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BIODIVERSITY RESEARCH

Spread of common species results in local-scale floristic homogenization in grassland of Switzerland

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ABSTRACT

Aim We assess changes in plant species richness and changes in species dissimilarity at local scale in Swiss grassland between the time periods 2001–2004 and 2006–2009. Further, we provide an ecological interpretation of the observed taxonomic homogenization of vascular plants.

Location Switzerland.

Methods Changes in species richness and changes in Simpson dissimilarity index of vascular plants in grassland (meadows and pastures) were examined. The analyses were based on species lists recorded on 339 10-m^2 sample plots from a systematic sample covering the entire Switzerland. Each sample plot had been surveyed once in 2001–2004 and once in 2006–2009 with 5 years between the first and the second survey. Changes in species dissimilarity were interpreted by comparing the relative contribution of several indicator species groups.

Results Mean species richness of vascular plants in grassland increased during the study period. In contrast, species dissimilarity of plants decreased, suggesting local-scale floristic homogenization of grassland in Switzerland. It was mostly because of the spread of common species, namely the species that are tolerant to high nutrient levels, the species of low conservation value and the species adapted to moderate temperature levels that led to taxonomic homogenization. Target species for conservation did only marginally affect taxonomic homogenization. In contrast to the predictions from studies of taxonomic homogenization on larger scales, the taxonomic homogenization of grassland at local scale was not explained by the spread of neophytic species.

Main conclusions The biotic diversity of grassland in Switzerland changed considerably between 2001–2004 and 2006–2009. The observed taxonomic homogenization was merely because of the spread of common species. Local-scale changes in land use regimes implemented by agri-environmental schemes and other conservation efforts on parts of the entire grassland area were, apparently, not enough to prevent the total grassland from recent taxonomic homogenization.

Keywords
Beta diversity, biodiversity monitoring, biotic homogenization, grassland, meadows, Simpson index.

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INTRODUCTION

Taxonomic homogenization is the decrease in species dissimilarity between sample units over time (Olden & Rooney, 2006). It is a simple prediction that follows from human-induced changes of environments that favour few winning species and negatively affect many others (Smart *et al.*, 2006; Rooney *et al.*, 2007). So far, studies on taxonomic homogenization have been mainly conducted by comparing extant and historic species lists among large grid cells, counties, countries

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or even continents, i.e. on large spatial scales (e.g. Kühn & Klotz, 2006; Schwartz *et al.*, 2006; Melo *et al.*, 2009). In such studies on large spatial scales, taxonomic homogenization has been shown to take place in various species groups and has often been attributed to the invasion of alien species or the replacement of specialist species by generalist species (Wiegmann & Waller, 2006; Kerbiriou *et al.*, 2009; Qian & Guo, 2010).

In contrast to many studies on a large spatial scale, only few studies on taxonomic homogenization have been conducted on a local scale, i.e. by comparing study plots of about one hectare (Smart *et al.*, 2006; Lambdon *et al.*, *2008*; Arevalo *et al.*, 2010; Naaf & Wulf, 2010). However, to understand the effect of human-induced environmental changes on biodiversity, studies on local scale are equally important as studies on large spatial scale. First, this is because changes in land use regimes or changes in conservation planning are often implemented at a local scale (Margules & Pressey, 2000; Naaf & Wulf, 2010). Furthermore, it is at the local scale that interactions between species and their physical environment are strongest and thus local-scale studies provide insights into ecological mechanisms and allow predictions of how human activities will affect biodiversity (Huston, 1999). Second, local-scale studies on taxonomic homogenization are needed because it could be challenging or even misleading to predict effects of human activity on biodiversity at the local scale from studies of taxonomic homogenization on large spatial scales. A variety of different processes affect biotic diversity only some of which may operate equally at all spatial scales. For example, species richness generally decreases at the global scale but often increases at the local scale (Sax & Gaines, 2003). Similarly, opposing trends of taxonomic homogenization at different spatial scales may become apparent, as soon as more studies on taxonomic homogenization at the local scale are available. For example, the invasion of alien species that is one of the major causes for taxonomic homogenization at large spatial scale seems unlikely to be a major driver for taxonomic homogenization at local scale (Smart *et al.*, 2006; Lambdon *et al.*, 2008).

