

A Vegetation-Based Classification of Habitats in Võigaste Forest, Matsalu Nature Reserve, Estonia

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The study presents an overview of habitats and plant communities of the Võigaste Forest in Matsalu Nature Reserve, Western Estonia. 700 ha of deciduous forest, abandoned wooded meadows, fens and grassland were characterised by vegetation relevés and species indicator values and grouped into 11 vegetation types. These differed mainly in structure, light and moisture conditions, with highest species numbers in semi-open habitats. The area contributes to Estonia's variety of ecosystems; its mosaic structure and species diversity can be preserved by resuming moderate management on suitable abandoned sites.

Key words: Matsalu Nature Reserve, semi-natural plant communities, species diversity, wooded meadows, conservation management, vegetation relevés

Introduction

Nature has been subject to human influence for thousands of years, resulting in semi-natural ecosystems that provide special habitats and have become refuges for many endangered species. An instructing example is the Võigaste Forest in Matsalu Nature Reserve, Western Estonia. Most of the area of 700 ha had been managed for agriculture and forestry in earlier times, favouring the development of semi-natural deciduous forest, semi-open woodland, fens and grassland. The aim of this study was to gain better knowledge of the structural and floristic diversity of the Võigaste Forest.

A specific feature of the region are wooded meadows: sparse natural stands of deciduous trees and shrubs with a regularly mown herb layer. Typically, tree canopies cover 20–40% in small irregular patches, providing a variety of microhabitats (Kukk and Kull 1997, Luhamaa *et al.* 2001) for animal and plant species. They are presently overgrowing, so for comparison with intact wooded meadows, two sites outside of Võigaste (Laelatu, Allika) were investigated.

Due to the limestone bedrock, the study area is dominated by neutral and slightly calcareous soils (Luhamaa *et al.* 2001). The groundwater table is high and fluctuates significantly during the year: large parts are flooded in winter and spring (Luhamaa *et al.* 2001, Lotman 1998). The climate is moderately continental (mean annual temperature 6°C, precipitation 650 mm). The Võigaste Forest is mostly uninhabited today and belongs partly to the limited management zone of the

nature reserve. Only restricted forestry activities are allowed, leaving forest and grassland at different stages of succession after abandonment.

Material and methods

For vegetation analysis, vegetational surveys after Braun-Blanquet (1964) were used. This method aims at a characterisation of a stand of vegetation by a combined cover-abundance estimation of each species within a defined, representative and uniform sample plot. The data are taken separately for each stratum of vegetation (e.g. field layer, bushes, trees).

For this study, relevés in the Võigaste Forest were taken in June and July 2002. Plot sizes were usually 100 m² for forests and 60–100 m² for open land, in accordance with the literature (Pfadenhauer 1997). Only vascular plants were included; nomenclature is referring to Schmeil (2000). At each site, light conditions were characterised with the help of a horizontoscope, a small glass half dome with a stereographic projection of the sun's path in the sky. This design can account for any type of obstructions on the horizon and determines potential (i.e. for cloudless sky) hours of direct sunlight on a site.

For the following calculations, only the field layer of relevés was considered. As a first step, the average Ellenberg indicator values for each relevé were calculated. Ellenberg *et al.* (1992) derived indicator values of plant species for light, temperature, continentality, soil moisture, soil acidity and nutrients. The indicated soil nitrogen content is often correlated with

all major nutrients. The numerical values range in each case from 1 (parameter weak/low) to 9 (parameter strong/high), resp. to 12 for moisture. From these figures, the abiotic habitat conditions can be derived approximately, keeping in mind that the indicator values have originally been validated for central Europe only. Here, the average indicator values of relevés were calculated as quantitative means: species were weighed according to their per cent coverage. For detailed explanations see Ellenberg *et al.* (1992).

With the help of indicator values, light conditions and observations in the field, the relevés were grouped into distinct vegetation types. They were distinguished and named by a combination of physiognomic and floristic features, especially the cover of trees / shrubs and dominating species. These vegetation types are not necessarily consistent with usual phyto-sociological nomenclature.

Results

In total, 115 vegetation relevés were made, and the resulting species list of the Võigaste Forest contains 335 species of vascular plants. The most varying indicator values were for light and moisture. Figure 1 shows the even distribution of the relevés among dry and wet habitats, covering a broad range of moisture conditions.

