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Retrospective assessment of frequency changes in Swiss bryophytes over the last two centuries

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We present a method that permits the retrospective assessment of frequency changes in species, based on the evaluation of specimens in biological collections. The method assumes that the increase and decrease in the frequency of a species is reflected in the number of collected specimens. A comparison of the specimen numbers from different time periods allows for an evaluation of the frequency changes of a particular species, provided that the specimen numbers are corrected for the general collecting activity of each time period. We used a reference data set consisting of 10 521 specimens of 85 species to reflect general collecting activity. For 42 species of bryophytes in Switzerland, we calculated the 'relative collecting activity', i.e. the number of specimens of an individual species as a percentage of the number of specimens from the reference data set. We examined changes in the relative collecting activity between the periods 1850-1939 and 1940-1999, using a permutation test. The calculated results were further assessed, taking all background information on each single species into account. In seven cases, the resulting assessments differed from the test results. According to the assessments, 16 species showed a decline and four had increased. The frequency of seven species was considered stable. For the remaining 15, mainly rare species, reliable assessments depend on further study of their former and actual frequencies. When species analysed were arranged into three classes of rare, medium and high frequency, the results showed that the rare and medium frequency species underwent significant decline, whereas the common species were stable. The fact that 12 species of medium or high frequency have most probably declined is of particular interest.

A central question in nature conservation is whether the frequency of a particular species is stable, decreasing or increasing. For example, assess the Red List status of a given species inclusion of information based on its frequency trends is of paramount importance (IUCN 2001). There are a number of different approaches for analysing frequency changes in species:

Search for populations that are known from former times

This has been done, for example, for the Species Action Plan for endangered bryophytes of Switzerland (Bisang and Urmi 1994, Urmi et al. 1997). The method has proved to be time consuming, particularly in the case of inconspicuous organisms like bryophytes. Furthermore, the locality information given on specimen labels is often not very precise and the ecology of many rare species is insufficiently known, which makes searching for them difficult. In addition, other reasons such as migration might account for the disappearance of a particular population in a particular place.

Permanent plots

Species occurrences are repeatedly surveyed at predetermined localities, as was done in a project started recently with the objective of monitoring biodiversity in Switzerland (Hintermann et al. 2002, www.biodiversitymonitoring.ch). Such approaches, however, require many years of intensive field work and will cover only a comparatively short time period.

Interpretation of distribution patterns

Wilson et al. (2004) showed that decreases and increases can be deduced from current species distribution alone, using occurrences in grid cells at two different spatial scales. They were able to relate declining species to sparse, fragmented current distributions for a certain distribution size, and expanding species to denser, more aggregated distributions. This approach does not require historical information. However, it remains unclear how naturally sparse (or aggregated, respectively) but stable distributions can be distinguished from distribution patterns resulting from range contractions or expansion processes.

Comparison of distribution data

In many cases historical data are available and provide a reliable basis for estimates of frequency changes in species. The data might be acquired from literature (Engler and Bauer 2002), biological collections (Reznick and Baxter 1994, Mac Dougall et al. 1998, Shaffer et al. 1998, Denys 2000, Hürlimann et al. 2001, Auderset Joye et al. 2002, Willis et al. 2003, Ungricht et al. 2004), or sometimes from other sources, such as documented observations from mapping projects or excursions (Arnolds 1997, Boujon 1997, Kirchhofer 1997, Vellinga 2000). Methods based on biological collections need to consider variations in collecting intensity over time in order to provide reliable information about frequency changes in nature (Stroot and Depiereux 1989, van Swaay 1990, Urmi 1992, McCarthy 1998, Burgman et al. 2000, Hedenäs et al. 2002).

In the present study we developed a method for assessing frequency changes based on herbarium collections of bryophytes in Switzerland. Our main interest lies in common species for which little is known about frequency changes and which were not included in conservation measures. Rare species were also included in this study, to allow for a comparison of frequency changes between rare and frequent species. The following questions were addressed:

1. Does the frequency of common bryophyte species in Switzerland change and if so, does it increase or decrease?
2. Can these changes be quantified?
3. Are frequency changes in common species different from those in rare ones?

Material and methods

Species selection and data basis

Forty-two species of hornworts, liverworts, and mosses were selected for analyses (Table 1, Fig. 2). The main criterion for selection of species was the presence of at least one-third of their populations on the Swiss Plateau (Fig. 3:1). Because this is the most intensively cultivated part of Switzerland, which has suffered the highest level of habitat destruction, we expect frequency changes in bryophytes to be particularly distinct. Additional criteria for species selection were: all main habitat types should be considered (woods, wetland, arable land, dry meadows, grassland, rocky places) and more or less equal numbers of common, medium frequent, and rare species should be surveyed.

The most important source of information on spatial and temporal distribution of bryophytes was the database of the inventory of Swiss bryophytes 'NISM' (Urmi et al. 1990), which is housed at the University of Zürich. This database, created in 1984, contains 89 798 records (July 2002) from different sources, of which ca 23 000 are historical records (collected before 1984). Recent records (collected 1984 and later) originate from systematic and non-systematic fieldwork that was conducted during the course of the 'NISM' project, and from two national surveys: the mire monitoring project (Grünig et al. 2004), and the biodiversity monitoring project (Hintermann et al. 2002). Historical records were mainly acquired by revising herbarium specimens. For this study we considered specimens from regional herbaria in Aarau, Altdorf, Frauenfeld, Winterthur, Schwyz, St. Gallen, Zug and from BAS, BERN, CHUR, G, LAU, LUG, NEU, NMLU, S, Z, ZT (abbreviations according to Holmgren and Holmgren 2001), as well as the private herbaria of the 'NISM' collaborators. All historical specimens were taxonomically verified.

Reference data set and preparation of data

We assume that the number of collected specimens in biological collections reflects increases and decreases of occurrences in nature. However, general collecting intensity varies with time, and the number of collected specimens of an individual species does not directly indicate changes of its frequency in nature. Collection numbers for individual species thus need to be compared with the general collecting activity of the respective organism group from the chosen area. As a measure of the general collecting activity we used a reference data set. Species of which all historic records were included in the 'NISM' database served as the basis for the reference data.

For the method chosen, the species and records of the reference data set must meet the following requirements: (1) the collection year of all records must be indicated; (2) the locality of all records should be roughly known to detect duplicates; (3) the records should be based on non-biased collecting; (4) all available specimens of each species should be included to equally represent all time periods and regions. Furthermore, the reference data set must contain enough records from the time periods to be analysed to allow for statistical analyses. The precise number depends on the targeted temporal resolution and the specific analysis method used (Hedenäs et al. 2002).

In order to implement these requirements we excluded the following records from the database specified above:

- records without collection year;
- records which could not be allocated to either a square kilometre, or a geographic unit of Switzerland (for the current mapping project ('NISM') 413 geographic units have been distinguished (Urmi and Schnyder 1996), each covering an area of approximately 100 km^2 with more or less homogenous geology and climate);
- duplicates from the same year and the same square kilometre or the same geographic unit; to prevent bias by multiple collections (e.g. by different people on the same excursion);
- records from systematic relevés for NISM (Urmi et al. 1990), mire monitoring (Grünig et al. 2004), and biodiversity monitoring (Hintermann et al. 2002), i.e. investigations for which all species in a predetermined area had to be collected. These records cannot be compared with records based on 'free collecting' (i.e. according to the interest of individual bryologists), because all species within the systematic relevé area have to be sampled (compare 'Assumption 3' below);
- records of species which are over- or underrepresented in a particular time period or a particular region. We used the "Kennarten-Index" in the programme VEGEDAZ (Küchler 2004) to identify species that are typical for categories, in our case space and time. This programme was originally designed to compare vegetation relevés, and the 'Kennarten-Index' is an algorithm that denotes species typical for groups of relevés;
- records before 1850, because the data basis for the period 1800 to 1849 was too poor for a statistical analysis (Fig. 1).

