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RESEARCH ARTICLE

Reconstructing the collapse of wetland networks in the Swiss lowlands 1850–2000

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Abstract In Central Europe vast wetland areas have been converted into agricultural land over the past few centuries. Long-term spatially explicit reconstructions of wetland cover changes at regional scale are rare but such information is vital for setting appropriate wetland conservation and restoration goals. In this study wetland cover change over the past 150 years was analyzed for the Canton Zurich (Switzerland) using information from historical and current topographical maps. Mapping instructions changed significantly over time, i.e., wetlands were mapped more conservatively on older maps. Therefore a technique was developed to account for changes in mapping instructions and to reconstruct a series of comparable maps spanning 1850–2000. Wetland cover dramatically decreased from 13,759 ha in 1850 (more than 8% of the total study area) to 1,233 ha in 2000 (less than 1%). Largest loss is observed for the first half of the twentieth century when more than 50% of the total wetland loss occurred. In 1850, almost all wetland patches were connected in two large networks defined by a 500 m buffer around all wetland patches to account for typical dispersal distances of wetland animals. Despite extensive wetland loss, this networks remained largely intact until 1950, but then collapsed into many medium and small networks consisting of only few wetland patches. In addition to the direct loss of wetland habitats increased habitat fragmentation is limiting metapopulation dynamics and hindering genetic exchange between populations. Amphibians and other wetland animals are particularly prone to habitat fragmentation because of their limited migration abilities. This may lead to time-delayed extinction in the future because current species occurrence might rather reflect historical than current wetland cover and habitat configuration. Future restoration efforts should focus on reestablishing connectivity between remaining smaller wetland networks.

Keywords Connectivity · Drainage · Historical maps · Landscape fragmentation · Landscape history · Land-use change · Wetland loss

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Introduction

Wetlands fulfill important ecosystem services as habitats for specialized animal and plant species, as buffers in the regional hydrological and climate system, and as significant pools of soil organic carbon. Up to half of the original wetland area has been lost worldwide due to human activities (Mitch and Gosselink 2000). The reconstruction of historical changes in wetland cover is essential for the assessment of long-term dynamics of regional carbon pools (Clymo et al. 1998; Beilman et al. 2009) because disturbance of wetlands result in a rapid loss of carbon that had been accumulated at much slower rates over centuries or millennia (Janssens et al. 2005). Information on historical wetland extent provides vital reference data for setting appropriate wetland conservation and restoration goals (Gibbs 2000; Stein et al. 2010). Still, long-term spatially explicit reconstructions of wetland cover changes at regional scale are rare (Van Dyke and Wasson 2005; Grossinger et al. 2007).

In Central Europe wetlands have been under pressure since people started to expand their agricultural activities by draining marshes, fens, peatlands and floodplains. Over the past few centuries, rates of wetland loss accelerated in response to a high demand for cropland and the development of efficient large-scale drainage techniques (Moser et al. 1996). Conversion of wetlands into agricultural land is among the most important type of land conversion in Central Europe over the past few centuries (Küster 1999). Additionally, many wetlands have been exploited for peat mining. In Switzerland peat mining started at some places in the early eighteenth century and experienced a last peak during the Second World War (Grünig 1994).

Recent high rates of landscape conversion by anthropogenic activities have led to increasing loss and fragmentation of natural habitats. Habitat fragmentation is a critical issue for landscape planners especially in densely populated regions (DiGiulio et al. 2009). Wetland animals (e.g., amphibians) are particularly susceptible to fragmentation effects as they are known to have very limited dispersal abilities (Gibbs 2000; Smith and Green 2005).

Historical maps are a powerful source for reconstructing land-use and land-cover changes (LUCC) (e.g., Sanderson and Brown 2007). Maps have been used to reconstruct historical conditions or time series for specific habitat types such as forests (Ludwig et al. 2009; Wulf et al. 2010) or wetlands (Van Dyke and Wasson 2005; Grossinger et al. 2007). However, the use of historical maps requires source critical approaches (Manies et al. 2001), including careful interpretation of the map content and combination with other sources. This is particularly important when combining different types of historical maps originating from different periods (Levin et al. 2009).

The goal of this study is to quantify wetland cover change in Canton Zurich over the past 150 years and to assess landscape ecological consequences by addressing the following specific research aims:

(a) Extracting wetland cover information for Canton Zurich for 1850, 1900, 1950 and 2000 based on information from historical and modern topographical maps.
(b) Developing and applying a procedure to take different mapping standards into account and to build comparable map series.
(c) Analyzing spatial patterns of wetland change and evaluating extent of wetland habitat fragmentation.
(d) Discussing the relevance of observed changes for future wetland conservation and restoration efforts.

Materials and methods

Study area

The study area Canton Zurich is located in northeast Switzerland, and covers 1,729 km^2 (Fig. 1). It is situated north of the Alps with some alpine foothills in the eastern and southern part (highest peak 1,292 m a.s.l.). Most of the canton consists of shallow valleys which drain north toward the river Rhine. The City of Zurich and the second largest City of Winterthur form a partly contiguous urban agglomeration covering large areas of the central parts of the canton. During the last glacial period most of the study area was covered with ice and after their retreat, the glaciers left typical post-glacial landscapes including features such as moraines, drumlin fields and vast wetland areas (Hantke 1980).

