



Calcareous pine forests on Gotland, their typology and main soil properties

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Paal, J., Rajandu, E. 2014. Calcareous pine forests on Gotland, their typology and main soil properties. – *Forestry Studies | Metsanduslikud Uurimused* 60, 5–23. ISSN 1406-9954. Journal homepage: <http://mi.emu.ee/forestry.studies>

Abstract. The calcareous pine forests have one of the highest species diversity among the forest communities in northern Europe. We analysed their classification structure and the relationship with principal environmental variables on Gotland Island, South East Sweden. There were 14 species recorded in the tree layer, 60 species in the shrub layer, including 18 species of tree saplings, 273 species in the field layer and 80 species in the moss layer. The former classifications of the Gotland's calcareous pine forests are conducted too coarsely or without statistical justification of established community types. In the current study the stands were classified into four community types, 1) *Arctostaphylos uva-ursi*-*Tortella tortuosa* type, 2) *Brachypodium sylvaticum*-*Rhytidadelphus triquetrus* type, 3) *Carex montana*-*Scleropodium purum* type and, 4) *Geranium sanguineum*-*Scleropodium purum* type. All these community types have significantly different species content and they are mutually distinct also by numerous considered environmental variables. The species variation in the shrub, field and moss layers was related primarily with three rather strongly correlated variables: tree layer height, abundance of *Picea abies* (L.) H.Karst. and soil humus horizon depth. Soils were mainly the Sceletic Regosols or Calcaric Gleyic Regosols, but also Rendzic Leptosols.

Key words: basicole forests, basiphilous forests, biodiversity, Calcaric Regosols, Rendzic Leptosols.

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Introduction

Gotland Island is famous among the plant ecologists due to its peculiar flora and vegetation (Sterner, 1922; Pettersson, 1958, 1965). Though the alvar grassland communities have been there the most exciting objects for botanists already from the 18th century (Linnaeus, 1745; cited by Gimingham *et al.*, 1966), the calcareous pine forests constitute a major element of the landscape covering around 60% of the area (Björndalen, 2002). These forests developed on shallow calcareous soils, usually having sparse and stunted tree layer, and the insolation to the ground is high (Engelmark &

Hytteborn, 1999). The floristic composition of Fennoscandian calcareous pine forests is complex, containing elements from a variety of floristic/ecological species groups (Pettersson, 1965; Björndalen, 1980, 1985; Engelmark & Hytteborn, 1999).

The Scandinavian scientists have used several terms for naming these forests – calcicolous woods (Pettersson, 1965), basiphilous forests (Björndalen, 1980, 1985), basicole forests (Engelmark & Hytteborn, 1999) or forest on calcareous ground (Påhlsson, 1998). In Estonia the respective 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). Taking into account that in Sweden the term '*alvar*' is traditionally used only for open grasslands on limestone pavements and/or Rendzina soils (Albertson, 1946; Hæggström, 1983, Rosén & Borgegård, 1999) we call these communities in the current paper for avoiding further confusion as calcareous pine forests.

Considering that (i) these stands include numerous rare and red-listed species and present one of the highest species diversity among the forest communities in the whole Nordic area (Bjørndalen, 1980) and, (ii) these forests are at the same time seriously threatened in many regions (Bjørndalen, 1985, 2002; Nitare, 2009), a more detailed analysis of their typology and relationship with habitat conditions will enhance also their better management and protection practice. Effective conservation of plant communities cannot be obtained without a thorough knowledge of their diversity, representativeness and rarity (Margules, 1986; Paal, 1998). From the other side, detailed vegetation classification, mapping and description form the basis from which informed and scientifically defendable decisions can be made for infrastructure and management in the area (Aleksandrova, 1969; Shimwell, 1971). It is also of help in assessment of the anthropogenic impact on vegetation and its monitoring for protection or development purposes.

Along ecological and phytogeographical gradients in Fennoscandia numerous subtypes of calcareous pine forests can be recognized (Bjørndalen, 1980). Still, the typological variation of these forests in Gotland has been treated rather superficially and ambiguously, or without statistical testing of the established community types. In our earlier paper (Paal *et al.*, 2014) we compared the Gotland's calcareous forests with respective forests on Saaremaa Island and established their joint typology

and ecological analysis. In the current paper we aim (i) to perform a detailed analysis of calcareous pine forests only on the ground of Gotland's data, (ii) to establish the typology of these forests on the basis of multivariate methods and, (iii) to compare our results with the classifications of former scholars.

Material and Methods

Data collection

Gotland Island is located in the Baltic Sea ca 60 km from mainland of southeastern Sweden and is formed of highly calcareous Cambro-Silurian strata (Pettersson, 1965). The majority of calcareous pine forests on this island are affected by intensive grazing or of recent cuttings, but our interest in the current study was to analyse forests without obvious anthropogenic impact. Therefore, we carried out first an inventory of these forests over the whole island, and in the final selection only 34 stands at least 0.5 ha in area were found suitable for analysis (Figure 1). Vegetation analyses were performed with round sample plots of an area of 0.1 ha (radius 17.8 m), which were fitted within homogeneous forest patches.

Tree layer average height and canopy closure were evaluated visually. The basal area (BA) of trees with a diameter at breast height (1.3 m) of 5 cm and larger was measured by species using the Bitterlich relascope. In every sample plot, the basal area measurement was repeated in 4–5 random locations and averaged per site. Young trees, having a height below 5 m and/or a diameter at breast height less than 5 cm were considered as saplings. Shrubs and saplings were recorded by counting their stems on five randomly placed subplots with a radius of 2 m. The total projective cover of shrub, field and moss layer was evaluated visually. For field and moss layers a total species list over the 0.1 ha sample plot was compiled and their cover-abundance rating was estimated according

to the following scale: 0.1 (single specimens), 1 (average cover $\leq 1\%$), 2 (1–5%), 3 (5–10%), 4 (10–25%), 5 (25–50%), 6 ($> 50\%$).

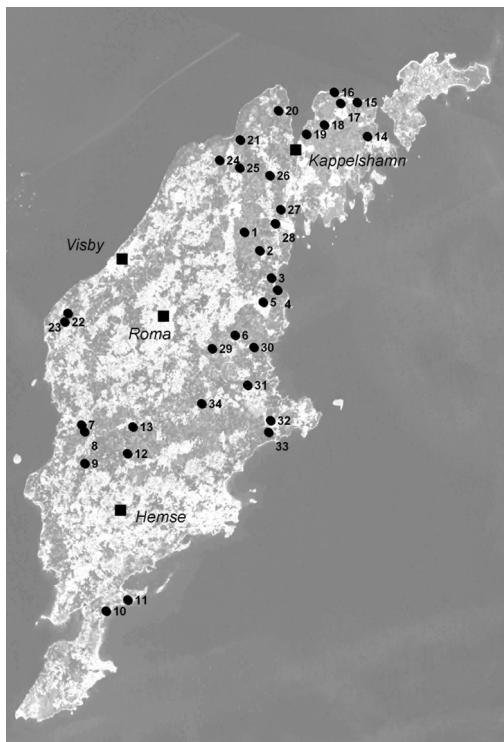


Figure 1. Location of the sample plots on Gotland Island.

