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A 150-year-old herbarium and floristic data testify regional species decline

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ABSTRACT

Old herbarium specimens and historical floristic data give insight into regional floras for given time periods. They often cover historical time periods for which few other data are available. Herbaria thus allow the study of changes of the flora of a region across time. Using a 150-year-old regional herbarium together with a historical publication, we investigated to which extent the flora of the Swiss canton of Schaffhausen has changed, which habitats were particularly affected by local extinction, what the environmental requirements of extinct plants were and whether conclusions about the respective drivers such as land use change can be drawn. A total of 987 species were historically recorded in the study region of which 154 are currently no longer reported and are regionally extinct. This means that about one species disappeared from the region every year. Species that are currently in a high category of endangerment on the Swiss Red List have declined markedly in the canton of Schaffhausen, showing that Red Lists well portrait the endangerment of species. Looking at plant strategies, the more stress-tolerant and less competitive plants have disappeared. In addition, wetland, pioneer, ruderal and mountain species as well as agricultural weeds and light-demanding species showed highest extinction rates. In contrast, forest species had a low extinction rate, and species from fertilized meadows showed no decline. Our evaluation of a regional herbarium helps to inform nature conservation about particularly endangered habitats and possible drivers of species decline.

1. Introduction

Information taken from herbaria and other biological collections has increasingly been used for a variety of purposes during recent years. There are several reviews (for example Lang et al., 2019; Lavoie, 2013; Pyke and Ehrlich, 2010; Rocchetti et al., 2020; Winker, 2004) on the use of herbaria, a fact which lend Heberling et al. (2019) to suggest that we have entered a distinctly new era for the application of museum specimens. Besides traditional uses in systematics, taxonomy and biogeography and newly emerged topics such as DNA analyses, scientists utilise herbaria specimens to conduct research on climate change (e.g. changes in the distribution area of species), patterns of pollution (e.g. historical levels of pollutants) and the spread of non-native species or invasive diseases (e.g. first occurrence and subsequent spread in a country). Likewise, the use of herbarium data to address biodiversity or conservation issues has recently increased, e.g., in documenting species decline or population trends as well as in site selection for protected areas, restoration or reintroduction (Heberling et al., 2019; Lang et al., 2019; Lavoie, 2013; Shaffer et al., 1998; Thiers, 2019, Van Calster et al., 2008). According to Winker (2004) incorporating applied research and conservation issues into their portfolio allows natural history museums to meet societal challenges such as the biodiversity crisis.

With regard to such biodiversity issues, smaller herbaria (<100,000 specimens) often contain information that refers to biodiversity at the regional scale, which is neither found nor duplicated in larger herbaria (Lughadha et al., 2018; Marsico et al., 2020). Furthermore, it is exactly the regional or even the local scale where investigations of changes in biodiversity are especially useful for conservation purposes as practical measures are mostly implemented at these spatial scales (Snow, 2005). A floristic assessment across time, i.e., a comparison of the species occurring in a given region during different time periods can show whether plant species have disappeared and whether their distribution and/or abundance have changed, which gives insights to areas of occupancy and fragmentation, therefore providing information and guidance for conservation actions (Lughadha et al., 2018; Rocchetti et al., 2020). By using herbarium specimens McDonough MacKenzie et al.

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(2019) assessed the loss of native plant species in several areas of new England (USA) across time, Dolan et al. (2017) showed floristic change as a result of urbanization in Indianapolis, Kolp et al. (2020) compared the loss or gain of native and non-native plants, respectively, in a natural area in Central Michigan (USA) and Stehlik et al. (2007) used an herbarium to study species loss in a single municipality in Switzerland across 150 years and focussed on floristic changes in different habitat types. The latter authors found a dramatic overall decline in the number of species of 28%. In more detail, species of meadows were lost at a rate of 22%, species of disturbed sites at 23% and species of wetlands at 28%, respectively. In contrast, forest species only showed a decline of 13% in species number. These local scale results mirror extinction at the national level in Switzerland (Bornand et al., 2016; Kempel et al., 2020).

An old herbarium covering a regional scale was established by Johann Conrad Laffon (1801–1882) for the whole canton of Schaffhausen in Switzerland in the years 1820–1847. Laffon's aim was to document the flora of this canton as completely as possible (Laffon, 1847a). In addition, Laffon (1847b) published a commented species list of the plants of the canton of Schaffhausen. As the current flora of the canton of Schaffhausen is well known (www.infoflora.ch), the rather complete herbarium of Laffon and his published species list offer the unique chance to assess the floristic changes in a time span that parallels the end of the abandonment of the three-field system in agriculture including the abandonment of general grazing on fallow fields and common land and the start of intensified industrialisation in Europe and North-America (Ellenberg, 2009; Langer et al., 2021) as well as Northern Switzerland (Bronhofer, 1958); a time period for which distinct and complete regional floristic information is often not available.

