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Five-year changes in Swiss mire vegetation

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Abstract To assess whether short-term changes in mire vegetation can be detected using the phytosociological approach, paired vegetation relevés from two surveys of 112 mire sites of Switzerland were assigned to phytosociological alliances through a numerical approach. About 30% of the plots were assigned to different alliances in the two surveys. These transitions were analysed based on species frequencies and interpreted ecologically using Landolt's indicator values. Transitions between different alliances were more frequently related to the appearance of new species rather than to the disappearance of species. Transitions from and to peat bog communities were frequent. Many plots with fen vegetation were transformed into other wetland types. Fen-grassland increased in abundance, mainly at the cost of small-sedge fens. To re-establish the function of the Swiss mires as peat producers, we recommend to raise the mean summer water table to a maximum depth of 10 cm.

Keywords Community transition · Species frequency · Landolt's indicator values

Veränderung der Schweizer Moorvegetation innerhalb von fünf Jahren

Zusammenfassung Um zu klären, ob kurzzeitige Vegetationsänderungen in den Mooren mit pflanzensoziologischen Analysen erfasst werden können, wurden gepaarte Vegetationsaufnahmen aus zwei Erhebungen mit einem numerischen Verfahren den pflanzensoziologischen Verbänden zugewiesen. Es wurden Flächen in 112 Moore untersucht. Etwa 30% der Flächen wurden in den beiden Erhebungen verschiedenen Verbänden zugewiesen. Veränderte Zuweisungen bei Erst- und Zweiterhebung wurden hinsichtlich veränderter Artfrequenzen untersucht und anhand von Zeigerwertanalysen ökologisch interpretiert. Die unterschiedlichen Klassierungen sind eher mit einwandernden Arten verbunden als mit verschwindenden Arten. Übergänge von und zu Hochmoor-Gesellschaften sind häufig. Die häufigsten Veränderungen sind Flachmoorgesellschaften, die sich zu anderen Feuchtgebietstypen umwandelten. Nasswiesen nahmen hauptsächlich zu Lasten von Kleinseggenrieden zu. Um die Funktion der Schweizer Moore als Torfproduzenten wieder herzustellen, empfehlen wir, den mittleren Grundwasserpegel im Sommer auf eine maximale Tiefe von 10 cm anzuheben.

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Introduction

Wetland vegetation in Switzerland has decreased by 90% of its area since 1800 (Grünig 1994), and all remaining sites considered to be of "national importance" are protected by Swiss legislation. The aim of this protection is twofold: Wetlands are to be conserved quantitatively by maintaining their overall surface and they should be conserved qualitatively by retaining their characteristic species composition. An extensive monitoring project was initiated in 1996 in order to assess whether these two aims have been achieved.

Whereas the law requires wetlands to remain unchanged, the design of the monitoring also has to consider

anticipated changes caused by past and recent land use and climate change. Detailed predictions of the effects of climate change on biodiversity in Switzerland for the next 50 years exist (OcCC 2007). Climate change will probably cause some species to disappear in some wetland types and emerging in others, causing transformations of wetland communities. According to Bühler and Schmid (2001) early signs of vegetation change are often changes in species abundance due to demographic processes, while species composition persists. Therefore our monitoring approach must use the species approach as well as the community approach (Guisan and Zimmermann 2000). Any statement about shifts in species occurrence will refer to the community level: Because legal regulations concern vegetation types, they represent our final reference system.

While the law considers vegetation types only, various investigations report alterations in species composition not affecting assignments to types: Bergamini et al. (2009) found in *Caricion davallianae* stands a decrease of habitat specialists, even if the traditional management was maintained. Ter Braak and Wiertz (1994) observed in *Junco-Molinion* stands a decrease of many species which are typical for wetland habitats due to a loss of moisture and an acidification of the soils. Gunnarsson et al. (2002) observed in a 40-year study drier surfaces and an increased availability of nitrogen together with an increased tree cover and a decrease of many low-growing species of wet microhabitats in Swedish mires. Nordbakken (2001) found after 5 years an increasing abundance of dwarf-shrubs in hummocks and upper lawns and a decreasing cover of peat mosses in a Norwegian bog. Pauli et al. (2002) found after an application of nutrients a rapid colonisation by generalists and a decrease in the abundance of sedges. *Succisa pratensis*—as a habitat specialist—reduced its production of biomass.

Most of the previous studies concerned particular mire communities. Community transitions were hardly assessed, and if so, this was mostly done in a historical context (e.g. Svensson 1988). In our study we present an overview of ongoing changes in all mire communities of Switzerland. We specifically address the following questions:

- Which communities are becoming more frequent, which less frequent?
- Are trends the same for the entire country, or are there regional differences?
- Which site factors change?
- Which species become more frequent or less frequent in plots with community transition and in those with stable classification?

Materials and methods

The phytosociological system

There are various definitions of mires (Broggi 1990; Steiner 1992; Hájek et al. 2006). For the present study we refer to the national inventory of fens which lists the phytosociological entities of mires, but we add some further alliances which are often embedded in the mire ecosystems or which can be regarded as degraded mire vegetation (Graf et al. 2010). We used the database „Pflanzengesellschaften der Schweiz" (Pantke 2003) as a reference data set to classify the records. This database defines a comprehensive syntaxonomic system for the entire Swiss vegetation. The database consists of species lists for 654 associations, 160 alliances, 82 orders and 52 classes. These species lists are derived from published classified relevés. Species are included if their constancy is at least 20%. The species are labelled according to their diagnostic type i.e. a species is a companion, a differential species, a high constancy species, a character species, etc. We adapted Pantke's database to fit the data of the Swiss mire monitoring (Graf et al. 2010).