Meadows and pastures (that we refer to as grassland) are probably among the habitat types that are most severely affected by land use regimes and have high priority in conservation planning (Jacquemyn *et al.*, 2003). Grassland with high biological diversity used to be common in central Europe, but intensification of land use has severely reduced the biotic diversity of most grassland areas in the last century (Marini *et al.*, 2008). In the last few decades, considerable conservation efforts, for example in the form of agri-environmental schemes and the legal protection of habitats, are targeting grassland with the aim of increasing their biotic diversity (Kleijn & Sutherland, 2003; Oster *et al.*, 2009; Foen, 2010). The central instruments of the implementation of measures to conserve grassland are contracts between farmers and authorities or conservation bodies. These contracts contain agreements on land management, conservation, maintenance measures and the financial compensation for all efforts (Foen, 2010). However, it is an open question whether the local-scale changes in land use regimes induced by agri-environmental schemes and other conservation efforts on parts of the entire grassland area were enough to prevent the total grassland area from further decline in species richness and from taxonomic homogenization. Alternatively, factors known to have a strong and usually negative effect on biodiversity at large spatial scales, such as climate change or the introduction of neophytic (i.e. alien plant) species, may have led to taxonomic homogenization of grassland also at a local scale.

In Switzerland, meadows and pastures are habitat types of high priority for conservation, and more than 93,000 ha of grassland have been registered as ecological compensation areas and are under contract with farmers (Foen, 2010). Several studies in different regions of Switzerland have reported a positive effect of ecological compensation areas on plant species richness (Herzog *et al.*, 2005; Knop *et al.*, 2006; Roth *et al.*, 2008). Our first goal in this study was to assess recent changes in biotic diversity of Swiss grassland across the entire range of land use regimes. Our second and main goal was then to identify potential mechanism that may explain the observed temporal changes in species dissimilarity. We investigated the temporal change in species richness and species dissimilarity of vascular plants at the vegetation plot level between the two time periods 2001–2004 and 2006–2009, using the data from the Swiss biodiversity monitoring programme (BDM, Weber *et al.*, 2004). As conservation is targeting species that became rare, we expected that because of conservation efforts in the last decade, an increase in distribution of the group of rare species should have led to both an increase in plant species richness and an increase in plant species dissimilarity. Specifically, we asked (1) whether taxonomic homogenization (i.e. a decrease in species dissimilarity) occurred in the grassland of Switzerland over the last decade, (2) whether the change in species dissimilarity in grassland depended on the altitudinal levels, on the species richness of the sample plots or on the relevance of the sample plots for conservation (i.e. grassland habitat of high conservation relevance vs. grassland habitats of low conservation relevance), (3) whether the change in species dissimilarity was differentially driven by groups of species assumed to reflect processes that act locally (i.e. species groups indicating different nutrient levels and species groups reflecting different levels of conservation value) and (4) whether the change in species dissimilarity was differentially driven by groups of species assumed to reflect processes that act globally (i.e. species groups indicating different temperature levels or neophytic species vs. indigenous species).

METHODS

Study site and field protocol

The study took place between 2001 and 2009 in Switzerland. The country covers approx. 41,000 km^2 in central Europe and altitudes from 193 to 4634 m a.s.l. About 70% of Switzerland is mountainous (60% Alps and 10% Jura Mountains). We used

the data from the Biodiversity Monitoring of Switzerland (BDM, http://www.biodiversitymonitoring.ch) which were launched in 2001 to monitor Switzerland's biodiversity and to meet the Convention on Biological Diversity of Rio de Janeiro (Hintermann *et al.*, 2000). In the BDM scheme, vascular plants are one of three species groups investigated on a systematic grid with random origin, covering 1650 circular 10-m^2 plots. Every year, one-fifth of these sample plots are surveyed and each plot is surveyed every 5 years. Thus, between 2001 and 2009, four-fifths of the 1650 plots were surveyed twice.

Fieldwork was highly standardized and was carried out by qualified botanists that recorded all plants on a surveyed plot. Each surveyed plot was visited two times per field season, except for plots at high altitudes with short vegetation period where only one inspection per field season was conducted. For each sample plot, the botanists identified the type of habitat according to the definition developed for Switzerland (Delarze & Gonseth, 2008). Further, the land use category was identified using a system of 32 pre-defined land use categories similar to the CORINE Land Cover system (Büttner *et al.*, 2004). For annual reporting of the BDM results, the 32 land use categories were then aggregated to six main types of land use, i.e. forests, meadows and pastures, arable land, settlements, alpine pastures and mountains.

For the present study, we analysed a subset of the 1650 BDM sample plots that were surveyed once between 2001 and 2004 (i.e. the first survey) and a second time between 2006 and 2009 (i.e. the second survey), and of which the land use category was either 'meadows and pastures' or 'alpine pastures' in both surveys. It should be noted that the definition of grassland applied for this study is, thus, defined by the management regime and independent of the species association found on the plots. The sample size was 339 grassland plots in total (Fig. 1).

