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Secondary succession in a Swiss mire after a bog burst

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Abstract Severe natural disturbances can lead to the recovery of the original vegetation or the shift to new vegetation types. While post-disturbance succession is well documented for regularly disturbed ecosystems, little is known about the pathways and rapidity of vegetation dynamics after rare events such as peat mass movements in bogs. We monitored the floristic changes in a mire subject to a bog burst in 1987 for two decades through the repeated sampling of permanent plots. The mean species number per plot increased continuously, while the evenness increased only in the first decade and then slightly decreased. Declining species were mostly mire species, while colonist species were mostly wet meadow species. Species turnover was higher in the first decade after the disturbance, and was also higher in the area of peat erosion than in the area of peat accumulation. Changes in plant species composition indicate a succession towards tall-forb vegetation (*Filipendulion*), acidic fen vegetation (*Caricion fuscae*) and swamp willow forest (*Salicion*). We conclude that the effects of the disturbance are still ongoing, and that the mire's potential for recovery is therefore difficult to predict.

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Résumé Les perturbations naturelles sévères peuvent conduire soit au rétablissement de la végétation d'origine, soit au déplacement vers un nouveau type de végétation. Alors que la succession végétale est bien documentée pour les écosystèmes régulièrement perturbés, la dynamique de la végétation après des événements rares comme les glissements de terrain dans les hauts marais est peu connue. Nous avons suivi pendant 20 ans les changements floristiques dans un marais soumis à un glissement de terrain en 1987 en effectuant des relevés sur 98 carrés permanents. La végétation perturbée consistait en un mélange de groupements végétaux de haut marais et de bas marais acide et basique. Le nombre moyen d'espèces par carré permanent a augmenté continuellement alors que l'abondance relative des espèces n'a augmenté que la première décennie et a légèrement diminué la deuxième. Les espèces en déclin sont principalement des espèces de marais alors que les espèces en expansion sont des espèces de prairies humides. Le turnover des espèces a été plus élevé la première décennie suivant la perturbation que la deuxième et a été aussi plus élevé dans la partie supérieure érodée que dans la zone d'accumulation de tourbe au bas du glissement. La zone perturbée s'est embuissonnée et est devenue plus sèche, plus riche en nutriments et plus acide. Les groupements végétaux montrent différentes tendances évolutives et nos résultats indiquent une succession vers le bas marais acide (*Caricion nigrae*), la mégaphorbiaie (*Filipendulion*) et la forêt de saules (*Salicion*). Les effets du glissement sont encore actifs et le potentiel de récupération du marais reste difficile à prédire.

Keywords Disturbance · Peat slide · Long-term monitoring · Species diversity · Species turnover · Ecological indicator values · Switzerland

Introduction

Ecological disturbance is associated with the partial or total destruction of plant biomass (Grime et al. 2007), and thereby creates an opportunity for new plants to become established (Sousa 1984). Some ecosystems are frequently affected by natural disturbances, such as windfall, flood, fire or landslides (Fischer 1992; Frelich and Reich 1995; del Moral and Jones 2002; Kenderes et al. 2007). In these systems, disturbance is usually followed by a rapid recovery of the previous vegetation (Fischer et al. 1990; Delarze et al. 1992; Guo 2003). Conversely, vegetation recovery is generally slow in ecosystems that rarely experience natural disturbances, such as mires. For example, long-term studies of post-fire succession on moors in England (Maltby et al. 1990) and heathland in France (Clement and Touffet 1990) revealed that the vegetation had not yet developed to its pre-fire state after 10 years.

Post-disturbance vegetation recovery is often slow or even impossible if the topsoil has been disturbed in addition to the vegetation because succession takes place under altered abiotic conditions. One striking example are bogs in which peat harvesting has caused a total destruction of biomass, the complete loss of the soil seed bank and unfavourable microclimatic conditions (Salonen 1987). In a study of secondary succession following peat harvesting, the vegetation had not yet recovered its original composition after 50 years (Soro et al. 1999).

Natural soil disturbances of a severity comparable to peat harvesting may occasionally occur in bogs as a consequence of peat mass movements such as bog burst, bog slide or bog flow (Dykes and Warburton 2007). This particular type of disturbance also occurs in degraded mires characterized by artificial drainage as a consequence of mining activity or agricultural practices (James and Alexander 1998; Warburton et al. 2004).

Little research has been done on vegetation succession following bog burst. Such events have been reported in many locations in northern Europe, but these studies describe the morphological and geological aspects and give no information on vegetation changes. We have found only one study of vegetation changes following a bog burst in Ireland (Feehan and O'Donovan 1996). Improved drainage due to the erosion and removal of the area where the peat mud had accumulated resulted in an increased growth of heather, especially on the dislocated peat rafts, and a decreased abundance of graminoids such as the purple moor-grass (*Molinia* ssp.) and cottongrasses (*Eriophorum* ssp.).

