Quality loss of Swiss bog vegetation - the key importance of the margins

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SUMMARY

Swiss Bogs of National Importance were designated as protected areas in 1991. However, their quality was found to have decreased over a 5–7 year monitoring period. In this article we assess the quality of the vegetation and its changes in 80 bogs throughout Switzerland. To determine change over time, 2912 pairs of records from revisited plots were compared. The indicator for quality was the ratio of specialists to the full species list in each record. We performed linear regressions to assess the proportion of variance explained by the variables: bog area, distance to edge, bog density, altitude and draining structures within the bog core areas and their surroundings. To specify the site conditions, we analysed Landolt's mean indicator values for light, humidity and nutrients. Finally, we derived a raw estimate of the loss in bog area. Distance to edge, bog density and draining structures outside the bogs had the best explanatory power for the quality of bog vegetation. The quality increased with distance from the edge. It correlated better with nutrients indicator values than with humidity values. With regard to quality changes, humidity indicator values decreased mainly in the bog centres, whereas increasing nutrients values and decreasing light values mainly affected the margins. We estimated that the loss of high quality surface affected about 0.6 % of the total Swiss bog area.

KEY WORDS: bog area, density of bogs in landscape, distance to edge, specialist species, surrounding area

INTRODUCTION

Wetlands are considered to be among the world's most threatened habitats and the global loss of wetlands has been estimated at 50 % of those that existed in 1900 (Zedler & Kercher 2005). Mires in Switzerland, as in other countries of the temperate zone, suffered after the 1720s from peat mining and since the 19th century from hydrological control operations followed by the expansion of hydroelectric power plants, land reclamation and extensive drainage schemes. By the end of World War II agricultural intensification had started, along with activities relating to large settlements and the expansion of tourism. In this densely populated country, 90 % of the former mire area is estimated to have been lost during the last two centuries (Grünig 1994, 2007; Lachat *et al*. 2010, Wüst-Galley *et al*. 2015). This is even more than the 80 % loss estimated for the European continent as a whole (Finlayson & Spiers 1999).

The small mire remnants in Switzerland represent isolated island-like habitats in otherwise forested or agricultural landscapes. Hardly any of these mires are pristine. Most have been disturbed and thus have highly heterogeneous plant communities, depending on the extent and type of disturbance (Graf *et al*. 2010). Nevertheless, these mires still harbour a specialised flora. Species able to survive in them have adapted to the extreme conditions which are typically wet, nutrient-poor, partly anoxic and often acidic (Rydin & Jeglum 2006).

Mires are now regarded as having high ecological value. Therefore, Swiss mires of national importance were designated as protected areas in 1991. To determine whether the total surface area and quality of these habitats were being maintained, a monitoring programme was launched in 1997 and continued until 2008. The authors and co-workers conducted this programme jointly with the Federal Office of Environment (FOEN). The results showed that the quality of raised and transitional bogs of national importance had declined (Klaus 2007). They had become drier, poorer in organic matter content, richer in nutrients and showed increased shrub encroachment, although the area in need of preservation remained approximately the same. This article evaluates factors potentially affecting the quality of Swiss raised and transitional bogs on the basis of data from the monitoring programme.

The size of protected areas has been a subject of debate in conservation biology since the 1970s. Discussions have been held about whether Single Large Or Several Small (SLOSS) reserves are better for conserving biodiversity in a fragmented area (Diamond 1975, Rosenzweig 1995). Because large sites support more species richness, some experts consider site area to be one of the main determinants for biodiversity and, accordingly, for site quality (MacArthur & Wilson 1967, Magurran 2004). However, species richness alone is not a pertinent quality criterion for bogs. Pristine bogs sustain a low number of highly specialised species, whereas drained bogs harbour a larger number of species because more common species quickly invade such degraded sites. While habitat specialists may require a minimum area to develop a vital population (Lienert *et al*. 2002), it is not clear whether habitats offering suitable conditions for specialised species are present only in large bogs. Could it be a matter of location within the bog rather than bog size itself?

Habitats can vary considerably within a bog and generally show marked functional gradients from the border to the centre (Rydin & Jeglum 2006). We assumed that habitat quality is not equal throughout a bog and depends on location. Therefore, we took into account not only bog size, but also distance from the edges (natural margins) of the bogs. Connectivity between bogs may, however, be more important than the sizes of the sites, and small sites may contain even more species than larger ones (Peintinger *et al*. 2003, Richardson *et al*. 2015). As Swiss bogs are found across a wide altitudinal range, we also estimated the relative importance of altitude. Most Swiss bogs are dissected by drainage ditches and also influenced by nearby drainage systems (Grünig 1994). Therefore, we also investigated artificial drainage features (draining structures) within the bogs and in neighbouring areas. Since mire quality has declined during the last decade despite governmental conservation measures (Klaus 2007), we assessed temporal changes in ecological conditions using Landolt's indicator values for light, humidity and nutrients (Landolt *et al*. 2010), as well as the loss in area of high ecological value between the two surveys.

Our study addressed the following questions:

(1) Which factors affect the quality of bogs?

(2) Does the quality vary between different locations in the bogs?

(3) How do bog quality and changes in quality correlate with ecological conditions?

(4) How much of the bog area of high ecological value has been lost in the past few years?

