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Classification structure of floodplain forests in Estonia: a comparison of two classification approaches

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Flooded forests in 79 sample areas were studied in various parts of Estonia. Using the principal component analysis and cluster analysis, six community types were established: (i) *Tilia cordata–Mercurialis perennis*, (ii) *Ulmus laevis–Allium ursinum*, (iii) *Populus tremula–Convallaria majalis*, (iv) *Alnus incana–Cirsium oleraceum*, (v) *Alnus glutinosa–Filipendula ulmaria* and, (vi) *Alnus glutinosa–Carex acutiformis*. The species composition of these types partly overlaps but the abundance proportions of species are clearly different and all types have several significant indicator species. Another classification scheme was established by TWINSPAN analysis. Following the phytosociological approach, the communities belong to *Querco–Fagetea*, *Alno–Ulmion* (*Pruno–Fraxinetum, Ficario–Ulmetum, Pruno padi–Alnetum incanae*, the latter subdivided further into P.p.–A.i. var. *Frangula alnus* and P.p.–A.i. var. *Urtica dioica*), and to *Alnetea glutinosae*, *Alnion* (*Carici elongatae–Alnetum*, represented with two subassociations: C.e.–*A. typicum* and C.e.–*A. cardaminetosum*). Despite different concepts used for establishment of community types by either approach the obtained results are rather similar. The syntaxa of *Alno–Ulmion* show particularly high internal variability, although all recognised communities have unambiguous affinities with the assemblages described elsewhere from central and northern-central Europe.

Key words: indicator species, TWINSPAN, *Querco–Fagetea*, *Alno–Ulmion*, *Alnetea glutinosae*.

Introduction

Floodplain forests have very specific ecological conditions in the temperate zone (Klimo 2001, Hager & Schume 2001) and are usually uniquely characterized by a combination of high species diversity, high density and high productivity (Mitsch & Gosselink 2000). In Estonia, like in most European countries, floodplain forests have remained in comparatively small areas and they are recognised as strongly threatened communities (Paal 1998). According to the Habitat Directive (EC 1992), floodplain forests belong to the habitats of great importance (types 91E0 and 91F0) for nature protection on the European scale.

At the same time, Estonian floodplain forests have been characterised only sporadically and long time ago by Kull (1925), Lippmaa (1935), Lunts (1938) and Marvet (1967). According to the forest classification system adopted in Estonia, these forests are not singled out as an autonomous site type but are dealt with under the broad swamp forest site type (*sensu* Lõhmus 2004). Relationship of floodplain forests with other forest types has been treated briefly by Ilves (1969), Masing (1966, 1969), Marvet (1970), Paal (1997) and Paal *et al*. (2006) but not in a wider geographical scale or in terms of the phytosociological syntaxonomy largely used in western, central and southern Europe. Estonian forest site type classification follows Cajander's concept (Cajander 1909, 1926, 1930, Frey 1973, Lõhmus 2004) and any attempts to connect or compare that with phytosociological classification approach are almost lacking.

The aims of the current study are: (i) to establish a phytosociological classification of Estonian floodplain forests, (ii) to evaluate its correspondence to the classification scheme elaborated earlier on the basis of cluster and discriminant analyses (Paal *et al*. 2006, 2007) and, (iii) to compare the syntaxa of the Estonian floodplain forests with corresponding phytosociological units on a wider geographical scale.

Material and methods

Field study

In the current study we regarded as floodplain forests stands where floods occur regularly almost every year and last at least for a couple of weeks, while the amount of alluvial sediments was not a decisive criterion (Ellenberg 1996, Hager & Buchleitner 2001, Oszlányi 2001). All in all, 79 subnatural stands (= plant communities) were studied in the country, representing considerably well preserved floodplain forests with an area not smaller than 0.5 ha, and not having obvious human activities impact (only a little decaying stumps, even age tree layer, ditches, roads, lines). Forests satisfying these criteria are located in Estonia in five regions: (i) on the banks of the Rannametsa River in southwestern Estonia, (ii) along the Halliste and Raudna rivers in Soomaa National Park, (iii) in the Alam-Pedja Nature Reserve on the banks of the Pedja River and the ditched Loksu Rivulet, (iv) in the valley of the Jänijõgi in northern Estonia and, (v) in the valley of the Poruni River in the Puhatu Nature Reserve (Fig. 1). Floodplain forests can be found in several other places along the brooks or rivulets as well, but there they border the watercourses as very narrow strips, form only small groves and/or are intensively attenuated by cuttings.

In every stand one round sample plot of ca. 0.1 ha was analysed. A sample plot was established using a height and distance measuring instrument Suunto: one tree stem was treated as a central one and from that a radius of 17.8 m was measured in different directions. Ground vegetation was described by means of randomly located sample squares of 1 × 1 m, their number was 15 per stand. The total cover percentage of the herb and moss layers as well as of every plant species was estimated. For further characterization and classification of a respective stand (plant community) for ground vegetation the averaged values of 15 sample squares were used. If some species were recorded in a sample plot but were not found in the squares, they were included in the community species list conditionally with a coverage of 0.01%.

The number of shrub layer species stems was registered on five randomly located 2 × 2 m sample squares in every stand. Young trees (saplings) with a height of < 4 m and/or with a diameter of < 5 cm at breast height (1.3 m) were also interpreted as belonging to the shrub layer and treated as "species". Shrub species outside the randomly situated squares were taken into account with number 1. The tree layer was characterised by the mean basal area of every species, obtained as an average result of 3–5 measurements.

The nomenclature of vascular plant species follows Leht *et al*. (1999) and the nomenclature of bryophytes follows Ingerpuu and Vellak (1998).

