

Continuum of floristic composition between two plant communities – *Carici elongatae-Alnetum* and *Fraxino-Alnetum*

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Abstract. One of the crucial debates in vegetation ecology is whether plant communities are discontinuous, distinguishable units or whether they change continuously. Phytosociology assumes discontinuity and its methodology requires subjective sampling during vegetation inventories. For that reason, some researchers argue that phytosociology artificially creates discontinuity among plant communities. Our aim was to assess the continuity between ash-alder riparian forest (*Fraxino-Alnetum*), and alder swamp forest (*Carici elongatae-Alnetum*), and to check whether discontinuity observed between these two plant associations is an effect of subjective sample plot choice. We conducted 57 phytosociological relevés within a regular grid covering potential sites of both plant communities. All relevés were arranged in order of decreasing relative cover of the diagnostic species for each plant association resulting in a gentle gradient, indicating a continuous transition from *Fraxino-Alnetum* to *Carici elongatae-Alnetum*. Similar results were obtained by detrended correspondence analysis. The proportion of species from the *Quercus-Fagetea* class, typical to *Fraxino-Alnetum*, was decreasing with increasing proportion of species from the *Alnetea glutinosae* class, typical to *Carici elongatae-Alnetum*. This shift followed a gradient of ecological light-moisture indicator values. Our results confirmed continuous transition between two plant communities and led us to the conclusion that discontinuity resulted from the standard sampling protocol used in classical phytosociology. This protocol, however, is useful in searching for typological patterns, required for classification of plant communities, which is the main aim of phytosociology. Nevertheless, it does not provide full insight into the variability of vegetation and introduces uncertainty when trying to understand ecosystem dynamics. This uncertainty should be taken into account when phytosociological data are used for nature conservation recommendations and to draw conclusion about vegetation dynamics.

Keywords: phytosociology, vegetation ecology, sampling, ordination, methodology

1. Introduction

The proper selection and monitoring of valuable natural sites is the key issue of nature conservation. However, the selection of the most valuable sites is not possible without their prior assessment through the comparison and classification of various ecosystems. The classical phytosociological approach, however, is biased by shortcomings associated, amongst others, with subjectivism required in the selection of examined plots and disregard, during the research, of transitional zones between plant communities (Holeksa, Woźniak 2005; Austin 2013). This is due to the belief of phytosocio-

logists from the Braun-Blanquet school about the discontinuity of vegetation (Austin 2013), which in turn leads to the selection of plots in a preferential manner – for example, based on the diagnostic species occurrence in a given area (Lepš, Hadincová 1992; Holeksa, Woźniak 2003, 2005). On the one hand, such behaviour highlights differences between plant communities and leads to a discretionary assessment of species richness and diversity of the area under investigation (Chytrý 2001; Holeksa, Woźniak 2005). However, there is often a broad range of transitional forms between plant communities, which confirms the continuity between them: plant communities are formed by specific species whose ecological

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niches – often wide – cause blending of abstract units of phytosociological classification (Oksanen, Minchin 2002; Austin 2013). Notably, a belief in the continuity of vegetation does not exclude the possibility of classifying plant communities – the distinguishing of the idealised types of vegetation units, as it allows creating a simplified vegetation diversity diagram (Mucina 1997; Dzwonko 2007).

The mentioned shortcomings of the classical method bring multifaceted consequences, such as erroneous assessment of species richness (Holeksa 2005; Holeksa, Woźniak 2005) and incorrect classification of plant communities. They may prevent conducting conservation methods provided for a given type of plant community and, subsequently, result in its replacement by another plant community. For example, the misclassification of the community corresponding to *Vaccinio uliginosi-Pinetum* as *Ledo-Sphagnetum* may lead to its degradation because the conservation of open raised bogs *Ledo-Sphagnetum* depends on the removal of natural regeneration and shrubs, whilst the conservation of bog forests *Vaccinio uliginosi-Pinetum* depends on excluding the area from utilisation and on the conservation of forest stands (Rutkowski 2009; Pawlaczyk 2010; Stańko 2010). With a relatively smooth transition between these plant communities, the demarcation line established during the inventory of natural habitats is very clear: in open raised bogs, in contrast to bog forests, the crown closure of the tree layer does not exceed 50%. The dynamics of transition between the discussed plant communities is associated with climatic conditions and phases of dieback and renewal of pine stands on peatbogs (Eckstein et al. 2011). This may create doubts in preparing vegetation classification. What's more, a similar error in other natural habitats included in the Natura 2000 network might impede decision-making related to silvicultural and forest conservation activities on a given site, such as selection of species composition of tree stands (Rutkowski 2009).

The way to eliminate the problem of subjective choice of vegetation patches is to use the systematic methods, such as transects, or random selection methods. They enable the location of the sites where phytosociological relevés are to be conducted in a manner not affected by the error resulting from the visual assessment of a given patch, deciding about its inclusion in the classification of plant communities (Pawlaczyk 2010). This method is used, amongst others, in the studies on vegetation along environmental gradients (e.g. Dyderski et al. 2016). In an example of mountain plant associations, Holeksa and Woźniak (2003, 2005) demonstrated differences resulting from the use of the two abovementioned methods of relevé location in the field. More diagnostic species were recorded in the patches selected in a preferential manner, which usually results in underestimating the real variability of vegetation in a given area and emphasising the differences between plant communities (Chytrý 2001; Holeksa 2005). This suggests that the alleged discontinuity of vegetation is not as much the ef-

fect of its actual characteristics as of the deliberate location of the analysed patches in the areas corresponding to the researcher's earlier ideas about plant associations occurring in given area (Chytrý 2001). As the specificity of the mentioned studies conducted in mountain communities, it is not recommended to refer their conclusions to lowland areas without earlier confirmation of their applicability to other types of vegetation; they should be first confronted with the arguments of the authors proving the discontinuity of vegetation (e.g. Daubenmire 1966; Tabacchi et al. 1990).