The resulting reference data set consists of 10 521 specimens from 85 species, from the period 1850 to 1999. Twenty-eight of the 42 study species were included among the reference taxa. For a complete list of reference species the reader is referred to Urmi et al. (in press).

Relative collecting activity

We calculated the 'relative collecting activity' of a particular species n for each decade d as the percentage of the number of specimens of this species of the number of specimens of the reference data set (1) (Eq. 1).

In a species with stable frequency, the relative collecting activity is expected to be more or less constant. If a species increases or declines, it should be collected proportionally more or less often than the reference data. Changes in the relative collecting activity therefore indicate frequency changes in nature, provided no other factors are involved (compare 'Assumptions' below). The latter has to be carefully evaluated for each individual species.

Groups of species with similar frequency

We grouped the species according to their number of specimens used for the statistical analysis (Table 1, 1850–1999). Species with less than 30 specimens were classified as rare, those with 30–119 specimens as medium frequent, and those with 120 or more specimens as common. In each group all specimens of the comprised species were treated as one sample and changes in the relative collecting activity were examined for each group. The classification seems doubtful for *Dicranella staphylina,* which is grouped as rare, although it was found 14 times in systematic relevés of the NISM and can therefore be expected to be rather common (Urmi and Schnyder 2000). However, for reasons of consistency we decided to retain the groups.

Statistical analysis

For each individual species and each frequency group we tested whether the relative collecting activity before 1940 (values of 9 decades, 1850–1939) differed from that since 1940 (values of 6 decades, 1940–1999) using a permutation algorithm (10 000 permutations), which is part of the programme VEGEDAZ (Küchler 2004). As the specimen data are not normally distributed, we tested the rank sums, instead of the means, of the relative collection activity per decade. The result-

$$\text{Relative collecting activity} = \frac{\text{number of specimens of species n per decade d}}{\text{number of specimens of reference data set per decade d}} \quad (1)$$

Table 1. Investigated species and numbers of specimens used for the statistical analysis and the diagrams; see Material and methods for classification of common, medium frequent, and rare species; p(1940): probability of error, calculated by a permutation test to determine whether the decade values of the relative collecting activity before 1940 differ significantly from those since 1940 (compare Fig. 2); dimension: dimension of change, means of relative collecting activity since 1940 divided by respective means before 1940 (values > 1 = increase, < 1 = decrease, compare Material and methods); change: changes of the relative collecting activity: – significant decrease, + significant increase, ns not significant, at $p < 0.05$; assessm.: critical assessment of the results: ↓ decreasing, = stable, ↑ increasing,? trend uncertain. See Material and methods for further details.

	Species	1850–1939	1940–1999	1850–1999	p(1940)	dimen-sion	change	assessm.
common	*Cinclidotus fontinaloides* (Hedw.) P.Beauv.	82	67	149	0.026	0.5	–	↓
	Homalia trichomanoides (Hedw.) Schimp.	151	112	263	0.011	0.5	–	↓
	Orthotrichum diaphanum Brid.	75	92	167	0.036	0.7	–	↓
	Bryum argenteum Hedw. subsp. *argenteum*	118	481	599	0.387	1.4	ns	=
	Dicranella heteromalla (Hedw.) Schimp.	141	222	363	0.486	1.0	ns	=
	Frullania dilatata (L.) Dumort.	115	449	564	0.025	1.9	+	=
	Metzgeria furcata (L.) Dumort.	68	281	349	0.094	1.6	ns	=
	Scapania nemorea (L.) Grolle	126	132	258	0.518	1.0	ns	=
	Trichocolea tomentella (Ehrh.) Dumort.	91	109	200	0.447	0.9	ns	=
	Lophocolea heterophylla (Schrad.) Dumort.	67	315	382	0.0002	2.8	+	↑
	Orthotrichum lyellii Hook. & Taylor	51	150	201	0.042	1.7	+	↑
	Scorpidium scorpioides (Hedw.) Limpr.	68	73	141	0.267	0.9	ns	?
medium frequent	*Anthoceros agrestis* Paton	17	66	83	0.342	2.1	ns	↓
	Buxbaumia viridis (Lam. & DC.) Moug. & Nestl.	77	32	109	0.015	0.2	–	↓
	Ephemerum serratum (Hedw.) Hampe aggr. (inkl. *E. minutissimum* Lindb.)	53	40	93	0,008	0.3	–	↓
	Fissidens grandifrons Brid.	44	7	51	0.006	0.2	–	↓
	Fissidens rufulus Bruch & Schimp.	33	12	45	0.019	0.3	–	↓
	Grimmia crinita Brid.	54	19	73	0.013	0.3	–	↓
	Orthotrichum scanicum Grönvall	36	2	38	0.0003	0.01	–	↓
	Phaeoceros laevis (L.) Prosk. subsp. *carolinianus* (Michx.) Prosk.	13	22	35	0.381	1.0	ns	↓
	Pogonatum nanum (Hedw.) P.Beauv.	60	4	64	0.004	0.1	–	↓
	Hyophila involuta (Hook.) Jaeg.	44	32	76	0.404	0.7	ns	=
	Cinclidotus danubicus Schiffn. & Baumgartner	9	31	40	0.170	1.5	ns	?
	Cinclidotus mucronatus (Brid.) Guim.	17	17	34	0.357	0.7	ns	?
	Cinclidotus riparius (Brid.) Arn.	47	44	91	0.002	0.4	–	?
	Lunularia cruciata (L.) Dumort.	23	41	64	0.463	1.1	ns	?
	Metzgeria temperata Kuwah.	7	37	44	0.080	2.3	ns	?
rare	*Acaulon muticum* (Hedw.) Müll.Hal.	22	4	26	0.023	0.2	–	↓
	Ephemerum recurvifolium (Dicks.) Boulay	9	1	10	0.006	0.03	–	↓
	Meesia longiseta Hedw.	20	0	20	0.002	0	–	↓
	Scorpidium turgescens (T. Jensen) Loeske	9	1	10	0.340	0.2	ns	↓
	Campylopus introflexus (Hedw.) Brid.	0	23	23	0.146	–	ns	↑
	Sphagnum fimbriatum Wilson	1	14	15	0.007	6.7	+	↑
	Acaulon triquetrum (Spruce) Müll.Hal.	6	6	12	0.340	0.7	ns	?
	Brachythecium campestre (Müll.Hal.) Schimp.	5	2	7	0.382	0.3	ns	?
	Brotherella lorentziana (Molendo) Loeske	0	13	13	0.011	–	+	?
	Buxbaumia aphylla Hedw.	13	10	23	0.170	0.4	ns	?
	Dicranella staphylina H.Whitehouse	2	14	16	0.268	1.5	ns	?
	Ephemerum cohaerens (Hedw.) Hampe	5	1	6	0.187	0.1	ns	?
	Ricciocarpos natans (L.) Corda	6	6	12	0.489	0.6	ns	?
	Scapania compacta (A.Roth) Dumort.	3	1	4	0.499	0.5	ns	?
	Seligeria carniolica (Breidl. & Beck) Nyholm	1	0	1	0.598	0	ns	?
	all species	1789	2985	4774				
	reference data set	3808	6713	10521				

