table 1)

The heath moor VST (51), which should be associated with Gleysols [19], avoids these soils. During the field work, the heath moor was defined as a burned or intensively drained part of *Calluna*- raised bogs on deep R soils. Therefore, based on the soil data, the heath moor should be included in the hummock bog VST (52).

5 Conclusions

The great variety of soil types related to paludifying forests, peatland forests, mires and paludifying grasslands reflects the varied mosaic topographic and soil conditions of Saaremaa and Muhu islands: no large homogeneous areas are found. This is caused by post-glacial uplift and various sea transgression periods in the Holocene, and significantly influences the heterogeneity of the vegetation cover. All of these conditions make the prediction of the vegetation pattern very complicated.

Therefore we can conclusively say that our expectations concerning the predictability of VSTs and VSTGs on the base of soil types and topographical factors were not 100% fulfilled. Apart from the objective reasons such as the enormous variability of parameters and relatively low age of soils and vegetation in this particular region, additional reasons for the unexpected results are: occasional inadequacies in the definition and classification of VSTs, the incorrect determination of VSTs in the field, and mistakes on soil maps. We can, however, expect much improved spatial overlapping in future, when corrections in the classifications of soil types and VSTs are included.

Our results also show that the VSTs on non-typical soil types and/or texture classes create a variety of transitional VSTs. Further investigations should be undertaken to test the reliability of these overlapping classification units. Especially, VSTs, such as the *Oxalis* boreal and *Arctostaphylo*s alvar forest VSTs, brown coastal dune VST, moist alvar grassland, dry and moist boreo-nemoral grassland, wet floodplain grassland, and the species-poor paludifying grassland VSTs, which were expected to be typical for certain soil conditions, require more detailed analysis.

In the further analysis of vegetation pattern predictability, we plan to use the principal component analysis and canonical correspondence analysis for the determination of complexes of biophysical conditions that significantly influence the vegetation pattern. In addition, fuzzy classification technique in combination with artificial neural networks and machine learning programmes are promising techniques for obtaining more reliable results. These would help in the compilation of an adequate digital vegetation cover model of the islands of Saaremaa and Muhu.

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