A bog burst occurred in September 1987 in the mire of la Vraconnaz in the Jura Mountains in Switzerland (Feldmeyer-Christe and Mulhauser 1994) and provided a unique opportunity to study changes in community assembly and the dynamics of individual species. We started monitoring the vegetation in 1988. Since the disturbance produced a major change in the hydrological and pedological conditions, we expected a rapid decline in mire vegetation and an invasion of species from the neighbouring meadow and pasture areas. However, changes in vegetation were slower than expected. In 1998, after 10 years, differences in indicator values indicated a general eutrophication and desiccation and a closing of the herb layer in the slide area. We also noticed an increase in species richness. Re-colonisation on the bare peat progressed slowly and with random settlement at first. We concluded at the time that an observation period of 10 years was too short to detect clear successional trends in the vegetation (Feldmeyer-Christe 1995; Feldmeyer-Christe and Küchler 2002).

The first aim of the present study was to evaluate the recovery potential of the mire 20 years after the disturbance. Did alternative plant community types replace the original mire vegetation or has the disturbed area healed and recovered its previous composition? The second aim was to determine how the disturbance has affected species diversity. In a productive environment, the main factor limiting species diversity is competitive exclusion. Disturbance, by temporarily reducing competition, increases species diversity (Odion and Sarr 2007). In an unproductive environment such as a mire, where species growth is limited by abiotic stress due to low resource availability, disturbance can add to this stress and lead to a decrease in species diversity (Huston and Smith 1987; Chesson 2000; Pellerin et al. 2009). The third aim was to determine which species showed a persistent increase or decrease in abundance over time following the disturbance.

Materials and methods

Study area

The bog of La Vraconnaz is a sloping bog situated in the calcareous Jura Mountains (Switzerland) at a mean altitude of 1,090 m (Grünig et al. 1986; Broggi 1990). Mean annual precipitation is between 1,320 and 1,480 mm. Mean annual temperature is between 4 and 5°C, with frost possible in almost any month of the year. The mire has a surface of about 30 ha of raised bog, surrounded by 25 ha of fen. It is completely surrounded by agricultural land and forests dominated by *Picea abies*. Like most of the Jura bogs, it was cut for fuel until World War Two. When peat cutting ended in 1945, the mire was partially used for grazing. After the bog burst, farmers installed fences to prevent cattle entering the dangerous disturbed area.

The bog burst in 1987 affected about 15 ha on the western part of the mire (Fig. 1). It occurred after an

Fig. 1 *Upper part* of the mire of la Vraconnaz 1 year after the slide (Photograph E. Feldmeyer-Christe 1988)

exceptional climatic event, when after 3 weeks of drought, almost 180 mm of rain fell within one night. The aerial photograph shows how the mechanism of the peat slide was similar to the movement of a glacier (Fig. 2). Within one night, about 150,000 m^3 of peat slid along the weak slope for a distance of about 300 m (Feldmeyer-Christe and Mulhauser 1994; Feldmeyer-Christe and Küchler 2002). In the upper part of the slide, the peat was partly eroded down to the mineral sub-soil. Peat rafts were compressed in the lower part of the slide, so that cracks filled with water developed, separated by rolls of bare peat pushed up by the compression. The disturbed vegetation included various communities of bog plants (*Sphagnion magellanici*), *Calluna* heath, acidic and calcareous fen plants (*Caricion fuscae* and *Caricion davallianae*) and patches of tall-forb vegetation (*Filipendulion*).

Vegetation data

One hundred permanent plots were established in 1988 in the burst area and in the undisturbed neighbouring area. These squared plots are oriented north to south and are marked with a wooden stake at their northeast corner. The position of the plots was measured with an accuracy of ±5 cm. It was not possible to set up a random sample in the burst area because the deep fissures and cracks within the peat mass, as well as the unstable peat rafts, made some parts impossible to access. We chose the plots so as to include the most representative plant communities. Some of the plots (22) were set up in pioneer habitats like bare peat, mineral soil, new pond banks or new hollows. Two plots have been lost since 1988. The surface of most of the plots is 1 m^2 (78), some are 4 m^2 (17) and five plots in the forest area northeast of the slide are 25 m^2. The plot size of 1 m^2 was imposed by the soil fragmentation caused by the slide.

Two different sets of records were used in this study, depending on the type of analysis: one including all plots (set 1 = 98 plots) and another one (set 2 = 88 plots) excluding plots without vegetation at the beginning of the study.

Field sampling involved a full record of vascular plants and bryophytes according to Braun-Blanquet (1964). The vegetation records include cover estimations for trees,