Map selection and data preparation

Current wetland cover was extracted from the vectorized version of the Swiss National Map at scale 1:25,000 (swisstopo, Vector25). This map includes four categories of wetlands: pure wetland,

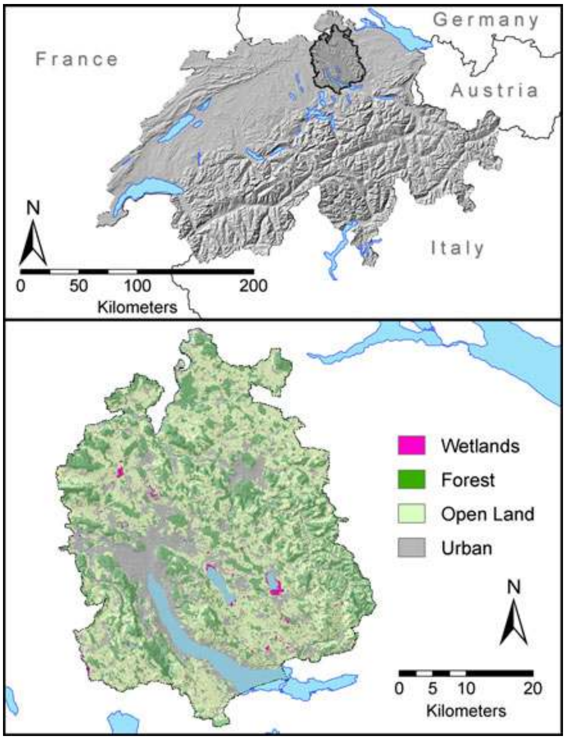

Fig. 1 Location of the Canton of Zurich within Switzerland (*upper map*) and current land cover (*data source* BFS 2001)

wetland with shrub, wetland with open forest, and wetland with forest. We combined all four categories into a single wetland class. To reconstruct wetland cover in the early and mid twentieth century, we used the forerunner maps of the modern National Maps, the so-called Siegfried maps, named after Colonel Hermann Siegfried who took charge of the Swiss Topographical Office in 1865 (Gugerli and Speich 2002). These maps have been repeatedly published from 1870 to 1949. The maps are at scale 1:25,000 and available as scanned and georeferenced GIS layers. We picked the last edition of this map series to generate a dataset for the mid twentieth century (map dates range from 1940 to 1946) by compiling multiple maps into one composite picture for the era. In the same way, we generated a dataset for 1900 using the maps edited at around the beginning of the twentieth century (map dates range between 1894 and 1907). Wetlands shown on the Siegfried maps were manually digitized as polygon features. The earliest dataset was reconstructed based on a dataset provided by the Department of Nature Protection of the Canton of Zurich based on digitized wetlands from the Wild Map (named after the cartographer Johann Wild). The survey for the Wild Map was conducted between 1843 and 1851 and the printed maps were edited from 1852 to 1865 at scale 1:25,000 (Grosjean 1996). The historic maps exhibit extraordinary high spatial accuracy. Both the Wild and the Siegfried maps were at the top of the cartographic art at that time and repeatedly gained international awards (Gugerli and Speich 2002). The Siegfried maps have already been successfully used for reconstructing landscape change (Kienast 1993) and transport infrastructure and settlement development (Bertiller et al. 2007) for Switzerland. However, mapping of wetland area leaves much more room for interpretation than mapping of roads and buildings.

Together these four datasets resulted in an initial unadjusted wetland cover time series for Canton Zurich. For clarity, we refer to these four datasets as wetland 2000, 1950, 1900 and 1850 (Fig. 2).

As an additional source of information on drainage, we used the drainage map of the Canton Zurich (Meliorationkarte Kanton Zürich, provided by the Department of Agriculture of Canton Zurich) which contains the location of drained areas and the timing of drainage based on an inventory of subsidies paid for agricultural meliorations starting in the 1870s. As drainage was by far the most important process leading to wetland loss, the drainage map provides vital information on when and where wetlands vanished in our study area.

Changes in wetland mapping

To establish consistent time series of wetland cover it is essential to ensure the comparability in wetland interpretation across the map types. We found similar minimal wetland size for all map types (about 0.1 ha), indicating a certain consistency in mapping scale and precision. To assess the quality of information for each map, i.e., what was actually mapped as a wetland in each survey, we consulted archival sources providing information on mapping instructions for each map type used. Metadata found for the different map types revealed that mapping instruction changed significantly over time. The instructions for the Wild map regarding wetlands simply stated that wetlands should be drawn on the maps in blue color and peat mining areas in brown (State Archive of the Canton of Zurich, STAZ NN66 No 14). This instruction was not fully

