Trends of vegetation change in colline and submontane climax forests in Switzerland

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Summary

1 The present study analyses overall trends of vegetation change during the second half of the 20th century in forests of the Swiss Midlands.

2 On an east-west transect across the Swiss Midlands, forest sites where the vegetation had been surveyed during the period 1940–1965 with the Braun-Blanquet method were resurveyed in 1998, excluding sites with obvious traces of forest management or other disturbance (in total 37 sites). Changes in species composition were evaluated in terms of presence or absence of species, species richness, growth forms and average ecological indicator values.

3 Species composition changed considerably between 1940–1965 and 1998, with 184 of the totally 241 species becoming less frequent and 44 species becoming more frequent. The average number of species per relevé decreased from 41 to 26 between the two periods.

4 According to average ecological indicator values, habitat conditions became moister, richer in nutrients, and generally darker. The observed trends generally point to more mesic conditions, which coincides with the natural life cycle of forests in increasingly mature stage.

5 A decreasing number of montane species, an increasing number of thermophilous species and the apparition of several evergreen broad-leaved exotic species together strongly suggest a change towards warmer conditions. This result is consistent with trends observed in other recently published studies on vegetation change within Swiss lowland forests and may reflect climate change.

Keywords: beech forest, climatic change, species richness, succession, vegetation relevé

Bulletin of the Geobotanical Institute ETH (2001), **67**, 3–12

Introduction

Vegetation is always subject to change. Even forest vegetation, which seems stable in the short term, shows considerable changes in the mid to long term. "Change seems to be the only constant over extended periods" (Gassmann *et al.* 2000), especially regarding species composition. If differences in species composition are observed between two periods, they may be interpreted (1) as consequence of the intrinsic dynamics of the system, (2) as an effect of external factors, or (3) as artefacts due to the method of vegetation survey.

Since environmental factors affect each species differently, conclusions about changes in environmental factors can be drawn from changes in the species composition of a given site (e.g. Olano *et al.* 1998; Philippi *et al.* 1998). However, several factors influence the vegetation and interfere with each other. It is often difficult to disentangle their combined effects, so that different interpretations of the same observed change may be possible (e.g. Werdenberg & Hainard 1988).

In the 1980s, many studies focused on the effects of atmospheric nitrogen inputs and acid rain on forest ecosystems (see e.g. Röder *et al.* 1996 and references therein). These studies mainly analysed changes in forest vegetation in terms of ecological indicator values for nutrients and acidity, assumed to reflect these environmental stressors. In the 1990s, the main focus of interest moved towards climate change (Klötzli *et al.* 1996; Walther 1997; Carraro *et al.* 1999; Dupouey *et al.* 1999; Burga & Kratochwil 2001). The effects of climate change on forest vegetation were studied with the same methodology as in the former studies – resurveying old vegetation relevés and analysing species change – but this analysis now included all ecological indicator values, so that a more comprehensive picture of changes in environmental conditions could be drawn. In Switzerland distinct changes in the species composition of lowland climax forest were detected in a 30-km wide transect from North to South (Fig. 1; Carraro *et al.* 1999). The aim of this study was to extend the previous survey to other parts of the country in order to provide a more general view on the vegetation change that took place in Swiss lowland forests during the past thirty years.

Material and Methods

SELECTION OF SITES

Vegetation relevés that had been recorded between 1940 and 1965 along an east-west transect from Lake Constance to Lake Leman were selected from the forest database of the Swiss Institute of Forest, Snow and

