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Floral free fall in the Swiss lowlands: environmental determinants of local plant extinction in a peri-urban landscape

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Summary

1 Local floras are being depleted by a host of human activities, including habitat destruction and fragmentation, eutrophication, and the intensification of agriculture. Species with particular ecological demands or life-history attributes are more prone to extinction than species with a broader niche.

2 We used an old herbarium from the municipality of Küsnacht (Swiss lowlands) as a historical record for comparison with contemporary plant diversity. This comparison revealed that 17% to 28% of all vascular plants that occurred between 1839 and 1915 were extinct by 2003.

3 Species of different habitats and life-forms had significantly different rates of extinction: wetlands, disturbed sites and meadows lost most species, whereas forests and rocky habitats were least affected; aquatics and annuals were most prone to extinction, geophytes and hemicryptophytes were intermediate, and phanerophytes and chamaephytes were least affected.

4 Species adapted to nutrient-poor soils suffered highest extinction in all habitats, indicating that eutrophication poses an urgent threat to species diversity. Light and soil moisture requirements also had significant effects on extinction, but the direction of the effect varied by habitat.

5 When species were grouped into IUCN categories of the red list of Switzerland, the rank order of the observed extinction matched the red list assignment.

6 Because many of the remaining species had high estimated extinction probabilities and because extinction is often delayed (extinction debt), a substantial part of the remaining flora of Küsnacht is likely to go extinct in the near future. This will increase the dominance of the common species that already comprise 81% of the local flora.

7 The rates and patterns of extinction in Küsnacht are probably representative of surrounding Swiss lowlands and peri-urban landscapes in most developed countries. Studies such as ours can serve as a call for action and form a basis for future monitoring of biodiversity.

Key-words: decrease in plant diversity, estimated extinction probability, extinction debt, fragmentation, habitat destruction, intensified agriculture, IUCN, physical indicators, trivialization of local flora

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Introduction

Local floras are being depleted as humans exert an ever-increasing impact on terrestrial ecosystems (Vitousek *et al*. 1997). However, the full extent of extirpation is unknown because it is rare to find historical records of the plant species that once occurred in a given locale. In the few cases where comprehensive historical records are present, comparisons with current species lists have revealed substantial losses of the original flora, ranging from 21% to 38% (Drayton & Primack 1996; Landolt 2001; Chocholoušková & Pyšek 2003; Van der Veken *et al*. 2004). Clearly, these are alarming numbers that

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must be additionally substantiated by using suitable historical records to estimate local extinction rates. Historical records can also be used to elucidate the primary causes of local extinction and to identify the ecological demands or life-history attributes that predispose plant species to extinction.

In heavily populated areas, habitat destruction and fragmentation are seen as the most important causes of local extinction (Tilman *et al*. 1994; Fahrig 1997; Thompson & Jones 1999; Brook *et al*. 2003). In contrast, eutrophication is a more subtle but pervasive cause of local extinction, particularly in industrial regions with high nitrogen deposition, and in intensively cultivated areas with high levels of nitrogen fertilization (Suding *et al*. 2005). The intensification of agriculture has also been shown to result in the extinction of species inhabiting old cultural landscapes (Chamberlain & Fuller 2000; Maes & Van Dyck 2001).

It is known that species with certain ecological demands or life-history attributes are more prone to extinction (Davies *et al*. 2000; Henle *et al*. 2004; Koh *et al*. 2004). For example, species with short life cycles (e.g. annuals) are more prone to extinction because they are subject to greater population fluctuations in variable environments (Fischer & Stöcklin 1997). It has also been suggested that species with particular resource requirements are more susceptible to extinction (e.g. plants with low nutrient demands; Colling & Matthies 2006). However, these hypotheses have not been fully tested because historical records rarely include a sufficient range of species and habitats.

Previous studies have used historical data to examine the causes of extinction for particular habitats and species (Lienert *et al*. 2002). For instance, revisitation of permanent plots revealed altered land use and fragmentation to be responsible for the extinction of short-lived habitat specialists in calcareous grasslands (Fischer & Stöcklin 1997; Garbutt & Sparks 2002), and single-species revisitation studies identified habitat destruction and isolation as causes of the extinction of local fern populations (Käsermann & Moser 1999; Landergott *et al*. 2000). However, because such studies are confined to a single habitat or species, they are of limited value in assessing the threats to local floras as a whole. In order to assess which species are most prone to local extinction, it is necessary to utilize historical records that contain large numbers of species from many different habitats and yet are confined to coherent geographical areas (Shaffer *et al*. 1998).

A herbarium in Küsnacht provides such an historical record. Küsnacht is a medium-sized municipality in the Swiss lowlands on the north-eastern bank of Lake Zürich. The local teacher's college (Seminar Küsnacht) was founded in 1832 and established and actively fostered its own herbarium. Küsnacht represents a cross-section of common habitat types in the Swiss lowlands. Thus, the herbarium of the Seminar Küsnacht provides a unique historical record of the plant species that once occurred in a large area spanning many different habitat types that were or are typical of the Swiss lowlands.

In this paper, we compare the historical record with the current complement of species to address the following five questions. (i) How many species have gone extinct since the beginning of the 20th century? (ii) Was extinction random across different habitats? (iii) What underlying environmental and landscape changes have caused extinction? (iv) What life-history attributes make a plant species more prone to extinction? (v) Which of the remaining species face the greatest risk of extinction?

Methods

DESCRIPTION OF THE MUNICIPALITY OF KÜSNACHT

Küsnacht is embedded in a landscape shaped by past glaciations. Its highest elevation (770 m a.s.l.) is part of a longer mountain chain (Pfannenstil), which originated as a lateral moraine of Pleistocene glaciers (Hantke 1980). Several streams carve deep ravines into the layered strata of Quaternary sediments on their way down to Lake Zürich (400 m a.s.l.). The biologically richest and most prominent ravine of the Lake Zürich area, the Küsnachtertobel, is located in the municipality of Küsnacht and has attracted many generations of botanists over the last two centuries (Schmid *et al*. 1937; Holderegger 1994). It also harbours a few rare, supposedly glacial relics such as *Saxifraga aizoides* or *Asplenium septentrionale* (Holderegger 1994). The multitude of different exposures, slopes and soils results in a diversity of natural habitats, including calcareous fens found on poorly drained marl. Küsnacht exhibits a number of these relatively rare but species-rich habitats, some of which are protected and categorized as regionally important.

