Revegetation dynamics after 15 years of rewetting in two extracted peatlands in Sweden

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SUMMARY

The restoration of extracted peatlands poses challenges with regard to their recolonisation by vegetation. The most significant problems are unstable water levels, destroyed propagule bank, and temperature fluctuations on bare peat surfaces. Rewetting is considered necessary for the re-establishment of peat-forming vegetation. Revegetation was investigated in a long-term field study at two rewetted extracted peatland sites in south-central Sweden, namely Västkärr (originally a lagg fen) and Porla (originally a bog). Both sites were expanses of bare peat before rewetting.

Rewetting procedures were applied in 1999 and strongly promoted plant colonisation. At Västkärr, colonisation started in the first year after rewetting, mostly by species that were not found during repeat vegetation surveys 15 years later. By 2014, Västkärr was a shallow lake surrounded by mesotrophic and eutrophic vegetation with species such as *Carex rostrata*, *Lemna minor*, *Typha latifolia*, *Phalaris arundinacea* and *Phragmites australis*. Revegetation of the Porla site was slower and started with *Eriophorum vaginatum* and *Polytrichum* spp. *Sphagnum* mosses appeared after six years and had established quite well after 13 years. A residual *Sphagnum* peat layer, inflowing surface water and groundwater provided spatially variable nutrient conditions. *Sphagnum* species and *E. vaginatum* established in nutrient-poor areas, while *C. rostrata*, *P. australis* and *Eriophorum angustifolium* colonised more nutrient-rich locations.

KEY WORDS: biodiversity, hydrology, nutrient status, re-vegetation, water chemistry

INTRODUCTION

Peatlands cover 3 % of the land area of the Earth (Lappalainen 1996) and store about one-third of global soil carbon (Gorham 1991). About 60 % of the peat bogs originally present in Europe have been affected by agriculture, forestry and peat extraction (Haapalehto *et al.* 2011). Approximately 50 % of these have been changed by agriculture, 30 % by forestry and 10 % by peat extraction (Vasander *et al.* 2003). For example, most of Ireland's large raised bogs have been drained and exploited over the past century, and only 7 % remain in a relatively intact state today (Crushell *et al.* 2008). Around 15 million hectares of peatland in boreal and temperate regions have been drained for forestry (Koskinen *et al.* 2011). In Finland, more than half the total area of peatland has been drained, mainly for this purpose. A similar area of peatland in north-west Russia, and large areas in Sweden and the Baltic countries, have also been drained (Koskinen *et al.* 2011). In Sweden, the area of peatland drained for agriculture may originally have been > 1 Mha, about 15 % of peatlands are influenced by forestry, and peat is extracted on around 0.1 % of the original mire area (Vasander *et al.* 2003).

Globally, human influence has directly altered approximately 25 % of peatlands and a tiny fraction (~ 1 %) of these have been used for peat extraction (Strack 2008). However, because peat extraction involves the drying of wet peat followed by collection, transport and storage of a somewhat drier product for use in horticulture, litter, fertilisers or fuel (Joosten & Clarke 2002), it leads to direct destruction of the peatland. Peat extraction is now carefully regulated and after-use/rehabilitation, e.g. restoration to new peat-forming ecosystems, is required.

Blankenburg & Tonnis (2004) argue that restoration of peat extraction areas does not return bogs to their pre-disturbance "original condition". However, they mention that restoration of abandoned extraction sites can sometimes generate valuable wildlife habitats and make an important contribution to European wetland conservation. The establishment of peat-forming vegetation on extracted peatlands is of great importance not only for biodiversity (Haapalehto *et al.* 2011), but also from a climate change perspective. Peatlands participate in climate regulation through carbon sequestration and storage; and because carbon storage has a cooling effect on climate, they are amongst the most important ecosystems in the context of global warming (Zhaojun *et al*. 2011, Bonn *et al*. 2014).

Drained and degrading peatlands are problematic environments for successful plant re-establishment because of dryness, aeolian erosion, increasing ground surface instability, changing water levels, frost heave and the presence of excess nutrients (Lavoie *et al.* 2003, Vasander *et al.* 2003, Nishimura & Tsuyuzaki 2014). Summer drought may not only have a direct adverse effect on the survival of bog plant seedlings, but may also lead to crust formation and cracking of the peat (Wheeler & Shaw 1995). Hence, the spontaneous revegetation of abandoned extracted peatlands is very slow, uneven and unpredictable (Tuittila *et al.* 2000, Triisberg *et al*. 2013, Nishimura & Tsuyuzaki 2014); and although self-regeneration of extracted peatland can occur, it often leads to only limited recovery of pre-extraction functions (Strack 2008).

The re-initiation of peat formation can take decades even after restoration measures have been applied (Bonn *et al.* 2014, Nishimura & Tsuyuzaki 2014). Nonetheless, some of the available data indicate that spontaneous revegetation can lead to the appearance of *Sphagnum* colonies (i.e. potentially peat-forming vegetation). *Eriophorum vaginatum* and *Polytrichum strictum* are often early colonisers of cutover surfaces, initiating different development pathways that favour the establishment of *Sphagnum* (Lavoie *et al*. 2003). Stable temperature and high relative humidity in the microhabitats provided by vascular plants (ericaceous shrubs and young trees) stimulate *Sphagnum* growth and hummock formation (Pouliot *et al.* 2011, Pouliot *et al.* 2012). However, the key factors for *Sphagnum* recolonisation and the development of different plant community structures on extracted peatlands are shallow water table and comparatively small water level fluctuations (Robert *et al*. 1999, Tuittila 2000, Lode 2001, Nishimura & Tsuyuzaki 2014). Hence, peatland rewetting can be a useful tool in promoting the regeneration of typical vascular plants and *Sphagnum* mosses. In general, if the aim is to reinstate an extracted *Sphagnum* peatland (bog), rewetting is usually needed to promote and facilitate the revegetation process (Lavoie *et al*. 2003, Gonzàlez *et al*. 2014).

Vasander *et al*. (2003) indicate that restoration actions can themselves have negative environmental consequences, e.g. the inundation of peat surfaces resulting from the rewetting process often increases phosphorus (P) leaching. The availability of plant nutrients is also significant for the revegetation of extracted peatlands. According to Wheeler & Shaw (1995), in cases where peat extraction has exposed fen peat, the chemical environment is likely to be conducive to the establishment of fen plants rather than bog vegetation. The exposure of peat by excavation results in higher nutrient concentrations in water and peat than were present in the original peatland (Nishimura & Tsuyuzaki 2014). Several investigations have shown that there is a link between environmental factors (especially the poor–rich fertility gradient) and species composition in mire vegetation (Wheeler & Shaw 1995, Rydin *et al*. 1999, Tahvanainen 2004, Rydin & Jeglum 2006, Avetov & Shishkonakova 2008, Hynninen *et al.* 2011, Avetov & Shishkonakova 2013, Kozlov & Avetov 2014).

Besides moisture conditions and water chemistry, the proximity of propagule sources is critical (Robert *et al*. 1999). In previous investigations it has been observed that restored habitats are most likely to be colonised by typical species if the restored areas are near existing sources of potential colonists (Vasander *et al*. 2003, Triisberg *et al*. 2013). A feature of many large-scale commercial peat extraction sites is limited availability of plants for recolonisation. Even if an abundant local source of propagules is present, recolonisation rates can be dramatically improved by the strategic introduction of plants (Quinty & Rochefort 2003, Blankenburg & Tonnis 2004).

In conjunction with the restoration (by rewetting) of two former peat extraction areas in southern Sweden, we carried out long-term observations of the revegetation process. Because the intention was to create bird lakes, we did not re-introduce plants. However, with time, sites that have been rewetted (only) can develop into peat-forming wetlands, so new mires may eventually be formed. The aim of this study was to investigate the initial development of plant cover, with focus on peat-forming plants, and to gain insights into the connection between plant species composition and water chemistry.

