ORIGINAL PAPER

Response of Swiss forests to management and climate change in the last 60 years

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Abstract
· **_Context_** Forest vegetation is forecasted to shift upslope several hundred metres by 2100 due to climate warming. However, only a small number of detailed assessments in selected regions have confirmed a climate response on the part of forest vegetation.
· **_Aim_**s This study aimed to analyse the relative contributions of temperature and other factors to range shifts in forest vegetation by comparing old and revisited relevés in Swiss forests.
· **_Methods_** In order to investigate such range shifts, we revisited 451 relevé plots in forests in all parts of Switzerland. Collected data comprise two independent samples, one dating from the 1950s (age 60 sample) on 126 plots and the other dating from the 1990s (age 15 sample) on 325 plots. We defined an indicator value for elevation to estimate the upslope and downslope range shifts of forest species. The influence of different site factors on range shifts was assessed by variance partitioning using Landolt's (2010) averaged species indicator values. Vegetation changes were analysed by balancing both increasing and decreasing frequencies of plant species.
· **_Results_** Our findings show significant differences between the two survey periods, where the averaged species indicator for elevation varied greatly in both the age-60 and the age-15 samples. In addition, a significant upslope shift in the herbaceous forest layer (herbs and tree regeneration) of about 10 m per decade since the mid-twentieth century is evident. Downslope shifts were detected in the shrub/tree layer at lower elevations, which may be explained by factors other than climate warming.
· **_Conclusions_** To date, the impact of global warming on tree species composition in Swiss forests has been weaker in comparison to the effects arising from forest management and land use change. Understorey vegetation, however, shows a strong signal of upslope shift that may be explained most adequately by a combination of climate change and other factors.

Key message An analysis of plant species range shifts in Swiss forests shows that, to date, the impact of global warming has been weaker in comparison to the effects arising from forest management and land use change. Forest species in understorey vegetation, however, have shifted upslope 10 m per decade.

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1 Introduction

Latitudinal and elevational margins of plant species occurrence indicate a close relationship to temperature (von Humboldt and Bonpland 1807; Randin et al. 2013). If a species' distribution area is assumed to be in equilibrium with climatic or more generally environmental conditions (Guisan and Zimmermann 2000), temporal changes in species distributions can be linked to environmental change or, more

specifically, to climate change if related variables clearly account for such changes (Walther et al. 2002; Lenoir et al. 2008). To detect temporal changes in plant species distribution, information on geo-referenced species occurrence at different times are needed. Ideally, locations of earlier vegetation survey studies serve as a first temporal reference, and these locations are then revisited for a second assessment at a recent date (e.g. Walther and Grundmann 2001). Since vegetation studies usually lack measurements of site conditions, species indicator values have often been used to both describe and interpret vegetation changes across spatial or temporal gradients (Diekmann 2003). Central European plant species have been assigned a set of indicator values expressing the average niches along environmental gradients such as light, temperature, continentality, nutrients, soil moisture and pH (Ellenberg 1974). For Switzerland, Landolt (1977, 2010) adapted these values to the broader range of site conditions present in the country and added indicators for humus content and soil aeration. Landolt's indicator values have frequently been used in comparative vegetation studies (e.g. Dzwonko 2001; Güsewell et al. 2012). Most often, the indicator values of individual species listed in vegetation relevés along an ecological gradient of interest are averaged, and the average value then is used to indicate the environmental conditions expressed by species composition (Schaffers and Sýkora 2000).

Statistical models have frequently been used in recent decades to describe individual species' spatial distributions (Guisan and Zimmermann 2000; Thuiller et al. 2005) and ecological ranges (Brzeziecki et al. 1993; Araújo and Guisan 2006; Zimmermann et al. 2010), as well as to predict potential future distributions of species or vegetation communities under various climate change scenarios (e.g. Brzeziecki et al. 1995; Bolliger et al. 2000; Theurillat and Guisan 2001; Dormann 2007; Hanewinkel et al. 2013). Regarding large scales, species distribution projections using both current and future climate scenarios generally yield plausible results (Walther 2010). In contrast, on a regional scale, i.e. at the level of individual European countries or provinces, the actual state of forest species occurrence may considerably differ from what is projected by models (Lenoir et al. 2010).