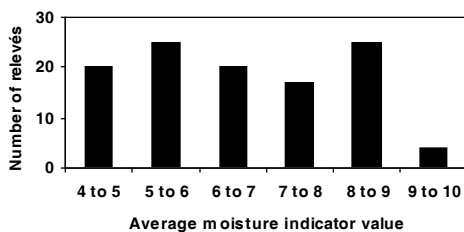


Figure 1. Distribution of Ellenberg indicator values for moisture among all relevés

In the case of the values for light, a modification seemed appropriate: Comparing indicator values to the horizonscope data (sunshine hours) and to the total coverage of trees and shrubs, indicator values only varied very little (partly due to the methodology of indicator definition). On the other hand, sunshine hours and coppice cover correlated satisfactorily (negative correlation; coefficient of determination $R^2 = 0.78$, not shown), so that the sunshine hours were used instead of indicator values for the following calculations.

Description of vegetation types

The combination of the parameters described above facilitates the grouping of the 115 relevés into 11 dis-

tinguishable vegetation types, not solely by their species assemblage, but first by physiognomic structure. Figure 2 shows the overview of these vegetation types, each with dominant and characteristic species. They form three main groups: open land, semi-open landscape with scattered (groups of) trees (cover 10-50%) and closed canopy forest (cover >50%). Within these groups, vegetation types were arranged according to soil moisture. Following this overview, each vegetation type will be described in detail. Additionally, minor habitats found scattered in the Võigaste Forest contribute to the forest's diversity (stone walls, ditches, erratic blocks, dead wood, ant hills, waysides, forest edges) or illustrate stages of transition (*Salix-Carex* shrublands, dense stands of *Phragmites australis*).

(A) Alvar grasslands of the Võigaste Forest dry out quickly in summer because of shallow soils. They are dominated by *Helictotrichon pratense*, *Sesleria caerulea*, *Carex tomentosa*, as well as *Primula veris*, *Galium boreale* and *Filipendula vulgaris*. Cessation of mowing or grazing results in the growth of *Juniper*, *Rhamnus* and other shrubs and suppresses more delicate, typical herbs like *Anthyllis vulneraria*, *Medicago lupulina*, *Polygala amarella*.

(B) The moist grasslands integrate communities of meadows and forest clearings. There are no species growing here exclusively, but the species assembly presents a high diversity due to its combination of species found in neighbouring forest (*Angelica sylvestris*, *Filipendula ulmaria*, *Rubus caesius*) and open land (*Campanula glomerata*, *Chrysanthemum leucanthemum*, *Alchemilla vulgaris*). Where human influence has ceased, tall herbs and shrubs start to dominate (up to 35% shrubs). Especially inside the forest, strong browsing of shrubs was observed and contributes to keeping these clearings open.

(C) The temporarily wet rich fen is characterised by fluctuations of the groundwater table, which allows for peat accumulation and a rather low nutrient availability. The vegetation is dominated by *Sesleria caerulea* and different *Carex* species (*C. hostiana*, *C. panicea*, *C. hartmanii*) in spring, until shoots of *Molinia caerulea* appear in July. Several other plants are less common, but very specific for these calcareous fens: *Carex davalliana*, *Primula farinosa*, *Gymnadenia conopsea*, *Epipactis palustris*, *Pinguicula vulgaris*, *Parnassia palustris*. Graminoid tussocks provide habitat for species less adapted to wet soil and for shrub sprouts. Together with tall forbs (*Lysimachia vulgaris*, *Filipendula ulmaria*, *Phragmites australis*) there are *Betula pubescens*, *Frangula alnus*, *Alnus incana* and *Salix spec.* invading.

