

ARTICLES

Saaremaa and Gotland: a Comparison of Calcareous Pine Forests

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Abstract

The pine forests on shallow calcareous rendzina-like soils have a limited distribution in the northern Europe. Due to the peculiar ecological conditions, these forests include different floroelements together with red-listed species and have high value for biodiversity conservation. The calcareous pine forests are well represented in two biggest islands of the Baltic Sea – in Saaremaa and Gotland. The aim of the paper was to compare the floristic composition and environment conditions of calcareous pine forests on these islands, to elucidate their typological similarities and divergence, and to estimate the characteristic/indicator species in the established forest types. In Gotland 34 stands and in Saaremaa 35 stands were studied on 0.1 ha sample plots. For data processing the detrended correspondence analysis, cluster analysis, the multi-response permutation procedure, the indicator species analysis and the multiple regression analysis were used. The soil humus horizon chemistry characteristics (pH, nitrogen and carbon content, and their ratio) in the considered forests vary within quite narrow limits; the difference of soils is mainly expressed by the humus horizon thickness, from which depends the soil water holding capacity. Climatically, Saaremaa has a lower average temperatures and more precipitation than Gotland. For calcareous pine forests on both islands numerous significant indicator species are characteristic, whereby this list is two times longer for Gotland. The total number of species in Saaremaa depends significantly (negatively) only on the dominating pine trees abundance, in the forests of Gotland the shrub layer coverage has cardinal importance. On the number of shrub layer species on both islands the shrub layer coverage has a significant impact but in Gotland also abundance of spruce has considerable effect. On the communities level the disagreement between the compared islands is even more conspicuous than on the species level: from nine established community types three are connected exclusively with one island, with Saaremaa or Gotland; on both islands only communities of two types are represented more or less evenly.

Key words: Alvar forests, classification structure, human impact, indicator species, Rendzinas, species diversity.

Introduction

In Baltoscandia, the forests on shallow calcareous Rendzina-like soils occur in western and north-western Estonia (Lõhmus 2004), in Sweden and Norway they have a wider geographical distribution but mostly an island-lake appearance (Bjørndalen 2002). The tree layer of these forests is usually dominated by Scots pine (*Pinus sylvestris*) (Lippmaa 1940, Karu 1956, Laasimer 1975, Bjørndalen 2002), along the ecological and phytogeographical gradients still numerous subtypes can be recognized (Karu 1956, Muiste 1957, Kaap 1964, Bjørndalen 1980). In Estonia, the re-

spective communities are called as ‘*loopealsed metsad*’ or ‘*loometsad*’ (Laasimer 1965, 1975, Paal 1997, Lõhmus 2004), translated into English or Russian as ‘alvar forests’ (e.g. Laasimer 1946, Cenn 1962, Kaap 1964, Paal, 1998). The Scandinavian scientists have used several terms for naming these forests – calcicolous woods (Pettersson 1965), basiphilous forests (Bjørndalen 1980, 1985), basicole forests (Engelmark and Hytteborn 1999) or forest on calcareous ground (Påhlsson 1998), using the term ‘alvar’ traditionally only for open grasslands on limestone pavements and/or Rendzina soils (Albertson 1946, Hæggsström 1983, Rosén and Borgegård 1999). To avoid further confu-

sion, we call these communities as calcareous pine forests in this paper.

Calcareous pine forests have been of great interest for scientists due to their peculiar ecological conditions and vegetation including different floroelements together with red-listed species (Sterner 1922, Pettersson 1958, 1965, Laasimer 1965, 1975, Bjørndalen 2002). They contain, e.g. species from forest-rim communities, calcareous shallow-soil communities, meadows, steppe communities, acidophilous pine forests and alpine *Dryas* communities (Bjørndalen 1985). In that way these forests have high value for biodiversity conservation (Bjørndalen and Brandrud 1989, Paal 1998, Bjørndalen 2002) but for sustainable management and elaboration of optimal protection measures a good knowledge of their peculiarities and variation is needed. The aim of this paper was to compare the floristic composition and environment conditions of calcareous pine forests on two biggest islands in the Baltic Sea – Saaremaa and Gotland. We wanted to elucidate also their typological similarities and divergence, and to estimate the characteristic/indicator species in the respective forests of both islands and in the established forest types.

Materials and Methods

Gotland and Saaremaa are both formed on the Silurian limestone deposits (Raukas and Teedumäe 1997, Calner et al. 2004). These two biggest islands in the Baltic Sea have an approximately even size (Gotland 2.994 km², Saaremaa 2.673 km²), and rather similar environmental conditions. Gotland is located apart from Saaremaa ca. 1° to S and 4° to W (Figure 1). Gotland is the only area in Fennoscandia, where calcareous pine forest constitute a major element of the landscape (around 60% or ca 1,800 ha of the area; Bjørndalen

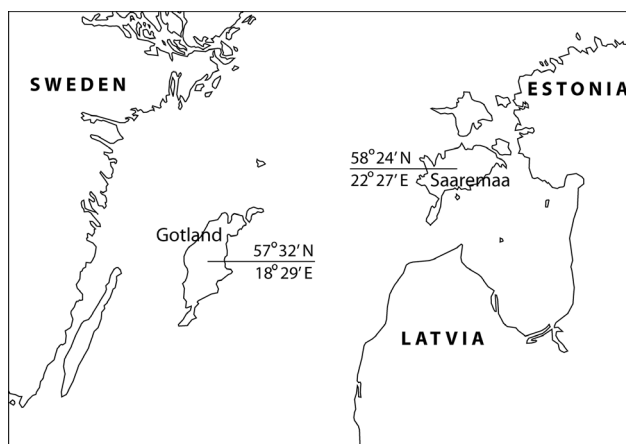


Figure 1. Location of Gotland and Saaremaa Islands and their centroid coordinates

2002), in Saaremaa these forests cover ca. 7,400 ha and there among them also pine stands prevail (Kaap 1964).

For the current study, forests without obvious indicators of recent cuttings or intensive grazing were selected. Therefore, in Gotland only 34 stands and in Saaremaa 35 stands located all over the islands were analysed. The early history of forest in Saaremaa Island was estimated from detailed topographic maps from the period of 1894–1920 (map scale 1:42000; the Estonian Land Board: www.maaamet.ee).

We used for vegetation analysis round sample plots with an area 0.1 ha (radius 17.4 m), which fitted within a homogeneous forest patch. All sample plots were located on areas with even topography. The tree layer was described by the basal area of tree-trunks and by the canopy closure. The basal area was estimated for every tree species at breast height (1.3 m) and only trees with a diameter at breast height (DBH) larger than 5 cm were registered. Young trees, having a height below 5 m and/or a DBH less than 5 cm were considered as saplings and recorded together with the shrub layer. In every sample plot, the basal area measurement was repeated in 4–5 random locations and averaged per site. The canopy closure, and in Gotland additionally the tree layer height were evaluated visually. The forest understory was described by counting stems of all species of shrubs and tree saplings on five randomly placed subplots with a radius of 2 m. Shrub species outside the subplots were taken into account with number 1. In the field (grasses + herbs + dwarf shrubs) and moss layer vegetation the species total list on 0.1 ha sample plot was compiled and the cover-abundance rating was conducted according to the scale: 0.1 (single specimens), 1 (average cover ≤1%), 2 (≤5%), 3 (≤10%), 4 (≤25%), 5 (≤50%), 6 (>50%).

For the morphological description of soils, a pit was dug in the middle of each sample plot. In the laboratory the following soil properties of the humus horizon were estimated: pH_{KCl}, the percentage of organic C content by oxidation of all organic matter with K₂Cr₂O₇ (according to Воробьева 1998), the percentage of total nitrogen by the Kjeldahl method (van Reeuwijk 1995). All analyses were performed from the fine soil fraction with a diameter less than 2 mm.

The nomenclature of vascular plant species follows mainly Mossberg and Stenberg (2003), by *Hieracium bifidum* and *H. caesium* Krall et al. (2007), by *H. murorum* Lid and Lid (2005); names of bryophytes are taken from Nationalnyckeln (2006, 2008).

Data processing

For ordination of the sample plots and environmental variables the detrended correspondence analysis

(DCA) was used (McCune and Mefford 1999). Cluster analysis was performed by the shrub layer and ground vegetation (field and moss layers) data, using the $\bar{\alpha}$ -flexible algorithm (McCune and Mefford 1999) and the Euclidean distance as the measure of dissimilarity. The clusters (= community types) were established on the basis of a dendrogram. Objectivity of relevés clustering was tested by the multi-response permutation procedure (MRPP) (McCune and Mefford 1999). Before the DCA and cluster analyses species occurring in data less than three times were filtered out.

The indicator values of the species in both islands as well as in community types were calculated by the Dufrene and Legendre (1997) method included into the program package PC-ORD (McCune and Mefford 1999). The statistical significance of the obtained indicator values were evaluated by the Monte Carlo permutation test ($N = 499$).

Differences in single soil properties and vegetation structure variables between the community types were tested by the univariate ANOVA and post-hoc Tukey HSD test (StatSoft Inc. 2011).

Dependency of species richness on environmental factors was ascertained by the stepwise forward multiple regression analysis (StatSoft Inc. 2011).

