



Topsoil removal in degraded rich fens: Can we force an ecosystem reset?



Willem-Jan Emsens^{a,*}, Camiel J.S. Aggenbach^{a,b}, Alfons J.P. Smolders^{c,d}, Rudy van Diggelen^a

^a Ecosystem Management Research Group, Department of Biology, University of Antwerp, Universiteitsplein 1C, 2610 Wilrijk, Belgium

^b KWR Watercycle Research Institute, P.O. Box 1072, 3430 BB Nieuwegein, The Netherlands

^c Department of Aquatic Ecology and Environmental Biology, Institute for Wetland and Water Research, Radboud University Nijmegen, Heyendaalseweg 135 1, NL-6525 ED Nijmegen, The Netherlands

^d B-WARE Research Centre, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

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ABSTRACT

Global land-use intensification and drainage has altered the biogeochemical properties of many peatlands, and concomitant eutrophication has led to a loss of low-competitive fen species. We investigated the hypothesis that removal of a degraded and eutrophied top peat layer, thereby exposing an underlying peat layer, can improve conditions for rich fen restoration. We studied the long-term (3–18 years) effects of past topsoil removal in six rich fens in Western Europe by comparing topsoil removal plots with (untouched) control plots. Overall, topsoil removal plots were characterized by lower bulk densities and soil nutrient pools of P and KCl-extractable NH_4^+ , while organic matter contents and soil C:N ratios were higher. Pore water concentrations of NO_3^- and NH_4^+ also decreased in the topsoil removal plots, while concentrations of base cations (Ca^{2+} , Mg^{2+} , Na^+ , K^+) and HCO_3^- increased. Furthermore, lower nutrient levels appeared to restrict herb biomass production in the topsoil removal plots, so that optimized light conditions led to the establishment of light-demanding target species and a significant increase in bryophyte cover. Multivariate analysis revealed that most variation in vegetation assembly was due to higher groundwater levels in the topsoil removal plots, closely followed by a higher relative light intensity (RLI) at surface level, lower pore water nutrient (NH_4^+) concentrations, and higher concentrations of base cations. We conclude that topsoil removal can be an effective mechanism to “reset” a degraded peatland to its initial state of nutrient limitation, base saturation and high availability of light, thereby improving the conservation prospects of endangered rich fen communities.

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1. Introduction

The global intensification of land use, a sharp increase in the use of artificial fertilizer, and an increase in anthropogenic nitrogen deposition is compromising the functioning of many nutrient-limited ecosystems, both in the aquatic and (semi-) terrestrial environment (Matson et al., 1997; Phoenix et al., 2006). As many endangered species are adapted to nutrient-poor habitats, eutrophication is considered a major threat to global species diversity (Wassen et al., 2005; Hautier et al., 2009).

Groundwater-fed peatlands (henceforth “rich fens”) are particularly vulnerable to land-use intensification and eutrophication. Typically, pristine rich fens are characterized by continuously wet,

base-rich and mesotrophic conditions and are dominated by low-competitive small sedges and brown mosses (Grootjans et al., 2006; Malson and Rydin, 2007). In Europe, however, most of the pristine rich fens have disappeared due to land use change, while degradation of the remaining fens leads to the gradual replacement of typical fen species with general wetland species (Kooijman 1992; Lamers et al., 2014). Therefore, both the conservation and restoration of the many degraded fens is a top priority for the long-term protection of this habitat type together with its typical species (van Diggelen et al., 2006). This is now legally acknowledged through the EU’s Habitats Directive (Romão, 1996).

In comparison with mineral soils, peatland eutrophication is a more complex process as nutrient enrichment is not necessarily related to an increased input from external sources alone (Bragazza et al., 2009). As peat soil mainly consists of reactive organic matter, the slightest alterations in hydrological conditions can have disproportional effects on fen chemistry. In this respect,

* Corresponding author. Tel.: +32 32652268.

E-mail address: willem-jan.emsens@uantwerpen.be (W.-J. Emsens).

desiccation is considered one of the major threats to rich fens (van Diggelen et al., 2006; Lamers et al., 2014). Desiccation can be triggered through direct local drainage (e.g., construction of drainage ditches), but it can also be the result of alterations in regional hydrology (e.g., increased rates of groundwater abstraction can reduce regional seepage fluxes (van Diggelen et al., 2006)). When peat soil desiccates, intrusion of oxygen becomes a driving force for increased rates of organic matter decomposition and mineralization (Brouns et al., 2014), which eventually results in nutrient release and eutrophication (Grootjans et al., 1986). Moreover, peat oxygenation triggers carbon loss (Laiho, 2006; Brouns et al., 2014), soil subsidence (Gambolati et al., 2006), regeneration of electron acceptors (Fenner et al., 2011), acidification (Beltman et al., 2001; Cusell et al., 2013), leaching of base cations (Laiho et al., 1999), shifts in vegetation assembly and a loss of typical biodiversity (Malson and Rydin, 2007; Malson et al., 2008). Long-term peat degradation can alter biogeochemical conditions to such an extent that successful fen restoration becomes notoriously difficult, even after restoration of the hydrological conditions (Zak et al., 2010, 2014; Brouns et al., 2014). Eventually, it is likely that the sum of these biogeochemical alterations in the top soil can trigger a shift toward a system that is governed by a different set of positive feedback mechanisms, possibly forcing the peatland toward an alternative degraded state (Suding et al., 2004).