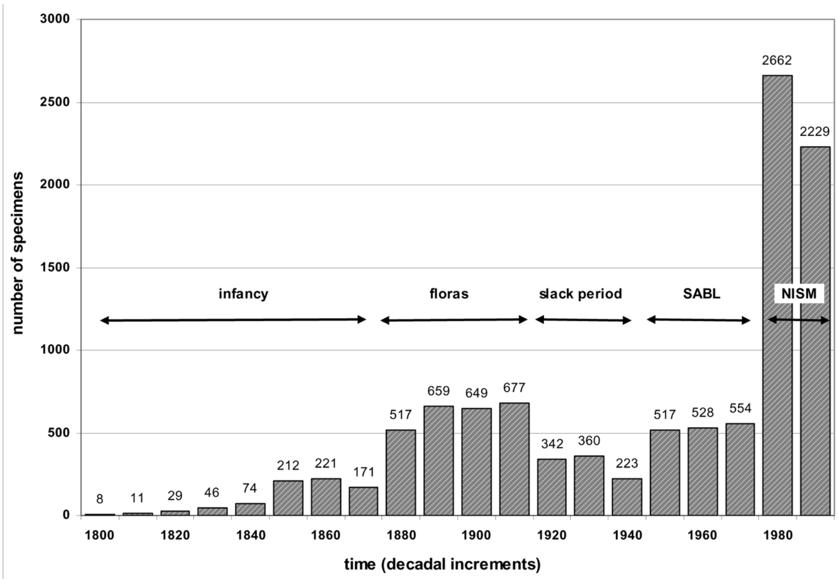


Fig. 1. General collecting activity in Switzerland from 1800 until 1999; data from 85 species with a total of 10 688 specimens. Data from 1850 to 1999 were used as reference data set (10 521 specimens); see Material and methods for further details. SABL = Swiss Association for Bryology and Lichenology; NISM = Swiss bryophyte mapping project.

ing p-values indicate the probability by which the respective distribution of the relative collecting activity before and since 1940 has occurred by chance. The beginning of 1940 was chosen as the time limit because many severe landscape changes, such as water pollution and drainage, took place before this time. Additional information about rank sum tests and permutation methods can be found in standard statistics textbooks (Stahel 1995).

Quantification of changes

To get an indication of the dimensions of the frequency changes in individual species, we calculated the quotient of the mean relative collecting activities of the six decades from 1940 to 1999 to the nine decades from 1850 to 1939 (Table 1) by Eq. 2.

We call this quotient "dimension of change". It indicates the scale and the direction of the changes (>1 increase, <1 decrease). For example, a value of 0.5 denotes that the proportional amount of specimens collected since 1940 was half of that in the period before 1940.

Final assessment of test results

The results were critically examined for each species on the basis of its ecology, habitat preferences, known changes in its habitat, distribution, susceptibility to environmental pollution, and any literature reports on frequency changes. The information considered is detailed in the species texts of the five example species (Results and discussion). Furthermore, we determined whether a species was at any time subject of a special investigation that would have raised the relative collecting activity, while leaving the frequency in nature unchanged. Special interests can be detected in the diagrams of the relative collecting activity (Fig. 2), where they produce peaks in a certain period during which most of the specimens were gathered by the same collector. Data from special investigations were not excluded, but their influence on the test result was evaluated (see *Example*: *Anthoceros agrestis*). In cases where we had strong evidence, based on our evaluations, that the number of collected specimens did not reflect the frequency in nature, the final assessments differ from the test results (seven cases).

Assumptions

The results of this investigation can be regarded as correct, if the following assumptions are true:

1. *The reference data set represents the general bryological collecting activity in Switzerland.*
   As the reference data set includes species of all taxonomic and all frequency classes and species that occur mainly in lower regions as well as those from

$$\text{Dimension of change} = \frac{\text{mean relative collecting activity of species n from 1940 to 1999}}{\text{mean relative collecting activity of species n from 1850 to 1939}} \quad (2)$$

higher altitudes, it can be regarded as a sample of the Swiss bryophyte flora, which represents the general collecting activity, independently of regional or other differences.

2. *There is no significant general decline of bryophytes.*
If all bryophytes were in decline, this would affect the reference data set and any comparison of a single species with the reference data set would be unreliable. For example, a species with constant relative collecting activity would then be interpreted as stable, although it would actually be decreasing in the same way as the reference data set. We consider the risk of such a methodical error to be negligible, as there is no indication of a general decline of bryophytes in Switzerland.

3. *The collecting behaviour of bryologists has not substantially changed.*
We believe that individual bryologists have certain but differing preferences in collecting (regarding species, regions, habitats, etc.), which can be described as the 'collecting behaviour' of a bryologist. Overall, however, all bryologists' visits in a certain area result in representative and unbiased collections of the species occurring in that area. Nevertheless, the collecting behaviour of bryologists can change under certain circumstances. Changes may be caused by (1) a new mapping method, (2) a special interest in a particular species, or (3) frequency changes in species, which may influence (2). (1) The aim of modern mapping methods is to treat all areas equally in order to obtain comparable data. Grid squares are often used as an objective basis for mapping. Each square is investigated, all species present are recorded, and voucher specimens are taken to check their identity. Such modern methods may lead to a drastic increase in specimens of common species and are distinctly different from former methods. In Switzerland this new mapping method was introduced in 1984 (Urmi et al. 1990). It implies that all bryophyte species in a given area at a given locality are sampled (systematic relevé). As specimens from systematic relevés are labelled, we were able to exclude them and thereby avoid a bias from common species due to a change in the mapping method. (2) A special interest in a particular species is easily detected as a peak in the diagrams of the relative collecting activity and was considered in the final assessment. (3) Frequency changes in species might also influence the number of collected specimens. If, for example, an easily recognized species becomes much more rare, it might be collected comparatively more often as bryologists will regard it as a special find. Such slow and general changes in the collecting behaviour are difficult to detect and remain a small source of uncertainty.

Results and discussion

The temporal distribution of the specimens of the reference data set gives a sense of the general collecting activity of bryophytes in Switzerland (Fig. 1). In the first half of the 19th century, bryological activity in Switzerland was minimal. From approximately 1880 until 1920, three bryologists, J. Amann, P. Culmann, and C. Meylan, collected bryophytes for their moss and hepatic floras of Switzerland (Amann et al. 1918, Meylan 1924). This can be seen in an increased general collecting activity during this period. In 1956 the Swiss Association of Bryologists and Lichenologists was founded, which again increased the general collecting activity slightly. A new era started in 1984 with the beginning of the Swiss bryophyte mapping project (NISM). Since then, more than four times as many specimens were collected per decade than previously.

Table 1 lists all species investigated, along with the number of specimens for the two study periods, the results of the permutation test (p(1940) and change), the dimension (i.e. a rough quantification) of the changes, and the final assessments, after considering all known information. The species have been grouped according to their frequency (1850–1999) and within groups according to the assessed trend in frequency changes. A diagram of the relative collecting activity for each species is presented in Fig. 2.

For the discussion, we distinguished five groups of individual species with similar trends in frequency alterations over time. For each group, we describe one example species in detail. In the species texts and the distribution maps (Fig. 3), we consider all available specimens for the particular species. The specimen numbers are therefore higher than those used for the statistical test (Table 1) and for the diagrams of the relative collecting activity (Fig. 2), from which some specimens were excluded (see Reference data set and preparation of data). Subsequently, we present the results of frequency changes as groups of rare, medium frequent and common species.

For a more detailed account of frequency changes in Swiss bryophytes, including comprehensive discussions of all investigated species, the reader is referred to Urmi et al. (in press).

I. Declining species – results of statistical analysis and assessments corresponding

Three rare and ten medium frequent or common species show a significant decline in the relative collecting activity, which, after consideration of all known background information, most probably reflects a decline in nature (Table 1: change –, assessment ↓). Neither the hornworts nor liverworts belong to this group.

