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# Profiteers of environmental change in the Swiss Alps: increase of thermophilous and generalist plants in wetland ecosystems within the last 10 years

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**Abstract** It has been predicted that Europe will experience a rise in temperature of 2.2–5.3 °C within this century. This increase in temperature may lead to vegetation change along altitudinal gradients. To test whether vegetation composition has already changed in the recent decade due to current warming (and other concomitant environmental changes), we recorded plant species composition in 1995 and 2005/2006 in Swiss pre-alpine fen meadows (800–1,400 m a.s.l.). Despite no obvious changes in the management of these fens, overall, plant species richness (cumulative number of plant species at five plots per site) significantly increased over this period. This was mainly due to an increase in the number of thermophilous, rich-soil-indicator and shade-indicator species, which corresponded to increased community productivity and shading within the vegetation layer. In contrast, fen specialists significantly declined in species numbers. The strongest species shifts occurred at the lowest sites, which overall had a higher colonization rate by new species than did sites at higher altitudes. Vegetation change along the altitudinal gradient was also affected by different types of land management: early-flowering species and species with low habitat specificity had high colonization rates in grazed fens, especially at low altitudes.

**Keywords** Altitudinal gradient · Fen meadows · Global change · Multi-factorial environmental change · Land management · Vegetation change · Land use

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## Introduction

Evidence is increasing that the rising concentration of greenhouse gases in the atmosphere may lead to significant changes in the European climate (Houghton et al. 2001). From 2001 until 2100, Europe is forecasted to experience a rise in temperature of 2.2–5.3 °C (Christensen et al. 2007) as well as more extreme temperature events (Kjellstrom et al. 2007). In Switzerland for example, an increase in the anomalies of monthly temperatures from 1941 to 2000 has been observed in comparison with a previous period from 1864 to 1923 (Schär et al. 2004) and, compared to the past 30 years, non-intervention scenarios predict a seasonal increase in mean temperatures until 2100 by 2.7–4.8 °C (CH2011 2011). The mean annual temperature has already increased by 0.4 °C per decade since 1961 and consequently from 1970 to 2006 the mean temperature has increased in total by 1.5 °C (North et al. 2007). Such drastic climatic changes may have an impact on plant diversity (Thomas et al. 2004; Lenoir et al. 2008) with mountainous regions having a high risk of losing species that may be competitively inferior toward thermophilous or more phenotypically plastic species (Thuiller et al. 2005; Sheldon

et al. 2011). Earlier warming events in history, causing relatively smooth upward shifts in the vegetation, had a much slower rate, e.g., 1 °C increase per century in the Peruvian Andes during the Pleistocene–Holocene (Bush et al. 2004). However, at the late Glacial–Holocene transition, 11,500 years ago, a rapid increase in temperature in the Alps by ca. 3–4 °C within ca. 50 years has been estimated based on oxygen-isotope records causing rapid shifts in tree species' dominance at the timberline (Tinner and Kaltenrieder 2005). Hence, to date, climate change is considered the second biggest driver of biodiversity change globally and the first for alpine ecosystems in the next few decades (Sala et al. 2000).

There are three basic ways in which species may respond to climatic change (Bazzaz 1996; Theurillat and Guisan 2001): (1) persistence in the changed climate, (2) migration to a more suitable climate or (3) extinction. Recent analyses indicate that some species have already responded to changing climatic conditions by changing their phenology (Fitter and Fitter 2002; Parmesan and Yohe 2003; Root et al. 2003) and/or by expanding or contracting their ranges (Grabherr et al. 1994; Parmesan and Yohe 2003; Walther et al. 2005; Wilson et al. 2005; Pauli et al. 2007; Lenoir et al. 2008; le Roux and Mcgeoch 2008; Parolo and Rossi 2008; Frei et al. 2010; Odland et al. 2010). Whereas some plant species appear to be constrained in moving along with the changing climate, others adapt well or move easily and prosper in their new areas. In high alpine ecosystems, especially wind-dispersed species were observed to be good colonizers of high alpine summits (Kudernatsch et al. 2005; Parolo and Rossi 2008; Vittoz et al. 2009). However, we still lack a comprehensive hypothesis to explain the differences in migration and establishment of plant species along altitudinal (Grabherr et al. 1994; Lenoir et al. 2008) or latitudinal gradients (Tamis et al. 2005). Ecological groups of plants, which may be differentially influenced by climate warming, have already been defined: (1) early-flowering species (Fitter and Fitter 2002) potentially profiting from an earlier start of the vegetation period; (2) late-flowering species (seed riskers; Molau 1993; Theurillat and Guisan 2001) potentially profiting from longer vegetation periods; (3) clonal species capable of long persistence; (4) fast-growing species that are invaders elsewhere and might be herbivore limited in their present range; (5) herbaceous plants (as opposed to woody plants; Theurillat and Guisan 2001) or, in general, species with a fast life cycle and fast population turnover (Lenoir et al. 2008). As changes in climate occur concomitantly with other environmental changes caused by human impacts (Botkin et al. 2007) such as habitat fragmentation and pollution (for example, by nitrogen deposition; Sala et al. 2000; Stockwell et al. 2003; Jump and Penuelas 2005; Thuiller 2007), these ecological groups, however, might still be at risk if they do not have the potential to cope with multi-factorial environmental change.