Discrepancies between projected or expected and actually observed changes in plant species distribution may emerge from correlations or interactions between variables used in the models. In particular, assessing the responses of plant species or communities to climate warming raises the question of whether, and to what extent, an observed or projected shift is actually caused by increased temperature or to what extent it may be explained by other factors that correlate with temperature. For instance, the nutrient supply in Swiss grassland soils is, according to several sets of vegetation records, higher in the lowlands than in the mountains (Güsewell et al. 2012). While this suggests that the nutrient supply is correlated with temperature, the actual cause is more intensive manuring and

nutrient input from densely populated regions in the lowlands. Similarly, data from the Swiss National Forest Inventory (Brändli 2010) indicate a strong negative correlation between management intensity and elevation and consequently temperature. However, management intensity depends on various abiotic site factors that may be correlated with temperature and therefore responses of species to climate are difficult to disentangle from responses to land use (Gimmi et al. 2010). In France, Bertrand et al. (2011) observed that the response of forest vegetation to climate warming in lowland areas is smaller than in mountain areas. They attribute this discrepancy to human land use, which tends to disturb ecological niches more frequently and intensively in the lowlands. Analyses of fossil remnants have shown that, already several thousand years ago, human impact more than climate change has altered tree species occurrence at the tree line (Gobet et al. 2010).

Applying the species indicator approach to evaluate climate change-induced elevational shifts of species or communities and community occurrences requires a reconsideration of the indicator values assigned to single species, leading us to consider two questions: (1) To what extent do these indicator values describe the responses of species to temperature? (2) To what extent do the responses refer to other site factors that depend on elevation and that are consequently correlated with temperature? All of Landolt's indicator values are assigned to the same roughly 3,000 plant species in Switzerland. Therefore, the indicator values statistically depend on each other. In order to account for these dependencies, we applied a combined evaluation of several indicator values.

In our study, we assessed the response of forest vegetation to changing site factors by using two sets of repeated vegetation relevés recorded across Switzerland and addressed the following questions:

- How much forest plant species elevation shift (in metres) has occurred in Switzerland during the last 60 years (1950–2011; 1995–2010)?
- To what degree did temperature account for elevational shifts in comparison with other factors over the study period?
- Were elevational range shifts in species' occurrences caused by the increase or decrease of species' frequencies over the study period?

2 Materials and methods

2.1 Study area

The study area extends over the forested territory (approx. 12,800 km^2) in Switzerland (41,285 km^2) with a strong elevational gradient ranging from 190 to 2,400 m a.s.l.

Climatic conditions include a moist oceanic climate north of the Alps (e.g. in Zürich, 426 m a.s.l.: 8.5 °C; 1,031 mm; all climate data: MeteoSwiss ©, 1961–1990), dry and continental-like conditions in the Central Alps (e.g. in Sion, 482 m a.s.l.: 9.2 °C, 598 mm) and Insubrian, i.e. a subtropical climate in the southern part of Switzerland (e.g. in Magadino, 203 m a.s.l.: 10.5 °C, 1,772 mm). The major climatic differences translate into pronounced elevational gradients, with more precipitation at higher elevations and an average temperature lapse rate of 0.5 °C 100 m^{-1}, which leads to a characteristic elevational zonation of vegetation (Zimmermann and Kienast 1999). Forests at lower elevations have a complex history of intensive human land use, whereas at higher elevations, forest vegetation is more natural. Today, forests cover about 31 % of Switzerland, with a maximum proportion of 51 % in the southern Alps and a minimum proportion of 25 % on the Central Plateau (Brändli 2010).

2.2 Data

Vegetation plots located throughout all forests in Switzerland were revisited (Fig. 1). Geo-referenced relevés containing abundance estimations of vascular plants and bryophytes growing on the soil served as baseline data (Braun-Blanquet approach; Braun-Blanquet 1964). The study comprises two independent old data sets, one 60 years old (age-60 sample) and one 15 years old (age-15 sample). To set up the age-60 sample, a total of 126 relevés from the 1940s and 1950s were

drawn from the Swiss forest vegetation database (Wohlgemuth 2012). Only relevés with reliable coordinates and continuous forest cover according to recent aerial photographs were considered for the study. To achieve an equal distribution over Switzerland, only one out of many records per quadrant of 5×5 km was chosen. The relevés stem from different studies that aimed at describing and classifying forest vegetation types in Switzerland (Ellenberg and Klötzli 1972; herein Etter 1943 and 1947; Trepp 1947; Moor 1952, 1954 and 1958; Braun-Blanquet et al. 1954; Kuoch 1954; Lüdi unpublished; Richard unpublished), which is why area sizes of the relevés in the age-60 sample vary. For the revisitation, we estimated the relocation accuracy of the plots to be 10 m. We chose the exact plot location of the earlier survey and assessed relevés on areas of 200 m^2.

For the age-15 sample, 325 plots were selected from the 4×4-km grid sample (729 circle plots 200 m^2 in size) of the Swiss National Forest Inventory (Wohlgemuth et al. 2008). The selection consisted of all 8×8-km grid points and of additional plots chosen either randomly or selectively from the rest of the 4×4-km grid points, thus ensuring an equal distribution of regions and elevations in Switzerland. Since all Swiss National Forest Inventory sample plots are permanently marked, and the plot coordinates are precise.