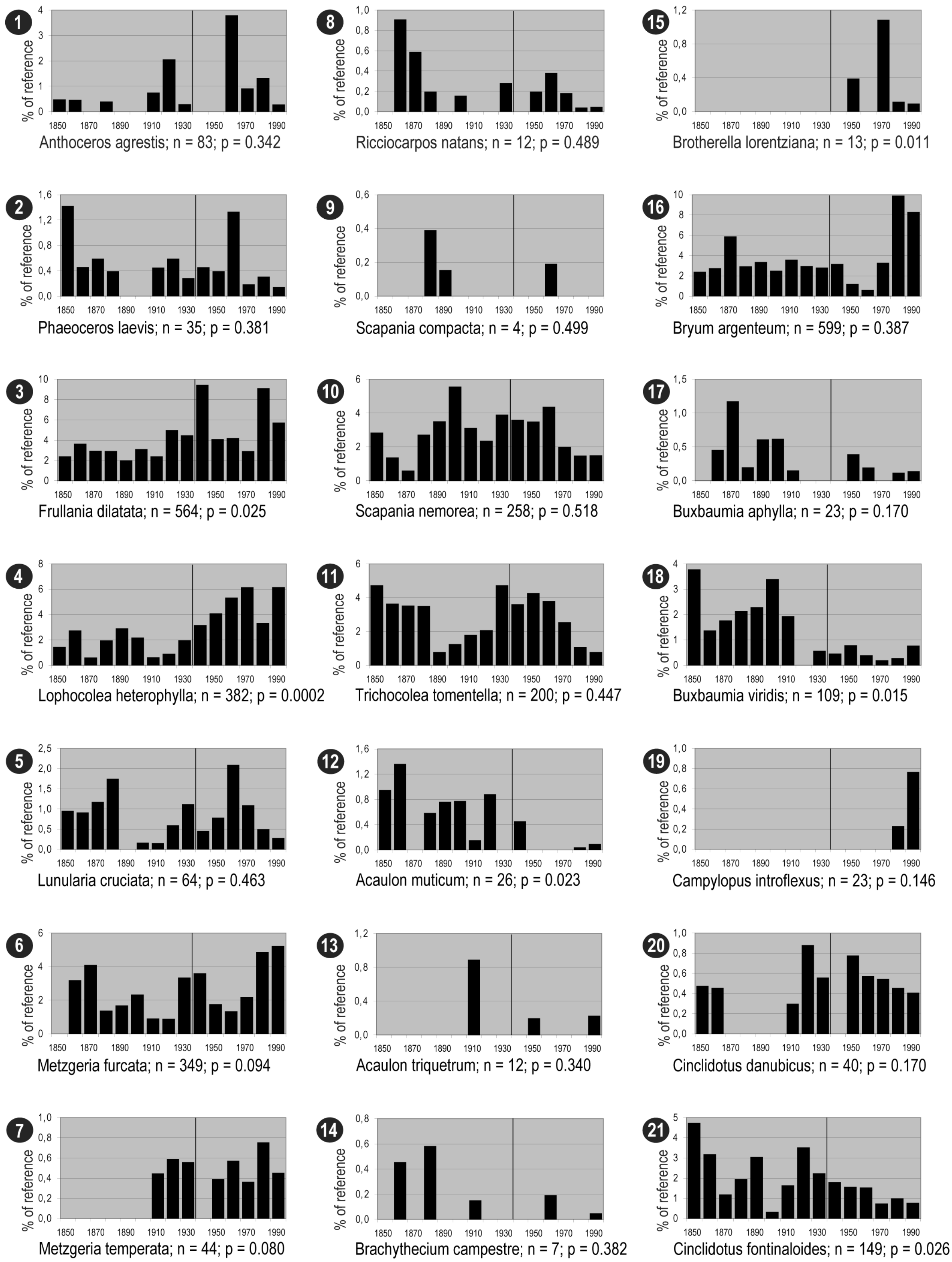
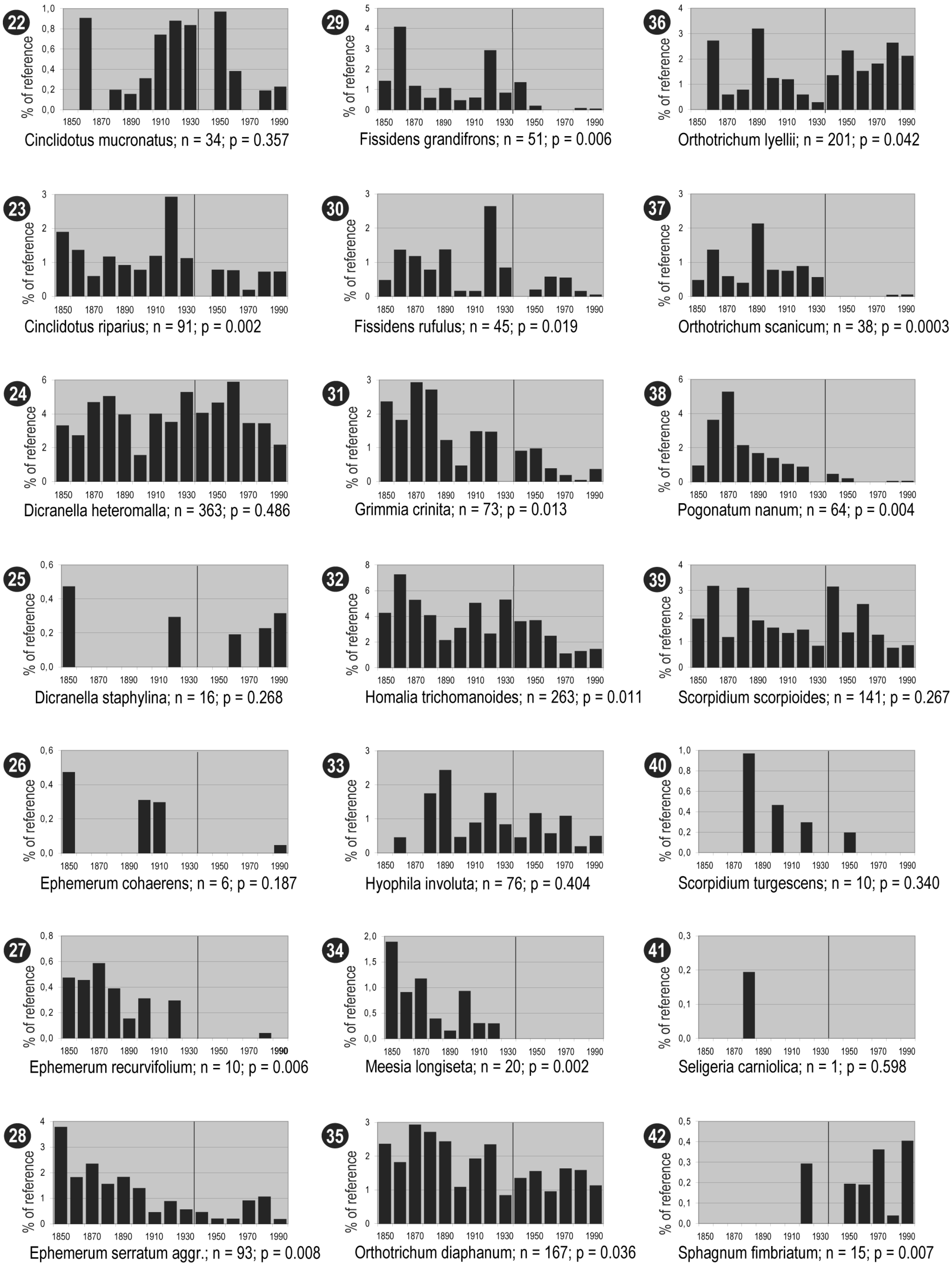


Fig. 2. Relative collecting activity of the investigated species (= the number of specimens of an individual species as a percentage of the number of specimens from the reference data set, calculated for each decade; Y-axes) as a function of time



(decadal increments; X-axes); p = result of the permutation test, probability of which the values before and since 1940 differ by chance. Note the different scales on the Y-axes.

Example: Homalia trichomanoides
Homalia trichomanoides occurs in Switzerland mainly in the Plateau (70% of all records) and the Jura Mountains (Fig. 3:2). It is comparatively rare in the Alps, and is mainly found at altitudes below 800 m. Above that altitude it becomes rare, with the highest record from 1540 m. With more than 400 records and 31 records from systematic relevés it is considered a common species.

Most of the populations grow on base-rich bark of ash, maple, elm, and beech. It can usually be found on the trunk base and bare roots of trees in forests with fairly high humidity. Much more rarely it grows on base-rich rocks and soil.