METHODS

Study areas

The two sites investigated were rewetted cutover peat areas at Västkärr (59° 06′ N, 14° 45′ E) and Porla (59° 01′ N, 14° 38′ E) in south-central Sweden (Figure 1). In both cases peat had been extracted using a sod peat cutting method. The two sites have similar climate with annual mean temperature around +6 °C, precipitation 800 mm and evapotranspiration 470 mm (long-term averages for 1961–1990) (Table 1). In the years after rewetting (2000–2013), precipitation was 9 % more and temperature 13 % higher than the long-term average value.

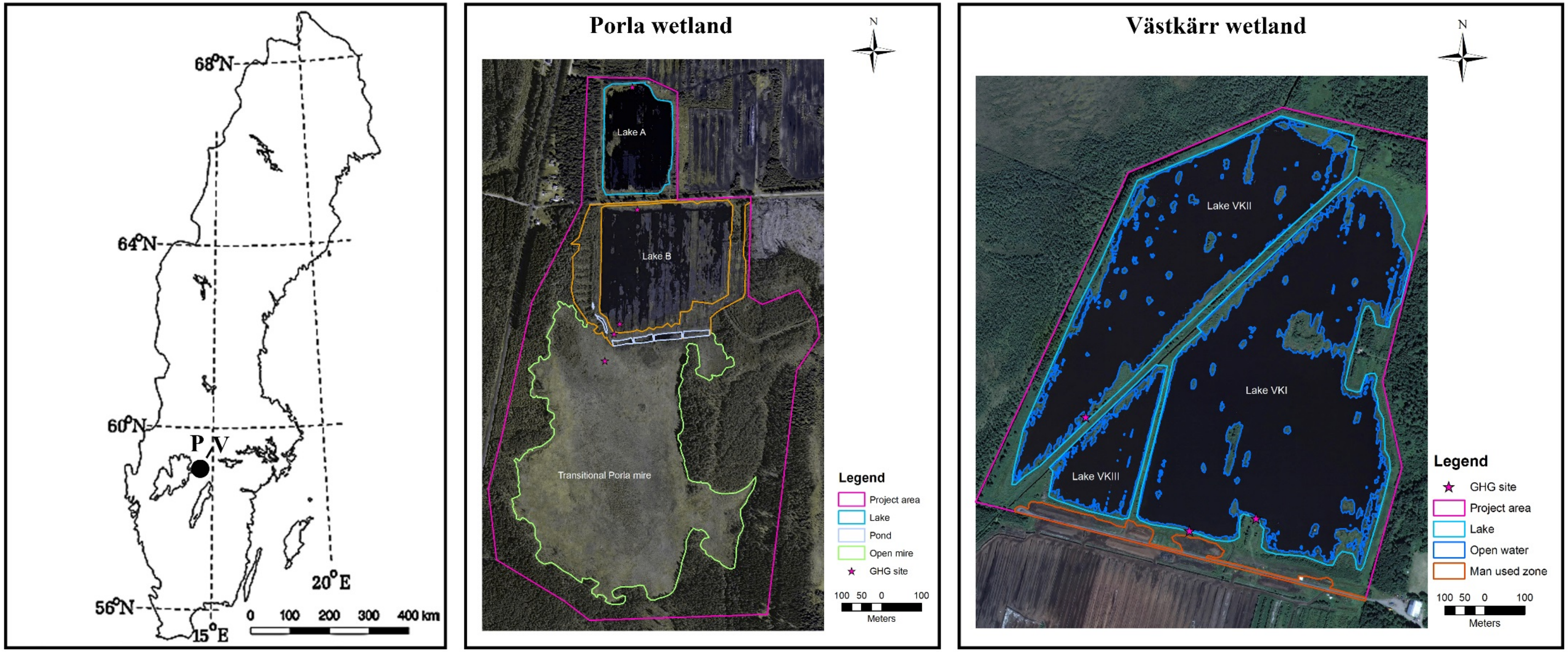

Figure 1. Map of Sweden showing the locations of the two rewetting areas Porla (P) and Västkärr (V), which are only 12 km apart. Västkärr is immediately to the east, and Porla 6 km to the south-west, of the raised bog known as Skagerhultamossen.

Table 1. Geographical and climate characteristics of the Västkärr and Porla wetlands (Raab & Vedin 1995). The meteorological data are mean values for the period 1961–1990.

Variable	Västkärr	Porla
Altitude (m a.m.s.l.)	65	85
Wetland area (ha)	80	17
Annual mean temperature (°C)	6	6
Vegetation period* (T > 5 °C) (days)	200	200
Annual precipitation (mm)	800	800
Annual evapotranspiration (mm)	470	470
Annual runoff (mm)	330	330

*Mean daily temperature > 5 °C for four consecutive days (Odin *et al*. 1983).

The Västkärr wetland (80 ha) lies between the raised bog Skagerhultamossen to the west and mineral soil grasslands to the east, and used to be the lagg fen of Skagerhultamossen. Before the peat was extracted it was cultivated for potatoes and cereal crops. The peat layer that remained after peat extraction was approximately 20 cm thick with a flat, even surface. Västkärr is now a single and more or less open shallow lake, although it is divided into three parts. Its main water supply is inflowing groundwater. The catchment area of Västkärr is not easily determined due to the presence of the large Skagerhultamossen bog, the slightly undefined groundwater inflow from the surroundings, and inflow from the nearby river Örebro Svartå. The river is also the outflow to Lake Hjälmaren and, beyond that, to Stockholm and the Baltic Sea.

Porla was originally a bog where peat extraction started in the 1880s, eventually transforming it to an excavated depression in a morainic landscape. Peat thickness varies considerably because of the stony mineral till underlying the peat. Boulders and stones can be observed in many places, and ordinary till hillocks and depressions form an uneven surface such that the remaining peat layer varies in thickness from zero to 2 m. Porla comprises two lakes/wetlands of area 2 ha and 5 ha, respectively, separated by a road. Water from the larger upstream area passes under the road and enters the smaller northern area, from which the outlet discharges to downstream watercourses. A poor sedge fen to the south supplies water to the Porla site. The total catchment area is 133 ha.

Peat extraction at Västkärr ceased in 1998. The ash content of the remaining peat layer varied spatially. Ash content was below 5 % in the upper peat (0–10 cm depth), whereas the underlying 10–20 cm of peat was partly mixed with clay and gyttja and its ash content was often above 15 %. The bulk density of the peat layer was mostly in the range 0.2–0.3 g cm^{-3}. Beneath the peat there was a 5 cm thick layer of gyttja with density 0.4–1.0 g cm^{-3} overlying postglacial clay.

At the Porla site, peat extraction stopped in 1999 leaving a peat layer that was more variable in thickness, as mentioned above. In places where the residual peat was up to 2 m thick it was topped by a *Sphagnum* layer which was mostly 0.4–0.6 m thick. Elsewhere there was only *Carex/Equisetum* peat up to 1.7 m thick directly overlying the till.

The chemical composition of peat differed between the two sites, Västkärr being more nutrient-rich than Porla. The C/N quotients were 21 and 45, but pH values (for peat) were initially quite similar at 4.8 and 4.5, respectively. The difference in pH increased after rewetting, when values of 6–7 were recorded at Västkärr and 5–5.5 at Porla. The concentrations of some other nutrients in the peat showed large differences between the sites (Table 2).

Rewetting procedure

In 1999, before rewetting started, both sites were prepared by soil and ground work which created a bare black peat surface with some patches of mineral soil. At Västkärr, the ditches were also filled in; and after pumping stopped, the water table rose rapidly over a few months. There was also rather heavy rainfall in 1999. As a result, after the winter of 1999/2000 a lake developed with water depths of 0.7–1 m just a few metres from the vegetated shore.

Porla was blocked by a road, and on the other side of the road a bund/wall was built and fitted with a high-level outlet. Subsequently, water discharging

Table 2. Characteristics of residual peat and chemical characteristics of upper-layer peat at Västkärr and Porla before rewetting. Samples were randomly located and distributed over almost the whole of each area.

