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Hypotheses of changes in palustrian plant communities under climate change. Specification of a model for European wetland habitats.

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Abstract

Marginal wetlands are particularly vulnerable to climate change. Changes in precipitation and temperature will impact on flooding patterns and water table fluctuations and will therefore modify vegetation communities and other ecological factors such as nutrient availability. A Space for time substitution was used as an approach dealing with the European scale. Inference of successional dynamic stages is only possible by relying on synchronic studies of multiple sites at different stages in dynamic trajectories. Because of this large scale, another surrogate was the Ellenberg indicator values used as a homogenous system to derive environmental factors. Multivariate analytical techniques (DCA/CCA) were used to depict the general pattern of wetland distribution and therefore to predict possible changes in plant communities, driven by climate change. In this deliverable, a test is made on palustrian standing water systems and perennial plant communities, from available phytosociological data sets through the European range. The objectives are bring out (1) the role/place of climate in the current distribution of wetland habitats in Europe in relation with other factors and (2) the possible changes in the distribution of European palustrian wetland habitats, that could be predicted regarding direct or indirect effects of climate change.

Data analyses shown that moisture is the main factor controlling ordination of plant communities both of meso-eutrophic and oligotrophic habitats. Other factors such as reaction, nutrient availability shown a clear distinction between meso-eutrophic and oligotrophic habitats. The widespread geographical distribution of plant species, and plant assemblages of the meso-eutrophic habitats in comparison with to the restricted distribution of most plant species and plant assemblages of oligotrophic habitats suggests that the ecological drivers, and then sensitivity to environmental change would be significantly different. Meso-eutrophic wetland habitats with a fertility value of $N > 5$, would not be affected by eutrophication process in relation with climate change and/or induced land-use changes. Oligotrophic habitats (fertility, $N < 4$) would be highly sensitive to climate change at a regional scale, both in terms of temperature increase, and of hydrological change. They would be also highly affected by increasing fertility in the palustrian wetlands in relation with eutrophication processes. A temperature increase might induce a shift

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from temperate or Atlantic oligotrophic habitat types towards eu-Mediterranean habitat types (oligo- or meso-eutrophic). Increasing nutrient availability, as an indirect consequence of increasing

temperature, might induce a shift from oligotrophic habitat types (either temperate or Mediterranean) to mesotrophic habitat types (temperate or Mediterranean), without change in hydrological functioning.

Introduction

It is now admitted through scientific studies that climate change is underway and could have a major impact on the nature and distribution of vegetation in the future (IPCC, 1996). The predicted changes in Europe are different between locations (e.g. Southern and Northern Europe, Semmler & Jacob, 2004). In addition to an increase of precipitation, as a result of a warmer climate (IPCC, 2001), increasing global surface temperatures are very likely to alter the hydrological cycle (Dore, 2005). In wetlands, hydrology, *i.e.* water level and water movement, is among the main factors that provide plant species growth and survival and therefore, determine the plant community composition, structure and dynamics (Clément & Proctor, 2006). Climate change will significantly influence wetlands by altering hydrologic regimes (increasing or decreasing water level, depth, duration, frequency, and seasonality of flooding). These changes will affect all wetland functions such as biological, biogeochemical, hydrologic and socio-economic functions (IPCC, 1996). Moreover, climate change may have, through change in land use, indirect effects that can worsen alteration. Geographical distribution of the wetland plant communities is likely to shift.

The objective of EUROLIMPACS WP1-Task 4 is to investigate the likely changes in wetland hydrology and to develop a simple model to predict changes in European habitats mainly based on plant communities typology depicted by the European habitat classification system (CORINE / [EUNIS](#), Devillers *et al.*, 1991; Davies *et al.* 2004).

Plant composition of the wetland communities is an integrative mirror of the ecosystem functioning and can be used as valuable predictors of number of fundamental ecosystem functions. According to different scales, plant assemblages, representing a plant community typology, may play a useful role as indicators of ecosystem status or ecosystem response to changing environmental conditions in the palustrine wetlands (Murphy *et al.*, 1994).

Wheeler and Shaw (1995) consider plants as “hydrologists”. Using plants and vegetation as indicators is a helpful tool for assessing the nature and effect on past or on-going hydrological change in wetlands (Ellenberg *et al.* 1992 ; Newbold & Mountford 1997).

The impact of climate change on vegetation has usually been analysed at an individual species level (Thuiller *et al.*, 2005) or on vegetation at a large zonal scale (e.g. Ozenda & Borel, 1990; Smith *et al.*, 1992). Few studies were carried on the response of plant communities or habitats to climate change. Comparisons of vegetation were done under similar climate but different regarding some constraints (temperature, hydrology...), as a basis to predict possible changes (Hill *et al.*, 1994; Duckworth *et al.*, 2000). In this deliverable we collected from the literature, available vegetation data on wetlands but restricted to palustrine habitats as a first stage of vegetation gradient analyses that may allow generating hypotheses regarding habitat and climate relationships.

Based on vegetation analyses, this deliverable aims to answer the following questions:

To what extent the climate is involved in the current distribution of wetland habitats in Europe in comparison with other factors such as nutrient availability, acidification and internal land-use? What changes due to climate warming, could be predicted in the distribution of European palustrine wetland habitats?

1 Material and methods

1.1 What are palustrine wetlands?

The term « wetland » is relatively recent and has a variety of definitions. According to the WP objectives, we retained the definition summarised through the figure 1. In this context, we are concerned especially with telmatic wetlands.

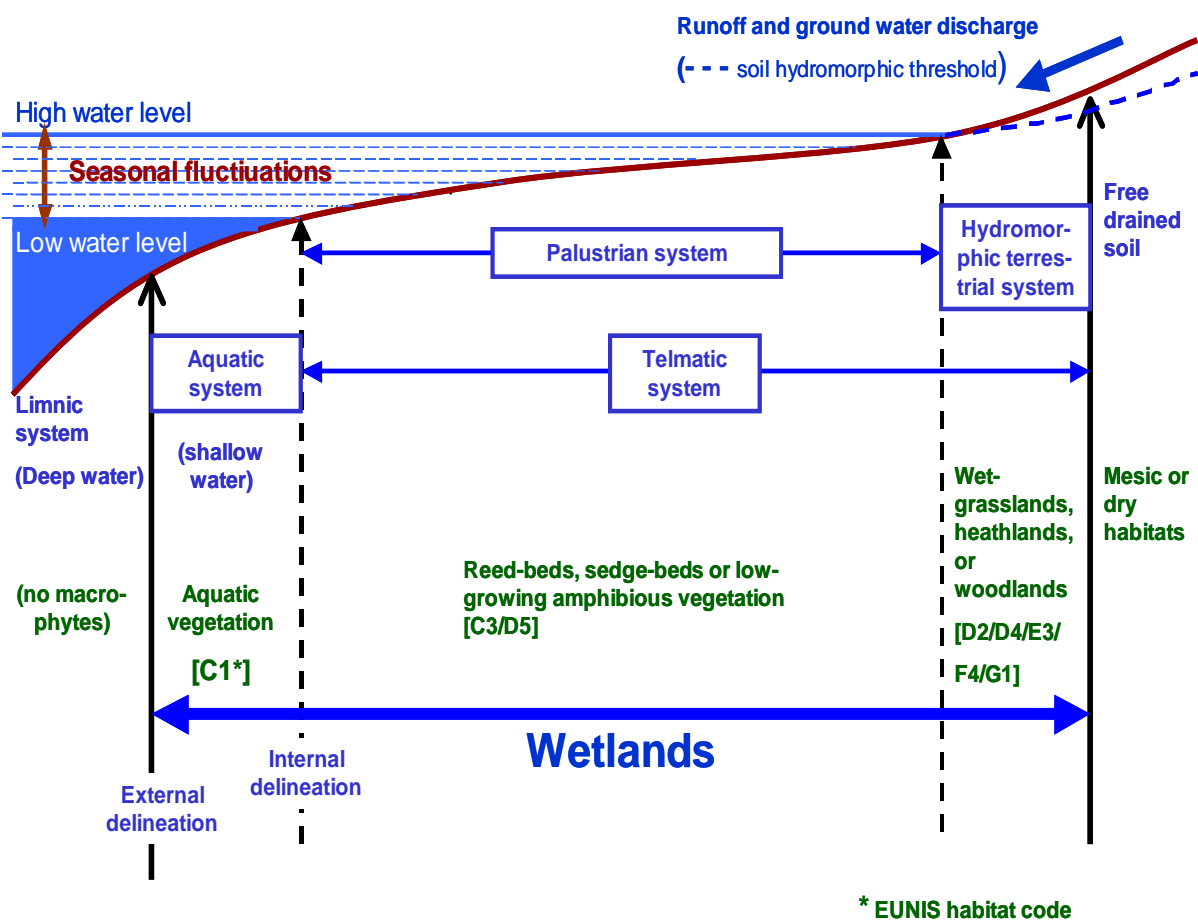


Figure 1. Wetland delineation in a hydrological ecocline,

Freshwater wetlands could be represented in a hydrological gradient, between limnic and free drained ecosystems, with two main types: aquatic wetlands (shallow water) and telmatic wetlands that are semi-terrestrial (Wheeler, 1999). Each subdivision along the hydrological gradient (or ecocline) corresponds to an hydroperiod or ecophase in time and an hydro-geomorphic unit (HGMU) in space. Telmatic wetlands can be subdivided in permanent, seasonal, and fluctuating wetlands, according to fluctuations in water flooding or waterlogging (Wheeler and Proctor, 2000).