METHODS

Study area

The Swiss inventory of raised and transitional bogs of national importance was compiled between 1978 and 1984 (Grünig *et al*. 1986). The basic unit is a 'bog site' classified as an object. Each object consists of one or several bog cores with a surrounding area. A 'bog core' is defined as an area covered with peat mosses and containing one of four typical bog vascular plant species (see Appendix). In order to include areas that do not bear typical bog vegetation but are still part of the bog biogeocoenosis (Gobat *et al*. 2010), a 'surrounding area' is defined in addition to the bog core. Parts of this area are, furthermore, considered to protect the bog core from harmful influences and to act as a "buffer zone". The inventory of raised and transitional bogs includes 1524 ha of bog core and 4014 ha of surrounding area (status 2008), i.e. the total surrounding area is more than twice the actual bog core area.

Vegetation survey and sampling sites

In the Swiss Mire Monitoring Programme the authors and co-workers conducted a first survey of 135 bogs and fens of national importance between 1997 and 2001, and a second survey in 2002–2008 (Klaus 2007). For the present study, we investigated 80 bog sites for which sufficient information was available (Figure 1). Together, these sites include 426 ha of bog core and 792 ha of surrounding area. The field data used here were recorded on 39 ha of bog core and 50 ha of surrounding area. Nomenclature follows Landolt *et al*. 2010.

Data collection

The data collected for the Swiss Mire Monitoring Programme consisted of aerial photographs and vegetation records. For the analysis of aerial imagery, it was assumed that similar ground vegetation looks similar on aerial photographs, which can thus be used to identify and delineate homogenous vegetation patches (Grünig *et al*. 2005). The field survey was restricted to a limited number of these patches, hereafter called plots, which were selected according to local stratified random sampling of each mire site (Ecker *et al*. 2008). Each plot was sampled in the first survey and re-sampled 5–7 years later in the second survey. The vegetation data consist of full records of vascular plants, mosses and liverworts over the whole surface of the plot, including abundance data on a logarithmic scale. The sample used in this study comprises 2912 pairs of records. The plot areas in the sample range from 25 to 2500 m^2, with a median of 189 m^2.

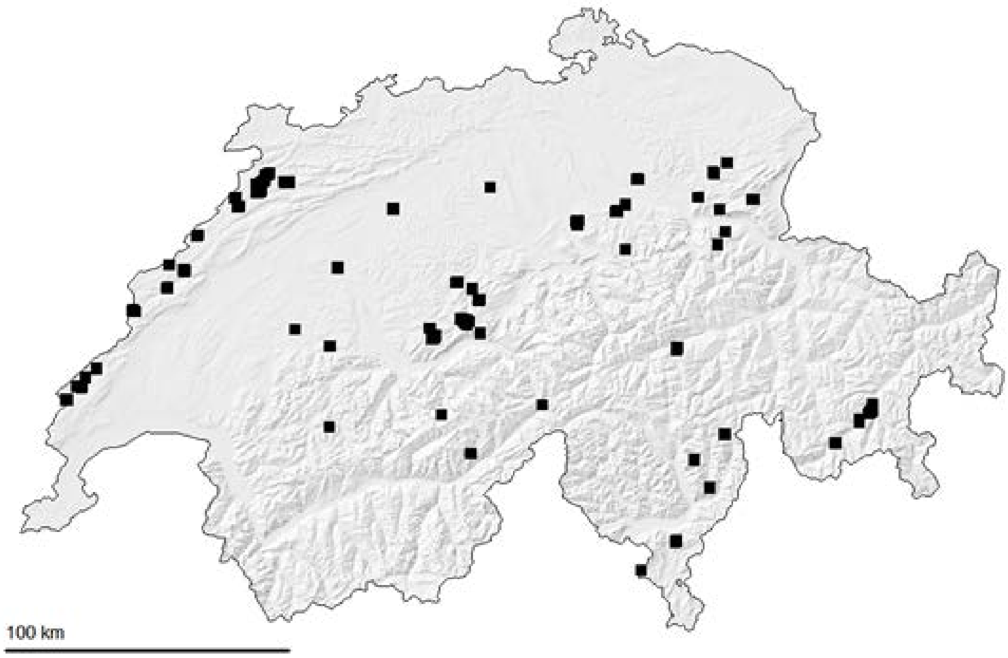

Figure 1. Distribution of the 80 bog sites studied in Switzerland.

Specialist species as indicators for quality

We defined the bog specialist species as those from two plant communities that form the hummock-hollow microtopography of the bog surface. This particular topography is associated with fine-scale patterns in the species composition with *Sphagnum* species dominant (Nordbakken 1996, Økland *et al*. 2008). At the level of plant communities, this corresponds to the alliances of Sphagnion magellanici for the vegetation in the rather dry hummocks, and of Caricion lasiocarpae (including Rhynchosporion albae) for the vegetation in the wetter hollows. Based on the list of characteristic species for these two alliances (Delarze *et al*. 2008), we selected a set of 40 specialist species including 21 mosses from the 1081 species present in our data (see Appendix).

Species richness in a bog is not a relevant indicator for bog quality (Gunnarsson *et al*. 2002). Typical bog vegetation is species-poor and is dominated by characteristic species (Appendix). The occurrence of many other species in a plot denotes disturbance, even if bog specialists are present. We chose the proportion (not the number) of specialist species as an indicator for quality. A high ratio of specialists to the full species list in each record was considered to represent a plot with bog vegetation in good condition. For analyses of quality at the bog site level, we averaged the proportions from all plots situated in each bog to obtain an indication of quality and took into account the frequency of species in each bog.