Joonis 1. Proovialade asukohad Gotlandi saarel.

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 and of the horizon under that were estimated: pH_{KCl} , the percentage of organic C content by oxidation of all organic matter with $\text{K}_2\text{Cr}_2\text{O}_7$ (according to Vorob'eva, 1998), the percentage of total nitrogen by the Kjeldahl method (van Reeuwijk, 1995), the percentage of free carbonates by titration (ISO 10693, 1994). Loss on ignition was determined at $500\text{ }^{\circ}\text{C}$ (Rowell, 1994). All analyses were performed from the fine soil fraction with a diameter less than 2 mm.

The names of vascular plant species are taken from Lid & Lid (2005) and Halliday & Beadle (1983), names of bryophytes from Nationalnyckeln... (2006, 2008). Nomenclature of soils follows WRB (2006).

Data processing

Cluster analysis was based on the shrub, field and moss layer data. For clustering the β -flexible algorithm (McCune & Mefford, 2011) and the chord distance as the measure of dissimilarity were used. Before the analysis species occurring in data less than three times were filtered out. The clusters (= community types) were established on the basis of a dendrogram. The objectivity of relevés clustering was tested by the multi-response permutation procedure (MRPP) (McCune & Mefford, 2011), taking into account the Bonferroni correction for multiple comparisons. An additional testing of the cluster analysis quality was conducted by the squared Mahalanobis distances between the type centroids, calculated on the ground of 10 first principal component scores (Discriminant analysis; StatSoft Inc., 2005).

The indicator values of the species in the clusters were calculated by the Dufrêne and Legendre (1997) method included into the program package PC-ORD (McCune & Mefford, 2011). The statistical significance of the obtained indicator values were evaluated by the Monte Carlo permutation test ($N = 499$).

Differences in single soil properties between the established soil types, as well as between the vegetation types were evaluated by the univariate ANOVA, post-hoc Tukey LSD test and discriminant function analysis (StatSoft Inc., 2005).

For ordination of the sample plots and environmental variables the detrended correspondence analysis (DCA) was used (McCune & Mefford, 2011).

Results

In tree layer we recorded altogether 14 species, in the shrub layer 60 species, including 18 species of tree saplings, in the field layer (grasses + herbs + dwarf shrubs) 273 species and in the moss layer 80 species. Soils were mainly the Skeletic Regosols or Calcaric Gleyic Regosols, but also Rendzic Leptosols.

The variation in the shrub, field and moss layers is determined primarily by three mutually rather strongly ($r = 0.44\text{--}0.66$) correlated variables: tree layer height, abundance of *P. abies* and soil humus horizon depth. That is well illustrated on the DCA ordination biplot (Figure 2); the first DCA ordination axis has the highest correlation with these variables (0.81, 0.74 and 0.57, respectively). The first ordination axis

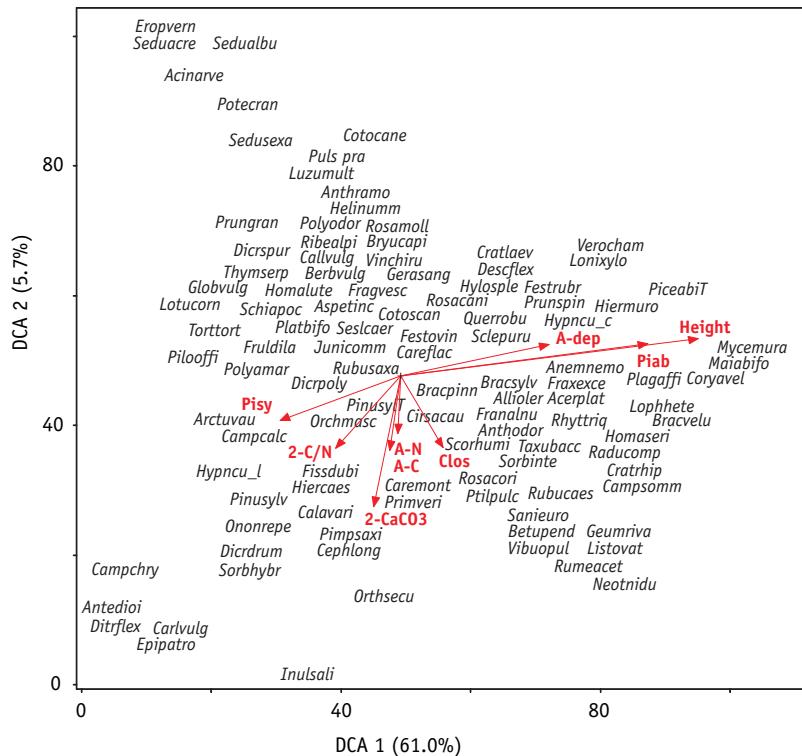


Figure 2. DCA biplot of species and environmental variables. Notations: A-dep – depth of soil humus horizon (cm), Piab and Pisy – basal area ($m^2 \cdot ha^{-1}$) of *Picea abies* and *Pinus sylvestris*, respectively, Height – height of tree layer (m), Clos – closure of tree layer canopy, A-N and A-C – nitrogen and carbon content in soil humus horizon, respectively, 2-CaCO₃ and 2-C/N – free carbonates content, and ratio of carbon and nitrogen content in soil horizon just below the humus horizon, respectively. Full species names are presented in Appendix 1.

Joonis 2. Liikide ja keskkonnategurite trendivaba vastavusanalüüs ordinaltsioonisekem. Tähistused: A-dep – mulla huumushorisondi paksus (cm), Piab ja Pisy – hariliku kuuse ja hariliku männi rinnaspind ($m^2 \cdot ha^{-1}$), Height – puurinde keskmise kõrgus (m), Clos – puurinde liitus, A-N ja A-C – mulla huumushorisondi lämmastiku- ja süsinikusisaldus, 2-CaCO_3 ja 2-C/N – vabade karbonaatide sisaldus ja süsiniku ning lämmastiku suhe mulla huumushorisondile järgnevas horisondis. Liikide täielikud nimetused on esitatud lisas 1.

