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Loss of habitat specialists despite conservation management in fen remnants 1995–2006

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Abstract

Many ecosystems of high conservation value have been shaped by human impacts over centuries. Today, traditional management of semi-natural habitats is a common conservation measure in Europe. However, despite traditional management, habitat remnants may still loose specialist species due to surrounding land-use change or atmospheric nitrogen deposition. To detect trends in species density (2-m^2 plot scale) and habitat quality in calcareous fens in the pre-Alps of Switzerland, we surveyed 36 traditionally managed fens in 1995/97 and again in 2005/06 (five plots per fen). The fens occurred at three altitudinal levels (800–1000, 1000–1200, 1200–1400 m asl) and were either extensively grazed or mown once a year. Despite these traditional management regimes, species density of fen specialists and of all bryophytes decreased during this decade (vascular plant specialists: −9.4%, bryophyte specialists: −14.9%, all bryophytes: −5.7%). Management had no effect on the number of Red-List species and habitat specialists of vascular plants per plot. However, bryophyte species density was more strongly reduced in grazed fens. Species density of vascular plant generalists increased between the two surveys (+8.2%) but not of bryophytes. Among vascular plants, Red-List species decreased from 1.01 to 0.78 species per plot. Furthermore, between the two surveys aboveground plant biomass, mean plant-community indicator values for nutrients and species density of nutrient indicators increased, whereas mean plant indicator values for soil moisture, light and peat, and species density for peat indicators, decreased. We attribute these changes and the loss of specialist species over the past decade mainly to land-use change in the surrounding area and to nutrient inputs. Thus, despite traditional management, calcareous fens in the pre-Alps suffer from ongoing habitat deterioration and endangered plant species remain threatened. For their long-term protection, we suggest to reduce nutrient inputs and, where necessary, to restore hydrology and adjust grazing management.

Keywords: Bryophytes; Calcareous fen; Grazing; Red-List species; Habitat specialist; Vascular plants

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Introduction

Europe has a long history of human modification of its ecosystems (Thomas, 1956). As a consequence,

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wilderness areas in Europe are rare and many European ecosystems of high conservation value have been shaped over the centuries by human impact. Hence, in contrast to other world regions, nature conservation in Europe strongly relies on the continuation of traditional management methods (Sutherland, 2002). Despite traditional management, however, conservation values still may decrease because of various direct and indirect threats to biodiversity such as nitrogen deposition or climate change. It is thus important to monitor whether conservation values within traditionally managed sites are maintained or if there is an ongoing deterioration despite protection efforts.

In this study, we focus on calcareous fens in the Swiss pre-Alps. Calcareous fens belong to the most species-rich grasslands in Europe and contain many habitat specialists and endangered species (Grünig, 1994; Ellenberg, 1996; van Diggelen et al., 2006). In the European Union Habitats Directive, they are considered a priority habitat for conservation. In Switzerland, all fens of national importance are protected since 1987 by the federal constitution and for most sites management contracts exist to ensure the traditional management (Grünig, 1994; Klaus, 2007).

Most calcareous fens in Switzerland are semi-natural, nutrient-poor habitats, which are not artificially fertilized and either mown late in the year or extensively grazed. Before legal protection, many fens have been destroyed by drainage and fertilization (BUWAL, 1990). Thus, the once large and continuous fen landscape in the Swiss pre-Alps has been converted into an archipelago of fen remnants. As a consequence and despite of traditional management, specialist species in fen remnants may suffer from isolation and altered abiotic conditions associated with edge effects (Lienert et al., 2002; Hooftman et al., 2003; Galeuchet et al., 2005; Bossuyt, 2007), from continuing land-use change in the surroundings (e.g. altered hydrological conditions: Fojt and Harding, 1995; Bollens et al., 2001), from nutrient spill-over from more intensively used areas as well as from atmospheric nitrogen deposition (Klötzli, 1986; Bergamini and Pauli, 2001; Pauli et al., 2002). In addition, they may be affected by global warming and associated climate change (Weltzin et al., 2003, Moradi et al., unpublished data). It is conceivable that all these factors affect habitat specialists negatively, whereas generalists may benefit (Fischer and Stöcklin, 1997; Pauli et al., 2002; Travis, 2003; Bennie et al., 2006). In fens, these latter species are often more productive and better adapted to disturbed sites than the specialists and thus put additional competitive pressure on the already disadvantaged specialists (e.g. Pauli et al., 2002).

The management of the protected fens, in combination with the factors mentioned above, may also affect the plant-species composition of the studied fens. We have previously shown that some fen taxa benefit from grazing and others from mowing (vascular plants: Peintinger, 1999; butterflies and grasshoppers: Wettstein and Schmid, 1999; bryophytes: Bergamini et al., 2001b). On the landscape level, a mixture of both management types was therefore recommended for the long-term protection of fen taxa (Peintinger, 1999; Wettstein and Schmid, 1999; Bergamini et al., 2001b). Given current threats such as eutrophication or climate change, however, favourability of management types may change.

In this paper, we concentrate on vascular plants and bryophytes, which are important components of calcareous fens in terms of species richness and biomass (Bergamini et al., 2001a; Peintinger et al., 2003). The two groups differ considerably in morphological, physiological, and ecological traits. Bryophytes are poikilohydric, and water and nutrients are absorbed over the whole surface (Schofield, 1985). Bryophytes may thus react differently to environmental changes than vascular plants and may indicate such changes earlier.

The aim of this paper was to study recent trends in species density of both vascular plants and bryophytes, and to identify their possible underlying environmental causes. We re-visited 36 calcareous fens, which we already studied in the mid-nineties of the last century (Peintinger, 1999; Bergamini et al., 2001b; Peintinger et al., 2003) and assessed species density at 180 plots in total as well as plant functional characteristics based on ecological indicator values (Landolt, 1977). Given the substantial governmental subsidies paid to the farmers for traditional management of fens, we particularly assessed (1) whether diversity of species of high conservation concern and habitat quality was maintained in the traditionally managed areas, and (2) whether species turnover over the 10-yr time span and changes in habitat quality differed between the two traditional management regimes grazing and mowing.

Materials and methods

Study sites

The study area covered approximately 3500 km^2 in the pre-Alps in the north-eastern part of Switzerland (for a map of the study area see Bergamini et al., 2001b). Within this area, more than 300 fens of at least 1 ha exist (BUWAL, 1990). In 1995, we randomly selected 36 fens with the restriction that they contained vegetation of the *Caricion davallianae* type (Ellenberg, 1996). The fens chosen were all traditionally managed, but differed in the type of management (mown vs. grazed) and altitude (800–1000, >1000–1200, >1200–1400 m asl) according to a balanced factorial design. Furthermore, the selection was done in a way to avoid a confounding of site area with the above classification factors (Bergamini et al., 2001b).

Vegetation monitoring

In each fen, five plots of $1 \times 2\,\mathrm{m}^2$ were sampled for bryophytes and vascular plants (in total 180 plots distributed over the 36 fens). The first survey of vascular plants was conducted in July and August 1995 (Pauli, 1998; Peintinger, 1999), the first survey of bryophytes between May and July 1997 (Bergamini et al., 2001b). Because in 1995 plots were not marked as permanent, plot locations for bryophytes and vascular plants were not identical in the first survey. However, for both groups the same random procedure was applied to select plot locations within fens: each fen was divided in 4 sectors and each sector was again split into 4 subsectors. Within each sector, one subsector was randomly chosen and one plot was then randomly located within that subsector. One additional plot was placed in the center of each fen. To avoid large differences in environmental conditions, plots that did not contain *Carex davalliana* (a frequent, small, tussock-forming sedge characteristic of the Caricion davallianae alliance, Ellenberg, 1996), were replaced by a new randomly selected, plot of the same subsector containing this particular species. A second survey of all 36 sites took place in July and August 2005 (24 sites) and July 2006 (12 sites). Shape and size of plots were identical to the first survey. At the second census, vascular plants and bryophytes were sampled on the same plots.