The diagram shows a clear decline in the relative collecting activity of this species, which is statistically significant (Fig. 2:32). The mean of the relative collecting activity since 1940 has decreased considerably to only half the amount before 1940 (Table 1: dimension). We also observed a clear reduction in fertility, which was confirmed by Born and Jordi (2005): whereas before 1940 82% of the specimens bore sporophytes, the proportion with sporophytes since 1940 was only 42%. This might be an expression of reduced vitality. Since we are not aware of other reasons that would explain this trend, we conclude that the species is indeed declining in nature. A decline of *Homalia trichomanoides* has also been discussed by Ahrens (2001) for Baden-Württemberg and Preston (1994) for southeast England. Sjögren (1995) on the other hand, found only a small decline of *H. trichomanoides* on boulders in Sweden, where the number of patches was nearly stable and only patch size was found to be decreasing slightly. However, the species might perform differently on tree trunks, which is its main substrate in Switzerland. Possible reasons for a decline in Switzerland are (1) an increase in acid rain, which causes the acidification of bark and has a strongly negative effect on epiphytes that prefer high pH values (Hallingbäck 1989, Sjögren 1995), such as *H. trichomanoides* (Düll 1991); (2) fertilization through nitrogen deposition, which promotes the spread of competitors like *Hypnum cupressiforme* (Stetzka 1994), at the cost of less competitive species.

Homalia trichomanoides is still a common species, and can be found in many localities in Switzerland in quite large populations. Urgent conservation measures are therefore not required. However, the populations should be monitored to detect future changes in frequency.

II. Declining species – results of statistical analysis and assessments not corresponding

Three species, the medium frequent hornworts and the rare *Scorpidium turgescens* are probably declining, although the statistical tests are not significant (Table 1: change ns, assessment ↓). In *Scorpidium turgescens* the specimen numbers are too low to give significant results. However, a decline is visible in the diagram (Fig. 2:40) and is supported by two facts: its habitat has suffered great losses and the species has not been re-located at several known sites. With respect to the hornworts, we know that the collecting activity was influenced by a special scientific interest (see example below). The test results therefore do not reflect the actual situation in nature.

Example: Anthoceros agrestis
Anthoceros agrestis has its main distribution in the Plateau, with 87% of all records. It also occurs rarely in Ticino Canton and the Jura Mountains (Fig. 3:3). It is restricted to lower altitudes between 200 and 1100 m, with two-thirds of the populations between 400 and 700 m. A total of 113 records are known, of which two are from systematic relevés. In this investigation it has been classified as a species of medium frequency.

In Switzerland it grows mainly in arable fields, where it prefers slightly acidic, loamy or sandy soil. It is predominantly found in autumn, after the crop has been harvested and light conditions and humidity are favourable for its development.

The diagram shows a strongly fluctuating relative collecting activity, but no significant change since 1940 was revealed (Fig. 2:1). The mean of the relative collecting activity has risen 2.1 times (Table 1: dimension). The trend towards increasing collecting activity since 1940 is mainly due to a particular interest in this species by Albrecht-Rohner in the 1960s (Albrecht-Rohner 1969) and Bisang in the 1980s (Bisang 1992, 1995, 1998). Both collected more than half of the specimens during their respective decades. On the other hand, we have evidence from older publications that the species was under recorded at the beginning of the 20th century (Bisang 1992, Urmi et al. 1993). With this background information it becomes obvious that the relative collecting activity before 1940 is too low, whereas it is too high after 1940 to reflect the situation in nature. In this case we have good evidence to conclude that *A. agrestis* is not stable, but is rather decreasing in Switzerland.

III. Increasing species

For three species (*Lophocolea heterophylla, Orthotrichum lyellii, Sphagnum fimbriatum*) the statistical analysis demonstrates a significant increase, which is in accordance with the assessment including background information (Table 1: change +, assessment ↑). Whereas *Lophocolea heterophylla* and *Orthotrichum lyellii,* were

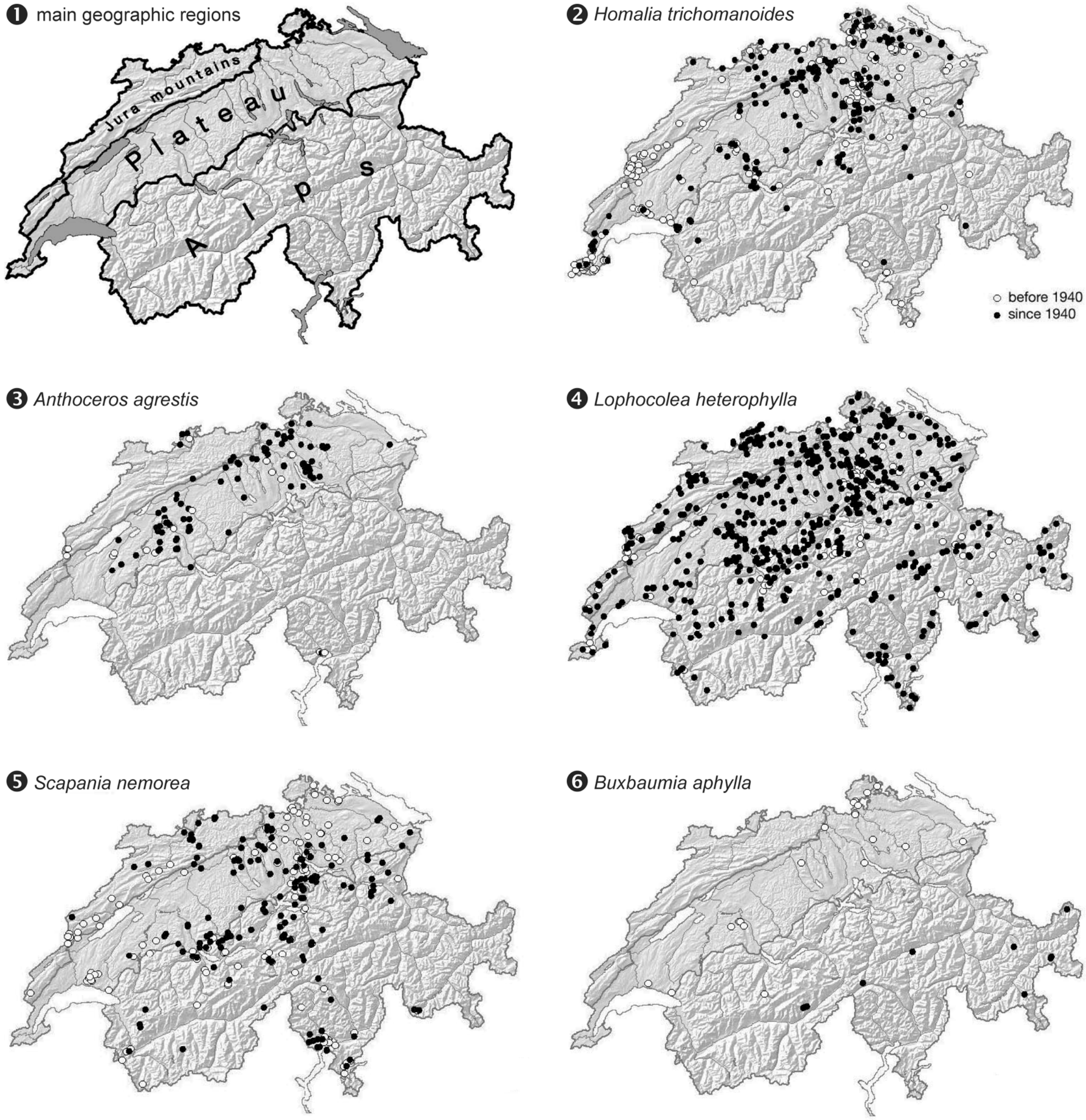


Fig. 3. Main geographic regions of Switzerland (according to Gutersohn 1973, modified) and distribution maps of the example species.

fairly frequent or even common in former times, *Sphagnum fimbriatum* is a rare species, which has only recently been found more often in Switzerland. It is also on the increase in some other European countries, such as Austria (Schröck and Krisai 1999), Germany (Paul 1997), and Hungary (Szurdoki and Ódor 2004). Its population dynamics in Europe (Szövenyi et al. 2006) as well as its population genetics (Itten 2006) are the subject of current investigations.

