

A phytosociological classification of Swiss mire vegetation

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Abstract The mapping and monitoring of Swiss mires has so far relied on a classification system based on expert judgement, which was not supported by a quantitative vegetation analysis and which did not include all wetland vegetation types described in the country. Based on a spatially representative sample of 17,608 relevés from 112 Swiss mires, we address the following questions: (1) How abundant are wetland vegetation types (phytosociological alliances) in Swiss mires? (2) How are they distributed across the country—is there a regional pattern? (3) How clearly are they separated from each other? (4) How clear and reliable is their ecological interpretation? Using published wetland vegetation relevés and lists of diagnostic species for phytosociological units (associations and alliances) established by experts, we developed a numerical method for assigning relevés to units through the calculation of similarity indices. We applied this method to our sample of 17,608 relevés and estimated the total area covered by each vegetation type in Switzerland. We found that vegetation types not included in previous mapping were either rare in Switzerland (partly due to mire drainage) or poorly distinguished from other vegetation units. In an ordination, the Swiss mire vegetation formed a triangular gradient system with the *Sphagnion medii*, the *Caricion davallianae* and the *Phragmition australis* as extreme types. Phytosociological alliances were clearly

separated in a subset of 2,265 relevés, which had a strong similarity to one particular association, but poorly separated across all relevés, of which many could not be unequivocally assigned to one association. However, ecological gradients were reflected equally well by the vegetation types in either case. Overall, phytosociological alliances distinguished until now proved suitable schemes to describe and interpret vegetation gradients. Nevertheless, we see the urgent need to establish a data base of Swiss wetland relevés for a more reliable definition of some vegetation units.

Keywords Numerical allocation · Ordination · Similarity · Transformation · Regional distribution

Zusammenfassung Kartierung und Monitoring der Schweizer Moore beruhten bislang auf expertenbasierten Klassifikationssystemen, welche nicht durch quantitative Vegetationsanalysen abgestützt waren und nicht alle im Land beschriebenen Vegetationstypen für Feuchtgebiete umfassten. Basierend auf einer repräsentativen Stichprobe von 17608 Relevés aus 123 Mooren stellen wir folgende Fragen: (1) Wie häufig sind die Vegetationstypen der Feuchtgebiete (pflanzensoziologische Verbände) in den Schweizer Mooren? (2) Wie sind sie über das Land verteilt – gibt es ein regionales Muster? (3) Wie gut sind sie voneinander unterschieden? (4) Wie klar und verlässlich ist ihre ökologische Interpretation? Wir entwickelten eine numerische Methode um Relevés durch die Berechnung von Ähnlichkeitsindizes pflanzensoziologischen Einheiten zuweisen zu können. Als Trainingsdaten verwendeten wir publizierte Feuchtgebietsrelevés und als Referenzdaten Listen diagnostischer Arten der pflanzensoziologischen Einheiten (Assoziationen und Verbände). Wir wandten diese Methode auf unsere Stichprobe von 17,608

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Relevés an und schätzten die Gesamtfläche von jedem Vegetationstyp. Wir fanden, dass die in früheren Übersichtsdarstellungen nicht berücksichtigte Vegetationstypen entweder selten waren (z.T. wegen alten Drainagen selten geworden) oder nicht gut von den anderen Typen unterscheidbar. In einer Ordination bildet die Vegetation der Schweizermoore ein dreieckiges Gradientensystem mit *Sphagnion medii*, *Caricion davallianae* und *Phragmition communis* als Extremtypen. In einer Teilstichprobe von 2265 Relevés mit hohem Ähnlichkeitsindex zu einer bestimmten Assoziation konnten die Verbände gut separiert werden. In einer Zufallsstichprobe derselben Grössen gelang dies nicht mehr so gut weil die Zuweisung mancher Relevés zu einer Assoziation nicht mehr so eindeutig war. Die ökologischen Gradienten wurden jedoch in beiden Fällen gleich gut abgebildet. Insgesamt erwiesen sich die bis jetzt unterschiedenen pflanzensoziologischen Verbände als gut geeignet, um die Vegetationsgradienten zu beschreiben und zu interpretieren. Trotzdem sehen wir für die verlässlichere Abgrenzung einiger Vegetationseinheiten dringenden Bedarf für eine Datenbank schweizerischer Feuchtgebietsrelevés.

Introduction

Vegetation maps representing the spatial distribution and extent of vegetation types are an essential tool in nature conservation. They are used to plan conservation measures as well as to monitor vegetation changes over time. The establishment of such maps requires a uniform and reliable classification system for the definition and identification of vegetation types (Bruehlheide and Chytrý 2000). The phytosociological system has been widely used for this purpose. However, the system has limitations, partly due to being based on local data sets, collected without statistical considerations and interpreted according to expert opinion. Having recognized these limitations, vegetation scientists in many countries presently try to revise and improve the traditional system based on the numerical analysis of large vegetation data sets.

The mire vegetation of Switzerland has been mapped as part of the establishment of national inventories of fens and bogs using a simplified phytosociological classification scheme (Grünig et al. 1986; Broggi 1990). This system distinguishes the most frequent vegetation types at the level of phytosociological alliances. A similar classification was used in the comprehensive overview of Swiss habitats (Delarze et al. 1999). These widely applied classification schemes are, however, not based on a quantitative analysis of vegetation data, nor do they include all wetland vegetation types described in more detailed phytosociological

studies of Swiss wetlands (Pantke 2003). Thus, it is possible that regionally important vegetation types were not included or that important ecological gradients are insufficiently represented.

The opportunity to revise the present classification system emerged from the collection of a large data set for a long-term mire monitoring program (Klaus 2007). These data, intended to represent the initial state for monitoring fens and mires, were collected in the form of a stratified random sample of vegetation relevés encompassing all plant species recorded in the field. They provide an unbiased, representative sample of the fens and mires of Switzerland. Hence, the following questions can be answered by statistical inference: (1) How abundant are wetland vegetation types (phytosociological alliances) in Swiss mires? (2) How are they distributed across the country—is there a regional pattern? (3) How clearly are they separated from each other? (4) How clear and reliable is their ecological interpretation?

Vegetation can be classified in numerous ways. The phytosociological system, developed since the 1920s based on vegetation surveys and classification efforts of many authors, provides a coherent classification system that has been applied in large parts of the world. However, given its heterogeneous origin, it does not provide clear rules for the assignment of vegetation relevés to vegetation types. Although specific rules for classification have been given (Mueller-Dombois and Ellenberg 1974), the outcome always reflects the preference of individual experts. To avoid this subjectivity in our revision of the Swiss mire classification, we wished to use rules that lead to a unique and reproducible solution while being as close as possible to the traditional expert system.