(D) The permanently wet rich fen resembles (C) to a certain extent, but is distinguished by its perma-

	NAME	TREES	SHRUBS	DOMINANT SPECIES (field layer)	CHARACTERISTIC SPECIES (field layer)	AVERAGE SPECIES No. (field layer)
A	Alvar grassland	---	<i>Juniperus communis</i> <i>Rhamnus cathartica</i>	<i>Helictotrichon pratense</i> <i>Sesleria caerulea</i> <i>Filipendula vulgaris</i>	<i>Plantago media</i> <i>Anthyllis vulneraria</i> <i>Pimpinella saxifraga</i>	32
B	Moist grassland	---	<i>Frangula alnus</i> <i>Populus tremula</i> <i>Betula pubescens</i>	<i>Galium boreale</i> <i>Inula salicina</i> <i>Centaurea jacea</i>	<i>Scorzonera humilis</i> <i>Anthoxanthum odoratum</i> <i>Carex pallescens</i>	39
C	Temporarily wet rich fen	---	<i>Frangula alnus</i> <i>Salix cinerea</i> <i>Betula spec.</i>	<i>Molinia caerulea</i> <i>Carex panicea</i> <i>Sesleria caerulea</i>	<i>Carex hartmanii</i> <i>Carex davalliana</i> <i>Primula farinosa</i>	25
D	Permanently wet rich fen	---	<i>Frangula alnus</i> <i>Alnus incana</i>	<i>Carex elata</i> / <i>lasiocarpa</i> <i>Lysimachia vulgaris</i> <i>Molinia caerulea</i>	<i>Carex flava</i> <i>Potentilla palustris</i> <i>Eriophorum angustifolium</i>	17
E 1	Abandoned wooded meadow, dry	<i>Populus tremula</i> <i>Quercus robur</i> <i>Fraxinus excelsior</i>	<i>Frangula alnus</i> <i>Corylus avellana</i> <i>Populus tremula</i>	<i>Calamagrostis epigejos</i> <i>Convallaria majalis</i> <i>Brachypodium pinnatum</i>	<i>Hepatica nobilis</i> <i>Dactylis glomerata</i> <i>Mercurialis perennis</i>	42
E 2	Abandoned wooded meadow, wet	<i>Populus tremula</i> <i>Quercus robur</i> <i>Fraxinus excelsior</i>	<i>Frangula alnus</i> <i>Populus tremula</i> <i>Fraxinus excelsior</i>	<i>Calamagrostis epigejos</i> <i>Convallaria majalis</i> <i>Brachypodium pinnatum</i>	<i>Aegopodium podagraria</i> <i>Deschampsia cespitosa</i> <i>Geum rivale</i>	34
F	Temporarily wet rich fen, overgrowing	<i>Betula pubescens</i> <i>Populus tremula</i>	<i>Frangula alnus</i> <i>Salix cinerea</i> <i>Betula spec.</i>	<i>Molinia caerulea</i> <i>Carex panicea</i> <i>Lysimachia vulgaris</i>	<i>Carex hartmanii</i> <i>Cirsium heterophyllum</i> <i>Inula salicina</i>	30
G	Hardwood forest	<i>Quercus robur</i> <i>Corylus avellana</i> <i>Tilia cordata</i>	<i>Corylus avellana</i> <i>Tilia cordata</i> <i>Sorbus aucuparia</i>	<i>Convallaria majalis</i> <i>Anemone nemorosa</i> <i>Mercurialis perennis</i>	<i>Acer platanoides</i> <i>Viola mirabilis</i> <i>Polygonatum spec.</i>	31
H	Wet deciduous forest	<i>Betula pubescens</i> <i>Fraxinus excelsior</i> <i>Alnus glutinosa</i>	<i>Frangula alnus</i> <i>Fraxinus excelsior</i> <i>Alnus glutinosa</i>	<i>Convallaria majalis</i> <i>Filipendula ulmaria</i> <i>Rubus caesius</i>	<i>Cirsium oleraceum</i> <i>Trollius europaeus</i> <i>Phragmites australis</i>	28
J	Swamp forest	<i>Alnus glutinosa</i> <i>Alnus incana</i> <i>Fraxinus excelsior</i>	<i>Alnus incana</i> <i>Alnus glutinosa</i> <i>Frangula alnus</i>	<i>Filipendula ulmaria</i> <i>Alnus glutinosa</i> <i>Deschampsia cespitosa</i> <i>Rubus caesius</i> <i>Scutellaria galericulata</i>	<i>Lycopus europaeus</i> <i>Galium palustre</i> <i>Lythrum salicaria</i> <i>Iris pseudacorus</i>	22
K	Intact wooded meadow	<i>Fraxinus excelsior</i> <i>Quercus robur</i> <i>Betula spec.</i>	<i>Corylus avellana</i> <i>Fraxinus excelsior</i> <i>Quercus robur</i>	<i>Convallaria majalis</i> <i>Melampyrum nemorosum</i> <i>Scorzonera humilis</i>	<i>Ohloglossum vulgatum</i> <i>Dactylorhiza spec.</i>	61

