

Recent changes in the plant composition of wetlands in the Jura Mountains

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Co-ordinating Editor: Gerald Jurasinski

Abstract

Aim: To assess vegetation changes in montane fens and wet meadows and their causes over 38 years.

Location: Wetlands, Jura Mountains (Switzerland and France).

Methods: Plots were inventoried in 1974 and re-located in 2012 (quasi-permanent plots) on the basis of sketches to assess changes in plant communities. The 110 plots belonged to five phytosociological alliances, two in oligotrophic fens (*Caricion davalliana*, *Caricion fuscae*) and three in wet meadows (*Calthion*, *Molinion*, *Filipendulion*). Changes between surveys were assessed with NMDS, and changes in species richness, Simpson diversity, species cover and frequency and the causes of these changes were evaluated by comparing ecological indicator values.

Results: Changes in species composition varied between alliances, with a general trend towards more nutrient-rich flora with less light at ground level. Species diversity declined, with a marked decreasing trend for the typical species of each alliance. These species were partly replaced by species belonging to nitrophilous and mesophilous grasslands. However, no trend towards drier conditions was detected in these wetlands. The largest changes, with an important colonization by nitrophilous species, occurred in the Swiss sites, where grazing was banned 25 years ago. As a result of floral shifts, many plots previously belonging to fens or wet mesotrophic meadows shifted to an alliance of the wet meadows, generally *Filipendulion*. Moreover, communities showed a slight trend towards more thermophilous flora.

Conclusions: The investigated wetlands in the Jura Mountains have suffered mainly from eutrophication due to land-use abandonment and N deposition, with a loss of typical species. Areas with constant land use (grazing or mowing) showed less marked changes in species composition. The most important action to conserve these wetlands is to maintain or reintroduce the traditional practices of extensive mowing and livestock grazing in the wetlands, especially in areas where they were abandoned 25 years ago. This previous land-use change was intended to improve fen conservation, but it was obviously the wrong measure for conservation purposes.

KEYWORDS

ecological indicator values, eutrophication, fens, grazing, land-use changes, N deposition, re-survey, semi-permanent plots, wet meadows

1 | INTRODUCTION

Drainage, habitat fragmentation, land-use change, atmospheric N deposition and climate change have caused the degradation and destruction of wetlands, particularly fens, in industrial regions (Chapman et al., 2003; Pauli, Peintinger, & Schmid, 2002; Van Belle, Barendregt, Schot, & Wassen, 2006). This deterioration has led to a global decline in species richness, with the extinction of some typical plants and animals (ter Braak & Wiertz, 1994; Guyonneau, 2010). Wetland habitats are among the most endangered of many regions around the world (Bergamini & Pauli, 2001; Pauli et al., 2002). In Switzerland, more than 90% of the wetlands have disappeared since 1800, replaced by agricultural or built-up areas (Grünig, 1994). Currently, even though the majority of Swiss wetlands are legally protected (Rausch, 2002), these habitats remain threatened due to continuous deterioration of their quality (Klaus, 2007; Pauli et al., 2002).

Vegetation changes in wet ecosystems have been studied in most Central European countries, e.g. in Switzerland (Bergamini & Pauli, 2001; Graf, Wildi, Küchler, & Ecker, 2010; Klaus, 2007), the Netherlands (ter Braak & Wiertz, 1994) and France (Bailly, Ferrez, Guyonneau, & Schaefer, 2007; Guyonneau, 2010), as in Northern Europe (e.g. Gunnarsson, Malmer, & Rydin, 2002 in Sweden). Generally, the species composition of low sedge fens (the phytosociological alliances of *Caricion davallianae* and *Caricion fuscae*), reed swamps (*Phragmition australis*) and tall sedge swamps (*Magnocaricion*) tends to shift towards wet meadows (mainly *Filipendulion*, *Calthion* and *Molinion*), which themselves tend to be transformed into mesophilous grasslands (Bergamini et al., 2009; Bollens, Güsewell, & Klötzli, 2001). Typical fen plant species (specialist species) have declined, and generalist species have increased (Bergamini et al., 2009; Gunnarsson et al., 2002).

Most previous studies have concluded that these transformations are due to drier conditions following land-use and/or climate changes (Bergamini et al., 2009; Bollens et al., 2001; Gunnarsson et al., 2002), affecting the nutrient availability in the soil (Koerselman, Van Kerkhoven, & Verhoeven, 1993; Wassen, Barendregt, Palczynski, de Smidt, & de Mars, 1990). More precisely, warmer and drier conditions accelerate organic matter mineralization, which releases supplementary nutrients (eutrophication) and, consequently, modifies species composition, particularly in nutrient-poor fens. Taller, more competitive species colonize the wetlands, resulting in less available light at soil level (Bergamini et al., 2009; Graf et al., 2010; Pauli et al., 2002). Altogether, these drier, darker and more eutrophic conditions lead to a decrease in the frequency and cover of the typical vascular plants and bryophytes of wetlands (Gough, Osenberg, Gross, & Collins, 2000; Morecroft, Sellers, & Lee, 1994). Eutrophication and decreases in water saturation may similarly be responsible for tree and shrub colonization, which is often observed (Gunnarsson et al., 2002), but simple forest recolonization may occur locally. Indeed, many wetlands in low to mid-elevations are secondary ecosystems derived from clearings performed to increase farmland before the 17th century (Küttel, 2002).