Nowadays most numerical approaches aimed at assigning relevés to predefined vegetation types replace the constancy classes of early phytosociologists by statistically derived resemblance indices. For example Hill (1989) uses an association table to derive an index considering the species composition as well as the dominance and the dominance constancy of a species within a vegetation unit. Bruehlheide (1995, 1997) in his “cocktail classification” proposes an iterative procedure by which species groups with high fidelity index u decide on the membership of relevés to the phytosociological units. Similarly, Tichý (2005) proposes a so-called frequency-positive index for species to any potential vegetation unit and van Tongeren et al. (2008) suggest using their “composite index.” Alternatively, Černa and Chytrý (2005) rely on a neural network for the allocation. We could not apply these procedures because they require comprehensive vegetation databases not available for wetlands in Switzerland. We therefore developed an assignment procedure based on standard resemblance measures between vegetation relevés

and a database of phytosociological units available for Switzerland.

In this paper, we first present the methodic development of the assignment procedure, i.e. the choice of data transformations and resemblance measures. We then apply the method to classify the Swiss mire vegetation. The resulting classification is then used to study the spatial extent and distribution of vegetation types as well as ecological gradients.

Definitions and data sets

Phytosociological system

As reference data set to classify the relevés we used the database “Pflanzengesellschaften der Schweiz” (Pantke 2003). This provides a syntaxonomic system of the entire Swiss vegetation. The database consists of species lists for all 654 associations included, the 160 alliances, 82 orders and 52 classes. The lists are derived from a variety of published classified relevés. The species are labelled according to their diagnostic type (Scott 1996), i.e., whether a species is a companion, a differential species, a species with high constancy, a character species, etc. Pantke included all species with minimum constancy of 20% into the definition of a given syntaxon. We removed all species of algae and lichens because these are not included in our data set. In Pantke’s database 13 associations are assigned to classes only, but neither to alliances nor orders. For these we completed the database by assigning them to the most similar alliance. As a result 143 alliances with 652 associations remained in the reference data set.

There are various definitions of mires and mire types (Steiner 1992; Hájek et al. 2006). For the present study we refer to the definition of the Swiss National Inventory of Fens listing the phytosociological types of mires (Broggi 1990). We included some more found in Pantke (2003) for our analyses. These mainly concern degraded mire vegetation. Finally we defined 21 alliances with 113 associations as mire vegetation and three alliances with eight associations as closely related vegetation types (Table 2).

Ecologically, mires can be subdivided into three types of ecosystems: Bogs (ombrotrophic ecosystem), fens (groundwater saturated ecosystem, systems having the potential to produce peat) and wet grassland (groundwater saturated ecosystems, usually not producing peat). We subdivided the alliances according to this distinction in our data analysis (Table 3).

Training data sets

In order to evaluate the best method for assigning relevés in the way the experts do it, we built a first training data set of

709 published, classified relevés taken from Klötzli (1969), León (1968) and from Dietl and Jorquera (2003). 18 relevés had to be excluded from the set because their phytosociological assignment was not specified in Pantke’s system. The phytosociological belonging of 691 relevés could be identified as associations sensu Pantke (2003). The authors considered their relevés belonging to 53 associations and 22 alliances respectively encompassing aquatic vegetation, riverine vegetation, bogs, fens, meadows, pastures and woodland of the colline, montane and subalpine belts. Eight alliances are represented by more than ten relevés, seven alliances are represented by seven to nine relevés and seven alliances are represented by one or two relevés only.

The second training data set was taken from the database “Österreichischer Moorschutzkatalog” (Steiner 1992). Steiner found 32 associations in 4,450 relevés. Some of these associations do not occur in Switzerland, or their definitions do not conform to Pantke’s system. 2,772 relevés could finally be assigned to 26 associations and 9 alliances, respectively, of Pantke’s (2003) system.

Data of the mire monitoring programme

Our mire vegetation data originate from the first survey of the Swiss mire monitoring programme (Klaus 2007). A stratified random sample of 125 sites was drawn from the total of 1,718 mire sites of national importance (BUWAL 1991, 1994). Stratification accords to the geographical regions, the altitudinal belts, the mire types (bog or fen and wet grassland) and the area of the sites (Grünig et al. 2005). For the present study, the data of 112 mire sites could be analysed.

The sampling design used a stratification based on remote sensing. Of each mire site an aerial colour infrared photograph was taken and interpreted using a stereoscope. Homogeneous patches in terms of colour and texture were delineated. The median of the area of the resulting patches was 212.6 m² (5% quantile = 49 m², 95% quantile = 1,506 m²). The patches were grouped by colour and texture. The number of groups was 1/3 of the number of relevés to be taken. To monitor the vegetation of a site, a random sample of patches was drawn so that all of the colour and structure groups would be represented. Patches adjacent to the mire were included to be able to identify the transitions from mire to non-mire vegetation statistically (and vice versa).

The vegetation of any site is described by about 130 relevés on average (18 for the smallest object; 935 for the largest object). A relevé is a comprehensive list of vascular plant species and bryophytes. The species cover is estimated on a 4-step logarithmic scale (1: $\leq 0.1\%$, 2: $\leq 1.0\%$, 3: $\leq 10\%$, 4: $\leq 100\%$). The entire data set of the 112 sites includes 17,608 relevés.

Methods

Assignment procedure

Relevés from both training sets were assigned to the vegetation associations and alliances of Pantke (2003) based on the comparison of species lists (relevés versus lists of diagnostic species) using similarity indices. Each relevé was given the membership of the unit to which it had the highest similarity value.

Before the calculation of similarity indices, data in species lists can be transformed in various ways to obtain scores that will be used in the calculations. Transformations determine how much weight is given to dominant species relative to subordinate species in the relevés, or how much weight is given to species with strong diagnostic value relative to species with weaker diagnostic value in the phytosociological system. We compared all combinations of various transformations for both lists (Table 1).

The similarity measures tested were the product moment (Pearson) correlation coefficient, Ochiai's index and van der Maarel's similarity index. The main difference between these indices is that correlation coefficients, being based on differences between species scores and mean species scores, give a similar importance to joint presences and joint absences in the two species lists being compared. In contrast, Ochiai index and van der Maarel's similarity index only take into account species that are present in at least one of the two lists and ignore joint absences (see Wildi and Orłóci 1996 for the exact definitions).