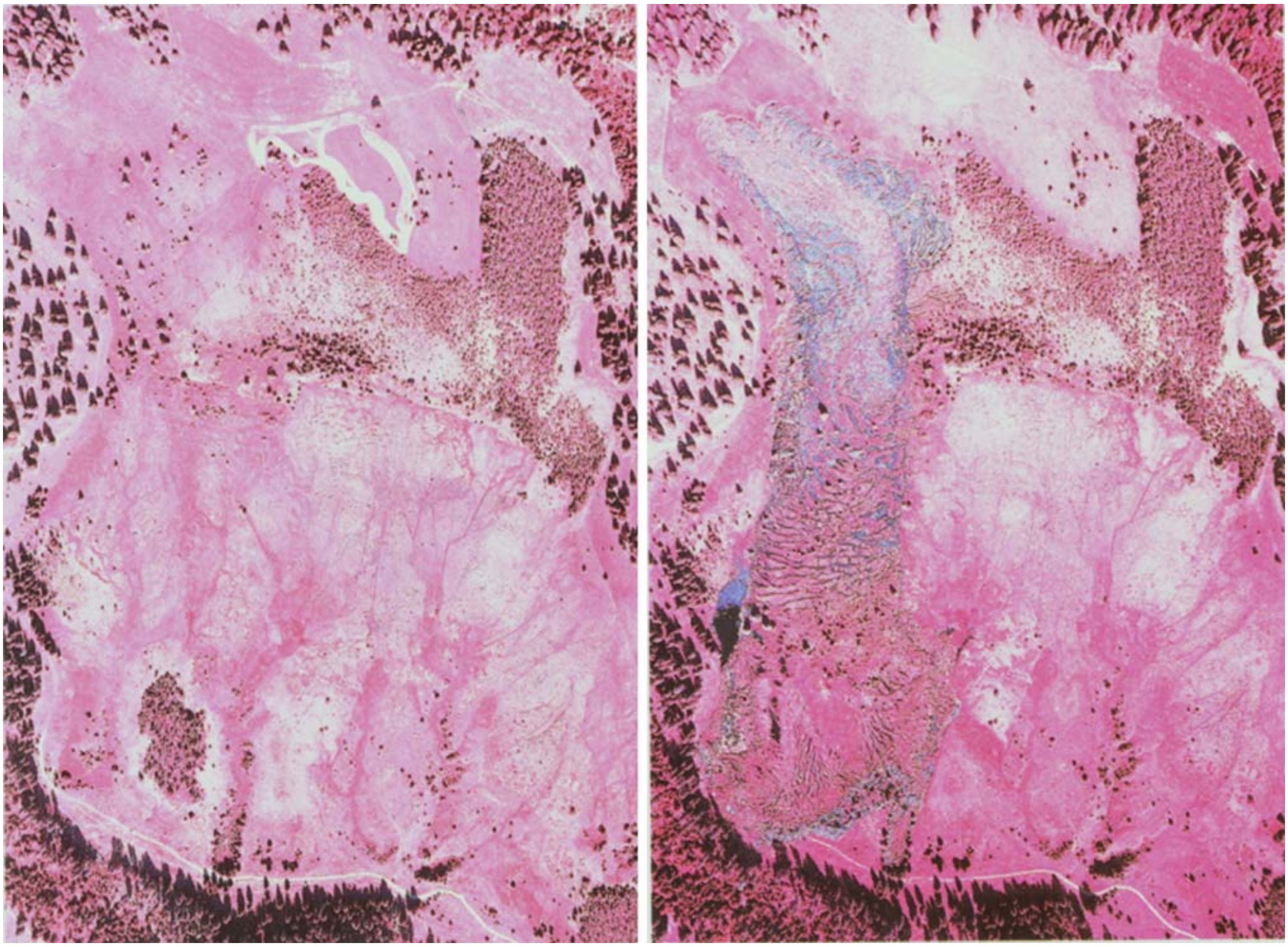

Fig. 2 Infrared false colour aerial photographs of the bog of la Vraconnaz on 31 July 1984, 3 years before the bog burst, and on 20 October 1987, one month after the disturbance. Photos taken by the Coordination Centre for Aerial Photographs, Dübendorf, Switzerland

shrubs, herbaceous and moss layers, bare peat and open water. The vegetation records of 1988 having been made in the first vegetation period following the burst should therefore reflect the same vegetation state as before the disturbance. Full samplings were performed in 1988, 1999 and 2007. To reduce phenological bias, we always sampled the vegetation in the first week of July. The database today contains 920 records. Nomenclature follows Aeschimann and Heitz (1996) for vascular plants and Schnyder et al. (2004) for bryophytes.

Statistical analyses

Species richness and evenness were calculated for 1988, 1999 and 2007. Evenness was expressed by the Shannon equitability index

$$J = \frac{-\sum_{i=1}^{s} p_i \ln p_i}{\ln s}$$

where s number of species, p_i abundance of the ith species expressed as a proportion of total cover.

For these calculations, we converted the Braun-Blanquet scale to cover percentages: $r = 0.03$, $+ = 0.3$, $1 = 2.2$, $2 = 11$, $3 = 35$, $4 = 60$, $5 = 87$.

We also performed variance analysis with polymonial contrasts to detect a trend in the changes (Lindsey 1994). A linear trend indicates a continuous increase or decrease. A quadratic trend indicates an acceleration or deceleration. Overall changes in species abundance were analysed by calculating species indicator values *INDVAL* (Legendre and Legendre 2006) for the years 1988 and 2007. This index measured to what degree a species' abundance in one year exceeded the abundance in the other year. Thus, a species' *INDVAL* for 1988 was calculated as $p_{1988} \times n_{1988}/(n_{1988} + n_{2007})$, where p_{1988} proportion of sampling plots occupied by the species in 1988, n_{1988} number of sampling plots occupied by the species in 1988, n_{2007} number of sampling plots occupied by the species in 2007.