In this study, we test the hypothesis that removal of the top layer of (disturbed) peat to restore rich fen ecosystems can trigger a system “reset” (i.e., after topsoil removal, biogeochemical conditions will become similar to initial pristine conditions), and that it improves conditions for the establishment of target plant communities. Although topsoil removal is a well-established measure in nature conservation on mineral soils (Allison and Ausden 2004; Olsson and Ödman 2014), the effect of topsoil removal in rich fens (in which an underlying peat layer is exposed) is only documented fragmentarily (Patzelt et al., 2001, 2007; Klimkowska et al., 2007, 2015), often with contrasting results. We believe this is due to the difficulty of predicting the effects of exposing an underlying high-quality peat layer after topsoil removal, as rapid peat mineralization and concomitant re-eutrophication is not unlikely (Brouns et al., 2014). To empirically test the effects of topsoil removal on abiotic conditions and rich fen development, we conducted a comparative field study in which we analyzed the mid-term (3–18 years) effects of past topsoil removal in six rich fens.

2. Methods

2.1. Study sites

Topsoil removal is an uncommon restoration measure for peatlands. Therefore, study site selection was determined mainly by the availability of suitable locations. Sites were included for sampling only if they met the following criteria: (1) peat-formation had started directly on mineral soils, thus excluding floating mires; (2) the peatland was fed by base-rich groundwater; (3) all peatlands were drained in the past, having led to topsoil degradation (Von post

humification topsoil > 8); (4) topsoil removal has taken place > 3 years ago and the area has re-vegetated; (5) after topsoil removal, a new underlying peat layer was exposed (excluding locations where all peat was removed down to the mineral subsoil); and (6) control plots (plots in which topsoil removal has not taken place) were available in the vicinity of the topsoil removal plots, to allow a meaningful comparison. In total, we located six fens in the Netherlands and Belgium that met all criteria (Table 1, Fig. 1). All sites have a history of agriculture that included haymaking and (limited) fertilization, while two of the sites (DA and PE) had also been rewetted by canal and ditch blocking.

2.2. Sampling design

In June 2013, within each study site we selected eight plots of 2 m × 2 m, resulting in a total of 48 plots. Four replicate plots per site were selected randomly in the zone where topsoil removal had taken place, and four replicate control plots were selected on nearby spots where the degraded topsoil had been left untouched. In each plot we recorded the cover of all species using the Londo scale (Londo, 1976). An Accupar LP-80 ceptometer (Decagon Devices Inc., Pullman, WA, USA) was used to measure relative light intensity (RLI) below the vegetation at surface level (=percentage of incoming photosynthetically active radiation as measured with a reference sensor above the canopy (Kotowski and van Diggelen, 2004)), averaged over 4 measurements per plot. This is an important measure as a sufficiently high availability of light (indicating limited herb productivity and thus less competition) is crucial for rich fen communities (Kotowski and van Diggelen, 2004; Kotowski et al., 2006). To ascertain that a high relative light intensity correlates with a decreased productivity at our study sites, we harvested the above-ground herb biomass in a randomly placed sub-plot of 0.4 m × 0.4 m within each of the larger plots. Next, four soil sub-samples per plot were taken from the upper 10 cm of the peat soil, and mixed into one homogeneous sample. Separate soil samples were taken for bulk density calculations. Element pool sizes in the soil are an indication of total long-term availability, but soil-bound elements are only partially plant-available. We, therefore, additionally collected pore water samples from the upper 10 cm of the soil in each plot using macro-rhizon samplers with a pore size of 0.15 μm (Rhizosphere Research Products, the Netherlands). Elements dissolved in the pore water are directly plant-available, but concentrations are much more subject to temporal variations. Pore water samples were stored at 4° until further treatment.

2.3. Chemical analyses

We measured pH and EC of all pore water samples directly in the field using portable field equipment (WTW multi 340i). Total inorganic carbon (TIC) was analyzed on an infrared gas analyzer (ABB Advance Optima): the resulting values were used to calculate HCO₃⁻ concentrations. Concentrations of NH₄⁺ and NO₃⁻ were determined on an auto analyzer 3 system (Bran + Luebbe) using ammonium molybdate, hydrazine sulphate and

Table 1

Study site location with coordinates, along with time (yr) since topsoil removal, and average depth (cm) of topsoil removal.