In the present study, we asked the following questions: (1) How many plant species that occurred in 1847 do no longer occur in the canton of Schaffhausen after the year 2000 (i.e. a time period of 153 years)? We thus checked whether the vascular plant species recorded by Laffon in his herbarium and species list (Laffon, 1847b) currently still occur in the canton. (2) Which factors were the potential driving forces of the species decline? We approached this question by analysing differences in the ecological indicator values, habitat preferences and plant strategies of the extinct species in comparison to those species still occurring in the canton of Schaffhausen. We hypothesised that changes in environmental conditions or habitats (e.g. increase in fertilized meadows, decrease in dry meadows, drainage of fens and bogs or change from coppiced woodlands to high forests) were indicated by the decline of species characteristic of the respective environmental conditions or habitats. (3) Did plant species that are nowadays threatened according to the Swiss Red List more often disappear in the canton of Schaffhausen than species that are currently not threatened in Switzerland? (4) What implications for nature conservation can be drawn from this comparison of a historical and a current regional flora?

2. Material and methods

2.1. Study region

The canton of Schaffhausen is located in the north of Switzerland (Fig. 1) and has an area of 298 km^2. Geologically, the majority of the canton consists of Jura limestone with shallow soils. To the east and south of the region are two exclaves (Stein am Rhein and Buchberg-Rüdlingen), where calcareous Tertiary rocks with molasse and glacial gravel predominate. The highest elevation in the canton is at 912 m a.s.l. The climate is temperate with an annual mean temperature of 8.8 °C. Since the canton lies in the rain shadow of the Black Forest, annual precipitation is comparatively low (Holderegger et al., 2019; Kummer, 1937) with about 900 mm (www.meteoschweiz.admin.ch). These conditions – a rather dry climate, permeable soils and a long period of land-use by humans – have led to the development of a rich regional flora. In particular, the canton harbours many species-rich extensive dry meadows and agricultural fields (Holderegger et al., 2019; Fig. 2). With

Fig. 1. Switzerland and the study area of the canton of Schaffhausen in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

42% of the cantonal area, the proportion of forest is markedly higher than the Swiss average of 30% (Abegg et al., 2020).

2.2. Laffon's herbarium and flora

Johann Conrad Laffon (1801–1882; Fig. 2) collected the first more or less complete herbarium and also published the first species list for the canton of Schaffhausen. He worked as a pharmacist in Schaffhausen. He was one of the founders of the Natural History Museum Schaffhausen and he bequeathed his herbarium to the museum, where it is still kept (herbarium SCH; Fig. 2). Laffon compiled his herbarium of vascular plants between 1820 and 1847. In total, his collection comprises almost 1000 specimens covering 852 plant species. Laffon wanted to create a complete collection of all the plant species occurring in the canton of Schaffhausen: “The cantonal herbarium […] contains all plants that have been found in the canton” (translation by the authors; Laffon, 1847a: 12). In addition to the herbarium, Laffon (1847b) published a commented species list of the flora of the canton of Schaffhausen. In this publication he listed 1053 plant species. The herbarium and the published species list are not entirely congruent; but there was no obvious bias with respect to certain ecological groups (e.g. water plants). Even if not all herbarium specimens or all entries in the published species list (Laffon, 1847b) indicate a distinct sampling locality, it can be assumed that they originated from the canton of Schaffhausen (Laffon, 1847a). It is, however, clear that the herbarium and the species list of Laffon (1847b) do not cover the complete flora of the canton of Schaffhausen in 1847. First, the current flora of the Canton of Schaffhausen harbours about 1400 vascular plant species (www.infoflora.ch) and there is no reason to assume that fewer species occurred in the canton in 1847 than today (except for some non-native species). Second, part of the collection of the cantonal museum was destroyed in the bombing of Schaffhausen during the Second World War. The extent to which the Laffon herbarium was affected is not known. Because of the potential non-completeness of the Laffon herbarium and of his published list (Laffon, 1847b), only changes in the occurrence or absence of those species explicitly sampled or stated by Laffon can be evaluated in a comparison with the current flora. Likewise, new additions to the flora of the canton of Schaffhausen cannot be evaluated. Furthermore, no changes in the abundance of species can be assessed as the herbarium labels and the entries in the published species list (Laffon, 1847b) rarely give information on the abundance of species within the canton of Schaffhausen. It might therefore be possible that some species were already rare or only had transient occurrences at Laffon's time.

Fig. 2. Top: Typical landscape in the canton of Schaffhausen with dry meadows, agricultural land, forests and rocky areas (in the back). Bottom left: specimen of *Cyperus flavescens* from the herbarium of Johann Conrad Laffon (now extinct in the canton of Schaffhausen). Bottom right: Johann Conrad Laffon.

2.3. Compilation of historical and current plant species

The existing herbarium specimens of the Laffon herbarium were compiled into a list and supplemented with species not present in the herbarium but mentioned in the published species list (Laffon, 1847b). A total of 81 cultivated species, which were designated as such by Laffon and which exclusively occur in cultivation today, were omitted from the list (e.g. *Amygdalus persica* or *Secale cereale*). However, species that might have formerly been cultivated but occur spontaneously today were included (e.g. *Fragaria moschata* or *Sinapis arvensis*). Six extremely improbable species mentioned in the published species list or clearly misidentified species were omitted (e.g. *Adonis vernalis* or *Ajuga pyramidalis*). The hybrid *Festuca loliacea* was also omitted. The final list included 987 species. Nomenclature followed Lauber et al. (2018).