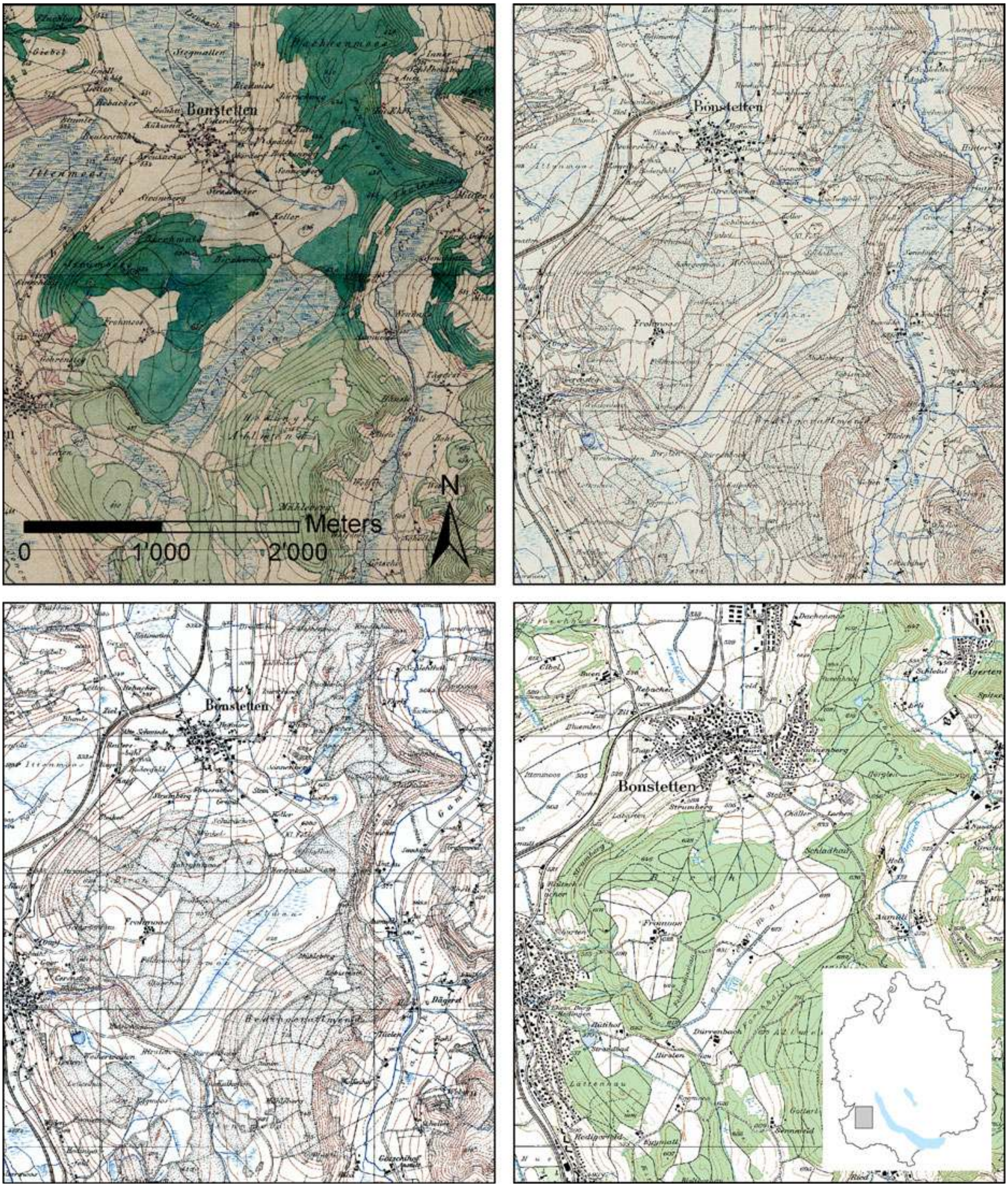

Fig. 2 A section in the western part of the study region as represented by maps used for this study. Wild Map from 1850 (*upper left*), Siegfried Map from 1898 (*upper right*), Siegfried Map from 1940 (*lower left*), and the modern National Map (*lower right*). The *grey rectangle* in the *inset map* shows the location of the detail area within Canton of Zurich. Formerly vast wetland areas (indicated by *blue horizontal line* patterns) have almost completely disappeared in the region, giving way to agricultural land and settlements. (reproduced with the permission of swisstopo: DV 033492.2 and DV 033594)

realized, as all wetlands have been drawn in blue without using a separate label for peat mining. For the Siegfried maps we found an instruction dating from 1873 in the Swiss Federal Archive in Berne that states that wet areas should be charted as soon as they could no longer be crossed on horseback (BA E27 22175). Wetland mapping on the modern National maps is based on aerial photograph interpretation. Wetlands are charted when typical wetland vegetation (e.g., reeds) is visible (pers. comm. swisstopo). This information suggests that modern instructions are less conservative; e.g., some of the wetlands depicted on modern maps could easily be crossed on horseback.

This assumption was confirmed by our observation that an essential part of modern wetland area was not represented on the earlier maps. Since we assumed no new wetlands being formed during our study period, we explain wetland expansion over time by changes in mapping definition rather than by real wetland expansion (see critical remarks on this in the "Discussion and conclusion" section). We conducted a simple consistency analysis by intersecting all unadjusted wetland covers with the immediate previous dataset. In case of uniform wetland mapping over time, theoretically all wetlands in one dataset should also be present in the previous dataset. This is the case with the 1950 and 1900 wetland covers (99.8% overlay) both derived from the same map type (Siegfried map), suggesting consistent wetland interpretation in early and late Siegfried maps. In contrast, only 50% of the wetland area mapped for 2000 (modern National map) is contained in the Siegfried maps around 1950 and 71% of 1900 wetlands (early Siegfried maps) can be found on the 1850. Wild maps indicating that only the wettest areas were mapped on the oldest map.