In addition, an increase in frequency is confirmed for *Campylopus introflexus*. It is a neophyte, which was first found in Europe in 1941 and is still spreading (Richards 1963, Frahm 1972). The first record from Switzerland dates from 1980.

Example: Lophocolea heterophylla

Lophocolea heterophylla can be found in all regions of Switzerland, except the highest parts of the Alps and the driest regions of Valais Canton (Fig. 3:4). Forty-six per cent of the specimens were collected from the Swiss Plateau. Its altitudinal range reaches from 200 to 2200 m, with three quarters of the specimens found between 200 and 1200 m. Based on the results of ca 1000 systematic relevés, we know that *Lophocolea heterophylla*, with 135 findings, is the most frequent liverwort in Switzerland (Urmi and Schnyder 2000). This is also reflected in the total of ca 770 specimens included in the study.

Its main substratum is rotten wood. It can be found in all types of forests, on dead stumps, logs, and branches, much more rarely on soil and rocks, and as an epiphyte.

The relative collecting activity since 1940 is significantly higher than before 1940 (Fig. 2:4). The mean relative collecting activity has risen 2.8 times (Table 1: dimension). It is very likely that this increase is due to an increase of *L. heterophylla* in nature, as was also observed by Sjögren (1995), who suggested that *L. heterophylla* benefits from acidic precipitation as it prefers substrata with pH below 5.5. Another possible explanation for its increase is a change in forest management. At the beginning of the 20th century, it was general practise to gather firewood from forests, which drastically reduced the amount of rotten wood (Bürgi 1998). In the second half of the 20th century, heating with oil or gas became more and more convenient and fallen wood was left in the forest. This offered plenty of new substrates for *Lophocolea heterophylla*. Moreover, its growth is promoted by airborne fertilization, as has been shown by Dirkse and Martakis (1992). *Lophocolea heterophylla* is a common species, which is favoured by environmental changes.

IV. Species with stable frequency

Seven species, three mosses and four liverworts, are considered as not having experienced frequency changes between the investigated time periods (Table 1: assessment =). Nearly all species are common, only *Hyophila involuta* is of medium frequency. For *Frullania dilatata* the assessment differs from the test result, which reveals a significant increase in the relative collecting activity. We believe that the latter is a consequence of detailed investigations on its distribution and ecology (Bisang 1985, 1987).

In 13 other species, which do not show significant changes, the lack of significance cannot be interpreted as stability because these species are represented by too few records (Table 1: change ns, assessment ?).

Example: Scapania nemorea
Scapania nemorea is widespread in Switzerland and occurs in the Jura Mountains, the Plateau (42% of all populations), and the Alps, except in the dryer central valleys (Fig. 3:5). It is frequent between 300 and 1400 m, with the highest record from 2000 m. *S. nemorea* was found seven times in a systematic relevé and is common in Switzerland, with a total of more than 300 specimens.

It grows on a number of different acidic substrates, usually in rather humid habitats like woods and ravines, but also rarely in more open places like marshes. It is most frequently found on loamy or peaty soil, boulders, rocks, walls, and rotten wood.

The relative collecting activity shows slight ups and downs but overall seems to be stable and without a significant trend (Fig. 2:10). The means of the relative collecting activity are equal (Table 1: dimension) indicating constant proportional specimen numbers. This seems to reflect the situation in nature, as this species occurs in habitats that were not much influenced by major environmental changes. Furthermore, we are not aware of any other factor that could have influenced the relative collecting activity, i.e. special scientific interest, or change in collecting behaviour. We therefore conclude that the frequency of *Scapania nemorea* has not changed in the last 150 years.

V. Species with uncertain frequency changes

For 15 mainly rare species, the data are not sufficient to either detect a clear trend, or to be certain of the stability of their frequency (Table 1: assessment ?).

Example: Buxbaumia aphylla
There are scattered records of *B. aphylla* from the Plateau, the edge of the Jura Mountains, and the Alps (Fig. 3:6). More than half of the total of 28 specimens were gathered from the Swiss Plateau. Because there are less than 30 finds, of which only one was made in a systematic relevé (gametophyte only!, Urmi 1996), it is classified as a rare species. Its altitudinal range extends from 400–800 to 1600–2200 m.

Buxbaumia aphylla grows in open places in sparse forests, forest edges, and dwarf shrub communities, usually on base-poor soil. The tiny gametophyte grows within the substratum and is more or less colourless, so that it is therefore usually only found if it bears sporophytes.

The relative collecting activity shows a decreasing tendency that is not statistically significant, probably due to the many zero values (Fig. 2:17). However, the mean relative collecting activity has decreased considerably to less than half the amount (Table 1: dimension) and no finds have been made in the Swiss Plateau since 1940 (Fig. 3:6). Forestry changes may account for a potential decrease of the species in the Plateau: woods have become darker and bare soil is rather rare because litter gathering is no longer practised (Bürgi 1998). Atmospheric nutrient input might also be a problem since it promotes more competitive species. Finally, environmental changes might lead to a reduction in fertility (Wiklund 2003, Greven 1992, Rao 1982),

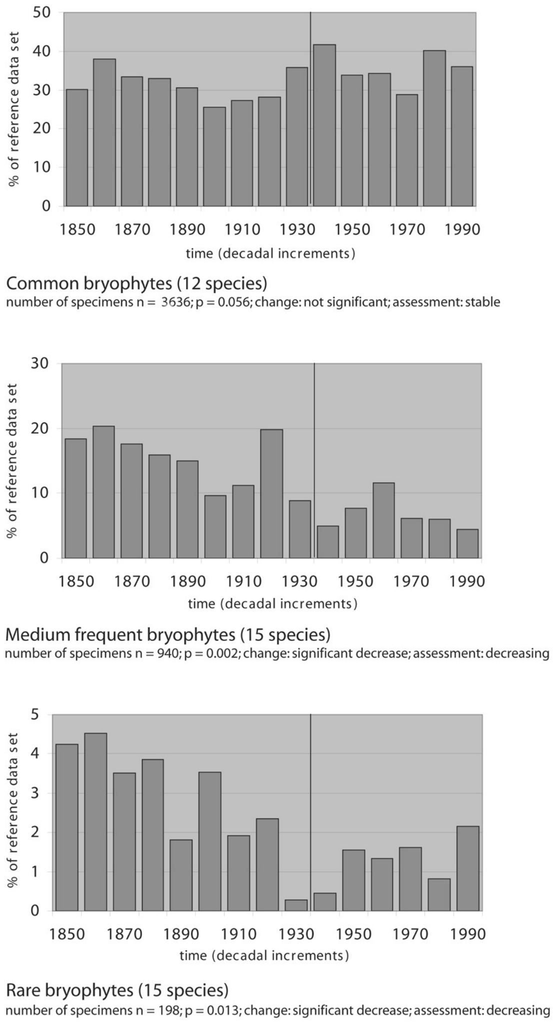


Fig. 4. Relative collecting activity of groups of species with similar frequency (= the number of specimens of the particular group of species as a percentage of the number of specimens from the reference data set, calculated for each decade; Y-axes) as a function of time (decadal increments; X-axes); p = result of the permutation test, probability by which the values before and since 1940 differ by chance; change: changes of the relative collecting activity based on the permutation test; assessment: critical assessment of the results by bryologists (see Material and methods for further details). Note the different scales on the Y-axes.

which would mean that the species cannot easily be found any longer.

However, as the outcome of the statistical test is not significant and only few older populations have been searched for, it is uncertain whether the species is really decreasing. Although this seems likely (at least in the Swiss Plateau) further investigations are needed to allow a more accurate assessment of the situation, especially of the observed shift of this species to higher altitudes.

Groups of species with similar frequency

Common species

The relative collecting activity for common species as a group is stable; the permutation test gives no significant result (Fig. 4). This was expected, since half of the common species are regarded as stable (Table 1). Three species are most probably declining, two are increasing and one shows an uncertain trend. On the other hand, the results show clearly that the common species in general are not increasing.