The mire vegetation is grouped into three categories: bog ecosystem (ombrotrophic ecosystem), fen ecosystem (groundwater saturated ecosystem, communities which have the potential to produce peat), and fen-grassland (mostly groundwater saturated ecosystem, communities which usually do not produce peat).

Mire vegetation data

We drew a stratified random sample of 125 objects from the sites listed in the federal mire inventories (Grünig et al. 1986; Broggi 1990). Stratification took into account the geographical regions, the altitudinal belts, the mire types (bog or fen) and the size of the sites. An aerial colour infrared photograph of each mire site was taken and interpreted on a stereoscope. Homogeneous patches of colour and structure were delineated on the picture. Patches adjacent to the mire were included in order to be able to identify the transitions from mire to non-mire vegetation statistically.

The vegetation of each object was described by about 130 relevés on average, depending on the size of the object. The delineated patches were classified by their colour and texture to describe the plots to be recorded. A stratified subsample of patches was taken to give equal weight to classes.

A relevé is a comprehensive list of vascular plant species and bryophytes of one entire delineated patch. The species cover is estimated on a four-step logarithmic scale ($1, \leq 0.1\%$; $2, \leq 1.0\%$; $3, \leq 10\%$; $4, \leq 100\%$). The median of

the record area was 212.6 m^2. Plots were surveyed a first time between 1997 and 2002, and a second time between 2003 and 2007. Records from both surveys are available for 8,024 plots in 112 mire sites. The time span between the surveys of each object was mostly 5 years, sometimes 6 years (29 mire sites) or 7 years (one mire object).

The names of vascular plants are according to Aeschimann and Heitz (2005), those of bryophytes according to Schnyder et al. (2004).

Assignment of relevés to the syntaxonomic system

The relevés were correlated with the species lists of all of Pantke's associations, assigned to the one with the highest (Pearson's) correlation coefficient and subsequently to the corresponding alliance. In Pantke's lists the species are weighted according to diagnostic types (Graf et al. 2010). The data transformation of the diagnostic weights and the species cover of the mire data was $\log(x + 10)^{2.5}$, where x is cover percentage of a species or the species weight in Pantke's list respectively. Absent species were set to 0. In a previous study (Graf et al. 2010) with this transformation we found the best match of computational assignments and expert classifications. In 12 plots the assignments to the alliances were ambiguous in at least one survey. These were disregarded in further analyses.

Gains and losses of alliances

As the assignment of relevés to predefined classes contains some uncertainty, a change in class may be arbitrary in some cases. To test this, we calculated the similarity of the relevé pairs. As similarity measure we took Pearson's product correlation. With a Wilcoxon test of independent samples we tested for each alliance the mean similarity of plots that remained within the alliances against the mean similarity of those that dropped out of the alliances.

The balance between each pair of alliances is calculated as the difference between transitions in both directions (cells symmetric to the diagonal in Table 1). For example the balance between *Sphagnion medii* and *Betulion pubescentis* is calculated as follows: 428 plots were assigned to *Sphagnion medii* in both surveys, 89 plots classified as *Sphagnion medii* in the first survey were classified as *Betulion pubescentis* in the second survey, and 65 plots classified as *Betulion pubescentis* in the first survey were classified as *Sphagnion medii* in the second survey. So *Sphagnion medii* lost on balance 24 plots to *Betulion pubescentis*.

The balances of the alliances for the different geographic regions and altitudinal belts (Hess et al. 1976) are calculated. The significance of changes was tested with a sign-test.

Within many mire sites, the alliances were often too sparsely recorded to test the significance of their balance. Nevertheless the results of transitions may be relevant for the conservation of the sites. Rather than relying on significance only, we decided that an alliance had a relevant change in frequency if it counted <90% or more than 110% in the second survey compared to the first survey. If an alliance remained within these limits in an individual mire site, we considered its status as not basically altered. We did this assessment only for the most frequent alliances (i.e. a total score of at least 500 records in both surveys together).

Change in site conditions

For lack of chemical analyses or physical measurements we assess the site conditions of a plot by Landolt's indicator values (Landolt 1977). We use a 10% trimmed mean of a presence/absence transformation of the species on a plot to account for possible misdeterminations of plants. Significance is tested with a Wilcoxon test.

Changes in species frequencies

Changes in plant communities are caused by the colonisation and the disappearance of species. We assessed the floristic changes in those plots that were reclassified in the second survey by analysing the changes in species frequencies: A Chi-squared test was applied to the frequencies in the first and the second survey inside a transition group against all other plots (i.e. for plots which dropped out of the community A the group A → B was tested against the group [A → A plus B → B plus B → A], whereas B is the sum of all other communities. In case of plots, which joined the community A, the tested groups were B → A and [A → A plus B → B plus A → B]). We assessed only species, which occurred in one of the surveys at least 10 times in the community A.

Population change of species in plots which remained in their alliance was assessed by a Wilcoxon test of paired samples with regard to their cover estimates.

Results

The records were assigned to 78 of the 160 alliances listed in Pantke (2003). 26.8% of the plots of the first survey and 27.7% of the plots of the second survey do not belong to mire vegetation (Table 1). This indicates that 1.2% of the total mire vegetation was lost within the 5–7-year period. The difference is not significant for the loss of mire vegetation (sign test $p = 0.121$), but it is for the increase of non-mire vegetation (sign test $p = 0.045$).