The difficulties connected with the proper classification of plant communities are particularly evident in the case of plant associations strongly related to each other, for example, in a series of toposequences or dynamic vegetation circles. The examples of such plant communities are alder forests *Carici elongatae-Alnetum* W. Koch 1926 ex Schwickerath 1933 and alder-ash forests *Fraxino-Alnetum* W. Mat. 1952, particularly strongly blending with each other at the spatial and habitat level and related with each other *via* dynamic vegetation circles, that is, groups of secondary plant communities that are able to replace primary vegetation type (Ellenberg 1988; Pawlaczyk 2004; Matuszkiewicz 2005, 2011; Ratyńska et al. 2010). This is due to the characteristics of the abovementioned plant associations, because in both of them, forest stands are composed mainly of *Alnus glutinosa*. Also shrub layer consists of the same species, for example, *Ribes nigrum* and *Padus avium*. Both associations can be found in the valleys of watercourses or in lake basins and their surroundings; they are also widespread throughout Polish lowlands (Ratyńska et al. 2010). The most important difference between alder forests and riparian forests is due to hydrological conditions: in alder forests the fluctuations of ground water table are vertical, whilst in riparian forests, these are also horizontal, which is linked with the direction of the watercourse. They also differ in species composition: the herbaceous layer of riparian forests is usually dominated by species of the *Quercus-Fagetea* class, whilst the herbaceous layer of alder forests is dominated by species of the *Alnetea glutinosae* class (Czerepko 2010; Ratyńska et al. 2010). A correct identification of the transition zone between them is crucial from the implementation of nature conservation tasks point of view, as alder-ash forests, unlike alder forests, are the natural habitats of included in the Natura 2000 network (Pawlaczyk 2004). The classification of plant communities affects not only the possibility of implementing conservation tasks appropriate for a given plant community but also the costs related to the monitoring of protected areas and the limitations of forest management (Pawlaczyk 2004; Rutkowski 2009).

The aim of the study was to analyse a continuous transition of vegetation between alder forests and alder-ash forests and to check whether the discontinuity of the floristic composition observed between these two plant communities may be the effect of a subjective choice of sample plots.

2. Materials and methods

2.1. Study area

The study area was covered by riparian and alder forests and was located around Młyński and Szeken Wielki lakes in the territory of the Międzychód Forest District, north-western part of the country (Regional Directorate of the State Forests in Szczecin). According to the natural-forest regionalisation, the area is situated in the Wielkopolska-Pomerania Region (III), Noteć Forest mesoregion (III.17) (Zielony, Kliczkowska 2012). The Międzychód Forest District is located in the temperate transi-tional (from maritime to continental) climate zone. According to the nearest meteorological station in Gorzów Wielkopolski, the mean annual temperature in 2001–2010 was 9.3°C and the mean annual precipitation was 572 mm (Central Statistical Office – GUS 2015). The length of the growing season in this region is 225 days (Żmudzka 2012). The study area is covered mainly by pine forests growing on podzolic and rusty soils, whilst the studied plant communities grow on murshic histosols, as well as on peat soils, typical to fens. No drainage activities were reported in the study area.

2.2. Fieldwork

Owing to the late development of vegetation in the plant communities of wetland ecosystems, fieldworks were carried out in September 2015 (Dzwonko 2007). Only one date (summer) was analysed in the study, because the spring aspect occurs only in the *Fraxino-Alnetum* association. Not taking into consideration of the spring aspect may be perceived as a short-coming affecting the results and their interpretation. Should the spring aspect that occurs only in one of the analysed associations be taken into account, the vegetation patches of *Fraxino-Alnetum* would become more distinguishable, which is linked with a relatively short-term seasonal occurrence of two geophyte species: *Anemone ranunculoides* and *Ficaria verna* (Jagodziński et al. 2016). In the summer time, when vegetation development reaches its optimum, the fully developed summer aspect observed in both communities could be compared.

On the basis of the orthophotomap and an earlier field inspection, three study sites were established in three forest habitat types (Lw, Ol, OIJ) where, in the Wielkopolska-Pomerania Region (III), the investigated forest communities (ORWLP 2004) might possibly occur. In order to avoid the preferential selection of patches, this area was covered with a regular 30 m × 30 m grid and the study sites were set in the centre of each square. In each of the points where forest vegetation occurred (excluding forest edge communities in gaps and reeds communities) was located in the field using a GPS receiver with an accuracy of 5 m, 10 × 10 m study plots were established using

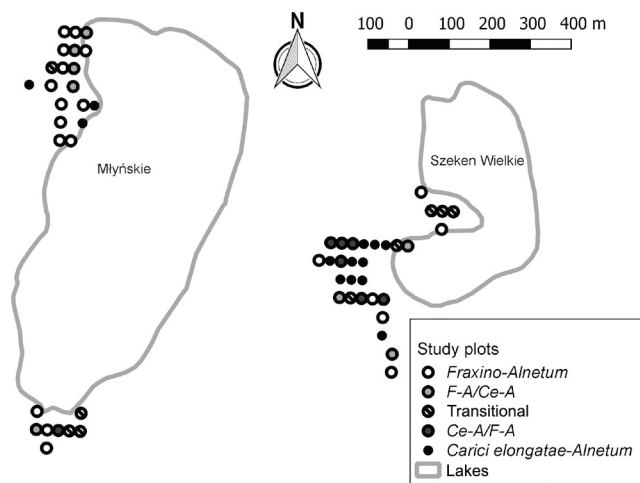


Figure 1. Distribution of the study plots (n=57) with diagnosis of the plant communities

a measuring tape and a compass (n = 57; Fig. 1). On each of the plots, a list of plant species was made including the assessment of plant cover using a modified 9-point Braun-Blanquet scale. Owing to a small distance between the study sites, the entire arrangement of study plots was considered to be a single observation; therefore, the results should be treated as a case study of the transition between the two specific plant communities.

