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Local extinctions of the wetland specialist *Swertia perennis* L. (Gentianaceae) in Switzerland: a revisitation study based on herbarium records

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Abstract

We studied population extinction of the locally abundant fen plant *Swertia perennis* in Switzerland and used up to 127-year old herbarium records to relocate 63 sites that had once hosted this species. We recorded current site characteristics and related them to the absence or abundance of populations. Fifty-four sites (86%) were still traditionally used (extensively mown or grazed). Fifteen populations (24%) had gone extinct. Extinction was more likely at lower altitude, in the peripheral distribution range of *S. perennis* (58% peripheral, 9% central populations extinct), on the smallest fens (75% extinct on fens <400 m^2) and on fens with intensified land use. However, even on traditionally managed wetlands 18.5% of the populations had gone extinct. Moreover, 40% of all remaining populations were smaller than 250 flowering plants. We conclude that both intensified agricultural practice and habitat fragmentation contributed to local extinction of *S. perennis*. Small populations, especially, may not be able to persist in the long term. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Altitude; Calcareous fens; Nutrient input; Habitat fragmentation; Small populations

1. Introduction

Calcareous pre-alpine fens belong to the few remaining semi-natural ecosystems of Central Europe (Ellenberg, 1978). These wetlands were traditionally mown in late summer or extensively grazed. Their vegetation (Caricion davallianae alliance) is characterised by a remarkable species diversity, with an average species richness of more than 100 vascular plants and an average density of more than 30 species per 2 m^2 (Peintinger, 1999). Moreover, wetlands harbour nearly 50% of all endangered plant species in Switzerland (Landolt, 1991). However, the persistence of many species, and especially of habitat specialists, is threatened by human activity (Ehrlich and Wilson, 1991). In Switzerland, all wetlands have undergone large-scale destruction, fragmentation, and deterioration through land use intensification (i.e. drainage, nutrient input) during the last century (Hintermann, 1992). Man-made impacts were more drastic in lower regions with higher human population density than at higher altitudes (Hintermann, 1992; Peintinger, 1999; Wettstein and Schmid, 1999; Bühler and Schmid, 2001).

Habitat fragmentation, which subdivides sites and isolates populations, also induces negative effects of small population size on population viability (Jennersten et al., 1992; Ellstrand and Elam, 1993; Young et al., 1996; Young and Clarke, 2000). The persistence of small, isolated populations is threatened by environmental, demographic and genetic stochasticity (Shaffer, 1987). Moreover, fragmentation may considerably change biotic interactions between species (Saunders et al., 1991). Negative effects of small population size on plant fitness (Allee effects, Allee et al., 1949) can further increase extinction risks of small populations (Courchamp et al., 1999; Stephens and Sutherland, 1999). Today, stochasticity and Allee effects affect many small remaining populations. Habitat specialists, which depend on particular habitat types, may be much more vulnerable than generalists, which occur in many different habitat types.

Swertia perennis L. (Gentianaceae) is a specialist of calcareous fens north of the Swiss Alps, where it can form large populations. However, because the overall

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fen area has decreased drastically in recent decades, population sizes today are probably much smaller than a century ago. Moreover, the geographic isolation of fens has increased considerably, and rates of local extinction of fen species most likely exceed rates of colonisation.

Local extinction can be studied by comparison of historical with current data (Ouborg, 1993; Bisang and Urmi, 1994; Byfield and Pearman, 1996; Leach and Givnish, 1996; Rich and Woodruff, 1996; Fischer and Stöcklin, 1997; McCollin et al., 2000). Here, we used plant herbarium records to locate sites that had once hosted *Swertia perennis*. To evaluate the extent of and possible reasons for local population extinction during the last century, we revisited these sites in 1998. We asked the following questions: (1) what is the current state of sites? (2) How many populations are extinct and how large are remaining populations? (3) Do site characteristics (altitude, position in the Swiss distribution range of *Swertia perennis*, site area, current land use, and presence of indicator species) explain the occurrence of local extinction or current population size? (4) Is the age of the herbarium record correlated with local extinction or population size? (5) Is the present protection status of sites correlated with local extinction or population size?

2. Materials and methods

2.1. Study species

Swertia perennis is a long-lived, iteroparous, herbaceous perennial, which grows in calcareous fens and very wet grasslands (Hegi, 1906). It has a wide, but discontinuous distribution from Central Europe through Asia to western North America, with a centre in the European Alps (Hulten and Fries, 1986). Although it can be locally abundant, it is considered endangered worldwide (Jäger and Hoffmann, 1997). In Switzerland, it only occurs in pre-alpine fens north of the Alps, i.e. in fens in the mountainous region situated between the Alps and the Swiss lowlands (Fig. 1; Welten and Sutter, 1982). The Red List classification status of *Swertia perennis* varies among Swiss regions from not 'endangered' to 'highly endangered' or even 'extinct' (Landolt, 1991).

Vegetative adults of *Swertia perennis* form a rosette of ovate leaves and can develop daughter rosettes from lateral meristems. A reproductive shoot has a single, 15–60 cm long stalk with up to 30 light-purple, star-shaped, proterandric flowers (Hegi, 1906). Plants of *Swertia perennis* flower from July to August, and attract a wide range of insects. Up to 50 winged seeds are produced in one ovate capsule per fruit. The above-ground parts die back in autumn as soon as they are covered by snow and re-emerge in April or May.