Figure 2. Overview of vegetation types in Võigaste Forest

nently wet soil; in places there is open water throughout the year. There is a well decomposed peat layer (10 to 50 cm), and the upper soil can be base-unsaturated. Some parts are rather eutrophic (*Carex elata* dominating), others mesotrophic (*Carex lasiocarpa* dominating). Species numbers can be very low. *Molinia caerulea*, *Carex panicea* and some tall forbs are present, but also specialists of flooded and nutrient-poor habitats: *Potentilla palustris*, *Menyanthes trifoliata*, *Eriophorum angustifolium*, *Carex nigra*, *Carex flava*.

(E) In many abandoned wooded meadows of the Võigaste Forest, the original structure is still clearly visible; tree coverage is 20 to 50%. *Frangula* and *Populus* shrubs are growing higher, and the field layer is largely dominated by vigorous *Calamagrostis epigeios* and *Brachypodium pinnatum* shoots. Beneath, shade tolerant *Convallaria majalis* and *Aegopodium podagraria* are widespread. There is a clear zonation along the light mosaic under and between trees.

The dry variant (E 1) shows the highest average species richness. Characteristic species in contrast to (E 2) and (F) are similar to the hardwood forest (G): *Lathyrus vernus*, *Hepatica nobilis*, *Mercurialis perennis*. The wet variant (E 2) shows no difference in structure, but the species spectrum here is shifted towards moisture indicators: *Carex acutiformis*, *Cirsium oleraceum*, *Geum rivale*, *Deschampsia cespitosa*, *Phragmites australis*.

(F) The overgrowing temporarily wet rich fen is corresponding to the rich *Molinia-Carex*-fen (C), but the stands here show 5 to 15 % coverage with young birch and aspen trees. As much as 30 % of the area is further covered with shrubs (*Frangula alnus*, *Betula spec.*, *Salix spec.*), and more fallow and shade-tolerant species than in (C) are present: *Inula salicina*,

Calamagrostis epigeios, *Cirsium heterophyllum*, *Convallaria majalis*, *Fraxinus excelsior*.

(G) Hardwood forest is often found on slight elevations drier than the surroundings. *Tilia cordata* and *Corylus avellana* are characteristic tree species. In the field and shrub layer *Acer platanoides*, *Crataegus rhipidophylla* and *Sorbus aucuparia* can be found regularly. Herb species are similar to type (E 1): *Hepatica nobilis*, *Lathyrus vernus*, *Viola mirabilis*, *Polygonatum multiflorum*. Under the dense tree foliage (especially *Corylus* poly-cormons), the ground vegetation is often dominated by high, vegetative shoots of a few shade-tolerant species (*Anemone nemorosa*, *Convallaria majalis*, *Mercurialis perennis*, *Melampyrum nemorosum*).

(H) The wet deciduous forest as the most common forest type in Võigaste displays a very variable species composition of only gradual differences. Under the mixed tree layer shrubs are standing densely in patches where more light falls in, especially *Fraxinus excelsior*, *Prunus padus* and *Frangula alnus*. The ground is often covered with *Convallaria majalis*, *Rubus caesius* and *Geum rivale*, out of which *Filipendula ulmaria* and *Angelica sylvestris* shoots are rising. There are no taxa strictly characteristic for this formation, but common species are *Carex panicea*, *Dactylorhiza fuchsii*, *Trollius europaeus*, *Cirsium oleraceum*. In lower areas, wetland species can be observed (*Carex acutiformis*, *Caltha palustris*, *Lysimachia vulgaris*). Tussocks around tree trunks provide habitat for plants sensitive to overflooding.