Factors that potentially influence the quality of bog vegetation

The factors considered in this article are: bog area, distance to edge, bog density in the landscape, and altitude above sea level, as well as the draining structures inside the bog core and in the surrounding area. The data were analysed at the bog site level as well as at the plot level.

Bog area was represented by the size of the bog core (0.013–129.2 ha, median 0.88 ha) recorded in the Swiss inventory of raised and transitional bogs. The edges of the bog cores were also recorded but, because these boundaries were drawn on a 1:25,000 map, their accuracy was limited. The width of the line (0.2 mm) corresponded to 5 m in the field. This, together with delineation inaccuracies, resulted in an unknown error. Nevertheless, we used these boundaries because they were drawn independently of our recordings.

The distance to the bog edge was computed for each vegetation plot as the distance from the middle of the plot to the closest boundary of a bog core. Plots situated inside a bog core were assigned positive distance values (0.25 to 129.7 m, median 13.9 m), while those situated in the surrounding area were assigned negative values (-0.20 to -359.5 m, median -24.0 m). Distance 0 denotes a position on the edge of a bog core.

To enable comparisons between different locations within the bog sites, we determined four concentric belts from the surrounding area to the centre of the bog (Figure 2). Belt A (outer

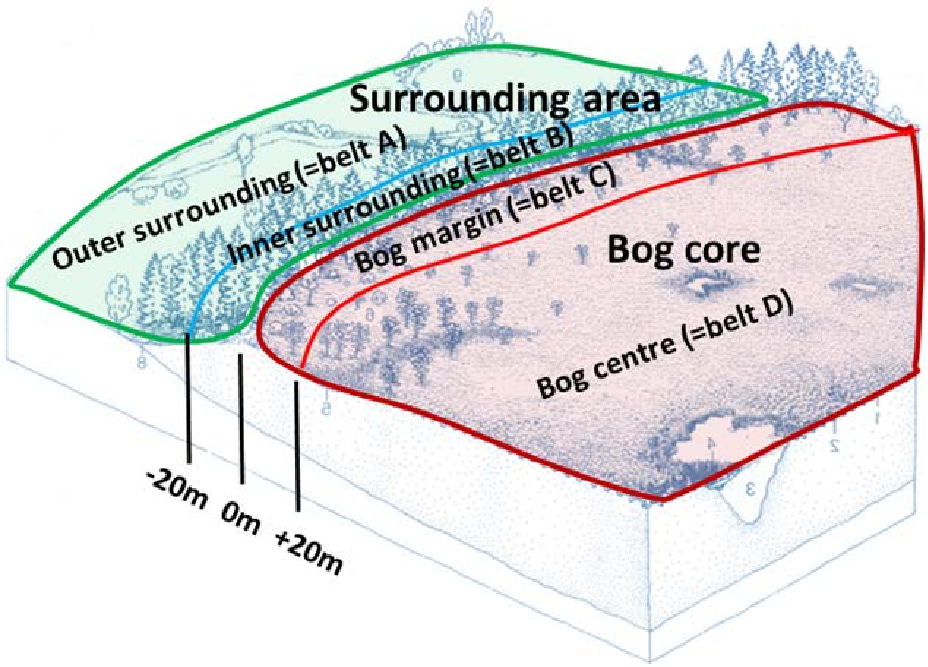

Figure 2. The four concentric belts within bog sites (adapted from Grünig *et al*. 1986).

surroundings) covered the surrounding area up to 20 m from the edge of the bog core. Belt B (inner surroundings) covered the surrounding area from 20 m outside the bog core to its edge. Belt C (bog margin) covered the bog core from the edge up to 20 m inside the bog core and Belt D (bog centre) covered the bog centre, i.e. the area situated inside the bog core at a distance of more than 20 m from the edge of the bog core.

To quantify bog density in the landscape (surrogate for connectivity), we used a relatively simple structural metric based on the number of habitats in the landscape (Tischendorf & Fahring 2000). We computed density as the number of bog cores (1 to 23, median 3) within a 1 × 1 km square around every vegetation plot. For the statistical tests at bog level, we averaged the square roots of these values.

The available data on draining structures were the roads and paths drawn on the 1:25,000 national map, and major ditches digitised from aerial photographs. The total lengths of these draining structures in the belts around the bog plots were recorded. To adapt the data to this study, we resampled the draining structures on a 25 m grid and computed their densities both inside the bog cores and in the surrounding areas.

Indicator values as surrogates for measurements of ecological conditions

To consider species composition from the point of view of the ecological conditions, we computed Landolt's mean indicator values for the plots (Landolt *et al*. 2010). We used Landolt's ecological indicator values for light, humidity and nutrients, ranging from 1 to 5. Ecological values should preferably be derived from geochemical and geophysical measurements, but the large number of sample plots made such measurements impossible. Indicator values were considered to be a valuable surrogate (Diekmann 2003) as they describe the responses of species to environmental conditions and not just the site conditions. Indicator values are, like other values derived from species, a representation of species composition in a reduced space. To avoid circular reasoning in the statistical modelling, species or values related to species were only permitted to appear in our analyses either in the response of a model or in the explanatory variables (Zeleny & Schaffers 2012, Wildi 2016).