Location	Coordinates	Time since topsoil removal (yr)	Average depth of topsoil removal (cm)
Leijer Hooilanden (LH)	52°38'33.73"N; 6°16'43.23"E	10	15
Hellen (HE)	52°0'33.94"N; 5°34'48.93"E	10	30
Drentsche Aa (DA)	53°0'49.65"N; 6°37'45.88"E	18	20
Holmers (HO)	52°54'12.41"N; 6°37'45.83"E	11	30
Peizermade (PE)	53°10'19.33"N; 6°30'12.19"E	3	30
Malendriesbeekvallei (MA)	50°50'56.48"N; 4°52'24.39"E	5	25

salicylate. Pore water sub-samples were acidified by adding 0.7 mL 65% suprapure HNO_3 per 100 mL sample and were analyzed on ICP (IRIS Intrepid II) for the following elements: Ca, Mg, K, Na, Fe, Mn, P, S, and Al.

Soil samples for bulk density ($10 \times 10 \times 10$ cm) were dried (72 h at 105°C) and weighed; results were expressed in kg L^{-1} . Soil organic matter content (%) was determined by loss-on-ignition for 4 h at 550°C . KCl-extractions and ammonium-oxalate extractions (in darkness) on moist soil allowed the determination of pH_{KCl} , $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ and P-oxalate (P_{ox}), respectively. The latter is a measure for reactive soil-P bound to amorphous components including Fe and Al. Oven-dry soil sub-samples (48 h at 70°C) were homogenized and ground in liquid N. C and N contents (%) were determined with a Carlo Erba NA1500 elemental analyser (Thermo Fisher Scientific). 200 mg of soil was digested with 4 mL HNO_3 (65%) and 1 mL H_2O_2 (30%) using a microwave labstation (Milestone srl) to measure total Ca, Mg, K, P, S, Fe, Al, and Mn with ICP. Values were calculated for dry weight soil. Above-ground herb biomass was oven-dried (48 h at 70°C) and weighed; results were converted to tons per hectare (t ha^{-1}).

2.4. Data analyses

As soil bulk density differs strongly between different fens, content of soil chemical parameters was expressed per volume unit (mmol L^{-1}). Values of KCl-extractable $\text{NO}_3\text{-N}$ were largely below the detection limit and were, therefore, excluded from further analyses.

Before statistical analysis, environmental data were checked for normality based on visual inspection of histograms and normal Q–Q plots. If needed, data were transformed using either logarithmic, square root, or inverse transformations to attain

approximate normal distributions. Species cover values from vegetation relevés were converted into percentages.

To test for the main effects of topsoil removal on biogeochemical parameters, we ran a mixed-effect model using restricted maximum likelihood (REML) estimation in which we treated the factor “topsoil removal” (no = 0, yes = 1) as a fixed effect and “study site” (LH, HE, DA, HO, PE or MA) as a random effect. The latter was a deliberate choice as our study sites can be considered a collection of random samples drawn from a (theoretically) large pool of rich fens to which we would like to extrapolate (Bennington and Thayne, 1994). This model, therefore, allowed to test for the main effects of the treatment “topsoil removal” while correcting for inter-site variation, in which we are not interested.

Vegetation data were stored in Turboveg 2.75 (Hennekens and Schaminee, 2001). Next, data were exported to the JUICE software (Tichy, 2002) in order to link Ellenberg light indicator values to each of the species in the dataset. For each plot, we then calculated an average “species’ light requirement index (henceforth “SLRI”)”. These indices were obtained by averaging the mean Ellenberg light indicator values for all individual species that were found within the same plot. To have a measure for restoration success after topsoil removal, we counted the number of target species per plot. A target species met at least one of the following two criteria: (1) the species is listed on the “red list” of either the Netherlands (van der Meijden et al., 2000) or Flanders (van Landuyt et al., 2006), or (2) the species can be considered typical for small-sedge and brown-moss rich fen vegetation in Western Europe. A list with typical species had been constructed in advance (Appendix A). This list is based on a broad assessment of rich fen relevés in which we included all species with a frequency of $>20\%$ in the relevés, combined with rare low-frequency species that are considered highly characteristic for rich fens (Schaminee et al., 1995).