Table 1 Transitions of mire alliances according to Pantke (2003); counts of classified records

	Sphagnion medii	*Oxycocco-Empetrion hermaphroditii*	*Betulion pubescentis*	*Caricion lasiocarpae*	*Rhynchosporion albae*	*Scorpidio-Utricularion minoris*	*Caricion fuscae*	*Caricion atrofusco-saxatilis*	*Caricion davallianae*	*Glycerio-Sparganion*	*Magnocaricion*	*Phalaridion arundinaceae*	*Phragmition communis*	*Cardamino-Montion*	*Caricion remotae*	*Convolvulion sepium*	*Filipendulp-Petasition*	*Calthion palustris*	*Juncion acutiflori*	*Molinion caeruleae*	*Violion caninae*	*Nardo-Juncion squarrosi*	*Salicion cinereae*	Other	Total counts 1st survey
Vegetation of bogs																									
Sphagnion medii	**428**	37	89	2	7	–	9	–	5	–	11	–	2	–	–	1	–	2	2	1	–	34	3	23	656
Oxycocco-Empetrion hermaphroditii	29	**153**	6	4	9	–	19	–	13	–	19	–	1	–	–	1	–	8	7	3	–	30	1	14	315
Betulion pubescentis	65	6	**276**	2	1	–	2	1	2	–	4	–	1	–	–	–	–	3	–	1	–	15	12	78	469
Caricion lasiocarpae	4	2	2	**46**	1	–	1	–	5	–	14	–	3	–	–	–	1	1	2	–	–	–	–	–	82
Rhynchosporion albae	6	0	1	2	**47**	–	–	1	2	–	7	–	1	–	–	–	–	–	–	–	–	1	–	1	69
Scorpidio-Utricularion minoris	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
Vegetation of fens (with the potential to form peat)																									
Caricion fuscae	18	30	5	2	3	–	**146**	8	21	1	26	–	1	–	–	–	1	38	12	5	–	23	–	41	381
Caricion atrofusco-saxatilis	3	2	–	–	1	–	4	**36**	32	–	4	–	1	2	–	–	–	4	–	–	–	1	1	3	93
Caricion davallianae	9	5	–	6	2	–	14	29	**749**	–	31	–	1	3	–	–	13	98	5	57	–	2	4	49	1077
Glycerio-Sparganion	–	–	–	1	–	–	–	–	–	**1**	–	–	–	–	–	–	–	–	–	–	–	–	–	3	5
Magnocaricion	16	16	6	21	11	–	18	–	32	–	**336**	2	30	–	–	–	15	69	6	5	–	2	29	26	641
Phalaridion arundinaceae	–	–	–	–	–	–	–	–	–	1	3	**7**	5	–	–	4	2	–	–	1	–	–	–	1	24
Phragmition communis	1	–	–	1	1	–	1	–	3	1	30	4	**168**	–	–	1	9	4	1	2	–	–	13	17	256
Vegetation of fen-grassland (without the potential to form peat)																									
Cardamino-Montion	–	–	–	–	–	–	2	1	8	–	2	–	2	**9**	–	–	–	5	–	–	–	–	–	8	37
Caricion remotae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	**0**	–	–	–	–	–	–	–	–	1	1
Convolvulion sepium	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	**8**	–	1	–	–	–	–	2	6	18
Filipendulp-Petasition	–	–	–	1	–	–	1	–	9	–	12	1	5	–	–	–	**59**	41	1	4	–	–	7	9	148
Calthion palustris	–	6	4	2	–	–	41	1	70	1	37	–	–	3	–	–	36	**882**	33	31	1	4	7	127	1285
Juncion acutiflori	–	3	–	2	2	–	12	–	1	–	2	–	–	–	–	–	1	22	**23**	3	–	3	–	3	75
Molinion caeruleae	–	1	1	–	1	–	1	–	24	–	5	1	6	–	–	1	17	37	–	**104**	–	–	2	26	227
Non-mire vegetation																									
Violion caninae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	3	4
Nardo-Juncion squarrosi	69	32	34	1	12	–	30	–	8	–	5	–	4	–	–	–	–	2	2	1	–	**152**	–	25	373
Salicion cinereae	3	–	15	–	–	–	–	1	1	–	13	–	13	–	–	2	3	2	1	–	–	1	**81**	26	153
Other	8	15	66	1	–	1	30	3	29	3	22	2	14	5	–	6	8	90	1	11	5	9	27	**1267**	1622
Total counts 2nd survey	659	308	505	93	95	1	331	80	1014	8	583	17	245	22	0	23	165	1310	96	229	5	276	189	1758	8012

Rows, 1st survey 1997–2001; columns, 2nd survey 2002–2007. The bold values represent the unchanged plots

Transitions of mire alliances

The records of 5,228 plots were assigned to a mire alliance at least in one survey. In 3,478 of these plots (=66.5%) the assignment to the alliance stayed unchanged; in 1,750 plots the assignment was different in the second survey (Table 1). For a part of these transitions the floristic similarity of the relevé pairs is nearly as big as for the cases of non-transitions (Fig. 1). They can be regarded as arbitrary, as a consequence of the uncertainty of the classification method. Nevertheless the mean floristic similarity of relevé pairs which dropped out of their alliance, is for most of the mire alliances significantly smaller than of those relevé pairs which remained within the alliance (Fig. 1).

In the first survey 1,592 records were assigned to one of the alliances of the bog-ecosystem, in the second survey the number was 1,661 (Table 1). This indicates a gain of 4.3% for the bog vegetation, but the difference is not significant (sign test $p = 0.066$). The biggest net losses were to non-mire vegetation types, net gains derived mainly from *Nardo-Juncion squarrosi*, *Carcion fuscae* and from *Magnocaricion* (Table 1). For the whole country, only the net increase of plots belonging to *Rhynchosporion albae* is significant, all other net changes of the alliances of the bog-ecosystem are not significant (Table 2). On the level of individual mire sites we observed a positive net change for *Betulion pubescentis*, a negative net change for *Oxycocco-Empetrion hermaphroditi* and a nearly even net change for *Sphagnion medii* (Table 3). The latter is a result of the losses of *Nardo-Juncion squarrosi* (Tables 1, 3).