(J) In the swamp forest, dominating trees are *Alnus glutinosa* (wettest parts) and *Alnus incana*, with shrubs of *Frangula alnus* and *Fraxinus excelsior*. The water table is rising above the surface in winter and spring. After the peaty soil has dried, a lush field layer develops, consisting of species adapted to the periodic flooding and rapid subsequent mineralisation of nitrogen: *Scutellaria galericulata*, *Solanum dulcamara*, *Lycopus europaeus*, *Mentha aquatica*, *Lythrum salicaria*.

(K) The investigated intact wooded meadows (Allika and Laelatu) are separated from the study area, but species pools are similar, and only few species were found solely on Allika or Laelatu. Main tree species are oak, birch, ash and hazel, growing in clumps on a yearly mown meadow. The abiotic conditions, physical appearance and even the species assemblage in the field layer are comparable to type E 1, but with a change in proportion: There are few dominants (*Convallaria majalis*, *Melampyrum nemorosum*, *Scorzonera humilis*), and a wide variety of accompanying species. This results in significantly higher species richness than all other vegetation types, favoured by

the competition-limiting management and the mosaic light pattern.

Comparison of vegetation types

Here, the 11 vegetation types described above will be contrasted in their main abiotic conditions. The differences in soil reaction (pH) and nitrogen/nutrient availability between the sites were hardly significant (graphs not shown). As for nitrogen, very few relevés show average values >6, which means that nowhere can the vegetation be called nitrophilous. On average, forest provides better nitrogen availability than grassland, especially alvars. The low values in intact wooded meadows are also remarkable. For reaction/pH, the species indicate a mostly homogeneous, slightly calcareous soil, with two exceptions: On alvars the influence of the limestone bedrock is reflected by calciphilous vegetation, while the rich fen (D) shows slightly acidic soil conditions.

As light and moisture were the main parameters used for classification, the bar charts reflect this configuration as expected on Figure 3.

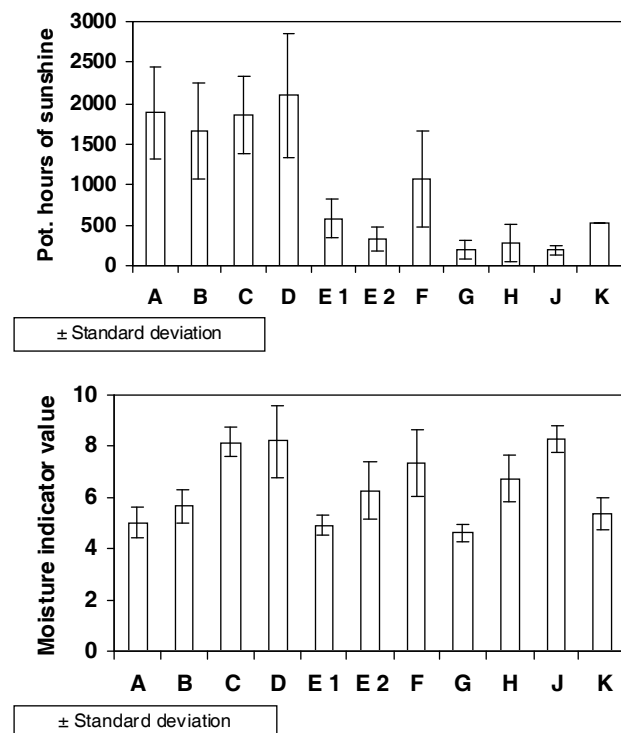


Figure 3. Potential hours of sunshine per growing period and moisture indicator values of vegetation types (field layer); A: Alvar grassland, B: Moist grassland, C: Temporarily wet rich fen, D: Permanently wet rich fen, E 1: Abandoned wooded meadow dry, E 2: Abandoned wooded meadow wet, F: Temp. wet rich fen, overgrown, G: Hardwood forest, H: Wet deciduous forest, J: Swamp forest, K: Intact wooded meadow

In open habitats, sunlight can last more than 15 hours per day. At the other extreme of a wide range, the forest ground layer often receives less than one hour of potential sunlight per day, but variation is high due to uneven spatial distribution of trees. This applies even more to the semi-open vegetation types (E) and (F), where average light conditions are between the two extremes, but varying intensely on a small scale. Within each group of similar light conditions, moisture indicator values are rising (from A to D, E1 to F, G to J). Considering the total range, no habitat can be characterised as generally dry, and the values for fens and swamp forests even indicate soddy soils with a temporary lack of oxygen.