2.3. Data analysis

Phytosociological relevés were entered into the Turboveg database program and classified into groups corresponding to plant communities based on the species composition of plants and their cover. The names of plant taxa were adopted after Szwed et al. (1999). Two approaches to the classification were used for the identification of the differences in the description of relationships between plant communities. In the classical approach (Dzwonko 2007), six relevés each, which would be taken into account during the standard inventory using phytosociological methods, were selected to best represent the alder and alder-ash forests in the investigated area. In the objective approach, all relevés including transitional patches were analysed. The syntaxonomical nomenclature was adopted after Ratyńska et al. (2010). Transitional plant communities were assigned to one of the three categories, alder forest/riparian forest, transitional community and riparian forest/alder forest, taking into account the highest abundance of plant species typical and distinct for *Quercus-Fagetea* and *Alnetea* classes.

The R program (R Core Team 2015) and ‘vegan’ package (Oksanen et al. 2013) were used for statistical analyses. In order to define the main trends in vegetation dynamics, a detrended correspondence analysis (DCA) was performed together with

passive vector fitting: the abundance-weighted averages of Ellenberg’s ecological indicator values (Ellenberg, Leuschner 2010) and the cover of plants of the main phytosociological classes. The coefficient of determination and statistical significance of the fitness was calculated using a permutation test implemented in the ‘envfit’ function of the ‘vegan’ package.

To assess the discontinuities between communities, the I coefficient proposed by Holeksa and Woźniak (2005) was used and adapted to the plant communities under study:

$$I = \frac{QF}{QF + Aln}$$

where:

QF is the total cover of plant species characteristic of the *Quercus-Fagetum* class,

Aln is the total cover of plant species characteristic of the *Alnetum* class.

This coefficient reaches the highest values in the patches of riparian forests most distinct from alder forests and the lowest values in alder forests where no species from *Quercus-Fagetum* occur. In the absence of a discontinuity between the investigated syntaxa, the distribution of I coefficient values arranged in ascending order is gentle (Holeksa, Woźniak 2003).

3. Results

In the studied area, plant communities list included alder-ash forests *Fraxino-Alnetum* (Table 1, Fig. 1) – 20 of 57 plots, pa-

tches with transitional communities between riparian forest and alder forest close to riparian forest (hereinafter: *F-A/Ce-A*; 8), plots with transitional communities (9), plots with transitional communities from alder forest to riparian forest (hereinafter: *Ce-A/F-A*; 7) and plots with alder forests (*Carici elongatae-Alnetum*; 13). In phytosociological relevés, 142 species of vascular plants, 14 species of mosses and 1 species of liverwort were identified. The occurrence and cover of distinguishing species and those characteristic of the associations and higher syntaxa were the basis for the classification of individual plant communities into vegetation types. In all vegetation types, the tree layer was made up of *A. glutinosa*. The most frequent shrub species was *Frangula alnus*; it occurred in nearly 70% of the phytosociological relevés of all distinguished plant communities (Table 1). The most frequent species (more than 50% relevés) in the herbaceous layer were *Dryopteris carthusiana*, *Urtica dioica*, *Solanum dulcamara* and *Brachythecium rutabulum*.

Alder-ash forests represented the most abundant plant community. The occurrence of species typical to *Alnion incanae* and species distinguishing *Fraxino-Alnetum* as well as the dominance of *Quercus-Fagetum* species over the *Alnetum glutinosae* species clearly show that they belong to this syntaxon. Species characteristic of other associations were scarce. The most frequent herbaceous species were *D. carthusiana*, *D. cespitosa* and *S. dulcamara*. The most abundant species allowing to distinguish the association were *Plagiomnium undulatum*, *Festuca gigantea* and *Chrysosplenium alternifolium*.

Table 1. Frequency and abundance of plant species in the distinguished vegetation units: left column shows species frequency (%), right – range of cover in Braun-Blanquet’s scale. Number in square bracket – number of study plots.

Species	Frequency (%)	<i>Fraxino-Alnetum</i> [20]	<i>F-A/Ce-A</i> [8]	Transitional [9]	<i>Ce-A/F-A</i> [7]	<i>Carici elongatae-Alnetum</i> [13]
Ch. Cl. <i>Alnetum glutinosae</i>						
<i>Alnus glutinosa</i> a	98.2	100 ³⁻⁵	100 ³⁻⁵	100 ³⁻⁵	100 ^{2a-5}	92 ^{2b-5}
<i>Alnus glutinosa</i> a2	15.7	15 ^{1-2m}	12 ¹	33 ¹⁻³	29 ^{2m-2a}	0
<i>Alnus glutinosa</i> b	61.7	50 ^{+2m}	38 ^{1-2m}	56 ^{1-2a}	86 ⁺³	85 ⁺⁴
<i>Alnus glutinosa</i> c	27.9	15 ^r	12 ⁺	11 ¹	71 ⁺	46 ⁺¹
<i>Solanum dulcamara</i>	72.0	80 ^{r-3}	62 ^{+2b}	56 ^{+2m}	100 ^{+2a}	62 ^{+2m}
<i>Lycopus europaeus</i>	47.4	50 ^{r-1}	50 ^{r+}	22 ⁺¹	57 ⁺¹	54 ^{r-1}
<i>Thelypteris palustris</i>	45.8	10 ^{1-2a}	25 ^{1-2a}	56 ^{1-2b}	86 ^{2m-3}	85 ¹⁻⁵
<i>Peucedanum palustre</i>	31.5	20 ⁺¹	50 ^{+2a}	33 ^{r-2b}	14 ⁺	46 ^{r-1}
<i>Scutellaria galericulata</i>	31.4	30 ⁺	25 ⁺¹	44 ⁺	14 ¹	38 ⁺
<i>Sphagnum palustre</i> d	21.1	10 ⁺¹	12 ^{2a}	0	29 ^{1-2m}	54 ¹⁻³
<i>Carex pseudocyperus</i>	19.2	0	12 ⁺	22 ⁺	14 ³	54 ^{+2a}