From the combined evidences (changes in mapping instruction and consistency analysis) we concluded that wetlands are generally underrepresented on historic maps when applying modern mapping standards. In other words, a direct comparison of the maps without taking changes in mapping instructions into account leads to an underestimation of the real wetland loss. The effect of changes in mapping instruction on actual wetland mapping is conceptually illustrated in Fig. 3. To allow for direct comparison of wetland maps from different periods, uniform mapping criteria have to be applied, i.e., wetland areas on historical maps have to be completed based on modern wetland definition. To address this, we developed a procedure for reconstructing consistent time series based on maps using different mapping criteria.

Reconstruction of consistent time series for wetland cover

The procedure to reconstruct consistent time series of wetland cover can be split into three steps. The first step is to estimate realistic rates of wetland loss. The rate of wetland loss between two points in time (t and $t + 1$) is determined to be the proportion of wetlands in one time (t) that is no longer indicated as a wetland in the subsequent time ($t + 1$), e.g., the portion of wetland cover mapped for 1950 but not represented as wetland on the 2000 maps (s1 in Fig. 4). In turn, we compute a target value for the wetland area at time t by dividing the wetland area $t + 1$ by ($1 -$ loss rate), e.g., we calculated the wetland area we would expect for 1950 when applying modern mapping standards. In a second step we adjusted the 1950 wetland cover by combining the two wetland layers as mapped in the topographical maps in 1950 and 2000 (s2). The remaining difference to the target value for 1950 was completed in a third step with the most suitable potential wetland areas that have been drained after 1950 evaluated by a habitat suitability model (see detailed model description below) (s3). This adjusted wetland cover for 1950 serves as the starting point to estimate wetland loss between 1900 and 1950 by evaluating the proportion of wetland cover mapped on the 1900 maps which is not represented in the adjusted

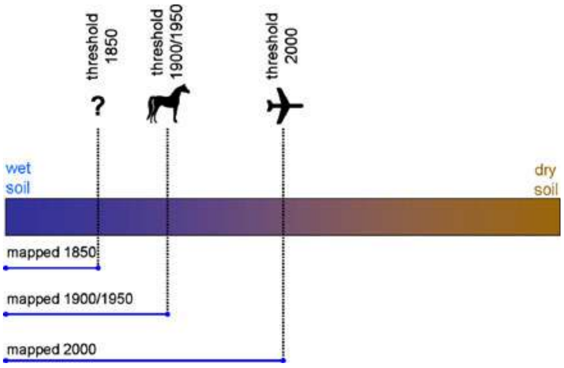

Fig. 3 Transect through a hypothetical landscape along a gradient in soil wetness. The conceptual diagram shows how changes in mapping instructions lead to different wetland interpretation (thresholds) and consequently to different wetland mapping

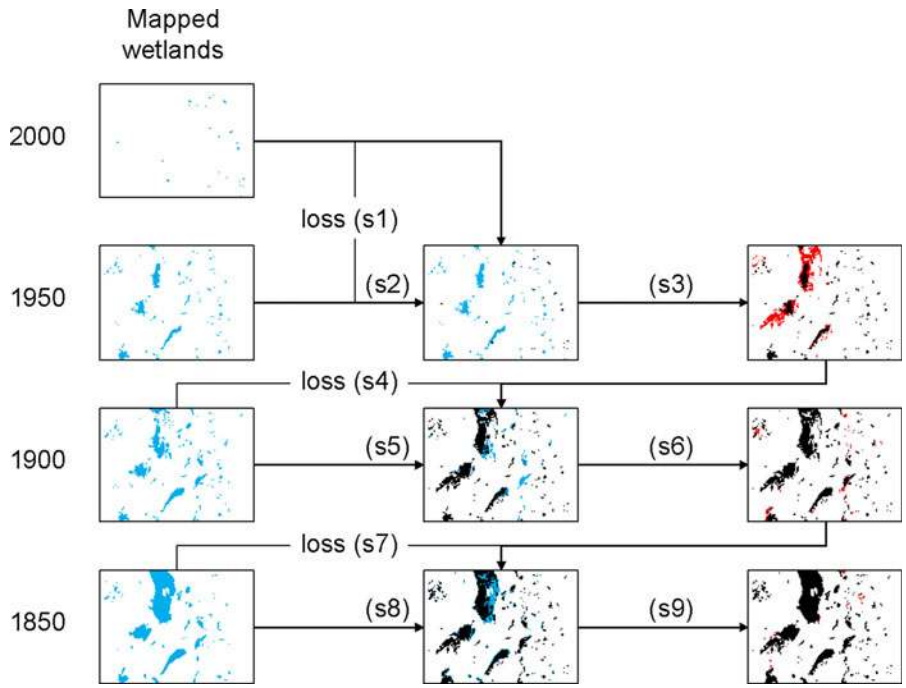

Fig. 4 Conceptual diagram illustrating reconstruction of comparable time series of wetland cover. Wetlands as represented on the maps are indicated in *blue*, wetlands adopted from previous reconstruction steps are shown in *black*, and wetlands gained from suitability models are shown in *red*

1950 wetland cover (s4). This procedure continues until the determination of the initial wetland cover in 1850 as it would presumably have been mapped with modern mapping standards (s9).

Our approach allows qualifying wetlands with into three different certainty levels (following the approach presented in Grossinger et al. 2007). We assigned the highest certainty label (definite) to wetlands depicted on the original maps. The second level (probable) describes wetlands adopted from subsequent maps (e.g., wetland not on 1950 original map but depicted on the 2000 map). Lowest certainty (possible) is assigned to wetlands derived from modeling.