Data processing

Our first floodplain forest classification (Paal *et*

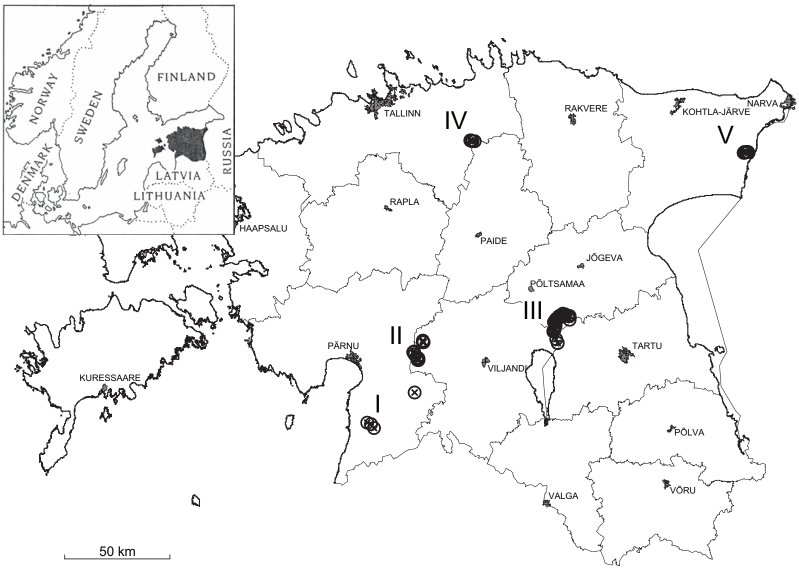

Fig. 1. Location of sample regions and sample plots.

al. 2006, 2007) was based on a cluster analysis where ten first principal components of plant communities' data (relevés) were used as input. These described 72% of the total variation in the data. A cluster analysis was performed using the minimal incremental sum of squares algorithm — MISSQ (Podani 2000), employing the chord distance as the measure of dissimilarity. Objectivity of clustering of every relevé was tested with a classificatory discriminant analysis (StatSoft Inc. 2001).

The second classification was carried out using the TWINSPAN algorithm (Hill 1979, Gauch & Whittaker 1981). Values 0, 2, 5, 10 and 20 were used as pseudospecies cut levels, corresponding to the default settings of the PC-ORD package (McCune & Mefford 1999). The obtained clusters were further interpreted in terms of phytosociology.

Indicator values of the species in clusters were calculated using the Dufrêne and Legrendre (1997) method. According to that, for each species its relative abundance and relative frequency in every group (= community type) was calculated. Multiplication of these two values, expressed as a percentage, yields an indicator value for a particular species in a particular group. The significance of each indicator value was assessed with the Monte Carlo permutation test (McCune & Mefford 1999).

A null hypothesis of absence of difference between corresponding vegetation types, established with the use of MISSQ and TWINSPAN methods, was tested using a multi-response permutation procedure (MRPP) (McCune & Mefford 1999). Communities were ordinated by means of a detrended correspondence analysis (DCA) (ter Braak & Šmilauer 2002); downweighting of rare species was applied.

Results

MISSQ analysis

Six clusters (community types) were established with the MISSQ analysis: (i) *Tilia cordata–Mercurialis perennis* type, (ii) *Ulmus laevis–Allium ursinum* type, (iii) *Populus tremula–Convallaria majalis* type, (iv) *Alnus incana–Cirsium oleraceum* type, (v) *Alnus glutinosa–Filipendula ulmaria* type, (vi) *Alnus glutinosa–Carex acutiformis* type.

Species composition, their indicator values, mutual relationships between types, as well as growth conditions of respective communities were discussed thoroughly by Paal *et al*. (2007). In general, it appeared that rather high internal variation is typical for *Alnus glutinosa–Carex acutiformis*, *Populus tremula–Convalla-*

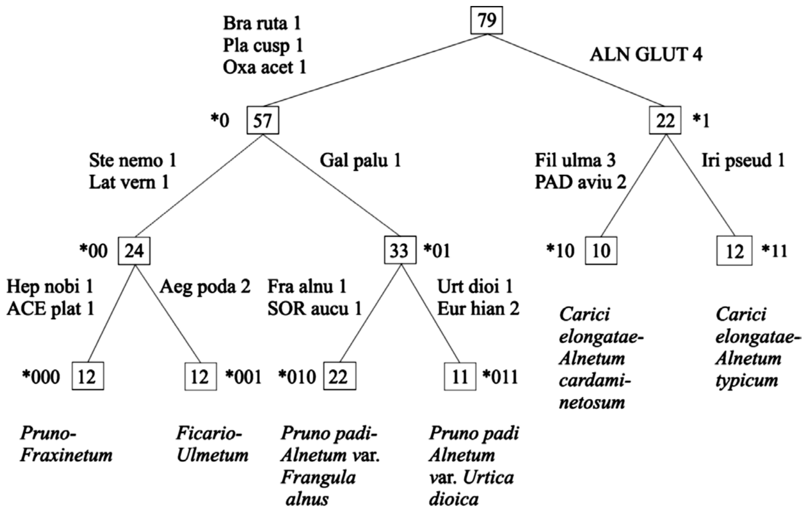

Fig. 2. Two-way indicator species analysis results by TWINSPAN classification with number of plots in each cluster and names of species delimiting descending divisions. Species: Bra ruta = *Brachythecium rutabulum*, Pla cusp = *Plagiomnium cuspidatum*, Oxa acet = *Oxalis acetosella*, ALN GLUT = *Alnus glutinosa* in tree layer, Ste nemo = *Stellaria nemorum*, Lat vern = *Lathyrus vernus*, Gal palu = *Galium palustre*, Fil ulma = *Filipendula ulmaria*, PAD aviu = *Padus avium* in shrub layer, Iri pseu = *Iris pseudacorus*, Hep nobi = *Hepatica nobilis*, ACE plat = *Acer platanoides*, saplings, Aeg poda = *Aegopodium podagraria*, Fra alnu = *Frangula alnus*, SOR aucu = *Sorbus aucuparia* in shrub layer, Urt dioi = *Urtica dioica*, Eur hian = *Eurhynchium hians*.

ria majalis, and *Alnus glutinosa–Filipendula ulmaria* community types. *Ulmus laevis–Allium ursinum* and *Alnus incana–Cirsium oleraceum* community types vary considerably less. All these community types as well as the *Tilia cordata–Mercurialis perennis* type largely overlap in a canonical correspondence analysis ordination plot (ter Braak & Šmilauer 2002). It means that the distinctness of these clusters is based not so much on their floristic differences but on different proportions of the species in the respective community types. Most common soils in Estonian floodplain forests are Gleysols, followed by Mollic Fluvisols. Locally Histic Fluvisols or Molli-Histic Fluvisols occur, the later have intermediate properties of the respective soils between Mollic Fluvisols and Histic Fluvisols. On floodplain terraces, submerged in floodwater for only a short time, Dystri-Gleyic Arenosols are present. Most soils have a light texture: on 49% of the studied stands the soils have a sandy texture, and 60% of the clayey soils have a sandy or gleic-sandy texture. The main factors determining variation in the vegetation are nitrogen and carbon content, as well as soil specific surface area for the uppermost soil horizon.