These two main parameters were further utilised to join all vegetation types in a two-dimensional illustration (Figure 4).

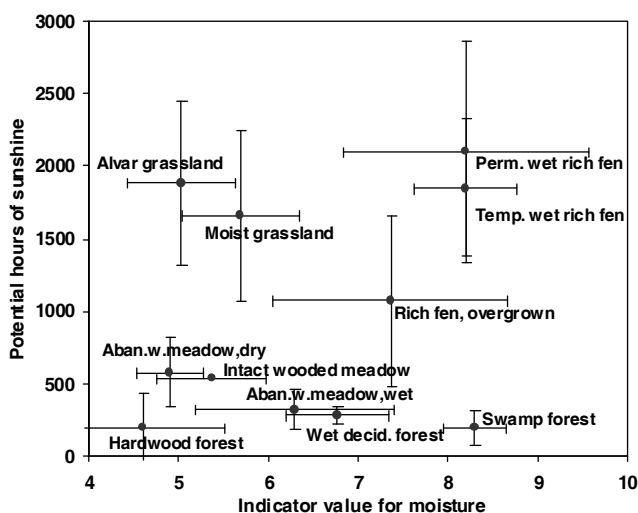


Figure 4. Two-dimensional ordination of vegetation types (field layer) for moisture and light conditions (potential hours of sunshine per growing period)

The standard deviation bars show wide variation within types. The swamp and hardwood forests are distinguished clearly from all others. They represent the dry and wet extreme of the closed-canopy sites, while the wet deciduous forest lies in between. At the other end of the scale of sunshine hours, the four open vegetation types are well delimited from the rest, forming a drier and a more humid group (grasslands and fens, respectively). The rich, overgrown fen shows less humidity than the open fen, although soil properties should be similar. The intact wooded meadow is situated next to the drier abandoned wooded meadows of Võigaste, confirming a close relation of these communities. On the other hand, the wet variant of abandoned wooded meadows resembles the common wet deciduous forest.

Species richness of vegetation types

Comparing the average species numbers of relevés in Võigaste vegetation types, the most obvious fact is the extraordinary large species number in intact wooded meadows (Figure 5). Next are dry, abandoned wooded meadows and moist grassland. On the other hand, rich fens (C and D) and swamp forests show low species numbers, while all other types are alike, taking into account the variability within types.

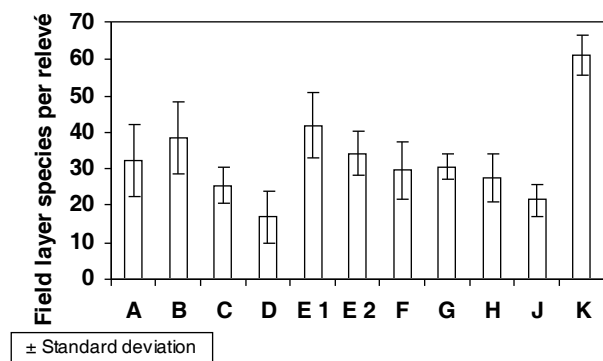


Figure 5. Species richness of vegetation types (field layer) A: Alvar grassland, B: Moist grassland, C: Temporarily wet rich fen, D: Permanently wet rich fen, E 1: Abandoned wooded meadow dry, E 2: Abandoned wooded meadow wet, F: Temp. wet rich fen, overgrown, G: Hardwood forest, H: Wet deciduous forest, J: Swamp forest, K: Intact wooded meadow

Protected species

A total of 13 vascular plant species found in the study area are protected in Estonia (Kukk 1998): *Cypripedium calceolus*, *Dactylorhiza fuchsii*, *Dactylorhiza incarnata*, *Dactylorhiza maculata*, *Daphne mezereum*, *Epipactis palustris*, *Gladiolus imbricatus*, *Gymnadenia conopsea*, *Listera ovata*, *Orchis militaris*, *Platanthera bifolia*, *Platanthera chlorantha*, *Viola elatior*. Most of these belong to protection category III (“could become threatened if picking and damaging are allowed”, Lilleleht 1998). They were found in all vegetation types but swamp forests, and several were exclusive to rich fens.