Many previous studies have explored floristic changes in large areas, with plots scattered far from each other and with very diverse

ecological conditions and historical management. This situation makes it difficult to identify differences in response patterns between vegetation types because processes can vary among regions, climates, geologies and agricultural management. Hence, studies on a local to regional scale that try to detect and interpret vegetation changes in a small area with homogenous climate are rare (Koch & Jurasinski, 2015), although understanding processes at this scale is essential to the ability to evaluate the relative sensitivity of the different wetland and fen types to environmental changes and to evaluate the potential for wetland conservation.

In this project, we studied vegetation change over four decades in wetlands scattered across two neighbouring valleys in the Swiss and French Jura Mountains. Five wetland types corresponding to different phytosociological alliances were assessed. We took advantage of the opportunity furnished by a wealth of older floristic inventories (mainly from 1974–1977) to compare these inventories with recent surveys (2012) to answer the following questions: (i) has fen and wet meadow vegetation changed in species composition in recent decades; (ii) which are the most sensitive communities; (iii) do the observed changes indicate ecologically directional shifts; and (iv) what are the most likely causes of these changes? We hypothesized that the vegetation changed between the two inventories, mainly in oligotrophic ecosystems, due to eutrophication and drainage, with denser grass cover and a decrease in the available light at ground level.

2 | METHODS

2.1 | Study sites

The three study sites are located between 1000 and 1110 m a.s.l. in the Jura Mountains and are separated from each other by <14 km (Figure 1). Two are in a Swiss valley called Vallée de Joux, La Burtignière (along the Orbe river and next to peat bogs) and Le Sentier (on the shore of the lac de Joux). One is in France, near Chapelle-des-Bois, in a short valley that is parallel to the Vallée de Joux. Both valleys are on calcareous sedimentary rock (Aubert, 1987) coated with impermeable marls and local ice moraines, respectively (Bichet & Campy, 2009).

The temperate climate of the study area is characterized by substantial annual rainfall (between 1500 mm and 1800 mm; Bailly et al., 2007) that is regularly distributed throughout the year, and by mean temperatures between -2°C in January and 15°C in July (Gallandat, 1982). Annual rainfall did not significantly change in the Jura Mountains between the inventories (1974–2013), but the mean annual temperatures increased by $0.39\text{--}0.45^{\circ}\text{C}$ per decade, for a total of approximately $+1.6^{\circ}\text{C}$ (see Appendix S1). Snow generally covers the ground from December to March. Both valleys are closed basins with lakes. This topography induces frequent fogs, with very cold temperatures at night, especially in winter, and frost is possible throughout the year (Bouët, 1957, 1985). Vegetative growth is generally possible from mid-April to mid-October.

The Swiss sites have been legally protected since 1987 (Rausch, 2002). Previously grazed or mown, with a few drains dug locally to increase available grassland, most of the areas are now fenced to protect

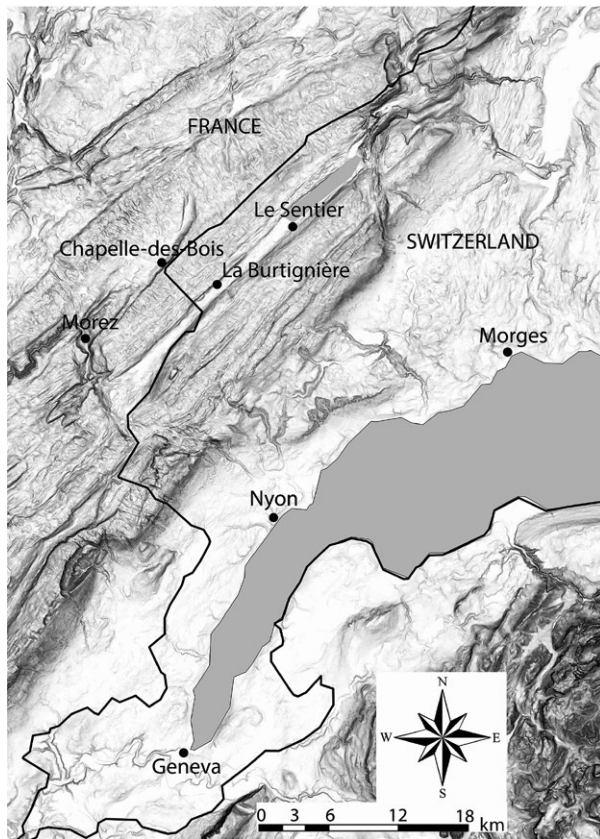


FIGURE 1 Study area with the three study sites: Chappelle-des-Bois (France, 1110 m a.s.l., 46°34'31 N, 6°05'39 E); Le Sentier (Switzerland, 1007 m a.s.l., 46°36'41 N, 6°14'53 E); La Burtignière (Switzerland, 1042 m a.s.l., 46°33'39 N, 6°10'15 E) (topographical map www.swisstopo.ch)

them from grazing. In contrast, the French site is farmed, with grazing by cattle (during a few weeks in summer and in autumn) or mowing (approximately twice a year), performed in accordance with the principles of organic farming. In none of the regions is fertilization of wetlands authorized, but the surrounding grasslands can be fertilized with manure, except for a buffer area around the wetlands. Historical data about past management is insufficiently detailed to be used, with irregular land use (grazing or mowing) in Chappelle-des-Bois.