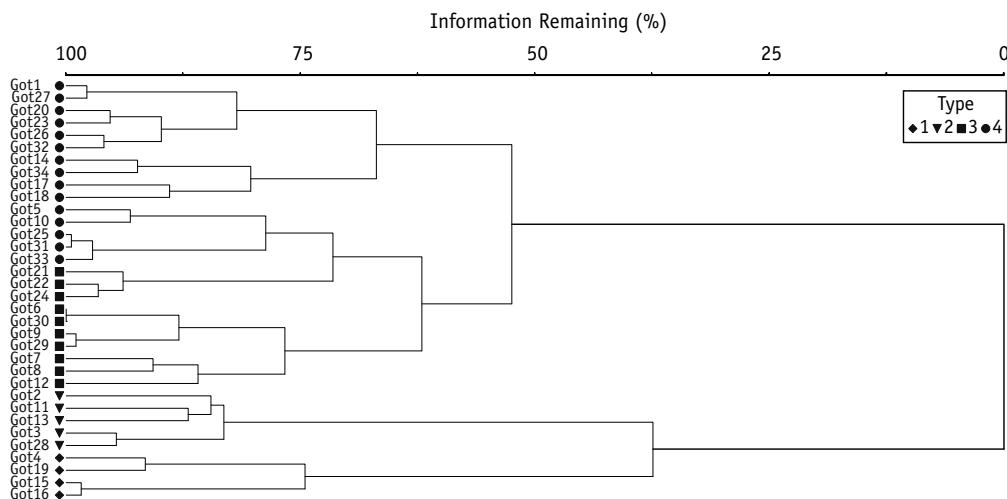


Figure 3. Cluster analysis dendrogram.

Joonis 3. Klasteranalüüsidi dendrogramm.

describes 61.0% of the species total variation. Variables correlating mainly with the second ordination axis (soil CaCO_3 , C and N content) characterize only 5.7% of the total variation.

The vascular plant species having the strongest positive relationship with the first ordination axis are *Mycelis muralis* (L.) Dumort., *Maianthemum bifolium* (L.) F.W.Schmidt, *Corylus avellana* L., *Aquilegia vulgaris* L., *Crataegus rhipidophylla* Gand. and of the bryophytes *Brachythecium velutinum* (Hedw.) B. S. et G., *Campylium sommerfeltii* (Myr.) J. Lange and *Lophocolea heterophylla* (Schrad.) Dum. In the opposite end of the first ordination axis are situated vascular plants such as *Antennaria dioica* (L.) Gaertn., *Epipactis atrorubens* (Hoffm. ex Bernh.) Besser, *Sedum acre* L., *Erophila verna* (L.) Chevall. and the bryophytes *Campylium chrysophyllum* (Brid.) J. Lange and *Ditrichum flexicaule* (Schwaegr.) Hampe (Figure 2).

The cluster analysis grouped the relevés into four community types (Figure 3) all having significantly ($p < 0.05$) different species composition by the MRPP tests, even taking into account the rather conservative Bonferroni correction for multiple comparisons. The significance of squared

Mahalanobis distances between the type centroids is < 0.005 , except between the 3rd and 4th type: there the p -value is 0.096, i.e. exceeds the conventionally acceptable limit. In conformity with that on the ordination biplot (Figure 4) the first three community types have all a well distinctive location, only the last type has larger variation and is partly overlapping with communities of the 3rd type.

Distinctness of community types established by their species content is similar also by the considered environmental variables: the significance of squared Mahalanobis distances between the type centroids is in all cases < 0.005 except the 3rd and 4th type where the respective value is 0.230. At the same time numerous environmental variables appeared to be significantly different for established community types not only by the ANOVA but also by the discriminant analysis (Table 1).

The fraction of dendrogram representing the 4th cluster includes in fact three „branches“, alluding to the potentiality of further splitting that cluster to three separate community types or subtypes; still on the basis of current data set distinguishing of these subclusters appeared statistically

Table 1. Community structure characteristics and soil properties in the established community types. Notations: X – arithmetical mean, SD – standard deviation, ANOVA – one way analysis of variance, DA – backward stepwise discriminant analysis, F – F-criterion, p – significance level; Height – height of tree layer (m), Closure – closure of tree layer canopy, Piab – basal area ($m^2 \cdot ha^{-1}$) of *Picea abies*, Pisy – basal area of *Pinus sylvestris*; Shrub, Field, Moss – projective cover of shrub, field and moss layers, respectively; A – soil humus horizon, 2 – soil horizon just below the humus horizon, A-depth – depth of soil humus horizon (cm), pH – soil pH measured in KCl solution, N, C and $CaCO_3$ – nitrogen, carbon and free carbonates content (%), C/N – ratio of carbon and nitrogen content, LOI – loss on ignition (%). In each row, different superscript letters denote significant differences between the community types by Tukey Unequal N HSD test.

Tabel 1. Kooslusetüüpide taimkatte struktuuri iseloomustavad karakteristikud ning mullaomadused. Tähistroosed: X – aritmeetiline keskmene, SD – standardhälve, ANOVA – ühefaktoriline dispercioonanalüüs tulemused, DA – tunnuste sammuväislise väljajätoga diskriminantanalüüs tulemused, F – F-kriiterium, p – olulisustõenäosus; Height – puurinde keskmene kõrgus (m), Closure – puurinde liitus, Piab – hariliku kuuse rinnaspind ($m^2 \cdot ha^{-1}$), Pisy – hariliku männi rinnaspind; Shrub, Field, Moss – vastavalt põõsa-, puhma-rohu- ja samblarinde üldkatvus; A – mulla huumushorisont, 2 – huumushorisondile järgnev mullahorisont. A-depth – huumushorisondi paksus (cm), pH – pH KCl lahuses, N, C and $CaCO_3$ – vastavalt lämmastiku, süsiniku ja vabade karbonaatide sisaldus (%), C/N – süsiniku ja lämmastikusisalduse suhe, LOI – kuumutuskadu (%). Tabeli igas reas on täheliste üleinideksitega tähistatud kooslusetüüpidele omased oluliselt erinevad vääritud Tukey ebavördse N HSD testi põhjal.