Results showed that the fit between numerical and expert assignment varies but slightly among procedures. The transformation $x' = \log(x + 10)^{2.5}$ for the relevés and for the list of diagnostic species yielded on average the best agreement (Table 1). In combination with this transformation, the product moment correlation coefficient performed slightly better than the alternatives (Table 2): the matching ratio of the numerical classification with the expert-based

Table 1 Weights ($x = \text{cover } \%$ or $x = \text{diagnostic value}$) initially attributed to species, and transformations applied to these weights to obtain species scores for the calculation of similarity indices. The last two rows indicate the overall hit rate (% of correct assignments to

associations) obtained with a transformation in the Swiss (CH) and Austrian (A) training data set and using correlation coefficient as similarity index

	Initial weight	$\log(x + 10)^3$	$\log(x + 10)^{2.5}$	$\ln(x + e)$	$\log(x + 10)^2$	$\log(x + 10)^{1.5}$	$\log(x + 10)$	Sign
Cover code mire monitoring data								
Absent	0	0	0	0	0.00	0.00	0	0
1	0.0316	1	1	1.01	1.00	1.00	1	1
2	0.316	1.04	1.03	1.11	1.03	1.02	1.01	1
3	3.16	1.4	1.33	1.77	1.25	1.18	1.12	1
4	31.6	4.25	3.34	3.54	2.62	2.06	1.62	1
Cover code Braun-Blanquet (training data)								
Absent	0	0	0	0	0.00	0.00	0	0
<i>r</i>	0.02	1	1	1.01	1.00	1.00	1	1
+	0.21	1.03	1.02	1.07	1.02	1.01	1.01	1
1	1.5	1.19	1.16	1.44	1.13	1.09	1.06	1
2	10	2.2	1.93	2.54	1.69	1.48	1.3	1
3	31	4.19	3.3	3.52	2.60	2.05	1.61	1
4	56	6.02	4.47	4.07	3.31	2.45	1.82	1
5	87.5	7.84	5.56	4.5	3.96	2.81	1.99	1
Diagnostic type according Pantke								
No diagnostic value	0	0	0	0	0.00	0.00	0	0
Regional character spec.	2	1.26	1.21	1.55	1.16	1.12	1.08	1
Denoting species ^a	4	1.51	1.41	1.9	1.31	1.23	1.15	1
Companion species	8	1.98	1.77	2.37	1.58	1.41	1.26	1
High constancy spec.	16	2.83	2.38	2.93	2.00	1.68	1.41	1
Differential species	32	4.28	3.36	3.55	2.63	2.07	1.62	1
Character species	64	6.53	4.78	4.2	3.49	2.56	1.87	1
Hit rates (CH)	0.326	0.494	0.495	0.475	0.491	0.501	0.465	0.427
Hit rates (A)	0.393	0.426	0.417	0.357	0.401	0.360	0.319	0.259

^a In German: "kennzeichnende Arten" (Pantke 2003). Species which are useful for diagnostic purpose only as a group

Table 2 Quality of numerical assignments: The left part of the table describes the hit rates of the Swiss (CH) and Austrian (A) training data sets when different similarity measures are used. The right part of the table describes the coherence of the resulting groups of the

Swiss monitoring data when different similarity measures are used. The internal correlation is the Pearson's product moment of the relevés assigned to one alliance. Data transformation is $\log(x + 10)^{2.5}$

	Hit rates						Internal correlations		
	<i>r</i> CH	<i>r</i> A	och CH	och A	vdm CH	vdm A	<i>r</i>	och	vdm
<i>Sphagnion medii</i>	–	0.730	–	0.728	–	0.684	0.350	0.372	0.371
<i>Oxycocco-Empetrium hermaph</i>	–	0.571	–	0.571	–	0.524	0.294	0.300	0.306
<i>Rynchosporion albae</i>	0.703	0.870	0.676	0.867	0.676	0.822	0.254	0.209	0.210
<i>Caricion lasiocarpae</i>	0.939	0.833	0.970	0.586	0.850	0.750	0.209	0.187	0.180
<i>Scorpidio-Utricularion minoris</i>	0.563		0.563	–	0.625		–0.749	–0.083	–0.104
<i>Sphagno-Utricularion</i>	–	–	–	–	–	–	0.961	0.356	0.316
<i>Betulion pubescentis</i>	–	–	–	–	–	–	0.344	0.360	0.359
<i>Caricion davallianae</i>	0.871	0.509	0.871	0.522	0.854	0.424	0.253	0.245	0.246
<i>Caricion atrofusco-saxatilis</i>	–	–	–	–	–	–	0.256	0.273	0.268
<i>Caricion fuscae</i>	0.143	0.571	0.143	0.614	0.143	0.630	0.241	0.211	0.211
<i>Magnocaricion</i>	0.672	0.843	0.672	0.837	0.696	0.851	0.161	0.181	0.178
<i>Phragmition communis</i>	0.667	1.000	0.667	1.000	0.778	1.000	0.384	0.419	0.408
<i>Phalaridion arundinaceae</i>	–	–	–	–	–	–	0.455	0.056	0.000
<i>Glycerio-Sparganion</i>	–	–	–	–	–	–	0.222	0.077	0.078
<i>Molinion caeruleae</i>	0.652	–	0.652	–	0.692	–	0.271	0.286	0.285
<i>Calthion palustris</i>	0.857	–	0.857	–	0.857	–	0.277	0.266	0.273
<i>Juncion acutiflori</i>	–	–	–	–	–	–	0.293	0.289	0.277
<i>Cardamino-Montion</i>	–	–	–	–	–	–	0.184	0.184	0.187
<i>Caricion remotae</i>	–	–	–	–	–	–	–	–	–
<i>Filipendulo-Petasition</i>	0.316	–	0.316	–	0.237	–	0.238	0.204	0.201
<i>Convolvulion sepium</i>	–	–	–	–	–	–	0.245	0.211	0.216
<i>Nardo-Juncion squarrosi</i>	–	–	–	–	–	–	0.374	0.374	0.366
<i>Violion caninae</i>	–	–	–	–	–	–	0.267	0.306	0.319
<i>Salicion cinereae</i>	–	–	–	–	–	–	0.190	0.139	0.137

r Pearson's product correlation, *och* Ochiai's index, *vdm* Van der Maarel's index, – not in the training data set

classification was on average higher than with the two other indices, and the resulting groups of the Swiss mire monitoring data were most consistent (Table 2). We further found that alliances were identified more reliably when relevés were first assigned to the associations, and the associations membership to alliances taken, than when the similarity between relevés and alliances was used for the assignment.

For the Swiss training data set with the correlation coefficient *r* as similarity measure used and the transformation $\log(x + 10)^{2.5}$ we got a hit rate of 69.8% on the level of alliances. On the level of associations the hit rate was 49.5%. Doing the same on the Austrian training data set from Steiner (1992) the hit rate was almost the same: 41.6% on the level of associations and 70.3% on the level of alliances.