Discussion and Conclusions

Diversity

The Võigaste Forest is a region of high structural diversity: forest, semi-open and open grassland form a mosaic landscape, and within the different vegetation types, a diverse horizontal structure develops (esp. in

semi-open habitats). Correspondingly, there is a high species diversity, favoured by many factors also mentioned in the literature (Dumortier *et al.* 2002, Kouki *et al.* 2001, Jensen & Hofmann 2002): the geographic location, age, area and structure of the forest, the variety of soil conditions and of micro-habitats, the proportion of dead wood, differentiated human influence, frequency of grazing animals. From the lower numbers in wet habitats, however, it should not be concluded that drier sites are more valuable: Many endangered species of fens and other flooded sites are “specialists” and occur nowhere else, among them several protected species (here for example *Dactylorhiza incarnata*, *Epipactis palustris*, *Orchis militaris*).

Furthermore, comparing species numbers between habitats is only one aspect and should not be taken as sole measure of diversity. Rather, diversity can be looked upon along different spatial and temporal scales, found especially on intact, but also on Võigaste’s abandoned wooded meadows: The light gradient causes a distribution of species according to their usual habitats, growth forms and life cycle strategies: In spots receiving much sunlight, species of open grassland are found. By their hemi-cryptophytic life form, they are adapted to the impacts by mowing or grazing, but susceptible to overgrowing. Other species are more shade-tolerant. They are often geophytes or hemi-cryptophytes and can take advantage of sunlight in spring, before the tree canopy closes. Therefore, they are also more tolerant to overgrowing by tall, late developing grasses and shrubs. Wooded meadows are ideal habitats for many animal species. Birds especially are dependent on vegetation structure and mosaic rather than on single tree species, whereas oak as a common tree on wooded meadows is the main habitat and food source of numerous specialised insects (Reif *et al.* 2000).

As a part of Matsalu Nature Reserve, the Võigaste Forest as a whole contributes to the overall diversity of the area, being refuge to many rare animal species - e.g. black stork (*Ciconia nigra*, own observation). Due to its “wilderness”, the forest offers habitats for territory-demanding mammals (beaver, elk, wolf, bear, lynx), as well as for amphibians, reptiles and invertebrates sensitive to environmental changes.

Succession

In nature protection management, species diversity is often a main objective, while undisturbed succession is sometimes desired, and sometimes a serious handicap. When grasslands or wooded meadows are abandoned, higher growing species can take over which cast shadow on the ground vegetation, spread

vegetatively, or whose seeds develop later in summer (Kukk and Kull 1997). This secondary succession can be recognised easily in Võigaste, where important fallow species are *Brachypodium pinnatum*, *Calamagrostis epigeios*, *Aegopodium podagraria*, *Melampyrum nemorosum*, *Mercurialis perennis*, *Inula salicina*, *Filipendula ulmaria*, *Phragmites australis*. However, it was not possible to determine exactly the different successional stages, and succession on wooded meadows could rarely be distinguished from that in other semi-natural communities. For the study area, some developments can be identified:

On unmanaged grasslands, aut-eutrophication occurs, rhizome- and tussock- forming species and geophytes are favoured (Kahmen *et al.* 2002). Together with fallow herb species, shrubs invade and various forest types can develop. According to Dierssen 1996), semi-open structures can attract grazing animals (deer, elks), and their role in repressing shrub growth in the Võigaste Forest should be taken into account.

In fens, the growth of shrubs is often repressed so that they may remain open for decades without human influence (Pfadenhauer 1997). In other cases, fens are only kept open by regular management. According to Ellenberg (1996), abandonment is first recognisable by invading tall forbs or *Phragmites australis* and *Carex* species. Woody species primarily colonise the drier tussocks of *Molinia* and *Carex*. This development is recognisable clearly in many fens within the study area.

In many parts of Võigaste, in the course of time the fast and densely growing “pioneer” bushes of *Frangula* and *Salix* will reach their maximum height (3-5 m) and then be outgrown by *Betula*, *Populus* and *Fraxinus* trees. Eventually, a deciduous forest will develop, but even inside these forests the coverage of tree canopies is not complete so that there are always patches suitable for more light-demanding plants. Periodical human and animal influence and the system’s internal mosaic cycle can provide heterogeneity of habitats and a basis for diversity on a larger spatio-temporal scale.