Plots from both the age-60 and the age-15 samples were revisited between 2008 and 2011, providing a second assessment of vegetation on circle plots which were 200 m^2 in size.
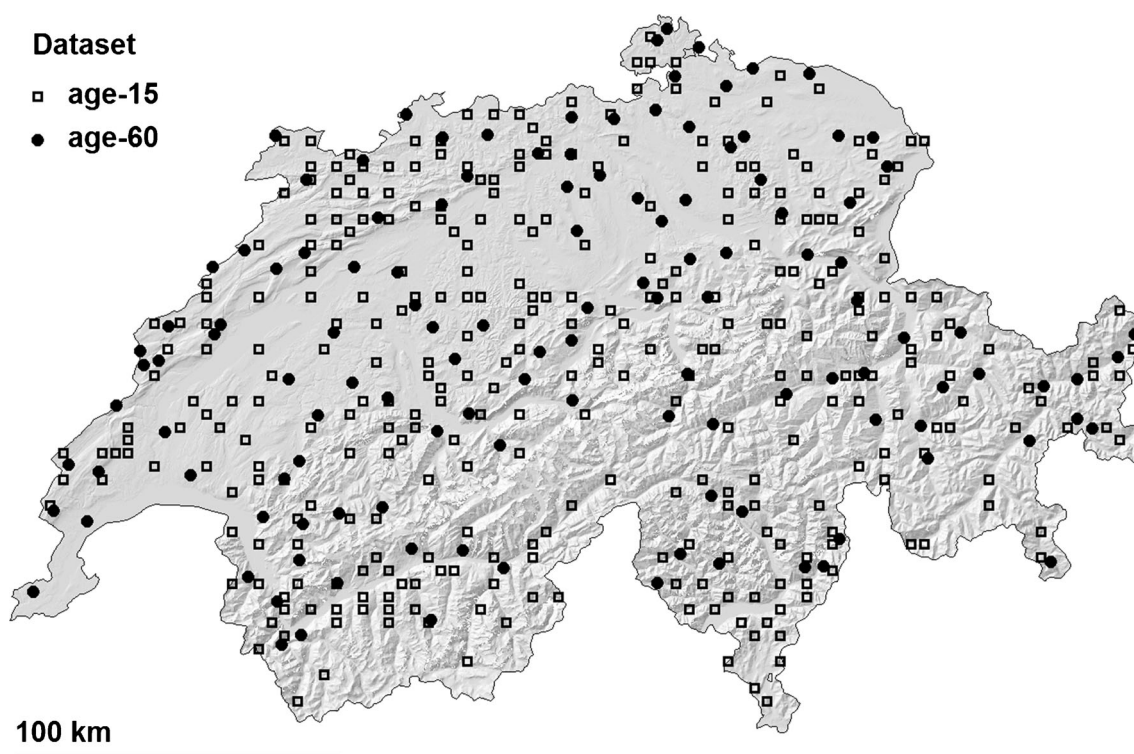

Fig. 1 Locations of the relevé plots chosen. *Black circle*: data from the 1950s (age-60 sample); *white square*: data from the 1990s (age-15 sample)

2.3 Indicator value for elevation

We deduced an indicator value for elevation from a reference set of 4,089 records from the Swiss Forest Vegetation Database (Wohlgemuth 2012). To ensure representativeness regarding the wide range of site conditions, reference records were drawn as an even sample across the gradient of Landolt's indicator values for temperature (T), light (L), moisture (F), nutrient supply (N), soil reaction (R), humosity (H) and soil aeration (D) (Landolt et al. 2010). For every species present at least five times in the reference data set, an indicator value for elevation was assigned by computing the 10 %-trimmed mean of the elevations of the species' occurrences. For shrub and tree species, we only took presence data regarding the herb layer into consideration. The resulting elevation indicators were then applied to the relevés from the age-60 and age-15 samples by averaging the corresponding species values in every relevé. No weighting of species abundance was applied. To enhance robustness and rule out extreme observations, we computed 10 % trimmed means. A difference between the averaged elevation indicators of the relevés from the first and second survey indicates a change in species composition, which we interpreted as an elevational shift. The averaged indicator of a relevé denotes the elevation at which similar vegetation can be found in the reference data set. If the elevation indicator of the second (i.e. recent) survey of one plot is lower than in the first, this implies that current species composition corresponds to reference data for lower elevations in comparison to the composition from the first survey. In other words, in this case, species composition has a temporal upslope shift. The amount of the shift is, however, underestimated because the range of the averaged elevation indicator values is smaller than the elevation range of the reference plots. Therefore, we compared the interquartile range of the averaged elevation indicators with the interquartile range of the actual elevations of the plots. We found that the elevational range indicated by the indicators was too small by a factor of 2.2 (Fig. 2). The differences between the elevation indicators from the first and the second surveys were thus multiplied by this factor.