INDVAL for 2007 was obtained similarly. Species whose *INDVAL* for 1988 was higher than that for 2007 were considered to have decreased or disappeared in 2007.

Conversely, species with higher *INDVAL* in 2007 were considered to be new or increasing.

To assess changes in species composition at the plot level, species turnover was calculated for the time spans 1988–1999 (early succession) and 1999–2007 (late succession) for each of the 98 plots. We used the Wilcoxon rank sum test to analyse the difference between the turnovers in the first and the second time span.

Turnover $T = (A + B)/(A + B + C)$

where A species present only at time $t = 0$, B species present only at time $t = 1$, C species present at both points in time, D $A + B$+C.

To interpret vegetation changes in terms of site conditions, we used Landolt's system of indicator values (Landolt 1977), adapted for mire biotopes (Feldmeyer-Christe et al. 2007). Mean indicator values were calculated for each relevé, and the significance of changes between 1988 and 2007 was tested by variance analysis with polynomial contrasts.

Vegetation succession was analysed by considering transitions between plant community types. We attributed each relevé to one phytosociological alliance and then built up a matrix of transitions between vegetation groups from 1988 to 2007. The attribution of relevés to alliances was made objectively based on external references, i.e. published vegetation records that had been classified into various alliances of bog, fen and meadow through phytosociological studies. For the alliances of *C. davallianae, C. fuscae* and *Filipendulion*, we used fen and wet meadow records from the Swiss Jura (Gallandat 1990). For the *S. magellanici*, we took mire records from Austria (Steiner 1992). Vegetation records of the *Cynosurion* were taken from Dietl and Jorquera (2003) and those of *Salicion* from the Swiss Jura (Richard 1975).

Table 1 Mean species richness and evenness in 98 plots for three time periods

	Species number	Mean species number per plot	Evenness index
1988	141	12.61 ± 8.68	0.56 ± 0.27
1999	169	16.95 ± 7.60	0.65 ± 0.16
2007	175	18.23 ± 6.54	0.61 ± 0.12

Differences between years are significant ($P < 0.0001$) for species number and the evenness index

We classified our vegetation data according to these references in the following way: first, the mean indicator values per record (Landolt 1977), adapted for mire biotopes (Feldmeyer-Christe et al. 2007), were calculated for the reference records as well as for our data. We then used the reference records as training data set for a generalized linear model (GLM). The GLM consisted in separate logistic (binomial) models with quadratic terms for each vegetation types. We chose for each plot the most probable vegetation type. All plots in the training data were assigned correctly. Finally we built a transition matrix of the vegetation groups between 1988 and 2007.

To enable spatially explicit analyses of the changes, we additionally determined the characteristic species for each vegetation group by calculating the Species Indicator Values *INDVAL* (Legendre and Legendre 2006) on the reference data. A species was considered as characteristic for a group if its *INDVAL* for that group was at least 0.25 and at the same time at least three times higher than its *INDVAL* for any other group. We followed the evolution of the vegetation groups in our data set by calculating the proportions of the cover of characteristic species in the entire vegetation cover. The changes were tested by variance analysis with polynomial contrasts.

To visualize the spatial distribution of changes, the data were smoothed with a window of variable side length. The width of the window was adjusted between 50 and 200 m in order to contain five values. If less than three values were found for a 200 m window, a missing value was generated. If more than five values were found for a 50 m window, the window size was maintained and all the values were evaluated. The smoothing consisted in averaging the

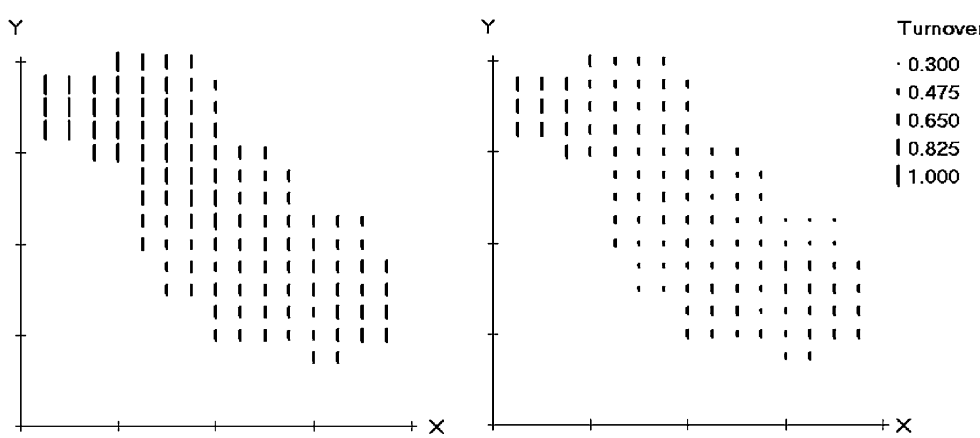

Fig. 3 Spatial distribution of the turnover intensity in the slide area calculated for 2 periods, 1988 to 1999 (*left*) and 1999 to 2007 (*right*); *X* axis and *Y* axis, coordinates of the Swiss National Grid; spacing of the data points = 50 m. Peat moved from the northwest (*top left* in the figure), where the zone of peat erosion is situated, to the south-east (*bottom right* in the figure), which corresponds to a zone of peat accumulation