In 1995, we started a comparative field study on the effects of altitude and management type (grazing vs. mowing) on wetland biodiversity using a network of 36 calcareous fen meadows identifiable by their typical *Carex davalliana* vegetation type (Wettstein and Schmid 1999; Bergamini et al. 2001a, b; Pauli et al. 2002; Peintinger et al. 2003; Bergamini et al. 2009a). To screen for possible shifts in species compositions, we repeated all vegetation surveys and measurements of soil abiotic variables in 2005/2006. By this re-monitoring after a decade, we investigated putative changes in vascular plant species richness (expressed as cumulative species richness in 5 plots per site) and species presence/absence within different plant ecological groups broadly defined as habitat-change indicators, climate-change indicators, soil-quality-change indicators and community-productivity-change indicators, each subdivided into more narrowly defined groups (Table 1).

Specifically, we investigated: (1) whether species richness changed at the different altitudinal levels over the 10-year period; (2) if so, which plant ecological groups responded positively or negatively; (3) whether changes in species richness of any group were correlated with changes in abiotic soil variables or with community-level changes, e.g., in biomass production.

## Materials and methods

Study sites and vegetation monitoring

We randomly selected 36 fen meadows in central and northeastern Switzerland out of a total of 309 fens in this area listed in a national inventory (BUWAL 1990; Bergamini et al. 2009a; Fig. 1). These fen meadows were grouped into three altitudinal classes (800–1,000, >1,000–1,200, >1,200–1,400 m a.s.l.). Altitude was defined as the altitude of the central plot at each site in m a.s.l. Our selection was based on an equal distribution of fens under two traditional land management regimes (mowing once a year in mid-September or non-intensive grazing by cows) and was done in a way to avoid a confounding of site area with the factors management and altitude (see Bergamini et al. 2001b).

Calcareous fen meadows belong to the most species-rich grasslands in Europe (Ellenberg 1996) containing many rare plant species (Wettstein and Schmid 1999; Bergamini et al. 2001a; Pauli et al. 2002) that are adapted to the nutrient-poor and moist site conditions (Dietl 1975). In Switzerland, all fens of national importance are legally protected since 1987 (Grünig 1994) and, for most sites, management contracts exist that should ensure an appropriate conservation management (BUWAL 2002). Therefore, protected fen meadows are not artificially fertilized and either mown once a year in early autumn or non-intensively grazed. We

**Table 1** Classification of the 229 recorded vascular plant species into mutually non-exclusive ecological groups based on phenological and ecological characteristics putatively influenced by climate and other drivers of environmental change such as change in soil variables and plant community aboveground biomass production

| Characterization | Group | Reference for classification | Description | Group size |
|---|---|---|---|---|
| 1) Habitat-change indicators | Fen specialists | BUWAL (1990) | Species characteristic of the *Caricetalia davallianae* vegetation type versus others | 24 species |
| | Species with low habitat specificity | Lauber and Wagner (1996) | Ubiquitous species versus species that occur only in a specific habitat type | 51 species |
| 2) Climate-change indicators | Early-flowering species | Lauber and Wagner (1996) | Species that start flowering early, (March–May) versus others | 42 species |
| | Late-flowering species | Lauber and Wagner (1996) | Species that start flowering in July–October versus plants that flower before | 35 species |
| | Thermophilous species | Landolt (1977) | Thermophilous, i.e., colline and southern European species versus alpine, subalpine and montane species | 37 species |
| 3) Soil-quality-change indicators | Acidic-soil indicators | Landolt (1977) | Acidic-soil indicators (pH 3–5.5) versus others | 40 species |
| | Variable soil humidity indicators | Landolt (1977) | Plants predominantly occurring on soils with varying humidity versus others | 132 species |
| | Rich-soil species | Landolt (1977) | Species predominantly occurring on medium to rich-soil versus poor-soil indicators | 114 species |
| | Peat indicators | Landolt (1977) | Peat-soil indicators avoiding mineral soils versus others | 31 species |
| 4) Community-productivity-change indicators | Light indicators | Landolt (1977) | Plants growing in full light versus half-shade–shade plants | 124 species |
| | Shade indicators | Landolt (1977) | Shade indicators occurring often under 10 % relative strength of illumination versus others | 17 species |