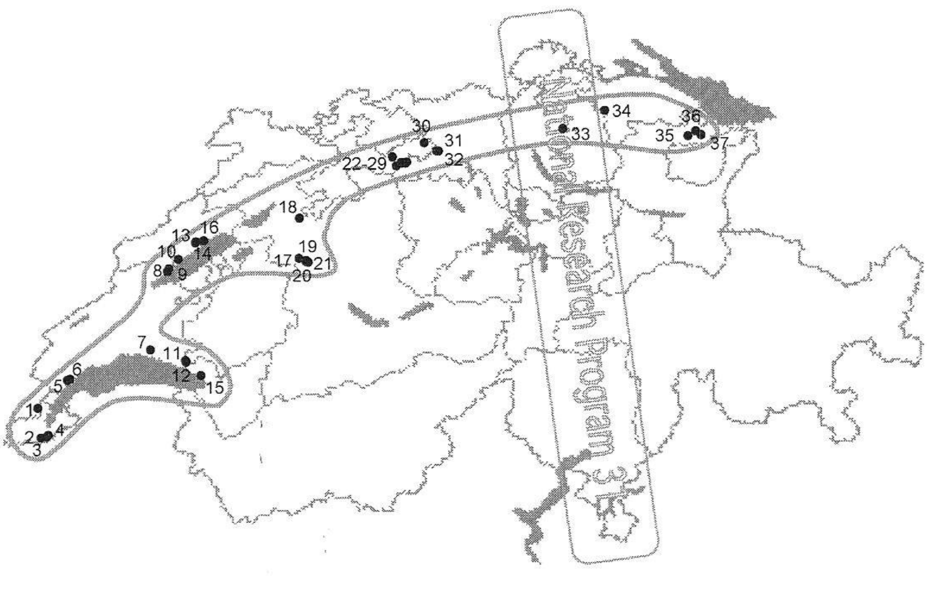

Fig. 1. Spatial distribution of the 37 investigated sites along an East-West transect across Switzerland. The North-South transect investigated as part of the National Research Programme 31 (Carraro et al. *1999) is also shown.*

Landscape Research (Wohlgemuth 1992). Of the 480 relevés located within the study area, only those (372) with an elevation lower than 800 m a.s.l. were retained. The localities of these 372 relevés were positioned on recent topographic maps according to their coordinates (Swiss National Maps 1:25.000, Federal Office of Topography). Ninety locality had to be excluded because they were not forested any more. In addition, 144 relevés were excluded from the investigation because they contained a high proportion of cultivated coniferous tree species (e.g. *Picea, Abies, Larix*), or tree species representing azonal vegetation (i.e. *Salix, Alnus, Fraxinus, Pinus*).

After this preliminary filtering process, 138 relevés were left to be verified in the field. As the "old" vegetation relevés were mainly from mature forests in the optimal stage, many of them had obviously been managed since the first survey. The selection of plots for resurvey was restricted to stands without obvious traces of recent management, so that changes in species composition would reflect only environmental change and not effects of management. Finally, 37 "old" relevés scattered along the east-west transect through Switzerland could be resurveyed (Fig. 1). The data set included relevés from Etter (1947), Trepp (1947), Moor (1952), Fritschi (1956), Richard (1961), Etter & Morier-Genoud (1963), Frehner (1963) and unpublished relevés from W. Lüdi, F. Klötzli, R. Kuoch, J.-L. Richard and A. Schläfli.

FIELD SURVEY

The resurvey in the field was carried out in June 1998 on plots of same size and with the same methodology as the "old" relevés. Thus, plot size ranged from 100 to 400 m^2. Within each plot the species composition was recorded separately for the herb, shrub and tree layer and the cover of each species within each layer was assessed visually according to the Braun-Blanquet method (Braun-Blanquet 1964).

DATA ANALYSIS

Changes in species composition within each vegetation layer were determined by comparing pairs of old and new relevés. For the analysis of species changes, only the presence or absence of species was considered, regardless of cover values. The number of sites in which a species had appeared (absent in the old relevé, present in the new one) or disappeared (present in the old relevé, absent in the new one) was taken as a measure of the species' change in frequency.

To display shifts in species composition for the entire data set, Principal Coordinates Analysis (PCoA) was performed with the statistical package Mulva-5 (Wildi & Orloci 1996). For this analysis the Braun-Blanquet codes were transformed into cardinal numbers (r–>1, +–>2, 1–>3, 2–>4, 3–>5, 4–>6, 5–>7), followed by square-root transformation. Resulting values were normalised by relevés (each relevé vector being adjusted to unit length). Species occurring in more than one vegetation layer entered the analysis several times as "different" species. PCoA was based on a similarity matrix of relevés with "van der Maarel's coefficient" (Wildi & Orloci 1996) as measure of similarity.