Table 2 List of species showing the highest values for the *INDVAL* index in 1988 (upper part) and in 2007 (lower part)

Species	*INDVAL*	Frequency	
		1988	2007
Group 1988			
Carex echinata Murray	0.25	33	11
Carex hostiana DC.	0.16	19	3
Menyanthes trifoliata L.	0.15	20	7
Danthonia decumbens (L.) DC.	0.08	9	1
Carex flacca Schreb.	0.06	8	2
Prunella vulgaris L.	0.06	7	1
Dactylorhiza fistulosa (Moench) Baum. & Künk.	0.05	5	0
Carex pallescens L.	0.04	4	0
Juncus alpinoarticulatus Chaix	0.04	4	0
Juncus articulatus L.	0.04	4	0
Lotus pedunculatus Cav.	0.04	4	0
Dicranum bergeri Hoppe	0.03	3	0
Holcus lanatus L.	0.03	3	0
Primula farinosa L.	0.03	3	0
Sphagnum palustre aggr.	0.02	3	1
Group 2007			
Cirsium palustre (L.) Scop.	0.45	10	53
Festuca rubra aggr.	0.42	3	44
Angelica sylvestris L.	0.36	2	38
Galium palustre L.	0.3	8	35
Polygonum bistorta L.	0.27	13	36
Crepis paludosa (L.) Moench	0.25	3	27
Filipendula ulmaria (L.) Maxim.	0.2	4	24
Rumex acetosa L.	0.14	1	15
Equisetum fluviatile L.	0.12	0	12
Picea abies (L.) H. Karst.	0.11	2	13
Trollius europaeus L.	0.1	0	10
Lathyrus pratensis L.	0.1	2	11
Hylocomium splendens (Hedw.) Schimp.	0.08	4	11
Genista tinctoria L.	0.07	1	8
Salix myrsinifolia Salisb.	0.06	0	6

values within the window with an inverse triangular weighting of the distance from the window centre.

All statistical tests were performed with Vegedaz (Küchler 2008) and S-Plus programmes.

Results

A total of 230 species were recorded during the three vegetation surveys (1988, 1999 and 2007). The total number of species recorded in the 98 plots in one year increased from 141 species in 1988, to 169 in 1999, and 175 in 2007 (Table 1). These changes in species richness were a result of both the arrival of new species (53 sedges, grasses, forbs and trees and 16 mosses) and species disappearances (24 sedges, grasses and forbs and 11 mosses). At the plot level, species richness increased on average by 4.3 species (+34%) between 1988 and 1999 and by 1.3 species (+7.5%) between 1999 and 2007 (Table 1). The evenness increased in the first period, followed by a slight decrease in the second period (Table 1).

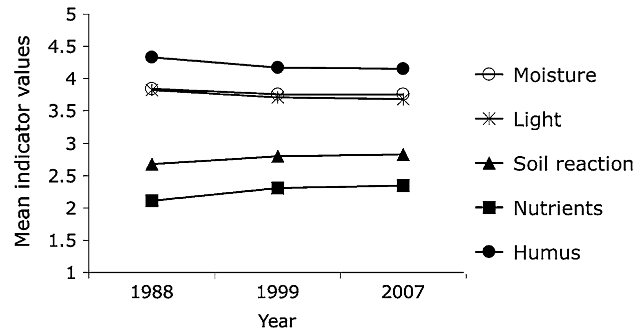

Fig. 4 Mean indicator values for moisture, light, soil reaction nutrients and humus calculated for 98 plots in 1988, 1999 and 2007. Changes are significant between years ($P < 0.001$) with a significant linear trend ($P < 0.001$) for all indicator values

Species turnover was significantly higher ($P < 0.001$) in the first decade (64.2 ± 0.13) than in the second one (55.5 ± 0.15). The level of turnover was much higher in the area of peat erosion in the upper part of the slide (top left in the figure) than in the area of peat accumulation in the lower part (Fig. 3).

Species that strongly decreased in frequency and cover between 1988 and 2007 were mostly mire species such as *Carex echinata, Carex hostiana* and *Menyanthes trifoliata,* while increasing species were grassland species (*Cirsium palustre, Festuca rubra, Angelica sylvestris, Polygonum bistorta* and *Trollius europaeus* as well as the tree species *Picea excelsa* and *Salix myrsinifolia* (Table 2; Fig. 4).