For the analyses, individual plants too small for reliable identification on species level were omitted. The proportion of the individual plants not identified on species level compared with the total number of recorded species per sample plot was small (mean ± SD of all sample plots: 5.6 ± 5.4% unidentified plants). However, the proportion of unidentified plants slightly decreased from the first survey to the second survey (mean ± SD difference: −1.4 ± 7.3% unidentified plants). As the proportion of unidentified plants was small and the temporal decrease in the proportion of unidentified plants did not depend on the classes of sample plots we analysed, i.e. altitude (ANOVA: $F = 0.8$, d.f. = 3, $P = 0.50$), species richness of the plots (Welch t-test: $t = 0.13$, d.f. = 295.3, $P = 0.89$) or relevance for conservation (Welch t-test: $t = 0.10$, d.f. = 308.5, $P = 0.92$), we were confident that the omission of unidentified plants did not bias our results on species richness or species dissimilarity.

Classes of sample plots and classes of species groups

Prior to analyses, we defined different classes of sample plots and classes of species groups that we assumed to behave differently in terms of temporal change in species richness or species dissimilarity. We assorted the 339 plots in three different ways. First, plots were classed according to four altitudinal levels based on the temperature zonation of Switzerland (Schreiber *et al.*, 1997), i.e. colline, montane, subalpine and alpine. Second, plots were classed according to their species richness as either species-poor (< 35 species, i.e. below the average species richness of the second survey) or species-rich (≥ 35 species). And third, plots were classed according to their relevance for conservation into plots of low relevance for conservation and plots of high relevance for conservation. Plots containing the habitat types 'nutrient-rich meadows' or 'nutrient-rich pastures' following Delarze & Gonseth (2008) were considered as being of low relevance for conservation. The remaining plots, i.e. the plots with high relevance for conservation contained different habitat types of dry or wet nutrient-poor sites that corresponded to the protected biotope types adopted by Swiss law since 2000 (Swiss Federal Council, 1991).

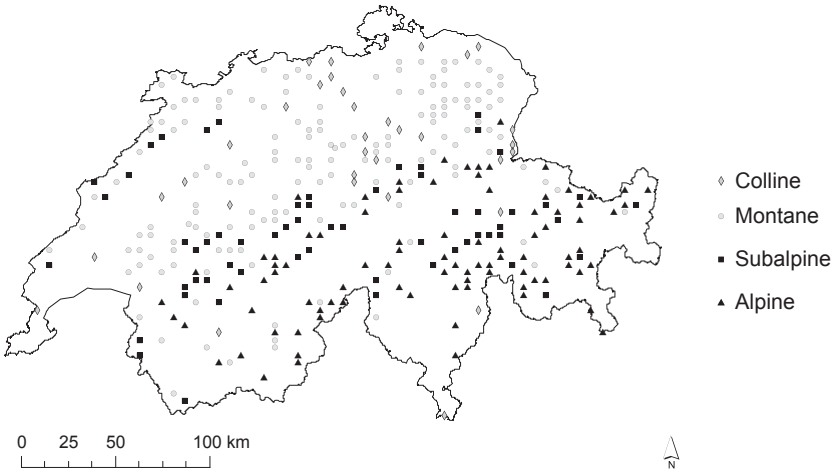

Figure 1 Map of Switzerland showing the distribution of the 339 grassland sample plots from the Swiss Biodiversity Monitoring programme used in this study.

We also assorted the species in four different ways (Table 1). We classed the species into species groups indicating different nutrient level, i.e. eutrophic, mesotrophic and oligotrophic species and into groups indicating species of different conservation value, i.e. very low, low and high conservation value. The rationale was that if local-scale factors such as changes in land use regimes or changes in conservation efforts had strong effects on species richness and species dissimilarity, we assumed that the temporal changes in species richness and species dissimilarity would differ between the species groups of different nutrient-level and the species groups of different conservation value. We further classed the species into groups with different altitudinal centres of distribution, i.e. species of warm, moderate and cold temperature levels and into neophytes, archaephytes and indigenous species. Here, the rationale was that if global-scale factors such as climate change or the introduction of neophytic species had strong effect on the observed species richness and species dissimilarity, we assumed that the temporal change in species richness and species dissimilarity would differ between the species of different temperature levels and between indigenous species and neophytes.

The analyses of the four species groups (Table 1) suggested that the observed taxonomic homogenization is mainly because of the spread of common species (see results). We therefore used the BDM data of all 1650 study plots to class the species into different categories of abundance and analysed the following groups of species separately: species recorded on less than 5%; on 5–25%, on > 25–50%, on > 50–75% and on > 75% of the 1650 sample plots.