Data analysis

Assessing the influence of the different factors on the quality of bog vegetation using commonality coefficients

To test the effects of the factors potentially influencing the quality of bog vegetation, we fitted multiple linear regression models with the proportion of bog specialist species as the response variable. The explanatory variables were: distance to edge (mean *per* bog core), bog core area, bog core density (proxy for connectivity), altitude, draining structures inside the bog cores and draining structures in the surrounding areas. To meet the need for normal distribution of errors in linear regressions, some of the explanatory variables were transformed. Bog core area and distance to edge entered the model as their logarithms, and bog core density as the square root.

The explanatory variables are, of course, correlated. Distance to edge must be correlated with bog core area because long distances can occur only in large bogs. The two variables are statistically dependent on each other. If an effect is found, it is not immediately clear which of the two variables is responsible for it. Size and altitude are also correlated because only small bogs occur at high locations. If explanatory variables are correlated, their respective effects on the response variable (here the proportion of bog specialists) have to be quantified specifically. We applied the R function "commonality coefficients" (Nimon *et al*. 2008) to the variables listed above. Using subsets of the explanatory variables, this function generates a combination of multiple linear regressions to estimate the proportion of variance exclusively and commonly explained by each explanatory variable (Ray-Mukherjee *et al*. 2014).

Stratified analysis of state and temporal changes

To investigate the quality of vegetation and the responses of vegetation to site conditions, we stratified the vegetation data according to the influencing factors described above. The distance to the edge was represented by Belts A, B, C and D (see Figure 2). For the remaining factors, the bog sites were assigned to equally sized high and low level subsets for each factor (e.g. > 3 bog cores *per* km^2 was high density, ≦ 3 bog cores low density).

Differences between the subsets and changes in time were tested for significance using rank sum tests. To avoid pseudo-replication, tests were performed at the bog level, i.e. the values (proportion of specialists and the indicator values of the plots) were averaged over the whole bog site or over a whole belt within a bog before analysis.

The changes in the proportion of specialists and in the indicator values through time could be quantified because the vegetation had been recorded at two different times (see above). The changes were tested for significance using signed-rank tests. The differences between the high and low levels of the factor subsets were tested using unsigned rank tests.

Loss of high-quality surface

The Swiss inventory of raised and transitional bogs defined the bog core area according to vegetation criteria assessed in the field (Grünig *et al*. 1986). If the quality of bog vegetation had decreased over the past decades, a new delineation would result in a shift of the external boundary and consequently a reduction of the bog area. We determined the relationship between distance along a gradient from the edge to the centre and vegetation quality using simple linear regression. The positions of all plots situated within Belt B (inner surroundings) and Belt C (bog margin) were regressed on the proportion of bog specialist species, and the mean change in the proportion of specialists between the first survey and the second survey was then projected to the regression line. The projection can be interpreted as a spatial shift in quality between the two surveys. The level of the regression line at position 0 (= boundary of the bog core) was taken as the threshold for high vegetation quality. An extrapolation of the lost surface could then be made for the whole Swiss inventory of raised and transitional bogs.

RESULTS

Influence of factors potentially affecting bog quality

Our regression model identified distance to edge, bog core density and draining structures in the surrounding area to be significant explanatory variables for bog quality (Table 1, last column). The relative importance of each variable can be read from the commonality coefficients (Table 1). Distance to edge turned out to be the variable with the most explanatory power (9.36 % of uniquely explained variance). The negative value of the shared component (-3.65 % of commonly explained variance) points to interactions with other variables, which is not surprising given the high correlation between distance to edge and bog core area (Table 2). Bog core area itself explained no variance uniquely.

Spatial gradients across the four bog zones

The proportion of specialist species increased from the outer surroundings (Belt A) to the centre (Belt D) (Table 3). The nutrients indicator values decreased from the outer surroundings to the centre, while the light and humidity indicator values increased.

The proportion of bog specialist species was highly correlated with the nutrients value in all belts and somewhat less with the light value. There was less correlation with the humidity value in Belts A, B and C, and almost none in Belt D (Table 4).

Influence of bog density on bog quality

In all belts the proportion of specialists was significantly higher in areas with a high density of bog cores than in areas with a low density of bog

Table 1. Commonality coefficients and regression coefficients of the six explanatory variables considered for the proportion of bog specialist species. Data: values from 80 bog cores. Significance levels for the regression coefficients: ** <0.01, * <0.05.

	Uniquely explained	Commonly explained	Total	Regression coefficients of the full model
Altitude	2.30 %	0.88 %	3.18 %	0.00005
Log bog core area	0.00 %	4.57 %	4.57 %	-0.0018
Mean (log distance to edge)	9.36 %	-3.65 %	5.71 %	0.2217 **
Sqrt (density)	5.57 %	2.91 %	8.48 %	0.0405 *
Drains inside	0.57 %	2.46 %	3.03 %	-0.0490
Drains outside	3.66 %	3.13 %	6.79 %	-0.1225 *
Full model			31.76 %	

Table 2. Correlations (Pearson's r) between the explanatory variables.

	Altitude	Log bog core area	Mean (log distance to edge)	Sqrt (density)	Drains inside	Drains outside
Altitude						
Log bog core area	-0.233					
Mean (log distance to edge)	-0.300	0.781				
Sqrt (density)	0.425	0.018	-0.113			
Drains inside	-0.120	0.410	0.452	0.073		
Drains outside	-0.078	0.286	0.405	-0.043	0.805	

Table 3. Site conditions in Belts A, B, C and D of the bogs studied.