Quantitative analysis of Swiss mire vegetation

To determine how abundant wetland vegetation types are in Swiss mires, and how they are distributed across the

country (research questions 1 and 2), each relevé was assigned to an association based on similarity indices calculated with the transformation $\log(x + 10)^{2.5}$. The number of relevés attributed to each phytosociological alliance was counted. We present results derived from all three similarity indices (Pearson's correlation coefficient, Ochiai index and van der Maarel's similarity index).

Because the sample inside a mire site was biased towards rare vegetation types (see above) the estimated area occupied by the associations and alliances in the observed sites was modelled with the help of aerial photographs. Colour and texture variables were regressed to the mean ecological indicator values (Landolt 1977) of the relevés. Using a general linear model (GLM) the mapped patches in the photographs were first assigned to the indicator values (Ecker et al. 2008; Küchler et al. 2004) and subsequently to the different associations and alliances. The surfaces were measured using ordinary GIS technique. In a second step the area of each alliance was extrapolated

to the total area of the national inventories of bogs and fens. The extrapolations were subsequently corrected for the differing portions of alliances within the mire sites of national and of regional importance according to the inventory of fens (Broggi 1990).

To show vegetation gradients and to assess the separation of vegetation units (question 3), we displayed relevés in ordination diagrams obtained through metric multidimensional scaling (Principal Coordinates Analysis) based on correlation coefficients calculated from the full set of species. These ordinations were performed on two different subsets of the data: (1) The “best fitting subset” was a sub-sample of all relevés fitting best to Pantke’s associations ($r \geq 0.2$ and quotient second/best fitting $q \leq 0.8$, to avoid ambiguity). A total of 2,265 relevés fulfilled this condition. (2) The “random subset” was a random sub-sample of the total set, with another 2,265 relevés drawn to match the size of the “best subset.” The first ordination, based on the “best fitting subset” would show whether disjunct groups emerge if only relevés are ordinated that fit best to the phytosociological classification. The second ordination, based on the “random subset” would show whether the phytosociological classification still appears as a group pattern when the entire set of relevés is ordinated.

For the ecological interpretation of the ordinations (question 4), mean ecological indicator values were projected into the ordinations by calculating the correlations between these indicator values and the first two ordination axes.

Results

Vegetation types of Swiss mires

The frequency of the alliances found in our data set differed slightly depending on the similarity function used (Table 3). This indicates that there is some uncertainty involved in the results. In fact, 58.8% of the relevés were assigned to the same alliance by all three similarity measures, 96.7% by at least two methods. The outcome when using van der Maarel’s versus Ochiai’s indices is rather similar: 90.1% of the assignments are identical. When van der Maarel’s and Ochiai’s index are compared with the product moment correlation coefficient r , the identical assignments are 61.3 and 63.1%, respectively.

Within the bog ecosystem complex the most frequent alliances are the *Sphagnion medii* and the *Betulion pubescentis*. The assignment to the *Sphagnion medii* is the most uncertain. Many of the relevés assigned to it by the correlation coefficient are seen as belonging to the *Oxycocco-Empetrium hermaphroditi* when relying on van der Maarel’s or Ochiai’s coefficient. Transition mires (*Caricion lasiocarpae*) and hollows (*Rhynchosporion albae*) are rather rare.

The fens (having the potential to form peat) are mainly composed of two clearly dominating alliances, *Caricion davallianae* and *Magnocaricion*. Three more play an important role: *Caricion atrofusco-saxatilis*, *Caricion fuscae* and *Phragmition communis*.

Our relevés of the wet-grassland alliances (generally not forming peat) are not representative for Switzerland as they mainly stem from the borders of our biotopes. There are four dominating: *Molinion caeruleae*, *Calthion palustris*, *Juncion acutiflori* and *Filipendulion*.

Our estimates for the extent of mire vegetation in Switzerland range from 22,780 ha through 23,080 ha up to 23,430 ha (Table 3). The differences result from the ambiguous assignments of relevés considered mires in some solutions but not in others.

Spatial distribution of vegetation types

The mire vegetation types are not distributed equally over the country (Fig. 1). For example, *Caricion lasiocarpae* mainly occurs in the Jura Mountains and the foothills of the Alps. It seems to form a substitute of *Rhynchosporion albae* concentrating in the Central Alps. Other alliances such as *Calthion palustris*, *Magnocaricion* or *Molinion caeruleae* are dispersed across the whole country. The distribution pattern is of course dominated by the occurrence pattern of bogs and fens in general as can be seen in the last map of Fig. 1. In some cases elevation (in Switzerland highly correlated with temperature) is a limiting factor. An example for this is *Phragmition communis* mainly restricted to low elevations (Fig. 2).

Gradient structure and separation of mire alliances

To see how clearly alliances are separated from each other, the similarity pattern in terms of species composition of the relevés is represented in ordinations (Figs. 3, 4).

The ordinations based on the “best fitting subset” (see “Methods”) show that the phytosociological system applied to the Swiss mire vegetation forms a triangular gradient system (Fig. 3). The three extremes are represented by the *Sphagnion medii*, the *Caricion davallianae* and the *Phragmition australis*. In Fig. 3 the nine alliances represented best are ordered to follow this gradient system. Although all alliances form distinct groups, they overlap, indicating that a continuum exists. Disjunct sub-groups emerge in three alliances: the *Caricion davallianae*, the *Magnocaricion* and the *Phragmition australis*.

The random sample of relevés is used to reveal the gradient pattern of the entire sample (Fig. 4). The triangular gradient system is still visible, with the same alliances at the three extremes. However, alliances are no longer clearly separated but overlap considerably (Fig. 4).