Statistical analysis

For all classes of sample plots and all classes of species groups (see previous chapter), we calculated the mean changes in species richness between the first and second survey. Further, we computed a measure of temporal change in species dissimilarity (i.e. the 'differentiation diversity', sensu Jurasinski *et al.*, 2009). Among the many indices that measure species dissimilarity (or similarity), the Simpson dissimilarity index was among the ones with the best properties (Koleff *et al.*, 2003; but see Tuomisto, 2010). The Simpson dissimilarity index is especially useful when the species dissimilarity between sample plots should be expressed independently of the species richness of the sample plots (Lennon *et al.*, 2001, Kühn & Klotz, 2006). In this study, we aimed to analyse the change in species richness and the change in species dissimilarity independently from each other. Thus, we preferred to use the Simpson index instead of another commonly used index, the Jaccard dissimilarity index. However, as a basis for comparison, we also presented the results for the Jaccard index in the figures, but discussed mainly the results of the Simpson index. The Jaccard dissimilarity index between two sampling plots was calculated as

$$\beta_J = 1 - \frac{a}{a+b+c}$$

where a is the number of species shared between two sample plots, and b and c are the numbers of species only found in one or only in the other sampling plot. The Simpson dissimilarity index between two sampling plots was computed as

$$\beta_S = \frac{\min(b,c)}{\min(b,c)+a}$$

Thus, both the Simpson dissimilarity index and the Jaccard index range from 0, i.e. all species in common, to 1, i.e. no species in common.

Our measure of the temporal change in species dissimilarity of several sampling plots (Δ_{Sim}) was then the average difference

Table 1 Description of the classes used for the grouping of the 825 recorded species into species groups.

Indicator	Classes	Source
Nutrient level	Eutrophic = typically on nutrient-rich sites (171 species) Mesotrophic = no clear preference (251 species) Oligotrophic = typically on nutrient-poor sites (397 species) Not assigned = no indicator value available (6 species)	Landolt (2010)
Conservation value	Very low = ubiquitous, often dominant on intensely managed sites (27 species) Low = ubiquitous, 'standard' or commonplace grassland species (37 species) High = target- or indicator species for grassland according to conservation objectives of the Swiss authorities (235 species) Rest = remaining species not typically grassland species: no conservation value assigned (526 species)	BAFU & BLW (2008); Landolt (2010)
Temperature level	Warm = centre of distribution at colline and lower montane levels (281 species) Moderate = centre of distribution at montane level (160 species) Cold = centre of distribution at higher montane level or above (350 species) Not assigned = no indicator value available (34 species)	Landolt (2010)
Alien species	Neophytes = species introduced by humans after 1500 AD (14 species) Archaephytes = species introduced by humans before 1500 AD (37 species) Indigenous = species that appeared without assistance by humans (681 species) Not assigned = no indicator value available (93 species)	Landolt (2010)

of the Simpson dissimilarity index of the second survey (β_k^2) minus the Simpson dissimilarity index of the first survey (β_k^1) for all $k = 1, \ldots, K$ possible combinations of two sample plots from the totally N sample plots.

$$\Delta_{Sim} = 100 \frac{\sum_{k}^{K} (\beta_k^2 - \beta_k^1)}{K} \quad \text{with} \quad K = \binom{N}{2}$$

A positive value of Δ_{Sim} would indicate that the species composition between the two plots became less similar from the first to the second survey, i.e. taxonomic differentiation; a negative value of Δ_{Sim} would indicate that the species composition became more similar, i.e. taxonomic homogenization.

To get an estimate of the precision of the change in species dissimilarity Δ_{Sim}, we adopted a jackknife approach (Jones, 1974): we removed one sample plot from the analysis and again calculated Δ_{Sim} as described earlier. We repeated that procedure until every sample plot was once removed from the calculation of Δ_{Sim}. The 2.5% and 97.5% percentiles of all the calculated Δ_{Sim} each with one sample plot removed were taken as an estimation of a 95% confidence interval. The approach to estimate the change in species dissimilarity Δ_{Sim} and its precision as described here is the same as the one used to calculate the indicator 'Diversity of Species Communities' of the BDM (see indicator 'Z12', http://www.biodiversitymonitoring.ch).

Testing for group differences of the change in species dissimilarity using traditional tests such as *t*-test or ANOVA would lead to an inflation of sample size. This is because there are $N(N-1)/2$ elements in a dissimilarity matrix calculated from N sample plots (Naaf & Wulf, 2010). To avoid an inflation of sample size, we instead used a permutation test with 1000 permutations of the group identities of the sample plots (Manly, 2007). As a test statistic for the permutation test, we used the averaged residuals.