In both surveys, a complete species list was compiled for both vascular plants and bryophytes. Difficult-to-identify vascular plant species and all bryophyte species were collected for later determination. Nomenclature for vascular plants follows Lauber and Wagner (2001), for mosses Hill et al. (2006) and for liverworts Grolle and Long (2000). Vascular plants were grouped into four taxonomic-functional groups: sedges (Cyperaceae and Juncaceae), grasses (Poaceae), legumes (Fabaceae), and non-legume herbs (all other species, including tree seedlings). Bryophytes were assigned to the two main phylogenetic clades, liverworts (Hepaticae) and mosses (Musci). We considered all nationwide ‘critically endangered’, ‘endangered’, ‘vulnerable’, and ‘nearly threatened’ species as ‘Red-List species’. Red-List status for vascular plants was based on Moser et al. (2002) and for bryophytes on Schnyder et al. (2004). Red-List species included vascular plants such as *Herminium monorchis*, *Gentiana pneumonanthe*, *Scorzonera humilis* or *Swertia perennis* and bryophytes such as *Hamatocaulis vernicosus*, *Meesia triquetra* or *Cinclidium stygium*.

For the designation of vascular plants with high habitat specificity (habitat specialists), we used the 25 species listed as characteristic of the *Caricetalia davallianae* alliance in the appendix to the Swiss fen inventory (BUWAL, 1990, see Table 1). Because no similar list exists for bryophytes, we treated all bryophytes, which are typical for ‘calcareous fens’, ‘extremely rich fens’ and ‘rich fens’ according to Hajek et al. (2006) as habitat specialists. We found 16 such specialist bryophytes. Based on our own studies (A. Bergamini, unpublished data), we removed five species from this group because they also occur abundantly outside *Caricion davallianae* fens (*Calliergonella cuspidata, Chiloscyphus pallescens* [incl. *C. polyanthos*], *Aulacomnium palustre, Palustriella commutata, Sphagnum teres*). Based on further reference works (in particular Braun, 1968; Nebel and Philippi, 2000–2005; Berg and Dengler, 2005) and our own experience, we added eight species to the group of bryophyte specialists (*Brachythecium mildeanum, Brachythecium turgidum, Pseudocalliergon trifarium, Palustriella decipiens, Palustriella falcata, Meesia triquetra, Sphagnum contortum, Sphagnum warnstorfii*). Finally, the list contained 19 bryophyte species, which we considered habitat specialists (Table 1). All species not classified as habitat specialists were regarded as generalists.

Table 1. All species designated as habitat specialists for vascular plants (after BUWAL, 1990) and bryophytes (see Methods section).

Vascular plants	Bryophytes
Aster bellidiastrum	*Brachythecium mildeanum*
Bartsia alpina	*Brachythecium turgidum*
Calycocorsus stipitatus	*Breidleria pratensis*
Carex capillaris	*Bryum pseudotriquetrum*
Carex davalliana	*Calliergon giganteum*
Carex dioica	*Campylium stellatum*[a]
Carex flava	*Cinclidium stygium*
Carex hostiana	*Fissidens adianthoides*
Carex panicea	*Hamatocaulis vernicosus*
Carex pulicaris	*Meesia triquetra*
Eleocharis quinqueflora	*Palustriella decipiens*
Epipactis palustris	*Palustriella falcata*
Eriophorum latifolium	*Philonotis calcarea*
Juncus alpinoarticulatus	*Plagiomnium elatum*
Molinia caerulea	*Pseudocalliergon trifarium*
Parnassia palustris	*Scorpidium cossonii*
Pinguicula alpina	*Sphagnum contortum*
Pinguicula vulgaris	*Sphagnum warnstorfii*
Primula farinosa	*Tomentypnum nitens*
Schoenus ferrugineus	
Selaginella selaginoides	
Swertia perennis	
Tofieldia calyculata	
Trichophorum cespitosum	
Triglochin palustris	

Nomenclature for vascular plants follows Lauber and Wagner (2001) and for mosses Hill et al. (2006).

[a] Incl. *Campylium protensum*.

We further used indicator values after Landolt (1977) for vascular plants occurring in Switzerland to assign species to ecological groups. Landolt's indicator values follow an ordinal scale and range from 1–5 (low numbers represent low, high numbers high resource requirements). Indicator values for vascular plants have been widely used in vegetation ecology (Diekmann, 2003) and proven to be an important tool for analyzing environmental causes of changes in vascular plant species richness (Stehlik et al., 2007).

We used the following groups: indicators of wet soils (species with Landolt humidity values $\geqslant 4$), light indicators (species with Landolt light values $\geqslant 4$), indicators of nutrient-rich soils (species with Landolt nutrient values $\geqslant 3$), indicators of acidic soils (species with Landolt soil-reaction values $\leqslant 2$), peat indicators (species with Landolt organic content values $= 5$). Additionally, we calculated mean indicator values for soil moisture, light availability, soil nutrients, soil acidity and soil organic content based on presence/absence data of vascular plants for each plot in both surveys.

Aboveground biomass of vascular plants was harvested within the $1 \times 2\,\mathrm{m}^2$ plots in randomly chosen subplots of $18.5 \times 18.5\,\mathrm{cm}^2$ by clipping the plants just above the ground. In the first survey, aboveground biomass was sampled in four of the vascular plant plots per site and in three subplots within each plot. In the second survey, biomass was harvested in five plots and in one subplot within each plot. In both surveys, biomass was harvested at peak standing crop. Biomass samples were dried (70 °C, 48 h) and weighed.

In the first survey, we collected soil samples from both the vascular plant plots (two soil cores of approx. 10 cm depth and 6 cm diameter from each of 4 plots per site) and the bryophyte plots (three soil cores of approx. $3 \times 3 \times 3\,\mathrm{cm}^3$ from each plot per site). In the second survey, we collected from each plot one soil sample (approx. $5 \times 5 \times 10\,\mathrm{cm}^3$). The soil samples were dried as soon as possible at 70 °C (first survey: 40 °C) to constant weight. Stones and roots were removed and the soil was pulverized with an electronic mill. The soil pH was measured from water suspension 1:3 soil/deionized water (w/v) of approx 1 g soil. After mixing, test tubes were left untouched for 24 h before measurement (pH-meter 'Knick 761 Calimatic', Knick, Berlin, Germany).

Statistical analyses

We used mixed-model analysis of variance (ANOVA) to analyze effects of management, altitude, survey date (1995/97 vs. 2005/06) and their interactions on the response variables. Fixed effects of management and altitudinal class and their interactions were tested against the random effects of sites. Interactions between these factors and survey date were tested against the site x survey date interaction (random), and random effects of site and of the site x survey date interaction were tested against the residual variation between plots. If residuals were not homogeneously and normally distributed, we transformed the response variable (square root for counts, logarithm for continuous values, Sokal and Rohlf, 1995). We omitted one fen from the analyses because management changed from grazing to mowing between 1995 and 2005/06. For the same reason, we had to omit one plot from another fen in which management changed on part of the area of the site. The total number of replicates was thus only 348 instead of 360. For the analyses of vascular plant biomass and pH measured on the vascular plant plots, the total number of replicates was 313 because sampling was done on only four plots per site in the first survey. Because vascular plant biomass may strongly vary between years, we tested by *t*-tests whether differences between 1995 and 2005 (24 sites) and between 1995 and 2006 (12 sites) were consistent. All analyses were done with the statistical software R (version 2.6.0, R Development Core Team, 2007).