2.2. Selection of study region and sites

Northeastern Switzerland is rich in pre-alpine fens. Most herbarium records concerning this region are stored at Zürich University and at the Swiss Federal Institute of Technology (ETH Zürich). Here, we found 144 records of *Swertia perennis* from north-east-Switzerland in 1998. The description of 58 sites was so imprecise that we could not relocate them. All other collection sites were located near identifiable landmarks, such as small villages, rivers, and hills, but a further 25 sites were hardly accessible. The age of the herbarium records from the remaining 63 sites used in this study ranged from 5 to 127 years (mean 69, median 77 years). We revisited these 63 sites in July and August 1998, when plants of *Swertia perennis* were flowering.

To ascertain that the weather was not exceptional in 1998, we compared the meteorological data from two stations located within the distribution range of *Swertia perennis* with the data of the preceding 10 years. The mean annual temperature in 1998 was the same as the average from 1988 to 1997 at both stations [Ebnat-Kappel (629 m.a.s.l.) 8.1°C, and Einsiedeln (910 m.a.s.l.) 6.8°C]. Annual precipitation in Ebnat-Kappel was 5% lower than during the previous decade (1998: 1791 mm; 1988–1997 mean: 1886 mm). In Einsiedeln, the differences in precipitation between 1998 (1730 mm) and the last decade (1758 mm) were negligible. These data suggest that our study was not distorted by unusual weather conditions during the census year.

2.3. Data acquisition

To accelerate the inventory procedure we used a form with predefined classes incorporating also continuous variates (e.g. site area, population size; Table 1). Each site was classified as follows: (1) we read its altitude from a 1:25 000 map (Landeskarte der Schweiz, Bundesamt für Landestopographie, Wabern, Switzerland; Appendix). (2) We noted the position of each site in the Swiss distribution range of *Swertia perennis* (central or peripheral). Peripheral sites were those that occurred at the margins of this distribution (Fig. 1; Welten and Sutter, 1982). In eastern north-east-Switzerland all sites north of Appenzell and Gonten, south-west of the river Thur, and south-west of Stein (including Stein and Nesslau) were considered peripheral. In central north-east-Switzerland peripheral sites were considered to be those north of Biberbrugg, and west of the wetland Rothenturm (excluding the Rothenturm sites). (3) We classified site area into five classes (Table 1A). (4) Current land use was assigned to three classes (Table 1B). (5) We recorded the presence of six species indicative of intact fens and of six species indicative of fens that were subject to nutrient input and drainage. As fen indicator species we used *Carex davalliana*, *C. panicea*, *Parnassia* *palustris*, *Primula farinosa*, *Succisa pratensis* and *Tofieldia calyculata*, which prefer nitrogen-poor habitats (indicator values 2–3; Ellenberg, 1978) and typically grow in the Caricion davallianae alliance following the Braun-Blanquet system (Ellenberg, 1978; BUWAL, 1990). As nutrient indicator species we used *Angelica sylvestris*, *Cirsium oleraceum*, *Filipendula ulmaria*, *Polygonum bistorta*, *Ranunculus aconitifolius* and *Trollius europaeus*, which prefer nitrogen-richer habitats or are indifferent to this factor (indicator values 4–7; Ellenberg, 1978) and are characteristic of the vegetation types Calthion and Filipendulion (BUWAL, 1990). (6) Further, the age of the herbarium record associated with every site was assigned to five classes (Table 1C). (7) Finally, the protection status of every site was assessed as unprotected, protected or unknown. 'Unknown' denotes sites with apparently traditional management, which are not nature reserves but may be set-asides that are protected through governmental contracts.

We checked each site for the occurrence of *Swertia perennis*. Since flowering adults are very conspicuous, they were easy to detect. If we did not find flowers, we carefully searched for the equally conspicuous parallel-veined leaves of vegetative plants of *Swertia perennis* for maximally 1 h. If this search remained unsuccessful, we considered the population to be extinct. We could have missed 'remnant populations' (Eriksson, 1996), which survive unfavourable periods with underground organs or seed banks. However, since the census year was not exceptional with respect to climate, and since we found large and small populations of *Swertia perennis* in both subregions, it is unlikely that some populations did not produce above-ground parts in the 1998 season. Finally, we assigned the population size of *Swertia perennis* to seven classes (Table 1D).

2.4. Data analysis

All data were analysed with a multiple regression model using the statistical software GENSTAT 5 (release 3.2.; Payne et al., 1993). First, we analysed extinction from all sites (1), followed by extinction from still traditionally managed sites only (2). Finally, we analysed the size of remaining populations (3).

(1) The binary data of extinction of populations from all 63 sites were analysed with logistic regression (Payne et al., 1993), using the complementary-log-log link (Candy, 1986). Deviance changes follow the χ^2 distribution, which allows tests of significance of factors. Site area class was log-transformed prior to analysis. (2) To test for causes of extinction in traditionally managed wetlands only (i.e. in mown or grazed fens), we used a reduced data set (54 sites), from