Species	Frequency (%)	<i>Fraxino-Alnetum</i> [20]	<i>F-A/Ce-A</i> [8]	Transitional [9]	<i>Ce-A/F-A</i> [7]	<i>Carici elongatae-Alnetum</i> [13]
Ch. All. <i>Alnion incanae</i>						
<i>Plagiomnium undulatum</i> d	54.3	80 ^{+2a}	50 ^{+2a}	44 ¹⁻³	57 ^{+2a}	23 ^{1-2m}
<i>Chrysosplenium alternifolium</i>	34.9	55 ⁺⁴	62 ⁺³	33 ^{1-2a}	14 ⁺	0
<i>Festuca gigantea</i>	33.3	55 ^{r-1}	62 ⁺¹	11 ¹	29 ^{r+}	0
<i>Prunus padus</i> a2	5.00	0	12 ⁴	11 ^{2m}	14 ^{2a}	0
<i>Prunus padus</i> b	14.0	5 ^{2m}	25 ^{+2a}	33 ^{2a-3}	14 ³	8 ¹
<i>Prunus padus</i> c	14.1	10 ⁺	25 ^{r-1}	11 ¹	29 ⁺	8 ⁺
<i>Carex remota</i>	13.9	30 ^{+2m}	12 ^{2m}	11 ^{2b}	0	0
Ch. Cl. <i>Quercu-Fagetea</i>						
<i>Tilia cordata</i> a	1.8	5 ¹	0	0	0	0
<i>Tilia cordata</i> a2	8.8	20 ¹⁻³	0	11 ⁴	0	0
<i>Tilia cordata</i> b	12.2	25 ^{+2a}	12 ^{2m}	11 ³	0	0
<i>Tilia cordata</i> c	13.9	30 ^{r-1}	12 ^r	11 ⁺	0	0
<i>Atrichum undulatum</i> d	12.3	10 ⁺¹	12 ⁺	11 ¹	29 ⁺¹	8 ³
<i>Acer pseudoplatanus</i> b	5.2	0	12 ⁺	22 ¹	0	0
<i>Acer pseudoplatanus</i> c	10.5	5 ¹	25 ⁺	22 ^{r+}	14 ⁺	0
<i>Fraxinus excelsior</i> a	1.8	5 ¹	0	0	0	0
<i>Fraxinus excelsior</i> a2	1.7	0	12 ^{2a}	0	0	0
<i>Fraxinus excelsior</i> c	10.4	20 ^{r-2m}	12 ⁺	11 ^r	0	0
Ch. Cl. <i>Artemisietea</i>						
<i>Urtica dioica</i>	73.8	75 ^{+2a}	88 ^{2m-4}	78 ^{r-2b}	71 ^{+2m}	62 ⁺⁵
<i>Geranium robertianum</i>	64.7	75 ^{+2a}	62 ^{+2m}	78 ^{+2m}	71 ^{+2a}	38 ⁺
<i>Impatiens parviflora</i>	43.7	70 ^{r-3}	50 ^{1-2b}	44 ^{1-2m}	14 ⁺	15 ^{1-2m}
<i>Rubus caesius</i>	31.8	15 ^{r-2m}	38 ⁺¹	56 ^{r-2m}	43 ⁺¹	31 ^{r-1}
<i>Geum urbanum</i>	19.3	30 ⁺¹	50 ^{r-1}	11 ⁺	0	0
<i>Moehringia trinervia</i>	19.2	40 ⁺	12 ¹	22 ⁺¹	0	0
<i>Eupatorium cannabinum</i>	17.6	25 ^{+2a}	25 ^{r+}	11 ⁺	14 ⁺	8 ^r
<i>Galium aparine</i>	15.7	10 ^{r+}	25 ⁺	11 ⁺	29 ^{r-1}	15 ⁺
Ch. Cl. <i>Molinio-Arrhenatheretea</i>						
<i>Deschampsia caespitosa</i>	73.5	90 ⁺³	75 ^{+2a}	89 ⁺³	71 ¹⁻³	38 ^{r-2a}
<i>Cirsium palustre</i>	49.2	35 ^{+2m}	62 ^{r-1}	22 ^{r-1}	86 ^{r-1}	62 ^{+2a}
<i>Geum rivale</i>	45.8	55 ^{r-1}	75 ^{r-1}	67 ^{r-2a}	29 ⁺¹	8 ⁺
<i>Lysimachia vulgaris</i>	44.0	45 ^{r+}	38 ⁺	22 ⁺	43 ⁺¹	62 ^{r-1}
<i>Juncus effusus</i>	33.3	50 ^{+2b}	25 ^{1-2a}	0	57 ⁺¹	23 ⁺³