Results

On both islands in calcareous pine forests 410 species were recorded all in all; of them 127 were not found in Gotland and 97 in Saaremaa, thus, the overlapping species list included 186 species. The total list of Gotland's species comprised 278 taxa; five species in the tree layer, 40 species in the shrub layer, including saplings, 157 species in the field layer and 76 species in the moss layer. In Saaremaa altogether 312 taxa were discovered; seven species in the tree layer (*Populus tremula* and *Tilia cordata* were not recorded in Gotland), 36 species in the shrub layer, including saplings, 174 species in the field layer and 95 species in the moss layer. The gradient length by DCA on the ground of Saaremaa data is considerably larger than according to Gotland's data: along the first ordination axis 3.6 versus 2.4 standard deviations of species turnover and along the second axis 2.3 versus 1.9 standard deviations, respectively. But comparing the average number of species *per* community, the species richness appears to be higher in Gotland forests: the total number of species in Saaremaa stands is 53 and in Gotland communities 59, the number of shrub and sapling species 9 and 12, the number of field layer species 31 and 35, while the average number of bryophyte species is 12 in forests of both islands. In Gotland forests we found eight protected species of

orchids (<http://www.lansstyrelsen.se/gotland/Sv/djur-och-natur/hotade-vaxter-och-djur/fridlysta-vaxter-och-djur/Pages/fridlysta-vaxter-och-djur.aspx>): *Cephalanthera longifolia*, *Epipactis atrorubens*, *E. helleborine*, *Listera ovata*, *Neottia nidus-avis*, *Orchis mascula*, *O. spitzelii* and *Plantanthera bifolia*. In Saaremaa forests the number of protected species (http://et.wikipedia.org/wiki/Looduskaitse_all_olevad_liigid_Eestis) was even a bit longer; there were registered orchids such as *Cypripedium calceolus*, *Epipactis atrorubens*, *E. helleborine*, *Goodyera repens*, *Listera ovata*, *Neottia nidus-avis*, *Plantanthera bifolia* and *P. chlorantha* but also *Pinguicula alpina*, *Pulsatilla pratensis*, *Malus sylvestris* and bryophyte *Campylium calcareum*.

The floristic distinction of compared forests on both islands is statistically confirmed by the indicator species analysis: according to that numerous species are significantly characteristic either for respective forests in Saaremaa or Gotland (Table 1), whereby this list is two times longer for Gotland. Two indicator species of Gotland's forests, *Calamagrostis varia* and *Sorbus hybrida* are not presented in Estonian flora. Moreover, in Estonian flora one are lacking also numerous species or their subtaxa recorded by us in Gotland only in one or two communities: in the shrub layer *Cotoneaster simonsii*, *Mahonia aquifolium*, *Cerasus vulgaris* and *Juglans regia*, in the field layer *Anthericum ramosum*, *Cerastium pumilum*, *Crepis tectorum* var. *glabrescens*, *Globularia vulgaris*, *Luzula multiflora* ssp. *divulgata*, *Monotropa hypopitys* ssp. *hypophegea*, *Orchis spitzelii*, *Pilosella officinarum* ssp. *peleteriana*, *Ranunculus polyanthemus* ssp. *polyanthemus*, *Sanguisorba minor* ssp. *minor* and *Senecio jacobaea* ssp. *dunensis*, in the moss layer *Bryum torquescens*, *Cephaloziella divaricata* var. *asperifolia*, *Cephaloziella divaricata* fo. *striatule*, *Dicranum tauricum*, *Grimmia montana*, *Hedwigia ciliata* var. *ciliata*, *Schistidium laucifolium*, *Schistidium submuticum* var. *submuticum*. Most striking is the dissimilarity in the shrub layer: species such as *Cotoneaster scandinavicus*, *Prunus spinosus*, *Rosa canina* and *R. mollis* having in the Gotland forests rather high relative frequency (62%, 65%, 56% and 44%, respectively; Table 1) were not recorded in the corresponding forests of Saaremaa. At the same time, from species of Saaremaa forests only *Rosa subcanina* is not presented in Swedish flora and *Calamagrostis arundinacea* is substituted in Gotland with a vicariant species *Calamagrostis varia* (Mossberg and Stenberg 2003).

By the sensitivity to human impact, estimated from the standpoint of Estonian flora (Kukk 1999), among indicator species of vascular plants apophytes

Table 1. Indicator species of calcareous pine forests in Saaremaa (Saa) and Gotland (Got) Islands; only species occurring at least in three communities are presented. Notations: SHI – sensitivity to human impact (HF – hemeraphob, HD – hemeradiaphor, AF – apophyte, AnF – antropophyte), *p* – significance level, IV – indicator value, Frequency – relative frequency in group, Abundance – relative abundance in group

Species	SHI	Island	<i>p</i>	IV		Frequency		Abundance	
				Saa	Got	Saa	Got	Saa	Got
<i>Corylus avellana</i>	HD	Saa	0.0002	52	2	63	12	83	17
<i>Pimpinella saxifraga</i>	AF	Saa	0.0002	49	0	51	9	96	4
<i>Solanum dulcamara</i>	AF	Saa	0.0002	40	0	40	0	100	0
<i>Knautia arvensis</i>	AF	Saa	0.0004	44	0	46	6	97	3
<i>Verbascum thapsus</i>	AF	Saa	0.0004	34	0	34	0	100	0
<i>Daphne mezereum</i>	HD	Saa	0.0006	31	0	31	0	100	0
<i>Selinum carvifolia</i>	AF	Saa	0.0006	31	0	31	0	100	0
<i>Rubus caesius</i>	AF	Saa	0.0012	41	2	51	12	80	20
<i>Ribes alpinum</i>	HD	Saa	0.0030	39	2	51	9	77	23
<i>Valeriana officinalis</i>	AF	Saa	0.0050	23	0	23	0	100	0
<i>Sanionia uncinata</i>		Saa	0.0052	23	0	23	0	100	0
<i>Campanula persicifolia</i>	HD	Saa	0.0054	44	3	51	21	86	14
<i>Lathyrus pratensis</i>	AF	Saa	0.0090	25	0	26	3	96	4
<i>Hypochaeris maculata</i>	HD	Saa	0.0096	25	0	29	3	88	12
<i>Festuca rubra</i>	HD	Saa	0.0104	40	7	57	24	70	30
<i>Luzula pilosa</i>	HD	Saa	0.0114	43	7	60	24	71	29
<i>Pyrola chlorantha</i>	HF	Saa	0.0136	24	0	29	3	84	16
<i>Hylocomium splendens</i>		Saa	0.0136	57	33	94	85	61	39
<i>Hieracium bifidum</i>	HD	Saa	0.0142	27	2	37	6	73	27
<i>Vaccinium myrtillus</i>	HD	Saa	0.0152	36	5	46	24	79	21
<i>Pleurozium schreberi</i>		Saa	0.0154	52	22	86	56	61	39
<i>Viburnum opulus</i>	HD	Saa	0.0212	42	9	57	32	73	27
<i>Primula veris</i>	AF	Saa	0.0230	29	2	34	15	84	16
<i>Achillea millefolia</i>	AF	Saa	0.0236	17	0	17	0	100	0
<i>Calamagrostis arundinacea</i>	AF	Saa	0.0236	17	0	17	0	100	0
<i>Agrostis stolonifera</i>	AF	Saa	0.0258	17	0	17	0	100	0
<i>Stellaria holostea</i>	HF	Saa	0.0276	17	0	17	0	100	0
<i>Swida sanguinea</i>	HD	Saa	0.0432	17	0	20	3	87	13
<i>Platanthera chlorantha</i>	HD	Saa	0.0464	14	0	14	0	100	0
<i>Rosa subcarina</i>	AF	Saa	0.0474	14	0	14	0	100	0
<i>Phleum pratense</i>	AF	Saa	0.0486	14	0	14	0	100	0
<i>Pyrola rotundifolia</i>	HD	Saa	0.0494	23	1	31	3	74	26
<i>Cotoneaster scandinavicus</i>	HF	Got	0.0002	0	62	0	62	0	100
<i>Prunus spinosa</i>	HF	Got	0.0002	0	65	0	65	0	100
<i>Rosa carina</i>	AnF	Got	0.0002	0	56	0	56	0	100
<i>Rosa mollis</i>	HD	Got	0.0002	0	44	0	44	0	100
<i>Sorbus intermedia</i>	HD	Got	0.0002	7	59	43	71	17	83
<i>Anemone nemorosa</i>	HD	Got	0.0002	8	57	46	71	19	81
<i>Brachypodium sylvaticum</i>	HF	Got	0.0002	5	67	23	88	24	76
<i>Calluna vulgaris</i>	HD	Got	0.0002	0	49	6	50	3	97
<i>Festuca ovina</i>	AF	Got	0.0002	16	67	51	97	31	69
<i>Hieracium caesium</i>	HD	Got	0.0002	2	53	20	59	11	89
<i>Orchis mascula</i>	HD	Got	0.0002	0	44	0	44	0	100
<i>Ranunculus polyanthemus ssp. polyanthemus</i>	AF	Got	0.0002	3	62	23	71	12	88
<i>Rubus saxatilis</i>	HD	Got	0.0002	3	75	29	82	9	91
<i>Vaccinium vitis-idaea</i>	HD	Got	0.0002	7	52	26	74	29	71
<i>Vincetoxicum hirsutinaria</i>	HD	Got	0.0002	0	44	0	44	0	100
<i>Hypnum cupressiforme var. cupressiforme/filiforme</i>		Got	0.0002	13	69	57	88	22	78
<i>Hypnum cupressiforme var. lacunosum</i>		Got	0.0002	1	48	6	59	19	81
<i>Helianthemum nummularium</i>	HD	Got	0.0004	0	32	0	32	0	100
<i>Plantago lanceolata</i>	AF	Got	0.0004	0	49	9	50	2	98
<i>Poa pratensis ssp. angustifolia</i>	HD	Got	0.0004	0	35	0	35	0	100
<i>Brachythecium velutinum</i>		Got	0.0004	0	34	3	35	2	98
<i>Melica nutans</i>	HD	Got	0.0006	25	62	80	91	32	68
<i>Scleropodium purum</i>		Got	0.0006	27	59	77	91	35	65
<i>Helictotrichon pratense</i>	AF	Got	0.0012	4	44	17	59	25	75
<i>Scorzonera humilis</i>	AF	Got	0.0014	1	39	11	41	6	94
<i>Crataegus laevigata</i>	AnF	Got	0.0016	0	24	0	24	0	100