2.2 | Vegetation data

Gallandat (1982) studied the wetland vegetation of these three sites. He produced 1090 exhaustive floristic relevés between 1974 and 1988 (mainly 1974–1978) in the Jura Mountains, about half of them in the three retained sites. The plots were originally selected to be ecologically and floristically homogeneous and representative of the different plant communities encountered at the sites. Their size varied according to the conditions and the available area. He classified them into phytosociological alliances and associations (or lower units) according to the traditional method (Braun-Blanquet, 1964). Additionally, he mapped the vegetation at a scale of 1:6,000. Approximately 300 relevés could be re-located on the basis of written

indications and sketches in his field notebooks and maps. Only the relevés classified by Gallandat (1982) as belonging to two phytosociological alliances of fens (*Caricion davallianae*, *Caricion fuscae*) or three of wet meadows (*Molinion*, *Calthion*, *Filipendulion*) were retained. These alliances were selected because they contained the most common wetland communities in these valleys and represented a large gradient of soil humidity and nutrient content, including oligotrophic and basic for *Caricion davallianae*; oligotrophic and acidic for *Caricion fuscae*; oligotrophic with variable humidity for *Molinion*; mesotrophic and wet for *Calthion*; and eutrophic, wet and without exploitation for *Filipendulion*. Relevés with an area <10 m² (the minimum area to consider that the community is almost complete) or without complete information (dates, vegetation cover and precise sketches) were not considered. Among the retained historical relevés, 30 were randomly selected in each alliance, with the constraint that at least one relevé was retained in each association or lower unit observed by Gallandat (1982). In this way, we ensured covering the whole ecological range of each alliance. The relevé distribution between sites was not considered in this random selection because priority was given to a broad range of ecological conditions, and it would have been impossible to balance sites and alliances. Nor was land use (grazing, mowing, abandoned) considered because of insufficient historical data. Finally, the position of these 150 randomly selected relevés was controlled using historic (1979–1980) and recent (2008–2009) aerial photographs and in the field. Some relevés had to be abandoned because location was doubtful, with a too large difference between expected and observed vegetation (e.g. totally submerged in water, in dense shrub thicket, heterogeneous vegetation) or because landmarks indicated in the sketches (e.g. hedges, isolated trees, river shores, etc.) were no longer present. Of these successive steps of selections, 110 relevés were ultimately re-inventoried (see Table 1 for distribution of the relevés among alliances and sites and Appendix S2 for size of each relevé). With the help of the historical sketches, we can be confident that the location shift does not exceed a few metres and that the data can be considered as being from quasi-permanent plots (Kapfer et al., 2017).

All relevés were re-inventoried in 2012 or 2013. The same area as that of the original relevé was used. All vascular plant species were recorded, and their cover was estimated according to Braun-Blanquet's scale (1964; Table 2). Recent land use was recorded according to observations and discussions with the farmers. Categories had to be limited to “exploited” or “abandoned” because grazing and mowing can change from year to year in Chappelle-des-Bois (Table 1, Appendix S2).

2.3 | Statistical analyses

For each relevé, cover classes were replaced by the corresponding absolute mean cover (Table 2). The species cover was then transformed into the relative cover (sum of species cover in a relevé brought to 100%) to reduce the influence of differences in cover estimations between authors (Gillet, 2014).

The new relevés were automatically assigned to an alliance using the same classification as Gallandat (1982). This procedure compared each new relevé with the centroid relevés of the 85 units (associations



	Number of relevés	Chapelle-des-Bois	Le Sentier	La Burtignière
Alliances				
<i>Molinion</i>	22	17	5	-
<i>Calthion</i>	22	-	2	20
<i>Filipendulion</i>	28	2	3	23
<i>Caricion davallianae</i>	22	2	11	9
<i>Caricion fuscae</i>	16	-	-	16
Exploitation type				
Exploited	27	9	4	14
Abandoned	83	12	17	54
Total	110	21	21	68

TABLE 1 Distribution of the relevés among the phytosociological alliances (according to Gallandat, 1982), sites and present exploitation type (pers obs in 2012–13). The distribution of the recent relevés in alliances is given in Appendices S2 and S11

TABLE 2 Estimation of plant cover according to Braun-Blanquet's (1964) scale, with the corresponding absolute mean cover according to Gillet (2014) for statistical analyses

Braun-Blanquet scale	Plant cover (%)	Absolute mean cover (%)
r	1 or 2 individuals	0.01
+	<1	0.5
1	1–5	3
2	6–25	14
3	26–50	32
4	51–75	57
5	>75	90

or subdivisions) observed by Gallandat (1982). For each unit, this centroid relevé was calculated on the basis of the whole set of original relevés used to define the unit. Seven parameters (Appendix S3) were then used to calculate seven similarity indices between a new relevé and each of the centroid relevés according to the proportion of species shared (by accounting or not for their relative cover; Appendix S3; Tichý, 2005). These seven indices were averaged, and the new relevé was attributed to the unit (and the corresponding alliance) with which it had the strongest similarity (mean similarity index varying between 0 and 1).

To detect vegetation shifts between inventories, NMDS (*vegan* R library; Borcard, Gillet, & Legendre, 2011) were performed with all the relevés on the Bray-Curtis distance on relative cover. The mean shifts of the NMDS coordinates between the old and new relevés were calculated in three different ways: for the five alliances, the three sites and the two types of land use. The changes in heterogeneity within alliances between old and recent relevés were evaluated with multivariate dispersion (Anderson, Ellingsen, & McArdle, 2006) and the significance of the changes with the implementation given in the *vegan* R library (R Foundation for Statistical Computing, Vienna, Austria).

To evaluate the importance of the floristic shifts, the Bray-Curtis distance was calculated between pairs of old and new relevés based

on relative cover. ANOVAs were performed to compare changes at the alliance level and at the site level (La Burtignière, Le Sentier, Chapelle-des-Bois). Post-hoc Tukey tests were then conducted for all significant ANOVAs to highlight which alliances or sites differed from the others.