	Porla	Västkärr
Residual peat type	*Carex/Equisetum* and *Equisetum/Carex* peat overlain by *Sphagnum* peat	*Carex* peat mixed with wood peat
Residual peat depth (m)	0–2	0.1–0.2
Numbers of samples	5 samples in 0–0.2 m layer; 5 samples in 0.2–0.5 m layer.	10 samples in 0–0.1 m layer; 8 samples in 0.1–0.2 m layer At some locations there was only 0.1 m of peat on top of the gyttja/clay.
pH	4.5	4.8
C (%)	50	45
N (%)	1.1	2.1
C/N	45	21
NO_3-N (mg kg^{-1} dw)	1	50
NH_4-N (mg kg^{-1} dw)	50	0
K_{HCl} (mg kg^{-1} dw)	92	400
P_{HCl} (mg kg^{-1} dw)	320	600

from the upstream catchment filled the excavated depressions in the ground. Winter rainfall and very heavy rain in the year 2000 created two open water bodies with water depths of 1–2 metres. The lakes were shallower near their shores and only 0–20 cm deep in vegetated areas. In 2001 and 2002 there were mishaps which reduced the water depth. In 2001, leakage occurred at the water regulating device. In 2002, the bund broke but was quickly repaired. After the repair the water level recovered within a month or two and has remained stable since 2003.

The peat at Västkärr was fairly stable after rewetting, but in some locations at Porla it swelled up and in a few places even broke away from the lake floor and rose up to the surface. The vegetation of the resulting "floating rafts" was not studied, however.

Vegetation recolonised in the first year after rewetting at Västkärr but took longer to appear at Porla, partly due to the problems encountered in stabilising water levels.

Vegetation inventories

Vegetation surveys were carried out at Västkärr in 2000, 2001, 2003, 2006, 2008, 2009, 2010, 2012, 2013 and 2014. We selected two areas, shore and littoral, the shore area being situated above the water level and slightly drier than the littoral area. The littoral area was a water body with partial vegetation cover and water depth mainly 0–0.5 m. The vegetation was described in 1 m^2 plots within each area. The number of plots was 4–12 *per* observation year.

At Porla the ground surface consisted mainly of bare black peat throughout the period 2000–2005. The first vegetation surveys were carried out when vegetation started to become abundant in 2006, and they were repeated in 2008, 2010, 2012, 2013 and 2014. Generally, plots (1 m^2) were placed at 5–10 m intervals along transects starting near the shore and ending at the transition to open water, but in some cases we made an inventory of an isolated plot. The number of plots was 15–32 *per* observation year.

At both Västkärr and Porla we made lists of species and visually estimated the percentage of total canopy cover, as well as the percentage canopy cover of each species, bare peat and open water. Nomenclature for vascular plants followed the Nordic flora (Mossberg & Stenberg 2003).

Water levels

Water depths at the vegetation relevés were measured manually using a ruler. At Porla, water levels at the road and the outlet were also monitored using float recorders, later replaced with pressure loggers.

Water sampling

Water sampling was carried out in open water 0.2 m deep at both sites. At Västkärr three samples were collected on approximately four (2–6) occasions *per* year during all years, and at Porla monthly samples were collected at three locations in all years. The water samples were taken to the central laboratory in Uppsala within two days for chemical analysis according to Swedish standards (SIS 1986). They were analysed for pH, electrical conductivity, SO_4-S and total concentrations of carbon (C), nitrogen (N), magnesium (Mg), phosphorus (P), potassium (K), calcium (Ca), copper (Cu) and zinc (Zn).

Data analysis

Directions of vegetation development were identified by analysing data from 69 vegetation relevés at Västkärr and 133 at Porla using Detrended Correspondence Analysis (DCA), an indirect ordination method (Ramette 2007).

Detrended Canonical Correspondence Analysis (DCCA) (a direct ordination method, Ramette 2007) with Monte-Carlo permutation test (499 permutations) was used to check if there were significant differences in the vegetation relevés between a given year and the next year of observation (e.g. between 2000 and 2001, 2001 and 2003, *etc*.). For this purpose, only one environmental variable (year of observation) was used. DCCA with a Monte-Carlo permutation test (499 permutations) was also used to explore the environmental preferences of plant species.

Principal Component Analysis (PCA), an indirect method (Ramette 2007), was used to estimate differences in surface water chemistry between Västkärr (131 samples) and Porla (135 samples).

The computer programme Canoco 5 (Šmilauer & Lepš 2014) was used for all ordinations.

RESULTS

During observations at the Västkärr wetland in 2000–2014, 24 species of vascular plants (including seven species identified to genus) were recorded. In 2001, several unidentified species were combined into the category ‘other species’ and cover of this category was estimated. At Porla, ten species of vascular plants and moss species belonging to three genera (*Polytrichum*, *Scorpidium* and *Sphagnum*) were observed during the period 2006–2014.

There were significant differences in species composition between Västkärr and Porla. No mosses were found at Västkärr, and only three taxa (*P. australis*, *Carex* spp. and *Juncus* spp.) were common to both sites. However, it is emphasised that more than one species might be included in the taxa *Carex* spp. and *Juncus* spp.

Revegetation at Västkärr through time

At Västkärr, lake water depths during the growing season were more stable from 2005 onwards (0.5–1 m) than in 2001–2004 (0–2 m), although the water might be deeper in spring and autumn. Water depth in the littoral area could be up to 0.5 m but was mostly 0–0.2 m, and the water level was close to ground level in the shore area. Recording of plants started in the year after rewetting, so it was possible to identify major changes during the whole observation period (Table 3). The average plot cover initially increased from 30 % in 2000 to 40 % in 2006; in the period 2008–2013 it fluctuated between 42 % and 98 %; and in 2014 it was 62 %. The average cover of bare peat showed a decreasing trend with peaks in 2008 and 2010, and in 2014 its value was only 3 %. The average cover of open water fluctuated mostly between 10 % and 23 %, with two high peaks in 2009 (66 %) and 2014 (48 %).

The revegetation process started with around three species *per* plot in 2000. In 2001–2006 the count increased to six species *per* plot, then in 2008–2010 it decreased to 2–3 species *per* plot. In the last three years of observation there were 3–6 species *per* plot.

To examine changes in species composition, the species recorded at Västkärr were divided into four groups, namely: trees/shrubs, herbs, graminoids and sedges (Figure 2). The graminoids group had the highest representation (in terms of number of species) in the early stages after rewetting. At that time the most abundant graminoids were *Glyceria fluitans*, *Alopecurus geniculatus*, *Calamagrostis canescens*, *P. arundinacea* and *Poa trivialis*. From 2003 the number of graminoid species decreased and stabilised, and by 2014 *P. arundinacea* was the most abundant graminoid. Herb species tended to increase in number. In 2000 the most abundant herbs were *Equisetum* spp., *Potamogeton* spp. and *Ranunculus repens*, but these taxa were not recorded in 2014. Sedges appeared in the second year after rewetting and the representation of this group stabilised for the last five years at around 22–27 %. Trees/shrubs (*Salix* spp.) appeared only once, with very low abundance, in 2006. In 2014 the most abundant species were *L. minor* and *T. latifolia*. *P. australis* was observed for the first time in 2006. Later, *P. australis* increased in cover and expanded into open water.

A DCA of vegetation relevés showed a shift over the years (Figure 3), with a gradient in changes in plant composition running from left to right reflecting plant development from 2000 to 2014.

Table 3. Mean cover values (%) recorded through time after rewetting (in 1999) at Västkärr. Confidence intervals (95 %) are shown for plot cover, bare peat, open water and number of species *per* plot. Species are listed in alphabetical order. For each species, mean cover is calculated across all plots and frequency of appearance (no. plots with a record) is shown in brackets. "+" = cover less than 1 %; * = unidentified species.