The greater area of Lake Zürich is an old cultural landscape. Cultivation of a diversity of food crops on fields, pasture farming, and meadows used for hay production are common in Küsnacht. The south-exposed mountain side facing Lake Zürich is used for the cultivation of grapes, although most of the vineyards in Küsnacht have disappeared during the last century. The calcareous fens have been used to harvest mulch for lifestock over centuries, and forests were formerly subjected to a variety of different management methods (e.g. coppicing, fire wood collection, selective harvesting, wood pastures, and autumnal collection of leaf litter for lifestock).

Due to its proximity to Zürich (10 km), Küsnacht has undergone rapid urbanization over the last half century. Currently, one-third of its total area (12.36 km^2) is developed, but one-third is forested, and another third remains in agriculture, including meadows and fields (Statistics Agency of the Canton of Zürich 2006).

PAST SPECIES LIST

The herbarium of the Seminar Küsnacht contains approximately 2000 herbarium sheets for 454 local plant

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species and covers all of the habitats that had been present within Küsnacht's boundaries. The original purpose of the herbarium was twofold: (i) to familiarize teachers studying at Seminar Küsnacht with the local flora, and (ii) to document the collections of botanists who frequently visited Küsnacht due to the diversity of rare habitats and its proximity to Zürich. Thus, the herbarium includes records of many rare species, but fewer of the most common species, probably because most teachers were familiar with these common species or because they could be readily located near schools.

We inspected all vascular plant specimens collected for the herbarium of the Seminar Küsnacht (now at herbarium Z) during the period of 1839–1915 and compiled a list of specimens collected within the boundaries of Küsnacht. For each specimen, we verified the species determination. In rare cases of incorrect species identifications, we determined the correct names according to Heitz (1990). As past plant nomenclature and taxonomy are partially inconsistent with those used presently, we consolidated all taxa and names according to Aeschimann & Heitz (2005). We excluded species that were obviously cultivated or escaped from gardens. Hereafter, we will refer to all species on the past species list as recorded species.

CURRENT SPECIES LIST

The current species list was compiled in 2003 by R. Holderegger, a local resident with expert knowledge of the local flora (Holderegger 1994). As above, we excluded cultivated or escaped species from the current species list, as well as invasive species (neophytes) that probably colonized Küsnacht after the collection period of the herbarium. We do, however, include all invasive species in our current species list for future reference. During the last decade, Swiss farmers have been encouraged to sow seed mixtures of wild flowers along fields to increase plant and animal biodiversity (Herzog *et al*. 2005). Such fields occur in low frequency in Küsnacht. None of the species used in wild flower mixes in Küsnacht would, if not deliberately sown, be categorized as extinct (*Agrostemma githago*, *Anthemis tinctoria*, *Calendula arvensis*, *Centaurea cyanus*, *Consolida regalis*, *Legousia speculum-veneris*; R. Holderegger, personal observations). Plants of wild flower mixes thus either currently exist as naturally occurring species elsewhere in the municipality, or have never existed in Küsnacht. In the latter case, their status is similar to other cultivated or escaped species and, as such, we also excluded these deliberately sown plant species. To ensure that we did not falsely presume any rare species to be extinct, R. Holderegger verified the absence of supposedly extinct species by repeated searching for relict populations or individuals. For locations that were not developed or otherwise destroyed during the last century, he repeatedly visited the exact locations indicated on herbarium sheets between 1995 and 2003. Additionally, he also searched other suitable locations in the municipality's perimeter. Thus, we are confident that species we deem to be locally extinct no longer occur in Küsnacht.

The current species list contains many species that were not recorded in the herbarium of the Seminar Küsnacht. Most of these unrecorded species are common species that were probably not collected because they were uninteresting to collectors (see above). Hereafter, we will refer to species that are not included on the past species list as unrecorded species.

UPPER AND LOWER BOUNDS OF EXTINCTION

As we are confident that we have not falsely presumed any species to be extinct, we can accurately calculate the extinction rate of recorded species:

$$E_r = N_{r,\,extinct}/(N_{r,\,extinct} + N_{r,\,extant}) \qquad \text{eqn 1}$$

where $N_{r,\,extinct}$ is the number of past recorded species that went extinct, $N_{r,\,extant}$ is the number of presently recorded species, and E_r is the percentage of extinct recorded species.

However, we cannot accurately estimate the extinction rate for the entire past flora because it is possible that there were some rare species that remained unrecorded but subsequently went extinct. Nevertheless, we can calculate an accurate lower bound on the extinction rate of the entire flora as:

$$E_{min} = N_{r,\,extinct}/(N_{r,\,extinct} + N_{r,\,extant} + N_{ur,\,extant}) \qquad \text{eqn 2}$$

where $N_{ur,\,extant}$ is the number of extant but unrecorded species, and E_{min} is the minimum extinction rate for the entire flora. In other words, E_{min} would be the true extinction rate of the entire flora if there were no species that remained unrecorded through 1914 and subsequently went extinct. The true extinction rate is probably larger than E_{min}, and could be larger than E_r if the extinction rate among the unrecorded species was substantially higher than that of the recorded species. However, we assert that the true extinction rate lies between E_{min} and E_r, and is probably closer to E_{min}, because the unrecorded species were mostly common species. To substantiate this assertion, we used the IUCN red list for the eastern Swiss lowlands (Moser *et al*. 2002) to compare the extinction risk of unrecorded, extant species with the extinction risk of all recorded species (including extinct species). The results indicate that unrecorded species were less prone to extinction than recorded species (see Results).

DESCRIPTIVE VARIABLES

For each individual species, we assembled a suite of descriptive variables, including (i) habitat affiliation, (ii) life-form, (iii) resource requirements, and (iv) extinction risk.

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(i) Based on Ellenberg *et al*. (1991), we assigned each species to one of five categories that designate the habitat in which it typically occurs. The five habitat categories included forests, meadows, wetlands, rocks and disturbed sites (wild plant species growing in or at the edge of cultivated fields and settled areas). We combined species from deciduous forests, coniferous forests and shrublands into the forest category.

(ii) We assigned each species to one of Raunkiaer's life-form categories, including phanerophytes, chamaephytes, hemicryptophytes, geophytes, therophytes and aquatics (Ellenberg *et al*. 1991).