Species	Frequency (%)	<i>Fraxino-Alnetum</i> [20]	<i>F-A/Ce-A</i> [8]	Transitional [9]	<i>Ce-A/F-A</i> [7]	<i>Carici elongatae-Alnetum</i> [13]
<i>Climacium dendroides</i> d	26.2	15 ⁺³	25 ^{1-2m}	22 ¹	71 ⁺¹	23 ^{+2a}
<i>Ranunculus repens</i>	24.5	25 ⁺¹	25 ⁺¹	33 ^{r+}	57 ⁺¹	0
<i>Lysimachia nummularia</i>	21.1	30 ⁺¹	38 ^{+2a}	22 ⁺¹	14 ⁺	0
<i>Juncus conglomeratus</i>	19.2	10 ^{r-1}	12 ¹	22 ^{r-1}	43 ^{r+}	23 ⁺¹
<i>Rumex acetosa</i>	14.0	15 ^{r+}	12 ^{2a}	22 ⁺	14 ⁺	8 ^r
<i>Equisetum palustre</i>	12.2	0	0	33 ⁺¹	14 ⁺	23 ⁺¹
<i>Lychnis flos-cuculi</i>	10.5	5 ⁺	25 ^{r-1}	0	43 ^{r+}	0
<i>Cirsium oleraceum</i>	10.5	15 ^{r+}	12 ¹	0	14 ^{2a}	8 ^r
Ch. Cl. Phragmitetea						
<i>Galium palustre</i>	38.7	25 ⁺¹	38 ⁺	11 ⁺	71 ⁺¹	62 ⁺¹
<i>Carex paniculata</i>	36.7	15 ¹⁻³	25 ⁺¹	33 ^{+2b}	57 ^{+2b}	69 ⁺³
<i>Equisetum fluviatile</i>	22.8	15 ⁺¹	12 ¹	11 ⁺	57 ⁺	31 ^{r+}
<i>Carex acutiformis</i>	22.7	15 ^{r-2m}	0	33 ^{1-2m}	14 ⁺	46 ^{r-3}
<i>Phragmites australis</i>	15.7	10 ^{2m}	25 ^{r-2m}	11 ¹	14 ^r	23 ⁺³
<i>Mentha aquatica</i>	12.2	15 ^{+2m}	0	0	14 ⁺	23 ⁺¹
<i>Carex elata</i>	12.2	0	0	33 ^{1-2m}	29 ^{1-2m}	15 ^{2m-2b}
<i>Carex riparia</i>	10.5	10 ⁺	0	0	14 ⁺	23 ¹⁻⁴
<i>Carex gracilis</i>	10.4	10 ⁺¹	12 ¹	0	0	23 ^{1-2a}
<i>Acorus calamus</i>	10.4	0	0	0	14 ⁺	38 ⁺¹
Ch. Cl. Rhamno-Prunetea						
<i>Frangula alnus</i> b	75.5	75 ⁺⁵	75 ¹⁻⁴	89 ⁺⁴	100 ^{2m-5}	54 ^{+2a}
<i>Frangula alnus</i> c	70.2	65 ^{r-1}	50 ⁺¹	78 ⁺¹	100 ^{+2m}	69 ⁺¹
<i>Rubus plicatus</i>	12.2	15 ^{1-2a}	12 ^{2m}	22 ⁺³	0	8 ¹
<i>Sambucus nigra</i> b	12.1	15 ⁺³	12 ^{2a}	22 ¹	14 ¹	0
<i>Sambucus nigra</i> c	12.2	20 ^{r+}	12 ⁺	11 ⁺	14 ⁺	0
Ch. Cl. Scheuchzerio-Caricetea						
<i>Agrostis canina</i>	40.1	35 ⁺³	62 ¹	11 ^{2a}	71 ^{+2b}	38 ⁺⁴
<i>Hydrocotyle vulgaris</i>	29.9	15 ^{1-2m}	25 ^{+2a}	22 ^{2a-3}	86 ⁺⁴	31 ^{+2a}
<i>Polytrichum commune</i> d	10.5	0	0	11 ⁺	14 ¹	31 ^{+2a}
<i>Carex nigra</i>	10.5	5 ⁺	12 ⁺	0	0	31 ⁺³
Ch. Cl. Vaccinio-Piceetea						
<i>Pinus sylvestris</i> a	1.8	0	0	0	0	8 ⁺
<i>Pinus sylvestris</i> b	3.6	5 ^r	0	0	0	8 ⁺
<i>Pinus sylvestris</i> c	15.6	10 ^r	12 ⁺	0	14 ^r	38 ^{r+}
<i>Vaccinium myrtillus</i>	12.2	5 ⁺	12 ⁺	0	14 ⁺	31 ⁺¹

Species	Frequency (%)	<i>Fraxino-Alnetum</i> [20]	<i>F-A/Ce-A</i> [8]	Transitional [9]	<i>Ce-A/F-A</i> [7]	<i>Carici elongatae-Alnetum</i> [13]
Accompanying species						
<i>Dryopteris carthusiana</i>	80.9	90 ⁺⁴	88 ⁺³	78 ^{2m-3}	86 ^{1-2a}	62 ^{+2a}
<i>Brachythecium rutabulum</i> d	59.8	55 ^{+2a}	50 ¹⁻³	67 ^{+2a}	71 ⁺³	62 ¹⁻³
<i>Oxalis acetosella</i>	52.8	70 ¹⁻⁴	75 ⁺⁴	67 ¹⁻³	43 ¹⁻³	8 ⁺
<i>Rubus idaeus</i>	52.5	50 ^{r-2a}	50 ^{r-3}	100 ⁺³	71 ^{1-2b}	15 ⁺
<i>Bidens frondosa</i>	34.9	45 ⁺³	50 ^{+2m}	11 ⁺	14 ^r	38 ⁺¹
<i>Sorbus aucuparia</i> b	15.7	15 ⁺	25 ⁺¹	33 ⁺¹	14 ¹	0
<i>Sorbus aucuparia</i> c	28.0	40 ^{r-1}	38 ⁺¹	44 ⁺	14 ⁺	0
<i>Athyrium filix-femina</i>	21.0	40 ⁺³	25 ^{r-1}	22 ^{+2a}	0	0
<i>Quercus robur</i> b	1.7	0	0	11 ¹	0	0
<i>Quercus robur</i> c	19.3	25 ^{r+}	0	56 ^{r+}	14 ^r	0
<i>Rubus sprengelii</i>	19.3	20 ^{+2m}	25 ^r	33 ¹⁻³	29 ^{r+}	0
<i>Cystopteris fragilis</i>	17.4	5 ^r	0	11 ⁺	43 ^{r+}	38 ^{r+}
<i>Calliergonella cuspidata</i> d	17.4	5 ¹	12 ^{2b}	11 ^{2m}	14 ¹	46 ¹⁻³
<i>Polygonum hydropiper</i>	14.1	20 ^{r+}	0	0	0	31 ^{r+}
<i>Plagiomnium affine</i> d	14.0	20 ⁺¹	12 ^{2m}	22 ¹⁻³	0	8 ⁺
<i>Polytrichastrum formosum</i> d	12.2	10 ¹	12 ^{2m}	0	14 ⁺	23 ⁺¹
<i>Stellaria media</i>	10.5	0	25 ⁺	22 ⁺¹	29 ⁺	0