To evaluate whether these 987 species currently still occur in the canton of Schaffhausen, a list of all the vascular plant species reported after the year 2000 in the canton of Schaffhausen was extracted from "Info Flora" (June 17, 2020; www.infoflora.ch). Info Flora is the national data and information centre for wild plants in Switzerland; it digitally collects records of vascular plants from field botanists and professionals and reports them in on-line distribution maps and checklists, creates the Red List of vascular plants of Switzerland and cooperates with conservation authorities. The vast majority of Info Flora records are from the years after 2000. Note that neither the data from

Laffon's herbarium nor the information from his published species list is included in the database of Info Flora. There is no current published checklist of the flora of the canton of Schaffhausen. The list of species currently occurring in the canton of Schaffhausen and provided by Info Flora, was checked for completeness by the authors with expert knowledge of the regional flora. If there were any species in the study region currently not reported to Info Flora and not known by the authors with expert knowledge, they should only be few. In the final data set, found in Supplementary material A, a species still occurring in the canton of Schaffhausen today was assigned a 1, a species no longer occurring was assigned a 0.

2.4. Analyses

We first calculated the percentage of plant species that were lost in the canton of Schaffhausen during 153 years (i.e. between 1847 and 2000). Note that this species loss constitutes a minimum estimate as the historical species list of the Laffon's herbarium and published species list (Laffon, 1847b) was not complete (see above). Some extinctions might therefore not have been noticed. We further evaluated whether there was a difference in the percentage of extinction among different habitat types. We assigned species to certain habitat types according to Landolt et al. (2010). The categories considered were wetland plants, mountain plants, pioneer plants, water plants, weeds and ruderal plants, plants of dry meadows, forest plants and plants of fertilized meadows. The group of forest plants included all species that have their primary occurrences in Switzerland in forests and shrublands. Mountain plants were those species that have their main distribution above or just below timberline (subalpine and alpine; above 1200–1500 a.s.l.). Some of these mountainous plants grow at lower elevations on rocks or if they are indirectly favoured by human land use (e.g. *Gentiana verna* in dry meadows or *Primula farinosa* in bogs). Pioneer plant species included species that occur in open floodplains, on erosion slopes or on scree and gravel at low elevations. Aquatic plant species were those species with a life cycle in water, and wetland species comprised species predominantly occurring in fens, bogs or riparian habitats. Dry meadow plant species referred to plants characteristic on dry meadows and dry pastures with low-intensity agricultural use, while weeds and ruderal plants included species whose sites are regularly mechanically worked by humans such as fields and vineyards but also vegetable gardens. Finally, plants of fertilized meadows encompassed species whose main occurrence is in meadows and pastures on intensively used agricultural land fertilized by heavy input of manure or slurry. Differences among habitat types were analysed with Chi^2-tests with 10,000 Monte Carlo iterations in SPSS 26.0 (IBM, 2020), as samples sizes between classes were rather different.

We then checked whether there were differences in mean ecological indicator values between species that were extinct and species that still occurred in the canton of Schaffhausen. We used the ecological indicator values for Switzerland by Landolt et al. (2010), which are similar to the well-known Ellenberg indicator values. The following indicator values were used: continentality (K), light (L), moisture (F), soil reaction (R), nutrients (N) and temperature (T). The indicator values were not strongly correlated (Spearman rank correlation coefficients $|r| \leq 0.657$ in all cases; Dormann et al., 2013). Two-sided *t*-tests with 1′000 bootstrap iterations were used for statistical analysis, as sample sizes of extinct and extant species were different and normal distribution of the data could not be assumed. Note that the total number of species per test did not always sum up to 987, as for certain species no value for a specific indicator value was available. Similar t-tests were additionally used to check for differences in indicator values among extinct and extant species per habitat type.

Additionally, we performed an analysis of the CSR plant strategies of Grime (1977) given in Landolt et al. (2010). For this purpose, the categorical description of the CSR strategies was transformed into the three separate numerical dimensions “competition”, “stress” and “ruderality” with values of 0–3 (Boch et al., 2019). For instance, a species with a plant strategy of “csr” was transcribed into a competition value of 1, a stress value of 1 and a ruderality value of 1, while a species with “ccs” received values of 2, 1 and 0, respectively. Again, two-sided *t*-tests with 1000 bootstrap iterations were used for statistical analysis of the complete data set but also for each habitat type (see above) separately.

Finally, we checked whether there was a difference in Swiss Red List categories (Bornand et al., 2016) between extinct and extant species of the canton of Schaffhausen. We did so by applying a Chi^2-test with 10′000 Monte Carlo iterations. All statistical analyses were done with SPSS 26.0 (IBM, 2020).

3. Results

Of the 987 species mentioned by Laffon and which occurred in the canton of Schaffhausen between 1820 and 1847, 154 were now extinct (i.e. no localities of these species are currently known within the canton of Schaffhausen). This refers to an extinction rate of species of 15.6% within the canton and translates into one species disappearing every year averaged across the time period 1847–2000.

Regarding habitat preferences, wetland plants showed the highest percentage of extinction (27.8%; total number of wetland species $N = 144$), followed by mountain species (25%; $N = 36$), pioneer plants at low altitudes (18.9%; $N = 37$), water plants (18.9%; $N = 37$), weeds and ruderal plants (17.4%; $N = 258$), plants of dry meadows (16.8%; $N = 125$) and forest plants (5.4%; $N = 222$; Fig. 3). Plants of fertilized meadows showed no extinction (0%; $N = 43$; Fig. 3). Differences in the percentage of species extinction among habitats were highly significant (Chi^2-test: $p \leq 0.001$).