A common approach to test the reliability of historic reconstructions is to compare them with information from independent sources (Gimmi et al. 2008). In our study we compared our results with statistical information contemporary with the historical map.

Modeling wetland suitability

In order to determine the location of the computed wetland area which had not been inventoried on the old maps, we applied an ecological-niche factor analysis (ENFA) using BIOMAPPER 4.0. This software is typically used for modeling species habitat suitability maps with presence-only data (Hirzel et al. 2002, 2006). ENFA is a method based on a comparison between the environmental niche of a species and the environmental characteristics of the entire study area represented by ecogeographical variables (Lachat and Bütler 2009). In this study, we modeled the distribution of a habitat (wetland) instead of a species. For the model building we used all wetland areas that disappeared from the maps between 1850 and 2000. Seven ecogeographical variables have been selected: (i) altitude, (ii) curvature, (iii) slope, (iv) soil type, (v) soil permeability, (vi) soil depth and (vii) moisture index. The first three variables are obtained from the digital elevation model for Switzerland at 50 m resolution from the Swiss Federal Office of Topography (swisstopo, DEM50). Soil information is derived from the soil map of Canton Zurich (Bodenkarte Kanton Zürich 1998) and the national soil suitability map (Bodeneignungskarte der Schweiz, BFS 1992). Qualitative variables (soil type and permeability) have been transformed to quantitative variables.

Similar to the principal component analysis, ENFA computes a group of uncorrelated factors, summarizing the main environmental gradient in the region considered (Chefaoui et al. 2005, see Hirzel et al. 2002 for details). It calculates a measure of habitat suitability for a certain species for each cell based on an analysis of marginality (how the species' mean differs from the mean of all sites in the study area) and environmental tolerance (how the species' variance compares with the global variance of all sites) (Allouche et al. 2008).

Model evaluation is done by a cross-validation process available in Biomapper 4.0. It computes a confidence interval about the predictive accuracy of the model. The data are randomly partitioned into k mutually exclusive sets. $k - 1$ partitions will be used to compute a model and the left-out partition will be used to validate it on independent data. The outcome is k different habitat suitability maps which fluctuations are compared. Biomapper follows the method described by Boyce et al. (2002) and further developed in Hirzel et al. (2006). Each map is reclassified in b bins (by default, $b = 4$). Each bin i covers some proportion of the map's total area (Ei) and contains some proportion of the validation points (Pi). One then computes the predicted to expected ratio P/E for each bin as $Fi = Pi/Ei$. If the model is good, low habitat suitability (HS) should have a low F (below 1) and high HS a high F (above 1) with a monotonic increase in between. A way to measure the monotonicity of the curve is to compute a Spearman rank correlation on the Fi; which is called the Boyce index (Boyce et al. 2002; Hirzel et al. 2006). For our model, we get a Boyce index of 0.86 ± 0.13, which reflect the monotonicity of the curves and the good quality of the model.

Each cell of the modeled map (50 m $\times$ 50 m) contains a habitat suitability value ranging from 0 (low suitability) to 100 (high suitability). From the modeled map we extracted those areas that have been drained during a specific period (according to information derived from the drainage map). We then cumulated the cells with the highest suitability values until the target value for the adjusted wetland area is reached (see also description in the section above and Fig. 4).

Analysis of changes in wetland patterns

As wetlands typically occur in discrete patches within a matrix of upland habitats, many wetland species live in small isolated populations sustained through occasional migration (metapopulations). Therefore, not only absolute loss of wetland habitats is of relevance for biodiversity conservation, but also the changes in the spatial distribution and configuration of wetlands in the landscape (Gibbs 2000). To assess the landscape ecological relevance of historical wetland loss, we calculated selected landscape metrics relevant in the context of the island biogeography theory (MacArthur and Wilson 1967), including total wetland area, portion of wetlands in total landscape, number of patches, mean patch size, and largest patch size. To account for landscape fragmentation effects (Fahrig 2003), we calculated the mean distance to the nearest patch (edge to edge) and analyzed changes in wetland habitat networks. The metrics selected are known indicators for wetland stress (Torbick et al. 2006) and they enable straightforward interpretation of the relationship between observed changes in patterns and ecological processes (Li and Wu 2004; Kindlmann and Burel 2008). Average dispersal distance for many wetland animals (such as frogs, salamanders and small mammals) are generally less than 300 m (Gibbs 2000). In their review of dispersal and the metapopulation paradigm in amphibian ecology, Smith and Green (2005) found that one kilometer has appeared as a 'magic' number beyond which amphibian populations would be isolated from dispersal events. Similar figures have been identified for dispersal abilities of dragonflies (Chin and Taylor 2009). We therefore created wetland networks by applying 150 and 500 m buffers around existing wetlands for all periods and analyzed changes in wetland habitat networks.

Results

Wetland cover change

We estimate a wetland cover loss of 91% of the initial area (13,759 ha) over the last 150 years considering the adjusted maps (Table 1). In the first period from 1850 to 1900 wetland cover decreased only moderately by 2,600 ha (−19%). Highest absolute wetland loss is observed for the first half of the twentieth century when 6,400 ha of wetland disappeared, i.e., more than 50% of the total loss over the whole study period. Relative loss was still large in the second half of the twentieth century when 3,500 ha wetlands vanished (−74%), resulting in a remaining wetland area of 1,233 ha in 2000.