Significantly less alliances of the fen-ecosystem were found in the second survey than in the first one (sign test $p \le 0.001$). The number of plots assigned to them dropped from 2,477 to 2,278 or to 91.9% of the first survey (Table 1). The biggest net losses were transitions to *Calthion palustris*, to non-mire alliances and to *Molinion caeruleae*. Net gains derived mainly from plots belonging to the *Nardo-Juncion squarrosi* in the first survey (Table 1). On the level of individual mire sites the trend is even stronger: All alliances, which could be assessed, had a relevant frequency decrease (<90% of the first survey) in far more sites than a relevant frequency increase (>110% of the first survey). The ratio is between 1.2 times and twice as many sites (Table 3).

Fen-grassland alliances were found slightly more frequently in the second survey than in the first one, but the difference is not significant (sign test $p = 0.13$). The number of plots assigned to them increased from 1,791 to 1,845 (Table 1). The biggest net losses derived from transitions to *Salicion cinereae* and other non-mire alliances. Net gains derived mainly from plots which were assigned to *Caricion davallianae* and to *Magnocaricion* in the first survey (Table 1). *Calthion palustris* has a relevant frequency increase in many more sites than it has a frequency decrease (Table 3) even though this trend is not significant for the total score (Table 2).

For five out of 20 mire alliances we had insufficient data to assess trends in individual regions of Switzerland. An additional two of them occurred only in one region in a frequency which allowed assessing the trends. For ten alliances we observed remarkably different (even reverse) developments either in different regions of Switzerland or different altitudinal belts or both (Table 2). For example: the number of plots belonging to *Betulion pubescentis* increased significantly in two regions and decreased significantly in another one (Table 2). In the fen alliances we observed some regional differences too. For example the plots belonging to *Caricion fuscae* increased in the Southern Alps, but declined in all other regions (significant difference only in the Jura region). For the whole country we observed a significant decline of about 13% for the *Caricion fuscae* (Table 2).

Fig. 1 Resemblance (mean Pearson's correlation) of paired relevés. Significance of the difference between plots which remained within the community and of those which dropped out of it (Wilcoxon test of independent samples: *$p \le 0.05$, **$p \le 0.01$, ***$p \le 0.001$, ****$p \le 0.0001$)
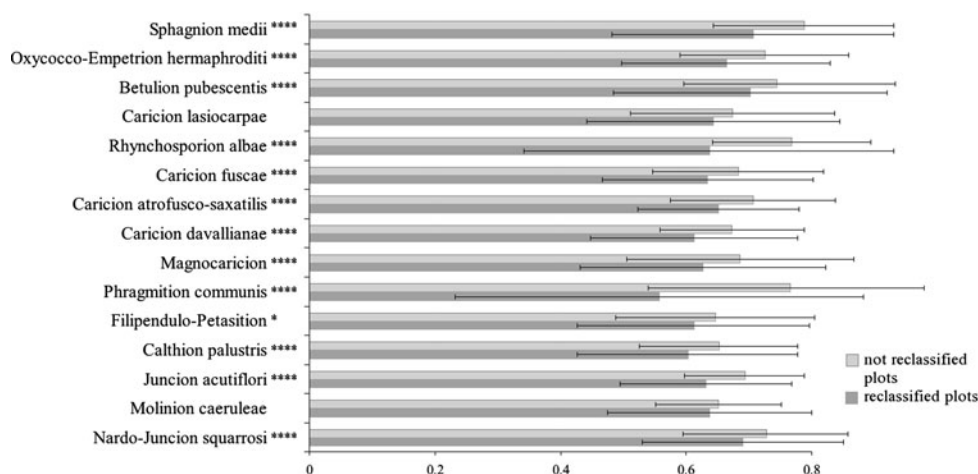
Table 2 Net change of mire alliances and related non-mire alliances in the geographic regions and altitudinal belts in percentage of the counts in the 1st survey

	Geogr. regions						Altid. Belts				
	Jura	Plateau	E-N-Alps	W-N-Alps	Central Alps	Southern Alps	Colline	Montane	Subalpine	Apline	Switzerland
Total counts of mire vegetation records in the 1st survey											
	1,169	1,031	1,544	1,410	1,001	235	823	3,078	1,877	612	6,390
Vegetation of bogs											
Sphagnion medii	−9	0	20*	−9	−10	22	–	0	−6	37*	0
Oxycocco-Empetrion herm.	–	–	−18	−11	9	–	•	−8	5	15	−2
Betulion pubescentis	21**	3	−23*	29*	–	–	−11	7	16	–	8
Caricion lasiocarpae	11	23	–	–	–	•	–	8	–	•	13
Rhynchosporion albae	•	–	–	–	20	–	–	–	0	22	38**
Scorpidio-Utricularion minoris	•	•	•	•	–	•	•	•	–	–	–
Vegetation of fens (with the potential to form peat)											
Caricion fuscae	−27*	−5	−2	−14	−15	10	–	−3	−15	−27*	−13*
Caricion atrofusco-saxatilis	•	–	•	–	−2	−35*	–	–	–	−12	−14
Carcion davallianae	–	−11	−4	−5	−10	–	−8	−14*	1	−10	−6*
Glycerio-Sparganion	–	–	•	–	•	–	–	–	–	•	–
Magnocaricion	−24**	−1	−12	17	−11	–	−6	−16*	−3	−2	−9*
Phalaridion arundinaceae	–	–	–	•	–	•	–	–	•	•	−29
Phragmition communis	26	−12	−15	–	25	•	−11	32	–	•	−4
Vegetation of fen-grassland (without the potential to form peat)											
Cardamino-Montion	•	–	–	–	−41	–	–	•	–	−23	−41*
Caricion remotae	•	–	•	•	•	•	•	–	•	•	–
Convolvulion sepium	–	–		•	–	•	–	–	•	•	–
Filipendulp-Petasition	0	23	28	–	–	•	56*	4	−26	•	11
Calthion palustris	8	6	−5	−2	71**	–	10	−1	4	48*	2
Juncion acutiflori	35	4	–	–	–	–	–	10	–	–	28*
Molinion caeruleae	−26	−8	−2	62*	0	–	−20	1	9	–	1
Non-mire vegetation											
Violion caninae	–	–	•	–	–	•	–	–	–	•	–
Nardo-Juncion squarrosi	–	−52*	−23*	−17*	−2	−77**	•	−41**	−17**	8	−26**
Salicion cinereae	32	25*	0	–	–	–	32*	13	–	•	24*