Regarding environmental preferences, the analysis of ecological indicator values showed that light-demanding species got more often extinct (extinct species: mean $L = 3.75 \pm 0.04$; extant species: mean $L = 3.40 \pm 0.03$; *t*-test: $p \leq 0.001$). This also held true for soil reaction, with extinct species preferring slightly lower soil reaction (extinct species: mean $R = 3.25 \pm 0.07$; extant species: mean $R = 3.46 \pm 0.03$; $p = 0.007$). Extinct species tended to favour lower soil nutrients (mean $N = 2.85 \pm 0.08$) than extant species (mean $N = 3.00 \pm 0.03$), but the difference was only marginally significant ($p = 0.084$). Indicator values for temperature, continentality and moisture showed no significant differences between extinct and extant species. The analysis of the change in plant strategies showed that extinct species were less competitive (extinct species: mean $C = 0.94 \pm 0.06$; extant species: mean $C = 1.20 \pm 0.03$; $p \leq 0.001$) and more stress-tolerant (extinct species: mean $S = 1.08 \pm 0.07$; extant species: mean $S = 0.88 \pm 0.02$; $p \leq 0.003$) than extant species. Ruderality showed no significant differences among extinct and extant species.

An evaluation of the indicator values per habitat showed that in forests the more light-demanding species predominantly became extinct (extinct species: mean $L = 3.03 \pm 0.19$; extant species: mean $L = 2.64 \pm 0.05$; *t*-test: $p = 0.021$). Among the pioneer plants those that are more light-demanding (extinct species: mean $L = 4.14 \pm 0.14$; extant species: mean $L = 3.63 \pm 0.14$; $p = 0.019$) and those preferring higher continentality (extinct species: mean $K = 4.00 \pm 0.00$; extant species: mean $K = 3.27 \pm 0.17$; $p = 0.02$) more often became extinct. Among the water plants, those preferring slightly wetter (extinct species: mean $F = 5.00 \pm 0$; extant species: 4.92 ± 0.03; $p = 0.036$) and colder conditions (extinct species: mean $T = 3.29 \pm 0.10$; extant species: mean $T = 3.62 \pm 0.09$; $p = 0.024$) were lost. Among wetland plants those that prefer wetter conditions (extinct species: mean $F = 4.25 \pm 0.05$; extant species: mean $F = 4.08 \pm 0.05$; $p = 0.027$) and less nitrogen (extinct species: mean $N = 2.45 \pm 0.13$; extant species: mean $N = 2.88 \pm 0.08$; $p = 0.006$) more often disappeared. In nutrient-poor and dry meadows species preferring warmer temperature (extinct species: mean $T = 4.17 \pm 0.12$; extant species: mean $T = 3.80 \pm 0,05$; $p = 0.006$) were more often lost. Finally, weeds and ruderal plants that are more light-demanding (extinct species: mean $L = 3.91 \pm 0.04$; extant species: mean $L = 3.77 \pm 0.03$; $p = 0.007$) and prefer higher temperature (extinct species: mean $T = 4.30$

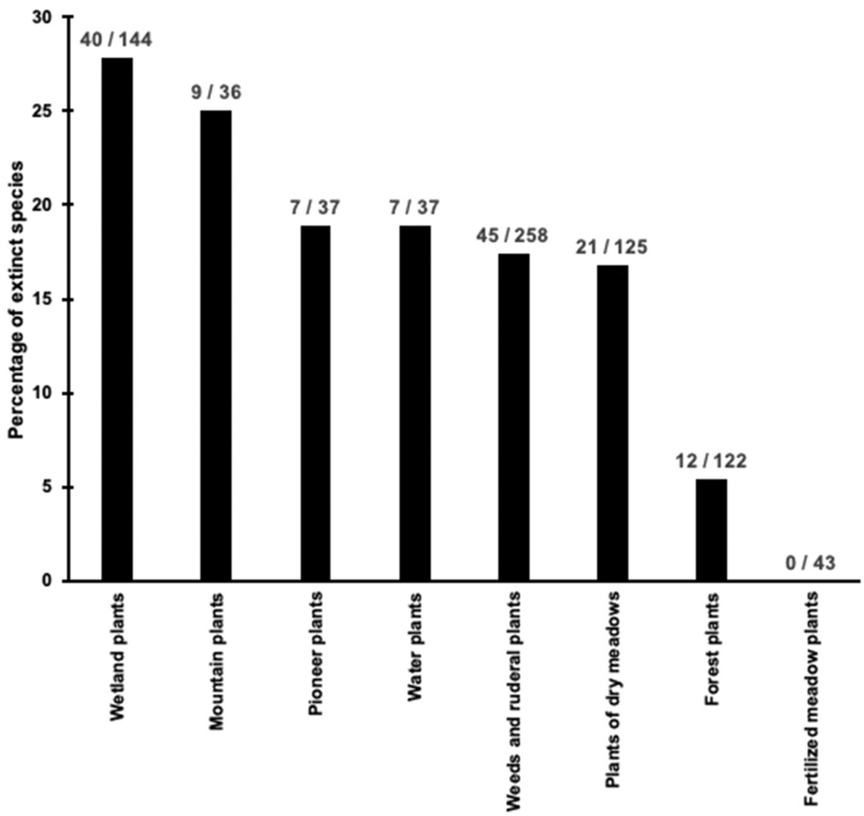

Fig. 3. Percentage of extinct vascular plant species in different habitat types in the canton of Schaffhausen present in Laffon's herbarium or species list (1820–1847) and extinct today (i.e. after the year 2000); numbers above bars show extinct species/total species per habitat type.