Species richness and Simpson index of the old and new relevés were compared at the levels of the full data set, the alliances and the sites and were tested with pair-wise Wilcoxon-Mann-Whitney tests. Mean ecological indicator values (Landolt et al., 2010) were calculated and weighted by species' relative cover for each relevé to assess the ecological factors related to the observed changes. Two indicators related to above-ground conditions (light, L; temperature, T) and four related to soil conditions (humidity, F; humus content, H; nutrient content, N; pH, R) were used. Similar to Ellenberg's indicator values (Ellenberg et al., 1991) but centred on the Alps, these values vary from 1 (low characteristics) to 5 (high characteristics). After testing the normality and homogeneity of the variance, pair-wise Wilcoxon-Mann-Whitney tests were performed to compare old and new inventories across the full data set, by alliances, by sites and by land use. The comparison at the alliance level was conducted according to the attribution of each new relevé to its original alliance.

Significant changes in species frequency (proportion of occurrences in old and new relevés) were tested by permutation tests (999 random permutations of the identity of the new relevés; Koch et al., 2017). The number of times that the change in observed frequency was smaller or equal to the randomized value served to indicate the significance level. This procedure was performed globally (on all relevés), at the alliance and site levels. Linear regressions were used to test whether the relative species cover changed between the old and new relevés. Only plants with a frequency $\geq 15\%$ were considered, considering little information available to evaluate cover changes on rare species. To interpret shifts in species composition, changes in frequency or cover were related to typical species of each alliance according to Delarze, Gonseth, Eggenberg, and Vust (2015), a reference listing the Swiss habitats with their respective characteristic species (Appendix S4).

All analyses were performed with R statistical software (v 3.0.2).

TABLE 3 Changes in mean ecological indicator values (Landolt et al., 2010), species richness and Simpson diversity index, overall, by alliances, by sites and by land use, between 1974 and 2012 in wetlands of the Jura Mountains. The significance of changes was tested with pair-wise Wilcoxon-Mann-Whitney tests: *, <0.05; **, ≤0.01; ***, ≤0.001 (significant changes in bold). A positive value indicates an increase in the corresponding value, and vice versa. T, temperature; L, light; F, soil humidity; R, soil pH; N, nutrients in soil; H, humus in soil

	T	L	F	R	N	H	Species richness	Simpson diversity
Total	0.039*	-0.056*	0.100**	0.042	0.206***	0.062	-3.9***	-1.87***
<i>Molinion</i>	0.079*	-0.115*	0.394***	-0.056	0.089	0.278**	-14.2***	-6.25***
<i>Calthion</i>	0.008	-0.057	0.077	-0.019	0.160	0.197	-2.0	-1.11
<i>Filipendulion</i>	0.030	-0.027	-0.033	-0.004	0.179	-0.118	-3.9**	0.09
<i>Caricion davallianae</i>	0.084	-0.015	0.035	0.017	0.229	-0.043	-0.2	-1.45
<i>Caricion fuscae</i>	-0.014	-0.080	0.052	0.361**	0.439**	0.037	2.1	-0.94
La Burtignière	0.025	-0.057*	0.053	0.099	0.235**	0.074	-1.1	-0.79
Le Sentier	0.016	-0.044	0.043	-0.145*	0.287*	-0.211*	-4.9**	-1.21
Chapelle-des-Bois	0.110**	-0.068	0.311***	0.045	0.027	0.295**	-12.4***	-6.06***
Exploited	0.066*	-0.066	0.060	-0.009	0.156	0.057	-1.1	-1.14
Abandoned	0.031	-0.053	0.113**	0.059	0.221***	0.063	-4.9***	-2.12***

3 | RESULTS

The species richness decreased significantly between the old and new relevés (old relevés: 27.9 ± 1.2 ; new relevés: 24.0 ± 1.0 ; Table 3). This decrease was significant in the alliances of *Molinion* (44.2 ± 2.3 – 30.0 ± 1.7) and *Filipendulion* (20.4 ± 1.3 – 16.5 ± 1.9), in the sites Le Sentier (26.1 ± 2.2 – 21.2 ± 1.6) and Chapelle-des-Bois (41.9 ± 3.3 – 29.5 ± 2.0) and in abandoned areas (25.7 ± 1.2 – 20.8 ± 1.1). Similarly, the Simpson diversity between the old and the new relevés significantly decreased overall (8.72 ± 0.50 – 6.85 ± 0.33 ; Table 3) in the *Molinion* (14.49 ± 1.18 – 8.24 ± 0.51), in Chapelle-des-Bois (13.97 ± 1.42 – 7.91 ± 0.59) and in abandoned areas (8.05 ± 0.52 – 5.93 ± 0.35 ; Table 3).

The ANOVA performed on the mean Bray-Curtis distances showed that the floristic shifts were of the same importance between alliances ($p = .051$) and between sites ($p = .065$; Appendix S5), with a mean value of 0.679 ± 0.016 . The first axis of the NMDS represents a nutrient gradient with the oligotrophic alliances on the left (*Caricion davallianae*, *C. fuscae*, *Molinion*) and the most eutrophic one (*Filipendulion*) on the lower right (Figure 2). Hence, the dominant shift between the old and new relevés towards the lower right quadrant of the graph corresponds to an increase of eutrophic plant species. However, the relevés classified in *Molinion* or located in Chapelle-des-Bois showed the opposite direction of shift compared to the other alliances and sites (Figure 2, Appendix S6). Plots under continued land-use regimes (grazing or mowing) appeared to be stable on average, as opposed to plots in abandoned areas that shifted to the lower right of the NMDS (Appendix S7). The multivariate dispersion of relevés in alliances remained unchanged for all alliances, except *Caricion davallianae*, which showed a slight significant increase of dispersion ($+0.057$, $p = .048$; Appendix S8).