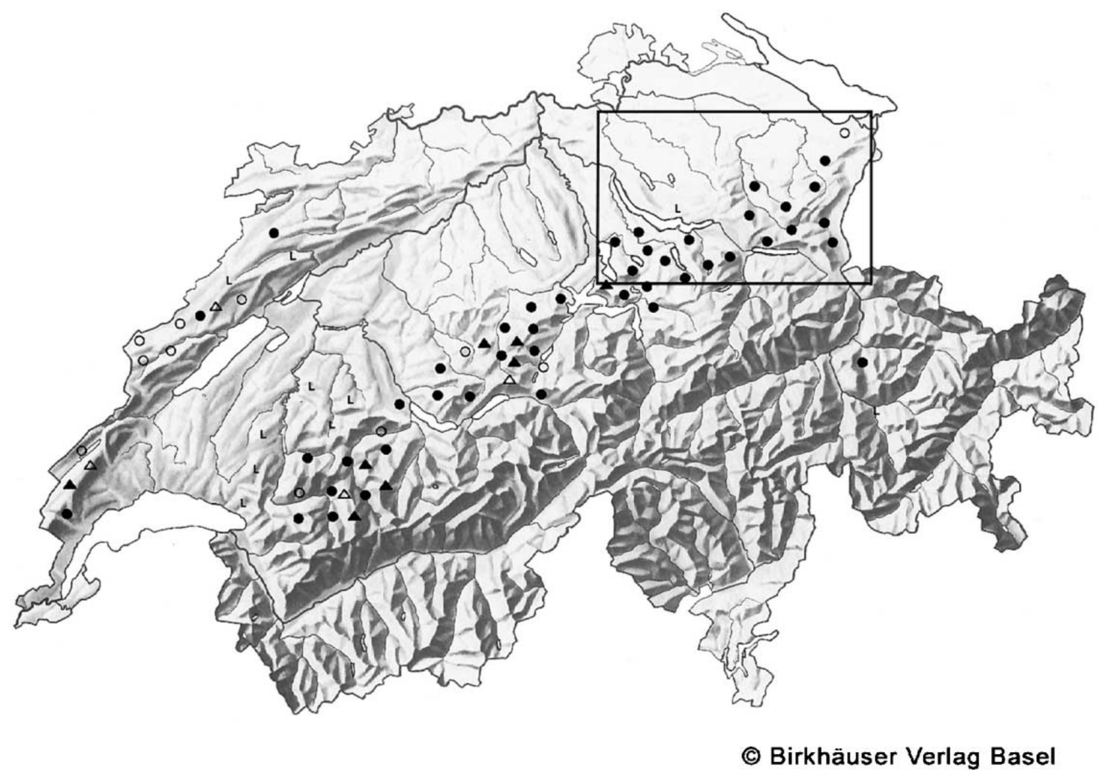

Fig. 1. Distribution of *Swertia perennis* in Switzerland (according to Welten and Sutter, 1982 © Birkhäuser Verlag, Basel) and location of our study region, which is depicted in more detail in Fig. 2. The symbols denote the occurrence of *Swertia perennis*: ●, in lowlands, frequent; ○, in lowlands, rare; ▲, in mountains, frequent; Δ, in mountains, rare; L, bibliographical reference.

which fertilised meadows, agricultural land and fallows were omitted. (3) Population size class (log-transformed) was analysed with an analysis of variance. Here, we only used the 48 sites that still hosted *Swertia perennis* populations.

To study the interdependencies between the different explanatory factors, we produced a correlation matrix of the pairwise relationships for each of the three data sets described earlier with the statistical software SPSS (release 8.0; SPSS Inc, Chicago, Illinois, USA). For the continuous variates (i.e. altitude, log-transformed site area class, number of fen indicator species, number of nutrient indicator species, age of record class) we used Pearson's correlation coefficient. Pairwise relationships between factors (distribution range and land use) and the continuous variates described earlier were analysed with one-way analysis of variance. The relationship between the two factors distribution range and land use was tested with the χ^2 test. The significance levels of all pairwise relationships were corrected for the Type 1 error with a sequential Bonferroni test (Dunn-Šidák method; Sokal and Rohlf, 1995).

Table 1
Classification of explanatory site characteristics and of population sizes of *Swertia perennis*: (A) site area, (B) current land use, (C) age of herbarium record associated with every site and (D) current population size

Class	Description of class
A	
0	Site destroyed
1	$\leqslant$400 m^2
2	401–2500 m^2
3	2501–10 000 m^2
4	10 001–250 000 m^2
5	$\geqslant$250 000 m^2
B	
0	Fertilised meadow or agricultural land
1	Mown fen
2	Grazed fen
3	Abandoned fen (fallow)
C	
1	$\leqslant$10 years (=1 record of the total census)
2	11–25 years (=2 records)
3	26–50 years (=8 records)
4	51–100 years (=48 records)
5	$\geqslant$100 years (=4 records)
D	
0	No *Swertia perennis* found
1	$\leqslant$10 flowering adults
2	11–25 flowering adults
3	26–50 flowering adults
4	51–100 flowering adults
5	101–250 flowering adults
6	251–1000 flowering adults
7	$\geqslant$1000 flowering adults

3. Results

3.1. Current state of sites

For most of the 63 locations land use had not changed during the last century. Fifty-four sites (86%) were still mown or grazed traditionally. Only four sites had been converted into fertilised meadows or agricultural land and only five sites were fallows. Five sites were classified as unprotected. Of the remaining 58 sites, 21 sites were protected and 37 were of unknown protection status.

3.2. Population extinction

On 15 of the 63 sites no populations of *Swertia perennis* were found (24%; Fig. 2). The likelihood of local extinction was independent of the age of the herbarium record (Table 2A). Extinction was more likely at lower than at higher altitude ($P<0.01$; Table 2A; Fig. 3A), in the peripheral (58% extinct) than in the central distribution range (9% extinct; $P<0.01$; Fig. 3B), on the smallest than on the larger sites (75% of populations extinct on fens <400 m^2; $P<0.05$; Fig. 3C), and on sites with intensified land use compared with mown or grazed fens and fallows ($P<0.05$; Fig. 3D).

All populations on unprotected sites were extinct (logistic regression: $n=63$, d.f.$=2$, deviance change$=7.95$, $P<0.001$). On the 21 protected sites, 19% of the *Swertia perennis* populations were extinct, and on the 37 sites with unknown protection status, 16% were extinct.