(iii) Landolt (1977) lists ordinal variables (equivalent to the well-known Ellenberg indicator values; Ellenberg 1996) that quantify the resource requirements of each species. We used the following three ordinal variables: soil moisture, light availability and soil nutrients. On a scale of 1–5, low numbers represent low while high numbers represent high resource requirements.

(iv) The IUCN red list of Switzerland (Moser *et al*. 2002) assigns all vascular plant species in the eastern Swiss lowlands to one of six ordinal extinction risk categories: regionally extinct (RE), critically endangered (CE), endangered (EN), vulnerable (VU), near threatened (NT), and least concern (LC).

STATISTICAL ANALYSIS

To test our assertion that the unrecorded species were less prone to extinction than the recorded species, we calculated the proportion of species in both groups that belong to IUCN's least concern category, and conducted a chi-square test to determine whether the proportions were significantly different.

To examine which characteristics predispose a species to extinction, we conducted several binary logistic regressions using three of the descriptive variables (i–iii) as predictors and status (1 = extinct, 0 = extant) as the dependent variable (SPSS 10.0; SPSS, Chicago, USA). We conducted three separate tests to assess whether a species' extinction risk depends on its habitat affiliation (i), its life-form (ii), or its resource requirements (iii). For multiple regression on resource requirements, we removed the non-significant interaction terms *a posteriori* using a stepwise procedure. We also conducted a regression using the IUCN red list categories (iv) to test whether they are significant predictors of extinction.

As a particular resource requirement (e.g. high light demand) may influence extinction risk in one habitat (e.g. field) but not in another (e.g. forest), we also grouped the recorded species by habitat affiliation and conducted separate regressions on each species group using resource requirements as predictor variables. Due to small sample size, we did not include species common to rocky habitats in this analysis.

In two cases the variation in extinction risk was non-linear with respect to a species' soil moisture requirements. In meadows and disturbed sites, highest extinctions were among species with very high and low soil moisture requirements, resulting in a U-shaped response pattern not compatible with linear logistic regression. Thus, we reduced Landolt's five ordinal categories down to three new ordinal categories. For category 3, we combined species with the lowest and highest soil moisture requirements (originally 1 and 5), for category 2, the species with the next highest and next lowest requirements (originally 2 and 4), and category 1 contained only species with intermediate requirements (originally 3). When recombined in this fashion, the data exhibited a linear response pattern, with the lowest extinction risk in category 1 (intermediate soil moisture requirements) and the highest in category 3 (extreme soil moisture requirements). We analysed the recombined data as described above. Note that in the results section we present unmanipulated figures along with statistics for the manipulated data.

We used the multiple regression coefficients to calculate the estimated extinction probability ($\hat{E}_i$) for each species i as:

$$\hat{E}_i = \frac{e^{c+c_m M_i+c_l L_i+c_n N_i}}{1 + e^{c+c_m M_i+c_l L_i+c_n N_i}} \qquad \text{eqn 3}$$

where M_i, L_i and N_i are the resource requirement variables, c_m, c_l and c_n are the corresponding regression coefficients, and c is the intercept. These estimated extinction probabilities can be calculated for extant species as well as extinct species and reflect differences in habitat affiliation, life-form and resource requirements. They thus provide a simple metric for assessing which of the remaining species are more prone to extinction, and why. Note that for species common to rocky habitats, we used regression coefficients obtained from the analysis in which species were not separated by habitat affiliation. Finally, to assess the goodness-of-fit, we sorted all recorded species in order of increasing extinction probability ($\hat{E}_i$), then divided them into four bins and calculated the mean $\hat{E}_i$ and the observed extinction rate within each bin.

CHANGES IN LAND USE

To assess the overall change in land use in Küsnacht, we used geo-referenced historical and present topographical maps (1 : 25 000; oldest available map, scanned Sigfried-Karte from 1881; most recent map, digitalized Landestopographie-Karte from 2003/2004). Land-use cover was assessed in ARCGIS 9.1 (ESRI, Redlands) using the following categories: developed area (including roads and gardens), forests, agricultural land including meadows, pastures, fields and orchards (different types of agricultural land can not be distinguished on the maps), larger ponds, fens and wetlands, and vineyards. From the obtained cover data, we calculated the percentage of land use change between 1881 and 2003/2004.

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Table 1 Number of extant and extinct plant species in the municipality of Küsnacht, along with an upper (E_r) and lower (E_{min}) bound on the extinction rate for the entire flora between 1915 and 2003

	Recorded species[a]	Unrecorded species[b]	All species
Extant	319	282	601
Extinct	127	0[c]	127
Total	446	282	728
Extinction rate	0.28 (E_r)[d]	0[3]	0.17 (E_{min})

[a]Recorded species were collected for the herbarium of the Seminar Küsnacht between 1839 and 1915.
[b]Unrecorded species were not collected, but were presumably present between 1839 and 1915 because they are commonly found in Küsnacht today (see text).
[c]Conservative assumption.
[d]The extinction rate of recorded species may be considered the upper bound on the extinction rate of the entire flora, based on the assertion that the extinction rate of unrecorded species was lower than for recorded species (see text).

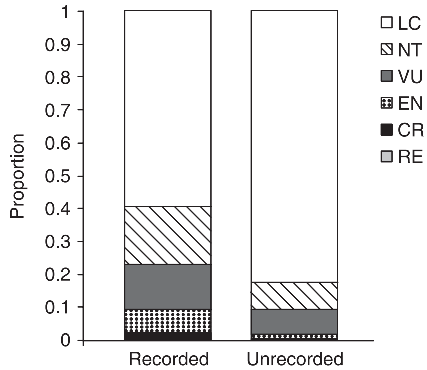

Fig. 1 Proportion of recorded and unrecorded plant species belonging to IUCN red list categories (Moser *et al*. 2002). Recorded species were collected for the herbarium of the Seminar Küsnacht between 1839 and 1915; unrecorded species were not collected during this period, but were presumably present at that time because they are commonly found in Küsnacht today. RE, regionally extinct; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern.

Results

PAST AND CURRENT SPECIES

About 20 collectors contributed to the herbarium of Seminar Küsnacht, many of whom were professors at the University of Zürich or at the Swiss Federal Institute of Technology Zürich (ETH). A total of 454 species were collected in the period 1839–1915 (median year = 1877; Appendix S1 in Supplementary Material). We excluded eight cultivated species or ornamentals, resulting in a total of 446 species on the past species list (Table 1; Appendix S2).