Randomised sign test: *$p \leq 5\%$; **$p \leq 1\%$

–, no statement because of too small sample in the first survey (<20)

•, not found in both surveys

E-N-Alps Eastern part of the northern Alps, *W-N-Alps* Western part of the northern Alps

Assessment of changes in site conditions and species composition

Based on changes in Landolt's indicator values, the plots which were classified as mire vegetation in the first survey generally experienced a decrease in moisture and reduced fluctuations in water level (Table 4). The loss of water was associated with a better aeration of the soils, indicated by lower values for dispersity (Table 4). As a consequence of this, the mire soils lost organic matter (Table 4, decline in humus value). Further we observed an increased availability of plant nutrients and a reduced availability of light (Table 4). All these trends were stronger in plots which were not classified any more as mire vegetation in the second survey, but they are also significant for the plots which remained mire vegetation. In plots which became mire vegetation in the second survey only, we observed some opposite trends: moisture increased and had bigger fluctuations as well and the aeration of the soils was reduced. Other opposite trends were not significant (Table 4).

Table 3 Transition of communities in single mire sites

	Sites with increasing frequency	Sites with decreasing frequency	Sites with almost stable frequency	Total sites	Total score
Vegetation of bogs					
Sphagnion medii	23	26	11	60	1,315
Oxycocco-Empetrion herm.	15	21	14	50	623
Betulion pubescentis	23	17	17	57	974
Caricion lasiocarpae	–	–	–	28	175
Rhynchosporion albae	–	–	–	27	164
Scorpidio-Utricularion minoris	–	–	–	2	2
Vegetation of fens (with the potential to form peat)					
Caricion fuscae	23	35	19	77	712
Caricion atrofusco-saxatilis	–	–	–	19	173
Carcion davallianae	16	32	29	77	2,091
Glycerio-Sparganion	–	–	–	10	13
Magnocaricion	29	41	17	87	1,224
Phalaridion arundinaceae	–	–	–	8	41
Phragmition communis	15	18	9	42	501
Vegetation of fen-grassland (without the potential to form peat)					
Cardamino-Montion	–	–	–	17	59
Caricion remotae	–	–	–	1	1
Convolvulion sepium	–	–	–	14	41
Filipendulp-Petasition	–	–	–	59	313
Calthion palustris	35	28	24	87	2,595
Juncion acutiflori	–	–	–	39	171
Molinion caeruleae	–	–	–	55	456
Non-mire vegetation					
Violion caninae	–	–	–	7	9
Nardo-Juncion squarrosi	13	34	6	53	649
Salicion cinereae	–	–	–	46	342

Number of mire sites with increasing, decreasing or almost stable frequency of communities, whereas increasing, >110% of the score of the 1st survey; decreasing, <90%; almost stable, 90–110%

Total number of sites where the community occurs, total number of relevés assigned to it in both surveys. Only alliances with a total score of at least 500 are assessed

We assessed the change in site conditions of 15 alliances which were found at least 60 times in both surveys. To complete the observations of change in site conditions we assessed changes in species frequency or in case of non-transitions changes in populations of single species.

The trends mentioned above were observed not only in a global view of the mire vegetation but in numerous alliances too: a significant loss of moisture was observed in the plots which dropped out of nine alliances, a significant increase was observed only in the plots which dropped out of *Betulion pubescentis* (Table 5).

Caricion lasiocarpae and *Rhynchosporion albae* are alliances with a similar ecology (except for soil reaction, Pantke 2003). They occur as regional or altitudinal variants (Graf et al. 2010). Whereas for the plots remaining in these alliances we could hardly find any significant change in site conditions, we observed a significant decline of the moisture values and humus values in plots dropping out of the alliances. In plots which dropped out of *Rhynchosporion albae*, we observed in addition a increased availability of nutrients and a reduced availability of light. In the same plots the frequencies of 33 species increased significantly, none decreased. Among the species with increased frequency there were seven mosses (but no *Spagnum* spec.). In the plots which dropped out of *Caricion lasiocarpae* the decrease of *Sphagnum contortum* was the only siginficant species change.

Plots joining these alliances had a reduced aeration of the soil. In those which joined the *Rhynchosporion albae* we found in addition an increased moisture value and a reduced availability of nutrients (Table 5).

Table 4 Mean changes in Landolt's indicator values between second and first survey and their significance (Wilcoxon test), calculated separately for plots that belonged to a mire alliance only in the first survey, in both surveys or only in the second survey

Counts of plots	Mire in survey 1		Mire in both surveys		Mire in survey 2	
	632		5,228		556	
	p	Δ	p	Δ	p	Δ
Moisture	<0.0001	**−0.07**	<0.0001	**−0.03**	<0.0001	**0.04**
Changing moisture	<0.0001	**−0.04**	<0.0001	**−0.01**	<0.0001	**0.03**
Dispersity	<0.0001	**−0.05**	<0.0001	**−0.01**	<0.0001	**0.03**
Humus	<0.0001	**−0.05**	<0.0001	**−0.01**	0.27	<0.01
Nutrients	<0.0001	**0.07**	<0.0001	**0.02**	0.36	<0.01
Soil reaction	0.32	<0.01	0.44	<0.01	0.001	**0.04**
Light	<0.0001	**−0.07**	<0.0001	**−0.02**	0.08	−0.01
Temperature	0.1447	>−0.01	0.0013	**<0.01**	0.2552	>−0.01
Continentality	0.03	**<0.01**	0.0455	**<0.01**	<0.0001	**0.03**

Other communities like the *Caricion davallianae* seem to be more sensitive to changing site conditions. We observed significant changes in nearly all indicator values in plots remaining within the alliance and in plots dropping out of it. In most cases the change was significantly bigger in those plots that dropped out than in those plots that remained within this alliance. In plots joining this alliance we observed some opposite trends (Table 5). These trends are reflected too in the decrease and increase of species (Table 6).