All alliances suffered a decrease in the frequency or cover of some of their typical species (Appendices S9, S10). Conversely, many of the increased species were widespread species that are not particularly

related to wetlands, such as *Rumex acetosa*, *Lathyrus pratensis* and *Festuca rubra* agr. In *Caricion fuscae*, typical species for this alliance decreased in frequency and/or cover (e.g. *Carex echinata*, *Eriophorum angustifolium*), whereas nitrophilous and basophilous species from *Calthion* and widespread species increased. Similarly, in *Caricion davallianae* typical species (e.g. *Primula farinosa*, *Eriophorum latifolium*) were replaced by large, nitrophilous species typical of the eutrophic alliances (e.g. *Valeriana dioica*, *Cirsium rivulare*, *Filipendula ulmaria*). In *Molinion*, *Molinia caerulea* increased in mean cover but decreased in frequency. Species with narrow leaves (*Agrostis capillaris*, *Koeleria pyramidata*) decreased in frequency and cover. The mesotrophic *Calthion* followed the same trend, with typical species decreasing in frequency (*Ranunculus aconitifolius*, *Silene flos-cuculi*), whereas a typical species of *Filipendulion* (*Valeriana officinalis*) increased. The *Filipendulion* lost typical species of *Calthion* and *Caricion davallianae*.

Landolt's ecological indicator values showed that, overall, the new relevés were composed of species indicating that soil is richer in nutrients (N, $+0.206$) and wetter (F, $+0.100$) than in the old relevés, and there is less available light at ground level (L, -0.056) and slightly warmer conditions (T, 0.039 ; Table 3). *Filipendulion*, *Calthion* and *Caricion davallianae* did not change, but *Molinion* contained in 2012 species indicating warmer ($+0.079$) and darker (-0.115) conditions, with wetter ($+0.394$) and humus richer ($+0.278$) soils than in 1974 (Table 3). In *Caricion fuscae*, species in the new relevés indicated that soils were richer in nutrients ($+0.439$) and with a higher pH ($+0.361$) than in 1974. The changes were quite heterogeneous between sites, with the most important shifts being an increase in the mean indicator values for nutrients at the Swiss sites (La Burtignière $+0.235$, Le Sentier $+0.287$) and in the values for humidity ($+0.311$) and soil humus content ($+0.295$; Table 3) in Chapelle-des-Bois (France). Finally, exploited areas contained a higher proportion of thermophilous species ($+0.066$) than before, whereas in abandoned areas, the present

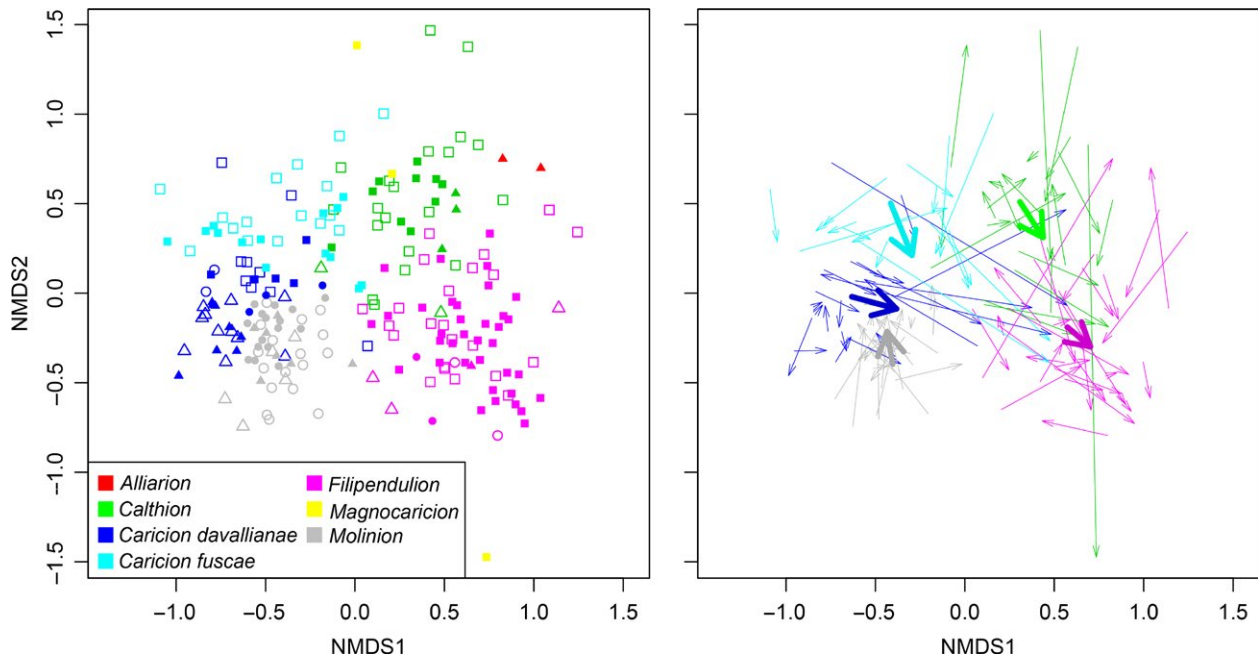


FIGURE 2 NMDS, based on Bray-Curtis distance, of old and recent relevés, according to their phytosociological alliance. Stress value = 0.212. On the left panel, sites are represented by different symbols: ■ La Burtignière (CH), ▲ Le Sentier (CH), ● Chapelle-des-Bois (FR); empty symbols are historical relevés and filled ones for recent relevés. On the right panel, pairs of relevés are linked by a thin arrow and the large arrows illustrate the mean shift of relevés belonging historically to the same alliance. Two alliances (*Magnocaricion* and *Alliarion*) were not retained among the historical relevés but were recognized by the automatic classification of five new relevés. The samples are too small to discuss further about these alliances

flora indicated wetter conditions (+0.113) and more eutrophic soils (+0.221) than in the past.