We found 643 species to be present today (Table 1; Appendix S1). We excluded 23 cultivated species or ornamentals, 13 neophytes/invasive species, and six species that were deliberately sown (Appendix S2). Thus, the present species list of Küsnacht comprised 601 species of vascular plants (Table 1).

EXTINCTION RATE

Of the 446 species recorded by 1915, 127 species were locally extinct by 2003. Thus, the extinction rate among recorded species (E_r) was 28% (Table 1). Given that there were an additional 282 unrecorded species, the minimum rate of extinction for the entire flora (E_{min}) was 17% (Table 1). The extinction rate of the entire flora was therefore likely to be between 17% and 28%, assuming that the extinction rate was lower among unrecorded species than recorded species.

EXTINCTION RISK OF RECORDED VS. UNRECORDED SPECIES

According to the Swiss IUCN red list, unrecorded species had significantly lower extinction risks than recorded species (chi-square = 9.82, $P < 0.01$; Fig. 1). Eighty-three per cent of unrecorded species were of least concern, whereas 59.5% of recorded species belonged to this category. Conversely, 39.5% of the recorded species belonged to higher-risk IUCN categories, whereas this was the case for only 17% of the unrecorded species.

Considering trees and shrubs as examples of common but unrecorded species, of the 54 tree and shrub species present in Küsnacht today, 33 were not recorded, including ubiquitous species such as *Acer platanoides*, *A. pseudoplatanus*, *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Picea abies*, *Corylus avellana*, *Crataegus monogyna*, *Ligustrum vulgare*, *Prunus spinosa* and *Sambucus racemosa*. Such species are unlikely to have migrated to Küsnacht during the last century, hence we assume that they were formerly present but not collected.

CHANGES IN LAND USE

Küsnacht has experienced drastic changes in land use over the last century. Developed areas have substantially increased (+75.4%; Table 2), particularly housing on former agricultural land. Accordingly, the agricultural land area has decreased by 33% (Table 2). Unfortunately, the available maps do not allow for an assessment of whether different types of agricultural land were affected differently. While vineyards were once a typical landscape feature of Küsnacht, they have declined by 77.5% in overall area (Table 2) and only two vineyards remain today. Fens and wetlands also suffered a substantial decrease (–72.8%; Table 2), mainly because the corresponding land became converted to agriculture. The area covered by larger ponds decreased by 14.7%, whereas forest cover slightly increased by 3.2%.

PATTERNS OF EXTINCTION

Species of different habitats had significantly different extinction rates (Wald statistic = 11.89, $P = 0.018$;

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Table 2 Habitat types of Küsnacht in 1881 and 2003/2004 and the percentage in land cover change per habitat type (1881 = 100%)

	1881	2003/2004	Land cover change
Developed area	2′613′093 m^2 (21.1%)	4′583′528 m^2 (37.1%)	+75.4%
Forests	3′707′643 m^2 (30.0%)	3′826′579 m^2 (30.1%)	+3.2%
Ponds	33′079 m^2 (0.3%)	28′232 m^2 (0.2%)	–14.7%
Agricultural land	5′783′489 m^2 (46.8%)	3′875′575 m^2 (31.1%)	–33.0%
Fens and wetlands	54′595 m^2 (0.4%)	14′874 m^2 (0.1%)	–72.8%
Vineyards	176′601 m^2 (1.4%)	39′712 m^2 (0.3%)	–77.5%
Total	12′368′500 m^2 (100%)	12′368′500 m^2 (100%)	–

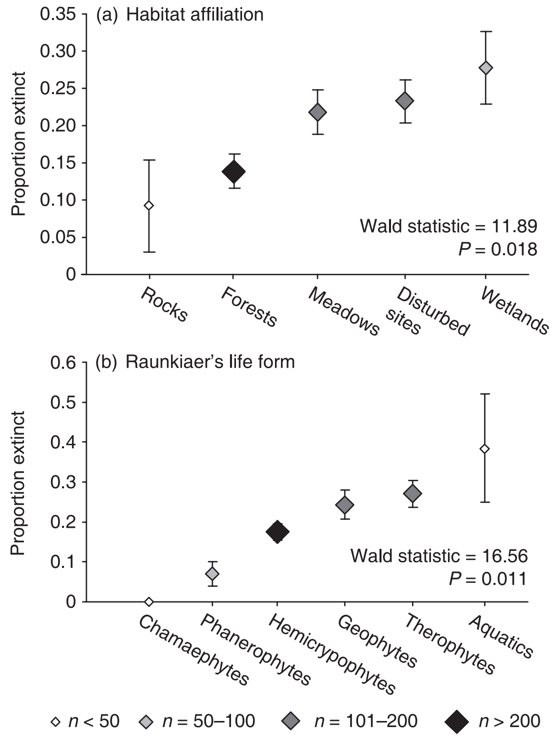

Fig. 2 Proportion of plant species by (a) habitat affiliation and (b) Raunkiaer's life-form that went extinct in Küsnacht between 1915 and 2003. Size and shading of diamonds refers to sample size per category (± SE).

Fig. 2a). Extinction was lowest among species common in rocky habitats (9%) and forests (13%), whereas species of meadows, disturbed sites and wetlands suffered extinction in excess of 20% (22%, 23%, 28%, respectively).

There was also a significant difference in extinction among different life-forms (Wald statistic = 16.56, P = 0.011; Fig. 2b). Aquatic species had the highest extinction (61%), chamaephytes and phanerophytes the lowest (0% and 6%, respectively), and the remaining life-forms had intermediate rates (hemicryptophytes, 17%; geophytes, 24%; therophytes, 27%).