According to EUNIS classification, habitats (higher levels) that can be encountered along the hydrological ecocline are as follow:

C1 : Surface standing waters (with aquatic macrophytes); C3 : Littoral zone of inland surface waterbodies (palustrine systems); D5 : Sedge and reedbeds, normally without free-standing water; D2 : Valley mires, poor fens and transition mires D4 : Base-rich fens and calcareous spring mires; E3 : Seasonally wet and wet grasslands; F4: Temperate shrub heathland; G1 : Broadleaved deciduous woodland. (For more detail, see annex 1)

1.2 Data

Available vegetation data have been collected mainly from phytosociological literature published about European wetlands. Data are represented by synoptic (syntaxonomic) tables of plant assemblages. These tables consist in a list of species (rows) and their occurrences in different syntaxa (columns). Each syntaxon was established on a number of relevés (or samples).

In this primary study, we have selected information only on palustrian wetlands that are classified in term of vegetation, into 4 phytosociological classes:

- § *Phragmiti australis* – *Magnocaricetea elatae* (**Reed and large Sedge beds**)
- § *Agrostietea stoloniferae* p.p. (**Spikrush beds**)
- § *Littorelletea uniflorae* (**non Mediterranean Low growing amphiphytic vegetation**)
- § *Isoetetea velatae* p.p. (**Mediterranean low growing amphiphytic vegetation**)

(For more information see annex 2)

Homologous class of *Littorelletea* for the temperate zone (non-Mediterranean) was represented by the class of *Isoeto-Nano-Juncetea bufonii* for the Mediterranean and South-Eastern Europe. But this class includes both perennial and annual plant species. Therefore it was preferable to separately distinguish these two groups (de Foucault, 1988). So, we chose to include only perennial plant communities in this primary analysis. Those plant communities belong to the new class proposed by de Foucault (1988) and called *Isoetetea vellatae*.(syn *Isoetion*, *Isoeto-Nano-Juncetea* p.p.); this class is only represented in the Mediterranean zone.

The corresponding EUNIS data base of European palustrian habitats was classified in two main categories:

- § C: littoral zone of inland freshwater and
- § D: Mire, bog and fen habitats (see annex 1 for details)

Reed beds, Sedge beds were found in this two main categories: C3 (Water- fringing reed beds and tall helophytes other than canes) and D5 (Sedge and Reed beds, normally without free-standing water).

The database have been built on the basis of 336 syntaxa (plant assemblages) with an average of 30 relevés sampled per syntaxon (total of 9977 relevés). The syntaxa have been gathered from European wetlands and some from adjoining countries (see figure 2). A letter was assigned to each syntaxon according to its physiognomic pattern (dominant plants).

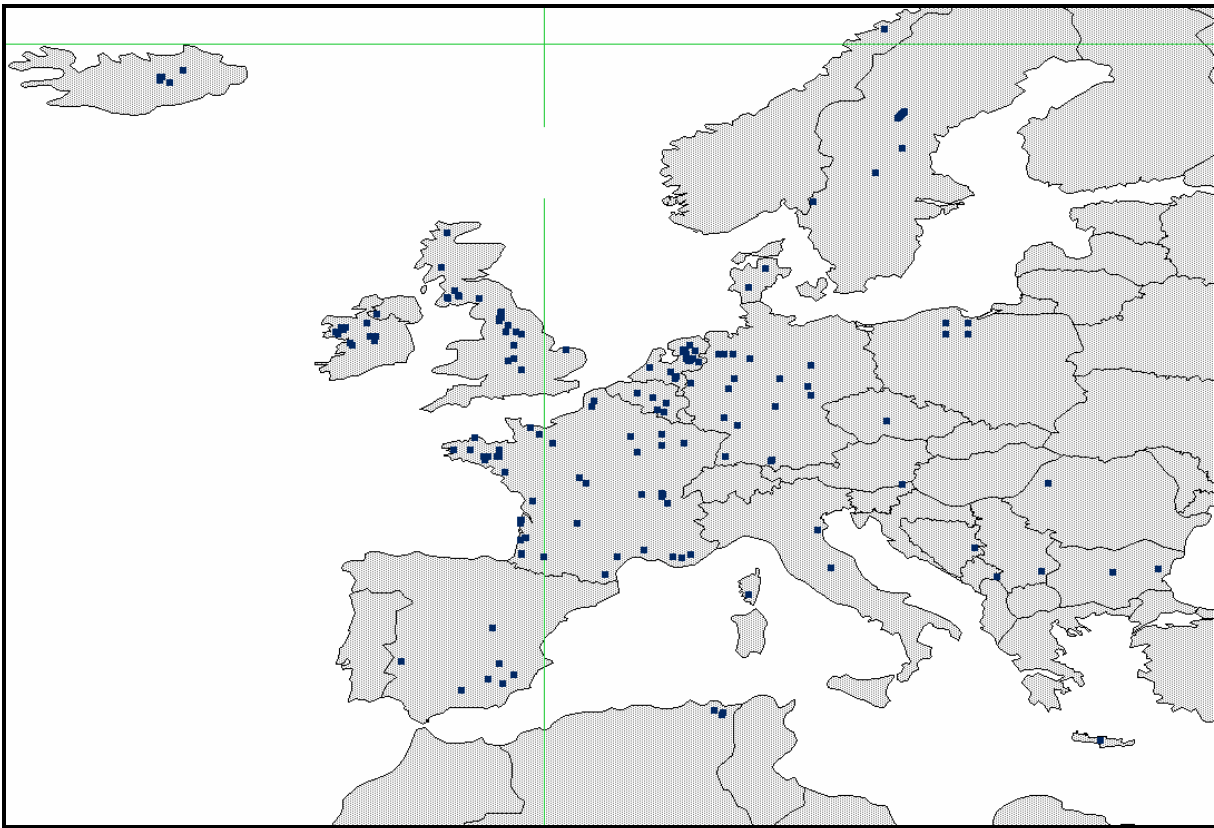


Figure 2. Map showing the mean central location of the collected data of palustrian wetland plant assemblages from Europe and the Mediterranean basin.

In order to reduce inherent bias of such data compilations from several studies, the data base was built according to the following criteria:

- § data consistency : eco-climatic and biogeographical representativity;
- § syntaxonomy validation according to the phytosociological status in relation with the used sampling design;
- § taxonomic relevance: because of existing species synonyms, the taxonomic list was standardised according to current used nomenclature of *Flora Europea* (Tutin *et al.*, 1964–80)..

1.3 Methods

Such vegetation data, based on phytosociological surveys, constitute a valuable source of information regarding the objective of the task at the scale of European area. Originally, the CORINE Biotope classification had been based on the hierarchical phytosociological classification (Devillers *et al.*, 1991).

This approach is based on the floristic composition using the concept of degree of fidelity of plant species to a plant community (Moravec, 1992). Characteristic groups of species are used to organize communities as plant assemblages into a hierarchical classification of syntaxa. A syntaxon is a classification unit at any level of the hierarchy. In the present case, syntaxa are used rather than relevés. Syntaxon groups were determined in phytosociological matrixes by successive

rearrangement of rows (species) and columns (syntaxa) until a clear hierarchical pattern. Columns (syntaxa) were compared to assess their degree of similarity, according to multi-dimensional analyses (see below) rather than the classical phytosociological procedure (Gehu and Rivas-Martinez, 1981). A group with a high degree of similarity constitutes a syntaxon group i.e. a community type. The final result of this procedure is a synoptic table representing the identified syntaxon groups. Each species is characterized by a frequency class indicated by a roman numbering from I to V as follows:

I: 1 - 20 % frequency, II: 21 - 40 %, III: 41 - 60 %, IV: 61 - 80 %, V: 81 - 100 %.

"Constant" species are those present in most of the plant associations, often with a high frequency level. The most important species for diagnostic are those which are present with a medium to high frequency, only in few syntaxa in those associations. They are called "differential species or "characteristic" species.

Syntaxa allow detection of multi-species responses along environmental gradients. Syntaxa can be regarded as 'fuzzy sets in an operational context for describing vegetation along ecological gradients in synthetic ways and can further the understanding of vegetation variation' (Biondi et al., 2004). Syntaxon groups are characterized by a recurrent combination of species which can be found in similar ecological conditions. Hence an important and valuable rule in the traditional phytosociological method is primarily the rigorous sampling of homogeneous stands of vegetation.