**Fig. 1** Distribution of 36 fen sites in central and northeastern Switzerland. The sites differed in management regimes (mown vs. grazed) and were classified into three altitudinal classes (class I: 800–1,000; class II: >1,000–1,200; class III: >1,200–1,400 m a.s.l.). Mown-class I: *white circles*, Mown-class II: *gray circles*, Mown-class III: *black circles*, Grazed-class I: *white triangles*, Grazed-class II: *gray triangles*, Grazed-class III: *black triangles*
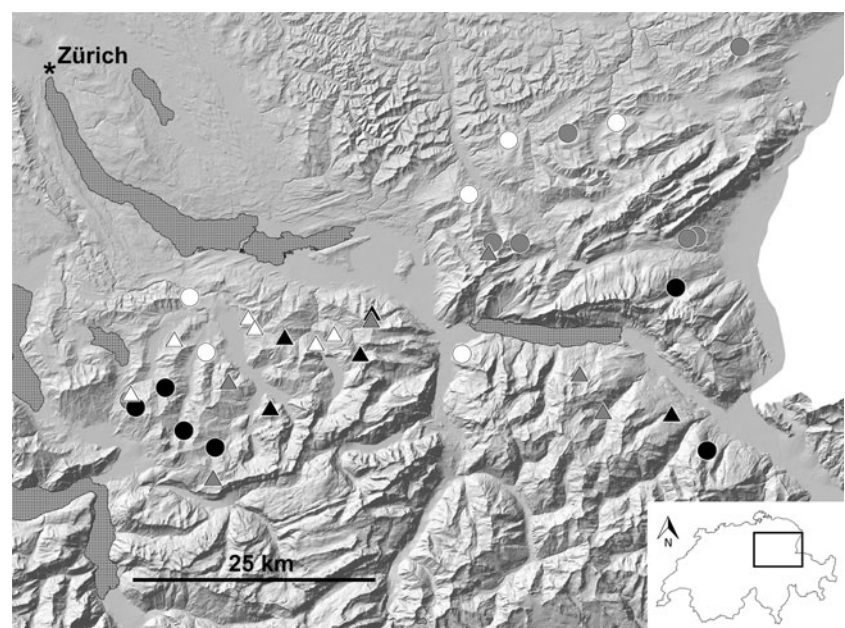
surveyed these montane calcareous fens of the phytosociological alliance Caricion davallianae (Ellenberg 1996) twice over a decade. The first and the second vegetation surveys were carried out by the same botanists (M.P. and A.B.). Vascular plant species presence and abundance were assessed in five randomly selected 1 × 2 m plots per site in summer 1995 and 2005 (24 fens) and July 2006 (12 fens). The same random procedure was applied to select plot locations within fens: each fen was divided into four sectors and each sector was again split into four subsectors. Within each sector, one subsector was randomly chosen and one plot was then randomly located within that subsector. One additional plot was placed at the center of each fen. To avoid large differences in environmental conditions, only plots that contained *Carex davalliana* (a frequent, small, tussock-forming sedge characteristic of the Caricion davallianae alliance, Ellenberg 1996) were chosen (see also Bergamini et al. 2009a). We calculated the cumulative species richness based on the presence/absence data of the five plots per site (in total 10 m$^2$). As the management changed in one of the mid-altitudinal sites from grazing to mowing within the study period, we excluded this site for the comparisons of species' compositional change. Similarly, also one plot was omitted from another fen in which management changed on a part of the site. The total number of replicate plots in the two surveys was thus 348 instead of 360 (36 sites × 5 plots site$^{-1}$ × 2 surveys; see Bergamini et al. 2009a).

Classification of plant species into ecological groups

The vascular plant species recorded were classified into different ecological groups based on phenological and ecological characteristics putatively influenced by climate and other environmental drivers such as airborne nitrogen deposition, which reaches deposition rates in the study area of 40 kg ha$^{-1}$ year$^{-1}$ (BAFU/BFS 2007). A complete list of all groups defined is provided in Table 1. Single species could belong to more than one group. However, none of the fen specialist species was at the same time a thermophilous or shade-indicator species and in only one case a fen specialist species (that also occurs in calcareous dry grasslands) was also considered a low habitat specificity species (*Molinia caerulea*, Table S1). The change in species number of each ecological group over the 10-year period, i.e., the colonization and extinction rates (see below), was calculated relative to the change of all species not belonging to that group.

The taxonomy followed Fischer et al. (2005). Most ecological data were obtained from Landolt (1977), who provided plant ecological indicator values for species occurring in Switzerland. These indicator values range from 1 to 5 on an ordinal scale (low numbers represent low, and high numbers high requirements; Table 1). Indicator values

have been shown to be an integrative tool for measuring habitat quality (Diekmann 2003) and allow a useful characterization of species into functional groups (Voigt et al. 2007). For the habitat specificity scoring (Table 1), values of habitat specificity between "low" versus "medium to high habitat specificity" were assigned to species by counting the number of phytosociological orders in which they occur in Switzerland according to Lauber and Wagner (1996) and by identifying their main habitat. Ubiquitous species with a low specificity scoring (Table S1) typically occur in four and more ecologically distinct habitats such as nutrient-rich meadows, nutrient-poor dry meadows, forests and agricultural fields (see also Fischer and Stöcklin 1997; Joshi et al. 2006) and typically occur in habitats other than wetlands. The phenological grouping of species was based on flowering data obtained from a Swiss flora (Lauber and Wagner 1996; Table 1). Species which produce rooted ramets were classified as clonal species (Rothmaler 1991; Table S1).

Abiotic environmental conditions

Abiotic site variables were recorded at each site. Soil nutrient analyses were done for two plots per site in 1995 and for five in 2005/2006; pH was measured in four plots per site in 1995 and in five plots per site in 2005/2006. In 1995, two soil cores were taken per plot and in 2005/2006 one soil core was taken per plot. Soil cores measured 6 cm in diameter and 10 cm in depth. The soil was dried at 70 °C to constant weight. $NO_3^-$ and $PO_4^{3-}$ were analyzed by standard methods (Anonymous 1997, 2004). The soil pH was measured in a water suspension 1:3 soil/deionized water (w/v) with a Hamilton Single PoresPlast electrode (Knick 761 Calimatic, Knick, Berlin, Germany). Total N was determined using a CHNS-Analyzer (LECO-932, St. Joseph, Mich, USA). In preparing soil samples, a slight change occurred in the second survey. In contrast to the first survey, fine roots were carefully removed from soil samples after grinding by using a fine sieve (0.5-mm mesh). Therefore, in the sequential statistical analysis, the "date of survey" effect contains a bias toward higher amounts of fine root material and thus nutrients in soil samples from 1995, but we assumed that the subsequently tested interactions of date of survey with altitude and management should not be affected by this bias. To overcome the bias, we tested whether the changes in soil variables per site after a 10-year period were significantly correlated with differences in extinction and colonization rates at different altitudes and under different management regimes.