Table 1 Changes in total adjusted wetland area including different certainty levels

	Adjusted wetland cover	Definite	Probable	Possible
2000	1,233 ha	1,233 ha (100%)	–	–
1950	4,762 ha	2,375 ha (50%)	617 ha (13%)	1,770 ha (37%)
1900	11,113 ha	6,993 ha (63%)	454 ha (4%)	3,666 ha (33%)
1850	13,759 ha	6,921 ha (51%)	2,385 ha (17%)	4,453 ha (32%)

Definite mapped on original maps, *Probable* mapped on subsequent maps, *Possible* modeled

Table 2 Changes in wetland area, percentage of total landscape (PLand), number of wetland patches, mean patch size, and size of the largest patch for the period 1850–2000

	PLand (%)	Number of patches	Mean patch size (ha)	Largest patch (ha)
1850	8.3	4,341	3.2 (±1.8)	977
1900	6.7	3,837	2.9 (±1.7)	558
1950	2.9	2,538	1.9 (±1.4)	234
2000	0.7	708	1.7 (±1.3)	191

Between 50 and 63% of the adjusted historical wetland area is effectively depicted on the historical maps (definite certainty level in Table 1). These were most likely the wettest parts of the landscape (see Fig. 3). In all adjusted datasets, approximately one third of the area consists of wetlands in the lowest certainty level (probable).

In the mid nineteenth century, wetlands covered more than 8% of the total study area, but by 2000 this portion had dropped below 1% (Table 2). Large contiguous wetland areas were especially prone to being converted. The largest contiguous wetland in 1850 covered 9.77 km^2 while the largest remaining patch today is less than 2 km^2. In 1850, almost 200 wetlands patches were larger than 10 ha, representing 63% of the total wetland area (Fig. 5). In 2000, only 17 patches larger than 10 ha remained and their contribution to the total wetland area decreased to 42%. Size distribution of today's wetlands is dominated by small and medium sized patches. Consequently, mean patch size has almost halved from 3.2 ha in 1850 to 1.7 ha in 2000.

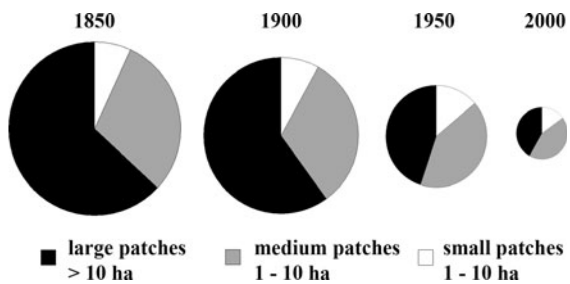

Fig. 5 Proportion of total wetland area by patch size classes. The size of the circle is proportional to the total wetland area for each dataset

Changes in wetland connectivity

Changes in habitat networks based on typical dispersal distances for wetland animals (0.3 and 1 km) are visually presented in Fig. 6. In general, the large connected wetland networks from the beginning of the study period collapsed into medium and small isolated units consisting of fewer habitats. At around 1850, almost all wetlands were connected in two large networks including 98.4% of all wetland patches and comprising 99.4% of the total wetland area at this time (Table 3; Fig. 6). Until 1950, these large networks remained largely intact although the total wetland area had clearly declined and holes (mainly the urban centers of Zurich and Winterthur) within the network had expanded considerably. The disintegration of the large network into smaller networks consisting of fewer patches occurred during the last 50 years. In 2000 the largest remaining network in terms of numbers of patches includes 72 wetland patches (10% of all patches) and the largest network in terms of wetland area included comprises 230 ha of wetland area though consists of eight patches. The mean distance (edge to edge) to the nearest neighboring wetland only moderately increased in the first 100 years of the study period from 80 m in 1850 to