Table 1. (Continued)

Species	SHI	Island	<i>p</i>	IV		Frequency		Abundance	
				Saa	Got	Saa	Got	Saa	Got
<i>Calamagrostis varia</i>		Got	0.0016	0	26	0	26	0	100
<i>Arctostaphylos uva-ursi</i>	HD	Got	0.0018	4	43	17	56	23	77
<i>Taraxacum officinale coll.</i>		Got	0.0020	2	45	17	50	10	90
<i>Pinus sylvestris</i>	HD	Got	0.0030	6	42	29	53	20	80
<i>Sesleria caerulea</i>	HD	Got	0.0030	18	57	60	82	30	70
<i>Anthoxanthum odoratum</i>	AF	Got	0.0034	0	23	3	24	1	99
<i>Geranium sylvaticum</i>	HD	Got	0.0034	0	24	0	24	0	100
<i>Carex montana</i>	HD	Got	0.0036	0	23	3	24	0	100
<i>Berberis vulgaris</i>	AF	Got	0.0038	0	26	3	26	1	99
<i>Cephalanthera longifolia</i>	HD	Got	0.0040	0	21	0	21	0	100
<i>Dicranum scoparium</i>		Got	0.0040	31	61	83	97	38	62
<i>Juniperus communis</i>	AF	Got	0.0046	35	58	83	100	42	58
<i>Asperula tinctoria</i>	HD	Got	0.0046	17	53	54	76	31	69
<i>Thymus serpyllum</i>	HD	Got	0.0058	3	36	14	47	24	76
<i>Sorbus hybrida</i>	AnF	Got	0.0060	0	21	0	21	0	100
<i>Tortella tortuosa</i>		Got	0.0066	2	38	26	41	7	93
<i>Carex flacca</i>	AF	Got	0.0076	23	54	63	85	37	63
<i>Polygala amarella</i>	HD	Got	0.0086	2	33	14	38	14	86
<i>Carlina vulgaris</i>	HD	Got	0.0108	0	18	0	18	0	100
<i>Fissidens dubius</i>		Got	0.0112	7	46	37	56	18	82
<i>Fruillaria dilatata</i>		Got	0.0152	0	18	0	18	0	100
<i>Rhamnus cathartica</i>	HD	Got	0.0162	17	48	46	76	37	63
<i>Filipendula vulgaris</i>	AF	Got	0.0216	20	51	63	74	31	69
<i>Crataegus rhipidophylla</i>	HD	Got	0.0220	0	15	0	15	0	100
<i>Quercus robur</i>	HD	Got	0.0260	18	49	54	74	33	67
<i>Hieracium murorum coll.</i>		Got	0.0236	0	17	3	18	1	99
<i>Acinos arvensis</i>	AF	Got	0.0262	0	15	0	15	0	100
<i>Hieracium murorum</i>		Got	0.0268	0	17	3	18	1	99
<i>Galium verum</i>	HD	Got	0.0328	21	51	63	76	33	67
<i>Hepatica nobilis</i>	HD	Got	0.0344	32	52	74	91	43	57
<i>Polygonatum odoratum</i>	HS	Got	0.0392	2	26	17	29	12	88
<i>Carex digitata</i>	HD	Got	0.0406	18	44	49	71	38	62
<i>Luzula multiflora ssp. divulgata</i>	AF	Got	0.0426	4	30	14	41	27	73
<i>Brachypodium pinnatum</i>	AF	Got	0.0430	10	35	29	53	34	66
<i>Taxus baccata</i>	HF	Got	0.0458	0	12	0	12	0	100
<i>Geranium sanguineum</i>	HD	Got	0.0466	10	36	31	53	32	68

(48%), followed by hemeradiaphors (45%) and hemeraphobs (7%), have predominance in Saaremaa. Among the respective species of Gotland hemeradiaphores constitute 60%, apophytes 26%, hemeraphobs 8% and antropophytes 6%. Cartographical analysis of calcareous pine forests in Saaremaa proved that 74% of studied stands have been about a century ago shrublands covered mainly by *Juniperus communis* (presumable on shallow soils) and *Corylus avellana* (on soils with thicker humus horizon) or wooded meadows, 14% were open areas, i.e. grasslands and only 11% forests.

The clear distinction of calcareous pine forests of the compared islands is well illustrated on DCA ordination plot – only two communities of Saaremaa are noticeably mingled with stands of Gotland (Figure 2). Moreover, the ordination scheme demonstrates the larger basal area of *Pinus sylvestris*, a higher canopy closure of the tree layer and a thicker humus horizon of soils in Saaremaa forests. Indeed the average thickness of soil humus horizon in the studied forests in Saaremaa is 16.1 cm versus 7.4 cm in Gotland, whereas the carbon content and C/N ratio is remarkable higher in forests of Gotland – 8.72% versus 13.55%, and 14.5 versus 19.4, respectively. According to the

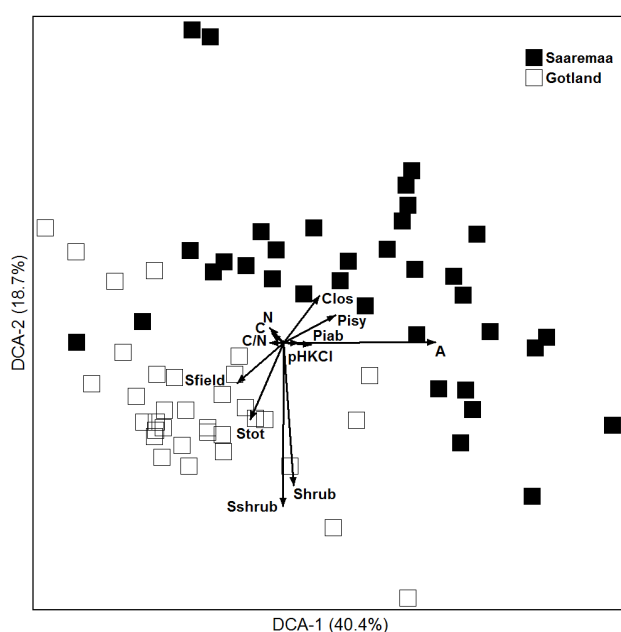


Figure 2. Ordination biplot of vegetation relevés and environmental variables

DCA results, the vegetation variation in calcareous pine forests is much more connected with the variables of vegetation structure (shrub layer coverage, tree layer closure and abundance of dominating tree species) than soil properties, except humus horizon thickness. Variables correlation with ordination axes affirms this statement explicitly (Table 2).

On the ground of multiple regression analysis it appears that the species richnesses in Saaremaa and

Table 2. Correlations of communities' structural variables and soil properties with ordination axes. Notations: r and τ – Pearson and Kendall correlation coefficients, respectively, S_{tot} – total number of species, S_{shrub} – number of shrub layer species, S_{grass} – number of field layer species, S_{moss} – number of moss layer species, Clos – tree layer closure, Piab and Pisy – basal area at breast height (1.3 m) of *Picea abies* and *Pinus sylvestris* trunks, Shrub – shrub layer coverage (%), A – thickness of soil humus horizon, pH_{KCl} – soil humus horizon pH in KCl solution, N and C – humus horizon carbon and nitrogen content (%), respectively

Variable	Axis 1			Axis 2		
	r	r^2	τ	r	r^2	τ
S_{tot}	-0.255	0.065	-0.164	-0.383	0.147	-0.248
S_{shrub}	-0.037	0.001	0.008	-0.559	0.312	-0.452
S_{field}	-0.297	0.088	-0.197	-0.276	0.076	-0.160
S_{moss}	-0.027	0.001	-0.011	0.044	0.002	0.099
Clos	0.262	0.069	0.381	0.300	0.090	0.319
Piab	0.231	0.054	0.249	-0.058	0.003	0.011
Pisy	0.315	0.099	0.219	0.230	0.053	0.168
Shrub	0.144	0.021	0.079	-0.522	0.272	-0.319
A	0.538	0.290	0.399	0.044	0.002	0.070
pH_{KCl}	0.169	0.028	0.116	-0.022	<0.001	0.025
N	-0.164	0.027	-0.090	0.172	0.030	0.193
C	-0.148	0.022	-0.091	0.130	0.017	0.153
C/N	-0.162	0.026	-0.210	0.024	0.001	-0.045

Gotland are driven partly by different factors. The total number of species in Saaremaa depends significantly (negatively) only on the abundance of dominating pine trees, whereas the shrub layer coverage and soil humus horizon thickness are left into regression model but they are not statistically significant (Table 3). In the forests of Gotland the shrub layer coverage has a cardinal importance, while significance level of the tree layer closure and the abundance of spruce in the tree layer is a little above the conventional critical limit; as non-significant variables are left into model also abundance of pine trees and carbon content in soil humus horizon. On the number of shrub layer species on both islands the shrub layer coverage has a significant impact, additionally in Gotland the abundance of spruce has considerable effect. In addition, in the forests of Saaremaa, carbon content in soil has a non-significant effect, whereas in Gotland abundance of spruce in the tree layer and nitrogen content in humus horizon have certain importance.