With respect to environmental determinants of extinction, soil moisture requirements had a significant effect on extinction rates, but the direction of the effect varied by habitat affiliation (Fig. 3). Among forest species, dry-adapted species had the highest extinction (marginally significant, Wald statistic = 3.46, $P = 0.063$), whereas the opposite was true for wetland species: 35% of species with the highest soil moisture requirements disappeared (Wald statistic = 5.00, $P = 0.025$). Among species common to meadows and disturbed sites, extinction was bimodal: extinction was greatest among species with very high and very low soil moisture requirements (meadows, marginally significant, Wald statistic = 3.49, $P = 0.063$; disturbed sites, Wald statistic = 10.98, $P = 0.001$). Light requirements also had a significant effect on extinction rates (Fig. 3), but only among species common to disturbed sites, where light-demanding species suffered more than others (Wald statistic = 5.91, $P = 0.015$). It is nevertheless noteworthy that even in forests, light-demanding species had higher extinction rates. In the case of soil nutrient requirements, the pattern was similar in all habitats (Fig. 3); extinction was highest among oligophilous species, although the effect was only significant in meadows and wetlands (meadows, Wald statistic = 13.98, $P < 0.001$; wetlands, Wald statistic = 6.30, $P = 0.012$).

The rate of extinction varied significantly among different red list categories (Wald statistic = 171.46, $P < 0.001$; Fig. 4). The only regionally endangered species once occurring in Küsnacht indeed disappeared. Two critically endangered species were still found in Küsnacht, whereas seven did not occur there anymore (80%). Three-quarters of endangered species became locally extinct, and 61% of vulnerable species were not present anymore. Among the near threatened species, more than a third became extinct (35%), whereas only 4% of species of least concern vanished. This extinction pattern resulted in an increase of common species (least concern), whereas species of all other categories decreased (Fig. 5).

ESTIMATED EXTINCTION PROBABILITIES

Our mean estimated extinction probabilities closely matched the observed extinction rates in all four species habitats (data not shown). Indeed, the relationship between the estimated and observed values was approximately linear with a slope of one and an intercept of zero, indicating that the model provides unbiased estimates of extinction risk.

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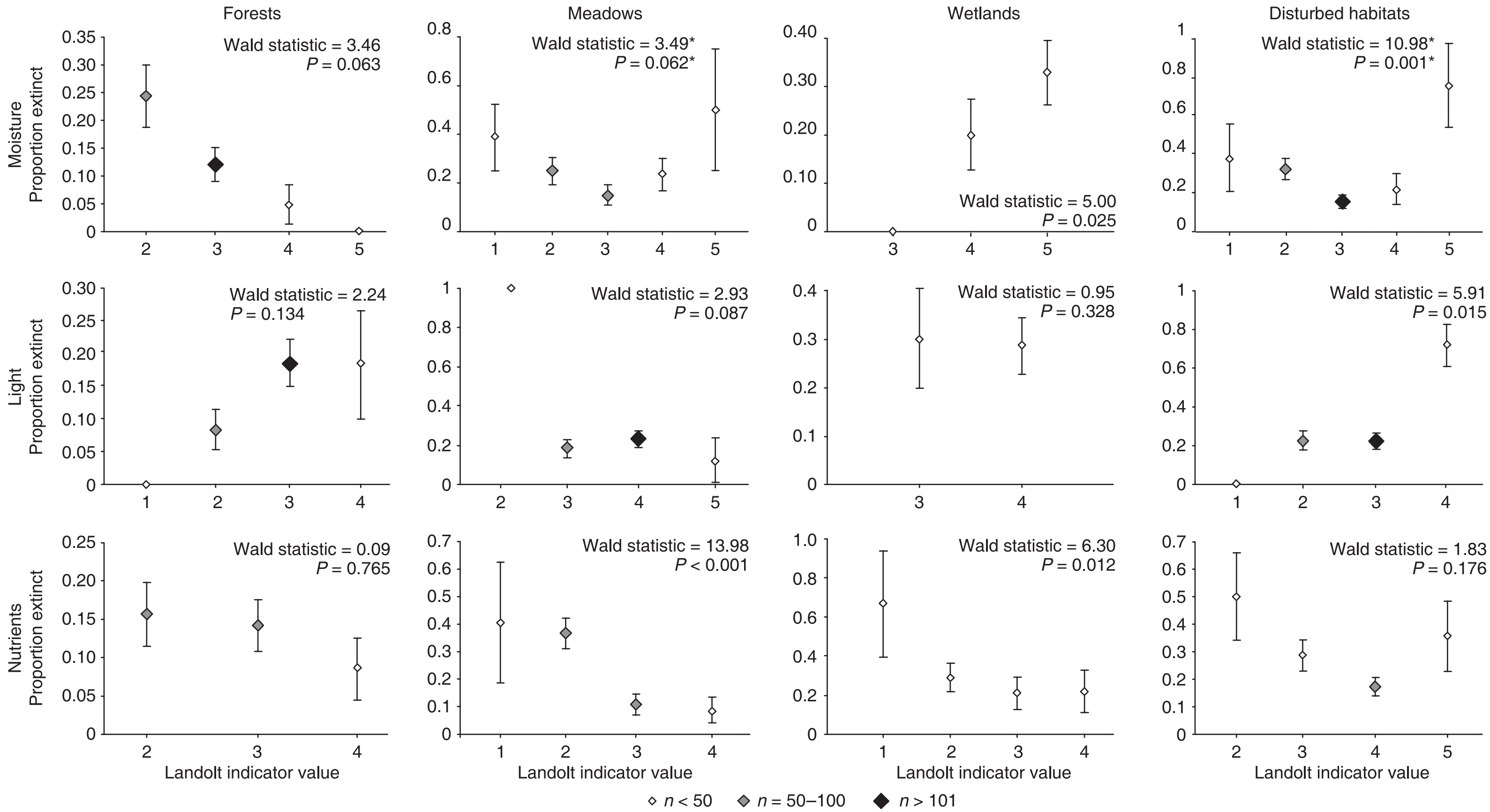

Fig. 3 Proportion of plant species that went extinct in Küsnacht between 1915 and 2003, plotted by habitat affiliation and resource requirements, as quantified by Landolt indicator values (Landolt 1977). On a scale of 1–5, low numbers represent low resources requirements, and high numbers represent high resource requirements. In some cases not all five values are shown because there were no species in certain categories. Size and shading of diamonds refers to plant sample sizes per category (± SE). *Multiple regression analysis is based on reduced Landolt's ordinal categories (see text for details).