TWINSPAN analysis

After the first division by TWINSPAN, all the communities are clearly spread between two classes: *Querco–Fagetea* and *Alnetea glutinosae*, both represented by one alliance, *Alno–Ulmion* and *Alnion glutinosae*, respectively. The communities of the first alliance are divided further into three associations: *Pruno–Fraxinetum*, *Ficario–Ulmetum* and *Pruno padi–Alnetum incanae*; the last association is represented by two variants in a sample — P.p.–A.i. var. *Frangula alnus* and P.p.–A.i. var. *Urtica dioica* (Fig. 2). The *Alnion glutinosae* is homotoneous (*sensu* Dahl 1960) and corresponds to the *Carici elongatae–Alnetum* association including two subassociation: C.e.–*A. cardaminetosum* and C.e.–*A. typicum*. Hence, Estonian floodplain forests have the following syntaxonomic structure (Appendix):

Cl. *Querco–Fagetea* Br.-Bl. et Vlieg. in Vlieg. 1937;
O. *Fagetalia sylvaticae* Pawl. *in* Pawl., Sokol. et Wallisch 1928;
All. *Alno–Ulmion* Br.-Bl. et Tx. *ex* Tchou 1948;
Ass. *Pruno–Fraxinetum* Oberd. 1953 (syn. *Ribeso sylvestris–Fraxinetum* Pass. 1958 and *Aegopodio–Fraxinetum* (Pass. 1958) Scam. et Pass. 1959);

Ass. *Ficario–Ulmetum* Knapp *ex* Medw.-Korn. 1952 (syn. p.p. *Querco–Ulmetum* Issler 1924);
Ass. *Pruno padi–Alnetum incanae* K.-Lund *ex* Aune 1973;
P.p.–A.i. var. *Frangula alnus*;
P.p.–A.i. var. *Urtica dioica*.
Cl. *Alnetea glutinosae* Br.-Bl. *ex* Tx. 1943 *ex* Westhoff *et al*. 1946;
O. *Alnetalia glutinosae* Tx. 1937 *em*. Oberd. 1953;
All. *Alnion glutinosae* (Malc. 1929) Meijer Drees 1936;
Ass. *Carici elongatae–Alnetum* Schwick. 1933;
Subass. C.e.–*A. cardaminetosum* Meijer Drees 1936;
Subass. C.e.–*A. typicum* Meijer Drees 1936.

The established syntaxa are separated from each other in the ordination plot quite well (Fig. 3). Only *Ficario–Ulmetum* and *Pruno padi–Alnetum incanae* var. *Urtica dioica* overlap slightly more than other clusters. At the same time, the latter syntaxon together with *Carici elongatae–Alnetum cardaminetosum* and *Carici elongatae–Alnetum typicum* have smaller internal variation than the remaining syntaxa.

Correspondence of the results of MISSQ and TWINSPAN

According to the results of the ordination (Fig. 3), the classification structures of the communities obtained with both methods generally harmonise fairly well. TWINSPAN yielded somewhat better discrimination and higher homotony of the clusters (*sensu* Dahl 1960), with a single exception of the *Ficario–Ulmetum* type, which displays higher variation than its counterpart, the *Ulmus laevis–Allium ursinum* type.

Pairwise comparison of the clusters using weighted mean within-group distances also proves, in four cases, their good agreement; only the *Populus tremula–Convallaria majalis* type and the *Pruno padi–Alnetum incanae* var. *Frangula alnus* have a significantly different structure of entities, while the difference between the *Alnus incana–Cirsium oleraceum* type and the *Pruno padi–Alnetum incanae* var. *Urtica dioica* slightly exceeds the conventional significance level (Table 1).

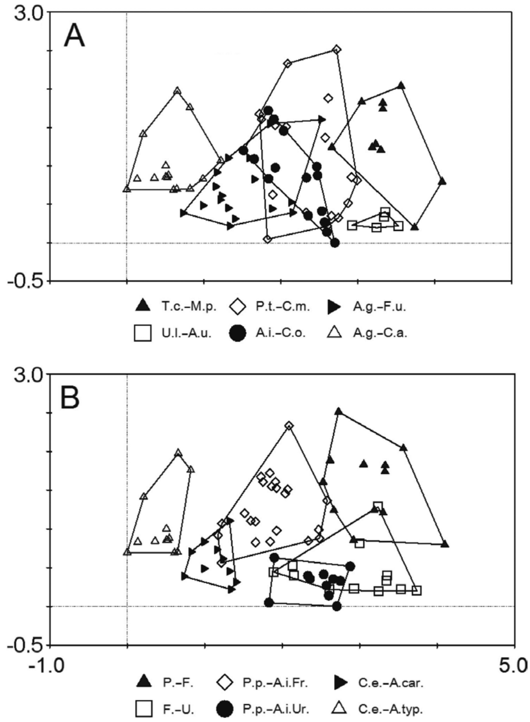

Fig. 3. DCA ordination of floodplain forests. — **A**: classification structure of communities obtained by MISSQ method. — **B**: classification structure of communities by TWINSPAN classification. Community types in part A: T.c.–M.p. = *Tilia cordata–Mercurialis perennis*, U.l.–A.u. = *Ulmus laevis–Allium ursinum*, P.t.–C.m. = *Populus tremula–Convallaria majalis*, A.i.–C.o. = *Alnus incana–Cirsium oleraceum*, A.g.–F.u. = *Alnus glutinosa–Filipendula ulmaria*, A.g.–C.a. = *Alnus glutinosa–Carex acutiformis*. Community types in part B: P.–F. = *Pruno–Fraxinetum*, F.–U. = *Ficario–Ulmetum*, P.p.–A.i.Fr. = *Pruno padi–Alnetum incanae* var. *Frangula alnus*, P.p.–A.i.Ur. = *Pruno padi–Alnetum incanae* var. *Urtica dioica*, C.e.–A.car. = *Carici elongatae–Alnetum cardaminetosum*, C.e.–A.typ. = *Carici elongatae–Alnetum typicum*.