To estimate the length of the vegetation period (VP), we used records of daily mean, minimum and maximum temperatures collected by the Swiss Federal Office of Meteorology and Climatology between 1959 and 2006 at three weather stations within our research area (Einsiedeln:

910 m a.s.l., Ebnat-Kappel: 623 m a.s.l., St. Gallen: 779 m a.s.l.). Because of missing data for some years at some stations, we only analyzed the period for which data were available for all three stations (daily mean temperature since 1959, daily minimum temperature since 1971 and daily maximum temperature since 1976). The length of the vegetation period (VP) was calculated based on daily mean and minimum temperatures: the beginning of the VP was estimated as at least 7 consecutive days with mean temperatures $\geq 5$ °C. The end of the VP was determined with at least 5 consecutive days with daily minimum temperatures $\leq 4$ °C or 1 day with minimum temperature $\leq -2$ °C (Primault 1992). Because of missing data for minimum temperatures at the Ebnat-Kappel station, the beginning of the VP was calculated since 1959 and the end and total length of the vegetation period since 1971, respectively.

Biomass

Aboveground biomass of vascular plants was harvested within the $1 \times 2$ m plots in randomly chosen subplots of $18.5 \times 18.5$ cm. In the first survey, aboveground biomass was sampled in four plots per site and in three $18.5 \times 18.5$ cm subplots within each plot. In the second survey, biomass was harvested in all five plots per site, but in only one subplot within each plot. In both surveys, biomass was harvested at peak standing crop. Biomass samples were dried (70 °C, 48 h), weighed and extrapolated to grams per square meter.

Statistical analysis

Data were analyzed using the statistical software R (Version 2.11.1 for Windows; R development core team 2010) with

mixed-model analysis of variance (ANOVA). The sequential analyses included main effects of management, altitude, survey date (1995 vs. 2005/2006) and their interactions (Tables 2, 3). Site, site × survey date interaction and plot were considered as random effects. It should be noted that adjacent plots of the same size and characterized by the presence of the fen specialist *Carex davalliana* were used in the two surveys (see Bergamini et al. 2009a) and thus the plot term was nested within the site × survey date interaction. The fixed effects of management and altitude and their interactions were tested against the random effects of sites. Interactions between these factors and survey date were tested against the site × survey date interaction (random). For the analysis of soil abiotic condition and biomass, the random effects of site and of the site × survey date interaction were tested against the residual variation among all plots (Tables 2, 3).

The number of colonizing species (CS) of locally extinct species (ES) and the extinction (ER) and colonization rates (CR) were calculated for each plant ecological group versus all other species over the 10-year period (Table 1). Species were counted as colonizing if they were absent at a site in the first survey (1995) and present in the second (2005/2006); if species were present in a plot in the first survey but absent in the second, they were considered locally extinct for the purpose of this analysis. Colonization and extinction rates were based on presence/absence data and calculated as $CR = 100 \times (CS \times 2)/(G95 + G05/06)$ and $ER = 100 \times (ES \times 2)/(G95 + G05/06)$, respectively, where G denotes the total number of species per group that was considered and 95 and 05/06 denote the survey (Nilsson and Nilsson 1982; Joshi et al. 2006). To test whether the colonization and extinction rate differed between each group versus other species and whether this difference was affected by altitude or management, we performed sequential ANOVAs similar

**Table 2** Effects of management (grazed vs. mown), altitude and survey date (1995 vs. 2005/2006) on aboveground community biomass per m$^2$ of vascular plants and five soil variables

| Source of variation | ln biomass | | | NO$_3^-$ | | | PO$_4^{3-}$ | | Total N | | Total C | | pH | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | df | SS (%) | F | df | SS (%) | F | SS (%) | F | SS (%) | F | SS (%) | F | df | SS (%) | F |
| Management (M) | 1 | 0.62 | 0.94 | 1 | 0.12 | 0.17 | 2.49 | 3.59 | 2.06 | 1.68 | 2.18 | 1.80 | 1 | 0.25 | 0.16 |
| Altitude (A) | 1 | 5.82 | **8.83**** | 1 | 0.06 | 0.08 | 0.10 | 0.14 | 0.25 | 0.20 | 0.17 | 0.14 | 1 | 0.25 | 0.16 |
| M × A | 1 | 2.12 | 3.21(*) | 1 | 0.06 | 0.09 | 0.49 | 0.71 | 0.05 | 0.04 | 0.01 | 0.01 | 1 | 0.28 | 0.18 |
| Site | 33 | 21.76 | **3.16***** | 33 | 23.67 | **2.14*** | 22.89 | **1.72*** | 40.39 | **4.70***** | 40.04 | **4.44***** | 33 | 51.19 | **9.16***** |
| Survey date (D) | 1 | 8.81 | **42.21***** | 1 | 0.51 | 1.52 | 0.68 | 1.68 | 1.31 | **5.05*** | 1.80 | **6.59*** | 1 | 1.18 | **6.98*** |
| M × D | 1 | 0.08 | 0.40 | 1 | 0.04 | 0.12 | 0.01 | 0.02 | 0.31 | 1.18 | 0.11 | 0.43 | 1 | 0.00 | 0.02 |
| A × D | 1 | 0.66 | 3.18(*) | 1 | 0.85 | 2.53 | 0.00 | 0.00 | 0.58 | 2.22 | 0.14 | 0.53 | 1 | 0.00 | 0.00 |
| M × A × D | 1 | 0.67 | 3.22(*) | 1 | 0.44 | 1.31 | 0.11 | 0.27 | 0.02 | 0.09 | 0.00 | 0.01 | 1 | 0.00 | 0.00 |
| S × D | 33 | 9.55 | 1.39(*) | 33 | 17.96 | **1.62*** | 5.33 | 0.40 | 11.32 | 1.32 | 9.63 | 1.07 | 33 | 7.06 | 1.26 |
| Residuals | 239 | 49.90 | | 168 | 56.30 | | 67.90 | | 43.71 | | 45.90 | | 235 | 39.78 | |