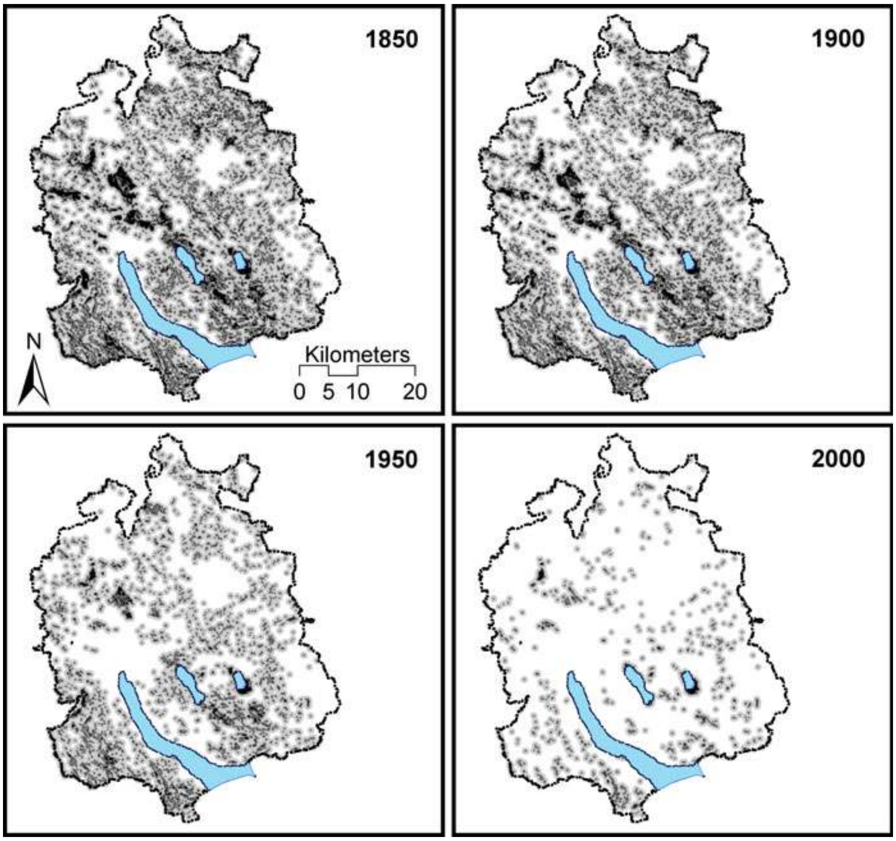

Fig. 6 Changes in wetland connectivity from 1850 to 2000. Wetlands are shown in *black*. Typical amphibian dispersal distances of 300 m and 1 km are indicated by buffers of 150 (*dark grey*) and 500 m (*light grey*)

Table 3 Changes in the number of networks and average number of wetland patches within a network applying 150 and 500 m buffers around wetland patches between 1850 and 2000

	Number of networks		Average number of patches within a network	
	150 m buffer	500 m buffer	150 m buffer	500 m buffer
1850	754	28	6	155
1900	802	30	5	128
1950	854	67	3	38
2000	355	139	2	5

100 m in 1900 and to 170 m in 1950 respectively. In the last 50 years, the value mounted to 360 m. This contrasts with the trend observed for wetland area, for which the highest rate of loss occurred in the first half of the twentieth century (Fig. 7).

Discussion and conclusion

Historical information used for land cover change reconstructions always requires critical interpretation (Egan and Howell 2001). Historical maps are particularly prone to be interpreted without necessary caution because the visual information appears clear at first view. This is also the case with our material where the signature for wetland cover is similar in all map types (see maps in Fig. 2). As mapping instruction significantly changed over time, a direct comparison of the mapped wetland areas would inevitably lead to misinterpretation of the real wetland loss. In order to obtain a consistent dataset for wetland cover changes over time, we developed a procedure to adjust for changes in mapping instructions. The procedure allows the implementation of certainty levels for wetland cover which offers a way to assess and quantify the potential error of historical mapping

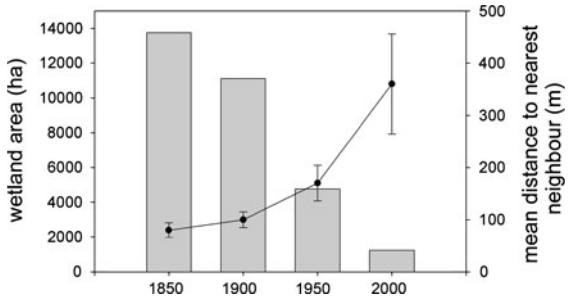

Fig. 7 Changes in wetland area (*bars*) and mean distance to the nearest neighboring wetland patch (points including standard error) for the period 1850 to 2000

efforts. Our results show that historical maps alone would clearly underestimate historic wetland loss. The 1950 and 1850 maps for example capture only about half of the wetlands area we estimated to be present at that time applying modern mapping standards (Table 1).

Our approach was based on several assumptions which we critically assess below.

An integral part of the reconstruction procedure is the assumption that all wetlands existing in a specific point in time should also be present in all previous points in time (exclusion of the possibility of wetland expansion). In theory, new wetlands could have been established either through natural or anthropogenic processes. However, natural establishment of wetlands within the study period can be excluded as the precipitation regime remained generally stable (Begert et al. 2005) and the demand for new agricultural land (Ewald and Klaus 2010) fostered draining existing wetlands, not creating new ones. Anthropogenic establishment of new wetlands, e.g., as ecological restoration projects, did not occur on a significant scale during the study period. A constraint in the wetland suitability model was that only areas that have been drained with federal and/or cantonal subsidies have been considered. We are convinced that this restriction is acceptable because it is not very likely that larger drainage projects would have been conducted without governmental financial support. The model without the supplementary drainage information would be able to localize potential wetland areas under natural conditions. With the help of the drainage map it was possible to enhance the spatial and temporal accuracy of the model results as the map provide helpful information on the timing and location of drainage activities, the most important process leading to wetland loss.

Inconsistencies between maps may be caused by other reasons than changes in mapping instructions. The seasonal timing of the map survey for example has potential impact on the mapping output. Although we do not have any information about the seasonal timing of the surveys for both the Wild and the Siegfried maps we don't expect a major effect on mapping results as seasonal wetlands is not a common type in study region as a consequence of the well balanced precipitation regime with a slight peak in summer. Further it's relevant if the survey was conducted in a particular dry or wet year. In our study this potential bias is buffered by the fact, that out datasets for the entire study area consist of a composite of maps dating from a period spanning more than a decade (e.g., the 1,900 data set combines maps from 1894 to 1907).