In order to point out the pattern of the syntaxon distribution, the vegetation data were analysed using Detrended Correspondence Analysis with detrending by segments (DCA, Hill, 1979; CANOCO package, ter Braak and Šmilauer, 1998). The extracted ordination can be interpreted as an environmental gradient that explain affinities between syntaxa regarding their species composition similarity.

To evaluate the importance of environmental and geographical factors, CCA (canonical correspondence analysis) was used. We chose the Ellenberg Indicator Values (IVs see below): F (moisture), N (productivity) and R (reaction/pH) as Environmental factors. Only these information is available through the whole European range as homogenous environmental features.

Latitude and longitude were used as geographical factors that could be linked with ecoclimatic / biogeographic zonation in Europe. Since we analysed syntaxa rather than relevés, the coordinates of syntaxon locations were estimated as a central point according to the importance of the sampling area of the syntaxon (fig. 2).

We used Ellenberg IVs introduced by Ellenberg for Central Europe (Ellenberg et al., 1992) and updated for British plants by Hill et al. (1999, available to [download](#)) that give the definition and derivation of Ellenberg values and a list of Ellenberg scores for British plant species. They are derived from the relationship between the presence of species and a characterisation of its environment. The three EIVs used in the present paper, are defined as follows:

F - Moisture

The F (from the German 'Feuchtigkeit') scale runs from 1 (plants living under extreme dryness) to 12 (plants permanently or almost continually under water). Intermediate conditions of moisture are: 5 Moist-site indicator, mainly on fresh soils of average dampness; 7: Dampness indicator, mainly on constantly moist or damp, but not on wet soils, 9: wet-site plant indicators with often waterlogged soil; 11: Plants rooted under water, or floating plants.

N - Nitrogen

Ellenberg N-values are considered as indicators of general fertility (Hill et al., 2000) rather than nitrogen availability in particular. Other authors (e.g. Shaffers & Sykora, 2000) found high correlation between N value and biomass production. The N value is used as indicator of trophic conditions. Its scale is between 1 indicating extremely low trophic and 9, indicator of extremely rich conditions.

R – Reaction

R value indicates soil pH, or water pH but does not mean pH values. The R scale, arbitrary defined, reflects conditions of acidity vs. alkalinity through the plant species composition of a given habitat, with values from 1 indicator of extreme acidity to 9 indicating basic reaction found in calcareous or other high-pH soils or water.

The use of Ellenberg IVs can usefully replace direct measurements of the variables of interest that are usually costly time consuming and therefore expert knowledge is often used instead. An advantage of Ellenberg IVs is that they may be more sensitive to the requirements of plants than it is to a selected variable.

Ellenberg IVs are used at plant community level rather than individual species. Although it is generally claimed that species respond individually to the environment, a vegetation community, representative of a local habitat, can be expressed as a species combination which is more integrative regarding the environment and therefore it is likely to have a stronger indicator value than any individual species (Clément & Proctor, 2006).

In habitat assessment the use of expertises based on indicator values is widespread. IVs can be used to provide information about abiotic environment of a certain plant species assemblage. Usually, many species occur together and one can expect that combinations of their IVs would give more reliable assessment of the environmental conditions than each of the species IVs.

The approach used is definitely a 'space for time substitution' which allows explaining time succession (diachronic process) using space gradients through synchronic approach.

In the context of the present task (WP1, task 4-2) objectives, this approach is based on the assumption that if a species is present in conditions of a warmer part of Europe, it is potentially able to spread into currently colder parts if temperatures increase. The same assumption or hypothesis could be made for plant communities and *in fine* habitats.

The aim of the 24 months investigation (this deliverable) is to determine the pattern of syntaxon distribution of habitats that are now designated by the European [EUNIS](#) classification (See annex 1 for details), which replaced the CORINE one. The habitats that are considered in this deliverable are palustrian wetlands.

2 Results

The first division retained separated meso-eutrophic habitats from oligotrophic ones.

2.1 Meso-eutrophic habitats

The first axis of the CCA ordination diagram of meso-eutrophic habitats (fig. 3) has an eigenvalue of 0.548 (Table 1) and represents a clear gradient of moisture, running from mainly common spikerush beds (C3.24A Eunis code) to those wetter of reed beds (C3.21/22/23 Eunis code) or *Cladium* beds (C3.28 Eunis code) (table 2). Regarding the F value, this gradient runs from 7/8 value in the negative part of the axis to 8/10.5 in the positive one. This is confirmed by the high correlation of 0.9344 ($p < 0.001$) between the first axis and the F variable (fig. 4).

The second axis (eigenvalue=0.345) is less clearly defined but appears to distinguish habitats with lower trophic level in the top of the diagram. This axis is highly correlated ($p < 0.001$) with the N and R values, respectively of 0.9582 and 0.8653 (table 1).

Table . 1 CCA axis eigenvalues and correlations for Meso-Eutrophic habitats.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.548	0.345	0.263	0.219	16.298
Correlations					
Longitude	-0.275	-0.517	-0.477	-0.294	
Latitude	0.383	0.460	-0.089	0.650	
Ellenberg Iv :					
F	0.934	-0.042	-0.163	-0.137	
N	0.064	-0.958	0.125	0.068	
R	-0.210	-0.865	-0.208	0.035	

	long	lat	F	N	R
Longitude	1.000				
Latitude	-0.578	1.000			
Ellenberg Iv :					
F	-0.123	0.251	1.000		
N	0.405	-0.388	0.062	1.000	
R	0.508	-0.447	-0.104	0.818	1.000