Year:	2000	2001	2003	2006	2008	2009	2010	2012	2013	2014
Years after rewetting	1	2	4	7	9	10	11	13	14	15
Number of plots	5	4	1	6	10	10	11	6	5	12
Plot cover (%)	30±33	112±40	126	40±9	75±13	42±10	59±8	79±13	98±50	62±14
Bare peat (%)	N/A	7±5	N/A	N/A	16±12	0±0	26±16	9±13	2±6	3±6
Open water (%)	N/A	N/A	N/A	N/A	10±9	66±10	20±15	23±16	16±29	48±9
Number of species *per* plot	3±1	6±1	6	6±3	3±0	3±1	2±1	5±2	6±1	4±1
Species and (abbreviations):										
Agrostis stolonifera (Agrostis)	-	1(1)	-	-	-	-	-	-	-	-
Alisma plantago-aquatica (Alisma)	-	-	15(1)	1(2)	1(1)	2(4)	1(4)	2(1)	+(2)	1(1)
Alopecurus geniculatus (Alopec)	7(1)	18(1)	-	-	-	-	-	-	-	-
Bidens tripartita (Bidens)	-	1(1)	-	2(4)	-	-	-	-	-	-
Butomus umbellatus (Butomus)	-	-	-	-	-	-	-	1(1)	+(1)	-
Calamagrostis canescens (Calam)	-	25(3)	-	-	-	-	-	-	-	-
Carex spp. (Carex)	-	1(1)	-	17(6)	36(8)	4(3)	27(6)	23(5)	22(3)	23(11)
Ceratophyllum demersum (Cerat)	+(1)	-	-	-	-	-	-	-	-	-
Equisetum spp. (Equiset)	4(1)	-	-	+(1)	-	1(1)	-	-	-	-
Glyceria fluitans (Glyc)	9(4)	27(4)	80(1)	5(3)	-	-	-	-	-	-
Hydrocharis morsus-ranae (Hydro)	-	-	1(1)	-	-	-	-	-	2(2)	+(1)
Juncus spp. (Junc)	1(3)	8(4)	-	-	2(1)	4(3)	1(1)	-	1(1)	1(2)
Lemna minor (Lemna)	-	-	5(1)	+(2)	-	+(3)	-	-	1(1)	15(8)
Lythrum salicaria (Lythr)	-	-	-	-	-	1(1)	1(3)	3(3)	1(3)	5(4)
Menyanthes trifoliata (Menyant)	-	-	-	-	-	-	-	1(1)	-	-
Phalaris arundinacea (Phal)	+(2)	11(4)	10(1)	-	17(8)	18(8)	16(6)	10(3)	4(2)	7(6)
Phragmites australis (Phragm)	-	-	-	6(4)	-	1(1)	-	28(6)	27(5)	1(1)
Poa trivialis (Poa)	-	12(1)	-	-	-	-	-	-	-	-
Potamogeton spp. (Potam)	6(3)	-	-	1(3)	-	-	-	-	-	-
Ranunculus repens (Ranunc)	3(1)	-	-	-	-	-	-	-	-	-
Salix spp. (Salix)	-	-	-	+(1)	-	-	-	-	-	-
Scirpus spp. (Scirpus)	-	-	-	-	-	-	-	+(1)	-	-
Sparganium spp. (Sparg)	-	-	-	3(3)	-	5(3)	-	2(3)	3(4)	+(2)
Typha latifolia (Typha)	-	-	15(1)	5(5)	21(8)	9(7)	14(6)	11(4)	36(5)	10(8)
Other species*	-	9(4)	-	-	-	-	-	-	-	-

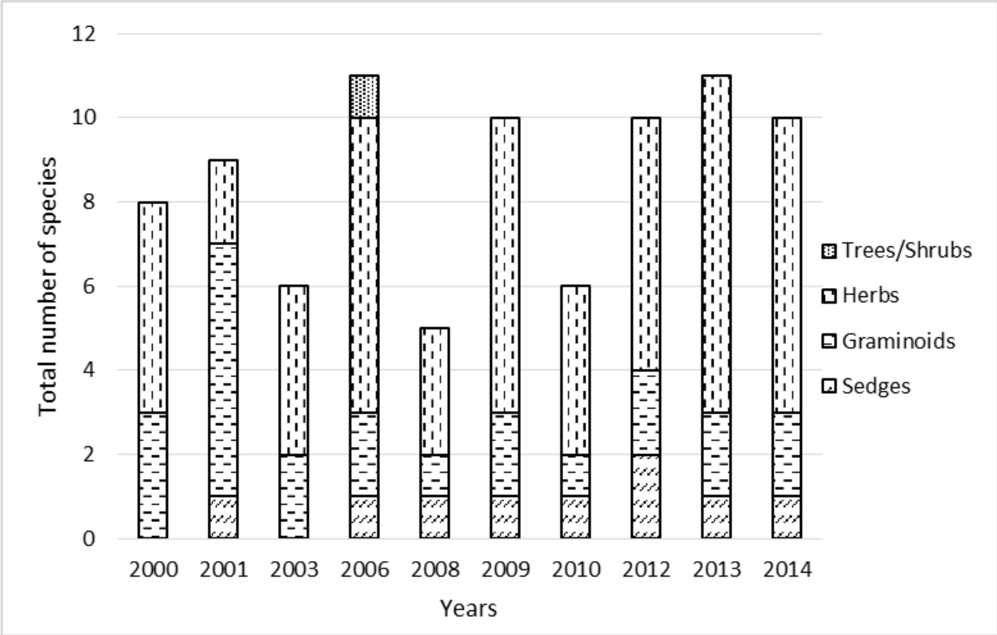

Figure 2. Total number of species according to plant group (trees/shrubs, herbs, graminoids or sedges) in the Västkärr wetland, 2000–2014. Species richness of the herb group tended to increase.