For all sites together, 20% of the new relevés did not belong to the same alliance as in the past (Figure 3, Appendix S11). The highest number of shifts between alliances was observed in the *Calthion* in La Burtignière, where seven relevés shifted to *Filipendulion* and three to *Magnocaricion*. Similarly, in La Burtignière, the *Caricion davallianae* lost four relevés, and the *Caricion fuscae* lost two relevés, all to *Filipendulion*. In Le Sentier, the *Caricion davallianae* lost three relevés towards *Molinion* or *Calthion*. The site of Chapelle-des-Bois was the most stable (Appendices S6, S11). Among the relevés historically classified in *Calthion*, eight of ten that shifted to another alliance are abandoned, whereas only one of 12 that stayed in *Calthion* is abandoned (Appendix S11).

4 | DISCUSSION

4.1 | Species composition

The study sites are still composed of wetlands, fens and wet meadows, and most of them are still worth preserving, because they are still dominated by typical wetland species. However, as expected, this study showed that the vegetation has changed from 1974 to 2012. Changes in species composition and cover in oligotrophic fens (*Caricion davallianae*, *C. fuscae*) indicated a shift towards more eutrophic habitats, with less available light at ground level. Wet meadows themselves were colonized by more nitrophilous species. Altogether, the changes were

important enough to produce a shift from one alliance to another for 20% of the studied plots, mainly from oligotrophic or mesotrophic alliances to *Filipendulion*, the most eutrophic alliance considered in this study. However, most of the other relevés also lost species and showed changes in their plant composition. This pattern is strongly visible in *Molinion*, which was quite stable from a phytosociological point of view but had the highest loss in species richness, the largest fluctuations in species frequency or cover and the most obvious changes based on the CWM ecological indicator values.

The higher mean indicator values recorded in 2012 indicated that nutrient availability increased since 1974. Eutrophication is a serious threat to these wetlands and fens, especially oligotrophic and acidic fens (*Caricion fuscae*). Eutrophication has been repeatedly observed to be a serious problem with a substantial negative impact on many European habitats, such as wetlands (Bollens et al., 2001; Graf et al., 2010; Kapfer, Grytnes, Gunnarsson, & Birks, 2011), oligotrophic meadows (Diekmann et al., 2014; Mauchamp, 2014) and alluvial forests (Gallandat, Gobat, & Roulier, 1993). Hence, although legally protected and managed for conservation goals, the quality of these wetlands is still decreasing, with a loss of diversity, especially in typical species. This alteration was accompanied by a general reduction in light, mainly in *Molinion* and at La Burtignière. This response has previously been observed in other wetlands (Bergamini et al., 2009; Gunnarsson et al., 2002; Kapfer et al., 2011; Pauli et al., 2002) and can be induced by eutrophication (development of larger plants) or by land-use shifts, particularly when mowing or grazing is abandoned (Diemer, Oetiker, & Billeter, 2001), a measure that is often thought

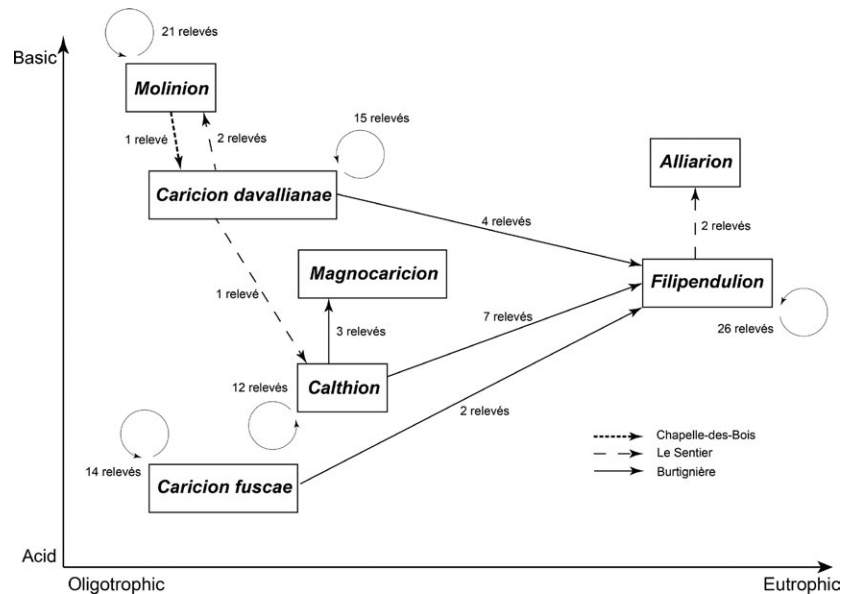


FIGURE 3 Number of relevés that shifted between phytosociological alliances (straight arrows) or stayed in the same alliance (circular arrows) in wetlands. Alliances are approximately distributed in the figure according to the two main ecological gradients (see comment in Figure 2 about *Magnocaricion* and *Alliarion*)

to favour the proliferation of more productive, nitrophilous and/or woody species (De Cauwer & Reheul, 2009). In our study, species with high, dense foliage, such as *Filipendula ulmaria*, *Valeriana officinalis* and *Molinia caerulea*, have shown increased species cover or frequency.