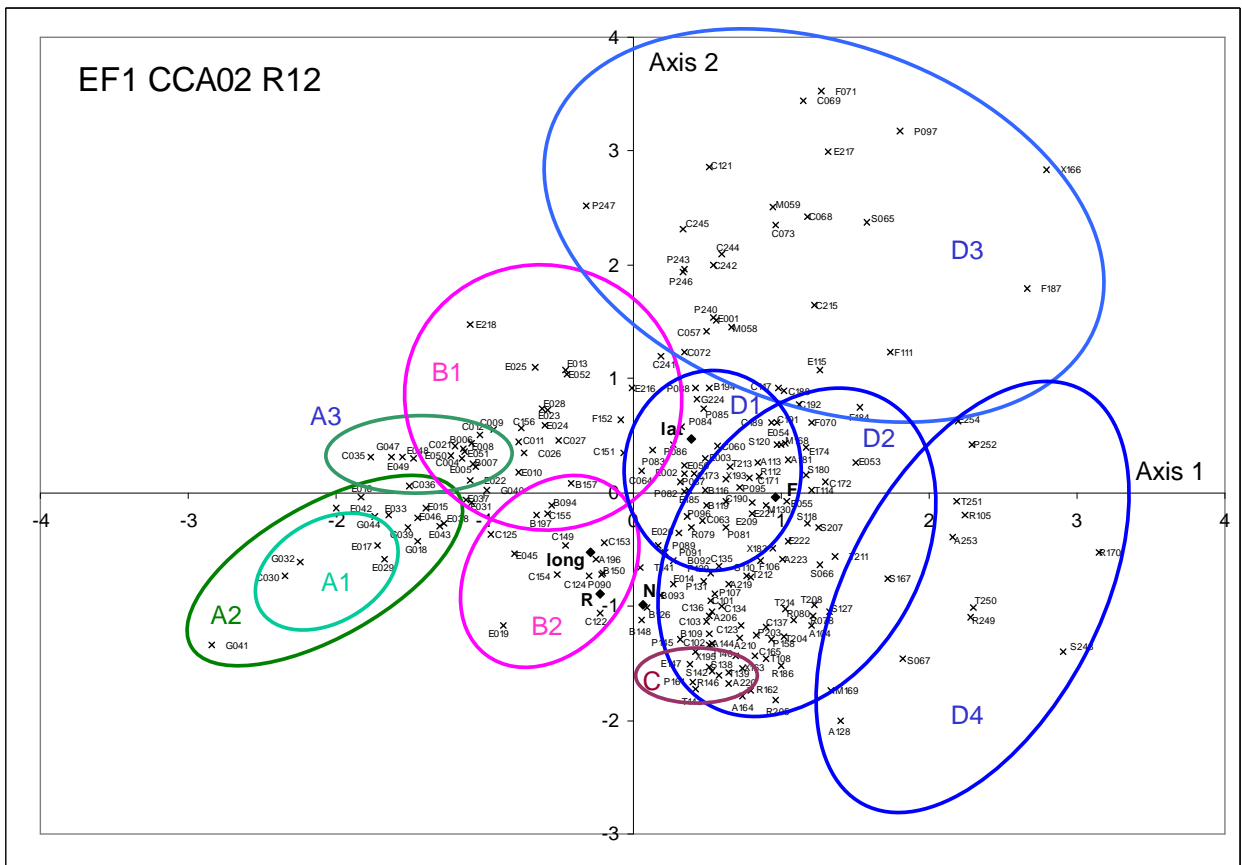


Figure 3. CCA Ordination diagram of the meso-eutrophic habitats

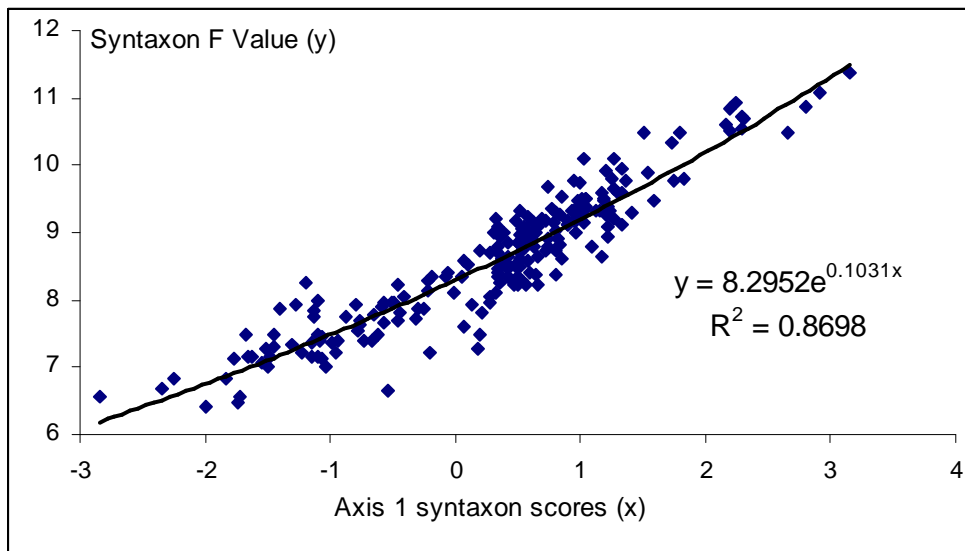
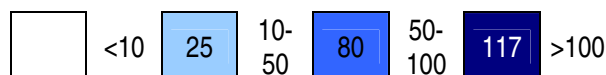


Figure 4. Regression between Ellenberg F value and the first ordination axis scores for the meso-eutrophic habitats.

Table 2. Identified syntaxon groups of meso-eutrophic habitats (see annex 4 for details)

Syntaxon groups	eA1	eA2	eA3	eB1	eB2	eC	eD1	eD2	eD3	eD4
Ellenberg IVs: Moisture (F)	7.1	7.0	7.3	7.6	8.0	8.7	8.4	9.1	9.2	10.4
Productivity (N)	5.4	5.4	5.0	5.0	5.5	5.9	5.6	5.6	3.9	5.7
Réaction (R)	6.6	6.4	6.5	6.2	6.4	6.6	6.4	6.4	5.6	6.5
Common/dominant Species										
Bromus racemosus, Cyperus longus										
Inula britannica, Beckmannia eruciformis.										
Allium angulosum, Cnidium dubium.										
Carex disticha, Senecio aquaticus										
Carex vulpina, C. otrubae, Filipendula ulmaria, Glyceria fluitans.										
Eleocharis palustris, Phalaris arundinacea, Carex acuta										
Phragmites australis, Equisetum fluviatile, Sparganium erectum, Typha latifolia, Glyceria maxima, Carex riparia, Schoenoplectus lacustris, Carex vesicaria, Carex acutiformis.										
Typha angustifolia, Cladium mariscus, Carex elata, Carex paniculata.										
Menyanthes trifoliata, Potentilla palustris, Carex rostrata, Hydrocharis morsus-ranae.										
Hippuris vulgaris, Apium nodiflorum										
Undetermined differential species										
Accidental species										
EUNIS references	EUNIS codes (frequent habitat in bold)									
Common spikerush beds	C3.24A					C3.24A				
Large sedge beds	D5.21					D5.21				
Phalaris beds						C3.26				
Phragmites, Schoenoplectus, Typha, water-fringing beds						C3.21/.22/.23				
Phragmites, Schoenoplectus, Typha normally without free-standing-water						D5.11/.12/.13				
Cladium beds						C3.28				

Density of frequency = total species frequency in the group / number of cells (in %)



The table 2 shows a summary of the synoptic table (annex 4) of meso-eutrophic syntaxon groups. This table is based on the ordination obtained from the multidimensional analyses (DCA and CCA, fig. 3).

The general structure of this table shows that the groups of syntaxa eA and eB mainly correspond to sedge beds with *Carex otrubae*, *C. vulpina*, *C. melanostachya*, *C. disticha*, and *Cyperus longus* (Large sedge beds: D5.21 Eunis code *p.p.*). These vegetation types are characterised by a lot of

wet grassland plants that tolerate no more than four months of flooding, during winter to mid spring, growing on longer time waterlogged and medium rich nutrient soils.

The eA1, eA2 and eA3 groups all encompass Mediterranean syntaxa, but their particularities are related to geographical variation from Balkans (eA1), Pannonian (see annex 3) region (eA2) to Central Europe (eA3).

The eB groups reflect a higher moisture level in comparison with the eA groups. No geographical gradient can explain the difference between eB1 and eB2. The group eB2 is differentiated by low frequencies of some reeds such as *Phragmites*, *Typha*, *Glyceria maxima* and large sedges such as *Carex riparia*, *C. vesicaria*. Presence of such tall helophytes indicates that eB2 may represent an intermediate group between medium tall beds and tall reed beds.

This eB2 group could be interpreted as a dynamic stage in term of succession, i.e. an early stage of reed beds predicting a possible change in relation with an increase in the flooding period, in late spring.

The eD groups represent reed beds, tall helophytes and large sedge beds, but also some common spikerush beds. No geographical variation could explain the difference between groups. The major difference is due to a moisture gradient (flooding duration) from about more than 5/6 months (for eD1) to permanently flooded (eD4). The F value (moisture) indicates a gradient (fig. 5) from 8.4 (eD1) to 10.4 (eD4).

eD1 group represents reed beds and large sedge beds associated with tall-herbs or forbs such as *Filipendula ulmaria*, *Valeriana officinalis*, *Epilobium hirsutum*, *Eupatorium cannabinum*... which indicate that those syntaxa belong to the Reed-Beds habitats (D5.1 Eunis code) or large sedge beds (D5.2 Eunis code) 'normally without free standing water'. The higher frequency of forbs and of some grassland plants shows the possible dynamics toward seasonally wet grasslands and tall forb habitats (E3 Eunis code).

eD2 group is a combination of standard or typical reed-beds and large sedge-beds. Moisture value of about 9 (fig. 5) could be considered as the moisture value of optimum development of such plant assemblages.

eD3 group corresponds to reed-beds and large sedge-beds and shows a similar requirement for moisture, but it is differentiated from eD2 by a lower reaction value R and a lower productivity value N (fig. 5). The high frequencies of *Menyanthes trifoliata*, *Potentilla palustris*, *Carex rostrata* and *Epilobium palustre* underline this observation.

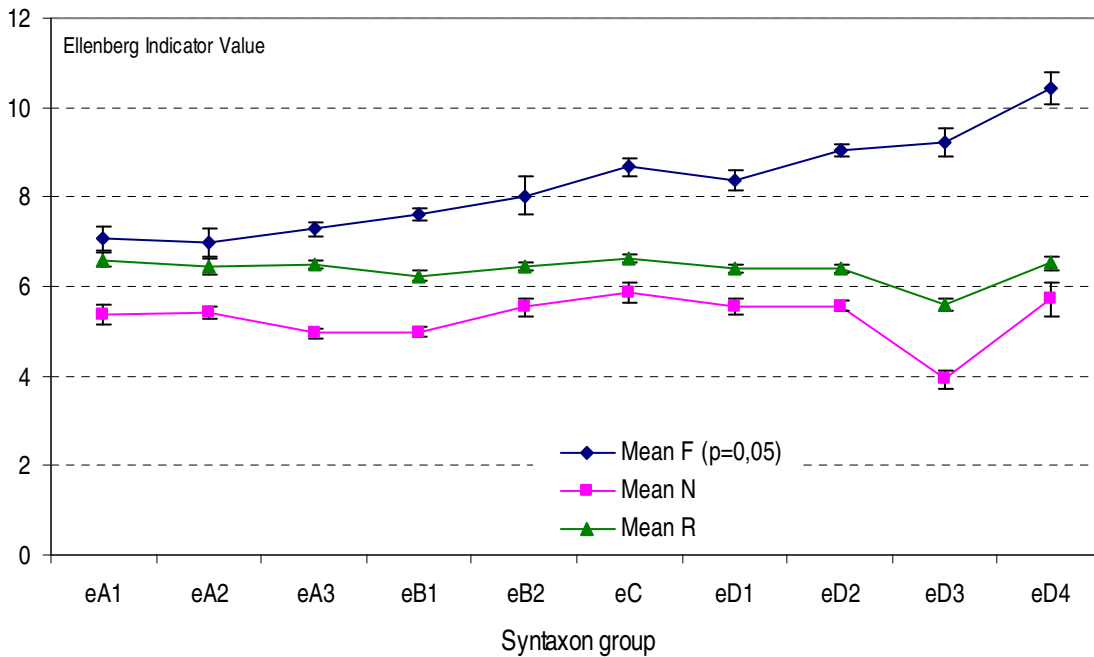


Figure 5. Ellenberg Indicator Values of the meso-eutrophic syntaxon groups.

eD4 group is characterised by the higher moisture value (mean F=10.5) and corresponds to early stage of colonisation of permanent standing water. This group is differentiated by associated aquatic plant species such as *Potamogeton spp.*, *Nymphaea alba*, *Nymphaea lutea*, *Hydrocharis morsus-ranae*...