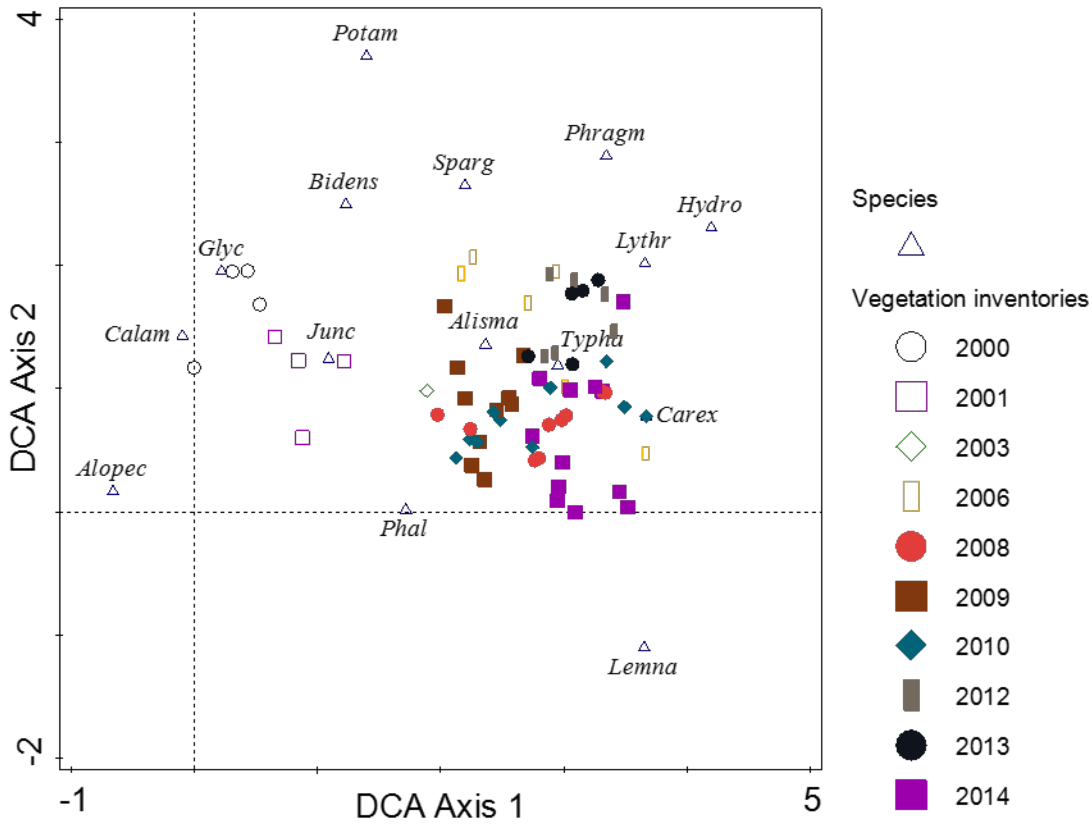

Figure 3. Detrended Correspondence Analysis (DCA) of 69 vegetation relevés in the Västkärr wetland. Empty triangles show the relative species positions. Species with relative weights from 1 % to 100 % are shown. Symbols show relative positions of vegetation relevés according to the year of observation. Scaling of axes is in SD units. Total inertia (variance) is 2.764. Eigenvalues of Axis 1 and Axis 2 are 0.535 and 0.298, respectively. Species abbreviations are shown in Table 3.

Species on the left, such as *G. fluitans*, *A. geniculatus*, *C. canescens*, *Bidens tripartita* and *Potamogeton* spp., were early colonisers but were not observed later. Species on the right (*L. minor*, *Carex* spp., *T. latifolia*) were the most abundant taxa in 2014.

A DCCA analysis showed that there were no significant differences between the vegetation relevés in 2000 and 2001 ($p = 0.104$), and 2001 and 2003 ($p = 0.062$). However, there were differences between relevés made in 2003 and 2006 ($p = 0.038$), 2006 and 2008 ($p = 0.001$), 2008 and 2009 ($p = 0.008$), 2009 and 2010 ($p = 0.042$) and 2010 and 2012 ($p = 0.003$). In 2012–2013, plant composition was stable and without significant differences ($p = 0.515$), but there were differences between the relevés recorded in 2013 and 2014 ($p = 0.001$). There was a difference of about one standard deviation (SD) between the vegetation relevés of 2000–2001 and 2006, probably because of the absence of vegetation inventories in 2002, 2004 and 2005. From 2006, despite the differences in plant composition shown by DCCA, the revegetation process developed more gradually.

Revegetation at Porla through time

Water depth at Porla was generally 1–1.2 m, and 2 m at the deepest place. On vegetation plots the water level was at ground surface level in most cases, with a few exceptions where 0–0.2 m of surface water was present (often with *E. vaginatum*). In the first years after rewetting (2000–2004), plant development was sparse. Until 2002 almost all of the area consisted of bare peat, although *Polytrichum* spp. and *E. vaginatum* were observed close to old ditches. Actual plant records for Porla started in 2006, seven years after rewetting (Table 4), when colonisation began to be more widespread. By 2006 the cover of *E. vaginatum* and *E. angustifolium* had gradually

Table 4. Mean cover values (%) recorded through time after rewetting (in 1999) at Porla. Confidence intervals (95 %) are estimated for plot cover, bare peat, open water and number of species *per* plot. Species are listed in alphabetical order. For each species, mean cover is calculated across all plots and frequency of appearance (number of plots in which the species was recorded) is shown in brackets. "+" = cover less than 1 %.

Year:	2006	2008	2010	2012	2013	2014
Years after rewetting	7	9	11	13	14	15
Number of plots	32	18	31	16	15	21
Plot cover (%)	40±9	60±12	70±9	74±12	77±18	76±12
Bare peat (%)	47±12	38±14	18±9	22±13	19±11	23±12
Open water (%)	13±11	5±9	11±7	7±7	14±12	10±10
Number of species *per* plot	2±0	2±1	2±1	3±1	4±1	3±1
Species and (abbreviations):						
Calluna vulgaris (Calluna)	+(2)	+(1)	+(2)	-	1(2)	+(1)
Carex spp. (Carex)	-	+(1)	+(1)	1(1)	3(2)	2(2)
Drosera spp. (Drosera)	+(7)	2(7)	3(11)	3(5)	4(6)	3(6)
Eriophorum angustifolium (EA)	17(27)	16(9)	23(16)	8(5)	5(7)	13(11)
Eriophorum vaginatum (EV)	18(22)	40(4)	31(22)	41(15)	32(13)	32(19)
Juncus spp. (Junc)	-	+(1)	1(2)	2(3)	1(2)	1(2)
Phragmites australis (Phragm)	+(1)	+(1)	1(1)	2(1)	6(4)	2(4)
Rhynchospora alba (Rynch)	1(4)	+(2)	1(3)	+(1)	1(2)	+(5)
Utricularia intermedia (Utric)	+(3)	-	2(3)	3(5)	3(5)	2(4)
Vaccinium oxycoccus (Vaccinium)	-	-	+(1)	-	-	+(1)
Polytrichum spp. (Polytric)	2(4)	+(4)	2(5)	1(3)	1(2)	+(2)
Scorpidium spp. (Scorpid)	-	-	+(1)	-	-	-
Sphagnum spp. (Sphagn)	+(2)	1(3)	5(7)	12(8)	22(8)	20(11)

increased to 35 % and the average plot cover at Porla was around 40 %. Then, in 2008, the average plot cover increased 1.5-fold to around 60 %, and after that it stabilised at 70–77 %. Bare peat cover on the plots was around 40–50 % during the 7–9 years following rewetting, but from 2010 it decreased to 18–23 % and remained stable at that level. Open water cover in the plots fluctuated from 5 % to 14 % during the whole observation period, but varied with seasonal water level/wetness.

In terms of species composition, Porla was much poorer than Västkärr. In 2006–2010, only 2–3 species were detected, on average, *per* plot; whilst in 2012–2014 the average number of species *per* plot was 3–4. There were no significant changes in the structure of plant communities over time (Figure 4). The species composition comprised six groups: shrubs, dwarf shrubs, herbs, graminoids, sedges and mosses. Species richness in each year of observation was stable for all groups except dwarf shrubs. One dwarf shrub species (*Vaccinium oxycoccus*) appeared in 2010 but was not observed again until 2014.

In 2006–2010 (7–11 years after rewetting) the most abundant species were *E. angustifolium* and *E. vaginatum*. *Sphagnum* species were observed in 2007 and had established quite well (12 % cover) by 2012. In that year, the most abundant taxa were *Sphagnum* spp. and *E. vaginatum.* By 2013 the average cover of *Sphagnum* spp. had doubled (to around 22 %), and *Sphagnum* spp. and *E. vaginatum* were still the most abundant species. In 2014, the cover of *E. angustifolium* increased to 13 % and it was the third most abundant species, after *E. vaginatum* and *Sphagnum* spp. (Table 4).

As we used transects to make vegetation inventories, some vegetation relevés were combined and 95 vegetation relevés instead of 133 were used for DCA. Statistical assessment with DCA showed changes in plant composition over time (Figure 5). Several of the vegetation relevés made in 2012–2013 (right of Figure 5) deviated strongly from the others (by up to two SD) due to the abundance of *Carex* spp. and *Juncus* spp. In 2014 the abundance of these species decreased. In the last three years of observation (2012–2014) some plots showed a trend towards *V. oxycoccus* and *Sphagnum* spp. Despite this, DCCA calculations showed that there were no significant differences between vegetation relevés recorded in different years ($p = 0.137$).