Variable / Tunnus	Community type / Kooslisetüüp								ANOVA		DA	
	1		2		3		4		F	p	F	p
	X	SD	X	SD	X	SD	X	SD				
Height	8.5 ^c	1.3	20.2 ^a	4.1	14.7 ^b	3.2	13.7 ^b	3.4	9.32	<0.001	0.40	0.753
Closure	0.5 ^{ab}	0.2	0.6 ^a	0.1	0.4 ^b	0.1	0.4 ^b	0.1	4.17	0.014	0.96	0.431
Piab	0.0 ^b	0.0	8.9 ^a	9.6	1.3 ^b	1.8	1.6 ^b	2.3	5.35	0.005	12.83	<0.001
Pisy	17.4	3.4	11.5	8.5	15.4	1.8	16.1	3.6	1.81	0.168	0.17	0.917
Shrub	17.0	17.1	43.0	28.2	27.0	6.7	37.0	11.9	3.27	0.035	1.75	0.190
Field	40.0 ^b	14.1	52.0 ^{ab}	23.9	72.0 ^a	14.0	51.3 ^b	20.7	3.93	0.018	2.44	0.094
Moss	33.8	28.1	59.0	27.5	51.0	19.7	57.2	23.7	1.07	0.376	0.55	0.652
A-depth	1.5 ^b	1.0	12.2 ^a	4.0	7.7 ^a	3.8	7.2 ^{ab}	4.8	5.17	0.006	0.37	0.774
A-pH	6.3	1.1	6.0	1.0	6.6	0.5	6.4	0.5	0.97	0.423	7.56	0.001
A-N	1.2 ^a	0.2	0.9 ^{ab}	0.4	0.4 ^c	0.2	0.6 ^{bc}	0.4	7.93	0.001	5.67	0.005
A-C	32.7 ^a	6.0	19.6 ^{ab}	10.9	6.2 ^c	2.4	11.4 ^{bc}	9.3	11.91	<0.001	6.69	0.002
A-LOI	65.6 ^a	30.3	65.0 ^a	17.5	20.0 ^b	6.3	33.4 ^{ab}	28.2	6.50	0.002	18.84	<0.001
A-CaCO ₃	7.9 ^a	2.3	4.8 ^{ab}	2.8	2.8 ^b	1.8	3.7 ^b	2.9	4.11	0.015	0.09	0.964
A-C/N	27.3 ^a	3.4	19.5 ^{ab}	5.0	17.4 ^b	3.8	18.6 ^b	4.4	5.32	0.005	4.36	0.015
2-pH	7.2	0.1	7.1	0.3	7.2	0.3	7.2	0.3	0.12	0.947	2.27	0.112
2-N	0.7	0.2	0.6	0.6	0.2	0.1	0.4	0.3	2.63	0.069	15.50	<0.001
2-C	15.2 ^a	4.1	10.1 ^{ab}	9.6	3.5 ^b	1.8	6.3 ^b	5.1	5.33	0.005	13.19	<0.001
2-LOI	39.6	19.0	28.8	27.8	15.3	4.6	19.5	14.8	2.59	0.072	13.72	<0.001
2-CaCO ₃	17.8 ^a	3.3	9.3 ^{ab}	5.3	7.7 ^b	4.6	7.5 ^b	5.4	4.50	0.010	0.19	0.902
2-C/N	23.0 ^a	4.2	15.5 ^b	3.1	14.0 ^b	2.1	15.3 ^b	2.4	11.36	<0.001	0.59	0.632

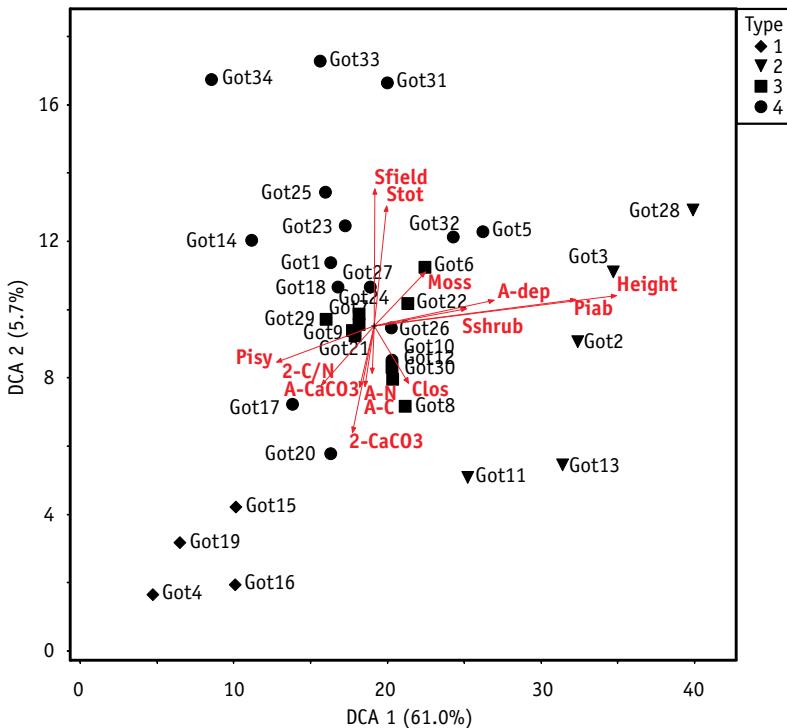


Figure 4. DCA biplot of sample plots and environmental variables. Notations: Stot, Sshrub and Sfield – total number of species, number of shrub layer and field layer species, respectively. Moss – total cover of moss layer. Other notations as in Figure 2.

Joonis 4. Proovialade ja keskkonnategurite trendivaba vastavusanalüüs ordinatsiooniskeem. Tähistused: Stot, Sshrub ja Sfield – liikide koguarv, põõsarinde liikide arv ja puhma-rohurinde liikide arv, Moss – sambalainde üldkatvus. Muud tähistused nagu joonisel 2.

unfounded. Considering the dominant and/or indicator species (Appendix 1), the community types can be labeled as: 1) *Arcostaphylos uva-ursi*-*Tortella tortuosa* type, 2) *Brachypodium sylvaticum*-*Rhytidiodelphus triquetrus* type, 3) *Carex montana*-*Scleropodium purum* type and, 4) *Geranium sanguineum*-*Scleropodium purum* type.

In the communities of *Arctostaphylos uva-ursi*-*Tortella tortuosa* type the tree layer is very stunted with an average height of 8.5 m and includes only *Pinus sylvestris* L. (Table 1). The projective cover of shrub, field and moss layer is comparatively tenuous (17%, 40% and 34%, respectively), and

the species number in field and shrub layers is lower than in other community types. The shrub layer is formed mainly by *Juniperus communis* L. and *Sorbus aucuparia* L. In the field layer additionally species such as *Vaccinium vitis-idaea* L., *Melampyrum pratense* L. and *Festuca ovina* L. should be mentioned, in moss layer *Rhytidadelphus triquetrus* (Hedw.) Warnst. and *Hypnum cupressiforme* Hedw. var. *lacunosum* Brid. (Appendix 1). Besides the title species, significant indicators in the field layer are *E. atrorubens*, *A. dioica* and *Pilosella officinarum* (Mérat) F.W.Schultz et Sch.Bip. ssp. *peleteriana*, in the moss layer *D. flexicaule* and

H. cupressiforme var. *lacunosum*. The soils of these communities have a very shallow humus horizon (ca 1.5 cm). The C and CaCO₃ content and the N/C ratio in the humus horizon but also in the horizon below are the highest among the studied samples (Table 1). Communities of the *Arctostaphylos uva-ursi*-*Tortella tortuosa* type were found in the northern and eastern Gotland (Figure 1).