Table 3. Dependency of species richness on environmental factors according to the stepwise forward multiple regression analyses. Notations: $AdjR^2$ – adjusted coefficient of multiple determination, p – significance level, β – standardized regression coefficient, B – raw regression coefficient, t – value of t -criterion (in brackets degrees of freedom); other notations as in Table 2

Variable	Total number of species							
	Saaremaa; $AdjR^2=0.148, p < 0.047$			Gotland; $AdjR^2=0.254, p < 0.019$				
	β	B	$t(31)$	p	B	$t(28)$	p	
Intercept		51.97	8.17	<0.001	53.21	5.62	<0.001	
Pisy	-0.35	-0.43	-2.17	0.037	0.35	0.81	0.221	
Shrub	0.25	0.15	1.53	0.136	0.51	0.31	3.13	0.004
A	0.17	0.29	1.06	0.297				
Clos					-0.40	-39.10	-1.94	0.062
Piab					0.50	1.12	1.81	0.082
C					-0.18	-0.16	-1.11	0.276

Variable	Number of shrub layer species							
	Saaremaa; $AdjR^2=0.203, p < 0.010$			Gotland; $AdjR^2=0.362, p < 0.001$				
	β	B	$t(32)$	p	B	$t(30)$	p	
Intercept		7.71	8.60	<0.001	13.92	6.08	<0.001	
Shrub	0.41	0.06	2.66	0.012	0.53	0.12	3.69	0.001
C	-0.26	-0.07	-1.68	0.102				
Pisy					-0.40	-0.33	-2.80	0.009
N					-0.19	-1.69	-1.35	0.188

By the relevés cluster analysis dendrogram (Figure 3) nine community types were distinguished, all having according to the MRPP tests significantly ($p < 0.05$) different species composition even taking into account the rather rigorous Bonferroni correction for multiple comparisons. Considering the indicator (Table 4) and/or dominant species (Table 5), the community types can be labelled as: (i) *Brachypodium sylvaticum*–*Rhytidiadelphus triquetrus* type, (ii) *Melampyrum pratense*–*Rhytidiadelphus triquetrus* type, (iii) *Vaccinium myrtillus*–*Dicranum polysetum* type, (iv) *Pimpinella saxifraga*–*Hylocomium splendens* type, (v) *Pteridium aquilinum*–*Hylocomium splendens*

ens type, (vi) *Arctostaphylos uva-ursi*–*Hypnum cupressiforme* var. *lacunosum* type, (vii) *Geranium sanguineum*–*Tortella tortuosa* type, (viii) *Deschampsia flexuosa*–*Scleropodium purum* type and, (ix) *Carex montana*–*Scleropodium purum* type.

(i) The first type includes communities both in Saaremaa and Gotland (Figure 3). In the dense shrub layer *Corylus avellana* dominates but the indicator

(ii) Communities of the *Melampyrum pratense*–*Rhytidiadelphus triquetrus* type were described only in Saaremaa (Figure 3). *Corylus avellana* is prevailing in the shrub layer, another indicator species is *Ribes alpinum* (Table 4) here. The field layer is rather modest, without salient species; in the moss layer *Hylocomium splendens*, *Pleurozium schreberi* and *Scleropodium purum* are also rather frequent (Table 5). The

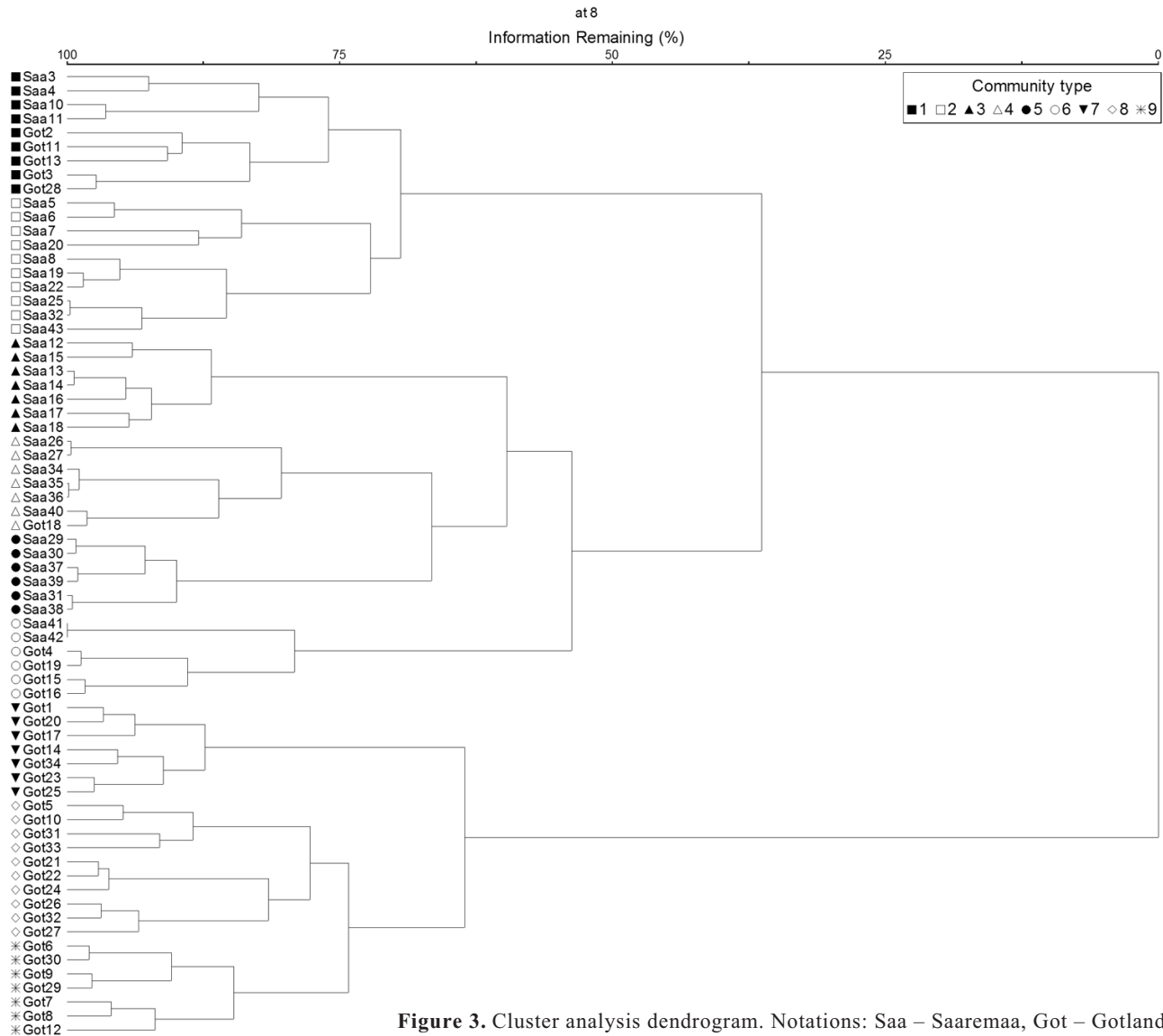


Figure 3. Cluster analysis dendrogram. Notations: Saa – Saaremaa, Got – Gotland

species is *Crataegus rhipidophylla* (Table 4). In the field layer beside title species *Anemone nemorosa*, *Convallaria majalis*, *Hepatica nobilis* and *Rubus caesius* are abundant; in the moss layer *Scleropodium purum* has almost the same cover as *Rhytidiadelphus triquetrus* (Table 5). Soil properties in these communities have an average value among the established types (Table 6).

humus horizon of soils in these communities has comparatively low nitrogen and carbon content (Table 6).

In all other communities, *Juniperus communis* dominates in the shrub layer.