± 0.08; extant species: mean $T = 4.0 \pm 0.03$; $p \leq 0.001$) predominantly disappeared. All other indicator values per habitat type showed no differences among extinct and extant species.

Regarding plant strategies per habitat type, the more stress-tolerant wetland plant species disappeared (extinct species: mean S = 1.53 ± 0.11; extant species: mean S = 1.24 ± 0.06; $p \leq 0.02$). In dry meadows the less competitive disappeared (extinct species: mean C = 0.081 ± 0.09; extant species: mean C = 1.01 ± 0.06; $p \leq 0.01$) and the more stress tolerant species (extinct species: mean S = 1.38 ± 0.11; extant species: mean S = 1.12 ± 0.05; $p \leq 0.03$) disappeared. For weeds and

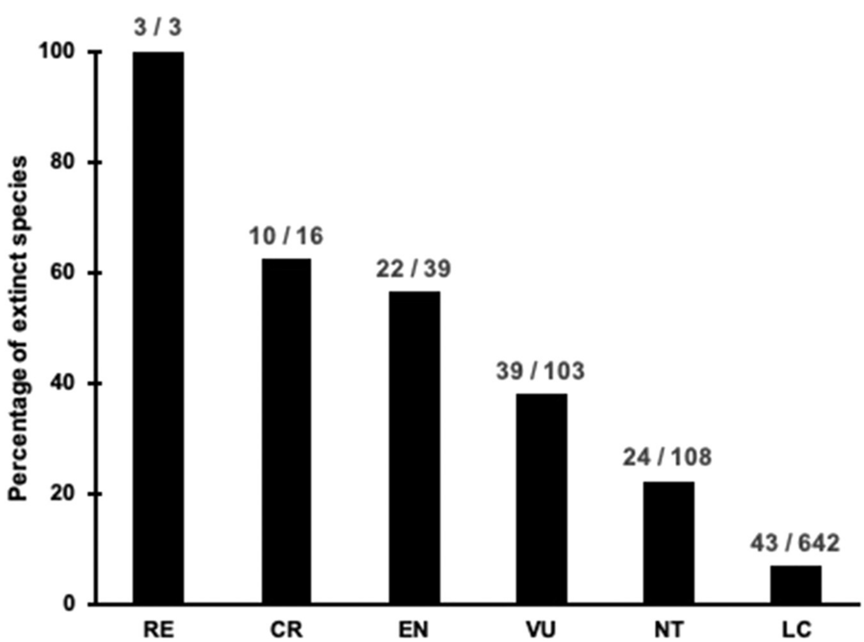

Fig. 4. Percentage of species, present in Laffon's herbarium or species list (1820–1847) and extinct today (i.e. after the year 2000) classified by categories of the current Swiss Red List of vascular plants (Bornand et al., 2016) in the canton of Schaffhausen (RE: regionally extinct; CR: critically endangered; EN: endangered; VU: vulnerable; NT: nearly threatened; LC: least concern). Numbers above bars show extinct species/total species per Red-List-category.

ruderal plants, the more ruderal plants (extinct species: mean $R = 2.18 \pm 0.12$; extant species: mean $R = 1.90 \pm 0.06$; $p \leq 0.033$) disappeared, while there was a trend for less-competitive (extinct species: mean $C = 0.56 \pm 0.09$; extant species: mean $C = 0.76 \pm 0.05$; $p \leq 0.056$) to became more often extinct.

Looking at the percentage of extinct species per category of the Swiss Red List of vascular plants (Bornand et al., 2016), those species that are currently listed in a higher category of endangerment were more likely to become extinct in the canton of Schaffhausen than did species with lower endangerment (Fig. 4). All species from the category of regionally extinct species in Switzerland (RE; total number of species; $N = 3$) were per definition extinct in the canton of Schaffhausen. 62.5% of critically endangered species (CR; $N = 16$), 56.4% of endangered species (EN; $N = 39$), 37.9% of vulnerable species (VU; $N = 103$), 22.2% of nearly threatened species (NT; $N = 108$) and 6.7% of species of least concern ($N = 642$) disappeared from the canton of Schaffhausen. A Chi^2-test indicated statistically significant differences in the percentage of extinct species among Red List categories ($p \leq 0.001$).