Table 3 Assigning of 17,608 relevés to the mire alliances using different similarity measures

	Counts of relevés			Estimated area (ha)		
	<i>r</i>	<i>och</i>	<i>vdm</i>	<i>r</i>	<i>och</i>	<i>vdm</i>
Vegetation of bog ecosystem						
<i>Sphagnion medii</i>	1,090	626	651	2,250	920	1,050
<i>Oxycocco-Empetrium hermaphroditii</i>	518	667	676	240	870	1,090
<i>Rynchosporion albae</i>	85	130	128	–	30	30
<i>Caricion lasiocarpae</i>	107	120	129	<10	40	40
<i>Scorpidio-Utricularion minoris</i>	2	6	5	–	–	–
<i>Sphagno-Utricularion</i>	3	8	6	–	–	–
<i>Betulion pubescentis</i>	895	1,040	1,050	2,700	3,260	3,320
Total bog vegetation	2,700	2,597	2,645	5,190	5,110	5,530
Vegetation of fen ecosystem						
<i>Caricion davallianae</i>	2,270	2,255	2,272	3,300	3,330	3,350
<i>Caricion atrofusco-saxatilis</i>	208	275	316	30	110	140
<i>Caricion fuscae</i>	756	861	784	330	430	330
<i>Magnocaricion</i>	1,299	1,038	953	1,390	1,610	1,550
<i>Phragmition communis</i>	516	218	210	1,090	330	320
<i>Phalaridion arundinaceae</i>	49	2	6	–	–	–
<i>Glycerio-Sparganion</i>	20	19	19	–	–	–
Total fen vegetation	5,118	4,668	4,560	6,140	5,810	5,690
Vegetation of wet meadows						
<i>Molinion caeruleae</i>	588	559	526	110	120	90
<i>Calthion palustris</i>	3,255	3,586	3,473	11,200	11,700	11,710
<i>Juncion acutiflori</i>	165	237	265	<10	10	20
<i>Cardamino-Montion</i>	86	93	84	–	–	–
<i>Caricion remotae</i>	2	0	1	–	–	–
<i>Filipendulo-Petasition</i>	341	510	571	140	320	390
<i>Convolvulion sepium</i>	46	62	60	–	–	–
Total wet meadows vegetation	4,483	5,047	4,980	11,450	12,150	12,210
Total mire vegetation	12,301	12,312	12,185	22,780	23,080	23,430
Groups close to mire vegetation						
<i>Nardo-Juncion squarrosi</i>	623	669	618	1,640	1,370	840
<i>Violion caninae</i>	16	58	61	–	–	–
<i>Salicion cinereae</i>	308	308	310	170	80	60
Other non-mire vegetation types	4,338	4,120	4,201	4,780	4,890	4,980
Total of non-mire vegetation	5,285	5,155	5,190	6,590	6,340	5,880
Classification ambiguous	22	141	233	–	<10	<10

Data transformation is $\log(x + 10)^{2.5}$. Counts of assigned relevés to the alliances and extrapolation of their area to Switzerland *r* correlation coefficient, *och* Ochiai's index, *vdm* van der Maarel's similarity index. – not enough relevés to estimate the area

To check whether the relevés not fitting the system are aberrant observations in ecological terms, we projected ecological indicator values (Landolt 1977) into the ordinations (Fig. 5). This confirmed that both ordinations reveal the same ecological gradients. The larger variation involved in the ordinations of the random sample does not blur the gradients. Apparently the relevés not fitting the phytosociological system are equally meaningful in ecological terms as far as the main gradients are concerned.

Discussion

Numerical assignments of relevés to an existing classification:

Trying to assign relevés to the phytosociological system is an ambivalent experience. On the one hand our results confirm that the group structure obtained helps in the interpretation of ordinations encompassing a large range of

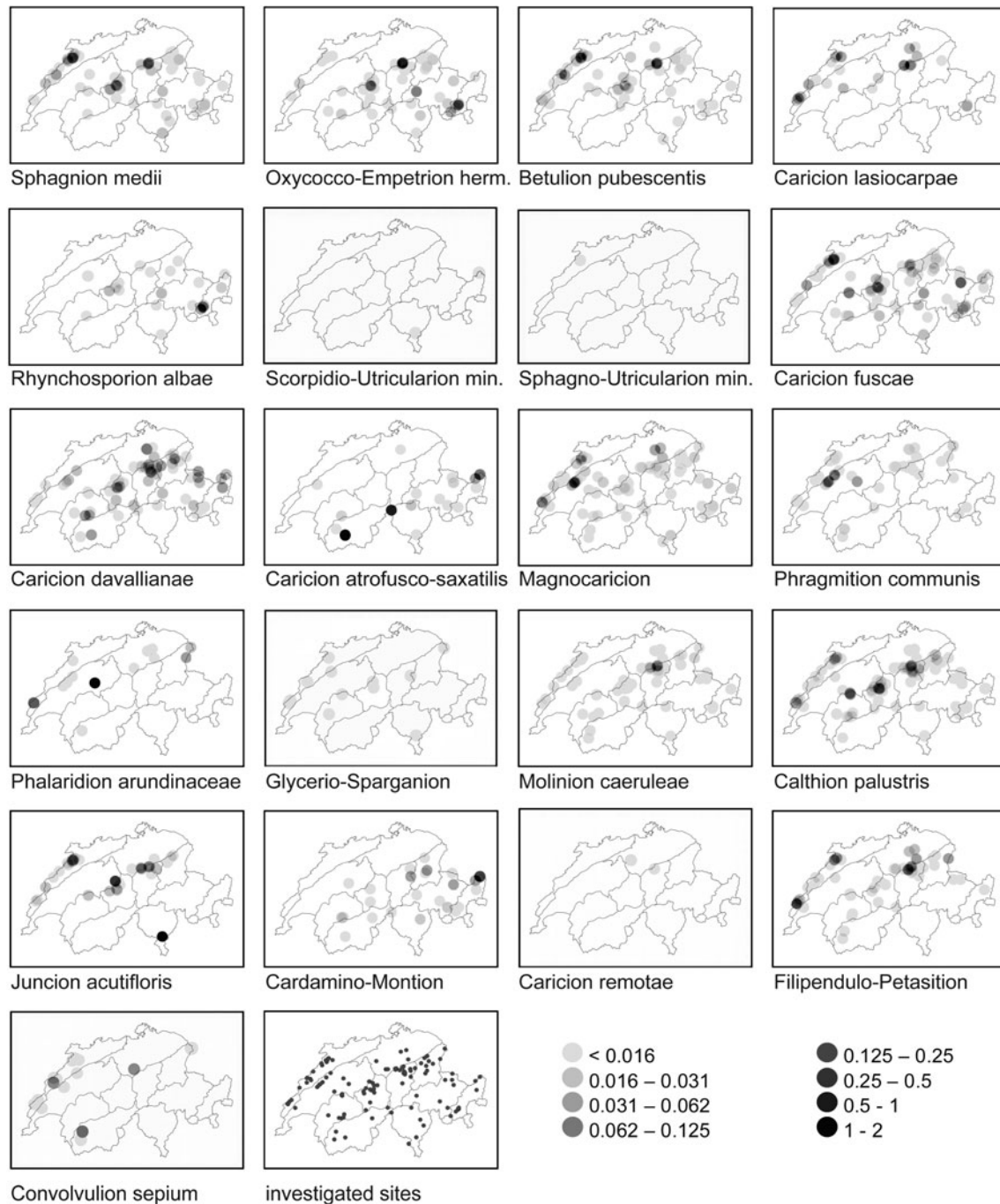
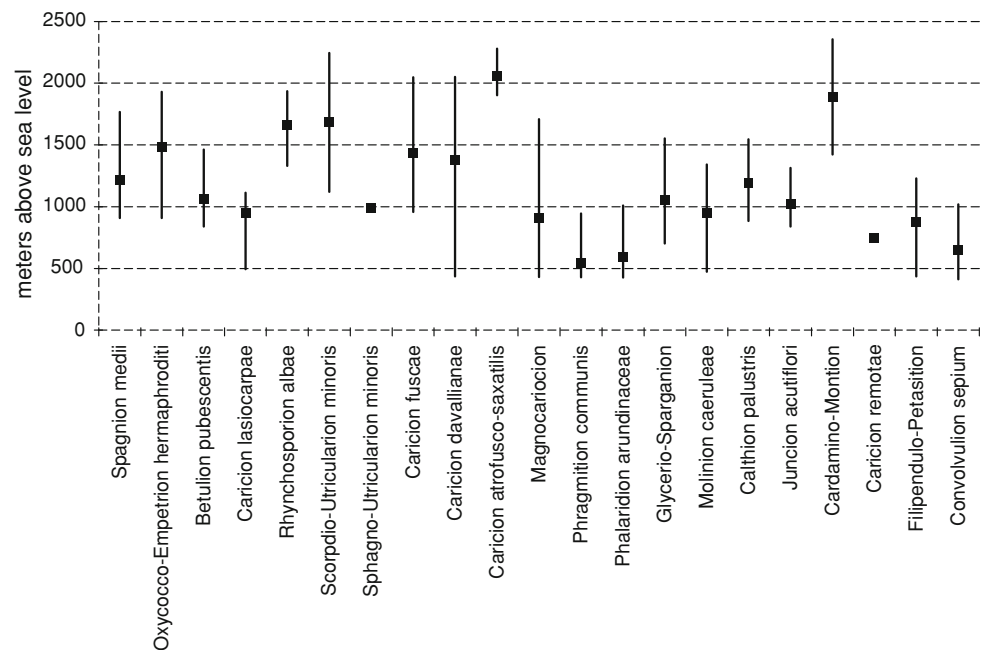