To interpret vegetation change in terms of changing environmental factors, weighted average ecological indicator values were calculated for all old and new relevés using indicator values and the calculation method given by Landolt (1977). Species occurring in several layers were represented by their maximum value. In addition, the relative importance of the different life forms (in %) was calculated as number of species with a given life form divided by the total number of species

Table 1. *Species of which the frequency decreased between old and new relevés, with the number of sites where the species occurred in both old and new relevés, only in new relevés or only in old relevés, and the resulting change in frequency. Indications on the ecology of species (in parantheses) are based on Landolt (1977); see legend in Table 2.*

Species (layer + species for woody plants)	Nr. of sites with the species present in: old and new relevés	new relevés only	old relevés only	Net change in frequency (Nr. of sites)	Species (layer + species for woody plants)	Nr. of sites with the species present in: old and new relevés	new relevés only	old relevés only	Net change in frequency (Nr. of sites)
S-*Rosa* sp.*	2		21	**-21**	*Helleborus foetidus*			6	**-6**
Solidago virga-aurea [F]	4		18	**-18**	*Platanthera bifolia* [A]			6	**-6**
Hieracium murorum [F]	3	1	17	**-16**	*Primula vulgaris*			6	**-6**
S-*Cornus sanguinea*	3	1	16	**-15**	*Ranunculus ficaria* [B]			6	**-6**
T-*Quercus* sp.	15		14	**-14**	S-*Fraxinus excelsior* *	6	5	10	**-5**
Phyteuma spicatum	10	2	15	**-13**	*Euphorbia dulcis*	5	4	9	**-5**
S-*Viburnum lantana* *	5		13	**-13**	S-*Prunus avium*	4	3	8	**-5**
S-*Viburnum opulus* *	1	3	15	**-12**	S-*Corylus avellana*	10	2	7	**-5**
Ajuga reptans	3	2	14	**-12**	H-*Ulmus scabra*	4	2	7	**-5**
S-*Crataegus* sp.*	11		12	**-12**	*Geum urbanum* [B]	2	2	7	**-5**
Neottia nidus-avis [C]			12	**-12**	*Melica nutans* [A]	4	1	6	**-5**
Viola silvestris	16	2	13	**-11**	*Primula elatior* [B]	4	1	6	**-5**
Vicia sepium [C]	5	2	13	**-11**	S-*Sorbus aucuparia*			5	**-5**
Carex flacca	6	1	12	**-11**	*Knautia silvatica*			5	**-5**
S-*Ligustrum vulgare* *	11		11	**-11**	*Mycelis muralis* [B/C]			5	**-5**
H-*Prunus avium*	4	6	16	**-10**	S-*Fagus silvatica*	18	4	8	**-4**
Geranium robertianum [B/C]	1	1	11	**-10**	*Poa nemoralis* [A]	2	4	8	**-4**
T-*Pinus silvestris*	4		10	**-10**	*Carex montana* [A]	4	3	7	**-4**
S-*Daphne mezereum*	1		10	**-10**	*Glechoma hederaceum*		2	6	**-4**
Veronica officinalis [A]			10	**-10**	S-*Rubus fruticosus* agg.	4	1	5	**-4**
S-*Lonicera xylosteum* *	16	2	11	**-9**	*Aegopodium podagraria* [B]	4	1	5	**-4**
S-*Evonymus europaea* *		1	10	**-9**	S-*Picea excelsa*	2	1	5	**-4**
Fragaria vesca [C]	8		9	**-9**	*Carex digitata*	8		4	**-4**
S-*Quercus* spec.			9	**-9**	*Vaccinium myrtillus* [A]	4		4	**-4**
T-*Prunus avium*	2	3	11	**-8**	S-*Clematis vitalba*	1		4	**-4**
S-*Abies alba*	4	2	10	**-8**	*Melampyrum pratense* [A]	1		4	**-4**
T-*Carpinus betulus*	7	1	9	**-8**	S-*Rhamnus cathartica*			4	**-4**
Melittis melissophyllum [C]	5	1	9	**-8**	S-*Rubus idaeus*			4	**-4**
S-*Prunus spinosa*	3		8	**-8**	*Luzula forsteri* [D]			4	**-4**
S-*Sorbus torminalis*	1		8	**-8**	H-*Abies alba*	9	4	7	**-3**
Sanicula europaea [F]	1		8	**-8**	T-*Acer pseudoplatanus*	8	3	6	**-3**
Potentilla sterilis			8	**-8**	S-*Sorbus aria*		3	6	**-3**
Luzula pilosa [A]	3	3	10	**-7**	*Polygonatum multiflorum*	20	2	5	**-3**
Lathyrus vernus	3	2	9	**-7**	*Pulmonaria* sp.	7	1	4	**-3**
T-*Picea excelsa*	7	1	8	**-7**	*Lilium martagon* [F]	1	1	4	**-3**
Prenanthes purpurea [F]	4	1	8	**-7**	T-*Sorbus aria*		1	4	**-3**
T-*Acer campestre*	3	1	8	**-7**	*Actaea spicata* [F]	2		3	**-3**
S-*Tamus communis* [C/D]	1		7	**-7**	T-*Larix decidua*	1		3	**-3**
Scilla bifolia [C]			7	**-7**	T-*Tilia cordata*	1		3	**-3**
Brachypodium silvaticum	11	2	8	**-6**	S-*Daphne laureola* [D]	1		3	**-3**
T-*Abies alba*	6	2	8	**-6**	*Lathyrus montanus* [A]	1		3	**-3**
Cephalanthera damasonium [A]	1	1	7	**-6**	S-*Coronilla emerus* [C]			3	**-3**
T-*Ulmus scabra*	5		6	**-6**	*Angelica silvestris*			3	**-3**
Luzula nemorosa [A]	4		6	**-6**	*Aquilegia vulgaris*			3	**-3**
Bromus benekenii	2		6	**-6**	*Campanula trachelium* [C]			3	**-3**
Majanthemum bifolium [A]	2		6	**-6**	*Dryopteris austriaca*			3	**-3**
Pteridium aquilinum [A/C]	1		6	**-6**					