2.4 Assessing the influence of different site factors using variance partitioning

We partitioned the variance of the averaged elevation indicator values of the relevés (response variable) to identify shared and independent components (predictor variables) through linear regression analyses. Partitioning referred to two groups of predictor variables: Landolt's indicator value for temperature T (group 1) and the remaining Landolt's indicator values (L, F, N, R, H, D; group 2). Goodness-of-fit was expressed as adjusted R^2. In a similar way, we partitioned the variance of the changes in the elevation indicator value (response) into

changes in temperature indicator value (dT; predictor group 1) and in the remaining indicator values (dL, dF, dN, dR, dH, dD; predictor group 2).

2.5 Increase or decrease in frequencies

An upslope range shift of a species' distribution can be caused by either an increased species frequency which occurs when colonising higher elevations or a decreased frequency at lower elevations due to competitive exclusion. Analogously, a shift towards denser forest stands is indicated by fewer light-demanding and more abundant shade-tolerant species. Such changes between the relevés from the first and the second survey are indicated by differences between the number and proportions of species with high or low values in particular (Landolt et al. 2010).

To reduce data, we expressed tree species composition in frequencies of conifers and broadleaf species (e.g. Brändli 2010). Changes between the two surveys were analysed in the same way as described for changes in indicator values.

2.6 Canopy layers and elevational belts

The data were analysed separately for shrub/tree and herb layers and for three elevational belts. The shrub/tree layer consists of woody plants, i.e. shrubs and trees taller than 50 cm (based on the Landolt et al. (2010) classification). The three elevational belts were delimited by dividing the data into three roughly similar elevational categories (low, mid and high elevation) with equal numbers of plots: 350–749, 750–1,199 and 1,200–2,300 m a.s.l. for the age-60 sample and 290–749, 750–1,249 and 1,250–2,190 m a.s.l. for the age-15 sample.

Data sets were analysed by using VEGEDAZ (Küchler 2014) and R version 3.0.0 (R Development Core Team 2013).

3 Results

3.1 Averaged indicator values for elevation

Changes in averaged indicator values for elevation differed with respect to both the three elevational belts and the shrub/tree and herb layers (Fig. 3). The age-60 sample showed marked uphill shifts in the herb layer for all three elevational belts (107, 44 and 58 m at low, mid and high elevations, respectively; averaging 65 m) and a downslope shift in the shrub/tree layer at low elevations (Fig. 3a). The age-15 sample showed a significant upslope shift in the herb layer only at mid-elevations and a significant downslope shift in the shrub/tree layer at high elevations (Fig. 3b).

Fig. 2 Observed elevations and averaged indicator values for elevation of relevés in the age-15 plots. **a** Scatterplot. **b** Boxplot; the *boxes* show the interquartile ranges
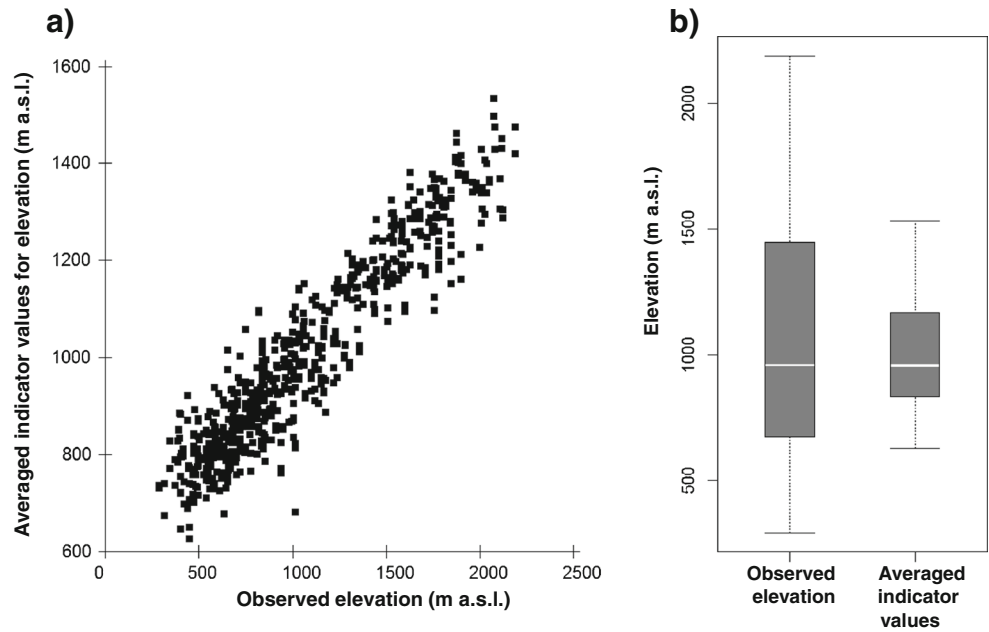
3.2 Variance partitioning of the elevation indicator value