(iii) In the *Vaccinium myrtillus*–*Dicranum polysetum* type communities field layer, in addition *Rubus caesius*, *Hepatica nobilis*, *Convallaria majalis*, *Calamagrostis arundinacea* and *Hieracium bifidum* are

Table 4. Indicator species of community types. Notations: Max type - community type where the indicator value is maximal, *p* - significance level

Species	Max type	p	Community type																	
			Relative frequency in community type									Relative abundance in community type								
			1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
<i>Veronica chamaedrys</i>	1	0.0004	78	10	43	0	0	0	0	50	0	53	1	14	0	0	0	32	0	
<i>Hepatica nobilis</i>	1	0.0026	100	50	100	71	100	33	100	100	86	19	4	15	10	10	2	16	12	12
<i>Anemone nemorosa</i>	1	0.0030	100	50	57	0	50	0	29	100	100	28	5	7	0	2	0	5	28	24
<i>Rhytidadelphus triquetrus</i>	1	0.0034	100	80	86	43	50	33	71	80	43	23	19	10	9	7	9	9	10	3
<i>Geum rivale</i>	1	0.0070	33	0	0	0	0	0	0	10	0	98	0	0	0	0	0	2	0	0
<i>Convallaria majalis</i>	1	0.0082	100	70	86	86	67	17	71	60	57	24	11	16	10	10	2	10	7	11
<i>Crataegus rhipidophylla</i>	1	0.0154	33	0	0	0	0	0	14	0	14	95	0	0	0	0	2	0	2	0
<i>Brachypodium sylvaticum</i>	1	0.0198	89	40	14	14	0	33	86	90	100	26	11	0	3	0	7	17	17	19
<i>Corylus avellana</i>	2	0.0002	78	100	29	14	83	0	0	0	14	43	46	8	0	2	0	0	0	0
<i>Plagiomnium affine</i>	2	0.0132	44	70	57	0	50	0	29	20	14	14	54	6	0	20	0	3	2	1
<i>Ribes alpinum</i>	2	0.0256	11	60	29	100	50	17	0	10	0	9	48	6	20	2	7	0	8	0
<i>Luzula pilosa</i>	2	0.0326	89	80	71	14	17	50	0	30	0	21	34	11	1	1	27	0	6	0
<i>Valeriana officinalis</i>	2	0.0332	22	40	29	0	0	0	0	0	0	27	67	6	0	0	0	0	0	0
<i>Vicia cassubica</i>	2	0.0352	0	30	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0
<i>Selinum carvifolia</i>	3	0.0002	22	20	100	0	0	0	0	0	0	29	10	61	0	0	0	0	0	0
<i>Solanum dulcamara</i>	3	0.0002	33	40	100	0	0	0	0	0	0	3	32	64	0	0	0	0	0	0
<i>Vaccinium myrtillus</i>	3	0.0002	44	60	86	0	0	33	0	30	43	9	16	59	0	0	1	0	6	9
<i>Hieracium bifidum coll.</i>	3	0.0004	11	10	100	29	17	33	0	0	14	7	6	46	10	1	22	0	0	9
<i>Rubus caesius</i>	3	0.0010	67	30	100	57	0	0	14	10	0	44	8	42	1	0	0	3	2	0
<i>Phleum pratense</i>	3	0.0016	0	10	57	0	0	0	0	0	0	0	24	76	0	0	0	0	0	0
<i>Calamagrostis arundinacea</i>	3	0.0038	11	10	57	0	0	0	0	0	0	1	34	65	0	0	0	0	0	0
<i>Juncus compressus</i>	3	0.0044	11	0	43	0	0	0	0	0	0	4	0	96	0	0	0	0	0	0
<i>Mycelis muralis</i>	3	0.0046	44	40	86	0	0	0	14	0	0	33	18	47	0	0	0	2	0	0
<i>Dicranum polysetum</i>	3	0.0048	33	50	100	71	100	50	100	70	71	4	5	25	8	17	16	9	7	9
<i>Ptilium crista-castrensis</i>	3	0.0292	22	0	43	0	33	0	0	0	0	32	0	63	0	5	0	0	0	0
<i>Festuca rubra</i>	3	0.0364	44	50	100	57	33	17	14	30	14	13	27	24	11	1	4	3	10	7
<i>Agrostis stolonifera</i>	4	0.0002	22	0	0	57	0	0	0	0	0	11	0	0	89	0	0	0	0	0
<i>Achillea millefolium</i>	4	0.0010	0	20	0	57	0	0	0	0	0	0	6	0	94	0	0	0	0	0
<i>Juniperus communis</i>	4	0.0012	89	60	100	100	83	100	100	100	100	5	3	9	18	13	10	15	14	13
<i>Pimpinella saxifraga</i>	4	0.0056	11	20	43	86	100	17	14	10	0	11	11	4	46	24	2	1	1	0
<i>Solidago virgaurea</i>	4	0.0202	11	30	0	57	67	0	29	10	43	1	2	0	61	15	0	11	7	3
<i>Inula salicina</i>	4	0.0250	0	10	0	43	33	0	14	0	29	0	2	0	67	5	0	22	0	4
<i>Lathyrus pratensis</i>	4	0.0268	11	20	14	43	33	0	14	0	0	3	5	4	76	8	0	4	0	0
<i>Rosa subcanina</i>	4	0.0326	0	0	0	43	33	0	0	0	0	0	0	0	56	44	0	0	0	0
<i>Knautia arvensis</i>	4	0.0410	22	30	43	71	50	0	0	20	0	14	23	19	36	6	0	0	2	0
<i>Hypochaeris maculata</i>	5	0.0002	11	10	29	14	83	17	0	0	0	9	8	23	1	57	1	0	0	0
<i>Pteridium aquilinum</i>	5	0.0002	11	20	0	14	100	0	14	50	29	5	4	0	3	44	0	6	22	16
<i>Picea abies</i>	5	0.0010	33	70	86	14	100	67	57	70	71	6	10	18	0	26	12	6	12	10
<i>Hylocomium splendens</i>	5	0.0114	78	90	100	100	100	67	100	90	86	7	9	16	18	18	3	8	10	9
<i>Neottia nidus-avis</i>	5	0.0118	11	30	0	29	67	33	0	10	29	12	3	0	3	58	20	0	1	3
<i>Campanula rotundifolia</i>	5	0.0174	11	10	0	86	100	17	43	10	14	2	1	0	31	36	2	6	1	20
<i>Encalypta streptocarpa</i>	5	0.0292	0	10	0	14	33	17	0	0	0	0	3	0	4	89	4	0	0	0
<i>Asperula tinctoria</i>	5	0.0390	33	40	29	71	100	67	86	90	86	3	3	2	7	21	7	20	17	20
<i>Arctostaphylos uva-ursi</i>	6	0.0002	0	0	43	14	17	100	100	50	29	0	0	7	3	3	47	26	10	3
<i>Epipactis atrorubens</i>	6	0.0012	33	10	71	29	100	100	29	0	14	2	0	21	14	18	38	7	0	1
<i>Antennaria dioica</i>	6	0.0014	0	0	0	14	50	67	14	0	0	0	0	0	14	5	67	14	0	0
<i>Vaccinium vitis-idaea</i>	6	0.0042	22	10	0	0	100	100	71	70	100	6	1	0	0	25	28	12	14	14
<i>Hieracium caesium</i>	6	0.0056	22	10	0	29	50	83	86	50	43	7	0	0	1	6	37	23	16	9
<i>Ditrichum flexicaule</i>	6	0.0158	0	0	0	29	33	67	43	0	0	0	0	0	40	3	54	4	0	0
<i>Ononis repens</i>	6	0.0238	0	0	0	0	0	33	0	10	0	0	0	0	0	0	77	0	23	0

Table 4. (Continued)