	Outer surroundings Belt A	Inner surroundings Belt B	Bog margin Belt C	Bog centre Belt D
Number of bogs	70	73	80	42
Proportion of specialists	8.87 ± 0.92 %	15.35 ± 1.05 %	21.93 ± 1.18 %	29.10 ± 1.96 %
Light indicator value	3.37 ± 0.03	3.43 ± 0.03	3.47 ± 0.02	3.56 ± 0.02
Humidity indicator value	3.60 ± 0.03	3.69 ± 0.03	3.72 ± 0.03	3.79 ± 0.04
Nutrients indicator value	2.39 ± 0.05	2.16 ± 0.04	1.97 ± 0.03	1.83 ± 0.05

Table 4. Correlations (Pearson's r) between the proportion of specialists and indicator values.

	Outer surroundings Belt A	Inner surroundings Belt B	Bog margin Belt C	Bog centre Belt D
Number of bogs	70	73	80	42
Light indicator value	0.27	0.42	0.41	0.31
Humidity indicator value	0.21	0.21	0.14	-0.04
Nutrients indicator value	-0.76	-0.79	-0.86	-0.81

cores (Table 5, 2nd data row). The nutrients indicator values were also significantly lower in all belts of bogs situated in areas with a high density of bog cores (Table 5, 5th data row). The light indicator value was significantly higher in the centre (Belt D) of areas with a high density of bog cores (Table 5, 3rd data row). We noted no significant differences in the humidity values between areas with a high density of bog cores and areas with a low density of bog cores.

Influence of draining structures on bog quality

In the inner surroundings and in the bog margin (Belts B and C), bogs with few draining structures in their surrounding areas showed a significantly higher proportion of specialists than bogs with many draining structures (Table 6, 2nd data row). The difference in nutrients values between bogs with few or many draining structures was significant only in the bog margin (Belt C) (Table 6, 5th data row).

Table 5. Site conditions in Belts A, B, C and D for high-density and low-density bogs. Significance levels for the differences between values for high and low density (rank sum test): *** < 0.001, ** < 0.01, * < 0.05, ' < 0.1.

	Density	Outer surroundings Belt A		Inner surroundings Belt B		Bog margin Belt C		Bog centre Belt D	
Number of bogs	high low	33 37		32 41		38 42		16 26	
Proportion of specialists	high low	11.44 ± 1.28 % 6.57 ± 1.21 %	***	18.03 ± 1.34 % 13.26 ± 1.49 %	**	25.26 ± 1.54 % 18.91 ± 1.65 %	**	36.68 ± 2.81 % 24.44 ± 2.24 %	***
Light Indicator value	high low	3.445 ± 0.036 3.316 ± 0.046	*	3.490 ± 0.032 3.387 ± 0.040	*	3.508 ± 0.029 3.445 ± 0.032	-	3.632 ± 0.026 3.519 ± 0.032	**
Humidity Indicator value	high low	3.618 ± 0.046 3.592 ± 0.040		3.717 ± 0.035 3.675 ± 0.042		3.734 ± 0.035 3.703 ± 0.036		3.858 ± 0.053 3.750 ± 0.064	
Nutrients Indicator value	high low	2.203 ± 0.056 2.565 ± 0.071	***	2.019 ± 0.034 2.269 ± 0.062	***	1.836 ± 0.034 2.088 ± 0.048	***	1.654 ± 0.060 1.938 ± 0.059	**

Table 6. Site conditions in Belts A, B, C and D for bogs with few and many draining structures. Significance levels for the differences between bogs with few and many draining structures (rank sum test): *** < 0.001, ** <0.01, * <0.05, ' < 0.1.

	Drains	Outer surroundings Belt A		Inner surroundings Belt B		Bog margin Belt C		Bog centre Belt D	
Number of bogs	few many	34 36		36 37		40 40		16 26	
Proportion of specialists	few many	9.78 ± 1.26 % 8.01 ± 1.34 %		17.45 ± 1.58 % 13.31 ± 1.33 %	*	24.75 ± 1.62 % 19.10 ± 1.62 %	**	33.99 ± 3.32 % 26.10 ± 2.28 %	-
Light indicator value	few many	3.333 ± 0.046 3.419 ± 0.039		3.427 ± 0.043 3.438 ± 0.034		3.451 ± 0.031 3.499 ± 0.031		3.572 ± 0.043 3.556 ± 0.028	
Humidity indicator value	few many	3.570 ± 0.041 3.636 ± 0.044		3.688 ± 0.042 3.699 ± 0.037		3.702 ± 0.034 3.733 ± 0.037		3.769 ± 0.071 3.806 ± 0.058	
Nutrients indicator value	few many	2.355 ± 0.078 2.432 ± 0.068		2.093 ± 0.052 2.224 ± 0.060	-	1.894 ± 0.040 2.042 ± 0.051	**	1.736 ± 0.061 1.888 ± 0.066	-

Changes in bog quality (proportion of specialist species) between the first and second surveys

The proportion of specialist species in all zones decreased between the first and second surveys (Table 7, 2nd data row). The light and humidity indicator values decreased significantly in the inner surroundings (Belt B) and in the centre (Belt D) (Table 7, 3rd and 4th data rows). In contrast, the nutrients indicator value increased in the inner surroundings and in the bog margin (Belts B and C), but showed a decreasing tendency in the centre (Belt D) (Table 7, 5th data row).