The full model explained 91 % of total variance in the age-60 sample and 93 % in the age-15 sample (Table 1). The temperature indicator value explained independently 34 % of total variance in the age-60 sample and 23 % in the age-15 sample. The remaining indicator values (*L, F, N, R, H, D*) explained 1 and 2 % of the variance uniquely. The shared variance of both groups accounted for a large part of total variance (56 % in the age-60 sample and 67 % in the age-15 sample), which suggests strong collinearity.

3.3 Variance partitioning of elevational shifts

To assess the extent to which forest plant species responded to temperature change as reflected in the elevational shift, variance of changes in the elevation indicator value was partitioned to separate changes in the temperature indicator value (group 1) from changes in the remaining indicator values (group 2; Table 2). Species in the herb layer at mid elevations (both samples) and high elevations in the age-60 sample exhibited a significant directed upslope shift (Fig. 3). The variance of this shift is explained, to a considerable

Fig. 3 Changes in averaged indicator value for elevation (10 % trimmed means) between the relevés from old and recent surveys from the **a** age-60 and **b** age-15 sample. Significance levels of signed-rank test, *p<0.05, **p<0.01, ***p<0.001
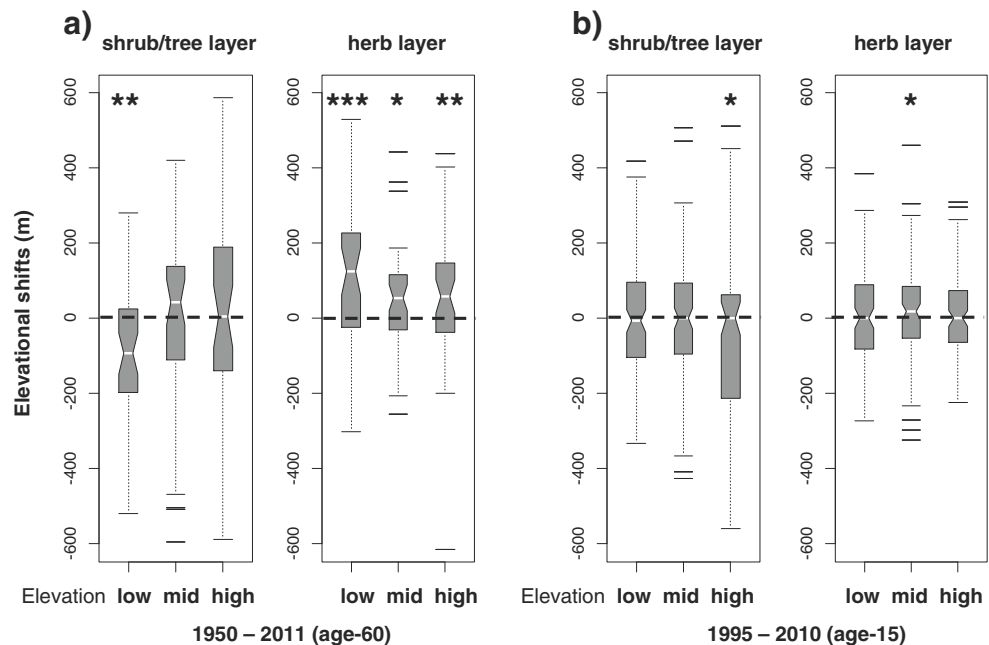
Table 1 Variance partitioning of the averaged indicator values for elevation (adjusted R^2, in %) between the temperature indicator value T and the remaining indicator values (L, F, N, R, H, D)

	Age-60 data	Age-15 data
Temperature indicator value T	90	91
L, F, N, R, H, D indicator values	57	69
Unique to T	34	23
Unique to L, F, N, R, H, D	1	2
Common	56	67
Full model	91	93
Unexplained	9	7

extent, uniquely by the temperature value change (dT). The marked upslope shift in the herb layer at low elevations in the age-60 sample (107 m) is predominantly explained by the change in factors other than temperature (52 % of the variance is explained independently by dL, dF, dN, dR, dH, dD). In the shrub/tree layer, the change in the temperature indicator value (dT) explained 29 % of the variance in the age-60 sample at low elevations and 17 % in the age-15 sample at high elevations, whereas the remaining indicator values (dL, dF, dN, dR, dH, dD) explained 12 and 18 % uniquely. A negative commonality (−5 %) was found for the shrub/tree layer at low elevations, indicating that the effects of temperature and other factors tended to compensate each other.