Species with frequency lower than 10%: **Alnetea**: *Calamagrostis canescens*, *Calla palustris*, *Ribes nigrum* b, *Salix cinerea* b, *Salix pentandra* b, *Sphagnum squarrosum* d; **Quercus-Fagetea**: *Brachypodium sylvaticum*, *Chaerophyllum temulum*, *Corylus avellana* b & c, *Dryopteris filix-mas*, *Gymnocarpium dryopteris*, *Poa nemoralis*, *Prunus avium* a2, *Ranunculus lanuginosus*, *Viburnum opulus* b & c; **Artemisietea**: *Epilobium hirsutum*, *Calystegia sepium*, *Chelidonium majus*, *Cirsium vulgare*, *Elymus repens*, *Equisetum arvense*, *Galeopsis tetrahit*, *Glechoma hederacea*, *Humulus lupulus*, *Lamium maculatum*, *Mycelis muralis*, *Stachys palustris*; **Molinio-Arrhenatheretea**: *Hypericum tetrapterum*, *Angelica sylvestris*, *Carex hirta*, *Cerastium holosteoides*, *Festuca rubra*, *Holcus lanatus*, *Lotus uliginosus*, *Lythrum salicaria*, *Myosotis palustris*, *Plantago major*, *Poa palustris*, *Poa pratensis*, *Potentilla anserina*, *Prunella vulgaris*, *Scirpus sylvaticus*, *Taraxacum officinale* agg., *Vicia cracca*; **Phragmitetea**: *Berula erecta*, *Glyceria nemoralis*, *Scrophularia umbrosa*, *Sparganium erectum*, *Typha angustifolia*, *Typha latifolia*, *Veronica beccabunga*; **Scheuchzerio-Caricetea**: *Epilobium palustre*, *Valeriana dioica*; **Vaccinio-Piceetea**: *Betula pubescens* c, *Dryopteris dilatata*, *Juniperus communis* b & c, *Picea abies* c; accompanying species: *Potentilla recta*, *Acer negundo* b & c, *Aesculus hippocastanum* a2, *Aulacomnium androgynum* d, *Betula pendula* a, b & c, *Bidens cernua*, *Brachythecium salebrosum* d, *Cardamine amara*, *Epilobium angustifolium*, *Fallopia convolvulus*, *Fraxinus pensylvanica* c, *Holcus mollis*, *Hottonia palustris*, *Hydrocharis morsus-ranae*, *Lemna minor*, *Marchantia polymorpha* d, *Mentha arvensis*, *Nymphaea alba*, *Oxalis europaea*, *Parthenocissus quinquefolia*, *Pohlia nutans* d, *Polygonum mite*, *Prunus domestica* c, *Prunus serotina* c, *Quercus petraea* c, *Ranunculus sceleratus*, *Rhizomnium punctatum* d, *Ribes rubrum* c, *Rubus corylifolius* agg., *Rumex aquaticus*

The ‘riparian forest/alder forest’ type of transitional communities was characterised by the species composition typical to *Alnion glutinosae*, simultaneous dominance of species typical of *Alnion incanae* and distinguishing species of *Fraxino-Alnetum*. The most frequent species in the herbaceous layer were *U. dioica*, *D. carthusiana*, *Oxalis acetosella*, *Geum rivale* and *D. cespitosa*. The most abundant species that allowed to classify the transitional community from riparian forests to alder forests were *Chrysosplenium alternifolium*, *Festuca gigantea* and *S. dulcamara*.

The transitional plant communities showed no dominance of diagnostic species for any of the analysed associations. The most abundant species in the herbaceous layer were *Rubus idaeus*, *D. cespitosa*, *U. dioica*, *Geranium robertianum* and *D. carthusiana*.

The ‘alder forest/riparian forest’ type of transitional communities was characterised by the species composition typical to *Alnion incanae*, the largest proportion of species typical of *Alnion glutinosae*, as well as distinguishing species of *Carici elongatae-Alnetum*. The most frequent species in the herbaceous

us layer were *Cirsium palustre*, *D. carthusiana* and *Hydrocotyle vulgaris*. The most abundant species that allowed to classify the community as transitional from alder forests to riparian forests were *Thelypteris palustris*, *U. dioica* and *S. dulcamara*.

Alder forests were characterised by the largest proportion of species typical of *Alnion glutinosae* and distinguishing species to *Carici elongatae-Alnetum*. The species typical to other associations were scarce. The most common species of the herbaceous layer were *F. alnus* and *Carex paniculata*. The most abundant species allowing to distinguish the association were *T. palustris*, *U. dioica* and *Carex pseudocyperus*.

The DCA of vegetation on the examined plots (Fig. 2) shows the variability of plant communities along the gradient of ecological light-moisture indicator values. With the increase of light-moisture indicator values along the axis DCA1, there is a decrease in the proportion of species from the *Quercus-Fagetea* class and the increase in the species from the *Alnetea* class. The occurrence of species from the *Quercus-Fagetea* class is associated with the occurrence of species from the *Artemisietea* class, whilst the occurrence of species from the *Alnetea* class is associated with the occurrence of species from the *Phragmitetea* class.

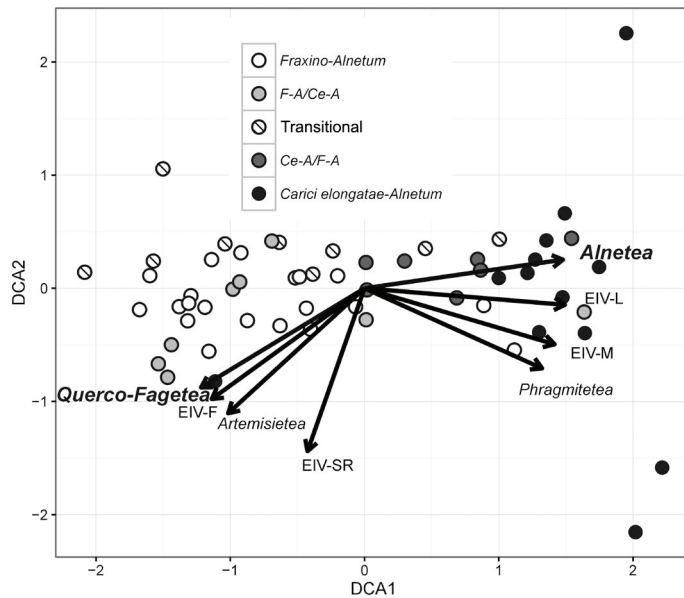


Figure 2. Result of Detrended Correspondence Analysis. Axis parameters: DCA1: eigenvalue 0.6532; DCA2: eigenvalue 0.3822. All vectors represent variables statistically significantly ($p < 0.001$) correlated with the ordination result: proportion of phytosociological classes and Ellenberg's Indicator Values: EIV-F – fertility, EIV-L – light, EIV-M – moisture and EIV-SR – soil reaction.