3.3. Population extinction from traditionally managed wetlands only

Of the 54 populations of *Swertia perennis* on traditionally managed sites (i.e. mown or grazed fens only), 10 (18.5%) were extinct. Here, extinction was more likely in the peripheral than in the central distribution range ($P<0.05$; Table 2B), and on the smallest fens than on larger ones ($P<0.01$). Moreover, extinction probabilities tended to be higher on grazed (20% extinct) than on mown fens (18% extinct; $P<0.1$).

3.4. Size of remaining populations of Swertia perennis

The sizes of the 48 remaining populations ranged from <10 to >1000 flowering adults. Populations were larger in fens with a larger area ($P<0.001$; Table 2C), and larger in fens in the central (median: 652 flowering adults) than in the peripheral distribution range (median: 176 flowering adults; $P<0.05$). All peripheral populations were smaller than 1000 flowering adults. Of the 48 remaining populations 40% consisted of fewer than 250 flowering adults (Fig. 2).

3.5. Pairwise relationships between explanatory site characteristics

The altitude of study sites was significantly correlated with the number of nutrient indicator species and with land use in all three data sets (Table 3), as well as with the distribution range in the first two data sets (Table 3A, B). This mirrors the fact that agricultural changes and human impact were less severe at higher altitudes and that the majority of sites in the peripheral distribution range occur at lower altitudes.

4. Discussion

4.1. Current state of sites

For up to 127 years, land use had remained unchanged for the majority of the studied fens, 86% of which were still mown or grazed traditionally. Only five sites were obviously unprotected. All other sites were either designated nature reserves, or their conservation status was unknown. Presumably, many of the latter fens are protected by governmental management contracts with the farmers. Thus, conservation practice in Switzerland seems to be able to impede direct destruction of entire sites and to preserve a more or less traditional land use. Nevertheless, wetlands were historically much larger and continuous than they are today and have been reduced by 90% since 1800 (Broggi and Schlegel, 1989). Moreover, even if the type of land use remained unchanged, its intensity has increased in many sites because of drainage, use of heavy machinery, premature mowing or larger cattle herds on grazed sites (Hintermann, 1992).

4.2. Extinctions

The likelihood of population extinction of *Swertia perennis* was independent of the age of the herbarium record, indicating that extinctions also occurred recently. While our method allowed us to study local extinctions, it did not allow us to detect colonisations. However, because in the last century fens have been very much reduced in number and size (Broggi and Schlegel, 1989), the potential sources for colonisation have drastically decreased. The increased isolation of remaining sites further reduces the likelihood of colonisation. Therefore, we consider it highly probable that the number of local extinctions is not balanced by recolonisations in our study area, i.e. that *Swertia perennis* forms a non-equilibrium metapopulation with higher local extinction than colonisation rates (Harrison, 1991). Presumably, many of the very old records stem from large wetlands, which are small and fragmented today, but which still exist as remnants. From industrialisation until legal protection in 1987 (constitutional protection of Swiss wetlands by the so-called

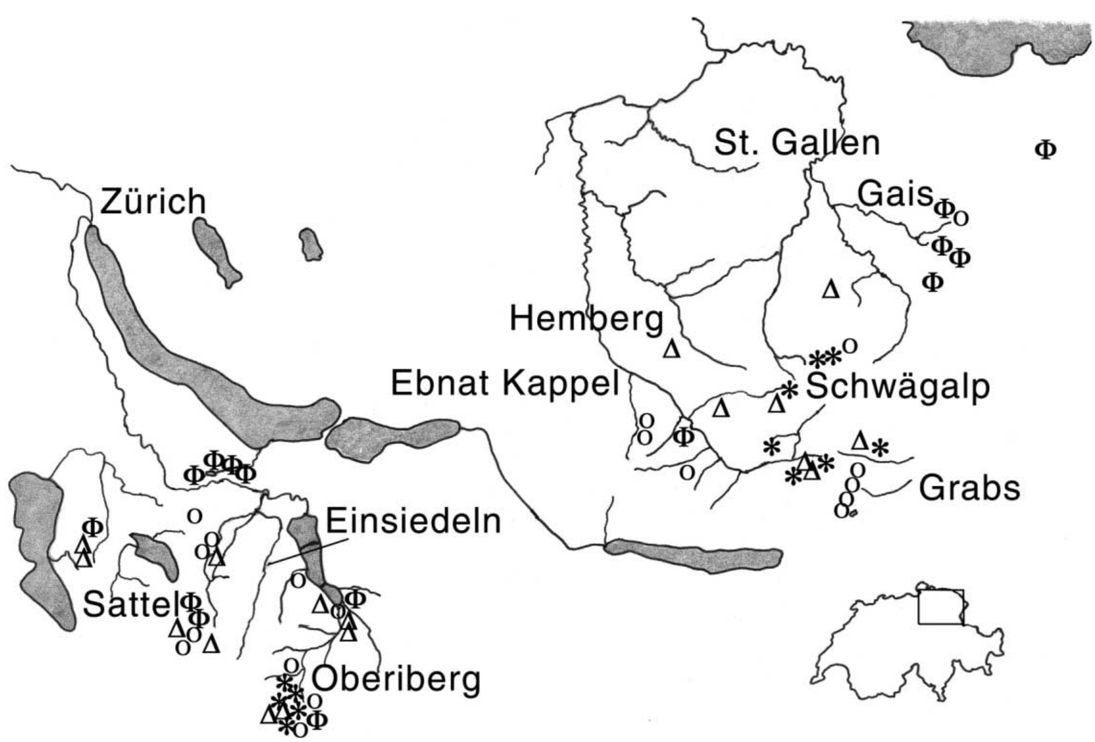

Fig. 2. Extinct populations and sizes of remaining *Swertia perennis* populations on 63 sites in Northeast Switzerland, from which herbarium records of *Swertia perennis* exist. Population size classes: Φ, extinct; ○, ⩽250 flowering adults; Δ, 251–1000 flowering adults; and *, ⩾1000 flowering adults. Insert: Switzerland with study region.