Results

Taxonomic-functional groups of vascular plants and bryophytes

Species density ($=$ species number per $2\,\mathrm{m}^2$) of all vascular plants did not change between the two surveys, but species density of herbs increased slightly over the 10-yr period (18.8$\pm$0.42 SE$\rightarrow$19.9$\pm$0.44 SE; Table 2). Species density of legumes remained almost constant in grazed fens (1.67$\pm$0.12$\rightarrow$1.61$\pm$0.13; Table 2), but increased in mown fens (2.04$\pm$0.12$\rightarrow$2.42$\pm$0.13; Table 2). Overall, species density of vascular plants was 14.5% lower in grazed than in mown fens (Fig. 1A, Table 2). This difference was mainly due to negative effects of grazing on species density of herbs (Fig. 1C, Table 2), and, to a lesser degree, legumes (Fig. 1B). Altitude had no effect on species density of any of the four taxonomic-functional groups of vascular plants (Table 2).

Species density of bryophytes declined from 1997–2005/06 (12.2$\pm$0.26$\rightarrow$11.5$\pm$0.23; Table 2). Management and altitude had no significant effects on total bryophyte species density (Table 2), but the interaction between these two factors was significant (Fig. 2A, Table 2). The decline of the bryophytes was mainly due to a decline in species density of mosses in grazed fens (grazed fens: 11.0$\pm$0.34$\rightarrow$10.1$\pm$0.27, mown fens: 11.8$\pm$0.31$\rightarrow$11.7$\pm$0.29; Table 2). In contrast to mosses, liverworts were slightly favoured by grazing (Table 2, Fig. 2B and C). However, for the liverworts, there was

Table 2. Results of mixed-model ANOVAs on the effects of management, altitude, date of survey and of interactions between these factors on species density of different taxonomic/functional groups in 1 × 2 m^2 plots.

		All vascular plants		Sedges		Grasses		Legumes	
	df	SS	F	SS	F	SS	F	SS	F
Management (M)	1	2291.2	12.57^{***}	28.41	2.98	0.69	0.05	30.91	6.87^{*}
Altitude (A)	2	669.1	1.84	57.08	2.99	44.74	1.60	21.88	2.43
M × A	2	840.3	2.30	17.41	0.91	14.85	0.53	18.16	2.02
Site (S)	29	5287.8	7.24^{***}	276.65	3.27^{***}	406.21	5.70^{***}	130.41	4.66^{***}
Date of survey (D)	1	116.1	3.14	10.00	2.85	6.08	2.18	2.42	2.68
M × D	1	117.5	3.18	0.49	0.14	0.44	0.16	4.15	4.60^{*}
A × D	2	183.1	2.48	3.55	0.51	1.49	0.27	2.73	1.51
A × M × D	2	16.4	0.22	4.21	0.60	1.18	0.21	0.83	0.46
S × D	29	1071.4	1.47	101.75	1.20	80.83	1.14	26.18	0.94
Residuals	278	6999.2		811.10		682.75		268.30	
		Non-legume herbs		All bryophytes		Liverworts		Mosses	
Management (M)	1	2191.1	20.56^{***}	38.6	1.81	5.29	3.97^{+}	119.9	7.23^{*}
Altitude (A)	2	568.6	2.67	80.8	1.90	6.55	2.46	42.8	1.29
M × A	2	519.3	2.44	152.6	3.59^{*}	8.95	3.36^{*}	73.4	2.21
Site (S)	29	3090.6	7.57^{***}	617.4	2.35^{***}	38.60	4.26^{***}	481.0	2.30^{***}
Date of survey (D)	1	98.3	5.31^{*}	33.5	6.02^{*}	1.04	2.98	22.3	5.15^{*}
M × D	1	55.3	2.98	13.2	2.37	0.41	1.18	18.0	4.16^{*}
A × D	2	94.8	2.56	3.7	0.33	0.10	0.14	2.8	0.32
A × M × D	2	33.1	0.89	3.8	0.35	2.14	3.07	7.0	0.81
S × D	29	537.4	1.32	161.6	0.62	10.09	1.11	125.2	0.60
Residuals	278	3911.5		2516.3		86.85		2003.4	

Species density of liverworts was square-root transformed prior to analysis.

$^{**}p<0.01$.

$^{+}p<0.06$.

$^{*}p<0.05$.

$^{***}p<0.001$.

also a significant interaction between management and altitude with species density being generally low in mown fens and in grazed fens at low altitude, but high in grazed fens at higher altitudes (Fig. 2C).

Specialists, generalists and Red-List species of vascular plants and bryophytes

Over the 10-yr period, species density of habitat specialists decreased by 9.4% in vascular plants (8.6 ± 0.23 → 7.8 ± 0.21; Table 3) and by 14.9% in bryophytes (4.4 ± 0.15 → 3.7 ± 0.15; Table 3). Density of vascular plant species of the Red List per 2 m^2 plot declined even by 22.7% (1.01 ± 0.07 → 0.78 ± 0.06; Table 3, Fig. 3A and B). The number of Red-List bryophyte species could not be analyzed, because too few plots contained such species. At both survey dates, species density of vascular plant specialists (but not of Red-List species) increased with altitude (low: 6.3 ± 0.20, intermediate: 8.8 ± 0.28, high altitude: 9.4 ± 0.26; Table 3). Management did not affect the reduction of specialist species density in vascular plants but in bryophytes specialist species density declined more strongly in grazed than in mown fens (Fig. 3C, Table 3). Species density of vascular plant generalists increased by 8.2% over the 10-yr period (23.8 ± 0.49 → 25.7 ± 0.57) and was 16% lower in grazed (22.5 ± 0.49 species per plot) than in mown fens (26.8 ± 0.53 species per plot; Table 3). Species density of bryophyte generalists did not change over time and was not affected by management (Table 3).

Ecological groups based on indicator values

Between the two surveys, mean species density of nutrient indicators increased by 18.4% (13.6 ± 0.40 → 16.1 ± 0.48) and of peat indicators decreased by 8.1% (3.7 ± 0.12 → 3.4 ± 0.12; Table 4, Fig. 4A and B). Species density of wet-soil indicators decreased over the 10-yr period in grazed (16.9 ± 0.33 → 15.7 ± 0.34), but not in mown fens (16.9 ± 0.35 → 17.1 ± 0.34; Table 4). No changes were found for the species density per plot of light indicators and of indicators of acidic soils (Table 4).

Species density of wet-soil indicators was particularly low at the lowest altitude (low: 15.5 ± 0.30, intermediate: 17.4 ± 0.25, high altitude: 17.2 ± 0.31; Table 4) indicating more disturbed hydrological conditions in these fens. Species density of light indicators increased with altitude in mown fens, but in grazed fens species density reached a maximum at intermediate altitude (mown fens: low: 19.6 ± 0.47, intermediate: 21.3 ± 0.49, high altitude: 23.3 ± 0.58; grazed fens: low: 16.3 ± 0.53, intermediate: 21.1 ± 0.57, high altitude: 17.5 ± 0.41, Table 4).