The eC group is located in the middle of the first ordination axis (fig. 3) and the synoptic table (tabl. 2 and annex 4). All the syntaxa in this group represent reed-beds and sedge-beds from Romania. Each syntaxon is characterised by both aquatic plants and grassland plants. The number of plants per syntaxon is about twice those of all other syntaxa. The explanation hypothesis is that most of the samples had been probably realized on large and non homogeneous area. Each syntaxon had been built on the basis of plant dominance; in consequence such data have been involved in the analyses as a heterogeneous data set, which amplified the species richness by association of grassland and aquatic plant species. For any of these reasons, the C group may be not used as a reference source.

2.2 Oligotrophic habitats

The ordination axis 1 of the CCA (fig. 6), with an eigenvalue of 0.753 (tabl. 3), corresponds, as for meso-eutrophic habitats, to a moisture gradient (fig. 7) with a highly significant correlation of this axis with the F value ($r=-0.929$; $p<0.0001$). The first axis represents also a geographic gradient, running from Northern European oligotrophic habitats to Mediterranean ones. The correlation of this axis with latitude is of $r=-0.644$ ($p<0.0001$). Hence, it appears a correlation between F value and latitude which can be explained by the existence within the Mediterranean group, of habitats with very short hydrophases indicating a low degree of moisture. The second axis with an eigenvalue of 0.345 but less clearly defined, is correlated with the N value. The CCA ordination diagram (fig. 6) and the synoptic matrix summary (tabl. 4) show a clear disjunction between the temperate and North-West plant communities (*Littoreletea uniflorae* Eunis code C3.41) and the Mediterranean plant communities (*Isoetea velatea* Eunis code C3.42).

Table 3. CCA axis eigenvalues and correlations for Oligotrophic habitats.

	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.753	0.453	0.348	0.243	11.759
Correlations					
Longitude	0.171	0.088	0.286	-0.103	
Latitude	-0.644	0.298	-0.188	0.403	
Ellenberg Iv :					
F	-0.929	-0.104	0.061	-0.045	
N	0.530	-0.518	0.431	0.204	
R	0.427	0.073	0.724	0.219	

	long	lat	F	N	R
Longitude	1.000				
Latitude	-0.012	1.000			
Ellenberg Iv :					
F	-0.174	0.585	1.000		
N	0.031	-0.567	-0.470	1.000	
R	0.226	-0.319	-0.418	0.717	1.000

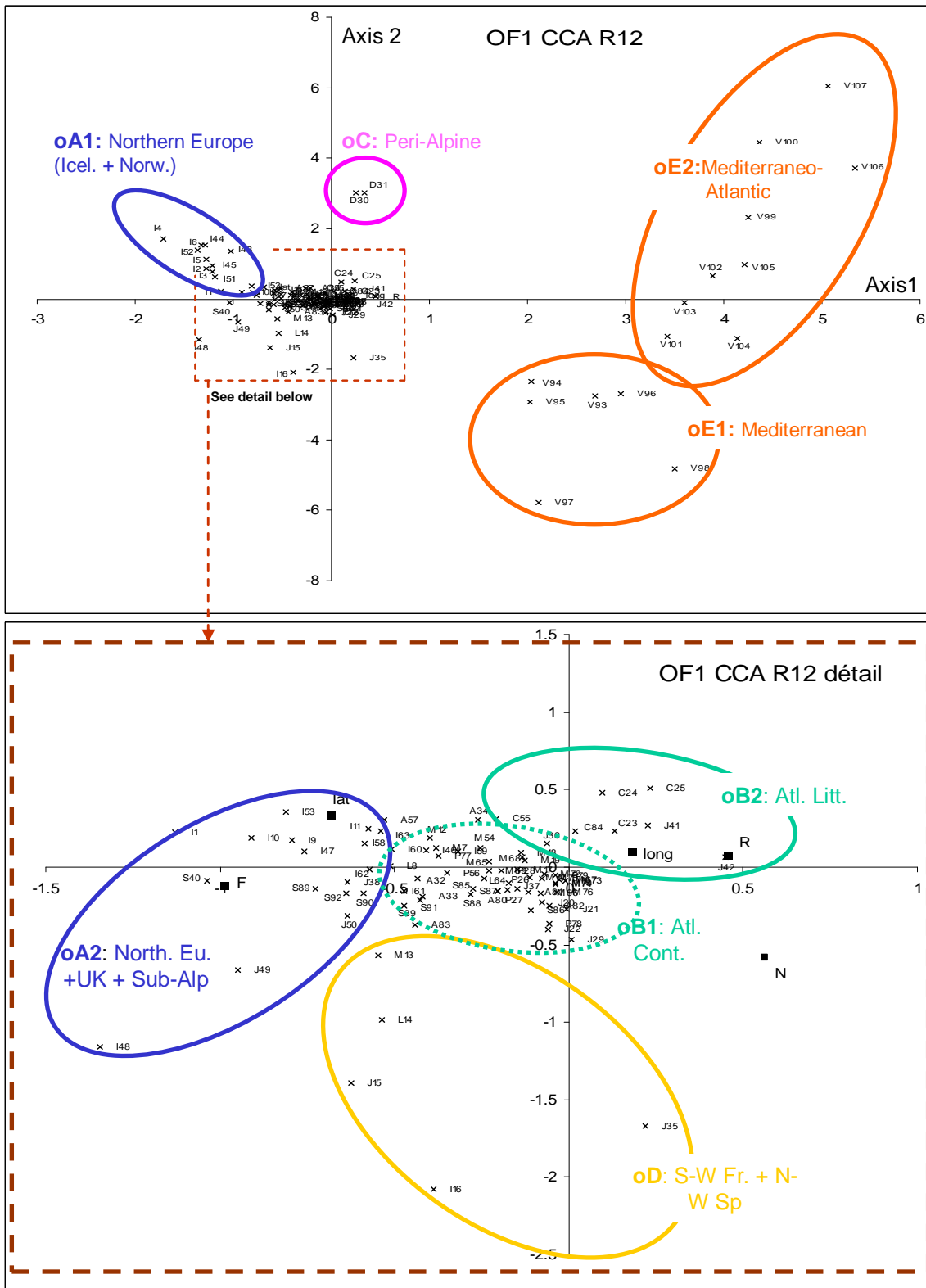
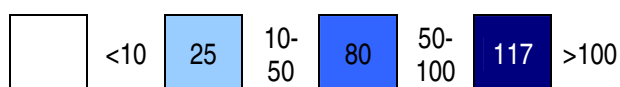


Figure 6. CCA Ordination diagram of the oligotrophic habitats

Table 4. Identified syntaxon groups of oligotrophic habitats (see annex 5 for details)

Syntaxonomical groups	oA1	oA2	oB1	oB2	oC	oD	oE1	oE2	
Ellenberg IVs: Moisture (F)	10.8	10.6	9.8	9.0	9.0	10.2	8.1	5.7	
Productivity (N)	2.6	2.9	3.1	3.6	3.4	4.0	5.1	3.9	
Réaction (R)	5.2	5.1	5.1	5.8	6.5	5.5	5.9	5.7	
Characteristic Species Group									
Isoetes muricata, Subularia aquatica, Ranunculus reptans, Ranunculus hyperboreus	Dark Blue	Light Blue			Dark Blue				
Isoetes setacea, Isoetes lacustris, Isoetes echinospora, Lobelia dortmanna, Sparganium angustifolium, Sparganium minimum, Eriocaulon aquaticum	Dark Blue	Dark Blue	Light Blue				Light Blue		
Carex viridula subsp. viridula, Samolus valerandi, Salix repens, Carex trinervis			Light Blue	Dark Blue	Dark Blue				
Deschampsia cespitosa subsp. littoralis, Myosotis rehsteineri, Juncus alpino-articulatus, Allium schoenoprasum					Dark Blue				
Juncus heterophyllus, Schoenoplectus americanus, Caropsis verticillatundatum, Isoetes boryana, Ranunculus omiophyllus							Dark Blue		
Eryngium galioides, Eryngium corniculatum, Eryngium pusillum, Mentha cervina, Pilularia minuta, Marsilea pubescens								Dark Blue	
Mentha pulegium, Isoetes velata, Isoetes delilei							Dark Blue	Dark Blue	
Ranunculus paludosus, Ophioglossum lusitanicum, Serapias lingua, Isoetes histrix, Isoetes durieui								Dark Blue	
Baldellia ranunculoides, Antinoria agrostidea			Light Blue				Dark Blue		
Littorella uniflora, Juncus bulbosus, Myriophyllum alterniflorum, Eleocharis acicularis, Pilularia globulifera	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue			
Baldellia ranunculoides subsp. repens, Hydrocotyle vulgaris, Apium inundatum, Eleocharis multicaulis, Potamogeton polygonifolius, Eleogiton fluitans, Luronium natans, Hypericum elodes		Light Blue	Dark Blue	Dark Blue	Dark Blue	Light Blue			
Deschampsia setacea, Ranunculus ololeucos, Molinia caerulea, Eriophorum angustifolium, Potentilla palustris, Anagallis tenella, Carex lasiocarpa, Utricularia intermedia, Carex panicea, Carum verticillatum			Light Blue	Light Blue	Light Blue	Light Blue			
Ranunculus flammula, Eleocharis palustris, Glyceria fluitans, Phragmites australis		Light Blue	Light Blue	Dark Blue	Light Blue	Light Blue			
Accidental species					Light Blue		Light Blue		
Eco-climatical zones	Northern Europe (Icel, Norw)	Northern Europe + North: UK + Sub-Alpine	Northern Europe + Continental	Atlantic	Atlantico-litoral	S-W Fr + N-W Sp	Peri-Alpine	Mediterranean	Mediterraneo-Atlantic
EUNIS Codes (see annex 1 for references)	C3.4115	C3.4112, 4114	C3.411, 412, 413	C3.4132	C3.4212 X C3.4112	C3.415	C3.4212	C3.4211	
	C3.4113								