For each subset of species (i.e. the analyses of the species groups), we calculated the change in Δ_{Sim} as follows. The Simpson dissimilarity index for the first survey for a given pair of sampling plots (β_k^1) was calculated exactly as above, including the records of all species. For the Simpson dissimilarity index of the second survey (β_k^2), however, we allowed to change only the species of the analysed species group, and the records of all the other species were held constant (i.e. as recorded during the first survey). The resulting Δ_{Sim} was then taken as a measure of the net effect on the change in species dissimilarity of the analysed species group only.

Sample sizes for the different groupings of sample plots, mean species richness of the first and second survey and the mean Simpson index of the first and second survey are given in Table 2. All analyses were performed with the statistical software R (R Development Core Team, 2010).

RESULTS

Over all plots, the species dissimilarity (Δ_{Sim}) of Swiss grassland decreased between the first and the second survey, suggesting recent and short-term taxonomic homogenization of grassland in Switzerland (permutation test: $P < 0.001$, Table 2). In contrast, the mean species richness of the same plots increased from the first to the second survey by 4.2% (mean increase of 1.4 species, paired *t*-test: $t = 4.3$, d.f. = 338, $P < 0.001$). Note, however, that the proportion of unidentified species slightly decreased from the first to the second survey, which could partly explain the increase in species richness between the first and the second survey.

Taxonomic homogenization of different groups of sampling plots

The temporal change in species dissimilarity depended on the altitudinal level (permutation test: $P < 0.001$), with highest taxonomic homogenization (i.e. the lowest values of Δ_{Sim}) found in montane and subalpine grassland, whereas no biotic homogenization was found at the colline level (Fig. 2a). Temporal change in species dissimilarity was not found to differ between species-rich and species-poor plots (permutation test: $P = 0.998$; Fig. 2b). However, this finding depended on the type of index used for the analysis. Using the Jaccard index instead of the Simpson index resulted in a higher degree of homogenization for species-poor plots compared with species-rich plots. Furthermore, the temporal change in species dissimilarity depended on the conservation value of the plots (permutation test: $P < 0.001$): strong taxonomic homogenization was found in plots of low conservation, while taxonomic homogenization was relatively weak in plots of high conservation value (Fig. 2c).

The increase in species richness was not found to differ between groups of different altitudinal levels (ANOVA: F = 0.9, d.f. = 3, $P = 0.46$, Fig. 2d) nor between groups of different relevance for conservation (Welch *t*-test: $t = 0.2$, d.f. = 267.4, $P = 0.81$, Fig 2f). However, the species richness of plots of low species richness tended to increase more than of plots with high species richness (Welch *t*-test: $t = 1.8$, d.f. = 286.5, $P = 0.07$, Fig. 2e).

Table 2 Given are the sample sizes (N), mean species dissimilarities of the first and second survey (Simpson index) and mean species richness of the first and second surveys of the different classes of sample plots that were analysed.

		Simpson index		Species richness	
Stratum	N	First	Second	First	Second
All types	339	0.723	0.715	33.6	35.0
Colline	34	0.534	0.536	25.2	25.1
Montane	156	0.506	0.494	29.9	31.5
Subalpine	60	0.685	0.674	41.3	42.7
Alpine	89	0.705	0.697	38.1	39.9
Species-rich	163	0.756	0.742	45.2	46.0
Species-poor	176	0.656	0.641	22.8	24.9
High-value	126	0.776	0.771	38.9	40.5
Low-value	213	0.542	0.530	30.5	31.8