3.4 Shifts in the frequencies of species

Both increases and decreases in the frequencies of species along the elevational gradient can lead to shifts in individual species' optima. In the age-60 sample, the number of species per relevé decreased at low elevations and increased at high

elevations over the time span of 60 years. Thus, at lower elevations, the mean temperature indicator value for species in the woody layer is reflected by a reduction of predominantly thermophile shrub and tree species (Fig. 4a). In contrast, the mean temperature value of species in the herb layer at low elevations mainly corresponds to the decreased frequency of species that have adapted to low temperatures (Fig. 4b). At higher elevations, the appearance of thermophiles was more marked than the increase of cold-resistant species (Fig. 4b). In both woody and herb layers, the mean nutrient indicator values at low elevations is mainly in line with the reduction in species with low nutrient requirements (Fig. 4c, d). In contrast, species with predominantly higher nutrient requirements appeared in the herb layer at higher elevations (Fig. 4d). The statistically highly significant decrease in the mean light indicator values in both layers at low elevations clearly corresponds with the decrease in light-demanding species and the increase in shade-tolerant species (Fig. 4e, f).

The proportion of conifer species increased in the wood/shrub layer at low elevations due to the increase in conifers and the decrease in broadleaf species (Fig. 5a). At higher elevations, the lowered proportion of conifers in the herb layer corresponds mainly to the appearance of broadleaf species (Fig. 5b).

4 Discussion

4.1 Elevational shifts of plant species in Swiss forests

Differences between current and earlier forest vegetation in Switzerland as measured by averaged indicators for elevation vary considerably in both the age-60 and the age-15 samples

Table 2 Variance partitioning (adjusted R^2; in %) of change in averaged indicator values for elevation between change in temperature indicator value (dT) and change in the remaining indicator values (dL, dF, dN, dR, dH, dD)

Elevational belt	Low elevation		Mid elevation		High elevation	
Age-60 sample (1950–2011)						
Elevational range in m	350–750		750–1,200		1,200–2,300	
Canopy layer	Shrubs/trees	Herbs	Shrubs/trees	Herbs	Shrubs/trees	Herbs
Unique to dT	29	20	29	37	18	42
Unique to dL, dF, dN, dR, dH, dD	12	52	5	10	8	0
Shared	−5	−1	29	8	35	17
Age-15 sample (1995–2010)						
Elevational range in m	290–750		750–1,250		1,250–2,190	
Canopy layer	Shrubs/trees	Herbs	Shrubs/trees	Herbs	Shrubs/trees	Herbs
Unique to dT	37	32	26	31	17	30
Unique to dL, dF, dN, dR, dH, dD	8	10	1	1	18	5
Shared	13	7	10	1	7	10