Fig. 1 Distribution and relative density of the mire alliances in Switzerland (findings per km² landscape)

vegetation types. On the other hand our sub-sample of relevés fitting best to the system has size $n = 2,265$ out of 17,806, a mere 12.8%. This happens when a stringent threshold is taken for assigning the relevés. The result is well-defined vegetation types with low dispersion (Fig. 3). When assigning all data collected in the framework of a statistical sampling design (“random subset”) then the threshold similarity has to be reduced drastically, resulting in vegetation types of high dispersion (Fig. 4).

Considering the allocation technique used, many of the relevés in the random subset had a low similarity to any of the alliances. If a stringent threshold was applied for the assignment, they would drop out of the phytosociological system. This may be partly related to the large size of the patches surveyed in the mire monitoring. Many of our relevés certainly would have been considered inhomogeneous in strict phytosociological terms and the species combination found there would have been discarded by phytosociologists.

Fig. 2 Altitudinal distribution of the mire alliances in Switzerland: mean altitude, 10 and 90%-quantile



The problem of relevés poorly fitting the phytosociological classification is, however, more general. Jandt (1999), Pflume (1999) and Täuber (2000) also discuss this issue and propose a two-step assignment procedure as a solution. In a first step they apply stringent criteria for assignments. Only in a second step the poorly fitting relevés are assigned too. For the same purpose Kočí et al. (2003) even change the method from the first to the second step. They start with Bruehlheide's (1995) Cocktail method and then apply a similarity-based assignment of relevés similar to what we do. Among 718 relevés they achieved 376 identifications of associations agreeing with expert opinion.

One limitation in the assignment is inherent flaws in phytosociological classifications (Kočí et al. 2003; Dengler et al. 2008). These are neither based on any consistent sampling scheme nor on a classification method (Legendre and Legendre 1998). The same holds for the assignment of new relevés. This has recently been much improved by computer-based procedures to yield stable solutions through iteration (Bruehlheide 1995, 1997). Assigning relevés by resemblance functions, as we do, results in a unique solution if a certain data transformation and a certain similarity index are used. However, using a different similarity index can considerably change the result. For example, in the Swiss mire monitoring data set, twice as many relevés were attributed to the *Phragmition communis* using the correlation coefficient r as similarity measure than with Ochiai's index (Table 3). The reason is that species-poor vegetation types, such as the *Phragmition communis*, are better recognised if the common absence of species is considered as "similarity" by the similarity index.

Our classification attempts showed that the phytosociological system is most consistent on the level of associations. Indeed, we found that assigning relevés to alliances directly results in much lower agreements compared to assigning relevés to associations and then deriving the alliance from the association. This roots in an inherent property of all hierarchical classifications but also in specific properties of the phytosociological classification. Examples are the alliances *Caricion davallianae*, *Magnocaricion* and *Phragmition communis* where some disjunct subgroups can be found (Figs. 3, 4). Further inconsistent group patterns found in Pantke's (2003) system are responsible for that as well. For example, the resemblance of the alliance *Oxycocco-Empetrium hermaphroditi* to *Spagnion medii* ($r = 0.55$) is higher than the average resemblance of associations within this alliance ($r = 0.38$). Another example is the alliance *Phalaridion* where the average internal correlation ($r = 0.49$) is not much higher than that to the *Glycerio-Sparganion* ($r = 0.41$). In all these examples even the best method of assignment cannot generate unambiguous solutions.

Given these flaws of the phytosociological classification, alternative classification procedures like the Cocktail method (Bruehlheide 1995, 1997) or its extension by Kočí et al. (2003) could be useful. Indeed, these do not only assign relevés to classifications but also carry the potential to change the classifications themselves if deemed necessary. To apply these procedures, however, we would need a database of relevés of the Swiss wetlands, unfortunately as yet missing.