Protection

The whole study area as a non-fragmented, diverse and well-structured landscape merits administrative, scientific and public attention as unique, complex woodland developing its internal mosaic of habitats, plant communities and successional stages. Of the natural vegetation types found in the Võigaste Forest, especially rich fens, swamp forests and old-growth deciduous forests are considered valuable and worth of protection by various authors (Külvik *et al.* 2001,

Paal 1998, Paal *et al.* 1998). Old forests are essential for the slowly colonizing 'ancient forest plant species', like *Anemone nemorosa* or *Polygonatum multiflorum* (Brunet *et al.* 2000, Verheyen and Hermy 2001). They also feature numerous key habitats for wildlife, such as dead wood, temporal waterbodies, rocks, ant hills (Külvik *et al.* 2001). The plant communities of semi-natural grasslands and wooded meadows are adapted to continuous management.

In a case study on abandoned wooded meadows by Mitlacher *et al.* (2002), species numbers in the field layer and also in the seed bank were found to drop sharply and grassland plants were substituted by forest species. Pärtel *et al.* (1999) investigated grassland in Hanila (Läänemaa) and state that 40-50 years are needed for its restoration (similar: Zobel *et al.* 1996). Thus, in the study area emphasis should be placed on protecting the existing communities rather than restoration of former ones.

There are four main methods discussed in nature conservation to restrict growth of woody species. Mowing is generally considered best for balancing the competition between species, but is also the most expensive. Mowing every third year can inhibit shrub growth (Hansson and Fogelfors 2000), but for conservation of high species diversity, yearly mowing would be necessary in most open vegetation types of the Võigaste Forest. Grazing leads to a more selective removal of plants; several species are not eaten at all. Further effects are trampling, manuring and seed dispersal. Burning is no traditional method of grassland management in northern Europe and effects are mostly undesired.

On wooded meadows, combining mowing and grazing has a long tradition, but discussion is continuing if this is necessary, neutral or harmful. Grazing does certainly not suffice to conserve wooded meadows and should not be too intense; mixed grazing of sheep and cattle may be ideal, also from an economical point of view (Hansson and Fogelfors 2000, Haeggström 1990, Paal 1998). In wetter habitats (e.g. fens) overgrowing is slowed considerably by the high groundwater level, and mowing frequency has to be adjusted.

As a part of Matsalu Nature Reserve, agricultural and forestry activities in the Võigaste Forest are already limited. It is suggested that wetland and forest areas be mostly left to their natural development, which may be one-directional, cyclic or stochastic. In drier habitats, the previous management should in parts be resumed, but conservation must have priority over restoration. Taking advantage of the large area, a variety of strategies and methods can be applied in order to leave space and time for diversity on all scales,

and to gain knowledge applicable to similar landscapes in the region.

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КЛАССИФИКАЦИЯ МЕСТ ПРОИЗРАСТАНИЯ НА ОСНОВЕ РАСТИТЕЛЬНОСТИ В ЛЕСУ ВЫЙГАСТЕ МАТСАЛУСКОГО ЗАПОВЕДНИКА (ЭСТОНИЯ)

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Резюме

Изучены растительные сообщества и места произрастания в лесу Выйгасте, находящиеся на территории Матсалуского заповедника в Западной Эстонии. Лиственный лес, неухоженные лесолуга, болота и луга, всего 700 га, характеризованы растительными сообществами и индикаторными показателями видов растений. Растительность разделили на 11 групп сообществ. На местах произрастания установлена разная структура растительности, а также разные условия освещенности и влажности. Самое высокое разнообразие растений оказалось в полукрытых сообществах. Разнообразие экосистем в лесу Выйгасте высокое. Мозаичная структура леса и обилие видов растений можно сохранять при помощи умеренного развития хозяйственной деятельности на неухоженных местах произрастания.

Ключевые слова: видовое разнообразие, лесолуга, Матсалуский заповедник, охрана природы, полудикие сообщества, растительные сообщества.