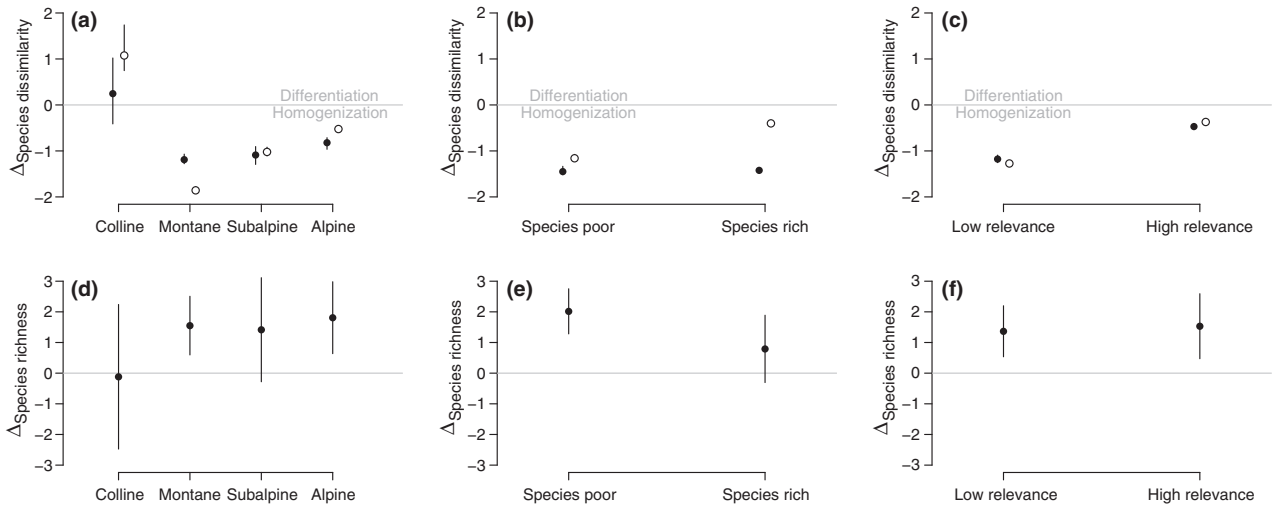

Figure 2 Temporal change in species dissimilarity and species richness between first and second survey in Swiss grassland. The sample plots are classed according to the altitudinal levels (a,d), according to the species richness of the second survey (species poor: below average species richness; species rich: above average species richness, b,e) and according to the conservation relevance of the meadow type (c,f). Shown are the mean ± 95% confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a–c), based on the Jaccard coefficient (open circles of a–c) and of the temporal change in species richness (solid circles of d–f).

Taxonomic homogenization of different groups of species

The analyses of the species groups that we assumed to indicate local land use regimes and local conservation efforts, i.e. the species groups reflecting nutrient-level and conservation value, suggested that it were mainly the eutrophic and mesotrophic species, and thus, the species of low conservation value that were responsible for the taxonomic homogenization in the grassland of Switzerland. In contrast, the changes in species dissimilarity induced by oligotrophic species or by species of high conservation value were only marginal (Fig. 3a,b). In terms of the change in species richness, however, all the different sets of species contributed to the overall increase in species richness (Fig. 3c,d).

The effect on change in species dissimilarity of the species groups we assumed to indicate climate change, i.e. the species groups of different temperature levels, seemed to vary strongly between the different species groups. Species that prefer warm temperatures (i.e. species with a distribution mainly at colline and lower montane levels) increased species dissimilarity, while species of moderate temperature level (i.e. species with

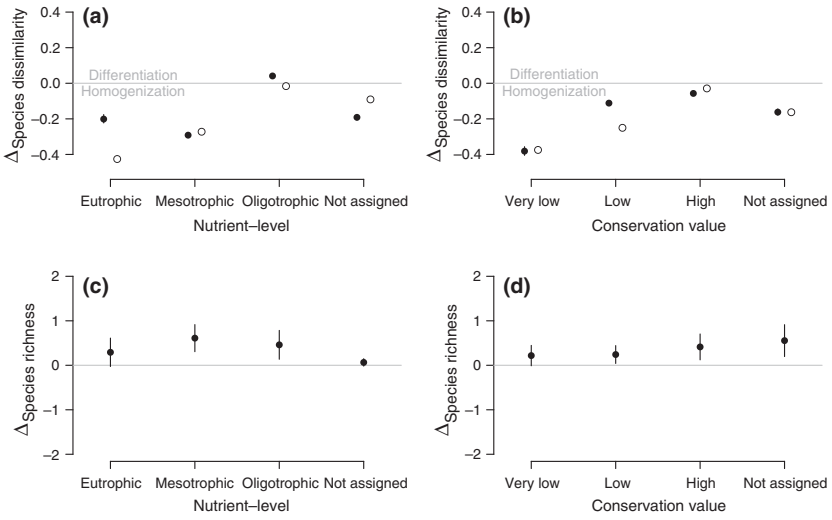

Figure 3 Temporal change in species dissimilarity and species richness between first and second survey for species groups that are assumed to reflect land use regime (i.e. nutrient level a,c) and conservation effort (i.e. species of different conservation value, b,d). Shown are the mean ± 95% confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a,b), based on the Jaccard coefficient (open circles of a,b) and of the temporal change in species richness (solid circles of c,d).