Discussion

The classification obtained by TWINSPAN outlines several features of Estonian floodplain forests:

i *Alnion* syntaxa of only fertile habitats (e.g. *Carici elongatae–Alnetum typicum*, C.e.–*A. cardaminetosum*) can be recognized;
ii No groups of wetland species indicating evident paludification (e.g. that of *Oxycocco–Sphagnetea* and *Scheuchzerio–Caricetea nigrae*) can be traced;
iii Typical species confined to river valleys in the Baltic region (e.g. *Humulus lupulus*,

Padus avium — the latter with high coverage and frequency) are spread almost among all communities;

iv In *Alno–Ulmion* no clear synsystematic differentiation occur amongst canopy dominants or co-dominants (e.g. *Fraxinus excelsior, Alnus incana, Ulmus glabra, Tilia cordata, Alnus glutinosa*): these species tend to coexist and delimitation of lower rank syntaxa is mostly based on the species of herb and moss layers;

v Communities of *Ficario–Ulmetum* and *Pruno–Fraxinetum* comprise species of relatively drier habitats as compared with *Pruno padi–Alnetum incanae*; this can be explained by the rather broad definition of a 'floodplain';

vi Although *Querco–Fagetea* and *Alnetea glutinosae* are clearly separated at the first division level of TWINSPAN, the latter syntaxa still maintain strong evidence of the nemoral vegetation — a feature uncommon for azonal *Alnetea glutinosae* outside river valleys in the eastern Baltic (Prieditis 1997a).

The clear delineation of the affinities of floodplain forest communities in Estonia, described here, is predetermined by two limitations: first, various sources (especially in Fennoscandia) follow different syntaxonomic approaches and, second, peculiar combinations of species and replacements of certain species may take place at the northern limit of the occurrence of deciduous broad-leaved forests. Nevertheless, the set of species in Estonian *Tilia cordata–Mercurialis perennis* communities overlaps largely with that in communities of the *Ulmo glabrae–Tilietum cordatae* association described from southern Scandinavia (Odland 1992, Dierßen 1996). Here it should also be considered that these communities have quite a wide distribution area and high internal variation. Moreover, forest communities where *Matteuccia struthiopteris* dominates in the herb layer, have been dealt with in different syntaxonomic units (Odland 1992). In central Europe, *Matteuccia struthiopteris* is a character species of the *Alnion glutinoso–incanae* suballiance *Alno–Ulmion* (Oberdorfer 1953, Dovotliková-Novotná 1961). Schwabe (1985), however, considers this species a nordic indication in her compendium of *Alnus incana* forest communities. Among the character species of *Alno–Ulmion* is also *Humulus lupulus* but according to our results, it appeared to be a statistically insignificant indicator species (p = 0.579) of *Alnus incana–Cirsium oleraceum* type communities instead. Undoubtedly, both *Humulus lupulus* and *Padus avium*, distributed over all communities of Estonian floodplain forests, are evident indicators of riverine vegetation. It should be mentioned that in Norway (Fremstad & Øvstedal 1978, Odland 1992) no essential differences were found between the *Matteuccia struthiopteris*-rich *Alnus incana* forests growing on river valleys or on mountain slopes. Some common features between Estonian *Tilia cor-*

Table 1. Pairwise comparison of the community types established by MISSQ and TWINSPAN methods. Pairs of types: T.c.–M.p. = *Tilia cordata–Mercurialis perennis*, P.F. = *Pruno–Fraxinetum*; U.l.–A.u. = *Ulmus laevis–Allium ursinum*, F.–U. = *Ficario–Ulmetum*; P.t.–C.m. = *Populus tremula–Convallaria majalis*, P.p.–A.i.Fr. = *Pruno padi–Alnetum incanae* var. *Frangula alnus*; A.i.–C.o. = *Alnus incana–Cirsium oleraceum*, P.p.–A.i.Ur. = *Pruno padi–Alnetum incanae* var. *Urtica dioica*; A.g.–F.u. = *Alnus glutinosa–Filipendula ulmaria*, C.e.–A.car. = *Carici elongatae–Alnetum cardaminetosum*; A.g.–C.a. = *Alnus glutinosa–Carex acutiformis*, C.e.–A.typ. = *Carici elongatae–Alnetum typicum*. δ_{Mi} and δ_{Tw} = the weighted mean within-group distance, T = test statistic, A = chance-corrected within-group agreement, p = probability of a smaller or equal delta.

MISSQ	TWINSPAN	δ_{Mi}	δ_{Tw}	T	A	p
T.c.–M.p.	P.–F.	43.1	40.2	1.794	–0.031	0.994
U.l.–A.u.	F.–U.	28.2	42.5	–0.321	0.007	0.321
P.t.–C.m.	P.p.–A.i.Fr.	34.3	39.1	–5.219	0.031	< 0.001
A.i.–C.o.	P.p.–A.i.Ur.	37.9	37.7	–1.779	0.019	0.052
A.g.–F.u.	C.e.–A.car.	37.4	37.6	0.771	–0.012	0.767
A.g.–C.a.	C.e.–A.typ.	27.6	28.3	2.308	–0.036	1.000

data–Mercurialis perennis forests and communities of the *Stellario–Alnetum glutinosae* subassociation *S.–A. g. mercurialietosum* (Moravec *et al*. 1982) in central Europe can also be asserted.