Vegetation and surface water chemistry

The physicochemical characteristics of the water at Västkärr changed over time. pH increased gradually from 6.1 in 2000–2001 to 6.7 in 2011–2013, although slightly higher values (pH = 7.0) were observed in 2007–2010. Electrical conductivity also increased, from 73 µS cm^{-1} in 2000–2001 to 109 µS cm^{-1} in 2011–2013. Total K and N concentrations decreased in the 3–4 years after rewetting, from 1.7 to 1.2 mg L^{-1} and from 2.07 to 1.66 mg L^{-1}, respectively; but by

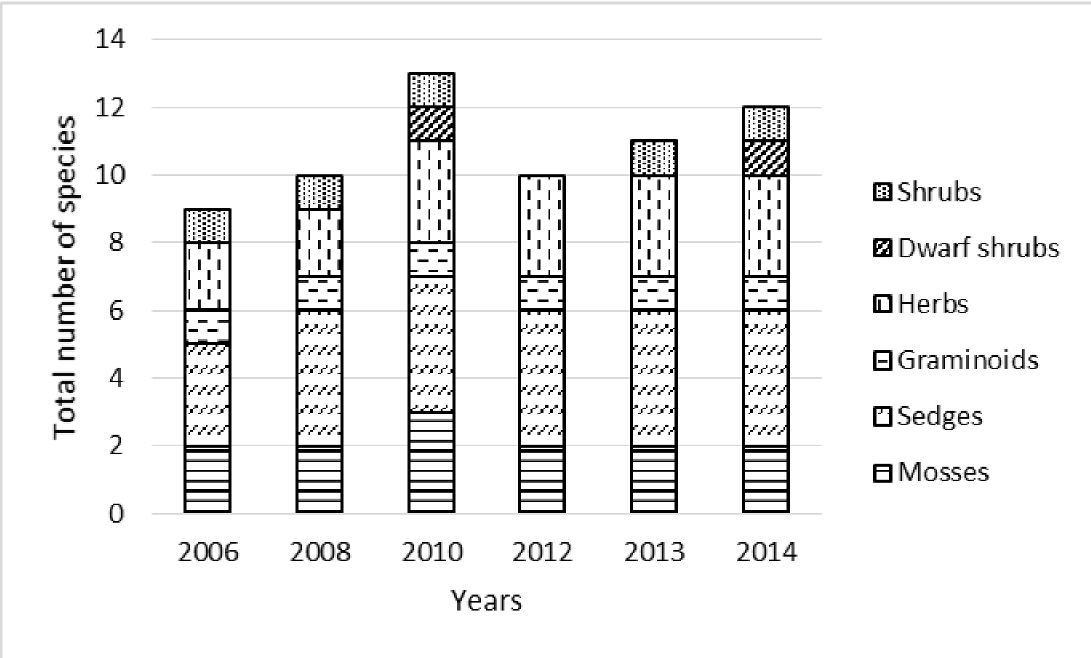

Figure 4. Total number of species in accordance with plant group (shrubs, dwarf shrubs, herbs, graminoids, sedges or mosses) in the Porla wetland, 2006–2014. The species richness of all groups except dwarf shrubs was stable. The dwarf shrub group appeared twice, with one species (*V. oxycoccus*), in 2010 and 2014.

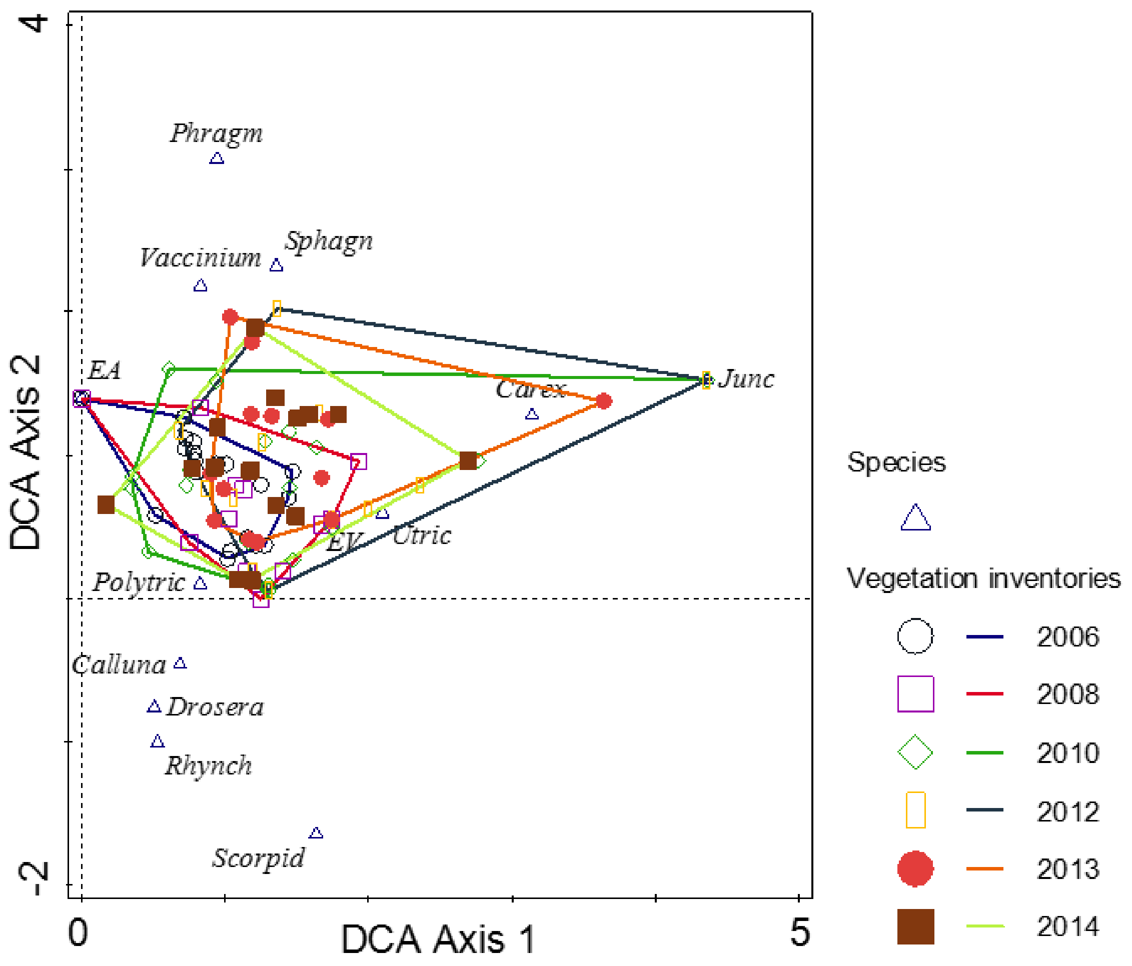

Figure 5. Detrended Correspondence Analysis (DCA) of 95 vegetation relevés in the Porla wetland. Empty triangles show relative species positions. Envelopes are plotted for symbols showing relative positions of vegetation relevés according to the year of observation. Scaling of axes is in SD units. Total inertia (variance) is 2.188. Eigenvalues of Axis 1 and Axis 2 are 0.516 and 0.277, respectively. Abbreviations of plant species names are given in Table 4.

2011–2013 they had increased again to 1.7 mg L^{-1} and 2.37 mg L^{-1}, respectively. The concentration of total P fluctuated between 0.051 and 0.124 mg L^{-1}.

The physicochemical characteristics of surface water at Porla did not fluctuate significantly after rewetting and values recorded during the period 2000–2013 were: pH 4.9–5.1, electrical conductivity 28–35 μS cm^{-1}, concentration of total K 0.44–0.50 mg L^{-1}, concentration of total P 0.017–0.021 mg L^{-1}. The concentration of total N gradually decreased from 1.51 mg L^{-1} in 2000–2003 to 1.08 mg L^{-1} in 2011–2013.

A PCA analysis of surface water chemistry (Figure 6), detected a strong poor–rich gradient in the whole dataset. Axis 1 explained 52.25 % of total variation, and the most important contributors to Axis 1 were total Ca concentration (0.969), electrical conductivity (0.967), total Mg concentration (0.938), pH (0.889), SO_4-S (0.857), total K concentration (0.829) and total N concentration (0.733). Axis 2 explained 10.81 % of total variation, which is much less than Axis 1, and indicated the importance of total C/N and total Zn concentration. Almost all samples from the Västkärr site had higher concentrations of major nutrients than samples from Porla, which was characterised by nutrient-poor conditions. Some of the Porla surface water samples had high total Zn concentrations.