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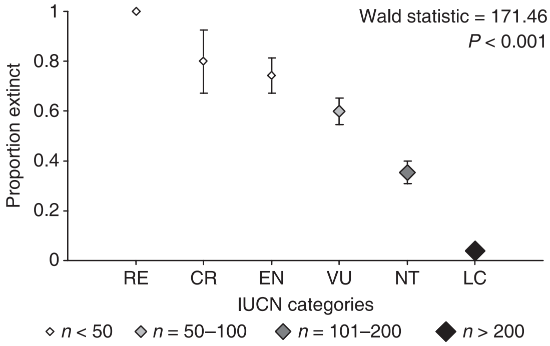

Fig. 4 Proportion of plant species by IUCN red list category (Moser *et al*. 2002) that went extinct in Küsnacht between 1915 and 2003. Size and shading of diamonds refers to sample size per category (± SE). RE, regionally extinct; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern.

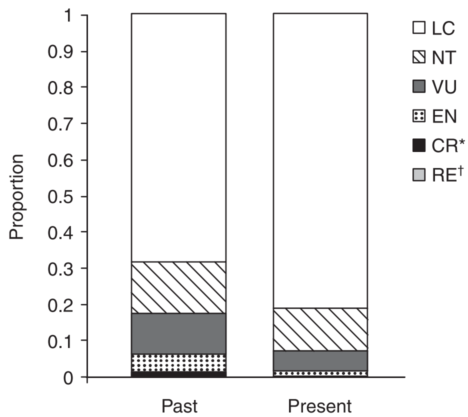

Fig. 5 Proportion of plant species on the past and present species list of Küsnacht belonging to each of the IUCN red list categories (Moser *et al*. 2002). RE, regionally extinct; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern. *Two critically endangered species remain. †The only regionally endangered species disappeared.

Discussion

MAGNITUDE OF EXTINCTION

A substantial fraction of vascular plants in Küsnacht went extinct during the 20th century (17% to 28%). This estimate is alarming, particularly because similar rates have been reported in other studies that covered a similar area in similar land-use settings (Drayton & Primack 1996, 38%, 4 km^2; Landolt 2001, 13%, 122 km^2; Chocholoušková & Pyšek 2003, 21%, 137 km^2; Van der Veken *et al*. 2004, 25%, 56 km^2). Local extinctions are the prelude to global extinction, and there is often a time lag before the last local population disappears (Hanski & Ovaskainen 2002; Carroll *et al*. 2004; Lindborg & Eriksson 2004). Hence, our study, and others like it, should serve as an early warning for impending regional extinctions. Indeed, the area we sampled was sufficiently large and diverse to suggest that these local extinctions reflect large-scale anthropogenic impacts on diversity, rather than local stochastic or exceptional events.

Examining the list of extinct species in Küsnacht reveals a formerly rich flora. Many species that are currently found only in particular regions of Switzerland and are regarded as typical for these landscapes (Becherer 1972), also originally occurred in Küsnacht. This indicates that the decrease in floristic richness was not only significant at the regional or even countrywide level (Moser *et al*. 2002), but that it was even more dramatic at the local scale. An example is given by the orchids of the genus *Ophrys*. Today, *Ophrys* almost exclusively occurs in dry and nutrient-poor meadows in the Swiss Jura Mountains. However, the former occurrence of three *Ophrys* species in Küsnacht suggests that similarly species-rich meadows once also occurred in the Lake Zürich area or, more generally, in the Swiss lowlands.

CAUSES OF EXTINCTION

Habitat destruction is the most obvious and widespread cause of local extinctions, especially in areas with high human population densities (Thompson & Jones 1999). As with most central European landscapes, Küsnacht has experienced its share of urbanization. While the area remained rural through the first half of the 19th century, its proximity to Zürich and scenic setting triggered the development of large houses with lake access or with a vista, the latter often in former vineyards. The development of such residential areas was almost completed by the middle of the last century. Wetlands suffered highest habitat losses, as the natural shoreline of Lake Zürich almost completely vanished by 2003 and, with it, species commonly found in open waters and marshlands (Landolt indicator value 5; Figs 2 and 3, e.g. *Eleocharis acicularis*). The almost complete destruction of vineyards probably led to the disappearance of species adapted to very sunny, dry and low-competition habitats (Fig. 3). Similarly, the species-rich meadows that once existed on the exposed slopes above Lake Zürich were developed. In particular, the extinct species *Aristolochia clematitis*, *Centaurea solstitialis*, *Melampyrum arvense*, *Nepeta cataria*, *Odontites vernus* and *Vicia sativa* are all Mediterranean species often associated with vineyards and dry meadows north of the Alps (Becherer 1972).

In addition to habitat destruction, there has also been substantial modification of several habitats. For example, the river running through the main ravine was modified by breaks put into the riverbed in 1895–1899 to decelerate the flow of water and prevent the erosion of steep slopes (Holderegger 1994). As a result, there are fewer of the erosion slopes and cliffs that have supported many of the extinct light-demanding species (e.g. *Anthericum ramosum*, *Aquilegia vulgaris*, *Centaurea montana*, *Cytisus scoparius*, *Gymnadenia odoratissima*, *Hieracium sabaudum* or *Peucedanum cervaria*; Fig. 3). Similarly, the total or partial drainage of fens has contributed to the extinction of many wetland species (e.g. *Drosera longifolia*, *Liparis loeselii*, *Gentiana utriculosa*, *Ranunculus flammula* or *Spiranthes aestivalis*).

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Our analyses suggest eutrophication (phosphorous and/or nitrogen; Wassen *et al*. 2005) is an important 'silent' agent of extinction. Indeed, oligophilous species were the only species that showed an elevated extinction rate across all habitats (Fig. 3). One likely explanation for this trend is that all habitats receive elevated inputs of nutrients via aerial deposition (Galloway *et al*. 1995; McCollin *et al*. 2000; Van der Veken *et al*. 2004). However, many oligophilous species that went extinct were commonly found in extensively managed meadows, pastures or fens. Nowadays, meadows receive large direct inputs of animal manure or fertilizers, whereas fens receive leached nutrients from upstream meadows or fields. This may explain why extinction was greatest among species common to these two habitats, including oligophilous species such as *Drosera longifolia*, *Liparis loeselii*, *Ophrys insectifera* or *Spiranthes aestivalis*.