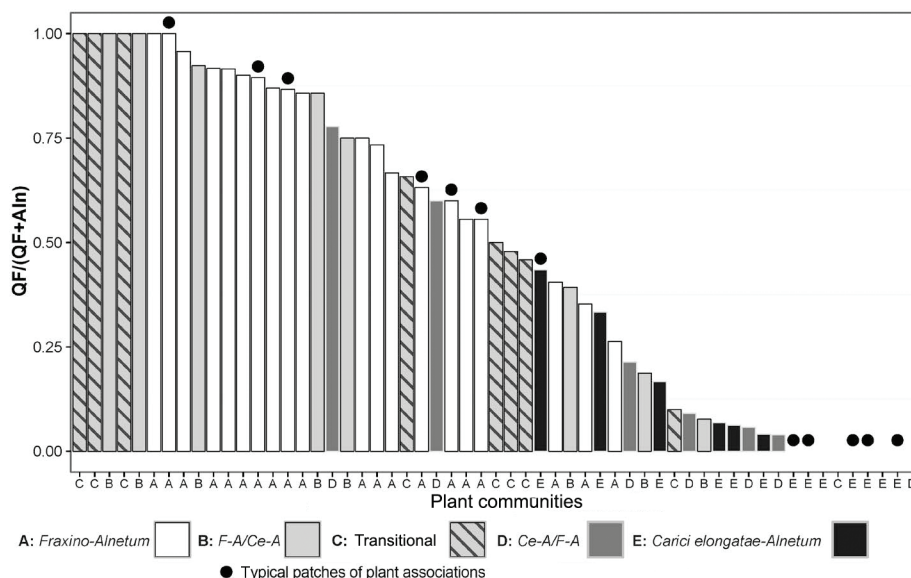


Figure 3. Arrangement of decreasing I index within the sample of 57 relevés. Black points indicate relevés selected as 'typical'.

The gradient of the species abundance, running along the DCA1 axis, representing both the investigated plant associations, is also reflected in the continuity coefficient I analysis of plant communities (Fig. 3), indicating a gradual transition from riparian forests *Fraxino-Alnetum* to alder forests *Carrici elongatae-Alnetum*. The use of the standard approach – that is, the choice only of the patches most consistent with the classification scheme – shows that there is a sharp transition between the associations under study, although one of the phytosociological relevés made in alder forests shows a higher value of the I coefficient.

4. Discussion

Spatial and habitat relationships between the studied associations

In the studied area, transitional vegetation patterns between alder forests and riparian forests were observed. Although the two plant communities are typical to different hydrological conditions, they are secondary communities for each other within their dynamic vegetation circles (Matuszkiewicz 2005; Ratyńska et al. 2010). This indicates that riparian forests may occur in potential habitats of alder forests and vice versa. Also the occurrence of species typical of alder forests in riparian forests and the occurrence of species typical to riparian forests in alder forests are thought to be the traits distinguishing these two associations (Matuszkiewicz 2005), even though they have wide ecological scales (Ellenberg, Leuschner 2010). On the other hand, the shift of riparian forests to alder forests and alder forests to riparian forests was described as a form of degradation of these plant communities, as in the case of hornbeam expansion (Czerwiński 1995; Czerepko 2010; Stachowski et al. 2015). The shift of riparian forests to alder forests can be both of zoogenic origin, associated with the activity of beavers, and of anthropogenic origin (Pawlaczyk 2004). This process is also considered an indicator of the natural dynamics of these plant communities associated with hydrological cycles. This would be a sign of the state of dynamic balance between the compared associations. Our results seem to support such an interpretation; however, because of lack of temporal replications, this is only a hypothesis.

According to Matuszkiewicz (2007), alder-ash riparian forests constitute a forest community with the lowest rate of changes in floristic composition, described by the dissimilarities in the species composition between the study dates and the length of time interval between dates. Maybe a small representation of dynamic states described based on few subjectively selected patches is the effect of the occurrence in the field of patches with a different degree of similarity to ‘typical patches’, that is, with a large number of diagnostic

species. In this case, both the standard approach and random sampling may lead to similar conclusions about the low rate of changes in riparian communities.

Czerepko (2008) presented a different point of view on the differentiation between alder forests and riparian forests, where DCA proved a discontinuity between the discussed plant communities, whilst Dyderski et al. (2015) demonstrated a smooth transition. Both studies differed in two aspects – the area where the studies were carried out and the method of selecting patches. Czerepko (2008) analysed changes in bog forest communities over time, whilst Dyderski et al. (2015) analysed the variability in forest communities within one date. The continuum observed by Dyderski et al. (2015) may have resulted from both degeneration of the discussed typological units and from the phytosociological approach defined by Dzwonko (2007) as ‘moderate subjectivism’. It consists in selecting the location of phytosociological relevés not only in ‘typical patches’ consistent with the ideas created by literature but also in the most frequent types of vegetation patches. Czerepko (2008) conducted relevés in the localities of former study sites from 1960 to 1970, when the choice of the best preserved patches was the common practice (Dzwonko 2007). Our results indicate that such an approach can artificially sharpen the demarcation lines between the distinguished syntaxa, which is also demonstrated in the studies by Holeksa and Woźniak (2003, 2005). It should, however, be noticed that because only one pair of plant communities was taken into consideration and because of the absence of replications, the conclusions cannot be directly transferred to other syntaxa, where different environmental factors may influence the sharpness of transition zones (Ellenberg 1988).