Rothenturm-Artikel) direct destruction of wetlands, drainage and fertilisation were common practice in Switzerland. Moreover, even during the last two decades pressure on the remaining wetlands has remained strong. For instance, in 91 Swiss wetlands nearly two 'relevant impacts' per km^2 (such as drainages, fertilisation and other agricultural influences, or new road and house constructions) were detected. Seventy-five per cent of these occurred after 1983 (national wetland inventory, Hintermann, 1992). However, the overall wetland area that is affected by these direct impacts is smaller than the area affected by indirect human impact, and only five of the 15 observed extinctions of *Swertia perennis* populations were attributed to direct destruction or abandonment of sites. Hence, indirect processes, such as increased nutrient input from surrounding farmland, drainage and habitat fragmentation, nowadays poses a larger threat to population persistence in wetlands than direct destruction of sites.

Table 2
Results of the logistic regression analysis on extinction (A, B), and analysis of variance on sizes (C) of *Swertia perennis* populations

Parameter	d.f.	Deviance change (A, B) or mean squares (C)
A		
Altitude	1	6.976**
Distribution range	1	9.530**
Site area	1	5.721*
Land use	3	10.676*
No. fen ind. species	1	1.253
No. nutrient ind. species	1	0.573
Age of record	1	0.075
Residuals	53	34.355
B		
Altitude	1	1.907
Distribution range	1	4.723*
Site area	1	7.240**
Land use	1	3.335†
No. fen ind. species	1	0.781
No. nutrient ind. species	1	1.407
Age of record	1	0.120
Residuals	46	32.238
C		
Altitude	1	0.034
Distribution range	1	0.503*
Site area	1	2.304***
Land use	2	0.185
No. fen ind. species	1	0.107
No. nutrient ind. species	1	0.092
Age of record	1	0.003
Residuals	39	0.121

(A) population extinction using the entire data set (63 sites); (B) population extinction using only the data on the 54 still traditionally managed wetlands; (C) population sizes using only the data on the 48 remaining populations. Note: the number of land use categories differs in each of the three analyses ($^{\dagger}P<0.1$; $^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$).

4.2.1. *Intensified agricultural practices*

Increased extinction probabilities of *Swertia perennis* populations at lower altitudes and in the peripheral distribution range (Fig. 3A, B; Table 2) can be explained by increased indirect agricultural pressure. Farming has been greatly intensified at the easily accessible lower altitudes. Here, wetlands are surrounded by intensively used agricultural land (Hintermann, 1992), whereas at higher altitude in north-east Switzerland, an increased proportion of sites with conservation relevance surrounds fens (Wettstein and Schmid, 1999). This also applies to the peripheral distribution range, which is confounded with altitude (Table 3).

Increased productivity can decrease species richness (Wheeler and Giller, 1982; Willems and Nieuwstadt, 1996; Pauli, 2000), possibly because plants with a low growth rate are outcompeted (Grime, 1973; Tilman, 1997). Since *Swertia perennis* is confined to narrow habitat conditions it is quickly excluded through competition when environmental factors change (Stoicovici, 1984). Thus, increased nutrient input as well as drainage at low altitude can lead to local extinction of *Swertia perennis* populations. Moreover, atmospheric nitrogen input, which was not assessed in our study, presumably also adversely affects species composition and eventually species richness of these low-productivity wetlands (Pauli, 2000). However, the situation concerning atmospheric nutrient input is not quite as severe in Switzerland as in other European countries (Fischer and Stöcklin, 1997). The hypothesis of increased nutrient input into fens at lower altitudes is supported by several studies in north-east Switzerland. Fertilisation of calcareous fens significantly affected species composition by changing the dominance of functional plant groups (Pauli, 2000). Moreover, with increasing altitude, the density of *Succisa pratensis* adults and seedlings (Bühler and Schmid, 2001) and the species richness of both fen plants and insects increased (Peintinger, 1999; Wettstein and Schmid, 1999). This was explained by an overall lower management intensity at higher altitudes.

4.2.2. *Habitat fragmentation*

Habitat fragmentation was presumably responsible for local population extinctions on still traditionally managed wetlands (Table 2B), since here the likelihood of extinction was highest on the smallest fens (Fig. 3C). Site area was not related to any other site characteristics (Table 3) and thus seems to be independent of increased productivity. Small site area is presumably the result of habitat fragmentation and of partial destruction of formerly larger sites. These smaller sites harboured smaller populations (Table 2C), which have increased extinction risks due to stochasticity (Shaffer, 1987) and

Allee effects (Allee et al., 1949; Courchamp et al., 1999; Stephens and Sutherland, 1999). Indeed, consistent with an Allee effect, we found in related studies that small site area combined with a high degree of spatial isolation negatively affected *Swertia perennis* populations: density of adult plants, genetic variability and several phenotypic fitness measures of *Swertia perennis* were all significantly reduced in small, isolated fens (Lienert et al., unpublished data). A combination of stochasticity with these genetic and demographic factors could eventually lead to population extinction.