4. Discussion

4.1. Extinction of species

The extinction of plant species and thus the loss of biodiversity in a certain region can be shown by a comparison of historical herbarium specimens and/or old floristic publications with the present-day situation (Drayton and Primack, 1996). We performed such an analysis for the canton of Schaffhausen in Switzerland and found a decline in the number of species of 15.6% in the 153 years between the establishment of the Laffon herbarium (1820–1847) including his published species list (Laffon, 1847b) and current species occurrence (after 2000) extracted from Info Flora, i.e., a total of 154 out of 987 species, disappeared from the study region. Comparing this figure with those of other studies comparing historical with current data reveals large differences with a range of extinction rates from 10.5% in the Mount Holyoke Range (Massachusetts/USA) in 150 years (Searcy, 2012) to as much as 38% in 99 years in Middlesex Fells, an area within Metropolitan Boston/USA (Drayton and Primack, 1996). These large differences are likely due to diverse causes: Within the last 150 years major changes occurred due to industrialisation, intensification of agriculture and forestry, landscape fragmentation, destruction and degradation of natural habitats, urbanization etc. However, the exact timing and intensity of these drivers differ among study regions. It is thus not particularly fruitful to compare studies from regions with drastically different land use histories. When comparing the floristic assessment of the Laffon herbarium and his published species list (Laffon, 1847b) with similar evaluations from Western Europe only, the figures of regional extinction of vascular plant species are more similar. Landolt (1999) detected an extinction of 14% of plant species during 160 years in the urban area of Zurich, the largest Swiss city, in the South of the canton of Schaffhausen. The city of Zurich's area also contains large natural habitats such as wetlands and forests (Landolt, 1999). Stehlik et al. (2007) detected an extinction rate of 28% in about 160 years in the municipality of Küsnacht near Zurich, and Spillmann and Holderegger (2008) found a similar value of 16% for a time span of about 100 years in the Tössbergland, a rural, mountainous area to the southeast of the canton of Schaffhausen. McCollin et al. (2000) also found a similar decline of 12.8% plant species disappearing in 65 years in Northamptonshire in the UK, whereas Van Calster et al. (2008) found a slightly higher figure of 19% extinct species for a time period of 110 years for a rural region in northern France. The rate of one species lost every year (averaged over the time period of 153 years) for the canton of Schaffhausen was slightly lower than the rate of one species lost every 0.8 years (averaged over a time period of 160 years) reported by Landolt (1999) for the city of Zurich.

4.2. Causes of extinction

Although there are many factors driving species extinction, its main cause is the loss and alteration of habitats due to change in land use (Applequist et al., 2007; Bertin, 2002; IPBES, 2018; McCollin et al., 2000; Stehlik et al., 2007). Data from herbarium specimens, combined with environmental or trait data can show the most likely threat to different habitat types (Lughadha et al., 2018). In the present case, we combined the extinction data with habitat types, ecological indicator values and plant strategies for Switzerland according to Landolt et al. (2010). At 27.8%, wetland species had the highest probability of extinction in the canton of Schaffhausen (Fig. 3). The canton harbours few wetlands such as fens and bogs, because of its comparatively dry climate and soils with low water capacity. However, between 80 and 88% of wetlands have disappeared in Switzerland since 1900 (Küchler et al., 2018). There is no reason why the canton of Schaffhausen should have been an exception to this general trend. In fact, a local botanist, Kummer (1945) gave a long list of wetlands that had already been destroyed in the 1940s due to drainage and destruction. For example, the only formerly known raised bog in the canton of Schaffhausen had been destroyed in 1905 (Kummer, 1945). According to our study, *Eriophorum gracile*, *Drosera rotundifolia*, *Carex diandra* and *C. lasiocarpa*, all typical species of raised and transition bogs, became therefore extinct in the canton of Schaffhausen. The loss of wetland species in our study is in line with other studies, showing that wetland plants were particularly affected by land use change (Bertin, 2002; Drayton and Primack, 1996; Holderegger et al., 2019; Scherrer et al., 2022; Stehlik et al., 2007). The significant difference between extinct and extant species in the indicator value for moisture for wetland and water plants shows that species preferring particularly wet conditions such as *Cicuta virosa*, *Potamogeton gramineus*, *Sparganium emersum* and *S. natans*, *Allium angulosum* or *Cyperus flavescens* disappeared from the study region. These results were supported by our analysis of plant strategies, in which the more stress-tolerant, i.e., the species with more extreme habitats, disappeared more often. This is also reflected by other studies. In 23% of Swiss wetlands, moisture in the reed and tall sedge vegetation decreased considerably and a further 34% showed a trend towards lower moisture. Similarly, 31% of wetlands exhibited a decrease in moisture throughout Switzerland (Küchler et al., 2018). In addition, nitrogen deposition and thus eutrophication increased in Switzerland. For instance, nutrient content increased considerably in 33% of the calcareous small sedge vegetation and a further 28% of this vegetation type showed a trend to become more nutrient-rich (Küchler et al., 2018). Again, this general trend for nutrients across Switzerland is well mirrored in our study where extinct species had significantly lower indicator values for nutrients than extant species.