The *Brachypodium sylvaticum*-*Rhytidadelphus triquetrus* type communities have the highest tree layer and the basal area of *P. sylvestris* and *P. abies* is almost equal, but some *Betula pendula* Roth and *Quercus robur* L. are represented as well (Appendix 1). These stands have the most dense canopy. In the shrub layer *C. avellana* and *Sorbus intermedia* (Ehrh.) Pers. are characteristic, in the field layer, in addition to *Brachypodium sylvaticum* (Huds.) P. Beauv. species such as *Anemone nemorosa* L., *Convallaria majalis* L. and *Hepatica nobilis* Mill. grow abundantly. Among essential indicator species also *Listera ovata* (L.) R. Brown, *M. muralis*, *Paris quadrifolia* L. and *Rubus caesius* L. are noteworthy (Appendix 1). Soils in these communities have the thickest humus horizon, their pH is comparatively low, whereas the N content and humus content have high values, almost equal to soils of the previous community type (Table 1). The *Brachypodium sylvaticum*-*Rhytidadelphus triquetrus* type communities are represented in various parts of the island (Figure 1).

The tree layer of the *Carex montana*-*Scleropodium purum* type communities has average height, comprises beside *P. sylvestris* only some single *P. abies* trees and its closure usually does not exceed 0.4. The shrub layer is rich in *J. communis* but includes numerous other species, e.g. *Berberis vulgaris* L., *Cotoneaster scandinavicus* B. Hylmö, *C. canescens* Vestergr. ex B. Hylmö, *Prunus cerasus* L., *Rosa mollis* Sm. etc. The field layer is well developed, its mean coverage is over 70%. Together with the title species prevail *Brachypodium pinnatum* (L.) P. Beauv., *Carex flacca* Schreb., *F. ovina*, *Calluna vulgaris* (L.)

Hull, *Galium boreale* L., *Scorzonera humilis* L. and *Sesleria caerulea* (L.) Ard. (Appendix 1). The pH of the humus horizon is subneutral (6.6), whereas the N, C, CaCO₃ content and the C/N ratio have the lowest value among the compared samples (Table 1). Substantial participation in field layer of *C. flacca* and *S. caerulea* indicates that soils are to some degree gleyed. The *Carex montana*-*Scleropodium purum* type communities are situated in eastern part of island in the surroundings of Slite but also in the central part of Gotland (Figure 1).

In the analysed data the *Geranium sanguineum*-*Scleropodium purum* type is represented with the largest number of relevés. Tree and shrub layers are quite similar with the communities of the previous type but the ground vegetation of these communities contains the largest number of species. The significant indicator species for this type are also *Filipendula vulgaris* Moench, *Briza media* L., *Helianthemum nummularium* (L.) Mill. non Grosser and *J. communis*, but to some extent the latter species are represented in all studied communities (Appendix 1). Moreover, relatively rather abundant are species such as *B. sylvaticum*, *B. pinnatum*, *C. flacca*, *F. ovina*, *Fragaria vesca* L., *S. caerulea* and *H. nobilis*. The soil properties of these communities have medium value, and like the soils of the 3rd community type, by the frequency of *S. caerulea* and *C. flacca*, here also some gleying is observable. The communities of *Geranium sanguineum*-*Scleropodium purum* type occur mainly in northern Gotland (Figure 1).

Discussion

The majority of authors have characterized the typological variation of the Gotland calcareous pine forests just casually or on a rather generalized level. According to Sernander (1894), the calcareous pine forests on Gotland can be defined as *pinetum herbidum*. Hesselman (1908) has pointed out that the *Arctostaphylos uva-ursi* (L.) Spreng.

pinewoods are typical to the northern Gotland, whereas herb-rich pinewoods (*pineta herbida*) occupy larger areas in other parts of the island. Marker (1969) has mentioned that in Gotland communities of *Peucedano-Pinetum* and *Melico-Pinetum* occur, and Kielland-Lund (1981) claims that Gotland's pine forests belong solely to the *Melico-Piceetum pinetosum* subassociation of the *Melico nutantis-Piceetum abietis* association. Pahlsson (1998) referred in general the respective forests to pine forests on calcareous ground.

According to the synchorological classification carried out by Bjørndalen (1980), these communities in Gotland are presented by the Baltic association of *Seslerio-Pinetum*. Later, in a more refined classification system Bjørndalen (1985) divided the so-called true basidophilous forests of the *Convallario-Pinetum* association into three main types distinguished by moisture conditions, and further into several geographical races. Gotlands race of xerophilous forests group includes species-rich forests where numerous southeastern species occur. A prevailing species is *A. uva-ursi*, typical are also *Calamagrostis varia* (Schrad.) Host, *Galium triandrum* Hyl., *H. nummularium*, *S. caerulea* and *Vincetoxicum hirundinaria* Medik. Forests of the Gotland's race of herb-rich (mesic) type are even richer in species and several of them can have a dominating position, e.g. *B. pinnatum*, *B. sylvaticum*, *C. varia*, *C. majalis*, *F. vulgaris*, *Geranium sanguineum* L., *S. caerulea* and *V. hirundinaria*. Forests belonging to the seasonal hygrophilous type are found in the southernmost part of Gotland. In these communities *Inula salicina* L. and calciphilous/hygrophilous species are more prominent.

The most detailed classification of Gotland forests has been published by Du Rietz (1925). He described altogether nine *P. sylvestris* dominated associations on more or less calcareous mineral soils: 1) *Pinus sylvestris-Arctostaphylos uva-ursi* association with four variants – (i) pure, on shingle, (ii) nor-

mal, (iii) grass-rich and, (iv) moss-rich; characteristic for the association are also *Campanula persicifolia* L., *Lathyrus vernus* (L.) Bernh. and *S. humilis*; 2) herb-rich variant of *Pinus sylvestris-Calluna vulgaris-Hylocomium* association on till covered rocks; 3) *Pinus sylvestris-Festuca ovina* association on talus slopes of the klint; 4) *Pinus sylvestris-Asperula tinctoria* association on shallow soils where also *G. sanguineum*, *Globularia vulgaris* L. and *F. ovina* occur, and what has certain similarity with communities of the first association; 5) *Pinus sylvestris-Hepatica nobilis* association, affine with previous association; 6) *Pinus sylvestris-Anemone nemorosa* association on soils with thicker layer of moraine on bedrock; 7) *Pinus sylvestris-Crataegus-Anemone nemorosa* association, comprising the most species-rich and lush pine forests on Gotland; 8) *Pinus sylvestris-Melica nutans* association in habitats where the bedrock is covered with moraine of various thickness and, 9) *Pinus sylvestris-Sesleria caerulea* association in habitats with nearly stagnant water. Still, with these community types we must consider that each of them has been established according to the state of art on the ground of a very scanty number of relevés and, therefore, from the statistical point of view they are not reliable.