4.3. Size of remaining populations

The survival of large populations of *Swertia perennis* in the central part of the distribution range and on large fens (Table 2C) suggests that reasonably large sites should be maintained to promote *Swertia perennis*. Forty per cent of all *Swertia perennis* populations consisted of <250 flowering adults (19 populations), and 25% (12 populations) were even smaller, with <100 flowering adults (Fig. 2). Persistence of such small populations is very uncertain. To be able to estimate the long-term survival probabilities of *Swertia perennis*, information on the longevity of the seed bank would be useful. Plants with longer-lived seeds have significantly lower local extinction rates than plants with short-lived seeds in Swiss calcareous grasslands (Stöcklin and Fischer, 1999). Unfortunately, published information regarding the seed bank of *Swertia perennis* is not available. However, population viability analyses (PVA) and estimates of minimum viable population size (MVP) suggest that extinction probabilities are high for populations of sizes comparable with our smallest *Swertia perennis* populations (Shaffer, 1987; Soulé, 1987; Simberloff, 1988; Menges, 1991). These theoretical predictions are strongly supported by the few existing plant studies that relate documented population extinction to original population size (Matthies, 1991) or that model real-world data (Oostermeijer, 2000; Young et al., 2000).

Moreover, in the smallest fen sites, an unfavourable edge-to-perimeter relationship increases nutrient influx from surrounding farmland, which enhances the adverse effects discussed earlier. In a related study, average vegetation height (as a measure of productivity) was 20 cm higher in fens smaller than 0.5 ha, than in fens larger

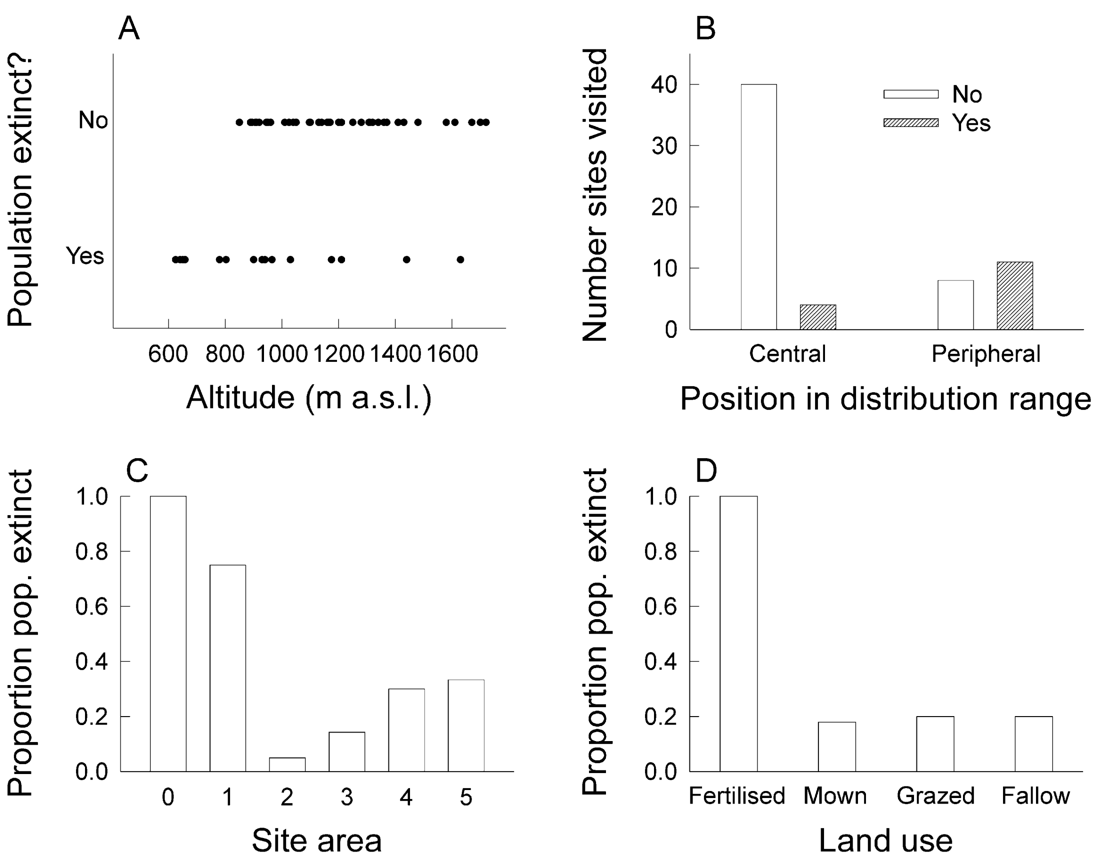

Fig. 3. Extinction of *Swertia perennis* populations using the entire data set (63 sites) as a function of (A) altitude ($P<0.01$; Table 2A); (B) position in distribution range ($P<0.01$); (C) present site area [$P<0.05$; 0: site destroyed (1 site); 1: $\leqslant 400$ m^2 (8 sites); 2: 401–2500 m^2 (20 sites); 3: 2501–10 000 m^2 (21 sites); 4: 10 001–250 000 m^2 (10 sites); 5: $\geqslant 250\,000$ m^2 (3 sites)]; (D) land use ($P<0.05$; 0: fertilised meadows or agricultural land (4 sites); 1: mown fens (39 sites); 2: grazed fens (15 sites); 3: abandoned fens (fallows; 5 sites).