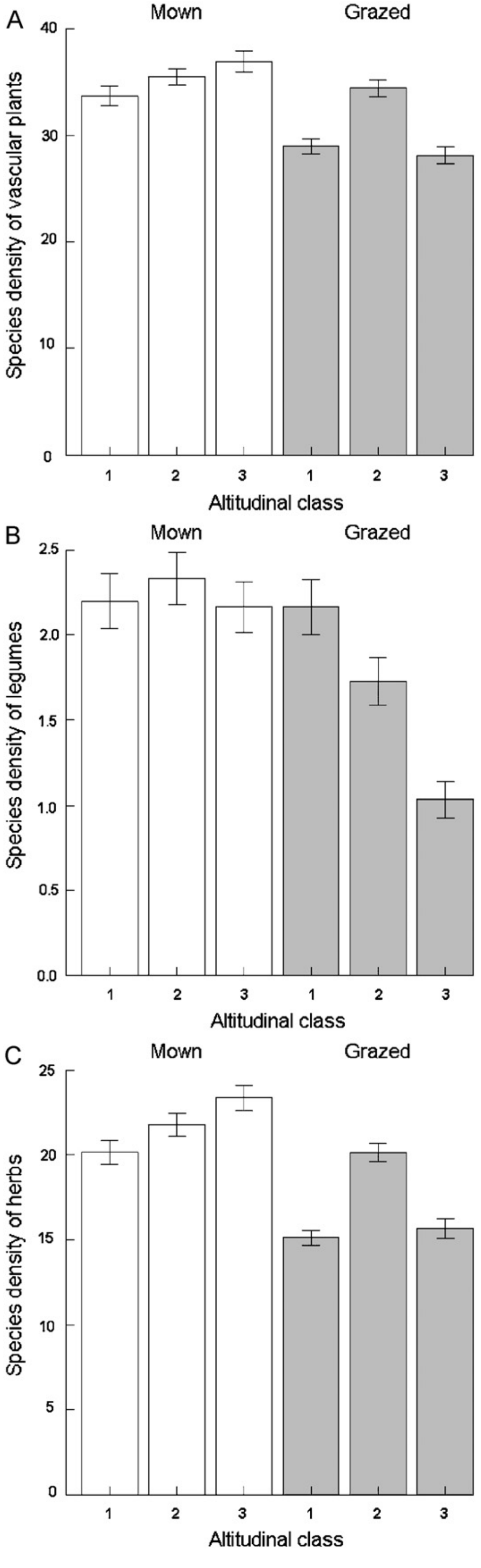

Fig. 1. Species density in 1 × 2 m^2 plots of vascular plants (A), legumes (B) and herbs (C) as a function of management and altitude in calcareous fens. Values are means over both survey dates (±SE). Altitudinal class 1: 800–1000 m asl; altitudinal class 2: 1000–1200 m asl; altitudinal class 3: 1200–1400 m asl. Species density of vascular plants, legumes and herbs was lower in grazed than in mown fens ($F_{1,29} = 12.57$, $p < 0.001$, $F_{1,29} = 6.87$, $p < 0.05$ and $F_{1,29} = 20.56$, $p < 0.001$, respectively).

Community biomass, pH and mean indicator values of vascular plants

In the second survey, aboveground biomass of vascular plants was almost 30% higher than in the first survey (254 ± 9.9 g m^{-2} → 329 ± 10.4 g m^{-2}; Table 5). Because in the second survey we sampled biomass in 2005 (24 fens) and in 2006 (12 fens), we tested whether both years had a higher vascular plant biomass than 1995; and this was the case (2005: $t = 3.24$, $p = 0.001$; 2006: $t = 3.90$, $p < 0.001$; Fig. 5). There was also a significant interaction between management and altitude, which was mainly caused by the very low biomass values in the grazed fens at the lowest altitude (Table 5). The soil pH in the second survey (6.00 ± 0.05) was slightly but significantly ($p < 0.05$) lower than in the first survey (vascular plant survey in 1995: 6.12 ± 0.05; bryophyte survey in 1997: 6.08 ± 0.04, Table 5).

Over the 10-yr period, mean plant indicator values changed significantly in the direction of reduced habitat quality for originally nutrient-poor fens (Table 6): indicator values for soil moisture, light availability, soil acidity and organic content of soils decreased whereas indicator values for soil nutrients increased (Fig. 6). In grazed fens, mean soil moisture values indicated wetter conditions than in mown fens (grazed fens: 3.72 ± 0.012, mown fens: 3.63 ± 0.011; Table 6) and average indicator values for light availability were higher at higher altitudes (low: 3.60 ± 0.012, intermediate: 3.64 ± 0.012, high altitude: 3.69 ± 0.011; Table 6).

Discussion

Decline of habitat specialists and Red-List species

Despite protection and traditional management, fen specialists of both vascular plants and bryophytes declined in the studied fens over a 10-yr period even at the small spatial scale of 2 m^2. In vascular plants, the relative decline was stronger for species of the Red List, emphasizing the higher extinction probability of these species. Declines in species richness of habitat specialists over a 5-yr period have been reported for different types of bogs in Switzerland (Klaus, 2007). Reduced richness of specialist species was also reported from other species-rich, semi-natural wet grassland habitats in Europe (Kooijman, 1992; Fojt and Harding, 1995; van Belle et al., 2006), but not over such short time spans as in this study. From a conservation point of view, the clear decline of habitat specialists in our case is particularly worrying because the sites are still traditionally managed. Moreover, because we only considered plots that contained the characteristic fen specialist *Carex davalliana*, i.e. plots or fen patches which lost this sedge were not even considered for monitoring, our estimates of the decline of habitat specialists and Red-List species may even be too conservative.

Causes of decline

The decline in habitat specialists and Red-List species at the study sites was correlated with a decline in habitat quality. The increased aboveground vascular plant biomass, changes in mean plant indicator values, the increase of nutrient indicators per plot and the decrease of peat indicators point to eutrophication and decreasing moisture: the fens became more productive, richer in nutrients, shadier at the ground and drier, thus making it difficult for small, non-competitive, fen-adapted species to survive. This decline in habitat quality is not specific to calcareous fens. Similar trends have also been observed in acidic fens and bogs and other habitats in Switzerland (Klaus, 2007; Stöcklin et al., 2007). In the following we discuss which factors could cause such effects.

Nutrient enrichment is widely recognized as an important driver of vegetation change in various types of wetlands (DiTommaso and Aarssen, 1989; Bobbink et al., 1998; Bedford et al., 1999) and it has been shown that both nitrogen and phosphorous can limit aboveground biomass in fens (Verhoeven et al., 1996; Boeye et al., 1997; Pauli et al., 2002). Lowered light availability under more productive conditions has been suspected to be the main reason for the decrease of fen specialist species (Kotowski et al., 2001), although increased