In plots remaining within their alliance we observed 141 species with significantly altered populations in mostly one or two alliances. We summarize the following observations (Table 7):

- Twice as many species populations were increasing than decreasing. In *Sphagnion medii* and *Caricion davallianae* this ratio was more than seven.
- In the alliances of the bog ecosystem *Sphagnum* mosses, dwarf shrubs and trees have significantly increasing populations. Decreasing populations were not observed.
- Bryophyte species had twice as many decreasing populations as increasing ones.
- It seems that *Cyperaceae* species are replaced by grass species: *Cyperaceae* species had declining populations in most of the alliances, whereas increasing populations were observed only for one species each in *Sphagnion medii* and in *Caricion davallianae*. Grass species increased their populations in most of the alliances.
- Tall forbs increased their populations in *Caricion davallianae* and in alliances of fen grassland. Decreasing tall forb populations were observed only in *Calthion palustris*.

Discussion

"Pseudo" community transitions or "true" community transitions?

Any classification of vegetation stands assumes boundaries to exist in a continuum. If a continuum exists, discrete classification is always arbitrary to a certain extent. Numerical assignments of relevés to a predefined system is prone to misinterpretation for two reasons: first some of the classes may be very similar (Graf et al. 2010; Kočí et al. 2003; Dengler et al. 2008) and second some of the relevés may be intermediate (Graf et al. 2010; Jandt 1999; Pflume 1999; Täuber 2000). In both cases observed community transitions in plots could be caused by minimal floristic differences. We observed a drastic change in the assignments of plots to the mire communities. Over 30% of them belonged to a different community in the second survey compared to the first one. We found for the majority of alliances the floristic resemblance of paired relevés to be significantly lower in plots changing community than in plots not changing community (Fig. 1). Despite uncertainty caused by weaknesses of classification this suggests that changes in species composition can in fact be assessed on the community level as well.

Vegetation of bogs

Sphagnum dominated mire vegetation has mostly been viewed as powered by autogenic processes leading towards a stable system (Weber 1902; Zobel 1988), persisting so for centuries or millenia (Rydin and Barber 2001; Kuhry 1997). Nevertheless recent floristic and stratigraphic

Table 5 Changes in site conditions (Landolt's indicator values) of plots which remained in the alliance and of plots which were reclassified in the second survey

	Sphagnion medii	Oxycocco-Empetrion hermaphroditi	Betulion pubescentis	Caricion lasiocarpae	Rhynchosporion albae	Caricion fuscae	Caricion atrofusco-saxatilis	Caricion davallianae	Magnocaricion	Phragmition communis	Filipendulo-Petasition	Calthion palustris	Juncion acutiflori	Molinion caeruleae	Nardo-Juncion squarrosi
Plots which remained within the alliance															
Count of plots	428	153	276	46	47	146	36	749	336	168	59	882	23	104	152
Δ-moisture	−0.02							−0.04				−0.02		−0.03	−0.02
Δ-changing moisture								−0.01		−0.05	−0.03	−0.02		−0.03	
Δ-dispersity	−0.01		−0.02					−0.01	−0.01	0.04		−0.02		−0.03	−0.02
Δ-humus	−0.02		−0.03		−0.03			−0.03		0.07		−0.01	−0.06	−0.02	
Δ-nutrients		0.03						0.02				0.03		0.03	
Δ-soil reaction			0.02					−0.01		0.05					
Δ-light	−0.03	−0.02				−0.03		−0.03				−0.02			
Δ-temperature						0.03									
Δ-continentality	0.01		−0.01					<0.01							
Plots which dropped out of the alliance															
Counts of plots	228	162	193	36	22	235	57	328	305	88	89	403	52	123	221
Δ-moisture	−0.03		0.04*	−0.08	−0.30*	−0.05	0.02*	−0.04	−0.01*	−0.13*	−0.05	0.01*	−0.07	−0.06*	−0.05
Δ-changing moisture							0.04	−0.04*	−0.03*	−0.03	−0.03	−0.02	−0.07*	−0.02	−0.03
Δ-dispersity	−0.04				−0.17*			−0.03*	−0.04*		−0.04		−0.08*		
Δ-humus	−0.08*		0.06	−0.06		−0.03*		−0.01	−0.07*	−0.03*		0.01*	−0.07		−0.04
Δ-nutrients	0.08*	0.03*			0.08*	0.03*		0.07*			−0.06	<0.01*	−0.05		
Δ-soil reaction	0.09*		0.05			0.02	−0.05*	−0.07*			−0.03			−0.04	0.06*
Δ-light	−0.05	−0.03			−0.13*	−0.02	0.05	−0.05*			0.03	−0.03	−0.04	−0.02	
Δ-temperature	0.03*	0.03*						0.01					−0.02	0.01	0.02*
Δ-continentality				0.04*				0.02*		−0.04*					
Plots which joined the alliance															
Counts of plots	231	155	229	47	37	185	44	265	247	77	106	428	73	125	124
Δ-moisture	−0.03		−0.05		0.08			<0.01*	0.07*		−0.04	−0.06*		−0.06*	−0.05
Δ-changing moisture								0.03*		0.04*		−0.03		−0.01	
Δ-dispersity	0.01*		−0.04	0.04*	0.04*		0.06	0.01*	0.03*						
Δ-humus	0.03*	0.02*	−0.02		0.02*	−0.03*		−0.01*		−0.03*	−0.04	−0.06*	−0.02*	−0.03	−0.04
Δ-nutrients	−0.04*	−0.03	0.04		−0.05			−0.02			0.05*	0.06*	0.04		
Δ-soil reaction	−0.05*	0.03					0.05	0.06*		0.07		<0.01			
Δ-light		0.03*	−0.05*			−0.02		0.01			−0.03*	0.01*		−0.05*	
Δ-temperature					0.08*					0.06*	−0.03	0.01		<0.01*	
Δ-continentality	0.02*	0.02*	<0.01*		−0.04	0.01		<0.01*	0.01*			0.01			