Species with medium frequency

The group of species with medium frequency shows a highly significant decline in relative collecting activity (Fig. 4). Nine species are assessed as declining (Table 1), only *Hyophila involuta* is stable and five do not show a significant change. No species is regarded as increasing.

Rare species

The relative collecting activity of the rare species is declining at a highly significantly rate (Fig. 4). Only three of the rare species showed a significant decrease based on the test (Table 1: change –), and only four were assessed as declining (Table 1: assessment ↓). The lack of significance is likely due to small sample size, and it is alarming to note that rare species as a group exhibit a significant decline. This suggests that quite a number of rare species with non-significant trends are probably diminishing.

However, two of the rare species, *Campylopus introflexus* and *Sphagnum fimbriatum,* are increasing (compare III: Increasing species).

Quantification of changes

In 11 species with significant declines, the mean relative collecting activity since 1940 has decreased to less than half its value before 1940 (Table 1: dimension < 0.5). The most extreme decrease is shown by *Meesia longiseta* (reduction to 0, a species which is nowadays assumed to be extinct in Switzerland), *Orthotrichum scanicum* (reduction to one hundredth, i.e. in the period since 1940 only one hundredths of the specimen numbers from the period before 1940 were collected), and *Ephemerum recurvifolium* (reduction to three hundredths). The significantly declining species with the smallest reduction in mean relative collecting activity is *Orthotrichum diaphanum*, which is reduced by 30%.

The increase in mean relative collecting activity can also be considerable. *Sphagnum fimbriatum* has the highest value, in which it increased nearly seven-fold (Table

1: dimension 6.7). In *Lophocolea heterophylla,* the mean relative collecting activity was roughly tripled and was doubled in *Frullania dilatata*. The species with the smallest significant increase is *Orthotrichum lyellii*, in which the mean relative collecting activity rose by 1.7.

In general, changes in mean relative collecting activity are more distinct in rare species than in common ones. Whereas the scale in rare species reaches from a reduction to one hundredth (*Orthotrichum scanicum*) to an increase by seven-fold (*Sphagnum fimbriatum*), in common species it extends only from a reduction to half (*Homalia trichomanoides, Cinclidotus fontinaloides*) to a three-fold increase (*Lophocolea heterophylla*).

In sum, the calculated changes in mean relative collecting activity are substantial in many species. An increase to a multiple as well as a decrease to a small fraction is no exception. As we assume that specimen numbers reflect the frequency of a species in nature, we conclude that the changes in frequency, too, are substantial in many species.

Conclusions

The questions raised in the introduction can be answered as follows:

1. Has the frequency of common bryophyte species in Switzerland changed and if so, has it increased or declined?
Yes, the frequency of approximately half of the investigated common bryophytes changed substantially, whereas the other half remained more or less stable. Two of the common species increased and three declined. Across the medium frequent and the common species, the majority of the species showed a decline (12 species declined, 7 were stable, 2 increased, and 6 were not assessable).

2. Can these changes be quantified?
Yes, the comparison of the mean relative collecting activity before 1940 with that since 1940 allowed a rough quantification of the dimension of the observed changes. It amounts from a reduction to one hundredth to a seven-fold increase.

3. Are frequency changes in common species different from those in rare ones?
Yes and no. Trends differed between groups of species with similar frequency: the common species group was the only one with constant frequency, whereas the medium frequent and rare species clearly declined. Also, with regard to quantity, changes in rare species were more distinct than in common ones. However, if we looked at single species, we found rare and common ones that were increasing, as well as those that were declining. The number of declining species in all groups was slightly higher than the number of expanding species. Of the three frequency classes, rare species were most often assessed as having an uncertain trend, which is likely due to low specimen numbers.

The results of this investigation clearly show that not only rare, but also some common bryophyte species are declining. In most cases the observed changes can be explained by man-made environmental changes whereas natural dynamics play only a secondary role. Species conservation in a wider sense should therefore also include common species.

Our method, based on the evaluation of biological collections, can be applied to all other organisms for which sufficient collections are available. It clearly demonstrates the usefulness of these collections and offers a strong argument for their maintenance.

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References

Ahrens, M. 2001. Neckeraceae. – In: Nebel, M. and Philippi, G. (eds), Die Moose Baden-Württembergs. Vol. 2, Ulmer, pp. 226–238.

Albrecht-Rohner, H. 1969. Zürcher Lebermoosflora, II. Teil. – Rev. Bryol. Lichénol. 36: 453–500.

Amann, J., Culmann, P. and Meylan, C. 1918. Flore des mousses de la Suisse. Part 2: Bryogéographie de la Suisse. – Herbier Boissier, Genève.

Arnolds, E. 1997. A quantitative approach to the Red List of larger fungi in the Netherlands. – Mycol. Helv. 9: 47–59.

Auderset Joye, D., Castella, E. and Lachavanne, J.-B. 2002. Occurrence of Characeae in Switzerland over the last two centuries (1800–2000). – Aquatic Bot. 72: 369–385.

Bisang, I. 1985. Zur Verbreitung und Ökologie der *Frullania*-Arten der Schweiz. – Bot. Helv. 95: 247–278.

Bisang, I. 1987. Zur Vergesellschaftung von *Frullania dilatata, F. tamarisci, F. fragilifolia* und *F. jackii* in der Schweiz. – Herzogia 7: 407–458.

Bisang, I. 1992. Hornworts in Switzerland — endangered? – Biol. Conserv. 59: 145–149.

Bisang, I. 1995. The diaspore bank of hornworts and its role in the maintenance of populations in cultivated fields. – Cryptog. Helv. 18: 107–116.

Bisang, I. 1998. The occurrence of hornwort populations (Anthocerotales, Anthocerotopsida) in the Swiss Plateau: the role of management, weather conditions and soil characteristics. – Lindbergia 23: 94–104.