Table 3
Pairwise relationships between explanatory site characteristics: (A) all 63 study sites; (B) only the 54 still traditionally managed wetlands (i.e. mown or grazed fens); (C) only the 48 sites with remaining populations

Parameter	Statistical test	Altitude	Site area	Fen ind. spec.	Nutrient ind. spec.	Age of record	Distribution range
A							
Site area	Pears. corr.	↓ 0.005					
Fen ind. spec.	Pears. corr.	↑ 0.060	↑ 0.019				
Nutrient ind. spec.	Pears. corr.	↓ 0.238***	↑ 0.032	↑ 0.023			
Age of record	Pears. corr.	↓ 0.004	↑ 0.005	↓ 0.046	↓ 0.005		
Distribution range	ANOVA	0.318***	0.000	0.102	0.014	0.015	
Land use	ANOVA/χ^2	0.487***	0.010	0.455***	0.369***	0.037	$0.196^{\dagger}$
B							
Site area	Pears. corr.	↓ 0.013					
Fen ind. spec.	Pears. corr.	↓ 0.001	↑ 0.043				
Nutrient ind. spec.	Pears. corr.	↓ 0.429***	↑ 0.044	↑ 0.004			
Age of record	Pears. corr.	↓ 0.000	↑ 0.002	↓ 0.022	↓ 0.001		
Distribution range	ANOVA	0.235**	0.000	0.001	0.026	0.005	
Land use	ANOVA/χ^2	0.417***	0.016	0.059	0.375***	0.001	0.078
C							
Site area	Pears. corr.	↓ 0.000					
Fen ind. spec.	Pears. corr.	↑ 0.019	↓ 0.001				
Nutrient ind. spec.	Pears. corr.	↓ 0.438***	↑ 0.006	↓ 0.009			
Age of record	Pears. corr.	↑ 0.001	↑ 0.001	↓ 0.049	↓ 0.008		
Distribution range	ANOVA	0.139	0.004	0.023	0.018	0.003	
Land use	ANOVA/χ^2	0.390***	0.003	0.029	0.392***	0.011	0.064

In the table we present r^2, the significance levels were corrected with a sequential Bonferroni test. Arrows (↑ pos./↓ neg.) indicate the direction of the relationship for the Pearson's correlation. For details of the statistical tests, see Section 2 ($^{\dagger}P<0.1$; $^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$).

than 5 ha (Lienert et al., unpublished data). Furthermore, small wetlands are often unprotected, which again increases the likelihood of extinction.

5. Conclusions

Although *Swertia perennis* is a fairly common plant in north-east Switzerland and occurred on 44% of 36 randomly selected fens larger than 1 ha (Peintinger, 1999; Pauli, 2000), survival of remaining populations is by no means certain. In the past, populations especially in the periphery of the distribution range and at low altitude have become extinct, even if the fens themselves still exist. Our study suggests that *Swertia perennis* populations are slowly retreating from the edges of an overall diminishing distribution range. Our study further suggests that this habitat specialist is sensitive to both intensified agricultural practices and to habitat fragmentation. Moreover, since many fen specialists depend on similar habitat conditions as *Swertia perennis*, these conclusions may also apply to other plant species, such as *Parnassia palustris*, *Primula farinosa*, *Succisa pratensis* and *Tofieldia calyculata*.

To avoid future extinctions, excessive nutrient input should be avoided. Since fens are often surrounded by intensively managed agricultural land, sufficiently large nutrient-buffer zones around the edges must be established. It is essential that recommendations for nutrient, as well as hydrological buffer zones (Marti et al., 1997) are effectively implemented (Findlay and Houlahan, 1997; Pauli, 2000). Furthermore, ongoing fragmentation and reduction of fen area must be avoided. We suggest, that even fens as small as 400 m^2 are worth protecting, since only populations on the smallest fens had increased extinction probabilities [also see Semlitsch and Bodie (1998), who recommend protection of wetlands >2000 m^2]. Our study demonstrates that population extinction is an ongoing process, which affects not only rare species, but also formerly common specialists confined to species-rich semi-natural wetlands.

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Appendix. Location, altitude, distribution range, management status, and population sizes of *Swertia perennis* for the 63 study sites[1]