Nevertheless, the *Arctostaphylos uva-ursi-Tortella tortuosa* type delimited in the current analysis has certain similarity with the grass-rich and moss-rich variants of the *Pinus sylvestris-Arctostaphylos uva-ursi* association established by Du Rietz (1925), but *C. persicifolia* and *L. vernus* had a very low frequency in all our sample, and *S. humilis* appeared instead to be an indicator species of the *Carex montana-Scleropodium purum* type.

Our communities of the *Brachypodium sylvaticum-Rhytidadelphus triquetrus* type have first of all a high affinity with the *Pinus sylvestris-Anemone nemorosa* association, and partly with the *Pinus sylvestris-Hepatica nobilis* association of Du Rietz (1925). According to Bjørndalen (1985), these communities belong to the Gotland's

race of herb-rich (mesic) type of the *Convallario-Pinetum* association.

The present *Carex montana-Scleropodium purum* type does not have an analogue among Du Rietz' (1925) associations; no type is presented there where *Carex montana* L. or *B. pinnatum* have a dominating position. By Björndalen (1985) this forest type is also embraced by the Gotlands race of herb-rich (mesic) type of the *Convallario-Pinetum* association.

The *Geranium sanguineum-Scleropodium purum* type is characterized by the largest internal variation, therefore it does not correspond well with any classification unit of the previous authors. A certain similarity can be followed by Du Rietz' (1925) associations of *Pinus sylvestris-Crataegus-Anemone nemorosa*, *Pinus sylvestris-Anemone nemorosa*, *Pinus sylvestris-Hepatica nobilis*, but also by *Pinus sylvestris-Sesleria coerulea*. Due to the locally occurring coherence with gleyic soils, communities of the considered type have partly an affinity with Gotland's race of seasonal hygrophilous basiphilous pine forests characterized by Björndalen (1985).

The community types described in the current paper are in good conformity with the respective types established in our previous paper dealing with comparison of calcareous pine forests in Saaremaa and Gotland Islands (Paal *et al.*, 2014). Despite of a larger sample, the difference is expressed only by the importance of some bryophytes as indicator species: instead of *Tortella tortuosa* (Hedw.) Limpr. in the current *Arctostaphylos uva ursi-Tortella tortuosa* type the *H. cupressiforme* var. *lacunosum* has higher indicator value, and in *Geranium sanguineum-Scleropodium purum* type the *T. tortuosa* is more prominent.

By reference to the analysis presented above we can conclude that the calcareous forests in Gotland are classified by former scholars whether too roughly, interpreting them all representing only one (Sernander, 1894; Hesselman, 1908; Kielland-Lund, 1981; Pålsson, 1998) or two (Marker, 1969) typological units, or splitting them into

many small associations (Du Rietz, 1925) whereby the statistical validity of established typological units has not been tested by anybody. We hope that the current paper will provoke in future more thorough studies of the peculiar calcareous forests in Gotland including aspects of their dynamics due to the anthropogenic factors.

Our results confirm the extraordinary species richness of calcareous pine forests among the nordic forest types. These forests surely need special attention in respect of biodiversity preservation (cf. Björndalen, 2002; Nitare, 2009). Similarly to the alvar meadows, the present calcareous pine forest on Gotland have been formed just due to the long-time human impact (Sernander, 1894; Pettersson, 1950, 1958, 1965; Nitare, 2009). A large part of these forests is continuously used for grazing but also for felling. If the grazing will be stopped, the stands with rather open canopy will develop towards higher closure and many heliophilous plant species will be outcompeted as it happens with overgrowing of alvar meadows by shrubs (e.g. Rosén, 1982; Hæggström, 1983; Rosén & Borgegård, 1999). Therefore the total cessation of human activities does not seem to be the best practice here.

Acknowledgements. We thank Mr. Jörgen Pettersson, the Chairman of the Botanical Society of Gotland for introducing us the island and numerous local plant species, Prof. Håkan Hytteborn for useful advices in preparing the manuscript, Mr. Rivo Rajandu for help in fieldwork, PhD Ain Kull for preparing the Figure 1 and Mrs. Kesti Unt for revising English. The study was supported by the Estonian Science Foundation grant 8060, target-financing project SF0180012s09 and by the Centre of Excellence FIBIR.

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Appendix 1. Centroids and indicator species of community types. After the community type number in brackets the number of relevés is pointed. Only species with mean abundance at least 0.3 in one type or having significant indicator value are presented. Notations: number of species – arithmetical mean ± standard deviation, Max type – type for what the indicator value is maximal, p – significance level, Abbrev. – abbreviation.

Lisa 1. Kooslusetiüüride tsentroidid ja indikaatoriüigid. Kooslusetiüübi numbri järel sulgudes on seda tiipi esindavate analüüside arv. Esitatud on ainult liigid, mille keskmise ohtrus vähemalt ühes tiibis on üle 0.3 või mille indikaatorväärtsuse olulisustõenäosus on väiksem kui 0.05. Tähistused: number of species – liikiide arv (arithmeetiline keskmene ± standardhääve), Max type – tiüp, milles indikaatorväärtsus on maksimaalne, p – olulisustõenäosus, Abbrev. – liigi lühendatud nimetus.

Species / Liik		Community type / Kooslusetiüüp				Indicator species analysis / Indikaatoriülide analüüs				Max type	p	Species relative frequency in type / Liigi suhetine sagekus kooslusetiüübisse			
		1 (4)		2 (5)		3 (10)		4 (15)							
		Number of species / Liikiide arv													
		48±12	59±3	61±7	65±10										
Full name / Täielik nimetus															
		Abbrev. / Lühend		Tree layer / Puurinne											
Column numbers / Veergude numbrid															
1	1	2	3	4	5	6	7	8	9	10	11	12			
<i>Betula pendula</i>		<i>BetupenT</i>	–	0.3	–	2	0.031	0	40	0	0	0			
<i>Picea abies</i>		<i>PiceabiT</i>	–	8.9	1.3	1.5	–	–	–	–	–	–			
<i>Pinus sylvestris</i>		<i>PinusylT</i>	17.4	11.5	15.4	16.1	–	–	–	–	–	–			
<i>Quercus robur</i>		<i>QuerrobT</i>	–	0.9	–	–	–	–	–	–	–	–			
Number of species / Liikiide arv															
		7±2	14±4	12±4	12±3	Shrub layer and saplings / Põõsarinne ja järelkasv									
<i>Berberis vulgaris</i>		<i>Berbulg</i>	–	–	0.3	0.4	–	–	–	–	–	–			
<i>Corylus avellana</i>		<i>Conyavel</i>	–	1.6	<0.1	–	2	0.003	0	60	10	0			
<i>Cotoneaster canescens</i>		<i>Cotocane</i>	–	–	0.1	0.3	–	–	–	–	–	–			
<i>Cotoneaster scandinavicus</i>		<i>Cotoscan</i>	–	0.6	1.5	1.7	–	–	–	–	–	–			
<i>Cotosimo</i>		<i>Cotosimo</i>	–	–	0.1	–	–	–	–	–	–	–			
<i>Crataeaev</i>		<i>Cratlaev</i>	–	0.2	<0.1	<0.1	–	–	–	–	–	–			
<i>Crathip</i>		<i>Crathip</i>	1.0	<0.1	<0.1	2	0.005	0	60	10	7	7			
<i>Franalnu</i>		<i>Franalnu</i>	–	0.6	0.8	0.8	–	–	–	–	–	–			