***Table 2.** Species of which the frequency increased between old and new relevés, with the number of sites where the species occurred in both old and new relevés, only in new relevés or only in old relevés, and the resulting change in frequency. Indications on the ecology of species (in parantheses) are based on Landolt (1977)*

Species (layer + species for woody plants)	Nr. of sites with the species present in: old and new relevés	new relevés only	old relevés only	Net change in frequency (Nr. of sites)
H-*Ligustrum vulgare* *	1	15		**15**
H-*Lonicera xylosteum* *		13		**13**
H-*Crataegus* sp.*		15	3	**12**
H-*Acer pseudoplatanus*	11	10		**10**
H-*Ilex aquifolium* [D]		10		**10**
H-*Fraxinus excelsior* *	18	11	2	**9**
H-*Viburnum lantana* *	1	10	1	**9**
H-*Rosa* sp.*	3	9	2	**7**
H-*Viburnum opulus* *	1	8	1	**7**
H-*Corylus avellana*	1	8	2	**6**
H-*Evonymus europaea* *		6		**6**
H-*Prunus laurocerasus* [E]		6		**6**
H-*Rubus fruticosus* agg.	8	9	4	**5**
Circaea lutetiana [B]	2	6	1	**5**
Dryopteris filix-mas [B]	3	7	3	**4**
H-*Acer platanoides*	2	6	2	**4**
Anemone nemorosa	19	5	1	**4**
Athyrium filix-femina	3	5	1	**4**
H-*Tilia platyphyllos*		4		**4**
Dryopteris dilatata [B]		4		**4**
S-*Acer pseudoplatanus*	7	5	2	**3**
H-*Fagus silvatica*	23	4	1	**3**
S-*Pyrus piraster*		3		**3**
H-*Cornus sanguinea*		3		**3**

Species (layer + species for woody plants)	Nr. of sites with the species present in: old and new relevés	new relevés only	old relevés only	Net change in frequency (Nr. of sites)
H-*Rubus caesius*		3		**3**
H-*Sambucus nigra* [B]		3		**3**
Dryopteris spinulosa		3		**3**
Impatiens parviflora [B]		3		**3**
T-*Hedera helix* [D]	3	5	3	**2**
S-*Ulmus scabra*	3	4	2	**2**
H-*Daphne mezereum*		4	2	**2**
S-*Lonicera periclymenum*	1	3	1	**2**
Carex pendula [B]	1	2		**2**
T-*Corylus avellana*		2		**2**
T-*Ilex aquifolium* [D]		2		**2**
S-*Evonymus latifolia*		2		**2**
S-*Prunus laurocerasus* [D/E]		2		**2**
H-*Juglans regia*		2		**2**
H-*Prunus* sp.		2		**2**
H-*Prunus spinosa*		2		**2**
Carex remota [B]		2		**2**
Urtica dioeca [B]		2		**2**
Single occurrence of exotic species:				
H-*Viburnum rhytidophyllum* [D/E]		1		**1**
S-*Lonicera japonica* [D/(E)]		1		**1**
S-*Mahonia aquifolium* [D/E]		1		**1**

Legend:

H = herb layer
S = shrub layer
T = tree layer

* = increase compensated by decrease in an other layer

[A] = species of nutrient-poor sites
[B] = species of nutrient-rich sites
[C] = heliophilous species
[D] = thermophilous species
[E] = exotic laurophyllous species
[(E)] = semi-evergreen broad-leaved species
[F] = (sub-) montane species

per relevé. Differences between means of old and new relevés were tested with Wilcoxon signed ranks test.