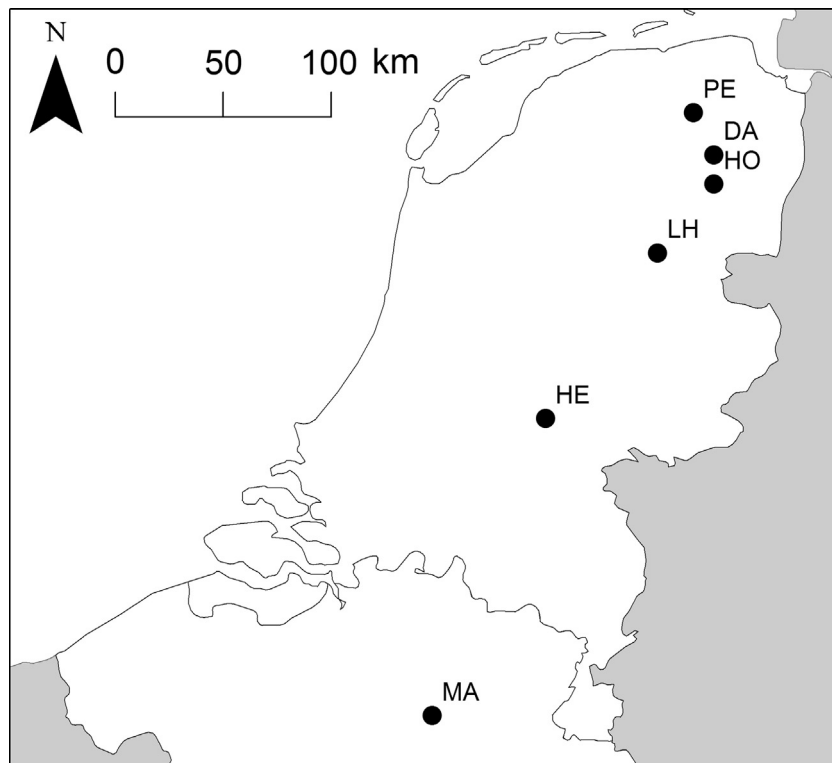


Fig. 1. Geographical spread of the study sites in Belgium and the Netherlands.

Table 2

Results of the mixed-effect model for the effects of topsoil removal on topsoil chemistry (mmolL^{-1}), corrected for study site. NS, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; and -, decrease at all sites; --, decrease at most sites; 0, no change; +, increase at most sites; ++, increase at all sites.

Effect	Dependent variable	d.f.	F-value	p-value	Direction
Topsoil removal	pH _{KCl}	1,41	18.55	***	+
	NH ₄ -N	1,41	13.82	***	-
	P	1,41	141.90	***	--
	P _{ox}	1,41	118.40	***	--
	C:N	1,41	71.52	***	++
	S	1,41	0.10	NS	0
	K	1,41	2.16	NS	0
	Ca	1,41	0.46	NS	0
	Mg	1,41	8.15	**	-
	Fe	1,41	29.66	***	-
	Al	1,41	14.92	***	-
	Mn	1,41	47.18	***	--
	Bulk density	1,41	30.26	***	-
	OM-content	1,41	36.94	***	++

The relationship between plant communities and abiotic characteristics in plots with and without topsoil removal was analyzed through multivariate analysis. First, species cover values were $\text{Log}_{10}(x+1)$ transformed. We then ran a detrended correspondence analysis to determine the total length of the gradient (length > 5). Next, abiotic variables were selected by forward stepwise selection in a canonical correspondence analysis (CCA) and a significance test based on permutations ($p < 0.05$ at 499 permutations). To account for site effects, permutations were restricted by adding the blocking factor “site” as a covariable. We used pore water variables rather than soil variables (pH and concentrations of dissolved HCO_3^- , Al, Ca, Fe, K, Mg, Na, Mn, P, S, NH_4^+ and NO_3^-) in the ordination because these are most relevant to rooting plants. Additionally, we included groundwater levels (“water level”) and relative light intensity at surface level (“RLI”). Extra variables were only added to the model if they showed no strong correlation with any of the preceding variables (inflation factor < 20).

Univariate statistical analyses were performed in SPSS 20 (SPSS Inc.). For multivariate analyses, we used CANOCO for Windows 4.5 (ter Braak and Šmilauer, 2002).

3. Results

3.1. Peat and pore water chemistry

Large differences in soil properties were found between plots with and without topsoil removal (Appendix B). Overall, the topsoil removal plots are characterized by a higher soil organic matter content ($F_{1,41} = 36.94$, $p < 0.001$) and lower bulk density ($F_{1,41} = 30.26$, $p < 0.001$) (Table 2), both of which are strongly correlated (Spearman's $\rho = -0.865$, d.f. = 10, $p < 0.001$). This observed decrease in bulk density correlates with a decrease in total pool size of all minerals, with the exception of stocks of Ca, K and S which remained unaltered. Interestingly, the most notable effects were found for total nutrient pool sizes: pools of total-P and oxalate extractable-P were drastically lower in topsoil removal plots at all sites (total pool size up to >6 times lower (P-total: $F_{1,41} = 141.9$, $p < 0.001$, P_{ox}: $F_{1,41} = 118.4$, $p < 0.001$)), while soil C:N-ratios increased ($F_{1,41} = 71.52$, $p < 0.001$) and KCl-extractable NH_4^+ -stocks decreased ($F_{1,41} = 13.82$, $p < 0.001$).