Only significant changes of indicator values are given (Wilcoxon test, $p \leq 0.05$). Significant differences between transitions and non-transitions are marked with * (Wilcoxon test, $p \leq 0.05$). In italics: value not significantly different from 0, but significantly different from the corresponding value of non-transition

Table 6 Change of species frequency in case of community transitions of *Caricion davallianae* and Landolt's moisture values

Plots which dropped out of *Caricion davallianae*				Plots which joined *Caricion davallianae*			
Species with decreased frequency	N value	Species with increased frequency	N value	Species with decreased frequency	N value	Species with increased frequency	N value
Aster bellidiastrum*	3	*Agrostis capillaris**	3	*Agrostis capillaris****	3	*Acer pseudoplatanus**	3
Bartsia alpina*	4	*Agrostis stolonifera* agg.*(ri)	x	*Juncus inflexus**	4	*Aster bellidiastrum***	3
Bryum pseudotriquetrum*	x	*Antennaria dioica**	2	*Leontodon helvet.**	3	*Campylium stellatum***	5
Calliergonella cuspidata*	4	*Athyrium filix-femina***	3	*Sagina saginoides**	3	*Carex davalliana***	5
Campylium stellatum***	5	*Carex leporina**	3	*Trifolium repens**	3	*Carex frigida**	5
Carex davalliana*	5	*Carex sylvatica***	3			*Carex hostiana**	4
Cratoneuron commut. agg.*	x	*Dactylis glomerata* agg.*	3			*Dactylorhiza fistulosa***	5
Dactylorhiza incarnata*	5	*Epilobium alpestre***	4			*Gentiana asclepiadea**	3
Dactylorhiza maculata*	4	*Festuca pratensis**	3			*Gentiana bavarica**	4
Eriophorum latifolium**	5	*Galeopsis tetrahit**	3			*Gymnadenia conopsea**	3
Euphrasia hirtella*	2	*Luzula multiflora***	3			*Linum catharticum**	3
Fissidens adianthoides agg.*	x	*Oxalis acetosella**	3			*Pinguicula vulgaris**	4
Gymnadenia conopsea**	3	*Plantago lanceolata**	2			*Platanthera chlorantha**	4
Pinguicula vulgaris*	4	*Poa trivialis***	3			*Primula farinosa***	4
Scorpidium revolvens agg.*	x	*Rhytidiadelphus loreus**	3			*Quercus robur**	3
Swertia perennis*	5	*Solidago virgaurea**	3			*Selaginella selaginoid.**	3
Tofieldia calyculata*	4	*Trifolium repens**	3			*Sphagnum warnstorfii**	x
		Veronica chamaedrys*	3			*Trifolium badium**	3
						Valeriana dioica*	4

ri reduced increase (lesser than expected value, i.e. a relative decrease). Only species with a minimum frequency of 10 in one of the two surveys are considered

x not known

χ^2 test: *$p \leq 0.05$, **$p \leq 0.01$.***$p \leq 0.001$

studies document changes in dominance and species composition of its vegetation (Svensson 1988; Gunnarsson et al. 2002). Sjögren and Lamentowicz (2008) found in a site in the Jura Mountains, that the bog vegetation is not older than 300 years and the major dominance of *Sphagnum* spec. was restricted to the period from ca. 1950 to 1985. Even pristine *Sphagnum* dominated bogs and fens are subjected to a strong dynamic in terms of species turnover, abundance change and pH-change (Gunnarsson et al. 2002). In our sample the communities of the bog ecosystem could keep their frequencies, or even increased it (Tables 1, 2: *Rhynchosporion albae*). Anyhow there was a big part of transitions in both directions and the trends were sometimes different in different geographical regions. Hummock communities could compensate their losses by transitions from *Nardo-Juncion squarrosi*. Transition mire and hollow communities had a compensation for their losses to a certain extent from *Magnocaricion*.

The observed loss of moisture in both plots dropping out of their bog alliances and plots remaining within it goes along with the observations of Bragazza (2006) on an southern Alpine bog and with the findings of Nordbakken (2001) and Gunnarsson et al. (2002) in Swedish mires.

Bragazza (2006) found autogenic reasons (mainly peat accumulation) for drying out, whereas Nordbakken (2001) and Gunnarsson et al. (2002) name change in site factors to be responsible for it (reduced rainfall, altered waterflow from the surroundings). Our observations support the findings of Nordbakken (2001) and Gunnarsson et al. (2002) rather than those of Bragazza (2006): At the same time as the plots were drying out, we observed a loss of soil humus content and increased soil-nutrient contents, indicating that peat is rather decomposed than accumulated. Gunnarsson et al. (2002) also found in Sweden increased soil nutrient availability and increasing populations of trees and dwarf shrubs. Whereas increased nitrogen deposition was held responsible for the increased tree growth in Sweden, Fosaa et al. (2010) regarded drainage-induced water deficit as the driving force for increased woody plant populations and increased nutrient availability in a blanket bog of the Faroe Islands. Our data (reduced moisture values) suggest that water deficit also contributed to the modification of Swiss bogs.