Density of frequency = total species frequency in the group / number of cells (in %)



Only two characteristic plant species of oligotrophic habitats, *Baldellia ranunculoides* and *Antinoria agrostidea* represent the linkage between the two classes. A wide ecological amplitude is also shown by *Eleocharis palustris*, a companion species, both found in oligotrophic and meso-eutrophic habitats. The Mediterraneo-atlantic group oD (S-W France) also indicates the transition between the temperate and the Mediterranean classes.

A synthesis of the synoptic table (annex 5) is given by the table 4, which identifies syntaxon groups of oligotrophic habitats and their link with the EUNIS classification.

Except for the group oB1 which represent a complex of different syntaxa from temperate area, an appropriate relationship is shown (Figures 6 and 7 and table 4) between syntaxon groups (oA1 to oE2) and their geographical location. The ordination of the oB1 syntaxon (table 4) is more or less linked with a hydrological gradient, the wetter on the left (Physiognomic plant assemblage 'S' with *Sparganium minimum*) to the wettest on the right (Physiognomic plant assemblage 'M' with *Eleocharis multicaulis*) (see annex 5).

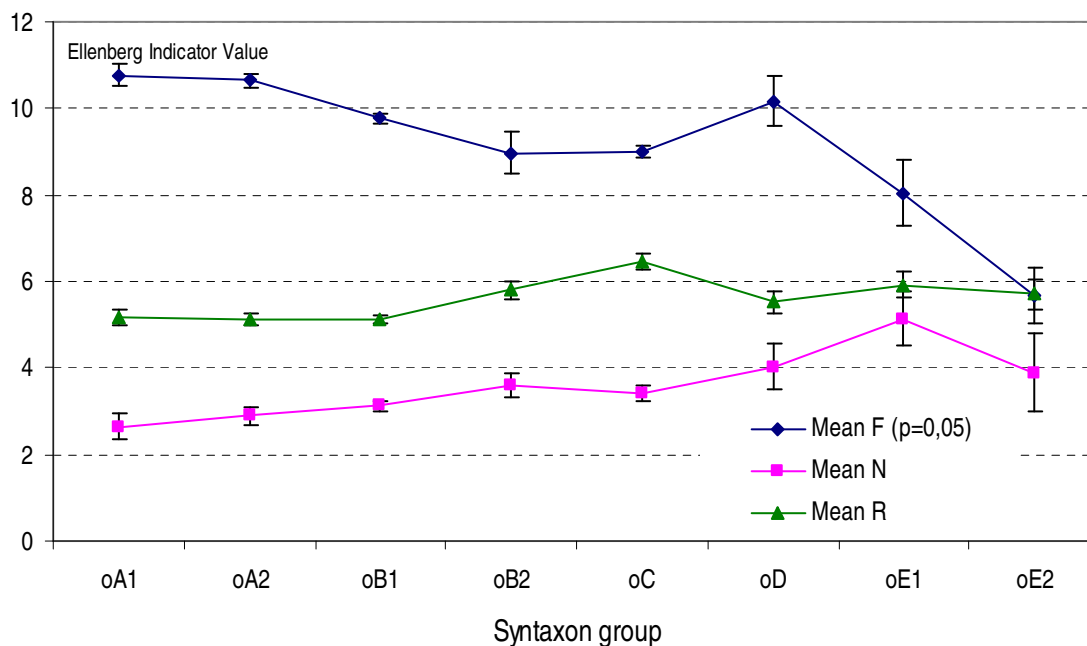


Figure 7. Ellenberg Indicator Values of the oligotrophic syntaxon groups.

3 Discussion

Hydrological factor is the main ecological driver which control plant responses in wetlands (Clément & Proctor, 2006). To minimize this huge factor, we chose to limit the data analysis, at the present stage, to palustrian wetlands as a reduced part of the hydrological gradient. Nevertheless,

moisture was the main factor in controlling ordination of plant communities in the analyses both in meso-eutrophic and oligotrophic habitats. As predictive assumption, such responses show clearly that palustrian vegetation and therefore palustrian habitats would be highly sensitive to hydrodynamic variations due to both direct (hydrophase variation) or indirect (hydromorphological change) effects of climate changes.

About other factors, data analyses shown a clearly major differences between meso-eutrophic and oligotrophic habitats.

Comparison of the respective CCA ordination diagrams (tabl. 2, 4 and fig. 3, 6) shown:

- § firstly that syntaxon groups of oligotrophic habitats are well discriminated and corresponding to different geographical locations while meso-eutrophic syntaxa shown fuzzy ordination groups.
- § secondly that latitude appears as the second factor in the distribution of the oligotrophic syntaxa while fertility (N values) and reaction (R values) are the second drivers in the meso-eutrophic data set.

Comparison of the synoptic tables (tabl. 2 and 4) reinforces this observation. The relative heterogeneity shown in the oligotrophic plant communities (tabl.4) could be explained by the clear distinction between each syntaxon group. This distinction is supported by characteristic plant species defining each group. The relative homogeneity of the table 2 of meso-eutrophic plant communities could be associated with the large assemblage of companion plant species, which belong to most syntaxon groups. The variability is mainly due to associated species (e.g. grassland plant species in eA and eB groups, and aquatic plant species in eD groups).

In conclusion, the widespread geographical distribution of plant species, and plant assemblages of the meso-eutrophic habitats in comparison with to the restricted distribution of most plant species and plant assemblages of oligotrophic habitats suggests that the ecological drivers, and then sensitivity to environmental change would be significantly different.

One can predict that meso-eutrophic wetland habitats that show a fertility value $N > 5$ would not be affected by eutrophication process in relation with climate change and/or land-use change; for instance, Typha beds (EUNIS code C3.23) were found either in northern temperate and Mediterranean regions. Such habitat is considered as the most fertile and the most productive and then it is always associated with eutrophic conditions. This does not mean that all reed or sedge beds respond in the same way; e.g. *Phragmites australis* beds, in spite of its known eutrophy, show a greater variation along the trophic gradient regarding other factors or characteristics.

Oligotrophic habitats (fertility, $N < 4$) would be highly sensitive to climate change at a regional scale, both in terms of temperature increase, and of hydrological change. They would be also highly affected by increasing fertility in the palustrian wetlands in relation with eutrophication processes. This ecological process is linked with increase of temperature in shallow water and increase of fertilising in surrounding areas of aquatic systems. These results confirm the hypotheses

mentioned by Dierssen (1983), considering the loss of *Littorelletea* communities in most European temperate areas

In Mediterranean areas, climate change will be reinforced by the risk of hydrological change, and reduction of the hydrophase in such amphiphytic oligotrophic habitat types.

Littorelletea and *Isoetetea* communities are characterised by small perennial limnophytic and amphiphytic plants, growing in the littoral (eulitoral to infralitoral) of oligotrophic to slightly mesotrophic tarns, lakes and pools, often surrounded by acid heathlands, swamps or mire communities.

The characteristic species have a low competitive ability and the communities are elements of the most endangered ecosystems.

The water table normally shows characteristic changes between the hydrophase and the terrestrial phase during parts of the vegetation period. Productivity is low because of the low concentration of nutrients. A long hydrophase and anaerobic conditions in the sediment might promote the availability of phosphorus and in this way an slight eutrophication. A long terrestrial phase and aerobic conditions results in the higher availability of nitrogen and in a sulfide oxidation. A slight eutrophication is, in most cases, greatly accelerated by artificial eutrophication processes.