Bold values indicate significant effects

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, (*) $P < 0.1$

**Table 3** Effects of management (grazed vs. mown), altitude and survey date (1995 vs. 2005/2006) on cumulative species richness of vascular plants per 10 m$^2$ (five plots of 1 × 2 m)

| Source of variation | df | F | P | SS (%) |
|---|---|---|---|---|
| Management (M) | 1 | 9.12 | *** | 18.36 |
| Altitude (A) | 1 | 1.22 | ns | 2.45 |
| M × A | 1 | 0.92 | ns | 1.85 |
| Site | 31 | 5.31 | *** | 62.44 |
| Survey date (D) | 1 | 7.41 | ** | 2.81 |
| M × D | 1 | 0.05 | ns | 0.02 |
| A × D | 1 | 0.84 | ns | 0.32 |
| M × A × D | 1 | 0.00 | ns | 0.00 |
| Residuals | 31 | | | 11.75 |

*ns* not significant

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$

to those described above, but with the additional terms "group versus other", "group versus other × altitude" and "group versus other × management", all fitted after site. These effects were tested against the final random term "group versus other × site".

To assess the significance of temporal trends in changes in the length of the vegetation period, the linear effect of "year" was tested against the residual variation among years.

To overcome the bias problem in soil analyses mentioned above, we tested whether the changes in soil variables per site over the 10-year period significantly correlated with extinction or colonization rate per site and compared these correlations between each group versus other species (ANOVAs with extinction or colonization rate per site as dependent variable, and change in soil variable, "group versus other" and interaction as explanatory terms).

Group-wise differences between extinction and colonization rates were compared by *t* tests (Fig. 4).

## Results

In total, we detected 229 vascular plant species belonging to 50 different plant families in our plots (see Table S1). Of these 229 species, 10 were tree species (mostly seedlings) and the majority of the non-woody species were perennials (only 5 species were short-lived annuals). Nearly two-thirds of the non-woody species (65.3 %; Table S1) were clonal.

### Biotic and abiotic environmental changes

In the second survey, aboveground biomass of vascular plants was almost 30 % higher than in the first survey (254 ± 9.9 vs. 329 ± 10.4 g m$^{-2}$; Table 3). This difference tended to be strongest at higher altitudes in grazed fens (Table 2).

Averaged over all sites, the soil concentrations of $NO_3^-$ and $PO_4^{3-}$ did not change from 1995 to 2005/2006, but total soil nitrogen and carbon significantly decreased from 1.61 ± 0.83 % to 1.44 ± 0.77 % and from 24.12 ± 0.22 % to 21.1 ± 0.19 %, respectively, and soil pH decreased from 6.12 ± 0.05 to 6.00 ± 0.05 (Table 2; however, see bias mentioned in "Materials and Methods"). Within-site changes in total soil carbon, soil $NO_3^-$ and soil $PO_4^{3-}$ over this time period were not significantly correlated with colonization or extinction rates of any ecological group (all $P > 0.1$). However, a within-site increase in total soil nitrogen content was correlated with a decrease in the extinction rate of species with low habitat specificity ($F_{1,30} = 4.29$, $P < 0.05$; Fig. S1) and the extinction rate of acid-soil indicators was positively correlated with the within-site changes in soil pH ($F_{1,30} = 5.10$, $P < 0.05$).

From 1959 to 2006, the average daily mean temperature per year measured at the three stations increased by 0.98 °C ($F_{1,45} = 10.56$, $P < 0.01$). The daily minimum temperature increased by 1.08 °C from 1971 to 2006 ($F_{1,34} = 11.13$, $P < 0.01$); and in the last 30 years (1976–2006), the daily maximum temperature increased by 1.28 °C ($F_{1,29} = 9.97$, $P < 0.01$). Accordingly, the length of the vegetation period increased by 25.9 ± 9.0 days from 1971 to 2006 ($F_{1,32} = 8.21$, $P < 0.01$). Whereas the beginning of the vegetation period did not significantly change from 1959 to 2006 ($F_{1,44} = 1.54$, $P > 0.2$), the end of the vegetation period from 1971 to 2006 shifted backward by 15.41 ± 5.1 days ($F_{1,34} = 9.16$, $P < 0.01$).

### Colonization, extinction and species turnover

Management, but not altitude, had a significant influence on cumulative plant species richness with a 12 % lower species density on average in grazed compared with mown fens (Table 3). Species density of all vascular plants increased from 60.31 ± 1.56 in 1995 to 63.51 ± 1.67 in 2005/2006 (Table 3). This increase in average species density occurred across altitudes and management types (no significant interactions with survey date; Table 3). The species density of non-specialist plants was 8 % higher in the second census (47.17 ± 1.43 in 1995 compared with 51.06 ± 1.56 in 2005/2006; $F_{1,31} = 13.24$, $P < 0.001$).