Fig. 4 Age-60 sample. Mean number of species per relevé in classes of indicator values (ranging from 1 to 5; *X* for species lacking an indicator value assignment), for shrub/tree and herb layers and for elevational belts (low, mid, high). Significance levels for an increase (+) or a decrease (−) in averaged indicator values between surveys (signed-rank test): *$p<0.05$, **$p<0.01$, ***$p<0.001$
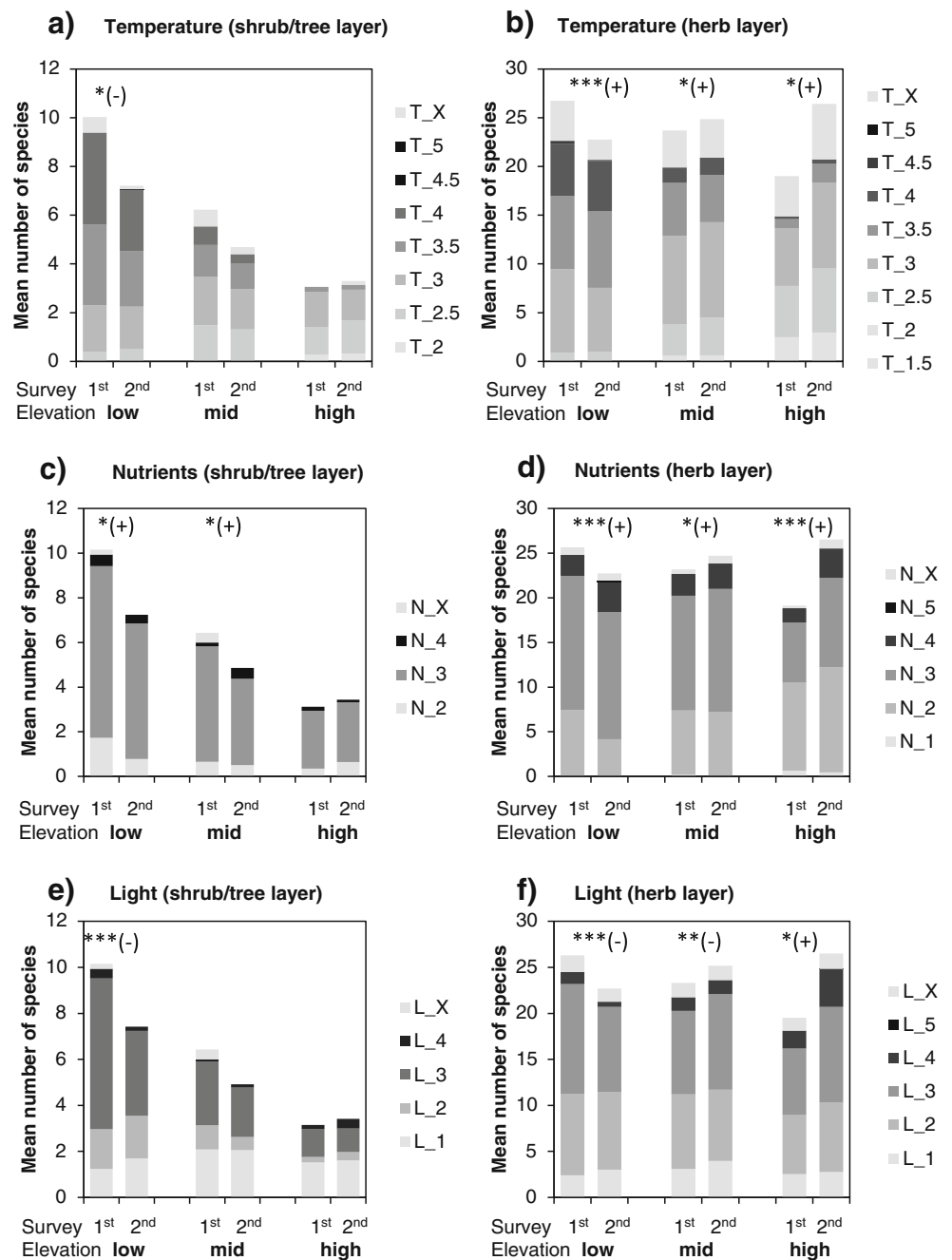

(Fig. 3). Some significant overall shifts are, however, apparent. According to our results, changes in the herbaceous layer correspond to an average upslope shift of 65 m, which corresponds to a rate of 10 m per decade since the middle of the twentieth century. In the same time period, the mean yearly temperature has risen by at least 0.15 °C per decade (Perroud and Bader 2013). This upslope shift rate is about three to five times smaller than predicted by earlier species and vegetation distribution projections (Brzeziecki et al. 1995; Zimmermann et al. 2006). Our observations of upslope shifting are consistent with a similar study from southern France (Lenoir et al.

2008), where an upslope shift of 29 m per decade was detected in correspondence with a temperature rise of 0.45 °C per decade.

In contrast to the clear signal in the herbaceous layer, a general upslope range shift in the shrub/tree layer is not evident. Below 750 m a.s.l. (Fig. 3a), even a conspicuous downslope shift is signalled by the species' range comparisons. The clear difference between shrub/tree and herb layers may, to some extent, be explained by the delayed response of long-lived species to climate change (Lenoir and Svenning 2013). On the other hand, the contrasting succession signals of

Fig. 5 Age-60 sample. Mean number of conifer and broadleaf species per relevé, for shrub/tree and herb layers and for elevational belts (low, mid, high). Significance levels for an increase (+) or a decrease (−) in the proportion of conifer species between surveys (signed-rank test): *p<0.05, **p<0.01, ***p<0.001
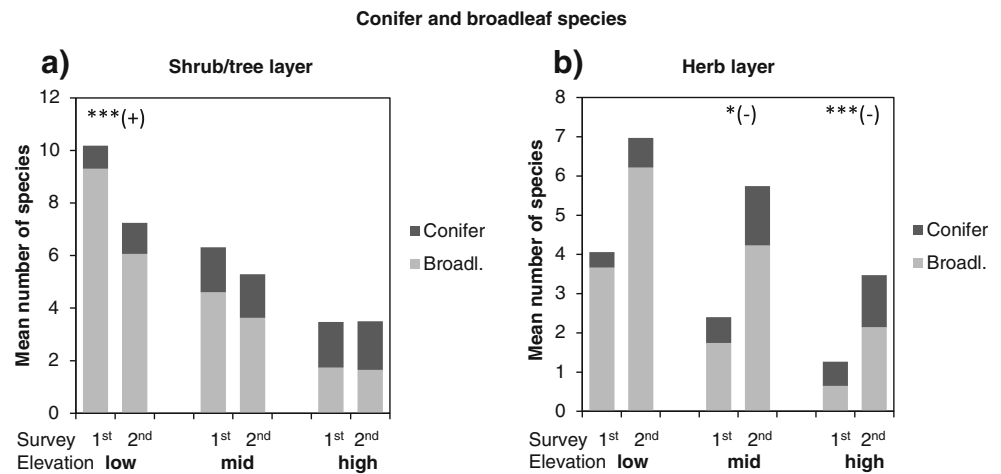
herbaceous and woody vegetation layers may also indicate that species composition in forests is affected by strong non-climatic factors, which, in the case of shrubs and trees, override the response to climate change.