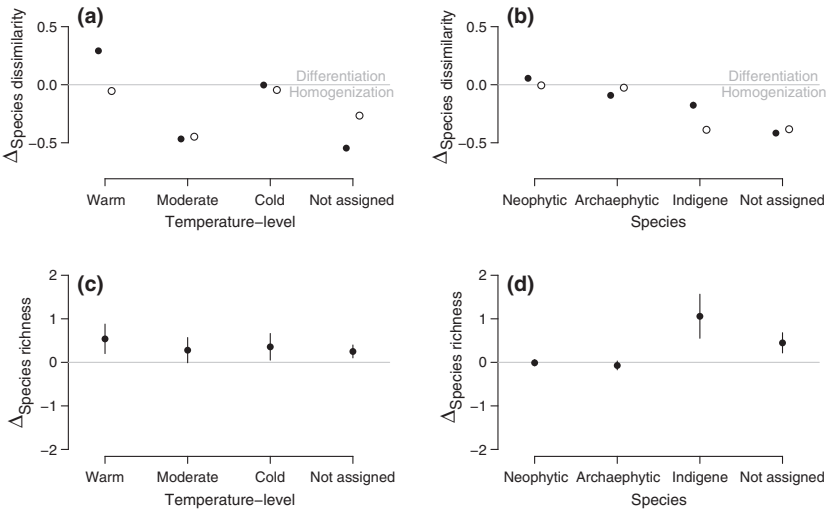

Figure 4 Temporal change in species dissimilarity and species richness between first and second survey for species groups that are assumed to reflect climate change (i.e. species groups indicating temperature level a,c) and the species group of neophytic, archaoephytic and indigenous species (b,d). Shown are the mean ± 95% confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a,b), based on the Jaccard coefficient (open circles of a,b) and of the temporal change in species richness (solid circles of c,d).

distribution mainly at montane level) led to taxonomic homogenization (Fig. 4a). The large differences in the temporal change in species dissimilarity found between the species of different temperature levels were not apparent when analysing the change in species richness: independent of the temperature level of the species, the species richness tended to increase (Fig. 4c).

The effect of neophytic species on the temporal change in species dissimilarity was only marginal and, contrary to expectation, it tended to increase species dissimilarity weakly (Fig. 4b). Overall, only few neophytic species were recorded in our data set and no change in species richness was recorded for neophytes between first and second survey (Fig. 4d).

The results for taxonomic homogenization of different species groups suggested that taxonomic homogenization was mainly because of the increase in common species, namely the species that are tolerant to high nutrient levels, the species of low conservation value and the species adapted to moderate temperature levels. We therefore directly analysed the effect of species groups that differ in their abundance. We found that the contribution to taxonomic homogenization strongly varied between species groups that differ in abundance (Fig. 5a). Although species of intermediate abundance and very abundant species equally increased in species richness (Fig. 5b), the increase in species of intermediate abundance resulted in higher species dissimilarity, while the very common species resulted in strong taxonomic homogenization.

DISCUSSION

In Switzerland, the mean plant species richness of grassland at local scale increased from 2001–2004 to 2006–2010, while during the same period, the species dissimilarity decreased suggesting local scale and short-term taxonomic homogenization of the grassland in Switzerland. Apparently, recent conservation efforts targeting Swiss grassland – for example in the form of agri-environmental schemes – were not able to counteract local-scale floristic homogenization. To our knowledge, this is the first study to demonstrate recent floristic homogenization of grassland for an entire country in spite of the sustained conservation efforts aiming at increasing biotic diversity of grassland.

The analyses of the different species groups suggested that the taxonomic homogenization was mainly because of an increase in already common and generalist species, namely the species that are tolerant to high nutrient levels, the species of low conservation value and the species of moderate temperature level. It is important to note that sample plots with change in land use between the first and the second survey had been excluded from the analyses. Therefore, the observed taxonomic homogenization took place in sites continuously managed as grassland. Unlike habitat destruction, taxonomic homogenization within a habitat is evidence for a rather inconspicuous change in biotic diversity that took place in a short time period.

From a conservation perspective, several of our findings are important. On the one hand, overall species diversity of grassland has increased including sites of high conservation value. Furthermore, part of the increase in species richness was because of an increase in target species for conservation. These results on its own may be considered as a success of conservation efforts. On the other hand, the spread of a limited number of ubiquitous generalist species has lead to more uniform species assemblages, i.e. taxonomic homogenization. To some extent,