A dystrophisation happens mainly in smaller pools, surrounded of acid heathlands and mires.

Isoetid growth forms disappear as soon as pressure of more competitive species, reed swamp species i. e., as well as bentic algae, mud accumulation occurring during eutrophication, and by overgrowing of *Sphagnum* species in dystrophic sites (*Isoetion* and *Lobelion*).

In the three other alliances, helophytic or amphiphytic species predominate but the more productive helophytes (reeds and/or sedges) occupy to some extent the same ecological niche on mesotrophic sites and may succeed in the course of eutrophication through higher competitive ability of meso-eutrophic species.

At the European scale, distinction between meso-eutrophic habitats and oligotrophic ones were done according to their sensitivity to climate characteristics and nutrient availability.

Nevertheless, a hypothesis could be tested in an European area in which the transition between the two systems could be observed. The South-West of Europe offers this opportunity.

Both, the shift of characteristic species and, in contrast, the invariable species could be used for modelling. Invariable or companion species between two habitat types justify the link between the two different systems.

Figure 8 represents a model built according to comparisons between those systems, on the basis, both of phytosociological and EUNIS classifications. Homologous habitat types exist in Mediterranean area (Southern France and Spain and temperate area N-W Spain and S-W France). Two main ecological gradients explain the link between the four habitats types. Notice

that in EUNIS structure, only one type (C3.24A, Common Spikerush beds) represent the two vicariant alliance categories in the high trophic level. Only one species (Common Spikerush: *Eleocharis palustris*) is a constant species belonging to the four different habitat types with different frequency and abundance.

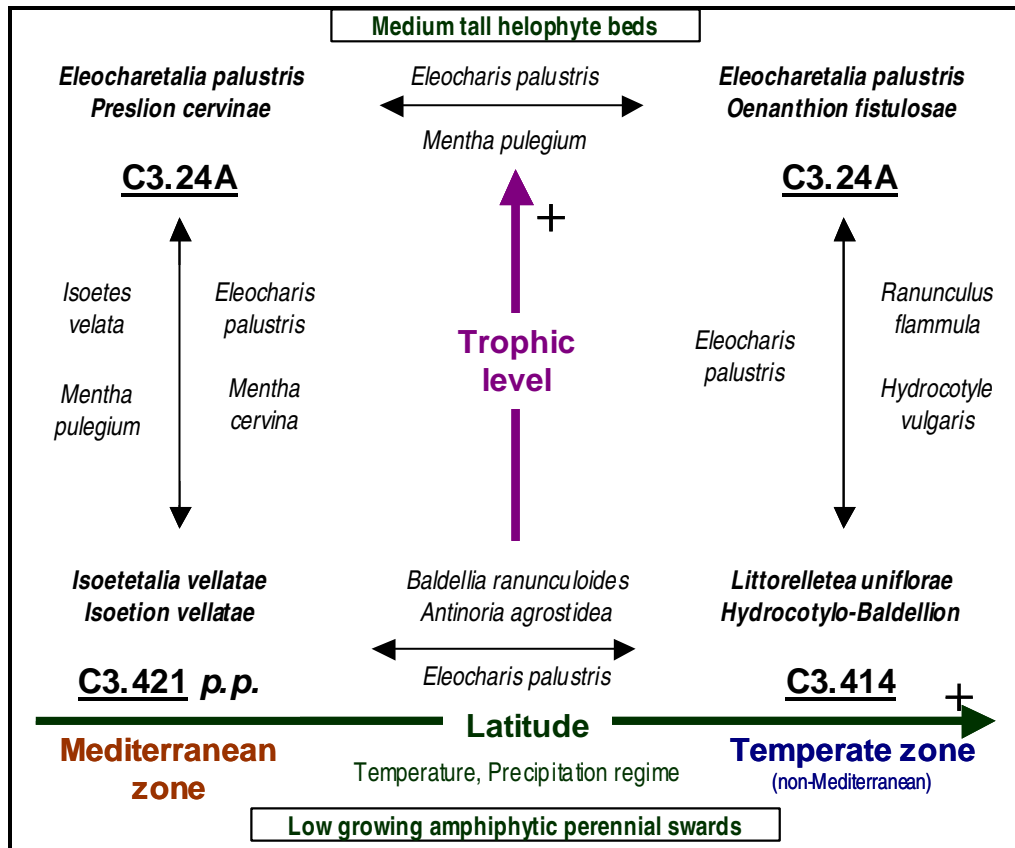


Figure 8. Model specification of potential shift in palustrian habitat types in response to climate and nutrient availability changes.

Underlined: EUNIS habitat codes

Species between the main habitats are their common invariable or companion species

A temperature increase might induce a shift from temperate or Atlantic oligotrophic habitat types towards eu-Mediterranean habitat types (oligo- or meso-eutrophic).

Increasing nutrient availability, as an indirect consequence of increasing temperature, might induce a shift from oligotrophic habitat types (either temperate or Mediterranean) to mesotrophic habitat types (temperate or Mediterranean), without change in hydrological functioning.

In case of hydrological change, other shifts are likely to occur (fig. 9). Longer standing water or reduction of water level balance might cause development and growth of reed beds (C3.21). By contrast, reducing standing water or increasing terrestrial phase might cause the substitution of perennial beds or swards by annual plant communities: dwarf annual swards of the *Nano-Juncetea bufonii* [EUNIS code C3.51] in oligotrophic systems and tall annual non-graminoid communities of the *Bidentetea tripartitae* [EUNIS code C3.52] in meso-eutrophic systems, within periodically inundated shores [C3.5]. This hypothesis needs to be validated later by empirical analyses.

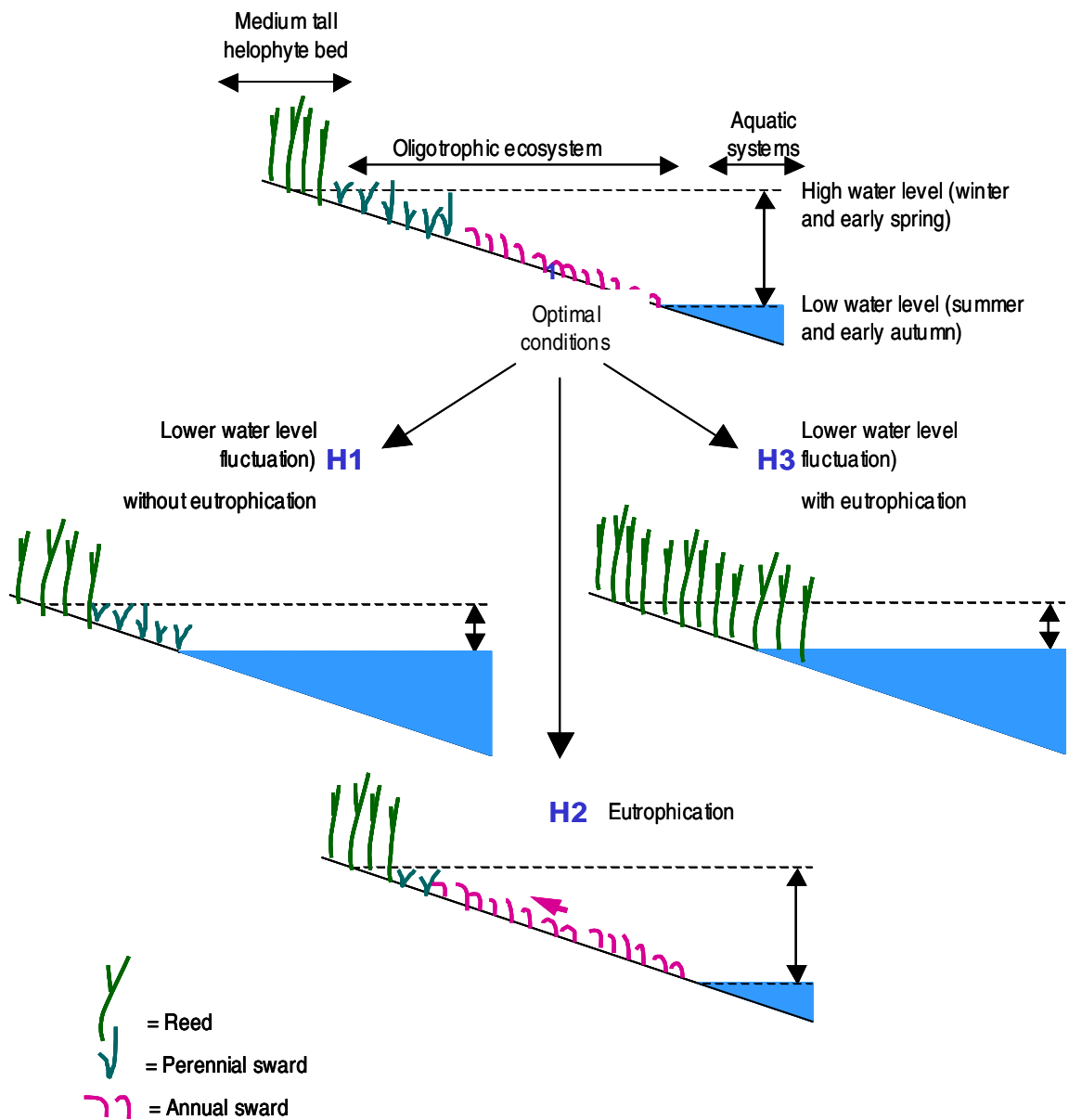


Figure 9. Ecological trend hypotheses in palustrine system dynamics in response to hydrological or/and trophic changes.