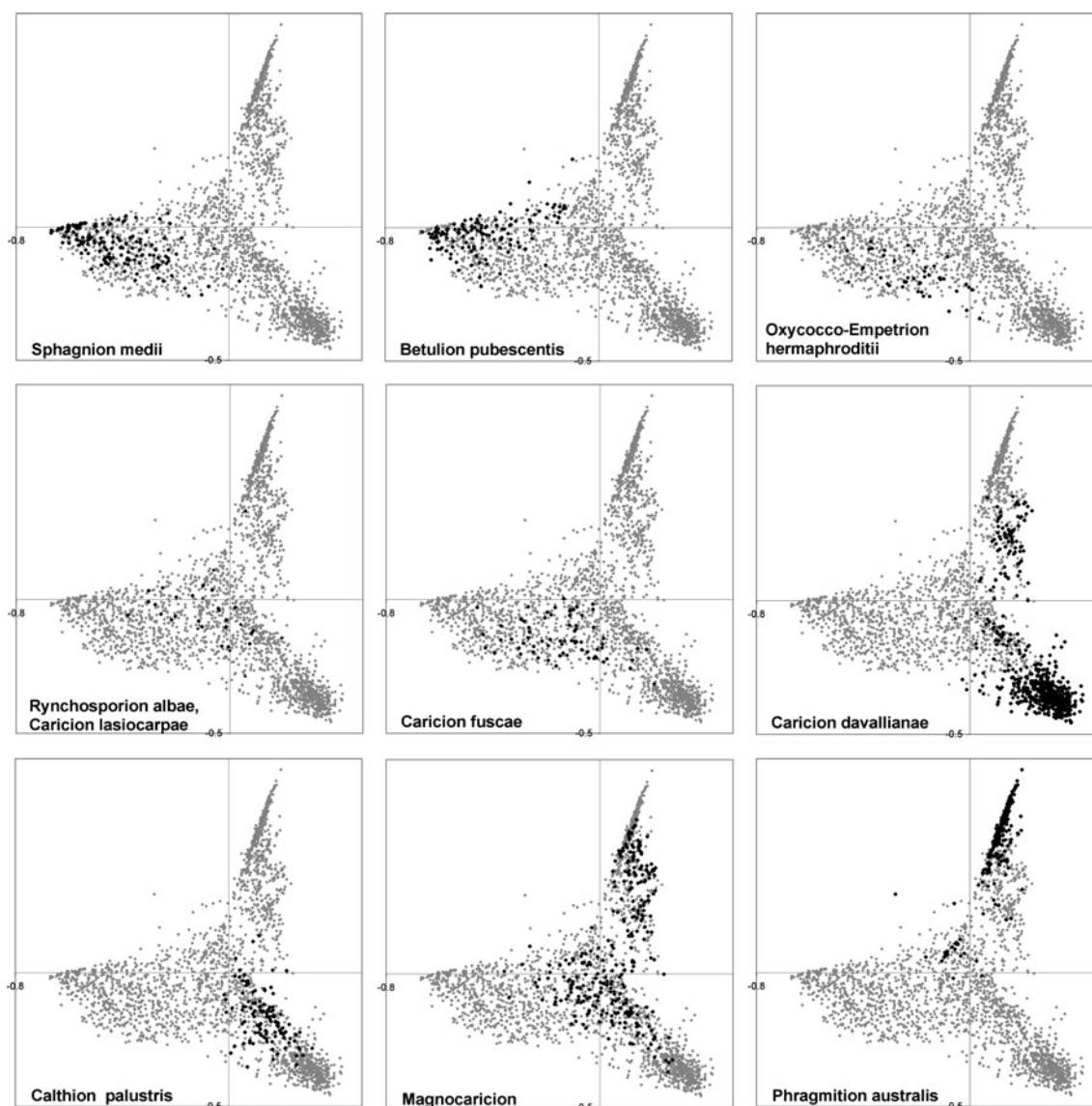


Fig. 3 Ordination of the sub-sample of relevés fitting best to the phytosociological system ($n = 2,265$). The most frequent mire alliances are highlighted

Distribution and abundance of mire vegetation types in Switzerland

Despite obvious potential for improvement the assignment of the wetland sample to the phytosociological system proves to yield an excellent overview of the major mire types in Switzerland, in terms of spatial distribution (Fig. 1) but also in terms of abundance (Table 3).

We found a regional pattern of distribution which can be explained for some alliances by their preferred altitude: For example *Caricion lasiocarpae* seems to be a regional replacement of *Rynchosporion albae* (Fig. 1) but in fact it is an altitudinal replacement. 90% of all findings of *Rynchosporion albae* are above 1,300 m

(Fig. 2) and so it is restricted to the alpine regions, whereas 90% of the findings of *Caricion lasiocarpae* are below 1,120 m (Fig. 2) and its main distribution is the Jura mountains. These two alliances were considered to be ecologically equivalent by Delarze et al. (1999) but in fact, they differ in their mean ecological indicator values (Landolt 1977) for light, soil reaction, nutrients, humus and temperature (not shown, all differences more than 0.2).

Some of the mire vegetation types are very rare. As for the alliances of bog-pools (*Sphagno-Utricularion* and *Scorpidio-Utricularion minoris*) their rarity might be explained by the fact that most of the bogs of Switzerland were drained or even exploited for peat production in the