Clustering of Estonian floodplain forests within *Querco–Fagetea* has been found particularly complicated. Among the syntaxa (e.g. *Alnetum incanae*, *Pruno padi–Alnetum incanae, Circaeo–Alnetum*, *Carici remotae–Fraxinetum, Pruno–Fraxinetum*, *Stellario–Alnetum glutinosae*, and *Ficario–Ulmetum*), normally ascribed to similar habitats in central and northern Europe (Matuszkiewicz 1977, Moravec *et al*. 1982, Schwabe 1985, Härdtle 1995, Dierßen 1996, Rychnovská & Bednář 1998), we found it possible to distinguish three associations: *Pruno–Fraxinetum*, *Ficario–Ulmetum*, and *Pruno padi–Alnetum incanae*.

Alnetum incanae (Schwabe 1985), according to its original diagnosis, has insufficient elements of the central European flora in Estonian habitats. *Carici remotae–Fraxinetum, Circaeo–Alnetum* and *Stellario–Alnetum glutinosae* (Moravec *et al*. 1982, Härdtle 1995) lack essential diagnostic species (e.g. *Carex remota*, *Circaea* spp., and some more species which do not reach the Baltic area). Nonetheless, we consider that, although not supported by the relevés of the present study, communities of both *Carici remotae–Fraxinetum* and *Circaeo–Alnetum* may reach Estonia as they are commonly found in southern Latvia (Prieditis 1997b).

High internal variability of all *Alno–Ulmetum* communities in Estonian floodplain forests is evident. Despite this, the investigated relevés display unambiguous similarity to the syntaxa described already from the southwestern regions of Europe both in terms of species and habitat. Hence introduction of any new syntaxa in these assemblages may not be warranted.

Some distant affinities at the level of forest site types can be noted between Estonian *Quercus robur–Convallaria majalis* forests and *Querco–Piceetum*, more widespread in eastern Europe (Matuszkiewicz 1977) as well as in southern Scandinavia (Kielland-Lund 1981). The counterpart of Estonian *Ulmus laevis–Allium ursinum* forests in southern Scandinavia could be *Ulmo–Fraxinetum* (Klötzli 1975) communities. The latter is interpreted as *Ficario–Ulmetum* in the present study.

Forests of the *Alnus incana–Cirsium oleraceum* type belong to *Pruno padi–Alnetum incanae* (*Alno–Prunetum*; Aune 1973) of *Alnion incanae* what is also supported by TWINSPAN clustering. *Alno incanae–Fraxinetum* (Dierßen 1996), another syntaxon suggested for such an assemblage, is characteristic of Gleysols alongside rivulets and can also grow on warm slopes, formed of till, and on seashores.

The highest similarity, as expected, occurs among floodplain swamp forests — azonal *Alnetea glutinosae* communities are distributed all over Eurosiberia (Kreeb 1983, Dierßen 1996). Distribution over large areas is characteristic also of a number of associations of *Alnion*, although numerous subassociations and variants identified within it diverge by their site ecology, peculiarities of distribution and sets of species (Moravec *et al*. 1982, Prieditis 1997a, 1997b, Wiebe 1998). One can note a clear correspondence of Estonian *Alnus glutinosa* communities with the communities of *Carici elongatae–Alnetum typicum* or *Carici elongatae–Alnetum cardaminetosum* in Latvia (Prieditis 1997a, 1997b), Denmark, southern Sweden (Brunet 1991, Dierßen 1996), southern Norway (Kielland-Lund 1981), Poland (Solińska-Górnicka 1987, described this formally under the name *Ribo nigri–Alnetum*), Czech Republic (Moravec *et al*. 1982), Germany (Scamoni & Passarge 1963, Döring-Mederake 1991, Wiebe 1998), where one of the character species is *Carex elongata*, often supported by a set of good additional diagnostic species (e.g. *Solanum dulcamara, Lycopus europaeus*, *Iris pseudacorus*).

Summarizing, we can conclude the following:

i According to the cluster analysis, Estonian floodplain forests constitute five community types: (1) *Tilia cordata–Mercurialis perennis*, (2) *Quercus robur–Convallaria majalis*, (3) *Ulmus laevis–Allium ursinum*, (4) *Alnus incana–Cirsium oleraceum*, and (5) *Alnus glutinosa–Filipendula ulmaria*. Despite some overlapping of species in communities of different types, there is a characteristic abundance proportion of species as well as a set of statistically significant indicator species in every community type.

ii According to TWINSPAN, four distinct associations of forest communities, belonging to *Querco–Fagetea, Alno–Ulmion* (three ass.) and *Alnetea glutinosae, Alnion glutinosae* (one ass.), can be recognized.

iii Despite different concepts used for establishing community types by either approach the obtained results are rather similar.

iv Although certain geographic peculiarities are evident, Estonian floodplain forests generally show good agreement with analogous communities in neighbouring countries and in central Europe.

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Appendix. Synoptical frequency table of floodplain forest communities in Estonia established by TWINSPAN. Species abundance classes are defined by pseudospecies cut levels. If the average abundance of species of frequency class I is < 0.5, the centroids of syntaxa abundance is presented as +, and those of species of frequency classes II and III is presented as 1. Sapl. = saplings.