Appendix 1 continues / Lisa 1 järgneb

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Fraxinus excelsior</i>		<i>Fraxexe</i>	-	0.4	0.2	0.2	-	-	-	-	-	-
<i>Juniperus communis</i>		<i>Junicomm</i>	2.5	1.4	3.2	3.5	4	0.002	100	100	100	100
<i>Lonicera xylosteum</i>		<i>Lonixyl</i>	<0.1	1.0	0.1	0.7	-	-	-	-	-	-
<i>Picea abies</i>		<i>Piceabie</i>	0.8	1.0	1.0	0.9	-	-	-	-	-	-
<i>Pinus sylvestris</i>		<i>Pinusylv</i>	1.8	-	0.8	0.7	-	-	-	-	-	-
<i>Prunus cerasus</i>		<i>Pruncera</i>	-	-	<0.1	0.1	-	-	-	-	-	-
<i>Prunus spinosa</i>		<i>Prunspin</i>	-	1.4	0.7	1.3	-	-	-	-	-	-
<i>Quercus robur</i>		<i>Querrobu</i>	<0.1	1.0	0.9	0.8	-	-	-	-	-	-
<i>Rhamnus catharticus</i>		<i>Rhamcath</i>	0.5	1.2	0.5	1.5	-	-	-	-	-	-
<i>Ribes alpinum</i>		<i>Ribeaipi</i>	0.3	-	-	0.3	-	-	-	-	-	-
<i>Rosa canina</i>		<i>Rosacani</i>	0.3	0.4	0.2	0.5	-	-	-	-	-	-
<i>Rosa mollis</i>		<i>Rosamoll</i>	-	-	0.3	0.6	-	-	-	-	-	-
<i>Sorbus aucuparia</i>		<i>Sorbaucu</i>	1.5	1.6	1.0	1.2	-	-	-	-	-	-
<i>Sorbus hybrida</i>		<i>Sorbyhybr</i>	0.5	-	-	0.2	-	-	-	-	-	-
<i>Sorbus intermedia</i>		<i>Sorbinte</i>	0.5	1.8	1.2	1.0	-	-	-	-	-	-
<i>Viburnum opulus</i>		<i>Vibuopul</i>	<0.1	0.4	0.1	<0.1	-	-	-	-	-	-
Field layer / Puhma-tohurinne												
			28±10	32±4	35±4	39±8						
Number of species / Lihkide arv												
<i>Actinos anensis</i>		<i>Actinane</i>	-	-	<0.1	<0.1	-	-	-	-	-	-
<i>Allium vineale</i>		<i>Allivine</i>	-	-	<0.1	<0.1	-	-	-	-	-	-
<i>Anemone nemorosa</i>		<i>Anemnemo</i>	-	3.4	2.2	1.2	2	<0.001	0	100	100	60
<i>Antennaria dioica</i>		<i>Antedioi</i>	1.0	-	<0.1	1	0.002	75	0	0	0	7
<i>Anthericum ranosum</i>		<i>Anthramo</i>	-	-	0.1	0.2	-	-	-	-	-	-
<i>Anthoxanthum odoratum</i>		<i>Anthodor</i>	-	0.2	0.5	0.3	-	-	-	-	-	-
<i>Anthyllis vulneraria</i>		<i>Anthvuln</i>	-	-	<0.1	-	-	-	-	-	-	-
<i>Arabis hirsuta</i>		<i>Arabhiirs</i>	-	-	<0.1	-	-	-	-	-	-	-
<i>Arctostaphylos uva-ursi</i>		<i>Arctuvau</i>	4.8	-	0.6	1.7	1	<0.001	100	0	40	73
<i>Arenaria serpyllifolia</i>		<i>Arenserp</i>	-	-	<0.1	-	-	-	-	-	-	-
<i>Arrhenatherum elatius</i>		<i>Arrhelat</i>	-	-	0.1	-	-	-	-	-	-	-