Changes in bog quality between the first and second surveys, in relation to bog density

The proportion of specialists decreased significantly in the margins and centres of bogs in low bog density areas, whereas it decreased only in the outer and inner surroundings of bogs in high bog density areas (Table 8, 2nd data row). The changes in light value also affected different belts in low and high bog density areas, with a decrease in the inner surroundings and margins of bogs in low density areas, while bogs in high density areas showed a decrease in the outer and inner surroundings

Table 7. Changes in Belts A, B, C and D for all of the bogs studied. Significance levels (signed rank sum test): *** < 0.001, ** < 0.01, * < 0.05, ' < 0.1.

	Outer surroundings Belt A	Inner surroundings Belt B	Bog margin Belt C	Bog centre Belt D
Number of bogs	70	73	80	42
Proportion of specialists	-0.47 ± 0.46 % *	-1.07 ± 0.42 % *	-0.91 ± 0.41 % *	-1.24 ± 0.63 % *
Light indicator value	-0.014 ± 0.011	-0.038 ± 0.011 ***	-0.011 ± 0.010 '	-0.026 ± 0.013 *
Humidity indicator value	-0.024 ± 0.012 '	-0.022 ± 0.010 *	+0.001 ± 0.011	-0.040 ± 0.011 ***
Nutrients indicator value	+0.017 ± 0.014 '	+0.019 ± 0.012 *	+0.031 ± 0.013 **	-0.019 ± 0.018 '

Table 8. Changes of bog quality in Belts A, B, C and D, in relation to bog density, between the first and second surveys. Significance levels for the changes themselves (signed rank sum test), and for the differences between high and low density (rank sum test): *** < 0.001, ** <0.01, * <0.05, ' < 0.1.

	Density	Outer surroundings Belt A		Inner surroundings Belt B		Bog margin Belt C		Bog centre Belt D	
Number of bogs	high low	33 37		32 41		38 42		16 26	
Proportion of specialists	high low	-0.31 ± 0.85 % ** -0.31 ± 0.85 %	*	-1.31 ± 0.54 % * -0.89 ± 0.61 % '		-0.12 ± 0.60 % -1.62 ± 0.53 % **	*	-0.53 ± 0.87 % -1.68 ± 0.86 % *	
Light indicator value	high low	-0.031 ± 0.015 * +0.002 ± 0.015	'	-0.033 ± 0.013 ** -0.041 ± 0.016 *		+0.014 ± 0.014 -0.034 ± 0.014 **	**	-0.034 ± 0.017 ' -0.021 ± 0.018 '	
Humidity indicator value	high low	-0.013 ± 0.014 -0.033 ± 0.019 '		-0.027 ± 0.013 * -0.019 ± 0.014 '		+0.027 ± 0.015 ' -0.023 ± 0.014	'	-0.054 ± 0.013 ** -0.030 ± 0.015 *	*
Nutrients indicator value	high low	+0.012 ± 0.021 ' +0.022 ± 0.020		+0.012 ± 0.016 +0.025 ± 0.017 *		+0.036 ± 0.024 +0.026 ± 0.015 *		-0.002 ± 0.019 -0.030 ± 0.027	

(Table 8, 3rd data row). In addition, the bogs in low density areas showed a significant increase in nutrients value in the inner surroundings and in the bog margin (Table 8, 5th data row). The humidity value decreased in the centres of all bogs, regardless of high or low density (Table 8, 4th data row).

Changes in bog quality in relation to draining structures between the first and second surveys

We observed a loss in the proportion of specialists in the margins of bogs with many draining structures in their surrounding areas, whereas bogs with few draining structures were affected in their outer and inner surroundings, and centres (Table 9, 2nd data row). The nutrients indicator value increased in the inner surroundings and margins of bogs with many draining structures, while bogs with few draining structures were affected in their outer surroundings and centres (Table 9, 5th data row). The humidity value decreased in the centres of all bogs, regardless of draining structures (Table 9, 4th data row).

Surface area of high quality lost

Simple linear regression of the distance from edge of the plots in Belts B and C on the proportion of specialists gave the following estimated coefficients: y = -3.534 + 22.08 x, where y = distance from edge of the plots in Belts B and C, and x = proportion of specialists on the plots in Belts B and C.

Between the two surveys, the mean change in proportion of specialists for the plots in Belts B and C was -0.0072 ± 0.0019 (standard deviation). This corresponds to an estimated shift of 0.0072 × 22.08 = 16 ± 4 cm. The total bog surface area recorded in the Swiss inventory of raised and transitional bogs was 1523.7 ha. We calculated an inner buffer of 16 cm from the edges of the bog cores. Its surface of 9.8 ha may be interpreted as an estimate of the bog area lost during the 5–7 years between the two surveys. Considering the standard deviation (± 4 cm), the estimated loss is between 7.3 ha and 12.2 ha. Expressed as a percentage of the whole bog core area included in the inventory, the loss is estimated to be 0.65 ± 0.15 %.

DISCUSSION

The influence of habitat area on biodiversity is a major concern in vegetation science, and many studies have addressed the effects of habitat extent on plant communities (Oertli *et al*. 2002, Drakare *et al*. 2006). Studies conducted in Ontario wetlands (Findlay & Houlahan 1997) indicated that species richness increases with wetland area and it was concluded that, from the perspective of biodiversity conservation, bigger is better. However, these authors conceded that land-use practices around the wetland might be as important as the size of the wetland itself.