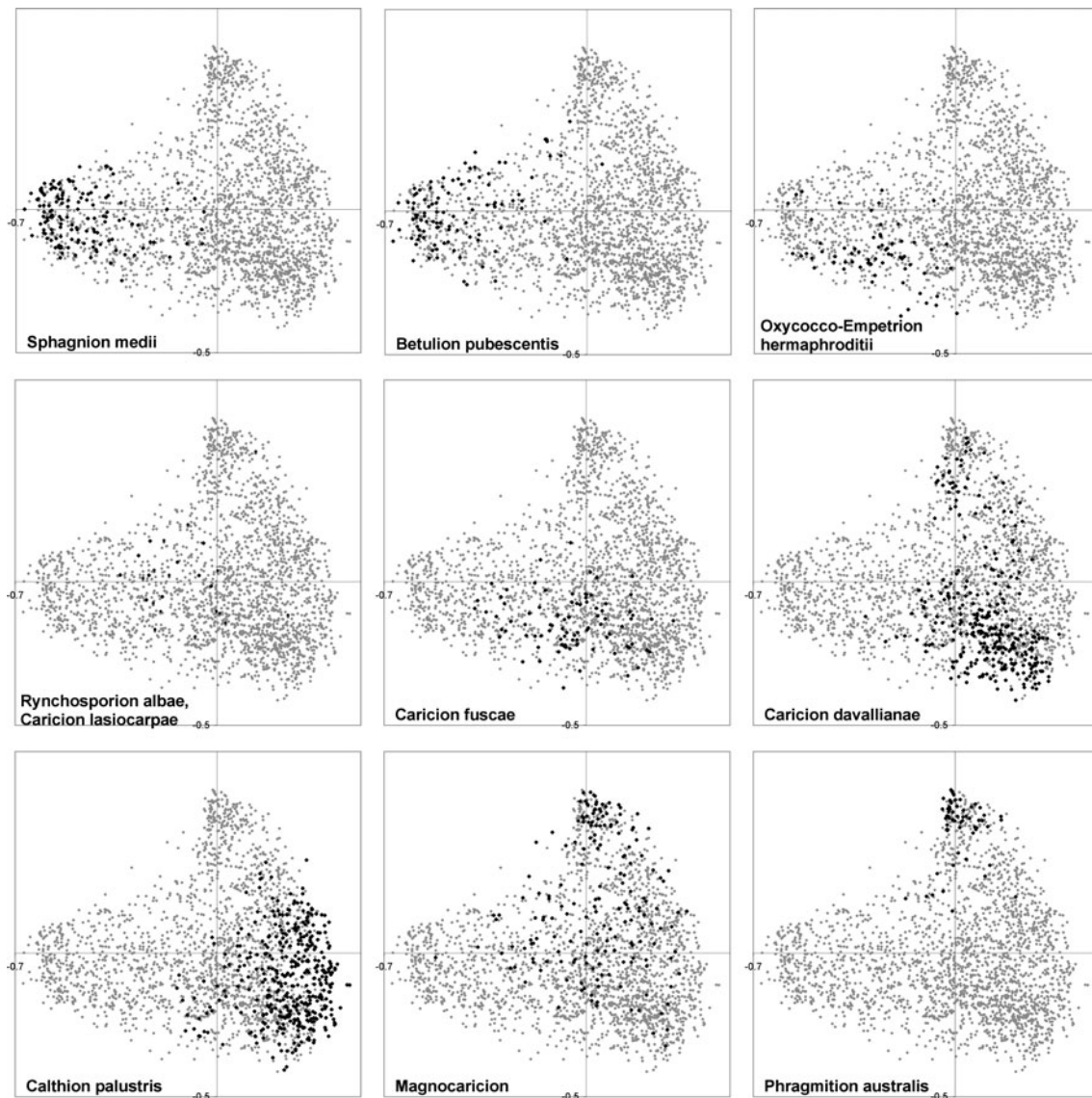


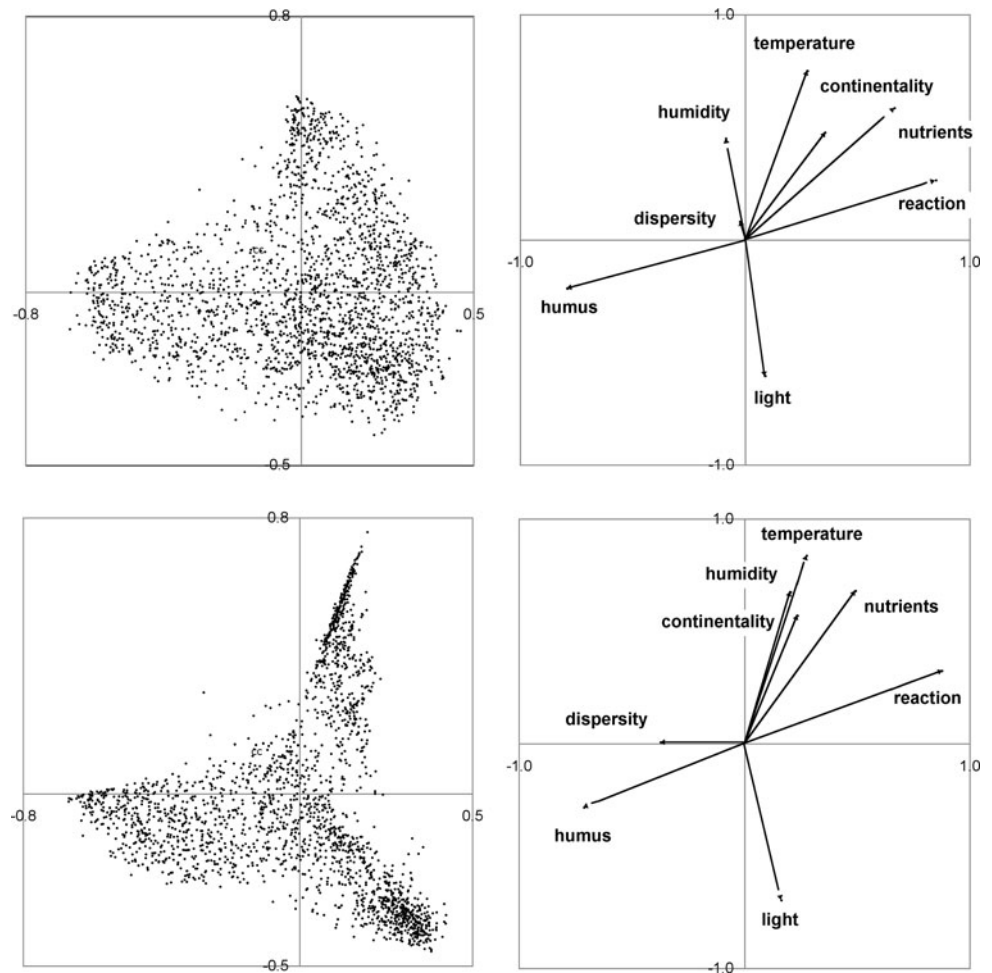
Fig. 4 Ordination of a random sub-sample of all relevés ($n = 2,265$). The most frequent mire alliances are highlighted. All relevés are assigned to alliances even if the assignments are very weak

past. Their water table still remains too low for these vegetation types to persist. Other alliances may occur sparsely because of the sampling design. Vegetation types tending to either grow in linear shape or in very small patches are likely to be underrepresented in a design where plots are used. This concerns, among others, all types of riverine and ditch vegetation (e.g. *Filipendulo-Petasion*, some associations of *Magnocaricion*), hollows and transitional mires (*Rynchosporion albae*, *Caricion lasiocarpae*) and spring vegetation on steep slopes occurring as short and narrow strips (*Cardamino-Montion*, *Caricion remotae*). A different type of sampling would be needed to assess these adequately.

Conclusions

Our study has shown that the numeric assignment of contiguous vegetation patches to phytosociological associations and alliances is a powerful method to study the spatial distribution and extent of mire vegetation types as well as ecological gradients. Overall, phytosociological alliances distinguished until now proved suitable schemes to describe and interpret vegetation gradients. However, our study has also revealed weaknesses in the current definition of mire alliances. A revision of the system using modern concepts and numerical methods would require a comprehensive database of vegetation relevés.

Fig. 5 Projection of ecological indicator values into the ordinations of the random subset (*upper graphs*) and the best fitting subset (*lower graphs*)



We therefore see the urgent need to establish a database of Swiss wetland relevés for a more reliable definition of some vegetation units.

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