In contrast to the results of many other studies (e.g. Bergamini et al., 2009; Graf et al., 2010), the considered fens and wet meadows were clearly not affected by drought. The new relevés indicated generally wetter conditions, particularly at the French site, where *Molinion* was the most common vegetation type. The high annual rainfall ensures a sufficient water supply, and the considered sites were less affected by drainage than other wetlands in Switzerland or neighbouring countries. As annual rainfall did not change in the region and, as far as we know, no modification was done to the hydrological system in this site, the significant increase in humidity indicated by mean value for humidity is difficult to explain. One possible explanation could be an artefact due to the weak correlation existing between nutrient (N) and humidity (F) indicator values for species with significant cover or frequency change in *Molinion* ($n = 37$, Spearman's $\rho = 0.329$, $p = .047$), as declining species largely prefer oligotrophic conditions (e.g. *Koeleria pyramidata*, *Carex caryophylla*, *Hippocrepis comosa*, *Carex sempervirens*), their decline may have induced a parallel increase in mean F indicator value.

4.2 | Possible causes of change

Because the studied fens and wet meadows do not show a shift towards lower humidity values, the indicated nutrient enrichment was probably not induced by an increase in the mineralization of organic matter by aerobic organisms, as may occur under drier conditions (Clymo, 1983; Holden, Chapman, & Labadz, 2004). Eutrophication through the direct application of mineral fertilizer can be excluded due to the legal prohibition of mineral fertilization of wetlands in both countries. Hence, other sources must be considered. Atmospheric N deposition has long been suspected to modify vegetation (Bragazza

et al., 2004; Pauli et al., 2002). It is considered an important driver of losses in ecosystems (CFHA 2005; Phoenix et al., 2012), such as in meadows (Bobbink et al., 2010), mountain grasslands (Mauchamp, 2014; Morecroft et al., 1994) and wetlands (Bragazza et al., 2004; Morris, 1991). For the study sites, the exact annual deposition is not known, but, according to extrapolations and models, it is approximately $15\text{--}20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (CFHA 2005). These values are able to strongly influence wetlands because they are in the magnitude of critical loads of N, $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for ombrotrophic bogs and $15\text{--}25 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for poor fens (*Caricion davallianae*, *C. fuscae*, *Molinion*; CFHA 2005). In addition, the deposition accumulates year after year, accentuating eutrophication in the long term (Thimonier, Schmitt, Waldner, & Rihm, 2005).

Another possible cause of eutrophication could be nutrients leaking from the surrounding grasslands (Pauli et al., 2002). This is probably not the major cause in the study sites because many fens and wetlands are too large to be impacted throughout their area, and farmers have to recognize a buffer zone, without fertilization, around wetlands.

Finally, eutrophication could derive from land-use changes such as mowing or grazing abandonment (Van Diggelen, Middleton, Bakker, Grootjans, & Wassen, 2006; Wyl, Stadler, & Leupi, 2002) or the intensification of agriculture (Wyl, Dieltl, & Wenger, 2002). Abandonment, most likely, is the prevailing cause at the Swiss sites. Indeed, the most important changes were in La Burtignière and Le Sentier, where grazing in wetlands was banned 25 years ago for conservation purposes. In these sites, as in abandoned relevés, a clear shift of vegetation towards more nutrient-rich flora was visible in the NMDS and in the mean ecological indicator values (Table 3, Figure 2). Conversely, in Chapelle-des-Bois, where many areas are still exploited by grazing or mowing, the changes in the NMDS were in the opposite direction, without visible eutrophication (Appendix S6). Moreover, in *Calthion*, the alliance that shifted most often, almost all relevés that changed are abandoned, whereas the areas with continued sustainable land use were globally stable. After abandonment, the accumulation of litter

stops the exportation of nutrients, which induces more production of above-ground biomass and, consequently, a reduction of light at ground level (Bergamini et al., 2009; Pauli et al., 2002). The process is worsened by N deposition, which is no longer balanced by N removal through fodder production. The consequences of grazing abandonment are clearly visible in the shifts of *Caricion davallianae* and *Calthion* towards *Filipendulion*, the typical alliance of unexploited wet meadows (Delarze et al., 2015), the eutrophication of *Caricion fuscae* or the decrease in diversity observed in *Filipendulion* and *Molinion* (De Cauwer & Reheul, 2009; Guyonneau, 2010). Similar decreases in species richness after abandonment have previously been recorded in wetlands and meadows (Bühler & Roth, 2011; Gough et al., 2000). These results suggest that a low-level practice of mowing or grazing is an important conservation measure for these ecosystems (Van Andel & Aronson, 2006). In the Swiss sites, not using this practice induced the loss of communities, although this management policy was intended to preserve them. Conversely, sustainable exploitation by organic farming in Chapelle-des-Bois maintained the wetlands closer to their historical species composition.

Climate change and, more precisely, temperature increase, has often been considered an important driver of changes in mountain plant communities in recent years (e.g. Matteodo, Ammann, Verrecchia, & Vittoz, 2016; Pauli et al., 2012). In mountain ecosystems, climate warming is expected to cause an upward shift of species, which, in mountain wetlands, could translate into an increase in thermophilous species. In this study, the 1.6°C temperature increase (Appendix S1) may have influenced the vegetation changes, as there was a small increase in the mean ecological indicator value for temperature, especially in *Molinion* at Chapelle-des-Bois. A similar trend was observed in other Swiss mountain fens (Moradi et al., 2012). However, this influence most likely remains weak compared with that of the other drivers, given that the changes in the mean values were small. Moreover, an indirect correlation cannot be excluded, as mountain species are more often associated with oligotrophic conditions than lowland species (Güsewell, Peter, & Birrer, 2012). Hence, it is not possible to conclude whether mountain species, such as *Carex sempervirens* or *Scabiosa lucida*, decreased because of warmer climate or eutrophication.