Finally, to interpret the ordination plot yielded by PCoA, Spearman rank correlations were calculated between the first two PCoA-axes and average ecological indicator values as well as geographic coordinates of relevés.

Results

Considerable change occurred at the species level between 1940–1965 and 1998. Out of the total of 241 species, 184 became less frequent or disappeared completely, while only 44 species increased or occurred newly in 1998, and 13 species showed no change in frequency. The number of species per relevé increased in 5 plots only, and decreased in all other plots. As a result the mean (± s.e.) number of species per relevé decreased from 41.0 ± 2.5 to 25.9 ± 1.2. Tendencies of individual species to increase or to decrease were related to their ecological requirements (according to Landolt 1977, see character supplements in Tables 1 and 2). Species characteristic of nutrient-poor sites (A) showed a decreasing tendency, whereas species characteristic of nutrient-rich or moist conditions (B) mostly increased. Several light-demanding species (C) declined, whereas thermophilous species (D) rather increased. In addition, some exotic evergreen broad-leaved species (E) were found for the first time in forest relevés in the investigated areas in 1998. By contrast, several (sub-)montane species (F) showed a decreasing trend.

The general trend of vegetation change at the investigated sites is reflected by PCoA (Fig. 2). The first axis represents 8.6% of the total variance and is positively correlated with average indicator values for reaction (r_s=0.81) and light (r_s=0.51) but negatively correlated