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Annex 1

Part 1: EUNIS habitats referring to wetlands (levels 1 & 2)

EUNIS habitats

- A – Marine habitats | out of Eurolimpacs
- B - Coastal habitats
- C – Inland surface water habitats
 - C₁ – Surface standing waters | partly wetlands
 - C₂ – Surface running waters
 - C₃ - Littoral zone of inland surface waterbodies (e.g. [Freshwater *Phragmites* beds](#), EUNIS code C3.2111 or [Common spikerush beds](#), EUNIS code C3..24A)
- D – Mire, bog and fen habitats
 - D₁ – Raised and blanket bogs
 - D₂ – Valley mires, poor fens and transition mires
 - D₃ – Aapa, palsa and polygon mires
 - D₄ – Base-rich fens and calcareous spring mires
 - D₅ – Sedge and reedbeds, normally without free-standing water (e.g. [Dry Freshwater *Phragmites* beds](#), EUNIS code D5.111)
 - D₆ – Inland saline and brackish marshes and reedbeds
- E – Grassland and tall forb habitat
 - E₃ – Seasonally wet and wet grasslands
 - E₅ – Woodland fringes and clearings and tall forb stands
 - E₆ – Inland saline and herb-dominated habitats
- F – Heathland, scrub and tundra habitats
 - F₁ – Tundra
 - F₄ – Temperate shrub heathland
 - F₉ – Riverine and fen scrubs
- G – woodland, forest and other wooded land
 - G₁ – Broadleaved deciduous woodland
 - G₃ – Coniferous woodland

G₄ – Mixed deciduous and coniferous woodland
Part 2: EUNIS habitats involved in deliverable 51

C – Inland surface water habitats

C₃ - Littoral zone of inland surface waterbodies

C_{3.2} – Water-fringing reedbeds and tall helophytes other than canes

C_{3.21} – [Phragmites australis] beds

C_{3.211} – Flooded [Phragmites] beds

C_{3.22} – [Scirpus lacustris] beds

C_{3.23} – [Typha] beds

C_{3.231} – [Typha latifolia] beds

C_{3.232} – [Typha angustifolia] beds

C_{3.24} – Medium-tall non-graminoid waterside communities

C_{3.241} – Arrowhead communities

C_{3.242} – Neglected bur-reed communities

C_{3.243} – Erect bur-reed communities

C_{3.244} – Sweet flag communities

C_{3.245} – Flowering rush communities

C_{3.246} – Dropwort-great yellowcress communities

C_{3.247} – Water horsetail beds

C_{3.248} – Water parsnip communities

C_{3.249} – Maretail beds

C_{3.24A} – Common spikerush beds

C_{3.24B} – Iris beds

C_{3.25} – Water-fringe medium tall grass beds

C_{3.251} – Sweetgrass beds

C_{3.252} – Eurasian [Leersia] beds

C_{3.253} – Eurasian [Scolochloa] beds

C_{3.254} – Water-fringe [Calamagrostis] beds

C_{3.26} – [Phalaris arundinacea] beds

C_{3.28} – Riparian [Cladium mariscus] beds

C_{3.4} – Species-poor beds of low-growing water-fringing or amphibious vegetation

C_{3.41} – Euro-Siberian perennial amphibious communities

C_{3.411} – Shoreweed lawns, lobelia ponds, quillwort swards

C_{3.4111} – Shoreweed lawns

C_{3.4112} – Lobelia ponds

C_{3.4113} – Euro-Siberian quillwort swards

C_{3.4114} – Floated bur-reed communities

C_{3.4115} – Boreo-Arctic lake mud communities

- C_{3.4116} – [Myriophyllum alterniflorum] communities
- C_{3.412} – Spike-rush shallow-water swards
- C_{3.413} – Acid pool fringe shallow-water swards
 - C_{3.4131} – [Eleocharis multicaulis] communities
 - C_{3.4132} – Dune slack shoreweed swards
 - C_{3.4133} – [Pilularia] swards
 - C_{3.4134} – [Juncus bulbosus] communities
 - C_{3.4135} – [Scirpus fluitans] communities
 - C_{3.4136} – [Apium inundatum] communities
- C_{3.414} – [Baldellia] shore swards
- C_{3.415} – Shore hairgrass swards
- C_{3.42} – Mediterranean-Atlantic amphibious communities
 - C_{3.421} – Short Mediterranean amphibious communities
 - C_{3.4211} – Terrestrial quillwort swards
 - C_{3.4212} – Mediterranean aquatic quillwort swards

D – Mire, bog and fen habitats

- D₅ – Sedge and reedbeds, normally without free-standing water
 - D_{5.1} – Reedbeds normally without free-standing water
 - D_{5.11} – [Phragmites australis] beds normally without free-standing water
 - D_{5.111} – Dry freshwater [Phragmites] beds
 - D_{5.12} – [Scirpus lacustris] beds normally without free-standing water
 - D_{5.13} – [Typha] beds normally without free-standing water
 - D_{5.131} – [Typha latifolia] beds normally without free-standing water
 - D_{5.132} – [Typha angustifolia] beds normally without free-standing water
 - D_{5.2} – Beds of large sedges normally without free-standing water
 - D_{5.21} – Beds of large [Carex] ssp.
 - D_{5.211} – Brown sedge beds
 - D_{5.212} – Slender tufted sedge beds and related communities
 - D_{5.2121} – Slender tufted sedge beds
 - D_{5.2122} – Lesser pond sedge beds
 - D_{5.2123} – Inn sedge beds
 - D_{5.2124} – Banat sedge beds
 - D_{5.2125} – Water sedge beds
 - D_{5.2126} – Brotero sedge beds
 - D_{5.2127} – [Carex melanostachya] beds
 - D_{5.2128} – [Carex hispida] beds

- D_{5.213} – Greater pond sedge beds
- D_{5.214} – Bottle, bladder and slender sedge beds
 - D_{5.214 1} – Bottle sedge beds
 - D_{5.214 2} – Bladder sedge beds
 - D_{5.214 3} – Slender sedge beds
- D_{5.215} – Tufted sedge and sward sedge tussocks
 - D_{5.2151} – Tufted sedge tussocks
 - D_{5.2152} – Sward sedge tussocks
- D_{5.216} – Greater tussock sedge tussocks
- D_{5.217} – Smaller tussock sedge tussocks
- D_{5.218} – Cyperus sedge tussocks
- D_{5.219} – Fox sedge tussocks
 - D_{5.2191} – True fox sedge tussocks
 - D_{5.2192} – False fox sedge tussocks

Annex 2

Phytosociological hierarchical classification of palustrian vegetation in Europe

- Class *Phragmiti australis* – *Magnocaricetea elatae* (**Reed and large Sedge beds**)
 - o Order *Phragmitetalia australis* (**Reed beds**)
 - § Alliance *Phragmition communis*
 - § Alliance *Oenanthion aquaticae*
 - § Alliance *Phalaridion arundinaceae*
 - o Order *Magnocaricetalia elatae* (**large Sedge beds**)
 - § Alliance *Magnocaricion elatae*
 - § Alliance *Caricion gracilis*
- Class *Agrostietea stoloniferae* p.p. (**Spikerush beds**)
 - o Order *Eleocharitetalia palustris* (**Spikerush beds**)
 - § Alliance *Oenanthion fistulosae*
 - § Alliance *Cnidion venosi* p.p.
 - § Alliance *Preslion cervinae*
 - § Alliance *Beckmannion eruciformis*
- Class *Littorelletea uniflorae* (**non-Mediterranean low growing amphiphytic vegetation**)
 - o Order *Littorelletalia uniflorae*
 - § Alliance *Littorellion uniflorae*
 - § Alliance *Lobelion dortmannae*
 - § Alliance *Elodo palustris*-*Sparganion* (syn *Hydrocotylo-Baldellion*)
 - § Alliance *Eleocharition acicularis*
 - § Alliance *Deschampsion littoralis*
 - §
- Class *Isoetetea velatae* p.p. syn. *Isoeto-Nano-Juncetea buffonii* p.p. (**Mediterranean low growing amphiphytic vegetation**)
 - o Order *Isoetetalia vellatae*.(syn *Isoetetalia durieui*)
 - § Alliance *Antinorio agrostidae* – *Isoetion velatae* (syn. *Isoetion* p.p.)
 - § Alliance *Ophioglossa lusitanici* – *Isoetion histricis* (syn. *Isoetion* p.p.)
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Annex 3

Biogeographical regions in Europe