4.3 | Possible limitations of the data

The repetition of plant inventories that are not based on permanent plots is always subject to the risk of mistakes in re-locating the relevé (Kapfer et al., 2017). One can never be sure that the new relevé is in the exact position to the old one, especially when topography (slope, exposure) cannot be used as supplementary indications (the wetlands mainly occur in flat areas). By retaining only relevés with a reliable sketch in the original field notebook, and still existing landmarks in the field, we largely restricted the possibility of mistakes in re-location. Moreover, by retaining only large relevés (mean area $28.9 \pm 22.6 \text{ m}^2$), we increased the chances that the new relevés at least partly covered the historic ones. Hence, we can be confident that the changes in floristic composition are mainly due to real changes in the vegetation rather than due to inexact plot re-location.

Another potential bias, common to all repetitions of floristic inventories, is due to mistakes in plant inventories (Vittoz & Guisan, 2007; Vittoz et al., 2010), either due to overlooked species or to differences in cover estimate. Most of the old and new relevés were recorded by one botanist, avoiding differences in time spent in looking for species (Vittoz & Guisan, 2007). However, we cannot exclude some potential differences because the aims behind old (community classification) and new (monitoring) relevés differed, with a potentially larger effort dedicated to avoid overlooking species in 2012. For this reason, comparisons of species diversity were calculated with the Simpson index, in which species with low cover (generally overlooked; Vittoz & Guisan, 2007) have little influence on the value, and possible differences in cover estimations were reduced by using relative cover (Gillet, 2014). Altogether, artefacts due to the inventories cannot be completely eliminated, but we reduced them as much as possible, and the remaining artefacts are not expected to have caused the observed directional shifts across our 110 plots.

Finally, considering shifts between alliances, which is often used as reference in management plans, is a conservative approach because many changes can occur in the floristic composition of plots without changing the classification at this level. Hence, the shift of areas from oligotrophic fens, representing conservation priorities, to eutrophic wetlands, which are of lower conservation value, is a clear indication of a serious loss in quality and is a signal understood by conservation managers.

5 | CONCLUSIONS

The studied wetland plant communities mainly indicated a shift towards more eutrophic habitat conditions during the past 38 years. This change produced a decline in oligotrophic species and the loss of typical wetland species, many of them with a high conservation value. For the two Swiss sites, the main cause of eutrophication was the abandonment of grazing – a measure adopted for conservation purposes 25 years ago. However, all the fens and wet grasslands were also likely impacted by atmospheric N deposition. Hence, the nutrient cycling in these wetlands is now strongly modified compared with the first half of the 20th century due to the absence of biomass exportation and the presence of a regular N supply. To date, temperature increase has had a minor influence, and species composition has not shown a trend towards drier soil conditions. The substantial distance separating the wetlands from the villages has probably ensured the favourable conservation of their water level.

One important result is the heterogeneity of the changes between sites and alliances. Oligotrophic plant communities suffered by far the strongest changes, with a substantial decrease in species richness in *Molinion* and strong eutrophication in fens. Indeed, *Caricion fuscae* had the largest increase in the ecological indicator values for nutrients, and 23% of the *Caricion davallianae* relevés shifted towards *Calthion* or *Filipendulion*. This heterogeneity is partly due to land-use changes, but areas that had no major land-use changes also suffered shifts in species composition.

To maintain these threatened wetland ecosystems, conservation measures need to limit nutrient accumulation, e.g. through re-establishing sustainable land-use practices such as grazing or mowing. These communities are generally the product of centuries of extensive farming after logging, and a low level of exploitation is necessary to export nutrients with litter and avoid colonization by shrubs, especially in the context of substantial atmospheric N deposition. Moreover, large buffer zones should be established between grasslands and wetlands to prevent N leakage. Finally, our study shows the importance of monitoring after changes in management for conservation purposes. This policy would have prevented the extended time needed to recognize the undesirable results of the management of the Swiss sites.

ACKNOWLEDGEMENTS

We are grateful to F. Gillet, R. Slobodeanu and M. Mulet, who helped with statistical analyses, to E. Feldmeyer-Christe, F. Gillet, G. Jurasinski and three anonymous referees for their valuable comments on a first draft of this manuscript, and to V. Flury, S. Giriens and S. Guenat for their participation in data collection. We thank the *Direction générale de l'environnement (Vaud)* for the authorization of inventories in nature reserves, the *Conservatoire Botanique de Franche-Comté* for advice and all farmers who let us work in their grasslands.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Trends in mean annual temperatures in western Jura Mountains

Appendix S2 Location, date, size and phytosociological assignment for each relevé

Appendix S3 Seven parameters used to calculate the similarity indices between new relevés and the centroids of the phytosociological units

Appendix S4 List of typical species of the five considered alliances

Appendix S5 Boxplots of Bray-Curtis distances between old and new relevés, classified according to their original alliance and by site

Appendix S6 NMDS of old and recent relevés, according to the sites

Appendix S7 NMDS of old and recent relevés, according to the land uses

Appendix S8 Multivariate dispersion of relevés in 1974 and 2012 in the alliances

Appendix S9 Species with significant changes in frequency for each alliance between inventories (2012 and 1974)

Appendix S10 Species with significant changes in relative cover between inventories (2012 and 1974)

Appendix S11 Historical and present distribution of the relevés in alliances and land use and observed shifts between alliances

How to cite this article: Rion V, Gallandat J-D, Gobat J-M, Vittoz P. Recent changes in the plant composition of wetlands in the Jura Mountains. *Appl Veg Sci*. 2018;21:121–131. <https://doi.org/10.1111/avsc.12338>