While mineral stocks in the soil were equal or lower in the topsoil removal plots than in the control plots, mineral concentrations in the pore water followed an opposite trend (Appendix C, Table 3). Concentrations of base cations Ca ($F_{1,41} = 20.77$, $p < 0.001$), Mg ($F_{1,41} = 15.85$, $p < 0.001$), Na ($F_{1,41} = 58.47$, $p < 0.001$) and K ($F_{1,41} = 10.25$, $p < 0.01$) as well as concentrations of HCO_3^-

Table 3

Results of the mixed-effect model for the effects of topsoil removal on pore water chemistry (μmolL^{-1}), corrected for study site. NS, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; and --, decrease at all sites; -, decrease at most sites; 0, no change; +, increase at most sites; ++, increase at all sites.

Effect	Dependent variable	d.f.	F-value	p-value	Direction
Topsoil removal	pH	1,41	15.79	***	+
	HCO_3^-	1,41	34.58	***	+
	NH_4^+	1,41	16.75	***	-
	NO_3^-	1,41	27.71	***	-
	P	1,41	2.52	NS	0/-
	S	1,41	29.54	***	--
	Na	1,41	58.47	***	+
	K	1,41	10.25	**	+
	Ca	1,41	20.77	***	++
	Mg	1,41	15.85	***	++
	Fe	1,41	4.98	*	+
	Al	1,41	5.52	*	-
	Mn	1,41	0.59	NS	0
	Groundwater level	1,41	116.85	***	++

($F_{1,41} = 34.58$, $p < 0.001$) and dissolved Fe ($F_{1,41} = 4.98$, $p < 0.05$) were generally higher in the topsoil removal plots, correlating with increased groundwater levels ($F_{1,41} = 116.85$, $p < 0.001$) and a higher pH ($F_{1,41} = 15.79$, $p < 0.001$). Furthermore, inorganic nitrogen concentrations (NO_3^- and NH_4^+) decreased ($F_{1,41} = 27.71$, $p < 0.001$ and $F_{1,41} = 16.75$, $p < 0.001$, respectively), but concentrations of dissolved phosphorus remained unaltered ($F_{1,41} = 2.52$, $p > 0.05$).

3.2. Floristic response to topsoil removal

In total, we registered 116 species of vascular plants (5 were identified to genus level) and 16 species of bryophytes (2 to genus level) (Appendix D). 37 of these species (28%) were classified as typical of rich fens and 15 (11%) were red list species. As most of the red list species were also classified as typical fen species (e.g., *Carex diandra*, *Menyanthes trifoliata*, . . .), there were 38 “target species” in our dataset (29% of total species count). The remaining 71% were considered general wetland or meadow species with a much broader amplitude (e.g., *Juncus effusus*, *Mentha aquatica*, . . .).

Compared with the control plots, topsoil removal plots have a lower herb biomass at all study sites ($F_{1,41} = 72.54$, $p < 0.001$, Appendix E, Table 4), which correlates with increased light intensity (RLI) at the surface level (Pearson's $r = -0.842$, $\text{df} = 10$, $p < 0.001$, Fig. 2). Consequently, we found an increase in bryophyte cover ($F_{1,41} = 19.58$, $p < 0.001$) and SLRI ($F_{1,41} = 28.43$, $p < 0.001$) in the topsoil removal plots. Both biodiversity (as defined by the total number of species) as well as the fraction of target species was higher in all of the topsoil removal plots ($F_{1,41} = 45.59$, $p < 0.001$ and $F_{1,41} = 37.63$, $p < 0.001$, respectively).

Canonical correspondence analysis resulted in a total of eight significant variables that partly explain variation in vegetation assemblages between the plots (Fig. 3): groundwater levels, RLI,

Table 4

Results of the mixed-effect model for the effects of topsoil removal on total herb biomass, total number of species, moss cover, fraction of target species, and the species' light requirement index (SLRI) per plot. NS, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; and --, decrease at all sites; -, decrease at most sites; 0, no change; +, increase at most sites; ++, increase at all sites.

Effect	Dependent variable	d.f.	F-value	p-value	Direction
Topsoil removal	Herb biomass (t/ha)	1,41	72.54	***	--
	No. of species	1,41	45.59	***	++
	SLRI	1,41	28.43	***	++
	Bryophyte cover (%)	1,41	19.58	***	+
	Target species (%)	1,41	37.63	***	++