Because we did not find any opposite trends in site factors between plots which dropped out of their communities and plots which remained within them, we are afraid,

Table 7 Number of species with increased or decreased populations in plots remaining in their alliances

	Sphagnion medii	Oxycocco-Empetrion hermaphroditi	Betulion pubescentis	Caricion lasiocarpae	Rhynchosporion albae	Caricion fuscae	Caricion atrofusco-saxatilis	Caricion davallianae	Magnocaricion	Phragmition communis	Filipendulp-Petasition	Calthion palustris	Juncion acutiflori	Molinion caeruleae	Nardo-Juncion squarrosi
Population increase															
Trees	2		3	2				1						1	
Shrubs									1						
Dwarf shrubs	5	1	1												3
Grasses	1	3		1		1		5	2	1	2	5		6	1
Cyperacee	1							1							
Rushes				1				1							
Sphagnum mosses	1		2												1
Other bryophytes	3		3					3				2			
Tall forbs								7	2	1		7		2	
Other plants	1	1	1	2		1	2	33	1	1	2	20	1	6	
Population decrease															
Trees															
Shrubs			1				1								
Dwarf shrubs				1	1										
Grasses				1	1	1					2	3		2	1
Cyperacee	2	2					3	4			1	6	1	3	1
Rushes												1			
Sphagnum mosses														1	
Other bryophytes	2	2	2		3	2	5	3			1	1	3	4	1
Tall forbs												4		1	
Other plants				2							1			1	

that the present equilibrium between gains and losses may switch to more losses in future.

Vegetation of fens and fen grassland

The fen communities have the biggest frequency declines. Even though these trends are not all significant, we observe declines in nearly all geographical regions and altitudinal belts (Table 2). The frequent communities (small sedge fens and *Magnocaricion*) all have a net change to *Calthion palustris*, and *Calthion palustris* itself has a net change to non-mire communities. As Bergamini et al. (2009) and Bollens et al. (2001), we observed an increased nutrient availability, a decreased soil humus content and a stabilisation of the moisture on a dryer level in those plots which dropped out of their community. At the same time we observed a reduction of light availability which goes along with the findings of Pauli et al. (2002), that the nutrient enrichment leads to a higher above ground biomass production. According to Pauli et al. (2002) habitat specialists do not react in a short time to altered site conditions but generalists increase their populations. Mälson et al. (2008) found 5 years after the drainage of a rich fen a decline of site typical mosses, followed by an increase of sedges and pioneer bryophytes and later of a few dominant species as *Molinia caerulea*, *Betula pubescens* and some *Sphagnum* species. As in Switzerland nearly all mires have been drained for decades, we cannot confirm Mälsons findings. Ter Braak and Wiertz (1994) found that reduced soil moisture leads to a population decrease of typical wetland species, whereas meadow species increased. In contrast to Pauli et al. (2002) and in accordance to ter Braak and Wiertz we found some decline of *Cyperaceae* and some increase in grass populations.

Because we did not find any opposite trends in the plots which remained in their community, we are afraid that their persistence will be only temporary.

Conclusions for nature conservation

Nardo-Juncion squarrosi is not considered a mire community as stated in the Swiss legislation. We found it almost only on peaty soils (Landolt's humus value around 4.5). According to Pantke's (2003) definitions the only exclusive species to separate it from the bog alliances are *Agrostis canina* and *Juncus squarrosus*. Because of its floristic and ecological proximity to the groups of *Oxycocco-Sphagnetea* and the big number of plots in transition from and to bog communities we recommend to take it as a bog community. If we do this, we will note that the bog communities too have declining frequencies, not only the fen communities.

Mires in Switzerland are suffering from a loss of soil moisture and a decrease of soil humus content. We interpret our observation of declining soil humus contents, that Swiss mires are no longer able to produce peat, but actually in contrast act as a source of CO_2. It is urgent to restore their hydrology to stop further peat losses (Dierssen and Nelle 2006). With regard not only to their future conservation but to the expected climate change as well, their function as peat producers should be re-established. It will be necessary to raise the mean water table in summer to a maximum depth of about 10 cm. At this level, fens start to produce peat again, whereas they loose peat if the water table is lower (Blankenburg et al. 2001). On the discharge of phosphorous from rewetted mires there are no statements in literature yet, which could be generalized (Koppisch et al. 2001). At least on alkaline peat, a rewetting of the soils will reduce the availability of phosphorous and potassium (Koppisch et al. 2001) and thus will counteract the observed nutrient enrichment. In Germany on formerly fertilised acidic peat an opposite effect of rewetting was observed: the availability of phosphorous increased (Rupp et al. 2004; Zeitz and Velty 2002). But we think, that this situation will hardly occur in Switzerland: here the mire sites which are nature reserves used to be treated rather as waste land by the farmers and they were never fertilized.

Mälson et al. (2008) observed after the rewetting of a drained fen only a tardy return to the original stage. Peat degradation, dispersal limitation and the presence of dominant species are the reason for it. After decades of deteriorated hydrology we cannot expect a rapid success in conserving our mire communities even if the restoration of the hydrology of the mire is done. Whereas the bogs often present a hydrological entity, fens and fen grassland usually make part of a larger hydrological system. Their conservation depends on the hydrogeological structure of the landscape (Grootjans et al. 2006, 1996; Wassen and Grootjans 1996; Grootjans and van Diggelen 1995), meaning, that mire conservation has to consider the surroundings as well as the mire sites themselves.

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