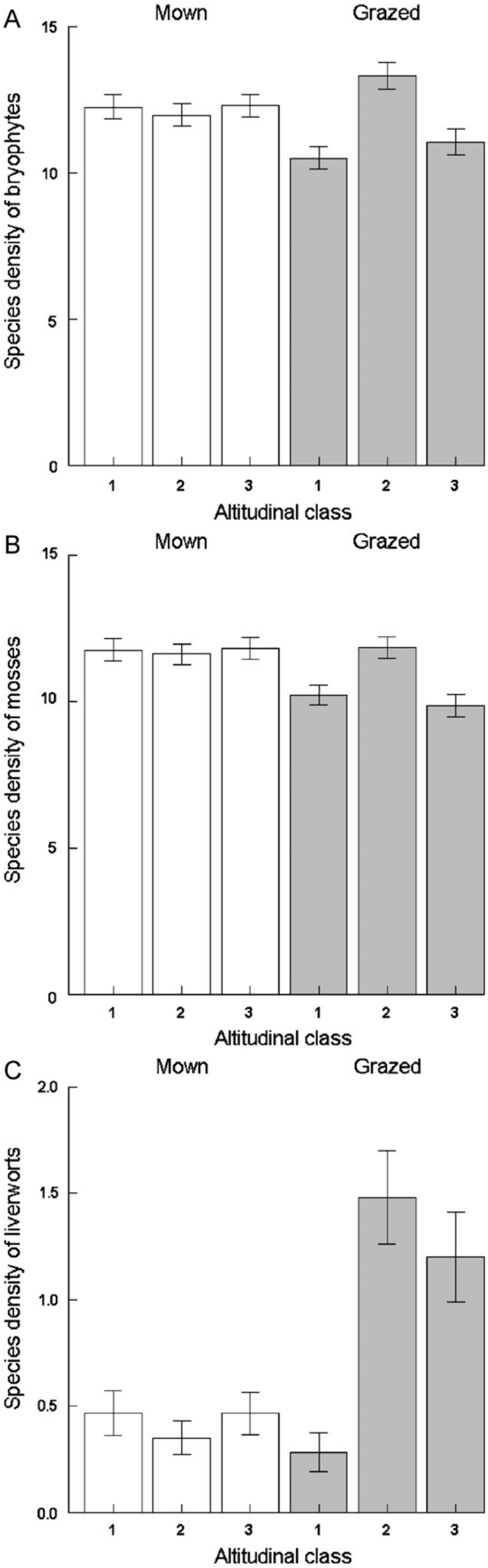

Fig. 2. Relationships between species density of bryophytes (A), mosses (B) and liverworts (C) and management and altitude (means over both survey dates ± SE). Altitudinal class 1: 800–1000 m asl; altitudinal class 2: 1000–1200 m asl; altitudinal class 3: 1200–1400 m asl Effects of management were significant for mosses ($F_{1,29} = 7.23$, $p < 0.05$), and marginally significant for liverworts ($F_{1,29} = 3.97$, $p < 0.06$). For both bryophytes and liverworts the management x altitude interaction was significant ($F_{2,29} = 3.59$, $p < 0.05$ and $F_{2,29} = 3.36$, $p < 0.05$, respectively).

Table 3. Relationships between management, altitude, date of survey and of interactions between these factors on species density of habitat specialists, generalists and density of Red-List species in $1 \times 2\,\mathrm{m}^2$ plots.

Vascular plants

		Habitat specialists		Red-List species		Generalists	
	df	SS	F	SS	F	SS	F
Management (M)	1	61.6	2.36	10.79	3.52	1601.7	7.32*
Altitude (A)	2	617.4	11.82***	1.55	0.25	472.8	1.08
M × A	2	113.9	2.18	2.69	0.44	401.5	0.92
Site (S)	29	757.4	5.68***	88.88	6.63***	6342.8	8.49***
Date of survey (D)	1	56.3	11.31**	4.60	6.11*	334.1	10.71**
M × D	1	8.6	1.74	0.13	0.17	62.4	2.00
A × D	2	26.1	2.62	0.42	0.28	75.1	1.20
A × M × D	2	26.5	2.66	0.87	0.58	10.8	0.17
S × D	29	144.4	1.08	21.81	1.63*	904.6	1.21
Residuals	278	1278.6		128.55		7159.4	

Bryophytes

		Habitat specialists		Generalists	
Management (M)	1	4.91	0.31	15.99	0.53
Altitude (A)	2	32.05	1.00	30.83	0.51
M × A	2	0.27	0.01	143.03	2.37
Site (S)	29	463.93	6.13***	875.62	3.56***
Date of survey (D)	1	37.35	17.12***	0.10	0.01
M × D	1	10.33	4.74*	0.18	0.02
A × D	2	0.15	0.03	5.19	0.35
A × M × D	2	0.81	0.19	3.52	0.24
S × D	29	63.26	0.84	217.12	0.88
Residuals	278	725.80		2358.70	

*$p<0.05$.
**$p<0.01$.
***$p<0.001$.

belowground competition may also contribute (Rajaniemi, 2002). In our calcareous fens, it has been experimentally shown that nutrient enrichment reduced bryophyte species density and biomass and increased vascular plant biomass within 1.5 years after application of either nitrogen alone or of a mixture of nutrients (NPK, Bergamini and Pauli, 2001; Pauli et al., 2002). Although Pauli et al. (2002) did not find a decrease in the number of habitat specialists during the course of their short-term experiment, they already observed an increase in generalist species, which might have out-competed the specialists in the longer term. In our study, the increase of the mean nutrient indicator value was caused by two processes: the decrease of habitat specialists and the increase of nutrient indicator species. The decrease of bryophyte species density in our study was likely caused by eutrophication that led to an increase of vascular plant biomass, but not of bryophyte biomass (see also Virtanen et al., 2000; van der Wal et al., 2005). Due to the experimentally shown N-limitation of aboveground biomass production in our fens (Pauli et al., 2002), high atmospheric nitrogen deposition has the potential to cause the observed changes (see also Stevens et al., 2004). Atmospheric nitrogen deposition rates in Switzerland exceed critical loads in 55% of the area covered with natural or semi-natural non-forest vegetation (BAFU/BFS, 2007). In the study region, deposition rates reach up to $40\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ (BAFU/BFS, 2007). Theoretically, increased phosphorus input could also lead to the observed changes, but given the diminished solubility of phosphates under base-rich conditions (Verhoeven et al., 1996; Larcher, 2003), this seems rather unlikely. However, phosphorus may also be released from microbes after drying and rewetting of the soil and it has been hypothesized that this process enhances the availability of phosphorus in regions with longer dry periods or more frequent cycles of wetting and drying due to climate change (Turner and Haygarth, 2001).

To assess whether the observed biomass increase was related to climatic differences between censuses (Knapp and Smith, 2001), we compared climatic data (daily precipitation and daily mean temperatures) from three weather stations within the study area (Alpthal:

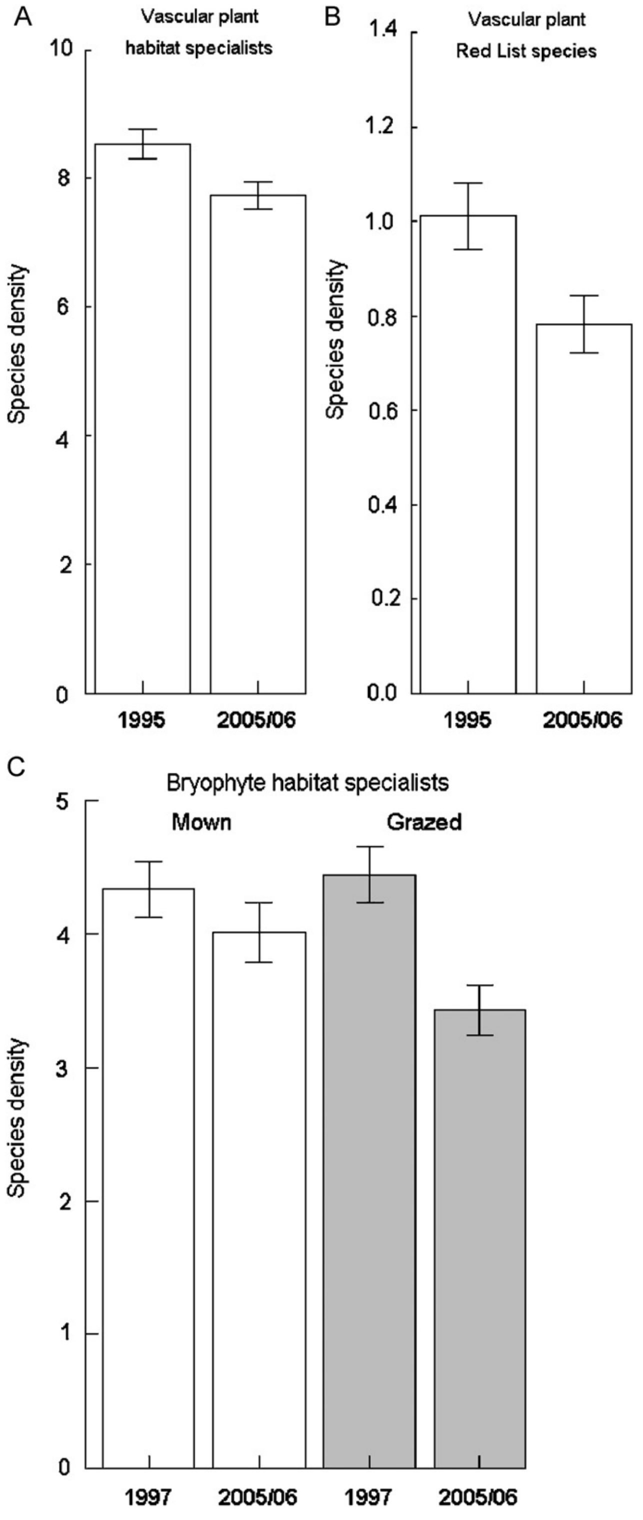

Fig. 3. Effects of survey date on species density of vascular plant habitat specialists (A) and Red-List species (B), and effects of survey date and management type on bryophyte habitat specialists (C; means ± SE). Habitat specialists and Red-List species all significantly declined 1995/97→2005/06 (Table 3). Bryophyte specialists declined especially in grazed fens ($F_{1,29} = 4.74$, $P < 0.05$).

1220 m asl, Einsiedeln: 910 m asl, Ebnat-Kappel: 623 m asl) for each month from March to August between 1995 (first survey) and 2005/2006 (second survey). Concerning precipitation, none of the mean daily amounts in the different months in 1995 was significantly different from those in 2005 or 2006 (Wilcoxon rank sum tests, data not presented). However, mean daily temperature in June (main growth period in these pre-alpine fens) 1995 was between 3.8 and 2.9 °C lower than in June 2005 and June 2006 at all three weather stations (Wilcoxon rank sum tests: $p < 0.01$ for all comparisons). Besides these rather extreme differences, there is a trend to increased temperatures during the growing period with a mean temperature increase per decade and month between 0.45 and 0.75 °C as regressions analyses for the period 1970–2006 showed for two of the weather stations ($p < 0.05$ in Ebnat-Kappel for April, May and June; in Einsiedeln for April, May, June, July and August; for Alpthal there were no long-term data available). If temperature, besides eutrophication, was the main driver of aboveground plant biomass production in these fens, then the predicted higher June temperatures for the coming decades (OcCC, 2007) may further increase fen productivity and threaten habitat specialists.

Lowering of the soil moisture is disastrous for fen vegetation (e.g. Grootjans et al., 2005), especially when combined with increased nutrient input (Fojt and Harding, 1995; Bollens et al., 2001). Although drainage is rarely part of the management contracts (Gonet, 2002), we observed in nearly every fen studied some traces of rather old (most probably built before legal protection of fens in Switzerland, i.e. before 1987), but still active drainage channels. However, there were no newly built channels. In addition to direct drainage of fens, disturbance of the hydrological regime in the surroundings of fens may also have severe effects on soil moisture within fens (Fojt and Harding, 1995; van Diggelen et al., 2006). Hence, altered hydrological site conditions may be one of the causes of the observed decline in mean soil-moisture indicator values. As for eutrophication effects, effects of changed hydrological conditions on fen specialists may also be mediated by increased biomass production of generalist, dominant vascular plants benefiting from those changes. The decreased organic content of the soil can also be a direct cause of the lowered soil moisture as well as of other processes such as increased atmospheric nitrogen deposition or global warming known to stimulate microbial decomposer communities and thus to enhance decomposition rates of organic material (Heimann and Reichstein, 2008). Furthermore, the lowering of the water table in fens increases the relative importance of rainwater, which may lead to an acidification of the uppermost soil layer (van Diggelen et al., 2006). This

Table 4. Dependence of species density of wet-soil indicators, light indicators, nutrient indicators, indicators of acidic soils and peat indicators in $1 \times 2\,m^2$ plots on management, altitude, date of survey and the interactions between these factors.

		Wet-soil indicators		Light indicators		Nutrient indicators		Acidic-soil indicators		Peat indicators	
	df	SS	F	SS	F	SS	F	SS	F	SS	F
Management (M)	1	43.6	1.62	946.3	17.35***	602.9	3.78	0.9	0.01	0.0	0.00
Altitude (A)	2	250.7	4.65*	619.0	5.67*	349.6	1.10	44.1	0.45	13.6	0.51
M × A	2	107.5	1.99	439.9	4.03*	220.7	0.69	0.6	0.01	1.1	0.04
Site (S)	29	782.2	3.55***	1582.1	5.18***	4625.8	8.54***	1433.4	12.80	387.5	8.92***
Date of survey (D)	1	17.0	2.09	13.7	0.79	546.3	27.50***	0.7	0.32	8.4	5.31*
M × D	1	46.9	5.75*	45.2	2.60	50.9	2.56	1.6	0.79	0.0	0.00
A × D	2	19.5	1.19	74.2	2.13	88.4	2.23	5.6	1.40	1.2	0.37
A × M × D	2	15.2	0.93	9.6	0.28	1.0	0.02	1.3	0.33	3.8	1.19
S × D	29	236.7	1.07	504.8	1.65*	576.0	1.06	58.3	0.52	45.8	1.06
Residuals	278	2113.1		2930.8		5190.7		1073.2		416.3	

Classification of species was based on the indicator values of Landolt (1977).

**$p < 0.01$.

*$p < 0.05$.

***$p < 0.001$.

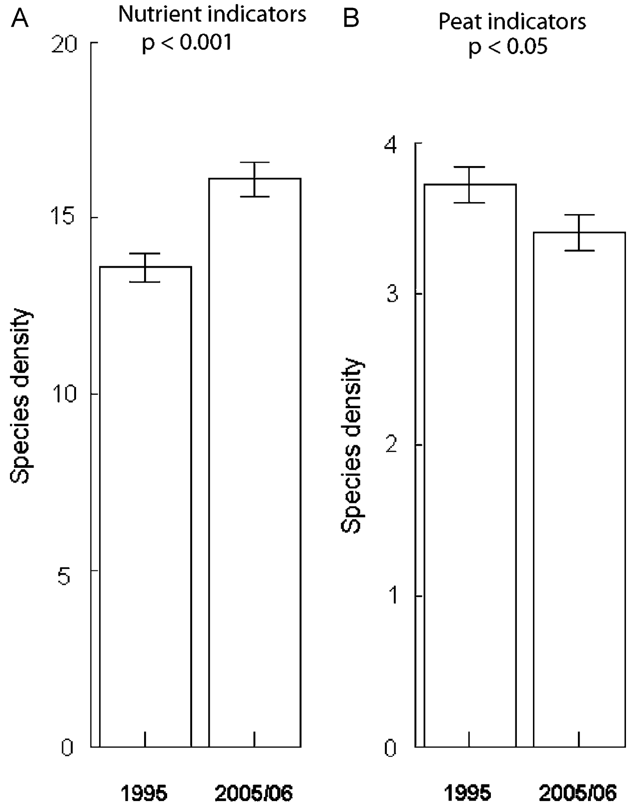

Fig. 4. Increase of average species density per plot of nutrient indicators (A) and concomitant decrease of peat indicators (B) 1995→2005/06 (means ± SE). Only vascular plants are considered.

may explain the decrease of the mean indicator values for acidity and of measured pH values over the last decade in the studied fens.