In particular, thermophilous as well as rich-soil-indicator and shade-indicator species had a substantially higher colonization rate than other species (Fig. 2) with the colonization rate of shade-indicator species being twice as high as that of others across all altitudinal levels (59.6 ± 5.9 % vs. 25.9 ± 1.3 %). Early-flowering species also had a marginally higher colonization rate than other species ($F_{1,31} = 3.60$, $P = 0.067$), especially colonized grazed fens at low altitude (management × altitude × group interaction: $F_{1,31} = 4.08$, $P = 0.05$). Similarly, also
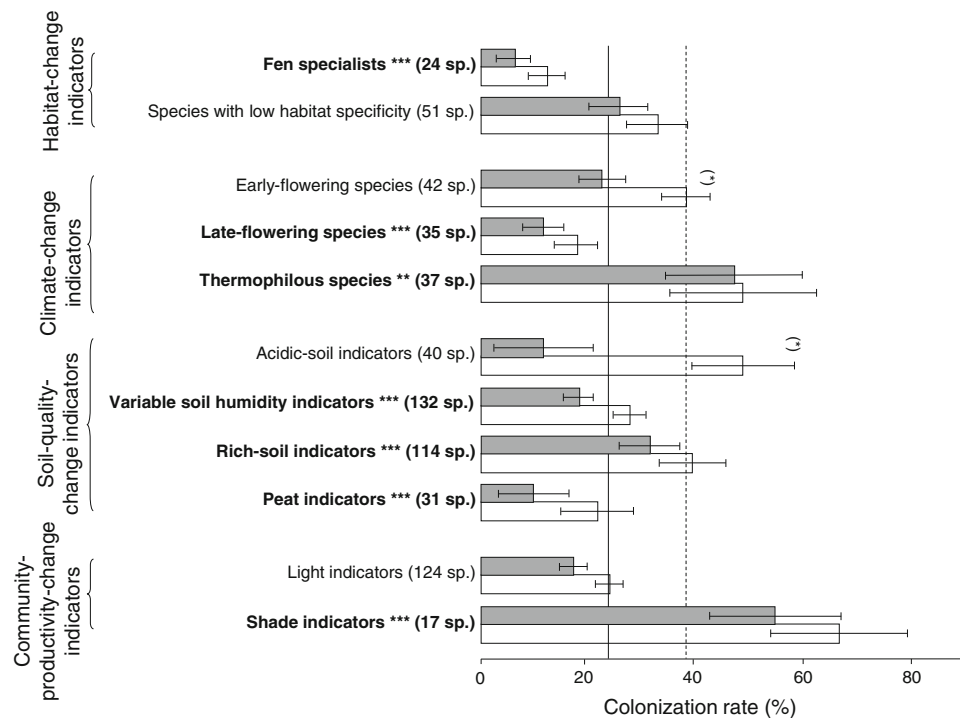
**Fig. 2** Colonization rates for each plant ecological group predicted at the lowest (800 m a.s.l.; *white bars*) and the highest altitude (1,400 m a.s.l.; *gray bars*; values fitted by regression analysis). *Numbers in brackets* after group names indicate the number of species in each ecological group. *Bold formatted group names* and *asterisks* indicate that the colonization rate was significantly different between species in the respective group versus other species. The *stars on the* *bars* indicate whether the interaction effect of altitude × group was marginally significant. The *vertical lines* show the overall mean of fitted values at 800 m a.s.l. (*dashed line*) and 1,400 m a.s.l. (*solid line*), respectively. The overall colonization rate was higher at low than at high altitudes ($F_{1,31} = 4.0$, $P = 0.05$). ***$P \leq 0.001$, **$P \leq 0.01$, (*)$P < 0.1$

species with low habitat specificity had an overall high colonization rate in grazed fens and especially colonized low-altitude fens (management × altitude × group interaction: $F_{1,31} = 5.02$, $P < 0.05$). In contrast to all these previous groups, fen specialists, variable-soil-humidity-indicator species, peat-indicator species and late-flowering species had lower colonization rates than other species (Fig. 2).

Extinction rates also varied considerably between plant ecological groups, but were generally not affected by management. Fen specialists had lower extinction rates than other species ($F_{1,31} = 9.76$, $P < 0.01$); combined with the lower colonization rates, this indicates a low turnover, presumably due to high habitat specificity. Late-flowering species also had lower extinction rates ($F_{1,31} = 22.71$, $P < 0.0001$), whereas thermophilous species had higher extinction rates than others ($F_{1,31} = 6.73$, $P = 0.01$). For acidic-soil indicators and for light-indicator species, the extinction rate was particularly high at low altitudes (Fig. 3). In contrast, extinction rates increased with altitude for rich-soil indicators and shade indicators (Fig. 3).

Comparing colonization and extinction rates (Fig. 4), the colonization rates of thermophilous, early-flowering and rich-soil species, as well as of species with low habitat specificity and shade indicators were significantly higher than their extinction rates. Of the different groups tested, only the colonization rate of fen specialists was lower than their extinction rate.

## Discussion

Despite legal protection and no obvious change in the traditional management system in the pre-alpine fen meadows investigated, we observed a significant increase in plant species richness between 1995 and 2005/2006. This increase in plant species richness was paralleled by an increase in small-scale plant species density (Bergamini et al. 2009a).

Within the last 30–50 years, daily mean, minimum and maximum temperatures increased significantly in the study region. The mean annual precipitation, however, remained relatively constant over this time period (Bergamini et al. 2009a).

Even though by 2070–2100, 31–51 % of subalpine species were predicted to lose more than 80 % of their suitable habitat (Engler et al. 2011), in the short term, an increase in