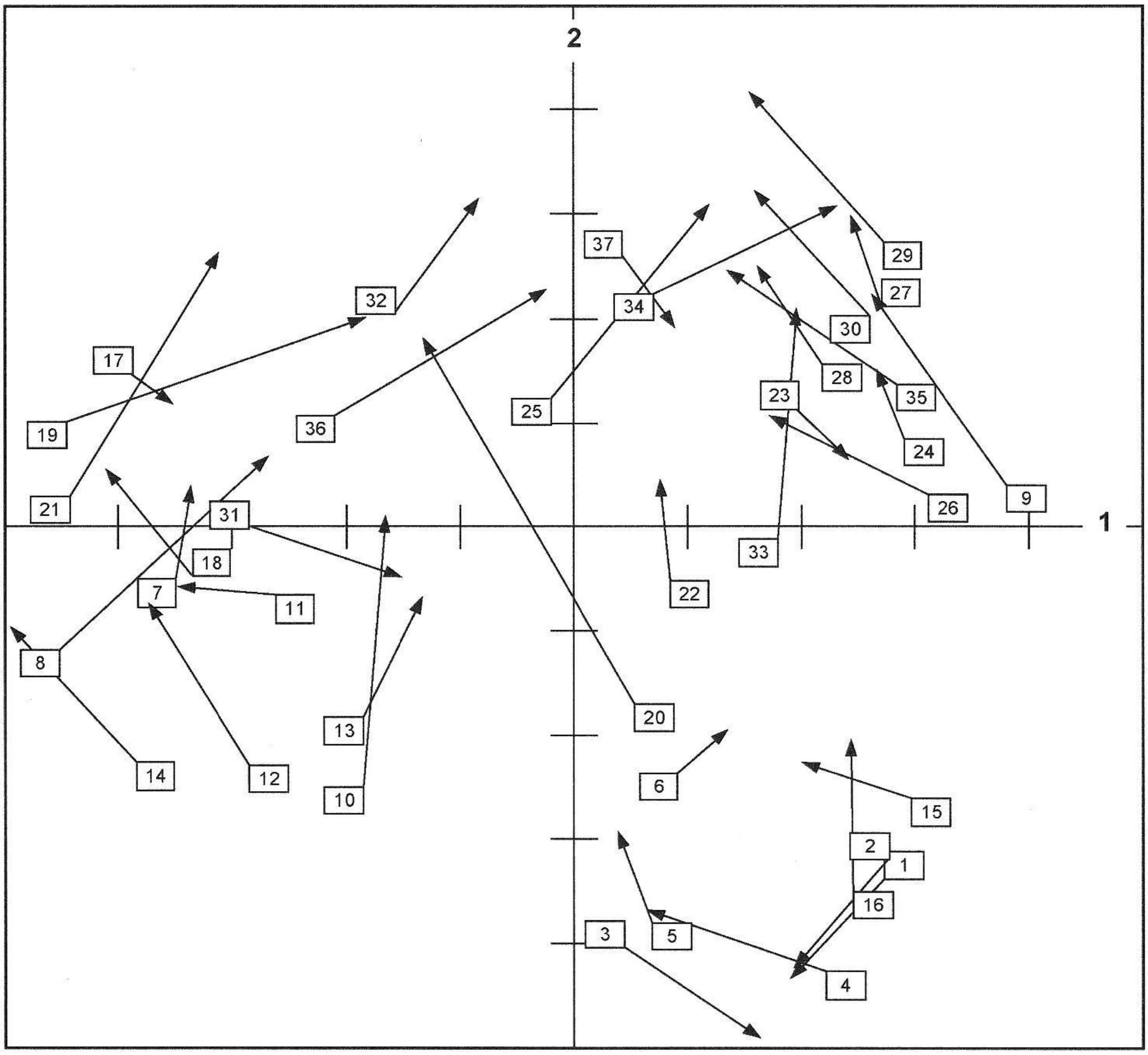

Fig. 2. *Ordination plot of relevés with the first and second axis of Principal Coordinates Analysis. Each of the 37 investigated sites is represented by an arrow, with the old relevé at the bottom and the new relevé at the top; numbers correspond to site numbers in Fig. 1.*

Table 3. Differences (a) in average ecological indicator values and (b) in growth or life forms between old relevés (1940–1965) and new relevés (1998). Data are means ± s.e. for 37 sites and P-values of the Wilcoxon signed rank test; only indices with significant differences are shown

	Old relevés	New relevés	*P*
(a) Average ecological indicator values			
Humidity value	2.89 ± 0.03	2.98 ± 0.03	0.002
Nutrient value	2.86 ± 0.04	2.95 ± 0.03	0.005
Dispersion value	3.91 ± 0.02	3.97 ± 0.02	0.009
Light value	2.29 ± 0.05	2.21 ± 0.05	0.025
Temperature value	3.34 ± 0.02	3.43 ± 0.03	0.001
Continentality value	2.67 ± 0.02	2.58 ± 0.02	0.000
(b) Proportion of growth or life forms [%]			
Evergreen phanerophytes	4.7 ± 0.6	10.3 ± 1.4	0.000
Deciduous nanophaneropyhtes	17.5 ± 1.6	21.0 ± 2.2	0.026
Hemicryptophytes	37.1 ± 2.2	27.9 ± 2.3	0.001

with the humus value (r_s=–0.71). The second axis (6.9% of total variance) correlates positively with average indicator values for humidity (r_s=0.57), nutrients (r_s=0.42) and humus (r_s=0.44), and negatively with the light value (r_s=–0.66) and the temperature value (r_s= –0.49). In addition, the second axis is correlated with geographic coordinates of sites (r_s=0.78 with latitude and 0.73 with longitude), which reflects a geographical gradient within the set of relevés. For most of the 37 sites a shift occurred along the second axis, new relevés having generally higher values than old relevés (see Fig. 2).

Compared across the whole data set (74 relevés), average nutrient and humidity indicator values were positively correlated with each other (r_s=0.87), and so were light and temperature indicator values (r_s=0.56). The humus indicator value was negatively correlated with the light value (r_s=–0.83), the reaction value (r_s=–0.78) and the temperature value (r_s=–0.61). The pairwise comparison of average indicator values between old and new relevés revealed a number of significant differences which suggested that the forest vegetation changed towards moister conditions with increased nutrient but decreased light availability, higher temperature and reduced continentality (Table 3a).

In terms of life forms, the main change between old and new relevés was a significant increase of evergreen phanerophytes, whose contribution to total vegetation cover more than doubled. Deciduous nanophanerophytes also increased, whereas hemicryptophytes decreased (Table 3b).