Table 5. Effects of management, altitude, date of survey and their interactions on aboveground vascular plant biomass in $18.5 \times 18.5\,cm^2$ plots and on pH measurements.

	Biomass			pH	
	df	SS	F	SS	F
Management (M)	1	0.47	0.98	0.26	0.15
Altitude (A)	2	4.33	4.55*	0.20	0.06
M × A	2	3.69	3.87*	2.46	0.71
Site (S)	29	13.80	3.04***	50.04	9.70***
Date of survey (D)	1	6.58	25.44***	1.19	5.00*
M × D	1	0.05	0.20	0.00	0.01
A × D	2	0.14	0.27	0.00	0.00
A × M × D	2	0.43	0.83	0.01	0.03
S × D	29	7.50	1.65*	6.90	1.34
Residuals	243/239	38.00		42.52	

There were only 243 degrees of freedom for the residuals because in 1995 biomass and pH was sampled only on 4 plots per site. In addition, for pH there were four missing values in 2005/06. Biomass was log-transformed for the analysis.

*$p < 0.05$.

***$p < 0.001$.

Effects of management and altitude on species density and habitat quality

Vascular plants

Although both forms of traditional management, grazing and mowing, are considered appropriate for these fens, each of the two has its specific effects on species composition and richness. Thus, the species density of all vascular plants was consistently higher in mown fens (see also Peintinger, 1999), but habitat specialists and Red-List species of vascular plants were not affected by management. These results are consistent with those of Stammel et al. (2003) from calcareous fens in southern Germany. In drier grassland sites low-intensity grazing usually has a positive or neutral effect on total vascular species density (Olff and Ritchie, 1998; Schläpfer et al., 1998; Fischer and Wipf, 2002). On wet soils, especially the effects of trampling on sensitive species may be much more severe than on dry soil (we observed gaps created by cattle hoofs of up to a depth of 25 cm in our fens, Bergamini et al., unpublished data) and the loss of these species may not be adjusted by the colonisation of gap depending species. For example Stammel and Kiehl (2004) found no species in hoofprints in fens which have not already been present in the surrounding vegetation and they hardly found any positive effects of hoofprints on species recruitments (see also Stammel et al., 2006). However, there are also reports of positive effects of artificially created gaps in fens on vascular plant germination (Kotorová and Leps, 1999; Poschlod and Biewer, 2005), but these artificially created gaps are presumably not directly comparable to hoofprints with their compacted and wet or even water-logged soil on the bottom. On dry soils, the creation of small disturbances by trampling, the spatially heterogeneous urine deposition and the selective defoliation by grazing ungulates all cause high habitat heterogeneity and are presumably responsible for the often positive effect on species density (van Wieren, 1995; Olff and Ritchie, 1998; Middleton et al., 2006). In our fens, the negative effect of grazing on vascular plants was mainly due to the decrease in species density of herbs and legumes; graminoid species were not affected, presumably due to selective grazing and better abilities for compensatory growth after trampling of grasses because of their basal meristems in contrast to legumes and herbs.

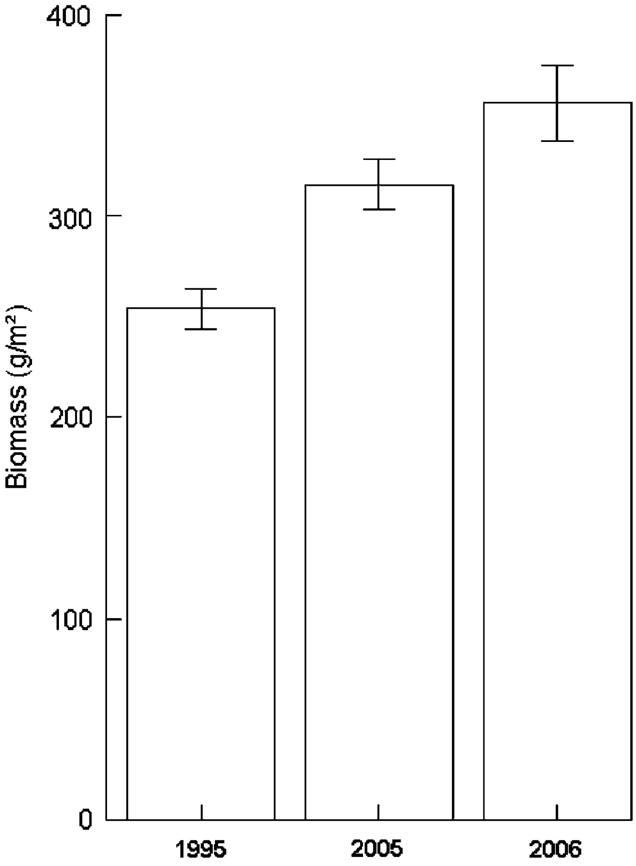

Fig. 5. Aboveground biomass of vascular plants significantly increased between the first and the second survey (means ± SE; $F_{1,29} = 25.44$, $P < 0.001$). The second survey was done in the years 2005 (24 sites) and in 2006 (12 sites).

Bryophytes

Species density of different bryophyte groups was differentially affected by management: grazing enhanced liverwort and mowing enhanced moss species density. In

Table 6. Relationships between mean indicator values per plot after Landolt (1977) and management, altitude, date of survey and their interactions.

		Moisture		Light		Nutrients		Acidity		Peat	
	df	SS	F	SS	F	SS	F	SS	F	SS	F
Management (M)	1	0.72	11.91^{**}	0.03	0.54	0.01	0.06	0.22	0.74	0.09	1.21
Altitude (A)	2	0.25	2.03	0.50	4.67^{*}	0.92	2.33	0.90	1.56	0.12	0.85
M × A	2	0.20	1.67	0.01	0.11	0.06	0.16	0.03	0.04	0.15	1.00
Site (S)	29	1.76	3.71^{***}	1.54	5.45^{***}	5.76	9.74^{***}	8.40	13.59^{***}	2.16	7.00^{***}
Date of survey (D)	1	0.14	6.34^{*}	0.52	37.67^{***}	0.38	15.01^{***}	0.18	9.30^{**}	0.14	8.17^{**}
M × D	1	0.03	1.28	0.01	0.52	0.01	0.34	0.00	0.01	0.00	0.00
A × D	2	0.02	0.47	0.04	1.37	0.02	0.36	0.01	0.36	0.05	1.38
A × M × D	2	0.02	0.45	0.02	0.71	0.03	0.53	0.04	0.90	0.01	0.37
S × D	29	0.64	1.35	0.40	1.42	0.74	1.24	0.57	0.92	0.50	1.65^{*}
Residuals	278	4.56		2.71		5.67		5.92		2.92	

Mean indicator values are based on vascular plant vegetation only.