Species	Max type	p	Community type																	
			Relative frequency in community type									Relative abundance in community type								
			1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
<i>Salix caprea</i>	6	0.0254	11	0	0	0	0	33	0	0	0	25	0	0	0	0	75	0	0	0
<i>Chimaphila umbellata</i>	6	0.0318	0	10	0	14	0	33	0	0	0	0	5	0	7	0	88	0	0	0
<i>Carlina vulgaris</i>	6	0.0366	0	0	0	0	0	33	43	0	14	0	0	0	0	0	85	11	0	4
<i>Pilosella officinarum</i> ssp. <i>peleterianum</i>	6	0.0376	0	0	0	71	50	67	43	20	0	0	0	0	19	3	39	33	6	0
<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	6	0.0394	0	0	0	43	0	67	100	50	43	0	0	0	20	0	37	20	14	9
<i>Pinus sylvestris</i>	6	0.0406	11	20	43	29	17	83	57	60	57	3	0	10	7	4	27	20	14	16
<i>Pyrola chlorantha</i>	6	0.0440	0	0	43	43	33	50	0	0	0	0	0	17	30	3	50	0	0	0
<i>Polytrichum juniperinum</i>	6	0.0476	0	0	0	0	17	33	14	0	0	0	0	0	0	8	86	7	0	0
<i>Empetrum nigrum</i> subsp. <i>nigrum</i>	6	0.0500	0	0	29	0	0	33	0	0	0	0	0	32	0	0	68	0	0	0
<i>Cotoneaster scandinavicus</i>	7	0.0002	11	0	0	14	0	0	100	60	86	6	0	0	3	0	0	42	26	24
<i>Geranium sanguineum</i>	7	0.0006	56	20	14	0	83	0	100	60	43	17	8	0	0	13	0	33	22	7
<i>Tortella tortuosa</i>	7	0.0008	11	10	14	43	67	67	86	30	0	0	0	0	1	6	33	48	11	0
<i>Rosa mollis</i>	7	0.0014	0	0	0	0	0	0	71	50	71	0	0	0	0	0	0	59	28	14
<i>Helictotrichon pratensis</i>	7	0.0028	33	20	0	29	0	33	100	50	71	11	3	0	14	0	8	31	14	20
<i>Vincetoxicum hirsutinaria</i>	7	0.0034	22	0	0	14	0	50	86	30	0	11	0	0	7	0	17	42	24	0
<i>Thymus serpyllum</i>	7	0.0090	11	30	0	29	0	67	71	20	57	4	14	0	1	0	13	45	4	20
<i>Frullania dilatata</i>	7	0.0096	0	0	0	0	0	0	43	20	14	0	0	0	0	0	0	73	25	2
<i>Prunella grandiflora</i>	7	0.0162	0	0	0	0	0	0	43	0	14	0	0	0	0	0	0	68	0	32
<i>Polygala amarella</i>	7	0.0170	22	10	14	14	0	50	71	20	43	9	1	1	1	0	25	43	8	12
<i>Festuca ovina</i>	7	0.0362	44	40	0	100	100	100	100	100	100	5	3	0	9	18	14	19	15	16
<i>Orchis mascula</i>	7	0.0446	11	0	0	14	0	17	57	70	14	10	0	0	1	0	15	41	31	1
<i>Fissidens dubius</i>	7	0.0476	56	20	57	43	33	67	100	40	14	11	5	2	7	1	36	26	5	6
<i>Prunus spinosa</i>	8	0.0002	44	0	0	14	0	0	29	100	71	21	0	0	0	0	0	8	56	15
<i>Deschampsia flexuosa</i>	8	0.0002	22	50	0	0	0	33	29	90	57	7	25	0	0	0	14	3	42	9
<i>Scleropodium purum</i>	8	0.0004	100	90	100	29	100	17	100	100	100	14	7	11	2	12	1	16	18	18
<i>Cotoneaster canescens</i>	8	0.0032	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0	100	0
<i>Carex flacca</i>	8	0.0170	78	40	71	43	100	33	100	100	100	9	3	10	4	16	6	15	21	17
<i>Anthoxanthum odoratum</i>	8	0.0206	11	10	0	0	0	0	14	50	14	10	1	0	0	0	0	12	52	25
<i>Rosa canina</i>	8	0.0210	44	0	0	14	0	17	57	70	29	15	0	0	9	0	10	27	37	2
<i>Helianthemum nummularium</i>	8	0.0260	0	0	0	14	0	0	43	60	14	0	0	0	14	0	0	43	42	1
<i>Anthericum ramosum</i>	8	0.0490	0	0	0	0	0	0	0	30	14	0	0	0	0	0	0	0	68	32
<i>Carex montana</i>	9	0.0002	11	10	0	0	0	0	0	0	100	3	0	0	0	0	0	0	0	97
<i>Scorzonera humilis</i>	9	0.0004	11	0	0	0	67	0	29	50	86	4	0	0	0	9	0	6	28	52
<i>Melica nutans</i>	9	0.0014	100	70	100	71	100	17	100	100	100	14	4	9	8	11	2	14	18	21
<i>Plantago lanceolata</i>	9	0.0022	11	0	0	14	17	17	43	70	86	1	0	0	1	1	1	20	28	49
<i>Calluna vulgaris</i>	9	0.0082	0	20	0	0	0	0	71	60	86	0	2	0	0	0	0	29	33	35
<i>Sesleria caerulea</i>	9	0.0082	33	50	57	86	100	33	100	90	100	1	3	3	15	14	3	20	17	24
<i>Hypnum cupressiforme</i> var. <i>cupressiforme/filiforme</i>	9	0.0110	67	80	14	71	83	50	71	100	100	18	5	0	13	7	4	8	21	25
<i>Viola riviniana</i>	9	0.0144	78	50	71	57	100	0	71	90	100	11	8	8	1	18	0	11	20	24
<i>Rubus saxatilis</i>	9	0.0174	44	20	0	71	50	50	86	80	100	9	2	0	4	7	9	24	22	24
<i>Ptilidium pulcherrimum</i>	9	0.0256	0	40	43	29	50	33	0	20	57	0	8	8	5	9	6	0	4	59
<i>Geranium sylvaticum</i>	9	0.0414	22	0	0	0	0	0	0	20	57	44	0	0	0	0	0	0	15	41
<i>Brachypodium pinnatum</i>	9	0.0452	22	10	29	14	67	0	57	80	86	5	1	11	0	22	0	11	24	25
<i>Galium boreale</i>	9	0.0456	78	70	100	100	100	0	100	90	86	8	9	9	6	12	0	16	17	23

more remarkable, in the moss layer *Hylocomium splendens*, *Pleurozium schreberi* and *Scleropodium purum* have almost the same abundance with the title

species (Table 5). The soil properties in these communities have an average value (Table 6). This type is inherent for Saaremaa (Figure 3).

Table 5. (Continued)

Species	Community type									
	1	2	3	4	5	6	7	8	9	
	Number of relevés									
	9	10	7	7	6	6	7	10	7	
<i>Scorzonera humilis</i>	0.1	-	-	-	0.2	-	0.2	0.7	1.3	
<i>Sedum acre</i>	0.1	-	-	<0.1	-	-	0.1	<0.1	-	
<i>Sedum album</i>	-	-	-	<0.1	-	-	0.3	0.2	-	
<i>Sedum sexangulare</i>	-	-	-	-	-	-	0.1	0.2	-	
<i>Selinum carvifolia</i>	0.6	0.2	1.2	-	-	-	-	-	-	
<i>Senecio jacobaea</i>	<0.1	-	-	-	-	-	0.1	-	-	
<i>Sesleria caerulea</i>	0.1	0.4	0.3	1.9	1.7	0.3	2.4	2.1	3.0	
<i>Solanum dulcamara</i>	<0.1	0.3	0.6	-	-	-	-	-	-	
<i>Solidago virgaurea</i>	<0.1	<0.1	-	0.9	0.2	-	0.2	0.1	<0.1	
<i>Stellaria holostea</i>	0.4	0.2	0.1	-	-	-	-	-	-	
<i>Stellaria nemorum</i>	0.3	0.1	0.3	-	-	-	-	-	-	
<i>Succisa pratensis</i>	<0.1	0.1	-	-	<0.1	-	<0.1	0.1	0.2	
<i>Taraxacum officinale</i> coll.	0.3	<0.1	-	0.1	<0.1	0.2	<0.1	0.1	0.2	
<i>Thymus serpyllum</i>	0.1	0.4	-	<0.1	-	0.4	1.3	0.1	0.6	
<i>Trientalis europaea</i>	0.3	0.2	-	-	-	-	-	-	-	
<i>Vaccinium myrtillus</i>	0.4	0.8	2.9	-	-	-	-	0.3	0.4	
<i>Vaccinium vitis-idaea</i>	0.4	0.1	-	-	1.8	2.0	0.9	1.0	1.0	
<i>Valeriana officinalis</i>	0.1	0.3	<0.1	-	-	-	-	-	-	
<i>Verbascum thapsus</i>	0.3	0.2	0.3	<0.1	-	-	-	-	-	
<i>Veronica chamaedrys</i>	0.7	<0.1	0.2	-	-	-	-	0.4	-	
<i>Veronica officinalis</i>	<0.1	0.2	-	0.1	0.1	-	0.3	0.1	0.3	
<i>Vicia cassubica</i>	-	0.1	-	-	-	-	-	-	-	
<i>Vicia cracca</i>	-	<0.1	-	<0.1	<0.1	<0.1	<0.1	0.1	-	
<i>Vicia sepium</i>	0.1	0.2	0.1	-	-	-	-	<0.1	-	
<i>Vincetoxicum hirundinaria</i>	0.2	-	-	0.1	-	0.4	0.9	0.5	-	
<i>Viola riviniana</i>	0.6	0.4	0.5	0.1	1.0	-	0.6	1.1	1.3	
<i>Viola rupestris</i>	-	-	-	<0.1	<0.1	-	-	-	-	
Moss layer										
<i>Amblystegium serpens</i>	<0.1	<0.1	-	-	<0.1	-	-	-	-	
<i>Aluacommium palustre</i>	-	<0.1	0.3	-	<0.1	-	-	0.2	0.1	
<i>Brachythecium glareosum</i>	<0.1	<0.1	-	-	-	-	<0.1	-	-	
<i>Brachythecium oedipodium</i>	<0.1	<0.1	-	<0.1	-	-	-	-	-	
<i>Brachythecium rutabulum</i>	0.3	0.2	<0.1	-	-	-	-	<0.1	-	
<i>Brachythecium salebrosum</i>	-	<0.1	-	-	<0.1	-	<0.1	-	-	
<i>Brachythecium velutinum</i>	0.3	<0.1	-	-	-	<0.1	<0.1	<0.1	0.1	
<i>Bryum caespiticium</i>	-	<0.1	-	<0.1	<0.1	<0.1	<0.1	-	-	
<i>Bryum capillare</i>	<0.1	-	-	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	
<i>Bryum flaccidum</i> (B. moravicum)	-	<0.1	-	-	-	-	-	<0.1	-	
<i>Calliergonella cuspidata</i>	0.2	-	-	-	-	-	<0.1	-	-	
<i>Campylopus calcareum</i>	-	<0.1	-	-	<0.1	<0.1	<0.1	<0.1	-	
<i>Campylopus chrysophyllum</i>	-	<0.1	<0.1	0.2	<0.1	0.2	<0.1	<0.1	-	
<i>Campylopus sommerfeltii</i>	0.2	-	-	-	<0.1	-	<0.1	-	0.1	
<i>Cirriphyllum piliferum</i>	0.1	0.1	-	-	-	-	-	-	-	
<i>Ctenidium molluscum</i>	-	-	<0.1	0.3	0.2	-	0.3	-	-	
<i>Dicranum drummondii</i>	-	-	0.2	-	<0.1	0.2	-	-	0.1	
<i>Dicranum montanum</i>	0.1	0.1	-	-	-	<0.1	-	0.1	0.2	
<i>Dicranum polysetum</i>	0.3	0.5	2.4	0.7	1.7	1.5	0.9	0.7	0.9	
<i>Dicranum scoparium</i>	0.7	0.5	0.9	1.6	0.9	1.5	1.6	0.9	1.0	
<i>Dicranum spurium</i>	-	-	0.3	-	-	<0.1	0.3	-	-	
<i>Ditrichum flexicaule</i>	-	-	-	0.4	<0.1	0.6	<0.1	-	-	
<i>Encalypta streptocarpa</i>	-	<0.1	-	<0.1	0.3	<0.1	-	-	-	
<i>Eurhynchium hians</i>	<0.1	0.1	-	-	-	-	-	-	-	
<i>Fissidens dubius</i>	0.3	0.1	0.1	0.2	<0.1	0.9	0.6	0.1	0.1	
<i>Frullania dilatata</i>	-	-	-	-	-	-	0.6	0.2	<0.1	
<i>Hedwigia ciliata</i>	-	<0.1	-	<0.1	<0.1	-	<0.1	-	-	
<i>Homalothecium lutescens</i>	-	0.1	-	<0.1	-	<0.1	0.2	-	-	
<i>Homalothecium sericeum</i>	0.1	<0.1	-	-	-	<0.1	-	-	-	
<i>Hylocomium splendens</i>	1.6	2.1	3.7	4.1	4.2	0.7	1.9	2.3	2.0	
<i>Hypnum cupressiforme</i>	1.0	0.3	<0.1	0.7	0.4	0.2	0.5	1.2	1.4	
<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>	-	-	-	0.7	-	1.3	0.7	0.5	0.3	
<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>	-	-	-	-	-	-	-	-	-	
<i>Isoetecium alopecuroides</i>	<0.1	<0.1	-	-	-	-	<0.1	-	-	
<i>Lophocolea heterophylla</i>	<0.1	0.1	<0.1	<0.1	<0.1	-	-	<0.1	-	
<i>Mnium hornum</i>	0.1	<0.1	<0.1	-	-	-	-	-	-	
<i>Nowellia curvifolia</i>	-	<0.1	<0.1	<0.1	<0.1	-	-	-	-	
<i>Plagiommium affine</i>	0.1	0.5	0.1	-	0.2	-	<0.1	<0.1	<0.1	
<i>Pleurozium schreberi</i>	0.2	1.7	3.1	1.4	3.0	2.2	1.1	1.8	1.7	
<i>Polytrichum formosum</i>	-	<0.1	-	-	-	-	-	0.1	-	
<i>Polytrichum juniperinum</i>	-	-	-	-	<0.1	0.2	<0.1	-	-	
<i>Ptilidium ciliare</i>	-	-	<0.1	-	<0.1	<0.1	-	-	-	
<i>Ptilidium pulcherrimum</i>	-	<0.1	<0.1	<0.1	0.1	<0.1	-	<0.1	0.3	
<i>Ptilium crista-castrensis</i>	0.2	-	0.4	-	<0.1	-	-	-	-	
<i>Racomitrium heterostichum</i>	-	-	-	-	<0.1	-	<0.1	0.1	0.2	
<i>Radula complanata</i>	0.2	<0.1	-	0.1	<0.1	-	<0.1	<0.1	0.2	
<i>Rhodobryum roseum</i>	-	0.1	<0.1	<0.1	-	-	-	<0.1	-	
<i>Rhytidiadelphus squarrosus</i>	0.1	<0.1	0.1	-	-	-	-	-	-	
<i>Rhytidiadelphus triquetrus</i>	3.9	3.2	1.7	1.6	1.2	1.5	1.4	1.7	0.4	