Discontinuity and continuity of plant communities – the impact of the phytosociological method

The phytosociological method generally requires focussing on vegetation patches that may be classified into specific vegetation units. When the researcher’s task is the investigation of the plant communities in a given area, such a procedure may facilitate fieldwork and ensure quick documentation of the vegetation state. At the same time, this leads to the belief that the distinguished units are distinct plant communities. The debate on continuity and discontinuity of vegetation has been going on in geobotany since the beginnings of this science and is related to the controversy over the continuum concept of vegetation in view of Clements’ approach to climax vegetation and Gleason’s dynamic equilibrium (Dzwonko 2007; Holeksa 2016).

The use of gradient analyses enabled the assessment of the variability track between different types of plant communities and detection of ecological niches of individual plant species that build a given plant community (Dzwonko 2007; Austin 2013). There is an established belief amongst

Polish vegetation ecologists that there is no continuity between plant communities. Despite of significant achievements in applying the quantitative methods to vegetation analysis in Poland (e.g. Kulczyński 1928, 1939), the tabular reports and the classical phytosociological analysis played an important role. The gradient analysis methods have been in use in Poland since the end of the 1970s (e.g. Dzwonko 1978; Brzeziecki 1984), although the multidimensional methods based on similarity coefficients (e.g. Matuszkiewicz 1973) were applied earlier. It is likely that such an approach has strengthened the belief amongst Polish geobotanists in discontinuity of vegetation, or this may be the question of the paradigm of the equilibrium of nature dominating in approaches of nature philosophy (Holeksa 2016). Despite this, the analysis of phytosociological relevés conducted with the classical method is still used as an argument in disputes on nature conservation methods (e.g. Brzeziecki et al. 2016; Jaroszewicz et al. 2017). The results obtained by the authors, such as those of Holeksa and Woźniak (2003, 2005), indicate to what extent the real variability of vegetation can be biased by preferential selection of study sites, resulting from the belief in discontinuity of vegetation. The problem with the proper naming of transitional stages of vegetation may be another potential reason for maintaining the belief of discontinuity between plant communities. In our studies, we draw attention to this issue and to the difficulty with assigning adequate names to three different transitional phases named as ‘alder forest/riparian forest’, ‘transitional community’ and ‘riparian forest/alder forest’. In fact, all the three phases are transitional communities, but they differ in the degree of similarity to the well-documented plant communities – abstract vegetation types. Assuming the continuity of vegetation may, therefore, lead to the multiplication of entities and problems with their naming and evaluation. Thus, for practical purposes, such as the mapping of the Natura 2000 natural habitats, or for the typology of forest habitats, it is necessary to adopt arbitrary, easily named units. This is particularly important because of the problems with adequate and correct naming of syntaxonomic units (Dzwonko 2007; Ratyńska et al. 2010).

Implications for nature conservation

The existing discontinuity between the associations under investigation has a significant effect on nature conservation. The *Fraxino-Alnetum* association is under protection as a priority habitat included in the Natura 2000 network, code 91E0 (Council Directive 92/43/EEC of 21 May 1992; Pawlaczyk 2004). Therefore, it requires setting the boundaries of its biochore within the Natura 2000 habitat conservation areas as well as periodic monitoring. The monitoring method requires that phytosociological relevés be conducted on the transect yet without providing any details concerning their

principles of location, except their representativeness. The occurrence and dominance of typical species are the criteria used to assess the state of the Natura 2000 habitats (Pawlaczyk 2010). As a result, the preferential selection of patches for monitoring, being consistent with the phytosociological methodology, poses two threats. First, it does not reflect the real dynamics and natural value of vegetation within a given plant community but recognised as a ‘typical patch’ within a delineated area. Phytosociologists generally select relevés on the sites with a large number of diagnostic species (Chytrý 2001; Holeksa, Woźniak 2003, 2005), hence, being not representative for the whole biochore of the association. Second, the application of the assessment criteria of natural habitats to transitional patches makes it impossible to obtain a FV note (favourable status), accounting for the proper state of the natural habitat. This results from one of the assessment criteria – the cover of diagnostic/typical plant species. Third, it also precludes proper selection of the conservation methods. The example of habitat 91E0 can be investigated in the framework of various schemes of forest management procedures that can either improve or worsen the actual state of the corresponding plant community (Rutkowski 2009). The identification of habitat 91E0 in alder forests may result in a biased selection of the conservation methods and lead to the loss of specific traits of the vegetation. Proper identification of the state of the habitat is important for conducting activities not only in a given forest stand but also in the catchment area of a given watercourse, for example, related to the small-scale water retention.

5. Summary

We observed a continuous transition between alder forests and ash-alder forest along the light-moisture gradient in the area under investigation. On the one hand, the discontinuity observed between the investigated plant communities may result from the preferential selection of patches; however, it is not a natural phenomenon. On the other hand, because of the lack of replications and non-considering of other vegetation units, care should be taken when attempting to transfer the discontinuity pattern to other plant communities where the continuous transition may be the effect of specific environmental conditions. The classical phytosociological method allows determining which model vegetation systems occur in a given area or in what forms of degradation they are. However, because of the exclusion of transitional patches, it does not account for a wide range of forms occurring in the area covered by inventory. The subjective and preferential choice of patches artificially creates a discontinuity amongst plant communities. From the point of view of phytosociology as a science, whose aim is to inventory and classify plant communities, such an approach allows distinguishing typological units that can be easily used in practice,

for example, in forest typology or nature conservation. However, it does not allow assessing a full vegetation diversity and makes it difficult to draw conclusions about the course of ecological processes. Moreover, through searching for rigid patterns, in the form of established schemes of diagnostic species, it is of great importance for the decision-making, concerning nature conservation of the Natura 2000 natural habitats. Therefore, in the phytosociological approach, the uncertainty as to the real state of investigated plant communities should also be taken into account when trying to assess the state of natural habitats and to draw conclusions about vegetation dynamics.

Conflict of interest

The authors declare the lack of potential conflicts.

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Author's contribution

A.M.J., M.K.D. – concept and methods of research; N.C., S.P., M.K.D. – fieldwork, data processing and analysis; N.C. and S.P. – literature review; N.C. and S.P. with participation of A.M.J., M.K.D. – manuscript preparation, editing; A.M.J. – revision and coordination.