Ordination of environmental and vegetation data for Västkärr and Porla revealed that the relationships between them were significant (p = 0.002 for Monte-Carlo permutation test) (Figure 7). In the diagram there is a strong poor–rich gradient from Porla to Västkärr, characterised mainly by SO_4-S, pH and total concentration of C and P. Total N could also be important for this gradient but due to high variance inflation factor (>20) is not plotted in the diagram.

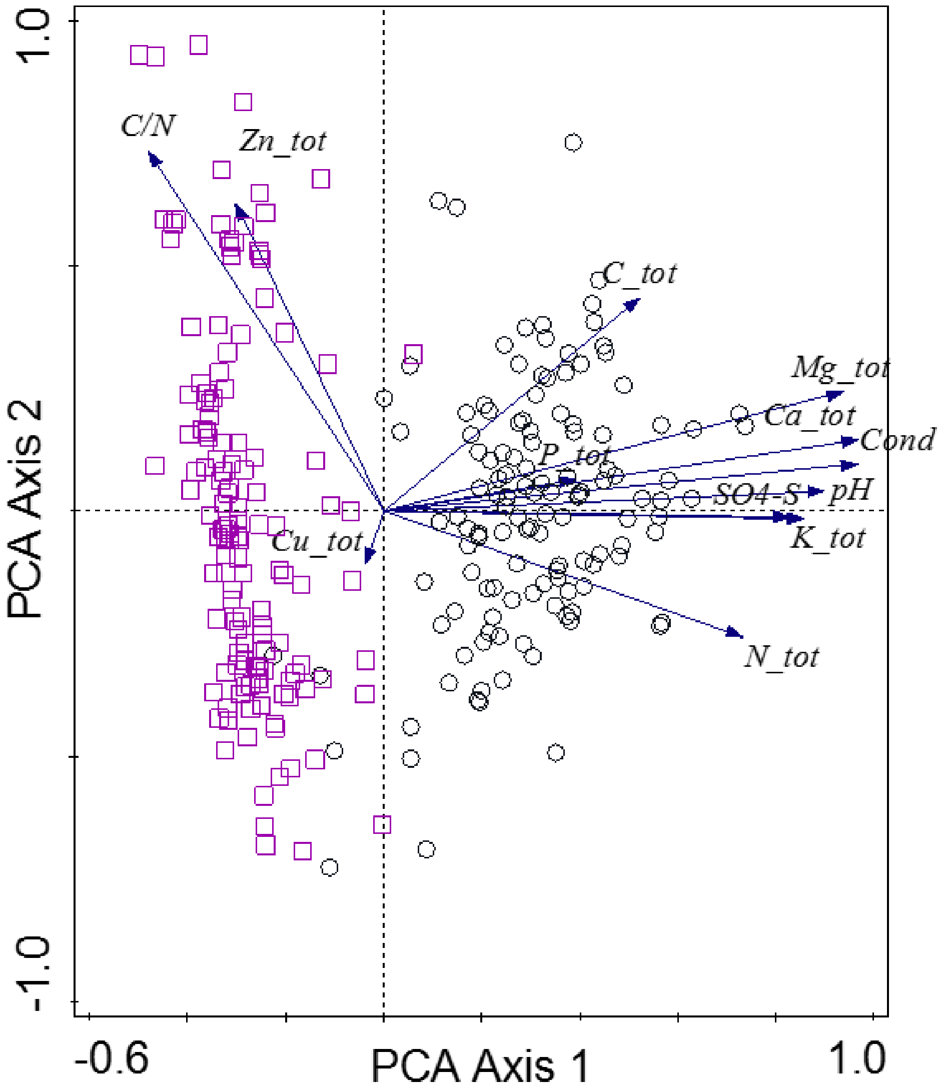

Figure 6. Principal Components Analysis (PCA) of 131 samples of surface water from Västkärr (circles) and 135 samples of surface water from Porla (squares). Axis 1 and Axis 2 explain 63.06 % of total variation. Arrows show the directions of environmental gradients. Surface water sample characteristics used in the analysis were: pH (*pH*), electrical conductivity (*Cond*), concentration of sulphate anion as sulphur equivalent (*SO4-S*), total carbon/total nitrogen quotient (*C/N*), total concentration of calcium (*Ca_tot*), magnesium (*Mg_tot*), potassium (*K_tot*), zinc (*Zn_tot*), copper (*Cu_tot*), phosphorus (*P_tot*), carbon (*C_tot*) and nitrogen (*N_tot*).

Axis 1 explained 16.56 % of total variation (eigenvalue is 0.850). Total concentrations of Cu and Zn were positively correlated with each other and slightly correlated (or even not correlated) with other environmental variables. Axis 2 explained only 2.53 % of total variation (the eigenvalue is 0.130).

The general species pattern could be interpreted as two separate groups of plant species with about one SD distance between them. The first group is situated on the right in Figure 7 and includes species preferring poor environmental conditions with low pH, total P and total N (high C/N ratio). All species in that group occurred only at Porla. The group on the left includes all other species, which prefer a more nutrient-rich environment with higher pH and total C concentration. Some of these (*T. latifolia*, *P. arundinacea*, *Carex* spp., *R. repens*, *Ceratophyllum demersum*) were related to higher concentrations of total Zn and SO_4-S, but most prefer a higher concentration of total P. Such species, e.g. *P. australis*, *Carex* spp. and *Juncus* spp., were present at both Västkärr and Porla and belong to the group on the left. They probably occur in association with higher nutrient levels at Porla.