Syntaxon	Cl. *Querco–Fagetea* All. *Alno–Ulmion*				Cl. *Alnetea glutinosa* All. *Alnion glutinosae*	
	Ass. *Pruno–Fraxinetum*	Ass. *Ficario–Ulmetum*	Ass. *Pruno padi–Alnetum incanae*		Ass. *Carici elongatae–Alnetum*	
			P.p.–A.i. var. *Frangula alnus*	P.p.–A.i. var. *Urtica dioica*	Subass. C.e.–*A. cardamine-tosum*	Subass. C.e.–*A. typicum*
Number of relevés	12	12	22	11	10	12
Total cover of tree layer (%)	83 ± 1	79 ± 2	74 ± 2	79 ± 1	71 ± 4	75 ± 2
Total basal area of tree layer (m^2 ha^{-1})	28 ± 1	28 ± 1	27 ± 1	30 ± 3	27 ± 1	29 ± 2
Number of shrub layer stems	18 ± 3	14 ± 1	16 ± 1	18 ± 2	8 ± 2	6 ± 1
Total cover of herb layer (%)	48 ± 4	65 ± 2	50 ± 2	49 ± 3	37 ± 8	29 ± 4
Total cover of moss layer (%)	14 ± 4	15 ± 5	28 ± 4	23 ± 4	6 ± 2	7 ± 2
Number of species	62 ± 3	59 ± 3	80 ± 4	69 ± 4	26 ± 3	31 ± 3
Diagnostic species of *Pruno–Fraxinetum* and *Ficario–Ulmetum*						
Fraxinus excelsior	V.2	V.2	III.1	IV.1	III.1	I.+
Fraxinus excelsior (sapl.)	V.2	V.1	V.1	V.1	IV.1	III.1
Ulmus glabra (sapl.)	IV.1	IV.1	III.+	IV.1	III.1	I.+
Ulmus glabra	IV.1	III.1	I.+	III.1	II.1	–
Ulmus laevis	–	III.1	I.+	IV.2	–	–
Ulmus laevis (sapl.)	–	II.1	–	II.1	I.+	–
Tilia cordata	III.2	III.1	II.+	II.1	I.+	–
Tilia cordata (sapl.)	III.1	II.+	II.+	–	II.1	I.+
Acer platanoides	III.1	I.+	–	–	–	–
Acer platanoides (sapl.)	V.1	II.+	I.+	I.+	–	–
Hepatica nobilis	V.2	–	I.+	I.+	–	–
Pulmonaria obscura	IV.1	I.+	–	I.+	–	–
Stellaria nemorum	V.1	V.2	I.+	II.1	I.+	–
Lathyrus vernus	V.1	IV.1	I.+	–	I.+	–
Mercurialis perennis	V.3	IV.2	I.+	II.1	–	–
Corylus avellana	IV.1	III.1	II.1	I.+	–	I.+
Matteuccia struthiopteris	III.2	V.2	I.+	–	I.+	–
Aegopodium podagraria	III.1	V.3	II.1	IV.1	I.+	–
Galeobdolon luteum	III.1	V.2	III.1	V.2	I.+	–
Allium ursinum	–	IV.3	–	–	I.+	–
Ranunculus ficaria	–	III.1	I.+	–	I.+	–
Diagnostic species of *Pruno padi–Alnetum incanae*						
Alnus incana	II.1	III.1	III.1	IV.2	II.1	I.+
Alnus incana (sapl.)	II.1	III.1	IV.1	IV.2	I.+	II.1
Padus avium (sapl.)	V.2	V.3	V.2	V.2	V.2	III.1
Padus avium	–	–	II.1	II.1	I.+	–
Climacium dendroides	II.1	I.+	V.3	III.1	III.1	II.1
Thuidium delicatulum	II.1	III.1	IV.1	III.1	I.+	–
Carex cespitosa	I.+	–	IV.2	III.1	I.+	I.+
Carex vaginata	I.+	I.+	III.1	–	I.+	I.+
Lysimachia vulgaris	–	I.+	IV.1	III.1	I.+	II.1
Viola epipsila	I.+	I.+	III.1	I.+	I.+	–
Calliergon cordifolium	I.+	–	III.1	II.1	I.+	I.+
Sorbus aucuparia (sapl.)	III.1	II.1	V.1	I.+	–	II.1
Galium palustre	I.+	II.1	V.1	V.1	II.1	I.+
Lysimachia thyrsiflora	–	I.+	III.1	III.1	II.1	I.+

continued

Appendix. Continued.

Syntaxon	Cl. *Querco–Fagetea* All. *Alno–Ulmion*				Cl. *Alnetea glutinosa* All. *Alnion glutinosae*	
	Ass. *Pruno–Fraxinetum*	Ass. *Ficario–Ulmetum*	Ass. *Pruno padi–Alnetum incanae*		Ass. *Carici elongatae–Alnetum*	
			P.p.–A.i. var. *Frangula alnus*	P.p.–A.i. var. *Urtica dioica*	Subass. C.e.–*A. cardamine-tosum*	Subass. C.e.–*A. typicum*
Diagnostic species of variants						
Frangula alnus	I.+	I.+	V.2	–	I.+	IV.1
Urtica dioica	III.1	V.2	II.1	V.2	IV.1	I.+
Diagnostic species of *Carici elongatae–Alnetum*						
Alnus glutinosa	V.2	IV.2	IV.2	I.+	V.4	V.4
Alnus glutinosa (sapl.)	I.+	I.+	I.+	–	I.+	IV.1
Solanum dulcamara	I.+	III.1	II.1	III.1	IV.1	V.1
Lycopus europaeus	–	II.1	IV.1	III.1	III.1	IV.1
Iris pseudacorus	–	I.+	III.1	II.1	I.+	V.1
Galium uliginosum	–	–	I.+	–	I.+	V.1
Carex vesicaria	–	–	II.1	II.1	I.+	IV.1
Carex acutiformis	–	–	I.+	–	–	III.2
Thelypteris palustris	I.+	I.+	I.+	I.+	–	III.2
Calla palustris	–	–	I.+	–	I.+	III.1
Veronica longifolium	–	–	–	–	–	III.1
Cardamine amara	I.+	I.+	I.+	–	I.+	II.1
Menyanthes trifoliata	–	–	–	I.+	–	II.1
Other accompanying tree species						
Betula spp.	V.2	V.2	V.3	III.1	V.2	V.3
Picea abies	V.3	II.1	V.2	II.1	I.+	III.1
Picea abies (sapl.)	II.1	I.+	III.1	–	I.+	II.1
Populus tremula	I.+	III.1	IV.2	III.1	II.1	II.1
Populus tremula (sapl.)	I.+	III.1	III.1	I.+	I.+	–
Quercus robur	I.+	I.+	III.1	I.+	I.+	I.+
Quercus robur (sapl.)	II.1	I.+	III.1	–	I.+	–
Betula pubescens (sapl.)	–	–	I.+	–	–	I.+
Other accompanying species						
Filipendula ulmaria	II.1	V.3	V.4	V.3	V.4	V.2
Calliergonella cuspidata	I.+	IV.1	IV.2	V.1	IV.2	V.3
Plagiomnium ellipticum	IV.1	III.1	IV.1	V.1	IV.1	V.1
Caltha palustris	I.+	III.1	IV.1	IV.1	IV.1	V.2
Ranunculus repens	II.1	III.1	III.1	IV.1	IV.1	IV.2
Chrysosplenium alternifolium	III.1	IV.1	III.1	II.1	IV.1	–
Equisetum pratense	V.2	IV.1	IV.1	III.1	I.+	–
Brachythecium rutabulum	V.1	V.1	V.1	V.2	I.+	I.+
Brachythecium salebrosum	IV.1	IV.1	IV.1	V.1	–	–
Cirriphyllum piliferum	IV.1	III.1	IV.1	III.1	–	–
Eurhynchium praelongum	V.1	III.1	III.1	V.1	I.+	–
Plagiomnium cuspidatum	V.1	V.1	IV.1	V.1	–	I.+
Plagiomnium undulatum	III.1	V.1	III.1	IV.2	–	–
Athyrium filix–femina	IV.1	IV.1	III.1	II.1	I.+	I.+
Convallaria majalis	III.1	II.1	III.1	III.2	I.+	I.+
Rhizomnium punctatum	III.1	II.1	III.1	II.1	–	I.+
Rubus saxatilis	V.1	II.1	IV.1	I.+	I.+	–
Cirsium oleraceum	III.1	IV.1	IV.2	V.2	I.+	I.+
Crepis paludosa	IV.1	V.1	IV.1	II.1	–	–