**Fig. 3** Extinction rates for each plant ecological group predicted at the lowest (800 m a.s.l.; *white bars*) and the highest altitudes (1,400 m a.s.l.; *gray bars*; values fitted by regression analysis). *Numbers in brackets* after group names give the number of species in each ecological group. *Bold formatted group names* and *asterisks* indicate that the extinction rate was significantly different between species in the respective group versus other species. The *stars on the bars* indicate whether the effect of altitude × group was significant. The *vertical lines* show the overall mean of fitted values at 800 m a.s.l. (*dashed line*) and 1,400 m a.s.l. (*solid line*), respectively.
\*\*\*$P \leq 0.001$, \*\*$P \leq 0.01$, \*$P \leq 0.05$, (\*)$P < 0.1$
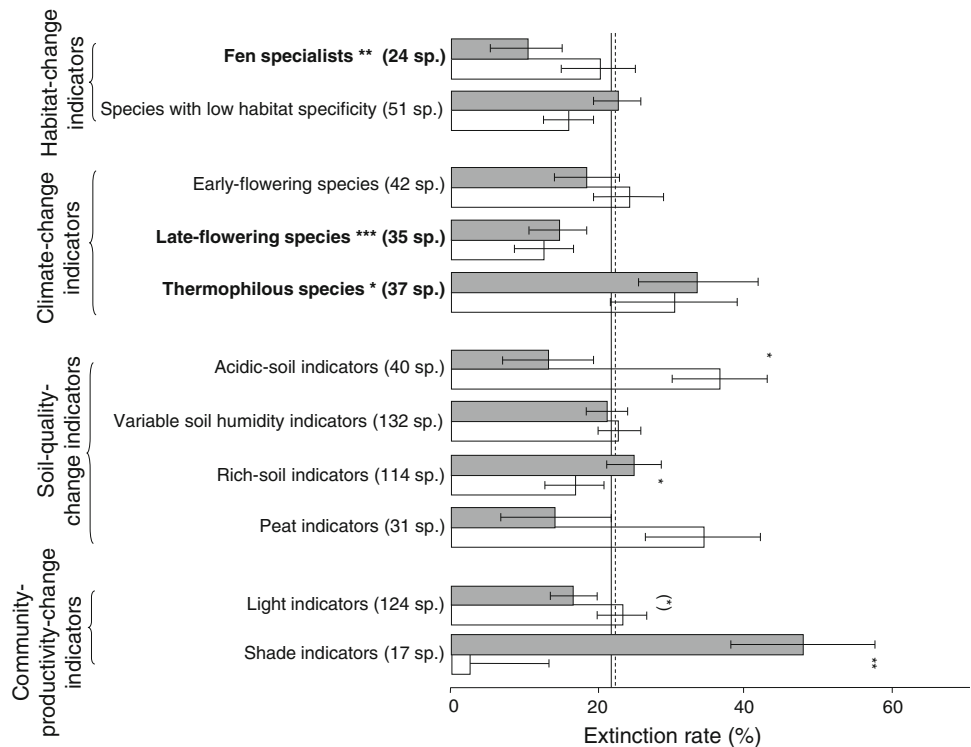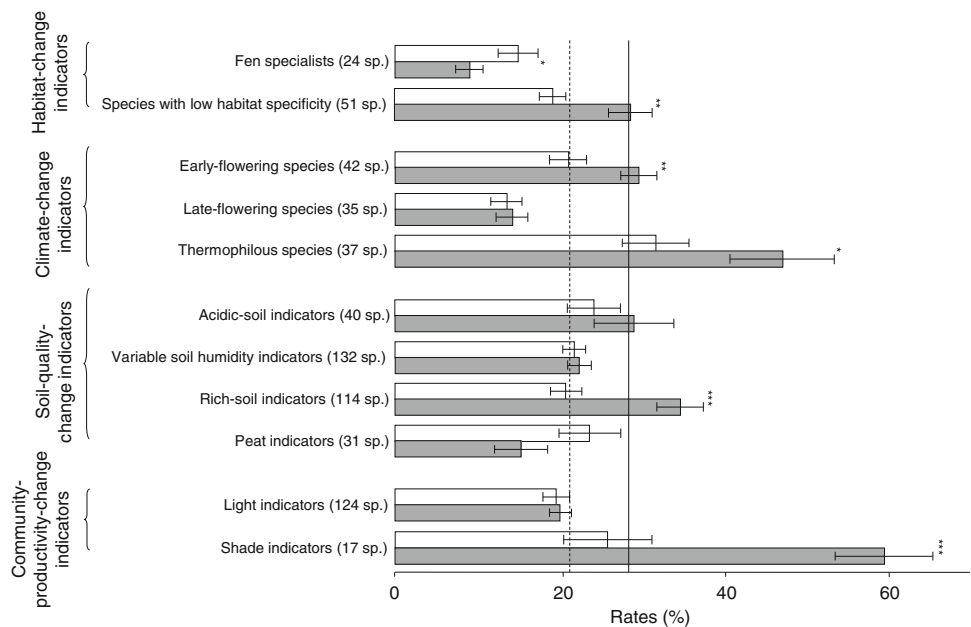


**Fig. 4** Differences between extinction (*white bars*) and colonization rates (*gray bars*) for each plant ecological group. The *stars on the bars* indicate significant differences (*t* test). The *vertical lines* show the overall mean of extinction rates (*dashed line*) and colonization rates (*solid line*), respectively.
\*\*\*$P \leq 0.001$, \*\*$P \leq 0.01$, \*$P \leq 0.05$



species richness along an altitudinal gradient is to be expected (Pearman et al. 2011), especially in pre-alpine areas under a scenario of climate warming and constant precipitation (Kienast et al. 1998). Such an increase in species richness of vascular plants has already been observed on a subantarctic island with the highest increase in species richness above 600 m a.s.l. (le Roux and Mcgeoch 2008), on Norwegian summits between 1,512 and 1,814 m a.s.l. (Odland et al. 2010), or on alpine summits (most pronounced between ca. 2,800–3,100 m a.s.l.; Grabherr et al. 1994; Frei et al. 2010) or within 10 years, 1994–2004, at high-altitude sites in the Austrian Alps (Pauli et al. 2007). In these high mountain ecosystems, the increase in floristic diversity has been attributed to recent climate warming, which has been twice as high in the Alps than at global scale (Pauli et al. 2007). An upward migration of

plant species with the highest increase in species richness in the transitional zone between alpine and nival ecosystems has also been observed during the past 50 years in alpine regions in northern Italy (Parolo and Rossi 2008). In our pre-alpine fen meadows, the colonization rates of early-flowering and thermophilous species, which as a group represent climate-change indicators, significantly exceeded their extinction rates (see Fig. 4). Also a monitoring of plant species distributions over 30 years across the British Isles showed that native plant species that became widespread during the recent past all exhibited earlier flowering (Hulme 2011).