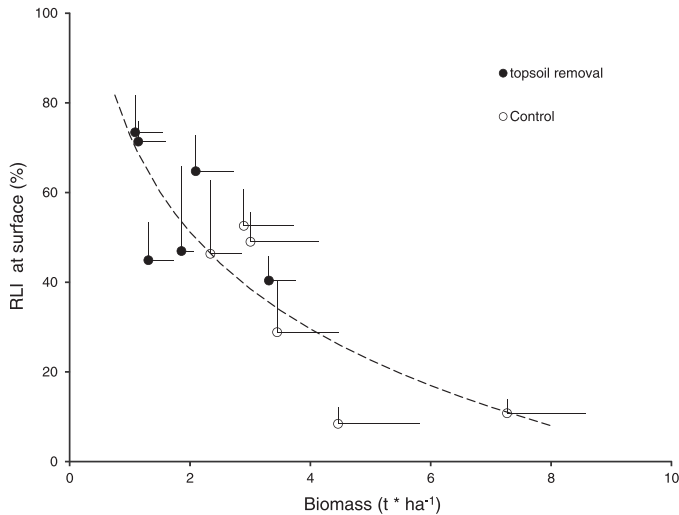


Fig. 2. Relationship between average herb biomass (t ha^{-1}) and relative light intensity at the soil surface (%), grouped for plots with and without topsoil removal ($y = -31.1 \times \ln(x) + 72.8$; $r^2 = 0.72$). Dots represent averages per site and treatment, bars represent standard deviations.

and pore water concentrations of NH_4^+ , S, Ca, K, Al and Mn. Axis 1 and 2 combined explain 42.1% of the total species–environment relation. Species–environment correlations with axis 1 (eigenvalue=0.49) and axis 2 (eigenvalue=0.35) equaled 0.95 and 0.93, respectively (total inertia=6.09). The plots with and without topsoil removal were largely separated along the horizontal axis (axis 1), which correlated best with groundwater levels ($r = -0.88$), RLI ($r = -0.50$) and pore water concentrations of NH_4^+ ($r = 0.60$), S ($r = 0.54$), Ca ($r = -0.43$), Al ($r = 0.35$) and Mn ($r = -0.26$). Some separation can also be observed along the vertical axis (axis 2), which correlates with pore water concentrations of K ($r = -0.74$, generally higher in the topsoil removal plots).

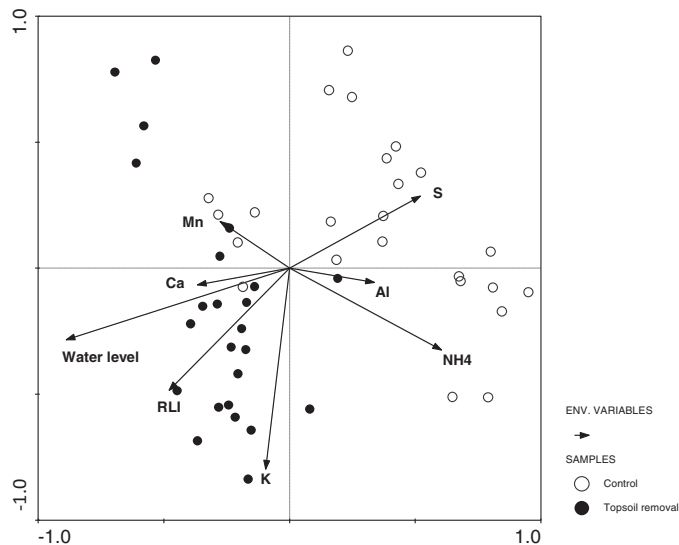


Fig. 3. CCA-biplot showing significant ($p < 0.05$) explanatory environmental variables (vectors) in relation to species composition in the 48 study plots (dots). Chemical variables were measured in the pore water, “Water level” = groundwater level and “RLI” = relative light intensity at surface level. Plots are grouped into topsoil removal or no topsoil removal (“control”). Study site was included as a blocking factor in the analysis (site blocks not shown in figure).

4. Discussion

Our results show that removal of a degraded and eutrophied top peat layer can considerably improve geochemical conditions for rich fen development. During the first two decades nutrient availability (either N, P or both) dropped sharply in each of the six study sites, whereas light availability (RLI) and base cation (Ca^{2+} , Mg^{2+} , Na^+ , K^+) concentrations in the pore water increased, correlating with higher groundwater levels. In response, bryophytes expanded and the number of rich fen target species increased.

4.1. Peat and pore water chemistry

In our study, hydro-geochemical conditions in the top soil differed markedly between plots with and without topsoil removal. One of the inherent effects of topsoil removal is the concomitant lowering of the soil surface level and an increase in relative groundwater levels, which we observed in all sites. The resulting increased influence of base-rich groundwater leads to a higher base availability and alkalinity (Boeye et al., 1995; Lamers et al., 2014), which corresponds with our observation of higher pore water concentrations of Ca^{2+} , Mg^{2+} , Na^+ , K^+ and HCO_3^- in the topsoil removal plots. Correspondingly, we observed significantly higher pH_{KCl} -values in the topsoil removal plots (ranging from 5.2 to 6.3).