continued

Appendix. Continued.

Syntaxon	Cl. *Querco–Fagetea* All. *Alno–Ulmion*				Cl. *Alnetea glutinosa* All. *Alnion glutinosae*	
	Ass. *Pruno–Fraxinetum*	Ass. *Ficario–Ulmetum*	Ass. *Pruno padi–Alnetum incanae*		Ass. *Carici elongatae–Alnetum*	
			P.p.–A.i. var. *Frangula alnus*	P.p.–A.i. var. *Urtica dioica*	Subass. C.e.–*A. cardamine-tosum*	Subass. C.e.–*A. typicum*
Oxalis acetosella	V.2	V.2	IV.1	IV.1	I.+	I.+
Drepanocladus revolvens	III.1	II.1	II.1	–	–	–
Eurhynchium angustirete	IV.2	V.1	IV.1	IV.1	–	–
Geum rivale	IV.1	III.1	V.2	III.1	I.+	–
Plagiomnium elatum	II.1	III.1	IV.1	II.1	–	–
Ranunculus cassubicus	V.1	V.1	III.1	II.1	–	–
Rhytidiadelphus triquetrus	IV.1	I.+	IV.2	II.1	–	I.+
Angelica sylvestris	III.1	II.1	V.1	IV.1	–	I.+
Homalia trichomanoides	II.1	IV.1	I.+	II.1	I.+	I.+
Impatiens noli-tangere	I.+	III.1	II.1	II.1	–	I.+
Amblystegium varium	III.1	III.1	II.1	III.1	I.+	–
Eurhynchium hians	III.1	V.2	IV.1	V.2	II.1	I.+
Paris quadrifolia	V.1	V.1	III.1	I.+	II.1	–
Viola mirabilis	III.1	III.1	III.1	III.1	I.+	I.+
Anemone nemoralis	III.1	V.2	II.1	–	I.+	–
Viburnum opulus	III.1	I.+	IV.1	III.1	I.+	I.+
Lonicera xylosteum	III.1	III.1	III.1	III.1	I.+	I.+
Dryopteris carthusiana	II.1	III.1	IV.1	IV.1	II.1	I.+
Maianthemum bifolium	IV.1	III.1	IV.1	I.+	I.+	I.+
Equisetum sylvaticum	III.1	II.1	III.1	I.+	–	I.+
Calamagrostis canescens	II.1	I.+	III.1	I.+	II.1	I.+
Gymnocarpium dryopteris	III.1	–	II.1	–	–	–
Melica nutans	II.1	II.1	II.1	III.1	–	–
Rubus idaeus	III.1	III.1	IV.1	III.1	I.+	II.1
Solidago virgaurea	II.1	–	I.+	I.+	–	–
Atrichum undulatum	II.1	II.1	II.1	II.1	–	–
Plagiochila asplenioides	III.1	I.+	III.1	I.+	–	I.+
Scutellaria galericulata	I.+	II.1	III.1	II.1	II.1	II.1
Lysimachia nummularia	–	I.+	III.1	V.1	I.+	IV.1
Humulus lupulus	I.+	II.1	I.+	III.1	II.1	I.+
Myosotis scorpioides	I.+	II.1	I.+	II.1	II.1	–
Carex elongata	I.+	I.+	IV.1	I.+	I.+	III.1
Hypnum cupressiforme	III.1	II.1	II.1	I.+	–	–
Plagiomnium medium	III.1	I.+	I.+	I.+	–	–
Ribes nigrum	I.+	I.+	II.1	III.1	–	I.+
Rubus nessensis	–	–	II.1	III.1	–	I.+
Trientalis europaea	III.1	–	III.1	II.1	I.+	–
Amblystegium subtile	I.+	I.+	III.1	II.1	–	I.+
Rhodobryum roseum	I.+	II.1	III.1	–	–	–
Daphne mezereum	I.+	–	I.+	I.+	–	–
Trollius europaeus	I.+	I.+	I.+	II.1	–	–
Brachythecium mildeanum	I.+	I.+	I.+	I.+	–	–
Dicranum scoparium	I.+	I.+	II.1	–	–	–
Drepanocladus cossonii	I.+	I.+	II.1	II.1	–	–
Hylocomium splendens	I.+	I.+	II.1	I.+	–	–
Mentha aquatica	I.+	I.+	I.+	–	–	–

continued

Appendix. Continued.