There are several possible mechanisms by which intensification of agriculture may have caused the extinction of species common to meadows and disturbed habitats. Increased fertilizer use probably eliminated a large number of oligophilous meadow species (see above; Schippers & Joenje 2002; Myklestad & Sætersdal 2004), and the increased use of pesticides decreased the number of weedy species in fields (agriophytes). Decreased connectivity among less intensively managed fields may have also contributed to the decline of agriophytes, because they are typically short-lived annuals that cannot survive short-term population fluctuations if there is no dispersal among fields (Eriksson 1996; Groom 1998; Lindborg & Eriksson 2004; Geertsema 2005). Some highly specialized agriophytes adapted to grow within crop fields figured prominently among extinct species (*Bromus arvensis*, *B. secalinus*, *Melampyrum arvense*, *Neslia paniculata*, *Papaver dubium*, *Ranunculus arvensis* or *Vaccaria hispanica*). They were probably also negatively affected by the use of non-traditional crops such as shade-casting corn (Fig. 3). Lastly, intensified mowing practices may have contributed to the extinction of late-flowering meadow species such as *Gentiana cruciata* or *G. germanica.*

FURTHER FLORAL FREE FALL: EXTINCTION DEBT

Saxifraga mutata is a rare species inhabiting calcareous rocks or erosion slopes in the major ravine of Küsnacht. A study conducted at this location (Holderegger 1996) indicated that *S. mutata* populations are declining because river breaks prevent the erosion on which the species depends for its establishment and recruitment. Therefore, *S. mutata* is doomed to extinction in the near future if the original disturbance regime is not restored. Indeed, the latest census (2003; R. Holderegger, personal observations) indicated that the population has declined to less than 30 plants, down from 200 in 1991.

This example probably reflects the trajectory of many extant species, including *Tanacetum corymbosum* (< 10 individuals in 2003), *Cotoneaster tomentosus* (one individual), *Cypripedium calceolus* (six individuals), *Aster amellus* and *Crepis praemorsa* (both < 20 individuals in 2003). Other species in Küsnacht may share a similar fate because they only occur in single, albeit larger populations (e.g. *Polygala chamaebuxus*, *Dactylorhiza incarnata* or *Gentiana ciliata*). Delayed extinction in relation to the onset of a disturbance, such as the construction of the river breaks in Küsnacht's ravine in 1895–1899, is a common phenomenon known as extinction debt (Hanski & Ovaskainen 2002; Carroll *et al*. 2004). Therefore, our forecast for the future is further floral free fall. Indeed, we believe that some (even common) species are likely to go extinct in the near future because they have high estimated extinction probabilities, e.g. the forest species *Campanula rapunculoides*, *Cotoneaster tomentosus* or *Melampyrum pratense* ($\hat{E}_i > 0.30$), the meadow species *Calluna vulgaris* or *Carlina vulgaris* ($\hat{E}_i > 0.50$), the wetland species *Eriophorum latifolium* ($\hat{E}_i > 0.50$), and the agriophytes *Amaranthus albus*, *Papaver rhoeas* and *Vicia tetrasperma* ($\hat{E}_i > 0.50$).

This predicted loss will accentuate the pattern of change between past and present: more rare species disappeared than common ones (Fig. 4), resulting in an increased fraction of common generalists and a trivialization of the vegetation (Fig. 5). Unfortunately, Küsnacht is probably not especially hard hit. It might have started out with higher levels of biodiversity as compared with other Swiss lowland municipalities (due to its diversity and extent of unusual habitats), but the environmental changes have occurred throughout most of the Swiss lowlands and indeed the industrialized world, with similar effects on local floras (Drayton & Primack 1996; Rich & Woodruff 1996; Fischer & Stöcklin 1997; Landolt 2001; Chocholoušková & Pyšek 2003; Van der Veken *et al*. 2004). Most areas, however, lack the historical records to assess the extent of floristic losses and thus to predict which species are most prone to future extinction. While IUCN red lists can provide a sound basis to determine which species to prioritize in conservation efforts, to conserve biological diversity, conservation efforts must be based not only on current species distributions but also on the landscape's long-term capacity to support populations (Carroll *et al*. 2004). Studies such as ours should serve as a call for action. For example, efforts are now being made in Küsnacht to allow for spatially restricted landslides that will restore early successional habitats on the slopes of the river. Additionally, studies that contain lists of extant species should be used for future monitoring of the impact of restoration measures, or, more pessimistically, to document further decreases in local biodiversity.

Conclusions

Using a unique local historical herbarium, we estimated that 17% to 28% of the vascular plant species in Küsnacht went extinct over the last century (Table 1). Extinction was non-random: species with different habitat affiliations and life-forms had significantly different

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rates of extinction. Losses in wetlands were highest, followed by those in disturbed habitats and meadows, whereas forests and rocks were least affected (Fig. 2a). Among different life-forms, aquatics and annuals were most prone to extinction, geophytes and hemicryptophytes less so, and phanerophytes and chamaephytes were least affected (Fig. 2b). Species adapted to nutrient-poor soils suffered highest rates of extinction in all habitat types (Fig. 3), hence eutrophication poses an urgent, yet stealthy threat to species diversity. Light and soil-moisture requirements also had a significant effect on extinction, but the direction of the effect varied by habitats (Fig. 3). When species were grouped according to Swiss red list categories, the rank order of the observed extinction rates was consistent with the rankings assigned by IUCN (Fig. 4). Extinction rates of species deemed rare by the Swiss IUCN red list were very high. Based on our estimated extinction probabilities, many of the remaining species (both rare and locally abundant) are likely to become extinct in the near future. This predicted decline is consistent with the notion that extinction is often delayed in relation to the onset of deterioration of environmental conditions (extinction debt). Hence, further extinction will increase the dominance of generalists already comprising 81% of all local species (Fig. 5). Unfortunately, the rates and patterns of extinction in Küsnacht are probably representative of surrounding Swiss lowlands and peri-urban landscapes in most developed countries.