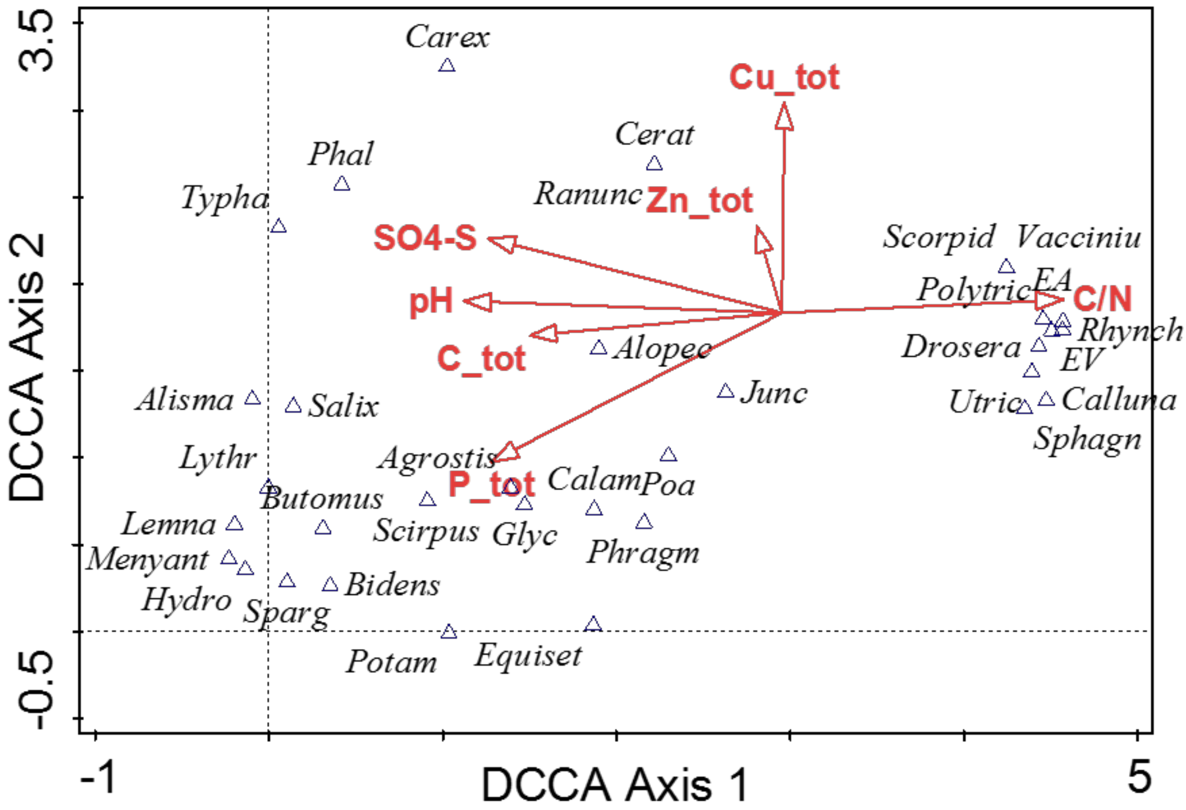

Figure 7. Detrended Canonical Correspondence Analysis (DCCA) of plant species and environmental variables based on 48 vegetation relevés at Västkärr and 80 vegetation relevés at Porla (22 vegetation relevés at Västkärr and 15 at Porla were excluded because of lack of environmental data). Relative positions of plant species are marked by unfilled triangles. Environmental variables (red arrows) with variance inflation factor ≤ 20 are shown. Total variation is 5.13. Explanatory variables account for 26.1 % of total variation (adjusted explained variation 21.8 %). Abbreviations of plant species are given in Tables 3 and 4, and of environmental variables in Figure 6.

DISCUSSION

Before rewetting, the bare black peat surfaces of both study areas were in the same condition as they had been when peat extraction stopped, because the dry soil conditions restricted the establishment of vegetation. At both Västkärr and Porla, rewetting significantly promoted colonisation by plants, and so made a considerable contribution to the revegetation of these extracted peatlands. However, the two sites are characterised by differences in the remaining peat substrate. While Västkärr has only fen peat with fairly high ash content, Porla has both fen peat and oligotrophic *Sphagnum* peat. This has resulted in differences in plant species colonisation patterns within the two restoration areas.

Vegetation development at Västkärr

According to other authors, significant changes in plant communities can be expected within the 3–10 years following peatland restoration works (Haapalehto *et al*. 2011, Poulin *et al*. 2013, González & Rochefort 2014). Revegetation of the Västkärr wetland started in the first year after rewetting and, during the following 14 years, significant changes in species composition and abundance occurred. By 2014, the vegetation of rewetted areas in the shallow lake at Västkärr included mostly *C. rostrata*, *L. minor*, *T. latifolia*, *P. arundinacea* and *P. australis*. In central Europe, *Carex* spp., *P. australis*, *Typha* spp., *Glyceria maxima* and *P. arundinacea* typically cover nutrient-rich wetlands which developed from fen grasslands after cessation of artificial drainage, opening dikes, or damming up of ground-surface water flow from adjacent catchment areas (Timmermann *et al.* 2006).

The strongest link between water chemistry (pH, electrical conductivity and Ca) and mire vegetation is along the bog to rich fen gradient (Rydin & Jeglum 2006). In our study pH, electrical conductivity and Ca concentration increased gradually during the 14 years following rewetting (2000–2013); pH from 6.1 to 6.7, electrical conductivity from 73 to 109 µS cm^{-1} and Ca from 12 to 17 mg L^{-1}. Lamers *et al*. (2015) showed that increased nutrient availability in rich fens leads to changes in vegetation composition caused by competitive interactions. For instance, fast-growing and highly competitive species become dominant and monopolise sunlight to the detriment of other species, leading to biodiversity loss (Lamers *et al*. 2015). In our investigations *T. latifolia* and *P. australis* colonised the lakeshore at the Västkärr wetland and actively grew out into the water. Stands of *T. latifolia* alternated with stands of *P. australis* within the flooded areas. Since the main purpose of rewetting was to create a bird lake, stands of *P. australis* are valuable. Wheeler & Shaw (1995) note that monotonous reed stands and *Salix* shrubs can be significant for the recovery of bird populations.

Active mesotrophic and eutrophic peat-forming species such as *T. latifolia*, *Carex* spp. and *P. australis* were observed at Västkärr, which means that the site may terrestrialise in the long term. The development of floating fen vegetation could, in turn, create suitable conditions for oligotrophic mire species (Wheeler & Shaw 1995), which would be the natural hydroseral succession. For instance, fen species may facilitate colonisation by oligotrophic species through the formation of accumulating substrates (peat) (Poschlod *et al*. 2007). However, the depth (0.5–1 m) of most of the open water at Västkärr wetland, which was designed as a bird lake, would be a constraint on fast terrestrialisation.

Vegetation development at Porla

At Porla, initial rates of colonisation by vegetation were low, and we can link this observation to water table instability during the period 2000–2002. A stable water table above or close to the soil surface is crucial for the regeneration and development of peatland vegetation (Robert *et al*. 1999, Tuittila *et al*. 2000, Lode 2001, Triisberg *et al*. 2013, Nishimura & Tsuyuzaki 2014). For instance, in England, studies of block-cut sections of peatland at Thorne Waste revealed that *Sphagnum* species colonised after the water table was artificially raised to a level 10 cm above the soil surface (Lavoie *et al*. 2003). Sufficient cover of *E. vaginatum*, *E. angustifolium* and *Polytrichum* spp. (up to 37 %) was critical for the appearance of other species.

At Porla, *E. vaginatum* seems to be the most important dominant component in colonisation of the bog by native oligotrophic plants. In particular, it has been reported that *E. vaginatum* (cottongrass) facilitates colonisation by other species, and most of the colonising species can be found close to cottongrass plants (Tuittila *et al*. 2000, Lavoie *et al*. 2003, Lavoie *et al*. 2005, Trinder *et*. *al*. 2008, Koyama & Tsuyuzaki 2012), although Lavoie *et al*. (2005) doubt that it can facilitate moss growth.

In Porla, the thickness of residual peat varied considerably and this influenced revegetation patterns, with species such as *E. vaginatum* colonising areas with thicker layers of remaining *Sphagnum* peat. In locations with mainly fen peat, *E. angustifolium* dominated the first recolonisation. Moreover, inflowing surface water and groundwater (which provided water for rewetting) contributed extra nutrients. This resulted in *Sphagnum* not developing everywhere and in some areas being covered mostly by *C. rostrata*, *P. australis* and *E. angustifolium.* The competitive balance may shift between *Sphagnum* mosses and vascular plants depending on the amount of nutrients, and thus influence the revegetation patterns of *Sphagnum* mosses (Poschlod *et al*. 2007, Hynninen *et al*. 2011, Nishimura & Tsuyuzaki 2014). Mesotrophic species such as *C. rostrata* and eutrophic species such as *P. australis* and *E. angustifolium* are indicators of an environment that is more nutrient-rich than an oligotrophic bog. However, several areas are covered by both *P. australis* and *Drosera anglica*, or by *E. vaginatum* growing with *E. angustifolium.* This reflects high heterogeneity in nutrient conditions for plants at Porla, which is a typical feature of vegetation development on extracted peatlands (Grishutkin *et al.* 2013).

CONCLUSIONS

Although the two extracted peatland sites studied here were rewetted with the primary intention of creating bird lakes, rewetting also facilitated and promoted revegetation.

Rewetting of Västkärr (originally a lagg fen) led to the formation of a shallow lake surrounded by stands of *T. latifolia* alternating with stands of *P. australis* along its shores. Special management is likely to be required to facilitate the development of more mesotrophic species.

At the Porla wetland (originally a bog), *E. vaginatum* was the most important early coloniser and probably facilitated the next successional stage. *Sphagnum* mosses established on their own without special management (such as applications of diaspore material) and started to grow out into the water. When water levels remained high and stable, *Sphagnum* growth in turn provided appropriate conditions for native bog vegetation.

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