Table 9. Changes in bog quality in relation to draining structures between the first and second surveys. Changes in Belts A, B, C and D in the bogs with few and many draining structures. Significance levels for the changes themselves (signed rank sum test) and differences between bogs with few and many draining structures (rank sum test): *** < 0.001, ** <0.01, * <0.05, ' < 0.1.

	Drains	Outer surroundings Belt A		Inner surroundings Belt B		Bog margin Belt C		Bog centre Belt D	
Number of bogs	few many	34 36		36 37		40 40		16 26	
Proportion of specialists	few many	-0.78 ± 0.74 % ** -0.18 ± 0.58 %	*	-1.01 ± 0.63 % * -1.14 ± 0.55 % '		-0.59 ± 0.62 % -1.22 ± 0.53 % *		-1.38 ± 1.11 % * -1.16 ± 0.76 % '	
Light indicator value	few many	-0.019 ± 0.019 -0.009 ± 0.011		-0.044 ± 0.013 ** -0.031 ± 0.017 '		-0.017 ± 0.016 -0.005 ± 0.012		-0.003 ± 0.022 -0.041 ± 0.015 *	
Humidity indicator value	few many	-0.029 ± 0.013 * -0.019 ± 0.020		-0.016 ± 0.013 -0.028 ± 0.014 *		+0.006 ± 0.016 -0.004 ± 0.014		-0.035 ± 0.017 * -0.042 ± 0.014 **	
Nutrients indicator value	few many	+0.028 ± 0.021 * +0.007 ± 0.020		+0.021 ± 0.018 +0.018 ± 0.016 *		+0.013 ± 0.015 +0.049 ± 0.022 *		-0.071 ± 0.032 * -0.013 ± 0.020	-

Proximity to the mire margin is also well recognised in mire ecology as one of the major gradients in mires (Malmer 1986, Økland 1990, Wheeler & Proctor 2000). This gradient has been described as the mire margin – mire expanse gradient in Finland and Norway, where it has been interpreted as a vegetation gradient (Pakarinen & Ruuhijarvi 1978, Økland *et al*. 2001).

According to our results, the quality of bog vegetation depends much more on distance to edge (Table 1) than on bog area, increasing with the distance from the edge (Table 3). Obviously, large bogs can offer larger distances to the edge than smaller ones, and thus potentially contain vegetation of better quality. Why, then, is distance to the edge a better quality index than area? The distance to edge takes into account the shape of the bog in addition to its area. A bog with a circular plan shape has shorter margins than a bog of the same area with an elongated shape. Almost all Swiss bogs have been heavily cut for peat in the past and hence have lost their original more or less regular shapes. Today they are not only small in size but also very irregularly shaped with long margins relative to their areas.

From their study on the ecological basis of the mire margin – mire expanse gradient in some bogs in the Italian Alps, Bragazza & Gerdol (1999) concluded that water-table depth was the most important factor. They considered the larger water-table depths along the mire margins to be responsible for the development of trees and/or shrubs along the mire margins, which is further favoured by the better-aerated conditions in the upper peat layers. Other researchers claim that the influx of nitrogen from the surroundings has played a major role in the decline of threatened ecosystems during recent decennia (Jacquemyn *et al*. 2003). This input might reduce the species richness of specialists whereas, in contrast, generalist species might survive better along the edges and consequently be more dominant there. The role of atmospheric deposition originating from soil dust and air pollution is widely acknowledged to be relevant (Damman 1990, Field *et al.* 2014), and may influence the development of raised bogs (Limpens *et al*. 2011). The mineralisation of the upper peat layers triggered by drainage results in unfavourable C:N and N:P ratios in ombrotrophic raised bogs (Bönsel & Sonneck 2012). Changes in these ratios in turn affect the species composition. *Betula pubescens*, and *Molinia coerulea* in particular, benefit from these new ratios and react with increasing biomass (Tomassen *et al*. 2004). Kapfer *et al*. (2011) observed changes in species composition in the vegetation along light and nutrient gradients in a boreal mire, possibly due to higher nutrient availability under drier conditions. The increase in shrubs and trees may also have caused altered light conditions, which is a disadvantage for short plants such as *Trichophorum cespitosum*, *Carex lasiocarpa*, *Drosera longifolia* and *Sphagnum palustre* (Kapfer *et al*. 2011).

Due to lack of water-table measurements and other environmental data in our study, we gained indications of soil moisture, light and nutrient availability from the mean indicator values of species (Landolt *et al*. 2010). We observed that the quality (expressed as the proportion of specialists) correlated best with nutrients indicator values, and more so than with humidity values (Table 4). As for the changes between the surveys, the humidity indicator values decreased mainly in the bog centres, whereas increasing nutrients values and decreasing light values mainly affected the inner surroundings and the bog margin. Even structures such as roads that dissect the mires or main drainage ditches in surrounding areas seem to have more effects at the level of nutrients than at that of humidity (Tables 6 and 9).

In the Swiss bog remnants, the degradation processes in the bog centres differ from those in the margins. The bog centres are still drying out, most likely due to small draining structures that are not visible on aerial photographs. Almost all Swiss bogs have been drained for peat cutting in the past, and such drainage ditches are often still active. In addition, many bog cores are isolated patches which have been left after peat cutting. These elevated bog remnants still lose water to the surrounding lower-lying and intensively used landscape. The bog margins have been affected by the invasion of trees and shrubs benefitting from the relatively dry conditions and increased nutrient supply. The increase in nutrients can be caused by peat mineralisation due to a lowered water table and by invading trees and shrubs, which enrich the site by producing litter and by drying the peat through increased evaporation. Further nutrient inputs may originate from the air and from the adjacent intensely used landscape, particularly if the site is accessible by car. The data used in this study did not allow assessment of the relative importance of these factors, which can all potentially cause eutrophication of bog margins.