Topsoil removal led to a drastic decline in nutrient concentrations: concentrations of nitrogen were lower both in the peat soil (lower NH_4^+ -N, higher C:N ratios) and in the pore water (NH_4^+ and NO_3^-) of the topsoil removal plots, and a similar distinct pattern was found for soil pools of total-P and oxalate-extractable P. Lower concentrations of nitrate after topsoil removal can be due to complete removal of the eutrophied top layer, but it can also be a consequence of wetter (more anoxic) conditions, which enhances denitrification by micro-organisms (Whitmire and Hamilton, 2005). Under such permanently wet conditions, however, reduced nitrification rates can lead to ammonium accumulation (Paulissen et al., 2005). One would, therefore, expect that the observed higher groundwater levels in the topsoil removal plots would correlate with higher concentrations of NH_4^+ , but we see the opposite. We assume that the higher NH_4^+ -concentrations in the control plots can be explained by (past) peat mineralization followed by the release and adsorption of ammonium to the cation exchange complex of the soil. In the topsoil removal plots, such accumulated soil-bound NH_4^+ is removed together with the mineralized topsoil. Also, the increased input of base cations by groundwater after topsoil removal enhances the desorption of NH_4^+ from the soil adsorption complex, allowing NH_4^+ to be washed out (Lucassen et al., 2006).

Concentrations of total phosphorus in the pore water were not lower in the topsoil removal plots, but we find up to six times lower soil pools of total-P and oxalate-P. Phosphorus is relatively immobile and tends to accumulate in an inorganic form in the top soil of degraded or fertilized fens (Graham et al., 2005; Zak et al., 2010), particularly when iron is abundant (Aggenbach et al., 2013). Such P-enriched layer is generally easily removed with topsoil removal, as is well known from restoration projects on mineral soils (Allison and Ausden, 2004). The discrepancy between lower P-concentrations in the top soil but unaltered P-concentrations in the pore water of the topsoil removal plots is possibly the result of lowered redox potentials that facilitate P-release in the form of PO_4^{3-} -P to the pore water (Zak et al., 2010; van de Riet et al., 2013).

4.2. Floristic response to topsoil removal

We observed an increase in biodiversity as well as in the fraction of target species in all topsoil removal plots. Moreover, target species that were already present in the control plots are

nearly always found in the topsoil removal plots as well, indicating activation of the seed bank after topsoil removal or rapid recolonization from nearby areas.

The multivariate analysis indicated that vegetation composition in the topsoil removal plots is strongly related to high groundwater levels, low pore water concentrations of NH_4^+ , a high availability of light (RLI), and high concentrations of base cations Ca^{2+} and K^+ . As discussed in Section 4.1, higher groundwater levels lead to rewetting, which correlates with higher concentrations of base cations and HCO_3^- . A continuous supply of both HCO_3^- (ensuring a high alkalinity and a buffered pH) and base cations is essential for rich fen species, which are vulnerable to acidification and base leaching (van Diggelen et al., 1996; Grootjans et al., 2006; Cusell et al., 2013). In this respect, a slight increase in concentrations of potassium may be of particular importance as K leaches relatively easily from degraded peat soils, thereby hampering fen restoration (van Duren et al., 1997). As many of the control plots were still suffering from (slight) desiccation, desiccation-related processes co-explain the limited occurrence of target species in the control plots. Furthermore, the low nitrogen levels (especially NH_4^+) in the topsoil removal plots are equally important for the establishment of rich fen communities: many rich fen species are easily outcompeted by competitive helophytes in N-enriched systems (Verhoeven et al., 2011), while excess ammonium accumulation can be phytotoxic to target species (Paulissen et al., 2005). Finally, the CCA unravels the significant effect of relative light intensity (RLI) on target community establishment, which is inversely related to productivity and nutrient availability. Site averages for the topsoil removal plots always exceeded 40% of RLI at surface level, whereas RLI in some of the control plots approached the 5% threshold of light compensation where respiration exceeds photosynthesis in herbs (Larcher, 2003). Under such conditions, light stress becomes a strong environmental filter for fen vegetation (Kotowski and van Diggelen, 2004). For typical rich fen communities of small sedges and brown mosses, thresholds lie generally around 40–60% of RLI (Kotowski and van Diggelen, 2004; Kotowski et al., 2006). Consequently, we observed a higher fraction

of light-demanding target species and an increase in bryophyte cover in the topsoil removal plots.

4.3. Site effects

We did not analyze different sites separately, but it appears that the strength of the effect of topsoil removal is somewhat site dependent. Moreover, depth of topsoil removal as well as time since topsoil removal varied between sites, and this may affect the outcome as well (Klimkowska et al., 2007). We have too few study sites to statistically disentangle all the different site effects that affect the magnitude of restoration success, but visual inspection of our data combined with the CCA-analysis suggests that higher groundwater levels and lower nutrient stocks play a major role, with most successful results on (previously) desiccated locations with a heavily-mineralized top soil (location LH, HE, HO and MA). The two locations that had been rewetted in the past (DA, PE) showed a less distinct, albeit positive, response to topsoil removal.