Appendix 1 continues / Lisa 1 järgneb

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Globularia vulgaris</i>		<i>Globbulg</i>	0.3	—	—	0.1	—	—	—	—	—	—
<i>Helianthemum nummularium</i>		<i>Helinumm</i>	—	—	0.1	0.5	4	0.044	0	0	30	53
<i>Helictotrichon pratense</i>		<i>Heliprat</i>	0.5	0.2	0.6	1.0	—	—	—	—	—	—
<i>Hepatica nobilis</i>		<i>Hepanobi</i>	0.5	2.6	1.6	1.9	2	<0.001	50	100	90	100
<i>Hieracium bifidum</i> agg.		<i>Hierbif</i>	0.5	—	0.1	—	—	—	—	—	—	—
<i>Hieracium caesium</i> agg.		<i>Hiercaes</i>	1.5	0.4	0.5	0.5	—	—	—	—	—	—
<i>Hieracium peleterianum</i> ssp. <i>peleterianum</i>		<i>Hierpel</i>	1.0	—	—	0.4	1	0.002	100	0	0	40
<i>Hieracium murorum</i> agg.		<i>Hiermuro</i>	—	0.6	—	0.3	—	—	—	—	—	—
<i>Listera ovata</i>		<i>Listovat</i>	—	0.6	—	<0.1	2	0.049	0	40	0	13
<i>Lotus corniculatus</i>		<i>Lotucorn</i>	0.5	—	0.1	0.2	—	—	—	—	—	—
<i>Luzula campestris</i>		<i>Luzucamp</i>	—	—	<0.1	—	—	—	—	—	—	—
<i>Luzula multiflora</i> ssp. <i>divulgata</i>		<i>Luzumult</i>	<0.1	<0.1	<0.1	0.3	—	—	—	—	—	—
<i>Luzula pilosa</i>		<i>Luzupilo</i>	0.3	0.4	<0.1	<0.1	2	0.026	25	80	10	13
<i>Maianthemum bifolium</i>		<i>Maiabifjo</i>	—	0.8	—	—	2	<0.001	0	80	0	0
<i>Melampyrum pratense</i>		<i>Melaprat</i>	1.5	0.2	0.9	0.7	—	—	—	—	—	—
<i>Melampyrum sylvaticum</i>		<i>Melasylv</i>	—	0.4	—	—	—	—	—	—	—	—
<i>Melica nutans</i>		<i>Melinuta</i>	0.3	1.6	1.9	1.5	3	0.014	25	100	100	100
<i>Mycelis muralis</i>		<i>Mycemura</i>	—	0.4	—	<0.1	2	0.005	0	60	0	7
<i>Neottia nidus-avis</i>		<i>Neotnidu</i>	0.3	0.2	<0.1	—	—	—	—	—	—	—
<i>Orchis mascula</i>		<i>Orchmasc</i>	0.3	0.2	<0.1	0.4	—	—	—	—	—	—
<i>Orchis spitzelii</i>		<i>Orchspit</i>	0.3	—	<0.1	—	—	—	—	—	—	—
<i>Orrhilia secunda</i>		<i>Orthsecu</i>	0.3	<0.1	<0.1	—	—	—	—	—	—	—
<i>Oxalis acetosella</i>		<i>Oxalacet</i>	—	0.4	—	—	—	—	—	—	—	—
<i>Paris quadrifolia</i>		<i>Parquad</i>	—	0.4	—	—	—	2	0.027	0	40	0
<i>Plantago lanceolata</i>		<i>Planlanc</i>	<0.1	—	0.5	0.4	—	—	—	—	—	—
<i>Poa angustifolia</i>		<i>Poaaangus</i>	0.3	0.4	0.4	0.3	—	—	—	—	—	—
<i>Poa compressa</i>		<i>Poacompr</i>	—	—	—	—	—	—	—	—	—	—
<i>Polygala amaraella</i>		<i>Polygamar</i>	0.5	—	0.2	0.3	—	—	—	—	—	—
<i>Polygonatum odoratum</i>		<i>Polyodor</i>	—	—	0.4	0.5	—	—	—	—	—	—

<i>Potentilla crantzii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Potentilla erecta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	40
<i>Primula veris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prunella grandiflora</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pteridium aquilinum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pulsatilla pratensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pyrola chlorantha</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ranunculus acris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ranunculus polyanthemos</i> ssp. <i>polyanthemos</i>	<0.1	1.0	0.7	0.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rubus caesius</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13
<i>Rubus saxatilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rumex acetosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Saxifraga tridactylites</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Scorzonera humilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sedum acre</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sedum album</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sedum sexangulare</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Senecio jacobaea</i> ssp. <i>dumensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sesleria caerulea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Silene nutans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Taraxacum officinale</i> agg.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Thymus serpyllum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vaccinium myrtillus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vaccinium vitis-idaea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Veronica chamaedrys</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Veronica officinalis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vincetoxicum hirundinaria</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Viola riviniana</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 1 continues / Lisa 1 järgneb

Moss layer / Samblarinne	1	2	3	4	5	6	7	8	9	10	11	12
Number of species / liikide arv												
<i>Aulacomnium palustre</i>												
var. <i>imbricatum</i>												
<i>Brachythecium rutabulum</i>												
<i>Brachythecium velutinum</i>												
<i>Campylium chrysophyllum</i>												
<i>Campylium sommerfeltii</i>												
<i>Campylium stellatum</i>												
<i>Ctenidium molluscum</i>												
<i>Dicranum drummondii</i>												
<i>Dicranum polysetum</i>												
<i>Dicranum scoparium</i>												
<i>Dicranum spinosum</i>												
<i>Ditrichum flexicaule</i>												
<i>Fissidens dubius</i>												
<i>Frullania dilatata</i>												
<i>Grimmia pulvinata</i>												
<i>Hylocomium splendens</i>												
<i>Hypnum cupressiforme</i> var. <i>cupressiforme</i>												
<i>Hypnum cupressiforme</i> var. <i>lacunosum</i>												
<i>Lophocolea heterophylla</i>												
<i>Plagiomnium affine</i>												
<i>Pleurozium schreberi</i>												
<i>Ptilium cristacastrense</i>												
<i>Ptilium pulcherrimum</i>												
<i>Radula complanata</i>												
<i>Rhytidiodelphus triquetrus</i>												
<i>Schistidium apocarpum</i>												
<i>Scleropodium purum</i>												
<i>Tortella tortuosa</i>												
	1.8	<0.1	0.3	0.9	1	0.003	100	20	20	20	47	

Gotlandi kaltsifiilsed männikud; nende tüpoloogia ja muldade peamised omadused

Jaanus Paal ja Elle Rajandu

Kokkuvõte

Kaltsifiilsed männikud on ühed Põhja-Euroopa liigirikkaimad metsakoooslused. Töös käsitletakse nende metsade klassifikatsioonistruktuuri ja seost peamiste mullaomadustega Rootsiga kauguosas paikneval Gotlandi saarel. Metsade puurindes tuvastati kokku 14 liiki, põõsarindes koos noorte puudega 60 liiki, puhma-rohurindes 273 liiki ning samblarindes 80 liiki taimi. Varasemate uurijate poolt on Gotlandi kaltsifiilseid männikuid käsitletud kas kuuluvatena ühe või kahte klassifikatsiooniüksusse, või siis on eristatud hulk väikesemahulisi assotsiatsioone, kusjuures ühelgi juhul ei ole testitud eristatud üksuste statistilist põhjendatust. Käesolevas töös klassifitseeriti käsitletud metsakoooslused nelja tüüpiga:

1) *Arctostaphylos uva-ursi-Tortella tortuosa*

tüüp, 2) *Brachypodium sylvaticum-Rhytidiodelphus triquetrus* tüüp, 3) *Carex montana-Scleropodium purum* tüüp ja 4) *Geranium sanguineum-Scleropodium purum* tüüp. Kõigile koolusetüüpide liigiline koosseis on statistiliselt oluliselt erinev, samuti erinevad nad oluliselt paljude keskkonnaraameetrite osas. Põõsa-, puhma-rohu ning samblarinde liigiline koosseis ning liikidevahelised ohtrussuhted sõltuvad peamiselt kolmest omavahel üsna tugevalt korreleeritud keskkonnategurist: puurinde kõrgusest, kuuse ohtrusest puurindes ning mulla huumushorisondi sügavusest. Mullad on enamasti rähksed rendsiinad või gleistunud rähksed rendsiinad, harvem paepealsed mullad.

Received July 31, 2014, revised September 3, 2014, accepted October 6, 2014