Independent information is of great importance for the calibration and interpretation of historical land cover reconstructions. However such information is often lacking or difficult to obtain. To check the reliability of our reconstruction, we compared the values with numbers from one independent contemporary statistical source. Our reconstructed wetland cover for 1900 (11,113 ha) fits well with numbers provided in official statistics found in the State Archive of Canton Zurich (Statistische Mittheilungen betreffend den Kanton Zürich 1910, STAZ III NNa3), i.e., litter meadows 9,200 ha; peat mining area 450 ha, especially when taking into account, that not necessarily all wetlands were used for one of these purposes. Our adjusted values are much closer to the statistical values than the unadjusted wetland cover for 1900 (6,900 ha), supporting our assumption that historical maps underestimate wetland cover compared to modern maps. Unfortunately, we found no suitable statistical records for an independent comparison with the 1850 and 1950 datasets. Another potentially useful approach to check the accuracy of map information is to calibrate them with other maps. Grossinger et al. (2007) for example reconstructed historical land cover in California's Santa Clara valley by compiling information from a set of very heterogeneous maps at different spatial scales. In our case, we had the opportunity to work with three map types being homogenous as such and covering the entire study area. The few local-scale maps found in the archives were not suitable for an independent calibration as no information on their wetland interpretation standards is given.

Our results show that Canton Zurich experienced a dramatic loss of wetland area over the past 150 years with accelerated loss rates in the twentieth century. Expansion of agricultural area was the main driver causing pressure on historic wetland area. Mechanization and technical innovations, such as the introduction of clay tubes in the late nineteenth century, allowed for more efficient lowering of water tables by subterranean drainage on larger areas. Lowering of lake levels played only a minor role in the study region. From 1900 to 1950, an increased demand for agricultural products especially during both World Wars and large infrastructural projects (namely the construction of the airport on the formerly largest contiguous wetland area of the canton) resulted in an exceptionally large wetland loss. Absolute wetland loss substantially slowed down in the last period because (a) there were simply not many wetlands left to drain, and (b) effective protection measures of the remaining wetlands came into force in the 1980s. In Switzerland wetland landscapes of national importance are under constitutional protection since 1987.

Whereas statistical information could also reflect these changes in wetland area, our approach allows for additional reconstruction of change in habitat connectivity, which is of high ecological relevance (Bender et al. 1998). Our results show that today's remaining wetlands are smaller and more isolated and we determined a collapse of wetland networks in the second half of the twentieth century. This has important impacts on metapopulation dynamics of wetland species because populations in isolated habitats are cut off from genetic exchange. Negative effects of habitat fragmentation on wetland plant species richness (Lopez et al. 2002; Lienert and Fischer 2003; Boughton et al. 2010) and fitness (Lienert et al. 2002) have been empirically demonstrated. The buffer distances (150/500 m) applied in this study represents a theoretical connectivity which in reality might be constrained by anthropogenic features (roads/settlements) and/or topographic features. The disintegration of large connected wetland networks is even more relevant when taking into account that the matrix between wetland patches changed considerably. The composition of the landscape matrix between habitats is crucial for assessing the ability of animals to migrate (Gustafson and Gardner 1996; Ricketts 2001). For example, Gibbs et al. (2005) associated urban development and high-intensity agriculture around frog and toad habitats with population disappearance. In addition, urban land use near wetland habitats can affect amphibian persistence negatively because of changed water regimes, road salt, pesticide inputs, and strong recreational use of the habitats (Gagné and Fahrig 2007). Results from the Swiss wetland monitoring program over the past decade identified problematic trends toward wetland degradation, such as increased nutrient inputs, drying, and shrub encroachment, in one third of all inventoried wetland habitats (Klaus 2007). Although we did not reconstruct land cover changes outside of wetlands, in our study area intensified agriculture, spreading urban land use, denser transport infrastructure and increased traffic volume have very likely amplified habitat fragmentation effects. Hamer and McDonnell (2008) reported in their review on amphibian conservation in urban landscapes that long distance dispersal (>1 km) of amphibians becomes virtually impossible in highly urbanized areas. In sum, the chance for occasional long distance dispersal was more likely in historical landscapes as the habitat networks were much denser and the matrix between wetland habitats was more permeable for wetland animal migration.

While habitat loss was the main threat for wetland ecosystems until the mid twentieth century, the main challenges today are declining habitat connectivity and increasing habitat degradation. In addition to the immediate effects of habitat destruction, the observed large loss of wetland habitat and reduction of habitat connectivity is very likely to cause time-delayed extinction of specialized wetland animal and plant species in the remaining wetlands—a phenomenon known as extinction debt (Tilman et al. 1994). In other words, current species occurrence might not be based on current wetland cover and habitat configuration but rather reflect historical conditions. Future wetland restoration efforts should clearly focus on reestablishing connections between existing wetland networks and removing dispersal barriers between habitats, without neglecting other current threats to wetland ecosystems such as nutrient input from nearby agricultural areas or shrub in growth (Klaus 2007). In this context, the creation of stepping stone habitats and migration corridors are crucial elements to enhance wetland connectivity. The effectiveness of connectivity measures in wetland management has recently been demonstrated for European tree frogs in Switzerland (Angelone and Holderegger 2009). The reconstruction of historical conditions can serve as reference points and in this way help set appropriate conservation goals and restoration priorities (Bolliger et al. 2004; Bürgi and Gimmi 2007).

The selection of specific locations for restoration projects should aim at re-establish as far as possible historical wetland connectivity and include a number of socioeconomic factors and practical considerations. Factors to be studied are present land use, land ownership and the willingness of land owners to participate, technical feasibility (removal of old drainages and raising of water tables without negative consequences for surrounding lands and land owners), and finally costs and the availability of funding options (agricultural schemes, local NGOs and sponsorship).

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