Syntaxon	Cl. *Querco–Fagetea* All. *Alno–Ulmion*				Cl. *Alnetea glutinosa* All. *Alnion glutinosae*	
	Ass. *Pruno–Fraxinetum*	Ass. *Ficario–Ulmetum*	Ass. *Pruno padi–Alnetum incanae*		Ass. *Carici elongatae–Alnetum*	
			P.p.–A.i. var. *Frangula alnus*	P.p.–A.i. var. *Urtica dioica*	Subass. C.e.–*A. cardamine-tosum*	Subass. C.e.–*A. typicum*
Poa nemoralis	I.+	II.1	III.1	II.1	–	–
Carex nigra	–	I.+	I.+	–	–	–
Fragaria vesca	I.+	–	II.1	I.+	–	–
Pleurozium schreberi	II.1	I.+	III.1	I.+	–	–
Milium effusum	III.1	III.1	II.1	–	–	–
Polygonatum multiflorum	III.1	III.1	I.+	I.+	–	–
Mycelis muralis	I.+	–	I.+	II.1	–	–
Pyrola rotundifolia	I.+	–	I.+	I.+	–	–
Taraxacum officinale	I.+	I.+	I.+	II.1	–	–
Valeriana officinalis	–	I.+	I.+	II.1	–	–
Amblystegium serpens	I.+	I.+	I.+	II.1	–	–
Brachythecium rivulare	I.+	II.1	II.1	III.1	–	–
Plagiomnium affine	–	I.+	I.+	I.+	–	–
Brachypodium pinnatum	II.1	–	I.+	II.1	–	–
Geum urbanum	I.+	II.1	I.+	III.1	–	–
Impatiens parviflora	–	I.+	I.+	I.+	–	–
Anthriscus sylvestris	I.+	–	II.1	III.1	–	–
Elymus repens	I.+	–	II.1	II.1	–	–
Orthilia secunda	–	–	II.1	II.1	–	–
Ranunculus flammula	–	–	II.1	III.1	–	–
Veronica chamaedrys	I.+	–	I.+	III.1	–	–
Salix fragilis	–	–	I.+	II.1	–	–
Ribes rubrum	–	–	I.+	III.1	–	–
Dryopteris filix-mas	I.+	–	I.+	III.1	–	–
Rhamnus catharcticus	I.+	–	II.1	II.1	I.+	–
Ranunculus auricomus	I.+	–	III.1	I.+	I.+	–
Campylium sommerfeltii	I.+	I.+	II.1	I.+	–	I.+
Campylium stellatum	I.+	I.+	III.1	II.1	–	I.+
Fissidens adianthoides	I.+	I.+	III.1	I.+	–	I.+
Cardamine pratensis	–	I.+	I.+	II.1	I.+	–
Lycopodium annotinum	–	–	II.1	II.1	–	I.+
Peucedanum palustre	–	–	I.+	I.+	–	I.+
Stachys palustris	–	–	II.1	III.1	I.+	III.1
Symphytum officinale	–	–	I.+	II.1	–	I.+
Viola uliginosa	–	–	I.+	I.+	I.+	–
Mentha × *verticillata*	–	I.+	I.+	I.1	–	I.+
Sium latifolium	–	–	I.+	III.1	–	I.+
Carex digitata	III.1	–	II.1	I.+	–	–
Glechoma hederacea	I.+	III.1	I.+	I.+	–	–
Stellaria holostea	II.1	I.+	I.+	–	–	–
Thelypteris phegopteris	III.1	I.+	I.+	–	–	–
Ribes alpinum	II.1	I.+	I.+	–	–	–
Calamagrostis arundinacea	III.1	–	I.+	–	–	–
Dryopteris expansa	III.1	–	I.+	–	–	–
Carex flava	–	–	II.1	–	–	–
Carex pallescens	–	–	II.1	–	–	–

continued

Appendix. Continued.

Syntaxon	Cl. *Querco–Fagetea* All. *Alno–Ulmion*				Cl. *Alnetea glutinosa* All. *Alnion glutinosae*	
	Ass. *Pruno–Fraxinetum*	Ass. *Ficario–Ulmetum*	Ass. *Pruno padi–Alnetum incanae*		Ass. *Carici elongatae–Alnetum*	
			P.p.–A.i. var. *Frangula alnus*	P.p.–A.i. var. *Urtica dioica*	Subass. C.e.–*A. cardamine-tosum*	Subass. C.e.–*A. typicum*
Dactylis glomerata	–	–	II.1	I.+	–	–
Deschampsia caespitosa	–	I.+	III.1	I.+	I.+	–
Equisetum palustre	–	–	I.+	–	–	–
Leucanthemum vulgare	–	–	II.1	I.+	–	–
Luzula pallidula	–	–	II.1	–	–	–
Luzula pilosa	I.1	–	II.1	–	–	–
Sphagnum squarrosum	–	–	I.+	–	–	–
Platanthera bifolia	–	–	II.1	II.1	–	–
Ranunculus acris	–	–	II.1	II.1	–	–
Scrophularia nodosa	–	–	II.1	III.1	–	–
Campanula latifolia	–	III.1	–	III.1	–	–
Geranium robertianum	–	–	I.+	I.+	–	–
Poa pratensis	–	–	I.+	II.1	–	–
Stellaria media	–	–	I.+	II.1	–	–
Agrostis gigantea	–	–	II.1	I.+	–	–
Salix myrsinifolia	–	–	I.+	I.+	I.+	–
Elymus caninus	I.+	–	II.1	II.1	I.+	I.+
Carex riparia	–	–	II.1	I.+	I.+	II.1
Galium elongatum	–	–	II.1	I.+	–	II.1
Lythrum salicaria	I.+	–	I.+	–	II.1	II.1
Phragmites australis	–	–	I.+	–	I.1	I.+
Carex acuta	–	–	I.+	I.+	–	II.1
Ranunculus lingua	–	–	I.+	I.+	–	III.1
Epilobium palustre	–	I.+	I.+	–	–	I.+
Viola riviniana	I.+	I.+	I.+	–	I.+	–
Agrostis stolonifera	–	I.+	I.+	–	–	I.+
Carex pseudocyperus	–	–	I.+	–	–	I.+
Thalictrum flavum	–	–	I.+	I.+	I.+	–
Equisetum fluviatile	–	–	–	I.+	I.+	III.1