Table 5. (Continued)

Species	Community type								
	1	2	3	4	5	6	7	8	9
	Number of relevés								
	9	10	7	7	6	6	7	10	7
<i>Sanionia uncinata</i>	<0.1	0.3	0.3	<0.1	-	-	-	-	-
<i>Schistidium apocarpum</i>	-	<0.1	-	0.1	<0.1	0.2	0.3	0.1	-
<i>Scleropodium purum</i>	3.4	1.8	2.9	0.6	3.0	0.3	4.1	4.6	4.4
<i>Tetraphis pellucida</i>	-	<0.1	-	<0.1	<0.1	-	-	-	-
<i>Tortella tortuosa</i>	<0.1	<0.1	<0.1	<0.1	0.2	1.2	1.7	0.4	-
<i>Tortula ruralis</i>	<0.1	-	-	<0.1	-	-	<0.1	-	-

(iv) Communities of the *Pimpinella saxifraga*–*Hylocomium splendens* type occur mostly in Saaremaa, although one community from Gotland was included into this type as well (Figure 3). The field layer of these communities is scanty like in the previous type (Table 5). A relatively low C/N ratio is characteristic to the soil humus horizon (Table 6).

(v) Communities of the *Pteridium aquilinum*–*Hylocomium splendens* type were described exclusively in Saaremaa (Figure 3). In the species rich field layer, *Asperula tinctoria*, *Brachypodium pinnatum*, *Festuca ovina* and *Vaccinium vitis-idaea* are prevailing, in the moss layer also *Pleurozium schreberi* and *Scleropodium purum* are frequent. Among others *Neottia nidus-avis* is also a significant indicator species (Table 4), a dense moss layer is formed beside the title species by *Pleurozium schreberi*, *Scleropodium purum* and *Dicranum polysetum* (Table 5). For the soil humus horizon, the largest thickness is characteristic (Table 6).

(vi) The *Arctostaphylos uva-ursi*–*Hypnum cupressiforme* var. *lacunosum* type is represented both in Saaremaa and Gotland (Figure 3). The tree layer is very stunted (with average height of 8.5 m); in the field layer species such as *Vaccinium vitis-idaea*, *Melampyrum pratense*, *Hieracium caesium* and *Festuca ovina* are quite abundant, in the moss layer *Pleurozium schreberi*, *Hypnum cypressiforme* var. *lacunosum* and *Dicranum* spp. are dominating (Table 5). An orchid *Epipactis atrorubens* also belongs to the indicator species of that type (Table 4). The soils of these communities have very shallow humus horizon (ca. 2.0 cm), its pH is relatively low, while the N and C content, and the N/C ratio are the highest among the studied samples (Table 6).

Communities of the last three types occur only in Gotland (Figure 3). The tree layer closure in communities of all these types is only 0.4 but the total number of species as well as the number of field layer species is usually higher than in previous types. The soil humus horizon is comparatively shallow (5.6–9.0 cm; Table 6), at the same time a quite high abundance of *Carex flacca* and *Sesleria caerulea* (Table 5) indicates soils gleying (Du Rietz 1925, Рейнтам 1976).

Table 6. Mean of species number, stand structural variables and soil humus horizon properties in community types. Notations: ANOVA – univariate analysis of variance, F – value of F-criterion, *p* – significance level; with uppercase letters are marked results of pairwise comparisons by post-hoc Tukey HSD test; *S*_{tot} – total number of species, *S*_{shrub} – number of shrub layer species, *S*_{field} – number of field layer species, *S*_{moss} – number of moss layer species, Clos – tree layer closure, Piab and Pisy – basal area at breast height (1.3 m) of *Picea abies* and *Pinus sylvestris* trunks; Shrub – shrub layer coverage (%), A – thickness of soil humus horizon (cm), pH_{KCl} – humus horizon pH in KCl solution, N and C – humus horizon nitrogen and carbon content (%), respectively

Variable	Community type									ANOVA	
	1	2	3	4	5	6	7	8	9	F	p
<i>S</i> _{tot}	58 ^{ab}	52 ^{ab}	46 ^a	58 ^{ab}	59 ^{ab}	47 ^a	66 ^b	63 ^b	55 ^{ab}	3.98	<0.001
<i>S</i> _{shrub}	12 ^{bc}	11 ^{abc}	7 ^a	11 ^{abc}	7 ^{ab}	7 ^{ab}	10 ^{abc}	13 ^c	11 ^{abc}	5.03	<0.001
<i>S</i> _{field}	35 ^{abc}	26 ^a	28 ^{abc}	34 ^{abc}	38 ^{bc}	27 ^{ab}	39 ^{bc}	39 ^c	35 ^{abc}	4.13	<0.001
<i>S</i> _{moss}	10	15	11	12	14	12	16	11	10	2.34	0.029
Clos	0.5 ^{ab}	0.7 ^b	0.6 ^{ab}	0.7 ^b	0.7 ^{ab}	0.5 ^{ab}	0.4 ^{ab}	0.4 ^a	0.4 ^{ab}	3.13	0.005
Piab	5.2	2.9	3.5	0.0	2.3	0.0	1.0	2.0	1.2	1.79	0.097
Pisy	14.3	21.7	21.2	14.6	16.8	16.6	15.8	15.6	15.5	1.45	0.196
Shrub	39.4 ^b	38.0 ^b	19.3 ^{ab}	36.4 ^{ab}	30.8 ^{ab}	12.0 ^a	32.9 ^{ab}	39.5 ^b	24.3 ^{ab}	3.15	0.005
A	16.2 ^{de}	15.7 ^{de}	13.0 ^{bcdde}	15.0 ^{cdde}	20.2 ^e	2.0 ^a	5.6 ^{ab}	9.0 ^{bcd}	7.9 ^{abc}	9.76	<0.001
pH _{KCl}	6.6	6.4	6.6	6.5	6.5	6.1	6.6	6.1	6.9	1.09	0.381
N	0.67 ^{ab}	0.41 ^{ab}	0.76 ^{ab}	0.75 ^{ab}	0.56 ^{ab}	0.94 ^b	0.68 ^{ab}	0.36 ^a	0.43 ^{ab}	2.74	0.012
C	12.57 ^{ab}	5.80 ^a	19.24 ^{ab}	10.16 ^{ab}	7.55 ^{ab}	22.85 ^b	12.93 ^{ab}	6.86 ^a	6.79 ^{ab}	2.86	0.009
C/N	15.5	16.3	19.8	12.8	13.7	21.7	17.7	19.2	15.9	1.36	0.235