All ecological indicator values showed significant changes between years ($P < 0.001$, with Bonferroni correction for multiple testing of five indicator values). Indicator values for humus, light and moisture decreased, while those for nutrients and soil reaction increased (Fig. 5). The decrease in humus and light values and the increase in nutrient values affected the whole mire. In contrast, moisture values decreased in the upper and lower parts of the disturbed area but increase in the south-east part, where a new pond developed after the slide. Reaction values increased to a varying degree in the whole area, except for the north-east part, which has an ombrotrophic bog directly above it.

The total cover of species that are characteristic of mire vegetation (*S. magellanici*, *C. davallianae*) decreased between 1988 and 2007, while the cover of tall-forb (*Filipendulion*) species increased (Fig. 6). The decrease in *S.*

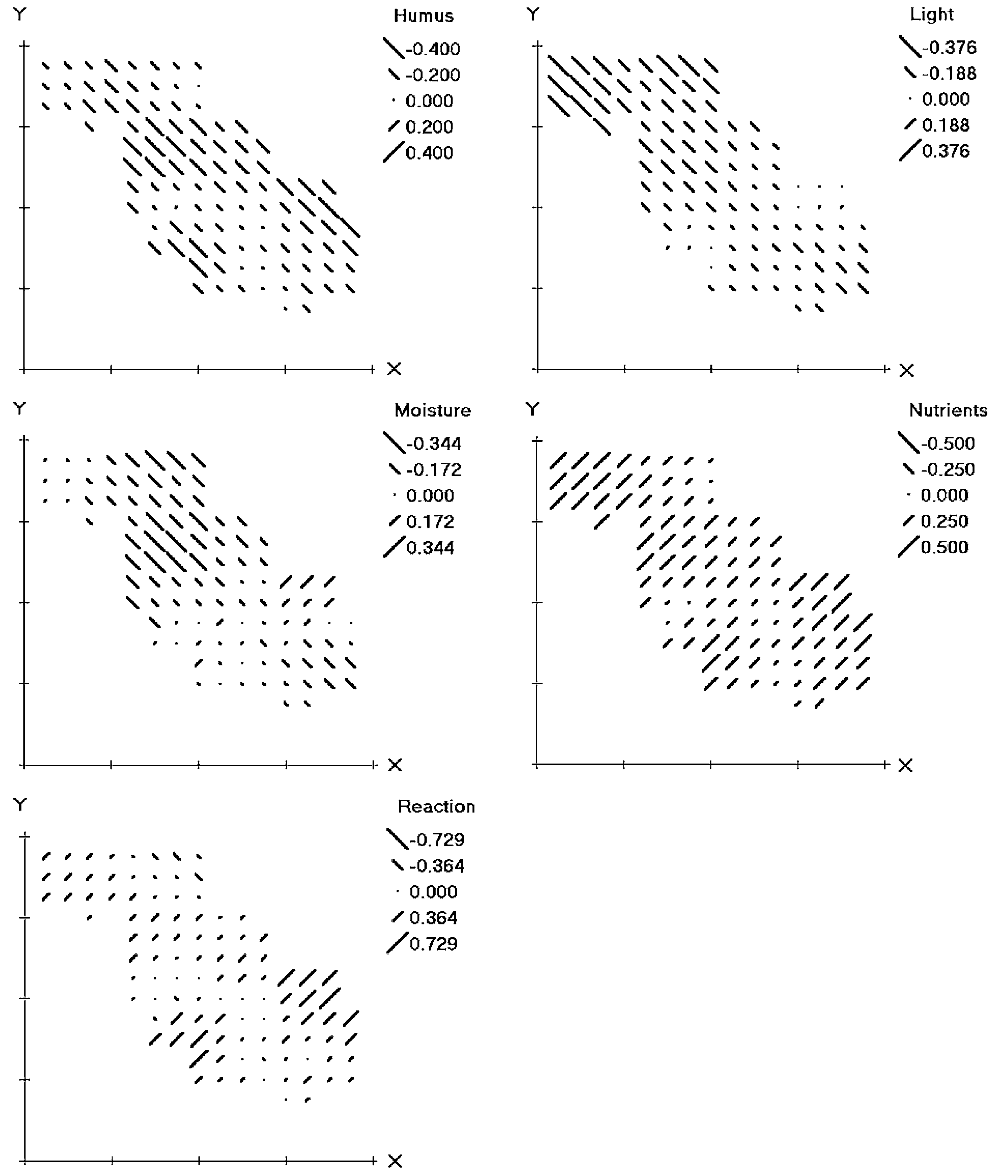

Fig. 5 Spatial distribution of indicator values changes between 1988 and 2007 in the disturbed area; *X* axis and *Y* axis, coordinates of the Swiss National Grid; spacing of the data points = 50 m. Peat moved from the northwest (*top left* in the figure), where the zone of peat erosion is situated, to the south-east (*bottom right* in the figure), which corresponds to a zone of peat accumulation