Pioneer species and to a lower degree weeds and ruderal plants also showed higher percentages of extinction. The group of the weeds and ruderal plants showed that the less competitive as well as the more ruderal species tended to disappear. Again, the species of more extreme conditions disappeared from the region. In other words, the less ruderal species survived. The habitats of pioneer and ruderal species, such as open soil in agricultural areas (fields, vineyards, vegetable gardens), roadsides, open floodplains, river banks and gravel pits, erosion slopes, scree and gravel etc., have disappeared due to the general intensification of human land use, the sealing of surfaces, river corrections, or the loss of un-managed wet and dry land (Delarze et al., 2015). In consequence, pioneer and ruderal species such as *Blysmus compressus*, *Myricaria germanica*, *Herniaria hirsuta* or *Blitum virgatum* are no longer reported from the canton of Schaffhausen. Although many new habitats such as walls, pavement, rubble sites, parks, backyards etc. have been created in urbanized areas and could provide substitute habitats for pioneer or ruderal plant species, they are often managed in an unsuitable manner, which deprives them of their role as potential habitat (Landolt, 2001). For weeds, agricultural intensification and mechanisation during the last 100 years, fertilizer application, seed cleaning, the almost complete loss of fallows and the ubiquitous treatment with herbicides has reduced suitable habitat dramatically (Baumann, 2011). These processes are the main causes for the decline of the arable flora or weeds (Richner et al., 2015). Consequently, weeds of arable fields and vineyards like *Chenopodium murale*, *C. urbicum*, *Picris echioides* or *Thymelaea passerina* have disappeared from the study region. Again, the trends shown for the canton of Schaffhausen are reflected by general trends across Switzerland (Richner et al., 2017) or Europe (Richner et al., 2015; Storkey et al., 2012). A particular case is the complete abandonment of flax (*Linum usitatissimum*) cultivation in the canton of Schaffhausen (Kelhofer, 1915). This led to the loss of the highly specialised weed or arable flora of flax fields. Accordingly, *Cuscuta epilinum* and *Camelina alyssum* became extinct in the canton of Schaffhausen. The evaluation of indicator values in our study showed that the pioneer, ruderal and weed plants adapted to more extreme environmental conditions more often became extinct (i.e. light-demanding species and, to a lower degree, species preferring higher temperatures).

Compared to the loss of species in other habitat types, forest plants showed a moderate extinction rate of only 5.4% in the canton of Schaffhausen. However, we showed that species that are particularly light-demanding, such as *Thesium rostratum* and *Campanula cervicaria*, no longer occur in the study region, pointing to a habitat change towards darker and denser forests. A comparatively low regional or local extinction rate of forest plants was also observed in other studies from Switzerland and Europe (Bürgi et al., 2010; Kempel et al., 2020; McCollin et al., 2000; Scherrer et al., 2022; Stehlik et al., 2007; Van Calster et al., 2008). Why is there higher species survival in forests? The area of forest has generally been protected in Switzerland since the year 1903 and the sustainable management of Swiss forests is the rule ever since (Rigling and Schaffer, 2015). However, the environmental conditions within forests changed substantially during the last 150 years and had clear impact on the floristic composition of forests (Bürgi et al., 2010). Many traditional forest management strategies or uses, such as coppiced woodlands, coppice-with-standards, forest pasturing, litter collecting, temporary agricultural use of forest clearings or collection of oak bark for the tanning of leather led to lighter conditions and poorer soils within forests (Kopecky et al., 2013). Many species have benefited from sparser forest with higher light conditions in the past, so that even species typical of dry meadows occurred within forests, where they found substitute habitats (Kummer, 1937; Peterken and Francis, 1999). This is reflected by the fact that Laffon noted forests as typical habitats on herbarium labels for species such as *Medicago falcata* or *Dianthus armeria*; nowadays these are typical species of dry meadows (Lauber et al., 2018) or sunny forest edges (www.infoflora.ch). Similarly, Laffon noted that *Calluna vulgaris* occurred in “all forests”. With the abandonment of traditional forest uses the importance of wood production for timber and fuel increased (Bürgi et al., 2020; Kopecky et al., 2013; McCollin et al., 2000). Correspondingly, the light availability within forests decreased significantly (Van Calster et al., 2008) and some forest species disappeared accordingly. This is evidenced by our indicator value analysis showing that the more light-demanding species in forests but also species preferring lower soil reaction indicating poorer soils became extinct. This result is mirrored by the results of Kopecky et al. (2013). These authors showed that with the abandonment of coppiced wood the flora of relatively open, nutrient-poor forests evolved towards a flora of nutrient-rich forests, and that it was primarily the light-demanding species that were most prone to local extinction.

It is noteworthy that the only habitat showing no extinction of plant species at all were fertilized meadows: not a single species disappeared from fertilized meadows in the canton of Schaffhausen since 1847. Fertilized meadows and pastures are by far the most common grassland type in Switzerland and Central Europe today (Ellenberg, 2009; Delarze et al., 2015; Zürcherische Botanische Gesellschaft, 2020). In marked contrast, non-fertilized dry meadows and pastures have decreased in area as well as in quality. For instance, they lost about 95% of their area in Switzerland since 1900 (https://www.bafu.admin.ch/tww). The habitat quality of dry meadows decreased due to agricultural intensification leading to more nutrient rich conditions with dense vegetation and due to atmospheric nitrogen deposition (Kosonen et al., 2019). In general, grasslands show less extreme, more mesic environmental conditions today. The most important remaining dry meadows and pastures of Switzerland are protected under Swiss law (https://www.bafu.admin.ch/tww). Although the canton of Schaffhausen is one of the regions of Switzerland that still harbours comparatively many dry meadows and pastures (Holderegger et al., 2019), our study showed that dry meadows lost 17.8% of their typical species in the canton of Schaffhausen during 153 years and that it was the more “extreme” species that vanished, that is the ones demanding higher temperatures, the more stress-tolerant and the less competitive species.