(vii) The communities of *Geranium sanguineum*–*Tortella tortuosa* type are peculiar first by their shrub layer, where *Cotoneaster scandinavicus* is characteristic, in addition *Rhamnus cathartica*, *Rosa mollis* and *Sorbus intermedia* are also rather frequent. In the field layer *Arctostaphylos uva-ursi*, *Brachypodium sylvaticum*, *Festuca ovina*, *Fragaria vesca*, *Hepatica nobilis*, *Rubus saxatilis* and *Sesleria caerulea* should be mentioned; in the moss layer *Scleropodium purum* is the most abundant species (Table 5). The total number of species in these communities is the highest; the average depth of soil humus horizon is less than 6 cm (Table 6).

(viii) To the shrub layer of the *Deschampsia flexuosa*–*Scleropodium purum* type communities besides *Juniperus communis*, also *Prunus spinosa*, *Cotoneaster canescens* and *Rosa canina* are notable. In the field layer *Anemone nemorosa*, *Brachypodium pinnatum* and *B. sylvaticum*, *Carex flacca*, *Deschampsia flexuosa*, *Festuca ovina*, *Sesleria caerulea*, *Filipendula vulgaris* etc. grow abundantly (Table 5). The soil humus horizon pH, nitrogen and carbon content in the respective communities are low (Table 6).

(ix) Communities of the *Carex montana*–*Scleropodium purum* type differ from the previous communities distinctly by the high abundance of the first title species (Table 5). The soil humus horizon nitrogen and carbon content are low like in the *Deschampsia flexuosa*–*Scleropodium purum* type but pH is the highest among all established types (Table 6).

Discussion and Conclusions

The results of the current paper demonstrate that despite of quite similar geological history (Calner et

al. 2004, Eliason et al. 2010), soil forming processes, geographical proximity and human impact (Sernander 1984, Kaar 1961, Kaap 1964, Pettersson 1965, Nitare 2009) several dissimilarities between the calcareous pine forests in Saaremaa and Gotland islands are notable. Usually the main factors determining differences in the species content and their richness in plant communities are the soil properties and climatic conditions. Though in the communities of types established in the current study the soil humus horizon chemistry characteristics (pH, nitrogen and carbon content, and their ratio) appeared to be significantly distinct, in general they varied in quite narrow limits. The difference was mainly expressed by the humus horizon thickness, depending first of all on the degree and depth of weathering underground limestone deposits (Reintam 1995, 1997). Due to the small amount of fine-textured material, the moisture holding capacity of Rendzinas is low, and, therefore, they dry up during the periods, when the amount of precipitations is inconsiderable. In that way, despite some properties of these soils are highly favourable for plants growth, their fertility is primarily determined by the adverse water regime due to the small depth of the soil profile and to the compact limestone bedrock (Rooma and Sepp 1972). In Saaremaa forests, the humus horizon was usually thicker than in Gotland ones and that is presumably the reason for the better growth of the tree layer (higher basal area and canopy closure) and many field layer species. Moreover, the amount of precipitations in Saaremaa (www.myweather2.com/City-Town/Estonia/Saaremaa-Island/climate-profile.aspx) exceeds 5–27 mm that in Gotland (www.myweather2.com/Motor-Racing/Sweden/Gotland-Ring/climate-profile.aspx) in all months, except May and June. At

the same time, the average temperature is some degrees lower from December to May in Saaremaa, while in summer and autumn it is almost equal on both islands. Albeit the pointed differences of temperature and precipitations are not very striking, in extreme conditions these continual small differences may have a crucial role for plants.

Comparing the floristical differences between two considered islands, we should take also into account the aspects of florogenesis. Numerous calcicolous and heliophilous species are growing in calcareous pine forests of Saaremaa and Gotland on their northern, north-western or western limits of geographical distribution (Kukk 1999, Mossberg and Stenberg 2003) but the plant geographical analysis is out of the scope of the current paper.

Somewhat higher percentage among the indicator species of Saaremaa apophytes, i.e. species preferring moderate to strong human impact, may approve there also to some respects more pronounced man-made effect on the forests studied than on Gotland. As the cartographic analysis showed, the majority of the recent calcareous forests in Saaremaa do not represent continuous ancient stands but have developed in the course of the last century. Though we did not have a possibility for analogous study of the forests history on Gotland, a rather severe human impact (grazing, cutting, pollarding, and cultivation) has been lasted there numerous centuries as well and has diminished after the II World War only (Pettersson 1950, 1965). The ceasing of grazing will be followed by overgrowing of open alvars or wooded meadows by shrubs or woods and the more closed canopy of woody vegetation will exterminate the heliophilous meadow flora (Pettersson 1965, Hægström 1983, Rosén and Borgegård 1999), but it offers also opportunity for enrichment vegetation with shadow-tolerant forest species. On different areas the human impact has had various intensity and history, and that together with even comparatively subtle habitat differences has created a network of forests with the richest species content in the northern Europe. In some respect, the larger species number in Gotland forest communities may be at least partly related to only late abandonment or still continuing grazing in these stands, while the larger total list of species in the considered forests of Saaremaa is explained by the about four times larger area of calcareous pine forests and connected with that wider variation of habitat conditions.

On the communities level the disagreement between the calcareous pine forests on Saaremaa and Gotland Islands is even more conspicuous than on species level. According to Bjørndalen (1985), the calcareous pine forests in Gotland and in Estonia are

closely related and they were classified by him to one broad *Convallario-Pinetum* association represented in Fennoscandia and Estonia in a rather wide geographical scope and with a considerable floristic variation between the different regions. Earlier, by a more explicit typology, these forests in Gotland and Estonia were distinguished as belonging to the *Seslerio-Pinetum* sub association (Bjørndalen 1980). In respect with the cited statements of J. E. Bjørndalen here one must be taken into account that he used as the Estonian reference only the data from 1920s collected by K. Linkola in neighbourhood of Hageri in the NW Estonia (Linkola 1929 1930). The current analysis of communities classification structure showed that from nine established community types three ones were connected exclusively with Saaremaa (*Melampyrum pratense-Rhytidiadelphus triquetrus* type, *Rubus caesius-Dicranum polysetum* type and *Pteridium aquilinum-Hylocomium splendens* type), while among the *Pimpinella saxifraga-Hylocomium splendens* type Gotland was represented merely with one community.

In the official Estonian forest typology elaborated by E. Lõhmus (2004), the calcareous (alvar) forests are represented with three site types named by a characteristic ground vegetation species as *Arctostaphylos*, *Calamagrostis* and *Sesleria* site type, divided further into the forest types by the dominating tree species. This typology has mainly a practical forestry issue (Kaar 1959) and to this day more detailed phytosociological studies of calcareous forests in Estonia are almost lacking. Therefore, all considered forest types were characterised in the current paper for the first time.

With Gotland only there were also bounded communities of three types (*Geranium sanguineum-Tortella tortuosa* type, *Deschampsia flexuosa-Scleropodium purum* type and *Carex montana-Scleropodium purum* type). According to Sernander (1894), all calcareous pine forests on Gotland can be defined as *pinetum herbicidum*. Numerous forest community types in Gotland were shortly characterised by Du Rietz (1925), but descriptions of these types are according to the state of art based on very few relevés. Marker (1969) has pointed on Gotland occurrence of *Peucedano-Pineetum* and *Melico-Pineetum* community types, whereas Kielland-Lund (1981) has merged all Gotland's pine forests to the *Melico-Piceetum pinetosum* subassociation of the *Melico nutantis-Piceetum abietis* association. Thus, three community types established by us were not described by anybody before, the same concerns communities of *Brachypodium sylvaticum-Rhytidiadelphus triquetrus* type and *Arctostaphylos uva-ursi-Hypnum cupressiforme* var. *lacunosum* type, represented more or less evenly on both islands.

We may conclude that notwithstanding the comparatively short geographical distance, generally similar soil and climatic conditions, the flora and classification structure of calcareous pine forest on Saaremaa and Gotland Islands is remarkable different. The reason for that is complex involving synergistic effect of man-made impact history, weathering extent of soil parent limestone deposits and the thickness of humus horizon covering it, soil chemistry properties but also certain differences in the precipitation amount in vegetation period, history of species distribution, closeness of shrub and tree layers etc. Due to the extreme habitat conditions, extremely rich and peculiar species content protection of calcareous pine forests needs more attention in future; so far they belong to the ordinary managed stands on both islands.

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