Bisang, I. and Urmi, E.1994. Studies on the status of rare

and endangered bryophytes in Switzerland. – Biol. Conserv. 70: 109–116.
Born, J. and Jordi, A. 2005. Nimmt bei Moosen die Fertilität ab? – Meylania 34: 21–24.
Boujon, C. 1997. Diminution des champignons mycorhiziques dans une forêt suisse: une étude rétrospective de 1925 à 1994. – Mycol. Helv. 9: 117–132.
Bürgi, M. 1998. Habitat alterations caused by long-term changes in forest use in northeastern Switzerland. – In: Kirby, K. J. and Watkins, C. (eds), The ecological history of European forests. CAB International, pp. 203–211.
Burgman, M., Maslin, B. R., Andrewartha, D. et al. 2000. Inferring threat from scientific collections: power tests and an application to western Australian Acacia species. – In: Ferson, S. and Burgman, M. (eds), Quantitative methods for conservation biology. Springer, pp. 7–26.
Denys, L. 2000. Historical distribution of 'Red List diatoms' (Bacillariophyceae) in Flanders (Belgium). – Syst. Geogr. Plants 70: 409–420.
Dirkse, G. M. and Martakis, F. P. 1992. Effects of fertilizer on bryophytes in Swedish experiments on forest fertilization. – Biol. Conserv. 59: 155–161.
Düll, R. 1991. Zeigerwerte von Laub- und Lebermoosen. – In: Ellenberg, H. et al. (eds), Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobot. 18: 175–214.
Engler , B. and Bauer, H.-G. 2002. Dokumentation eines starken Bestandesrückgangs beim Haussperling (Passer domesticus) in Deutschland auf Basis von Literaturangaben von 1850-2000. – Vogelwarte 41: 196–210.
Frahm, J.-P. 1972. Die Ausbreitung von *Campylopus introflexus* (Hedw.) Brid. in Mitteleuropa. – Herzogia 2: 317–330.
Greven, H. 1992. Changes in the moss flora of the Netherlands. – Biol. Conserv. 59: 133–137.
Grünig, A., Steiner, G. M., Ginzler, C. et al. 2004. Approaches to Swiss mire monitoring. – Int. Peat J. 12: 55–73.
Gutersohn, H. 1973. Naturräumliche Gliederung. – In: Imhof, E. (ed.), "Atlas der Schweiz", plate 23. Eidgenöss. Landestopographie, Wabern-Bern.
Hallingbäck, T. 1989. Bokfjädermossa, *Neckera pumila*, en försurningshotad mossa. – Svensk Bot. Tidskr. 83: 161–173.
Hedenäs, L., Bisang, I., Tehler, A. et al. 2002. A herbarium-based method for estimates of temporal frequency changes: mosses in Sweden. – Biol. Conserv. 105: 321–331.
Hintermann, U., Weber, D., Zangger, A. et al. 2002. Biodiversitätsmonitoring Schweiz BDM. Zwischenbericht. – Buwal, Schriftenreihe Umwelt No. 342, Bern.
Holmgren, P. K. and Holmgren, N. H. 2001. Index Herbariorum on the Internet. – http://www.nybg.org/bsci/ih/ih.html.
Hürlimann, J., Elber, F., Niederberger, K. et al. 2001. Historische Kieselalgenproben als biologische Referenzen zur Bewertung von Fliessgewässern des Schweizer Mittellandes — erste Ergebnisse. – In: Jahn, R., Kociolek, J. P., Witkowski, A. et al. (eds), Lange-Bertalot-Festschrift. Ruggel, pp. 401–415.
IUCN 2001. IUCN Red List Categories and Criteria: ver. 3.1. IUCN Species Survival Commission. – IUCN, Gland, Switzerland and Cambridge, UK.
Itten, B. 2006. Population biology and genetic diversity of *Sphagnum fimbriatum*, a bipolar species rare in Switzerland. – PhD thesis, Univ. of Zurich.
Kirchhofer, A. 1997. The assessment of fish vulnerability in Switzerland based on distribution data. – Biol. Conserv. 80: 1–8.
Küchler, M. 2004. Software VEGEDAZ. Programm für die Erfassung und Auswertung von Vegetationsdaten. Update 2004. – Beratungsstelle für Moorschutz, Eidg. Forschungsanstalt WSL, Birmensdorf.
McCarthy, M. A. 1998. Identifying declining and threatened species with museum data. – Biol. Conserv. 83: 9–17.
MacDougall A. S., Loo, J. A., Clayden, S. R.et al. 1998. Defining conservation priorities for plant taxa in southeastern New Brunswick, Canada using herbarium records. – Biol. Conserv. 86: 325–338.
Meylan, C. 1924. Les Hépatiques de la Suisse. – Beitr. Kryptogamenfl. Schweiz 6: 1–318.
Paul, A. 1997. Breitet sich *Sphagnum fimbriatum* Wils. in Nordhessen aus? – Philippia 8: 89–92.
Preston, C. D. 1994. *Homalia trichomanoides*. – In: Hill, M. O., Preston, C. D. and Smith, A. J. E. (eds), Atlas of the bryophytes of Britain and Ireland. Harley Books, Vol. 3, p. 223.
Rao, D. N. 1982. Responses of bryophytes to air pollution. – In: Smith, A. J. E. (ed.), Bryophyte ecology. Chapman and Hall, pp. 445–471.
Reznick, D. and Baxter, R. J. 1994. Long-term studies of tropical stream fish communities: the use of field notes and museum collections to reconstruct communities of the past. – Am. Zool. 34: 452–462.
Richards, P. W. 1963. *Campylopus introflexus* (Hedw.) Brid. and *C. polytrichoides* De Not. in the British Isles; a preliminary account. – Trans. Brit. Bryol. Soc. 4: 404–417.
Schröck C. and Krisai, R.1999. Verbreitung und Lebensräume ausgewählter *Sphagnum*-Arten im Bundesland Salzburg und seinen Nachbargebieten. – Abh. Zool.-Bot. Ges. Österreich 30: 153–158.
Shaffer, H. B., Fisher, R. N. and Davidson, C. 1998. The role of natural history collections in documenting species declines. – Trends Ecol. Evol. 13: 27–30.
Sjögren, E. 1995. Changes in the epilithic and epiphytic moss cover in two deciduous forest areas on the island of Öland (Sweden). – Stud. Plant col. 19: 1–106.
Stahel, W. 1995. Statistische Datenanalyse. Eine Einführung für Naturwissenschafter. – Vieweg, Braunschweig.
Stetzka, K. M. 1994. Die Waldbodenvegetation als Bioindikator für Umweltbelastungen unter besonderer Berücksichtigung der Moosflora: Lang- und kurzfristige Vegetationsvergleiche. – Diss. Bot. 232: 1–412.
Stroot , P. and Depiereux, E. 1989. Proposition d'une méthodologie pour etablir des 'listes rouges' d'invertébrés menacés. – Biol. Conserv. 48: 163–179.
Szövenyi, P., Hock, Zs., Urmi, E. et al. 2006. Contrasting phylogeographic patterns in *Sphagnum fimbriatum* and *Sphagnum squarrosum* (Bryophyta, Sphagnopsida) in Europe. – New Phytol. 172: 784–794.
Szurdoki, E. and Ódor, P. 2004. Distribution and expansion of *Sphagnum fimbriatum* in Hungary. – Lindbergia 29: 136–142.
Ungricht, S., Rasplus, J.-Y. and Kjellberg, F. 2004. Extinction threat evaluation of endemic fig trees of New Cale-

donia: priority assessment for taxonomy and conservation with herbarium collections. – Biodiv. Conserv. 14: 205–232.

Urmi, E. 1992. Verbreitungsdaten als Grundlage für Artenschutz bei Moosen. – Biol. Conserv. 59: 185–190.

Urmi, E. 1996. Welche Überraschungen bryofloristische Standard-Aufnahmen neben ihrem bekannten Nutzen noch zu bieten haben. – Meylania 10: 10–12.

Urmi E. and Schnyder, N. 1996. Puzzle statt Schach. Eine naturräumliche Mosaikkarte der Schweiz und Liechtensteins in digitaler Form. – Vierteljahrsschr. Naturf. Ges. Zürich 141: 123–131.

Urmi, E. and Schnyder, N. 2000. Bias in taxon frequency estimates with special reference to rare bryophytes in Switzerland. – Lindbergia 25: 89–100.

Urmi, E., Schnyder, N. and Geissler, P. 1990. A new method in floristic mapping as applied to an inventory of Swiss bryophytes. – In: Bohn, U. and Neuhäusl, R. (eds), Vegetation and flora of temperate zones. SPB Academic Publishing, pp. 21–32.

Urmi, E., Schubiger-Bossard, C. and Bisang, I. 1993. Veränderungen in der Moosflora der Schweiz. – Diss. Bot. 196: 263–279.

Urmi, E., Schubiger-Bossard, C., Schnyder, N. et al. 1997 ("1996"). Artenschutzkonzept für die Moose der Schweiz. – Dokumentation zur Schriftenreihe Umwelt No. 265. Buwal, Bern.

Urmi, E., Schubiger-Bossard, C., Schnyder, N.et al. in press. Zwei Jahrhunderte Bestandesentwicklung von Moosen in der Schweiz — Retrospektives Monitoring für den Naturschutz. – Bristol Schriftenreihe 18: 1–138.

van Swaay, C. A. M. 1990. An sssessment of the changes in butterfly abundance in The Netherlands during the 20th Century. – Biol. Conserv. 52: 287–302.

Vellinga, E. C. 2000. Mushroom recording in the Netherlands. – Mycol. Helv. 11: 99–119.

Wiklund, K. 2003. Phosphorous concentration and pH in decaying wood affect establishment of the red-list moss *Buxbaumia viridis*. – Can. J. Bot. 81: 541–549.

Willis, F., Moat, J. and Paton, A. 2003. Defining a role for herbarium data in Red List assessments: a case study of *Plectranthus* from eastern and southern tropical Africa. – Biodiv. Conserv. 12: 1537–1552.

Wilson, R. J., Thomas, C. D., Fox, R. et al. 2004. Spatial patterns in species distributions reveal biodiversity changes. – Nature 432: 393–396.