Our results also highlight the role of the bogs' density in the landscape, which is our proxy for connectivity. Many studies have underlined the importance of connectivity between isolated patches (Saunders *et al*. 1991, Debinski & Holt 2000). One possible impact of isolation may be that dispersal and immigration rates are reduced and species are lost as a result. Other studies have found that dispersal traits do not explain any of the variation in the distribution of bryophytes and vascular plants in a patchy landscape, and that environmental and biotic filters are more important than dispersal limitation (Udd *et al*. 2015). For example, many of the *Sphagnum* species are bog specialists with small wind-dispersed diaspores whose dispersal is not limited at distances of up to 40 km in the islands of the Baltic Sea (Sundberg *et al*. 2006). Many species have limited distribution ranges due to their unique ecological requirements (Frahm 2008) and restricted habitat availability, and are thus surrounded by large areas of unfavourable habitats (Brueckmann *et al*. 2010).

The effects of connectivity on bog quality found in our study could be due to the different geographical locations of the Swiss bogs. Nowadays, most bogs occurring in high densities are located in the Pre-Alps which are dominated, geologically speaking, by flysch (an almost impervious marine sediment) and almost impervious clay layers deposited by glaciers during the Late Glacial Maximum period. Soils on the flysch as well as on the ground moraine are usually shallow (Schlunegger *et al*. 2016). As a consequence the landscape in the Pre-Alps area is scattered with small and, sometimes, larger wetlands in which bog species could establish. In contrast, bogs in the Jura Mountains are like isolated islands in a calcareous landscape where their growth is limited by the layer of impervious marl. Such a landscape offers bog species little opportunity to establish populations in the surroundings. Due to intensive peat extraction since the 18th century together with subsequent drainage activities in both the 19th and 20th centuries (Grünig 2007), bogs in the Swiss Plateau are similarly isolated, with bog remnants surrounded on all sides by urban and agricultural surfaces where it is almost impossible for bog species to establish new populations.

Because Swiss bogs are widely distributed across altitude, we also tested whether altitude affects bog quality. It does not affect the proportion of specialist species much, and this is not really surprising. Plant communities in bogs are considered to be azonal. This means that the plant community structure and floristic composition are the result of hydrogeological conditions, whose influence on floristic composition, structure and dynamics overrides that of microclimate (Diekmann 1997, Brand *et al*. 2013).

CONCLUSION

In contrast to more or less pristine bog systems such as the ones in Canada (Howie & Tromp-van Meerveld 2011, Langlois *et al*. 2015), the borders of Swiss bogs are very long in proportion to area due to the bogs' past history and to high fragmentation. The high-quality surface area that was lost during the 5–7 years between the two surveys represents about 0.6 % of the total bog core area of the inventory. Environmental legislation in Switzerland requires mires of national importance to be surrounded by "a buffer zone that is sufficient from the ecological point of view". These zones are mainly designed to avoid nutrient enrichment from the neighbouring agricultural land, but our results indicate that they largely fail to fulfil this essential purpose. To improve or at least to preserve bog quality, it is essential but not sufficient to re-introduce natural hydrological regimes in the bog cores, as has already been done in some revitalisation projects in Central Europe (Tomassen *et al*. 2010, Sundberg 2014). It is equally indispensable to reduce nutrient inputs and nutrient formation by enlarging and strengthening the buffer zones surrounding the small and fragile cores of the Swiss bog remnants.

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Appendix

List of the characteristic species of the Sphagnion magellanici and Caricion lasiocarpae (including Rhynchosporion albae) alliances. The four typical bog species used for the Swiss inventory of raised and transitional bogs of national importance are marked with asterisks (*) and shown in ***bold*** type.

Vascular Plants	Bryophytes
****Andromeda polifolia***	*Aulacomnium palustre*
Betula nana	*Calypogeia sphagnicola*
Carex chordorrhiza	*Cephalozia connivens*
Carex diandra	*Cladopodiella fluitans*
Carex heleonastes	*Dicranum undulatum*
Carex lasiocarpa	*Gymnocolea inflata*
Carex limosa	*Kurzia pauciflora*
Carex pauciflora	*Mylia anomala*
Drosera intermedia	*Polytrichum juniperinum* aggr. (almost always *P. strictum*)
Drosera longifolia	*Sphagnum capillifolium* aggr. (incl. *S. capillifolium* and *S. rubellum)*
****Drosera rotundifolia***	*Sphagnum compactum*
****Eriophorum vaginatum***	*Sphagnum cuspidatum*
Juncus stygius	*Sphagnum fuscum*
Lycopodiella inundata	*Sphagnum magellanicum*
Potentilla palustris	*Sphagnum majus*
Rhynchospora alba	*Sphagnum papillosum*
Rhynchospora fusca	*Sphagnum russowii*
Scheuchzeria palustris	*Sphagnum tenellum*
****Vaccinium oxycoccos***	*Straminergon stramineum*
	Warnstorfia exannulata
	Warnstorfia fluitans