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References

Aeschimann, D. & Heitz, C. (2005) *Index Synonomique de la Flore de Suisse*. CRSF, Genève.
Becherer, A. (1972) *Führer durch die Flora der Schweiz mit Berücksichtigung der Grenzgebiete*. Schwabe, Basel.
Brook, B.W., Sodhi, N.S. & Ng, P.K.L. (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**, 420–423.
Carroll, C., Noss, R.E., Paquet, P.C. & Schumaker, N.H. (2004) Extinction debt of protected areas in developing landscapes. *Conservation Biology*, **18**, 1110–1120.
Chamberlain, D.E. & Fuller, R.J. (2000) Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agriculture, Ecosystem and Environment*, **78**, 1–17.
Chocholoušková, Z. & Pyšek, P. (2003) Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzeň. *Flora*, **198**, 366–376.
Colling, G. & Matthies, D. (2006) Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (*Scorzonera humilis*). *Journal of Ecology*, **94**, 959–972.
Davies, K.F., Margules, C.R. & Lawrence, K.F. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology*, **81**, 1450–1461.
Drayton, B. & Primack, R.B. (1996) Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. *Conservation Biology*, **10**, 30–39.
Ellenberg, H. (1996) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. Ulmer, Stuttgart.
Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Palissen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1–248.
Eriksson, O. (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, **77**, 248–258.
Fahrig, L. (1997) Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management*, **61**, 603–610.
Fischer, M. & Stöcklin, J. (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–85. *Conservation Biology*, **11**, 727–737.
Galloway, J.N., Schlesinger, W.H., Levy, H., Michaels, S. & Schnoor, J.L. (1995) Nitrogen-fixation – anthropogenic enhancement – environmental response. *Global Biochemical Cycles*, **9**, 235–252.
Garbutt, R.A. & Sparks, T.H. (2002) Changes in botanical diversity of a species rich ancient hedgerow between two surveys (1971–98). *Biological Conservation*, **106**, 273–278.
Geertsema, W. (2005) Spatial dynamics of plant species in an agricultural landscape in the Netherlands. *Plant Ecology*, **178**, 237–247.
Groom, M.J. (1998) Allee effects limit population viability of an annual plant. *American Naturalist*, **151**, 487–496.
Hanski, I. & Ovaskainen, O. (2002) Extinction debt at extinction threshold. *Conservation Biology*, **16**, 666–673.
Hantke, R. (1980) *Eiszeitalter 2*. Ott, Thun.
Heitz, C. (1990) *Schul- und Exkursionsflora für die Schweiz*. Schwabe, Basel.
Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.
Herzog, F., Dreier, S., Hofer, G., Marfurt, C., Schüpbach, B., Spiess, M. & Walter, T. (2005) Effect of ecological compensation areas on floristic and breeding bird diversity in Swiss agricultural landscapes. *Agriculture Ecosystems and Environment*, **108**, 189–204.
Holderegger, R. (1994) Flora and vegetation of the Küsnachtertobel – changes in the last 50 years. *Botanica Helvetica*, **104**, 55–68.
Holderegger, R. (1996) Intrapopulational size structure of the monocarpic species *Saxifraga mutata* and its relationship to succession. *Flora*, **192**, 151–156.
Käsermann, C. & Moser, D.M. (1999) *Merkblätter Artenschutz-Blütenpflanzen und Farne*. BUWAL, Bern.
Koh, L.P., Sodhi, N.S. & Brook, B.W. (2004) Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology*, **18**, 1571–1578.
Landergott, U., Schneller, J.J., Holderegger, R. & Kozlowski, G. (2000) Population history of the rare fern species *Dryopteris cristata*, Switzerland. *Botanica Helvetica*, **110**, 151–170.
Landolt, E. (1977) *Ökologische Zeigerwerte zur Schweizer Flora*. Veröffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rübel, Zürich.
Landolt, E. (2001) *Flora der Stadt Zürich*. Birkhäuser, Basel.
Lienert, J., Fischer, M. & Diemer, M. (2002) Local extinctions of the wetland specialist *Swertia perennis* L. (Gentianaceae) in Switzerland: a revisitation study based on herbarium records. *Biological Conservation*, **103**, 65–76.
Lindborg, R. & Eriksson, O. (2004) Historical landscape connectivity affects present plant species diversity. *Ecology*, **85**, 1840–1845.
Maes, D. & Van Dyck, H. (2001) Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biological Conservation*, **99**, 263–276.

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McCollin, D., Moore, L. & Sparks, T. (2000) The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation*, **92**, 249–263.

Moser, D.M., Gygax, A., Bäumler, B., Wyler, N. & Palese, R. (2002) *Rote Liste der gefährdeten Arten der Schweiz: Farn- und Blütenpflanzen*. BUWAL, Bern.

Myklestad, Å. & Sætersdal, M. (2004) The importance of traditional meadow management techniques for conservation of vascular plant species richness in Norway. *Biological Conservation*, **118**, 133–139.

Rich, T.C.G. & Woodruff, E.R. (1996) Changes in the vascular plant floras of England and Scotland between 1930 and 1960 and 1987–88: the BSBI monitoring scheme. *Biological Conservation*, **75**, 217–229.

Schippers, P. & Joenje, W. (2002) Modelling the effect of fertilizer, mowing, disturbance and width on the biodiversity of plant communities of field boundaries. *Agriculture, Ecosystems and Environment*, **93**, 351–365.

Schmid, E., Däniker, A.U. & Bär, J. (1937) Zur Flora und Vegetation des Küsnachtertobels. *Berichte der Schweizerischen Botanischen Gesellschaft*, **47**, 352–362.

Shaffer, H.B., Fisher, R.N. & Davidson, C. (1998) The role of natural history collection in documenting species declines. *Trends in Ecology and Evolution*, **13**, 27–30.

Statistics Agency of the Canton of Zürich (2006) https://data.statistik.zh.ch (last accessed November 2006).

Suding, K.N., Collings, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S. (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the USA*, **102**, 4387–4392.

Thompson, K. & Jones, A. (1999) Human population density and prediction of local plant extinction in Britain. *Conservation Biology*, **13**, 185–189.

Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, **371**, 65–66.

Van der Veken, S., Verheyen, K. & Hermy, M. (2004) Plant species loss in an urban area (Turnhout, Belgium) from 1880 to 1999 and its environmental determinants. *Flora*, **199**, 516–523.

Vitousek, P.M., Mooney, H.A., Lubchenko, J. & Melillo, J.M. (1997) Human domination of earth's ecosystems. *Science*, **277**, 494–499.

Wassen, M.J., Vanterink, H.O., Lapshina, E.D. & Tanneberger, F. (2005) Endangered plants persist under phosphorous limitation. *Nature*, **437**, 547–550.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Vascular plant species included in the past and current species lists for Küsnacht.

Appendix S2 Vascular plant species excluded from the past and current species lists for Küsnacht.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01246.x

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