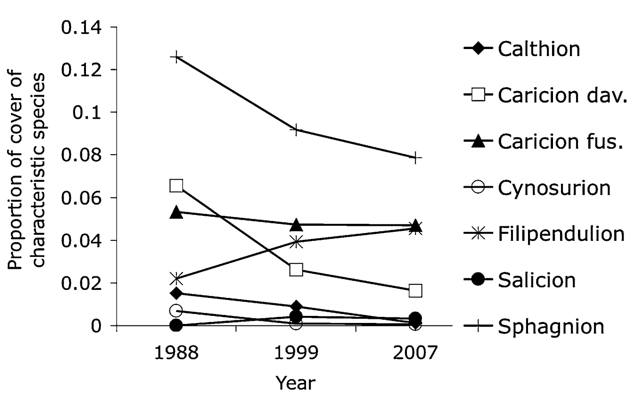

Fig. 6 Changes of the different vegetation groups after the bog burst. Data are given for the years 1988, 1999 and 2007. Changes are significant between years ($P < 0.05$) with a significant linear trend ($P < 0.05$) for *Caricion davallianae, Sphagnion magellanici* and *Filipendulion*

magellanici mainly resulted from the shift of this group towards acidic fen vegetation (*C. fuscae*), whereas the *C. davallianae* evolved partly towards *C. fuscae* and partly towards *Filipendulion* (Table 3). The increase in *Filipendulion* occurred at the expense of *C. fuscae* and *C. davallianae* (Table 3). The spatial distribution of these changes (Fig. 7) indicates that *C. davallianae* species decreased throughout the disturbed area, whereas *S. magellanici* declined only in the lower part of the disturbed area, where this type of vegetation had been moved to by the slide. *C. fuscae* generally decreased in the upper part of the slide but increased in the lower eastern part. The *Filipendulion* mostly increased in the lower part of the slide. *Calthion* decreased in the upper part of the slide, while *Salicion* developed in his area where the peat has been eroded down to the mineral subsoil.

Table 3 Frequency of transitions between vegetation types observed between 1988 and 2007 in individual plots

	Sm	***Fil***	*Cfu*	***Cda***	*Calt*	*Cyn*	Sum 1988
Sm	6	0	13	1	0	0	20
Fil	0	0	1	0	0	0	1
Cfu	3	6	31	1	1	0	42
Cda	1	6	8	7	0	0	22
Calt	0	1	1	0	0	0	2
Cyn	0	1	0	0	0	0	1
Sum 2007	10	14	54	9	1	0	88

Rows indicate vegetation types in 1988 and columns vegetation types in 2007; "sum" is the total number of plots assigned to each vegetation type in either year. *Sm*, *Sphagnion magellanici*; *Fil*, *Filipendulion*; *Cfu*, *Caricion fuscae*; *Cda*, *Caricion davallianae*; *Calt*, *Calthion*; *Cyn*, *Cynosurion*. Bold characters indicate vegetation types with statistically significant changes in frequency between the 2 years ($P < 0.05$)

Discussion

The bog burst in 1987 dramatically modified the edaphic conditions of the mire. The disturbed part of the mire became significantly drier, richer in nutrients and less acidic. The decrease in light value indicates a closing of the herb layer and the decrease in the humus value points to the loss of peaty soil. Following such a disturbance, we expected a rapid change in mire vegetation and its replacement with alternative vegetation types. Our results showed that although changes in vegetation composition did occur, they were slower than expected and did not affect all vegetation types in the same way. The main changes were an increase in species diversity and a general increase in the shrub and tree cover (*Salix myrsinifolia, Picea abies*). We also detected a general shift of the vegetation of bog and calcareous fen towards tall forbs.