4.2 Climate and non-climate factors as drivers

Statistically, elevational shifts were, to a large extent, explained by changes in Landolt's species indicator value for temperature (Table 2). However, changes in the indicator values for other site factors also explained a considerable part of the variance. Given the collinearity of Landolt's species indicators (Table 1) and the fact that Landolt's temperature value relies mainly on the elevational distributions of species (Landolt et al. 2010), a conservative interpretation is necessary. We believe that the explained variances shared between species indicator values for temperature and other indicator values (Table 2) is accounted for by factors other than temperature. We can only accept variance that is uniquely explained by the temperature indicator value as a valid indicator of a response to warming. This implies that the effects of warming may be hidden by opposing trends and possibly remain undetected. For instance, a continuously closing canopy results in more shade which may lead to a cooler microclimate (von Arx et al. 2012) and thus counteracts a response to a warming macroclimate. The results of the variance partitioning analysis suggest that climate change caused at least some of the significant upslope shifts in the herb layer at middle elevations (age-60 and age-15 samples) and at high elevations (age-60 sample). In contrast, factors other than temperature increases are likely to play a role in the marked upslope shift of herb vegetation at low elevations (+107 m, Table 2) in the age-60 sample.

4.3 Increases and decreases in the frequencies of species

In the age-60 sample, forest vegetation at low elevations changed mainly with both the decrease of light-demanding (L values 4, 5) and stress-tolerant species (N values 1, 2; Fig. 4). This result is consistent with Brändli (2010), who reports that lowland forests have generally become denser due to lower management intensity during recent decades. A discrepancy between temperature indicator values in the herb layer (increase) and in the shrub/tree layer (decrease) can be partly explained as the result of the plantation of spruce during the middle of the twentieth century (Bürgi and Schuler 2003). This management measure is visible in the age-60 data as an increase in conifers (Fig. 5) and as a downslope shift of shrub/tree composition at low elevations (Fig. 3).

In forests at higher elevations, both species with a high demand for nutrients, light and warmth in the herb layer and broadleaf tree species increased in numbers. In particular, an increase in species of tall herb communities and in non-coniferous species can be interpreted as the result of the abandonment of wood pastures and the direct and indirect effects of wind disturbances that created huge open areas in the Swiss Pre-Alps. An invasion of broadleaf species at mid and high elevations has also been reported in the Pyrenees (Hernández et al. 2013). Disturbance as a potential mechanism to explain downslope range shifts during periods of climate change has recently been noted by Lenoir et al. (2010). In addition, species may also expand or reduce their range margins due to legacy effects related to former management that has been altered in recent decades.

5 Conclusions

The results of this study indicate that the impact of contemporary global warming on tree species composition in Swiss

forests has been much weaker than that of management and other disturbance effects. Nevertheless, understorey vegetation shows a considerable upward shift, part of which can probably best be explained by global warming. Forest vegetation has sometimes been modified in unexpected ways, in particular as a reaction to former and actual land use. Evidence of current and future changes in forest vegetation due to climate warming can only be found through long-term monitoring of vegetation. We demonstrate that tree, shrub and herb canopies must be studied separately in order to comprehensively understand the effects of climate change and to disentangle climate change from other influencing factors such as succession and management. In particular, the response of trees and shrubs to climate change seems to have been either delayed or strongly affected by management.

Global temperature is a slowly changing factor that affects forest vegetation only very subtly. In contrast, windthrow, fire, disease and forest management result in clear and abrupt forest changes. Many of these factors interact, which makes forecasting future forest composition rather speculative. One strong indication of our study, however, is that disturbance and management influence woody vegetation more than contemporary and future warming. Hence, management by objectives will be one key approach to ensure that forests can adapt appropriately to a changing environment.

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