In contrast, late-flowering species (seed riskers) that might benefit from the observed longer vegetation period had comparatively low colonization as well as low extinction rates. In our data set, we had approximately the same number of early-flowering and late-flowering species (18.3 % early-flowering species belonging to 23 plant families vs. 15.3 % late-flowering species belonging to 18 plant families; Table S1). However, within the group of late-flowering species, 20 % are species that are consistently found in most of the fens (occurence in 30 or more fens, such as *Molinia caerulea*, *Succisa pratensis* or *Trifolium pratensis*) and 51 % are rare species that were found in three or less fens rendering an overall low turnover rate highly probable. In contrast, 41 % of the early-flowering species were also rare, but only 7 % were commonly found in most fens. More importantly, the late-flowering species might have been prevented from thriving under the potentially more favorable climatic conditions by the traditional mowing treatment in late summer.

Multi-factorial causes of changes in plant species richness

Over the 10-year observation period, our fen sites increased in productivity and therefore, presumably, shadiness increased as well. The increased productivity may have been caused by airborne nitrogen deposition as well as by lowered groundwater tables (as indicated by significantly decreased soil-moisture indicator levels; Bergamini et al. 2009a) and possibly also by increased species richness (Marquard et al. 2009), higher air temperature and a longer vegetation period. In low-arctic vegetation, for example, a greater resource investment in vegetative growth as a response to artificial warming by 1.5 °C during 4 years has been observed by Arft et al. (1999). The higher productivity in our fen meadows might in part explain the lower total soil nitrogen measured in the 2005/2006 than in the 1995 survey (in addition to the bias caused by removing fine roots more completely in the second survey); in biodiversity experiments, a higher primary productivity associated with higher species richness was correlated with lower soil nitrogen levels (Balvanera et al. 2006).

The high colonization rate of rich-soil indicators and the low colonization rate of peat indicators (see Fig. 2) also suggest a change in soil conditions away from the typical fen soil over the observation period from 1995 to 2005/2006. Desiccation of wetland soils leads to higher soil respiration and increased peat decomposition (Rydin and Jeglum 2006). Increased nutrient spillover from adjacent agricultural areas and increased airborne N-deposition as well as a disturbed hydrology has also been observed in a recent monitoring and quality assessment of protected fens and mires in Switzerland (Klaus 2007).

Fen specialists seem to be rather inflexible under environmental change (Saetersdal and Birks 1997), whereas species with a low habitat specificity presumably can react more plastically to such change. Thus, the latter indeed had higher colonization than extinction rates in our fen meadows. Putatively pre-adapted species (i.e., thermophilous as well as rich-soil species and shade indicators) had the highest colonization rates during the 10-year observation period and obviously were not negatively affected by the observed increase in temperature and other drivers of environmental change, such as nutrient spillover from intensively used adjacent areas and increased atmospheric nitrogen deposition (Klötzli 1986; Pauli et al. 2002) or changes in water regime (Bergamini et al. 2009a). The most successful colonizers during the observation period were thermophilous grass species with low habitat specificity, such as *Festuca rubra* and *Dactylis glomerata*, or generalist thermophilous herbs, such as *Leucanthemum vulgare*, which colonized between 17 and 23 % of the sites and either never became extinct (*F. rubra*) or only disappeared at two (5.7 %) of the sites (*D. glomerata*, *L. vulgaris*). An increased colonization indicating a latitudinal shift of thermophilous species was also observed during the final decades of the twentieth century in the Netherlands (Tamis et al. 2005) and a comparison of bryophyte species records in Switzerland from 1880 to 2005 showed an upward shift in altitudinal limits, which was mainly driven by low temperature-adapted species expanding their range to higher elevations with a slow ongoing extinction process, probably as a result of climate warming trends at lower altitudes (Bergamini et al. 2009b).

Altitudinal gradients

The main shift in vegetation composition occurred at low-altitude sites, which overall were affected by higher colonization rates than high-altitude sites (see Fig. 2). Indicators of soil-quality change (rich-soil species) and of differences in community productivity (shade indicators) became less often extinct at low than at high-altitude sites. Clear altitudinal gradients were observed in mown fens with, e.g., an increase in colonization of species with low habitat

specificity and an increase in extinction of peat indicators with decreasing altitude. Altitudinal patterns in grazed fens were less strong, probably because of masking effects of land-use changes correlated with altitudinal change (Körner 2007), such as differences in stocking rates and average cattle weight at different altitudes.

Our findings show that specific ecological groups of species in the calcareous fen meadows studied respond differentially, but predictably (Bazzaz 1996), to multi-factorial environmental change: thermophilous and generalist plant species with low habitat specificity often colonized new sites, particularly at low altitudes, whereas fen specialists often could not cope with the change and became extinct at a higher rate over the observation period. In a previous analysis of small-scale vegetation patterns, we already observed the decline of specialist species associated with disturbed hydrology and increased nutrient input (Bergamini et al. 2009a). The present analysis suggests that, in addition to changed soil conditions, the observed increase in temperature in the study region, leading to a prolonged vegetation period, as well as increased community biomass may be the causes of these shifts in species compositions.

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