It would be interesting to know during which time periods species disappeared. Such an analysis across time was only feasible if historical floristic data for several time periods existed. For instance herbarium collections and/or floristic publications specimens distributed across time were needed for such an analysis (Applequist et al., 2007). In fact, another herbarium dating from about 1900–1950 (Herbarium Kummer distributed across herbaria SCH; BERN and Z) and additional published floristic distribution data for the 1910s (Kelhofer, 1920) and 1940s (Kummer, 1937–1946) exist for the canton of Schaffhausen. However, all these historical floristic data would ask for extensive herbarium revision and data cleaning and curating before this information could be used. Applequist et al. (2007) performed such an analysis of species decline across several time periods. They used herbarium specimen of three arbitrarily chosen time periods (before 1950, 1950–1980 and after 1980) and showed that the probability of *Echinacea* species to be found at historical sites decreases with increasing age of herbarium specimens.

4.3. Red Lists reflect the historical extinction of species

The higher the category of endangerment of a species is on the current Red List of Switzerland (Bornand et al., 2016), the more likely it became extinct in the canton of Schaffhausen since 1847 (Fig. 4). Of the 154 species now extinct in the canton of Schaffhausen, 74 are currently listed as threatened or regionally extinct (categories RE, CR, EN, VU) in the Red List of Switzerland. This translates into an extinction rate of 46%. This is comparable to an evaluation by Stehlik et al. (2007) for a single Swiss municipality with an extinction rate of 39.5% for the same Red List categories. In accordance, Holderegger et al. (2019) compared the decline of locations (i.e. not species) of plant species in the canton of Schaffhausen and found that historical locations of threatened species were lost at more than 50%. It goes without saying that all species of the category regionally extinct (RE) disappeared from the study region. These were *Filago gallica*, *Camelina alyssum* and *Cuscuta epilinum*. Of the 16 critically endangered species (CR), ten were no longer present in the canton of Schaffhausen, including species such as *Lolium temulentum*, *Silene gallica* or *Thymelaea passerina*. However, some species of higher categories of endangerment (categories CR and EN) still occur in the canton of Schaffhausen, like *Gagea pratensis*, *Legousia hybrida*, *Asperula tinctoria* or *Adonis flammea*.

Lughadha et al. (2018) stressed that herbaria are a valuable source of species distribution data used for the compilation of Red Lists. The data used for the Swiss Red Lists also depended on available distribution data (Bornand et al., 2016; Landolt, 1991; Moser et al., 2002; Welten and Sutter, 1982; www.infoflora.ch) and on expert assessments. They also include information from selected herbaria and literature, but neither the Laffon herbarium nor his species list was used for Red List assignments in Switzerland. Therefore the present analysis showing that plant species classified in higher categories of endangerment are more likely to become extinct than plants in lower endangerment categories, exemplifies that national Red Lists well predict the regional endangerment of species as well (Kempel et al., 2020; Stehlik et al., 2007).

However, there is a drawback to our evaluation: some plant species might still occur in the study region, but in a few scattered individuals or in very small populations that do no longer reproduce regularly and could finally go extinct. Such delayed extinction refers to an extinction debt (Carroll et al., 2004; Hanski and Ovaskainen, 2002; Kuussaari et al., 2009). Extinction debts have been shown to occur in grasslands (e.g. Helm et al., 2006; Olsen et al., 2018) and wetlands (Jamin et al., 2020). Assuming an extinction gap, one could therefore expect more species to become extinct in the study region in the near future.

5. Conclusions

The Laffon herbarium (compiled between 1820 and 1847) and his published species list (Laffon, 1847b) were created with a primarily regional focus, which proves to be an auspicious occasion today: the restriction to a comparatively small and clearly defined region - as it is often the case with collections of smaller herbaria - enables to carry out research in biodiversity change within a given time period and a clear reference area (Pyke and Ehrlich, 2010; Snow, 2005). Such comparisons of the historical with the current flora of a region allow showing that species extinction was non-random and that particular habitats experienced a higher loss of species. They also allow studying which environmental requirements of species led to their extinction. In this way, possible drivers of species decline can be identified. In the case of the canton of Schaffhausen, wetland and water habitats, disturbed or ruderal sites as well as agricultural land showed particularly high species extinction. We also showed that light-demanding species generally showed a particularly high extinction rate. Based on such results, conservation management can be better informed. Depending on the time periods covered by historical resources such as herbaria or old publications one could define the time period when most species decline happened, even beyond the usual time horizon of the past few decades.

With regard to this last point, Laffon himself already noted the beginning of species decline in the canton of Schaffhausen in the first half of the 19th Century: "With the exception of bare rock faces and stony rubble heaps stripped of all soil, there is not a single uncultivated spot in the entire canton; the diligence of our land cultivators has taken possession of all cultivable land, as a result of which many rare plants have recently, if not completely disappeared, at least been greatly reduced in number" (translation by the authors; Laffon, 1847a: 10).

CRediT authorship contribution statement

Michèle Büttner: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing - Original draft, Visualization, Project administration
Urs Weibel: Resources, Writing - Review & editing
Michael Jutzi: Data curation, Writing - Review & editing
Ariel Bergamini: Writing - Review & editing
Rolf Holderegger: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - Review & editing.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

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