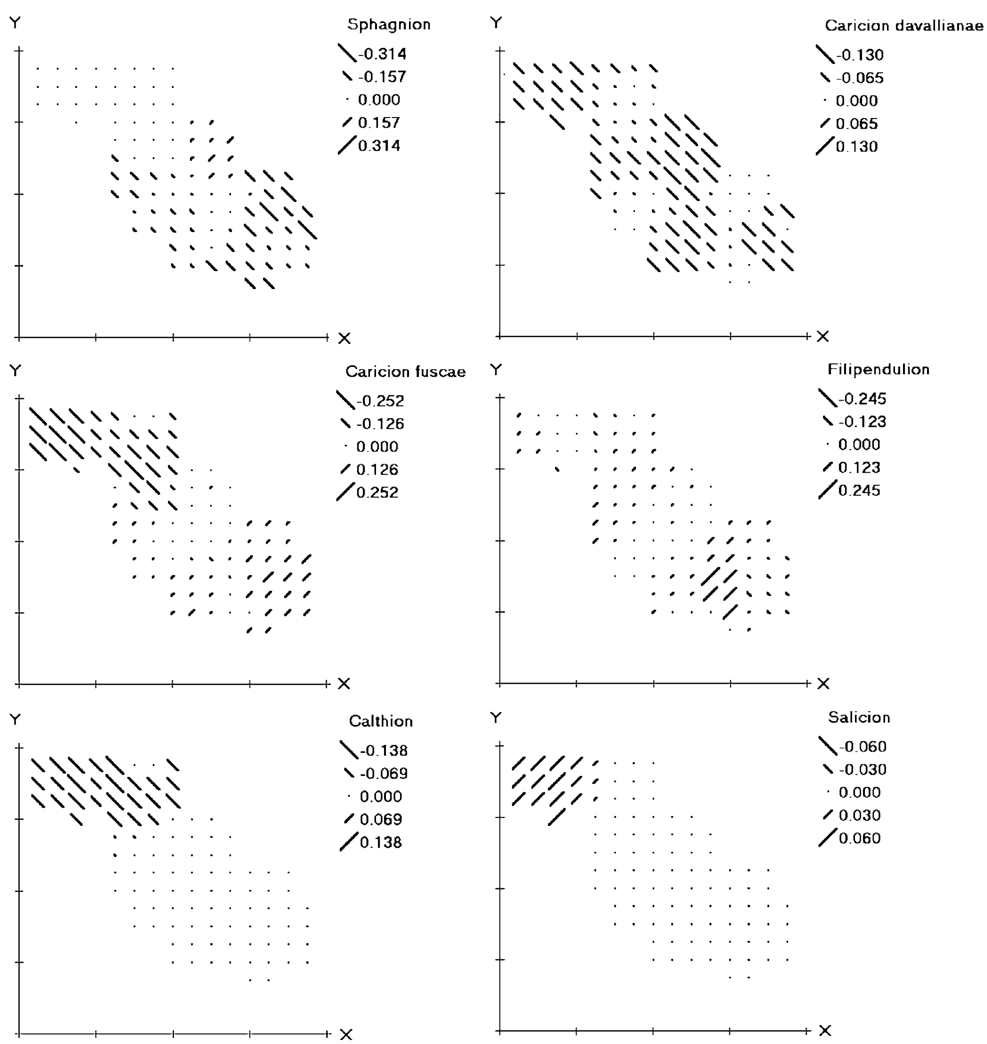

Fig. 7 Spatial illustration of the abundance changes in the characteristic species for six vegetation groups in the disturbed area. *X* axis and *Y* axis, coordinates of the Swiss National Grid; spacing of the data points = 50 m. Peat moved from the northwest (*top left* in the figure), where the zone of peat erosion is situated, to the south-east (*bottom right* in the figure), which corresponds to a zone of peat accumulation

The overall increase in species diversity observed in la Vraconnaz after the bog burst is in accordance with the findings of many authors that disturbance promoted species richness (Houssard et al. 1980; Fischer 1992; Güsewell et al. 1998; Hansson and Fogelfors 2000; Pierce et al. 2007) by avoiding the competitive exclusion of less competitive species (Grime 1973).

Our results seem to contradict other studies that associated disturbance in bogs with a decrease in species diversity. Such a decrease in the species diversity of ombrotrophic species following anthropogenic disturbances has been observed in Europe (Frankl and Schmeidl 2000; Freléchoux et al. 2000; Linderholm and Leine 2004) and North America (Pellerin and Lavoie 2003; Pellerin et al. 2009). The case of la Vraconnaz, however, is not comparable because even before the slide the mire was no longer a true ombrotrophic bog, but had already become a patchwork of various fen and bog communities. The increase in species richness may thus be seen as a direct effect of the peat slide that offered new open surfaces of bare peat and open water, providing a temporary habitat for pioneer species. Moreover, the increase in nutrient availability due to the mineralization of the peat allowed the establishment of less frugal species.

The bog burst led to a considerable species turnover, especially in the first decade. The higher turnover observed in the upper part of the slide reflects the intensity of the disturbance. It was higher in the area where the peat had been eroded to the mineral substrate, thus providing a temporary habitat for pioneer species, than in the lower part of the peat accumulation where the vegetation was displaced but suffered no destruction of biomass.

Species promoted by the disturbance were those common in nutrient-rich moist grasslands (*Polygonum bistorta, Rumex acetosa, Trollius europaeus, Angelica sylvestris, Cirsium palustre, Crepis paludosa, Filipendula ulmaria*), ubiquitous species (*Festuca rubra* and *Lathyrus pratensis*), pioneer species in ditches (*Equisetum fluviatile* and *Galium palustre*) and woody species (*Salix myrsinifolia* and *Picea abies*). All these species took advantage of the increase in nutrients, which became available when the peat was oxidised on sudden exposure to air. The upper part of the mire is also subject to eutrophication from the nearby agriculture. Since the bog burst, nutrients from the adjacent pastures could directly flow into the mire. Woody species further benefitted from the drier conditions.

On the other hand, the perturbation caused the decline or disappearance of many mire species. These mire specialists are adapted to a wet environment poor in nutrients and are weaker competitors under drier and more nutrient-rich conditions.

Thus, the vegetation has mainly developed away from that typical of bog and calcareous fen towards tall forbs. The acidic fen vegetation has remained about constant in spite of losses in favour of tall forbs because these losses have been compensated for by gains in previous bog and calcareous fen vegetation.

The vegetation is still changing, and we do not know yet if it will stabilize at a new equilibrium state or if there will be a backward development towards a prior state, i.e. away from tall forbs towards the previous bog and calcareous fen vegetation. Thus continued monitoring is needed for secondary succession in the mire to be assessed thoroughly.

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