$^{*}p < 0.05$.

$^{**}p < 0.01$.

$^{***}p < 0.001$.

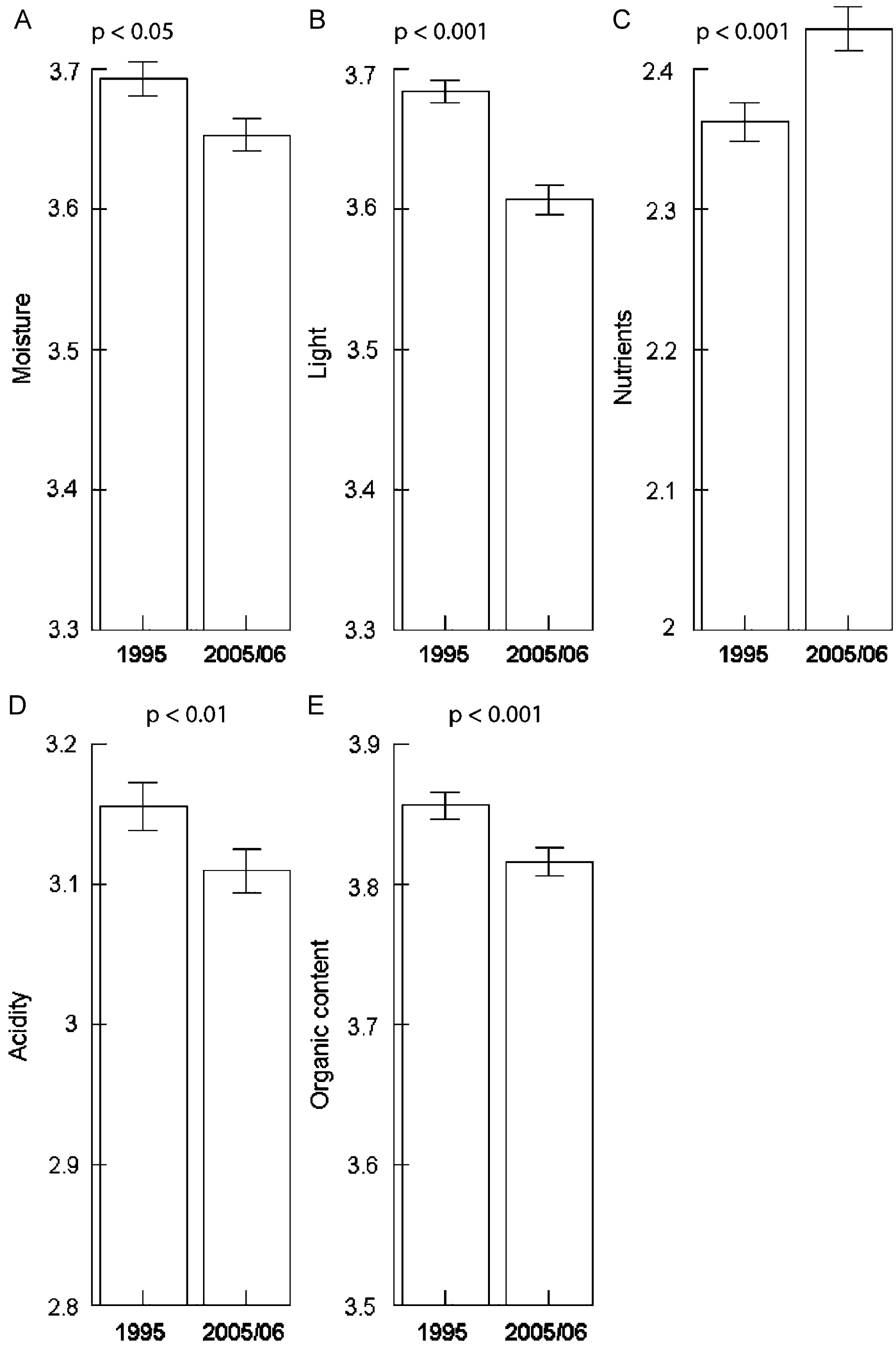

Fig. 6. Changes in mean indicator values for soil moisture (A), light availability (B), soil nutrients (C), soil acidity (D) and soil organic content (E) after Landolt (1977) between the two surveys (means ± SE).

contrast to vascular plant specialists, which showed a similar decline over the 10-yr study period both in grazed and mown fens, mosses and specialist bryophyte species declined strongly in grazed fens, but less so in mown fens. Separate ANOVAs (data not shown) showed that the differential decline for mosses was due to the specialists among them without a compensating response of generalist mosses. Whether the stronger decrease of the bryophyte habitat specialists in the grazed fens can be considered an early warning signal for similar changes in the vascular plant layer remains to be seen.

Liverwort species such as *Pellia endiviifolia*, *Riccardia multifida* or *Scapania* species were often found on the border and on the often steep walls of the small gaps created by the hoofs of the grazing cattle (Bergamini et al., unpublished data). Within the dense and thick moss layer of mown meadows however, liverworts were rarely found. In the lowest altitudinal class, grazing had a slightly negative effect on species density of liverworts.

The reasons for this different effect of grazing on liverwort species density in the lowest altitudinal class are not clear.

Management and altitude also had differential effects on habitat quality. Average indicator values indicated that grazed fens were wetter than mown fens, an observation also reported by Barth et al. (2000) and Stammel et al. (2003) and probably due to the compaction of the soil by the grazing animals. With increasing altitude, habitat quality of fens increased somewhat as indicated by the increasing average indicator value for light availability and the increase in species density of vascular plant specialists.

Conclusions

Despite traditional management, habitat quality and species density of habitat specialists and Red-List species of calcareous fens in the Swiss pre-Alps significantly decreased over only a decade from 1995 to 2006. The stronger decline of bryophyte habitat specialists in grazed fens than in mown fens may indicate that the current grazing intensity (but probably not grazing per se) is not a suitable conservation measure for these fens. Furthermore, specialized vascular wet-soil indicator plants declined only in grazed fens. On the other hand, grazed fens still contained many vascular plant and bryophyte species of high conservation value (see also Barth et al., 2000). Thus, also grazed fens are still important objects for fen conservation. A number of species are even dependent on grazed sites. For example, the dung mosses *Splachnum ampullaceum* and *Splachnum sphaericum*, which grow only on decaying cattle faeces in fens and bogs (Amann et al., 1918), are obviously not found in mown fens. Considering vascular plants, the herb *Ranunculus flammula* and the grass *Agrostis canina* are examples of species of conservation concern (both with Red-List status ‘nearly threatened’) which are mostly found in grazed sites.

Based on our diversity monitoring, the following recommendations can be made for long-term protection of these fens: (1) the traditional management has to be continued since abandoned fens loose habitat specialists (Diemer et al., 2001; Peintinger and Bergamini, 2006); however, grazing intensity (cattle breed, animal weight, stocking rate) should be adjusted to sustainable levels; (2) nutrient inputs should be reduced via the inclusion of unfertilized buffer zones around fens and measures that reduce atmospheric input of nutrients; (3) the often disturbed hydrology should be restored also in consideration of the predicted significant decrease in summer rains and increase of summer temperatures (OcCC, 2007) in the region, which will enhance the fragility of these specialized ecosystems adapted to high groundwater tables. Hydrological buffer zones around the fens may be an effective measure for the long-term protection of these fens.

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