Discussion

METHODOLOGICAL ISSUES

Permanent plots are often considered the best method to monitor long-term changes in species composition. Unfortunately, long-term forest monitoring on permanent plots started only a few years ago in Switzerland (Innes 1995). Hence, the repetition of vegetation relevés carried out years or decades ago without permanent marking of plots is the only available method for the analysis and interpretation of long-term changes in species composition at present. Thus, extensive information on the state of the forest in the first half of the 20th century is available in the WSL database of Swiss vegetation relevés (Wohlgemuth 1992) and was used for this study. The lack of permanently marked plots prevented a precise re-location of relevés, but thanks to coordinates and site descriptions given in the old relevés a good approximation could be achieved.

There is always the possibility that apparent changes in species composition are simply an artefact resulting from different methodologies. In our study, several shrub species increased in the herb layer while decreasing in the shrub layer (indicated by asterisks in Tables 1 and 2). These changes might simply reflect observer bias in the attribution of woody species to the different vegetation layers. An analogous problem is that minor changes in cover values may simply be due to different ratings of species cover by different authors. In this study the evaluation of changes at the species level only took into account the presence or absence of species. Thus, the observed shifts in species composition could hardly be due to observer bias, and could therefore be interpreted with reasonable confidence in terms of changes in habitat conditions.

CHANGES AT THE SPECIES LEVEL

In general, the species number per relevé was lower in the relevés of 1998 than in those of 1940–1965. Especially the more light demanding species have decreased, reflecting perhaps more mature forests with a more closed canopy. The decrease in species from nutrient-poor sites and increase in species from nutrient-rich sites corresponds to trends observed in a wide range of vegetation types (Ellenberg 1985; Klötzli 1986).

Although the shift of relevés along the second PCoA axis might suggest a trend towards lower temperature indicator values, a closer look at species composition rather suggests the opposite trend: the decreasing frequency of several montane species and the increasing frequency of thermophilous species, especially of evergreen broad-leaved exotic species (Table 2) strongly indicates a response of the vegetation to increasing temperature. This coincides well with the increasing expansion of exotic evergreen species that has been observed in other Swiss regions (Meduna *et al.* 1999; Walther 1999; Brodtbeck *et al.* 1997; Klötzli *et al.* 1996; Landolt 1993) and in Europe (e.g. Doyle 1999; Kovacevic 1998; Mazomeit 1995; Sukopp & Wurzel 1995). Obviously, the shift of relevés along the second PCoA axis must have been due to the decrease of light-demanding species and to the positive correlation between light and temperature indicator values across sites. This illustrates the difficulty of interpreting shifts along ordination axes when the latter are strongly correlated with more than one site factor (Philippi *et al.* 1998), and when they reflect both spatial and temporal variation, as was the case in our study.

In general, the changes in species and species groups mentioned above concur with the findings of Carraro *et al.* (1999) on a north–south transect across Switzerland, and this gives more confidence in their interpretation.

CHANGES AT THE ECOSYSTEM LEVEL

In this study inferences about changes in environmental conditions were derived from changes in average ecological indicator values between old and new relevés at the same location. In accordance with earlier investigations (e.g. Carraro *et al.* 1999 and references therein), results suggested three main trends:

- The forests investigated tended to more mesic conditions, as shown by increasing humidity and nutrient indicator values (Table 3). This change might simply reflect the natural regeneration cycle of forests with increasing age (see e.g. Fischer 1997). Alternatively, the change might be interpreted as a consequence of increased atmospheric inputs of nitrogen. However, both humidity and nutrient indicator values are strongly coupled, and the effects of the two site factors are therefore hard to disentangle.
- Light conditions in lower vegetation layers tended to deteriorate, probably due to a general ageing of the forest. The opposite trend might in principle have been expected because of a potential decrease in crown density due to aerial pollutants, but apparently the latter did not occur to any significant extent.
- Temperature indicator values increased on average between old and new relevés. In addition, the decline of montane species and the increase of thermophilous species, and in particular the new occurrence of exotic evergreen broad-leaved species point to warmer conditions. Indeed, a recent study comparing the meteorological conditions of the last thirty years with decades before 1960 showed an increasing trend for all permanent Swiss meteorological stations (Aschwanden *et al.* 1996).

The present study and the investigation of a north-south transect through Switzerland (Carraro *et al.* 1999) together provide a database of reasonable size for a trend analysis of vegetation changes in the last thirty years. The results can therefore be considered representative for a large part of Swiss lowland forest. The same trends are also likely to have occurred in other Central European forests with similar edaphic and climatic conditions.

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Received 6 December 2000
Revised version accepted 3 April 2001