4.4. Topsoil removal as a restoration strategy for organic soils

Topsoil removal on peat soils (thereby exposing an underlying peat layer) is an uncommon practice in nature restoration (but see Patzelt et al., 2001; Klimkowska et al., 2009, 2015), but our results show that it can significantly improve conditions for rich fen development. It should be noted that we cannot ascertain that topsoil removal triggers a complete “ecosystem reset” to pristine conditions, as this requires complete knowledge of the conditions prior to degradation. However, it is clear that hydro-geochemical conditions in the degraded fens shift toward conditions that are, at least, more typical for pristine rich fens (see Aggenbach et al., 2013), and that target species respond positively. At the same time, a complete removal of a degraded peat layer is irreversible and not without risk. Therefore, we provide a simplified decision flow-chart with criteria that should be met before topsoil removal is considered (Fig. 4). First, it is evident that topsoil removal is not feasible if the

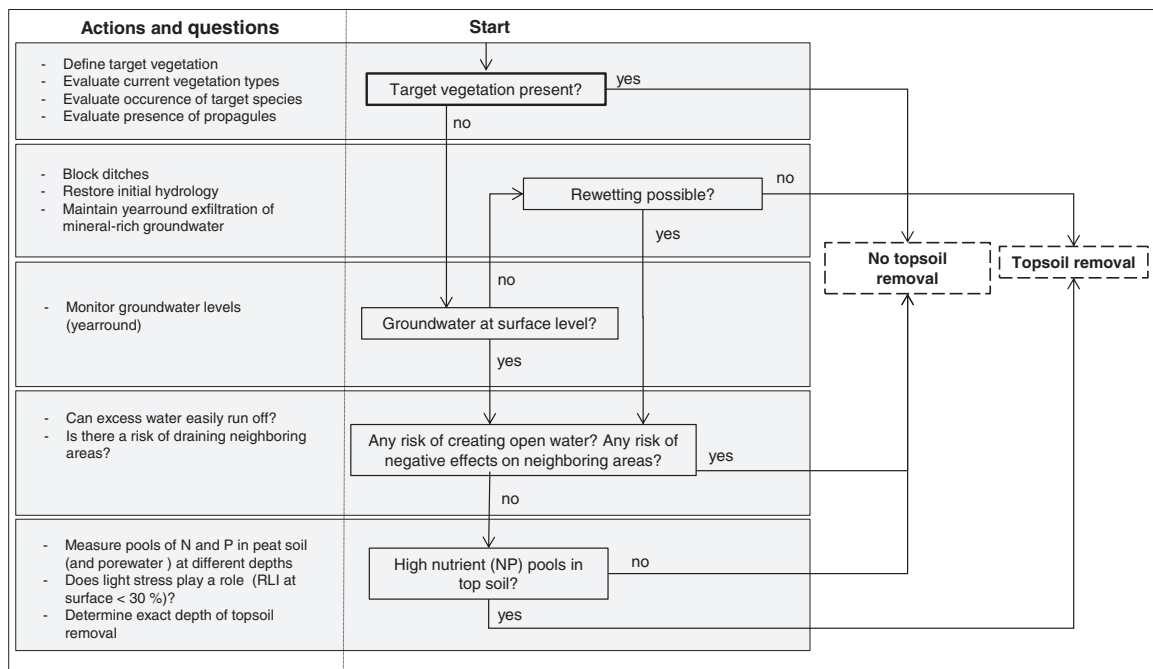


Fig. 4. Decision flow-chart with criteria on when to consider topsoil removal in degraded rich fens.

target rich fen vegetation is already present. Second, if other restoration strategies deserve priority (for rich fens this includes rewetting with minerotrophic water (van Diggelen et al., 2006)), then topsoil removal should be considered only if (1) rewetting is not possible or (2) nutrient (N or P) pools are so high that typical rich fen species are outcompeted by non-target species (Lamers et al., 2014). Finally, if topsoil removal is expected to negatively affect any neighboring area of high ecological value (e.g., through drainage effects), then potential gains in the restoration area must be balanced with potential losses in the neighboring area.

5. Conclusions

Our study has shown that topsoil removal on degraded peat soils can significantly improve conditions for rich fen development. We suggest that the best results are to be expected in areas where raising groundwater levels to the surface level is not possible, so that topsoil removal leads to immediate rewetting. Moreover, removal of the degraded top layer reduces soil bulk density and nutrient pools, thereby exposing an underlying peat layer of better physio-chemical quality. Generally, target species respond relatively fast. We propose that topsoil removal should be more frequently considered in degraded groundwater-fed peatlands. As most peatlands in Europe are already in a stage of severe degradation, such drastic measures may be crucial to improve the conservation prospects of these endangered habitats.

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Appendix. A Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2015.01.029>.

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