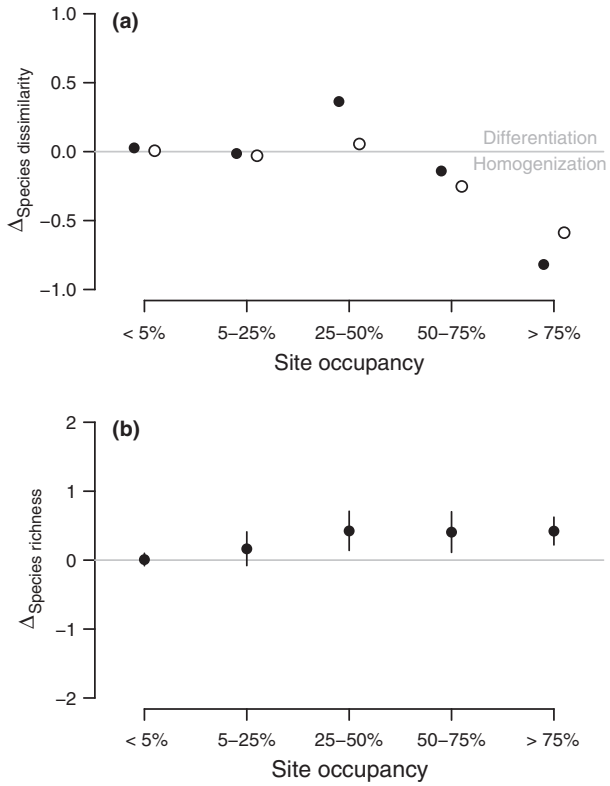

Figure 5 Temporal change in species dissimilarity and species richness between first and second survey for species that differ in total abundance over all habitats in Switzerland. Species are grouped according to proportion of the ca.1650 sample sites of the Biodiversity Monitoring Switzerland that are occupied by the species. Shown are the mean ± 95% confidence intervals of the temporal changes in species dissimilarity based on the Simpson index (solid circles of a), based on the Jaccard coefficient (open circles of a) and of the temporal change in species richness (solid circles of b).

taxonomic homogenization counteracts conservation objectives aiming to preserve locally typical species assemblages.

Taxonomic homogenization, however, is not always a negative indication of decreasing biodiversity (Rooney *et al.*, 2007). For the grassland in Switzerland, the taxonomic homogenization seemed to be caused mainly by an increase in common and generalist species. This finding is in accordance with results from other studies that found an increase in native ubiquitous, meso- or eutrophic species into species-rich grassland (Bennie *et al.*, 2006; Bergamini *et al.*, 2009) or temperate forest plant communities (Rooney *et al.*, 2004; Naaf & Wulf, 2010). But, as we found no indication that the increase in common species negatively affected species of conservation value in the last decade, the taxonomic homogenization of Swiss grassland presumably is not an indication of decreasing biodiversity. However, such an interpretation needs to be treated with caution, as a study period of only a decade might not be enough to demonstrate a decline of uncommon specialists caused by the spread of common generalists. For example in forest understory plant communities, the increase in species with a broad habitat range was accompanied by biotic impoverishment to a lower degree after two decades than after 50 years (Rooney *et al.*, 2004; Naaf & Wulf, 2010).

Taxonomic homogenization at large spatial scales has usually been attributed to the invasion of alien species or the replacement of specialist species by generalist species (Wiegmann & Waller, 2006; Kerbiriou *et al.*, 2009; Qian & Guo, 2010). However, in Switzerland, the taxonomic homogenization of grassland at a local scale could not be explained by the spread of neophytic (i.e. alien) species. This is in accordance with other local-scale studies that also did not find an effect of alien species on taxonomic homogenization (Smart *et al.*, 2006; Lambdon *et al.*, *2008*; Naaf & Wulf, 2010). Furthermore, in our case, the increase in common and generalist species within the last decade seemed not to have negatively affected specialist species of high conservation value. These results suggest that floristic homogenization in Swiss grassland was neither attributed to the invasion of neophytic species nor to the replacement of specialist species by generalist species. Therefore, our study adds also to the evidence that it is difficult to predict changes in taxonomic homogenization at the local scale from studies on large spatial scales.

Biotic homogenization is often linked to an increase in species richness (Rahel 2002; Olden, 2006; Smart *et al.*, 2006; Kerbiriou *et al.*, 2009; Naaf & Wulf, 2010). Similarly, in our study, the overall trend in the Swiss grassland was towards an increase in species richness but towards a decrease in species dissimilarity. In spite of the prevalence of studies that reported a negative correlation in the development of species richness and temporal change in species dissimilarity, the temporal trend of species dissimilarity has to be viewed as a process on its own and needs to be evaluated independently of species richness but in the context of other environmental factors (Smart *et al.*, 2006; Devictor & Robert, 2009; Filippi-Codaccioni *et al.*, 2010). In our study, the species richness of the group of species typical for warm temperatures and for low altitudes increased. This increase in species richness was positively linked to a moderate increase in species dissimilarity and indicates that both the species richness and the species dissimilarity diversity may increase.

We conclude that between the two surveys of 2001–2005 and 2006–2009, the species dissimilarity of Swiss grassland considerably declined suggesting local-scale taxonomic homogenization. The observed taxonomic homogenization was mainly because of the spread of common species. Local-scale changes in land use regimes implemented by agri-environmental schemes, and other conservation efforts on parts of the entire grassland area were apparently not enough to prevent the total grassland from recent taxonomic homogenization.

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