Site	Local authority	Canton	Latitude (m)	Longitude (m)	Altitude (m.a.s.l.)	Distribution range (c = central, p = peripheral)	Site area (classified as in Fig. 3)	Land use	Population size (number of flowering adults)
Gonten, Torfmoor	Gonten	AI	243 200	744 900	910	p	3	Mown fen	251–1000
Najenriet	Oberegg	AI	255 500	760 500	803	p	5	Fertilised meadow	0
Eggerstanden	Rüte	AI	243 850	753 100	940	p	1	Mown fen	0
Borstböhl, Potersalp	Schwende	AI	238 300	745 125	1200	c	2	Grazed fen	26–50
Kammhalde, Potersalp	Schwende	AI	237 100	743 550	1360	c	4	Mown fen	⩾1000
Sauböhl, Potersalp	Schwende	AI	237 150	744 200	1320	c	4	Grazed fen	⩾1000
Hirschberg	Gais	AR	246 600	754 350	1030	p	3	Fallow	0
Hirschberg	Gais	AR	247 075	753 825	965	p	1	Mown fen	0
Schwäbrig-Weiherchen	Gais	AR	249 850	754 075	1165	p	2	Mown fen	⩽10
Unter-Gäbris	Gais	AR	249 850	753 950	1175	p	2	Mown fen	0
Schwarzegg, Schwägalp	Urnäsch	AR	235 400	741 350	1280	c	3	Mown fen	⩾1000
Gräppelensee	Alt St. Johann	SG	230 550	739 850	1307	c	3	Grazed fen	⩾1000
Engialp	Ebnat-Kappel	SG	230 050	728 300	1040	p	2	Grazed fen	101–250
Steintal	Ebnat-Kappel	SG	231 700	728 600	850	p	2	Mown fen	26–50
Sommerigchopf	Gams	SG	230 900	748 500	1280	c	4	Mown fen	⩾1000
Alp Gamperfin	Grabs	SG	226 300	747 075	1310	c	2	Mown fen	⩽10
Gamperfin, Hochmoor	Grabs	SG	226 425	747 350	1320	c	3	Fallow	101–250
Ölberg, Herti, im Wald	Grabs	SG	227 250	746 900	1430	c	2	Fallow	26–50
Voralpsee	Grabs	SG	224 900	747 150	1130	c	2	Grazed fen	26–50
b. Hochmoor Scherb	Hemberg	SG	237 750	730 700	1100	c	2	Mown fen	251–1000
Rietbad	Krummenau	SG	233 900	735 950	920	c	2	Mown fen	251–1000
Wideralp	Krummenau	SG	234 625	741 450	1340	c	2	Grazed fen	251–1000
Nesslau	Nesslau	SG	231 250	732 800	780	p	3	Mown fen	0
Stein - Hinterlaad	Stein	SG	228 700	733 700	950	p	3	Mown fen	101–250
Lisighaus	Wildhaus	SG	229 400	743 350	1010	c	3	Mown fen	251–1000
Munzenriet	Wildhaus	SG	229 300	745 000	1025	c	5	Mown fen	⩾1000
Richtung Schwendiseen	Wildhaus	SG	228 625	743 800	1130	c	2	Mown fen	251–1000
Schönenbodensee	Wildhaus	SG	230 250	746 025	1097	c	3	Mown fen	251–1000
Schwendiseen	Wildhaus	SG	227 650	743 300	1160	c	4	Mown fen	⩾1000
Breitried, Studen	Einsiedeln	SZ	215 500	705 000	889	c	4	Mown fen	251–1000
Euthal	Einsiedeln	SZ	216 550	704 900	900	c	1	Mown fen	0
Rotmoos, Grosser Runs	Einsiedeln	SZ	217 950	700 750	960	c	2	Mown fen	101–250
Schachen, Euthal	Einsiedeln	SZ	215 750	704 700	890	c	3	Mown fen	101–250

(*continued on next page*)

Appendix *(continued)*

Steinbach	Einsiedeln	SZ	216 650	703 250	890	c	3	Mown fen	251–1000
Itlimoos-Weiher	Feusisberg	SZ	226 600	695 200	650	p	4	Mown fen	0
Chruthüttli, Hoch Ybrig	Illgau	SZ	206 500	700 400	1580	c	4	Grazed fen	⩾1000
Fuderegg, Hoch Ybrig	Illgau	SZ	207 750	702 100	1480	c	3	Mown fen	⩾1000
Hessisbohl, Hoch Ybrig	Illgau	SZ	206 350	702 450	1630	c	1	Grazed fen	0
Nielenstock, Hoch Ybrig	Illgau	SZ	206 450	700 800	1610	c	3	Grazed fen	251–1000
Seebli, Hoch Ybrig	Illgau	SZ	207 650	702 450	1430	c	3	Grazed fen	50–100
Änglisfang	Oberiberg	SZ	209 825	700 550	1200	c	2	Mown fen	⩾1000
Bändigstobel	Oberiberg	SZ	210 350	700 450	1250	c	1	Fallow	⩽10
Bueffen, Steinerboden	Oberiberg	SZ	209 450	701 100	1170	c	4	Fallow	⩾1000
Lauchern, Hoch Ybrig	Oberiberg	SZ	206 675	701 100	1700	c	3	Grazed fen	251–1000
Spirstock, Hoch Ybrig	Oberiberg	SZ	206 350	701 400	1720	c	2	Grazed fen	101–250
Windegg, Hoch Ybrig	Oberiberg	SZ	206 850	700 750	1670	c	3	Grazed fen	⩾1000
Äusser Altmatt	Rothenturm	SZ	220 800	694 950	906	c	3	Mown fen	251–1000
Vorder Mäderen	Rothenturm	SZ	214 725	693 200	1210	c	1	Grazed fen	0
Bannegg, Herrenboden	Sattel	SZ	213 650	693 650	1440	c	1	Grazed fen	0
Bärenfang, Hochstuckli	Sattel	SZ	213 425	693 250	1370	c	2	Mown fen	101–250
Mostelberg, Herrenboden	Sattel	SZ	213 550	692 300	1140	c	3	Mown fen	251–1000
Mostelegg, Schwand	Sattel	SZ	212 150	692 725	1210	c	1	Mown fen	⩽10
Haggenegg	Schwyz	SZ	212 050	694 750	1410	c	2	Mown fen	251–1000
Chilenried, Studen	Unteriberg	SZ	214 700	705 500	890	c	3	Mown fen	251–1000
Erlenmoos	Wollerau	SZ	226 900	695 450	625	p	4	Fertilised meadow	0
Bibersteg, Altmatt	Oberägeri	ZG	221 250	694 750	895	c	2	Mown fen	50–100
Raten	Oberägeri	ZG	221 910	693 600	1050	p	2	Mown fen	⩽10
Steinstoss, Altmatt	Oberägeri	ZG	220 500	693 850	920	c	3	Mown fen	50–100
Eigenried	Zug	ZG	219 850	683 025	960	p	5	Mown fen	251–1000
Hinterer Geissboden	Zug	ZG	220 675	683 000	945	p	2	Mown fen	251–1000
Schönfels	Zug	ZG	221 725	683 125	930	p	3	Fertilised meadow	0
Hüttnersee	Hütten	ZH	226 500	693 500	658	p	4	Mown fen	0
Weberrüti, Samstagern	Richterswil	ZH	227 150	694 650	641	p	0	Agricultural land	0

[1] Coordinates refer to the Swiss map grids.

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