Spontaneous revegetation of cutaway fens: can it result in valuable habitats?

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SUMMARY

Studies of spontaneous revegetation in cutaway peatlands with residual fen peat are relatively scarce in Europe. However, knowledge about the spontaneous recovery of vegetation and factors affecting the succession can be applied in wetland restoration and conservation of valuable, threatened habitats and species populations. We analysed spontaneous revegetation and influencing factors in six cutaway fens in Latvia. The results suggest that the major drivers affecting the composition of vegetation in the study sites are water table, soil water pH and time since peat harvesting ceased. Water table is the major variable that distinguishes success from failure in terms of fen recovery, while pH differentiates the outcome: poor fen and rich fen vegetation, together with age, define the 'typicalness' of the plant community. In alkaline conditions the sites can host numerous rare and specialist species. The outcome of self-restoration is site-specific, making the results difficult to generalise.

KEY WORDS: environmental factors, Latvia, peatlands, spontaneous succession, vegetation

INTRODUCTION

Fens are now among the most threatened habitat types in Europe. The area of natural fens, especially species-rich alkaline fens, has declined dramatically over recent centuries (Joosten & Clarke 2002, Klimkowska *et al*. 2010, Lamers *et al*. 2015), resulting in the loss of highly valuable habitats and related species. Cutaway peatlands are areas where the ecosystem has been severely damaged by drainage followed by removal of the natural vegetation, the active peat-forming layer (acrotelm) and most of the peat deposit (catotelm).

Most research on the recovery of mire vegetation in cutaway peatlands has concentrated on reinstating mire plant communities or spontaneous revegetation on *Sphagnum* peat (Gorham & Rochefort 2003, Poschlod *et al*. 2007, Triisberg *et al*. 2013, González & Rochefort 2014). Spontaneous revegetation in cutaway peatlands with residual *Sphagnum* peat is a fairly well-studied topic. In most cases, environmental variables such as water table, chemical properties of soil water (pH, macroelements, nutrients), residual peat depth, microtopography and decomposition rate have being investigated (e.g. Lanta *et al*. 2004, Poschlod *et al*. 2007, Triisberg *et al*. 2013).

Numerous studies have also demonstrated the results of applying management measures to restore drained or traditionally mowed and grazed fens (Güsewell *et al*. 2000, Güsewell & Le Nédic 2004, Klimkowska 2008, Klimkowska *et al*. 2010, Hedberg *et al*. 2014) and, lately, increasing attention has been paid to restoring fens by removing the eutrophic topsoil (Hedberg *et al*. 2014, Evasdotter 2011, Klimkowska *et al*. 2015). Fewer studies have focused on the restorability of cutaway peatlands with residual fen peat, although there have been several studies on cutaway fens in Canada (Cobbaert *et al*. 2004, Graf 2008, Graf & Rochefort 2008, Malloy & Price 2014) including field and greenhouse experiments on fen plant regeneration (Graf & Rochefort 2010). Studies of spontaneous revegetation on cutaway peatlands with residual fen peat (especially in alkaline conditions) are still rare. Especially, almost no published data are available concerning the variability of abiotic conditions and vegetation, apart from Canadian experience.

Cutaway peatlands have potential to recover as valuable habitats, and thus to partially compensate for the loss of natural fen areas and reduce fragmentation effects. However, the potential for restoring fens on cutaway peatlands is often under-estimated, at least in eastern Europe. This is partly due to lack of knowledge about the abiotic conditions and species diversity of abandoned peat extraction sites and their restorability. Also, there are no clear legal responsibilities for land reclamation on cutaway peatlands in former Soviet countries that were abandoned after land reform. Often, there is interest in other after-uses such as afforestation and biofuel plantations.

In this article we analyse the situations of several cutaway peatlands in Latvia which were abandoned without any intentional restoration measures, by exploring the current spontaneously recovered

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vegetation and some environmental variables. By analysing data from six cutaway peatlands with residual fen peat, we attempt to answer the following questions:

(1) What is the result of spontaneous revegetation in cutaway fens?

(2) Can the succession lead to valuable fen habitat?

(3) What criteria can be used to define a successful result of self-recovery of fen vegetation?

METHODS

Study sites

Six cutaway peatlands in Latvia were studied (Figure 1). These mires were originally ombrotrophic bogs or fens which had been extracted using the vacuum harvesting method. Peat extraction ceased 20–60 years ago, and no restoration measures were applied at that time or subsequently. The original vegetation of the sites and their vicinities was completely destroyed by drainage and peat extraction and no historical vegetation records were available, making it impossible to determine their natural condition. The thickness of the residual peat layer ranged from a few centimetres to 1–2 metres. In all cases, the conditions were similar to those of groundwater-fed fens (the residual peat layer consisted of fen peat and the substrate reactions were slightly acidic) because the ombrotrophic bogs had been extracted down to fen peat. The conditions are summarised in Table 1.

Vegetation plots

The vegetation was described using the Braun-Blanquet method (Braun-Blanquet 1965) in 5 × 5 m plots (total 155 sample plots). At five sites the plots were located on three separate transects of ten plots (10 m distance between the closest edges of plots). Thus, there were 30 plots in each study site except Elles purvs, which had a total of only five plots in a single transect (due to time and laboratory limits). The transects were located within typical areas for the particular site but not in areas that were completely overgrown with forest, and ran parallel to the cross drains. All taxa of vascular plants, mosses and lichens and their cover (%) were recorded once during the vegetation season (June to September) of 2014. Species were either identified in the field or (for most of the bryophytes and lichens) samples were taken and identified in the laboratory. Nomenclature follows Gavrilova & Šulcs (1999) for vascular plants, Āboliņa (2001) for mosses and Piterāns (2001) for lichens. The ecological character of species and their affiliation to certain habitat types was determined by

Figure 1. Locations of the study sites within Latvia.

applying generalised habitat types using literature sources (e.g. Eurola *et al*. 1984, Atherton *et al*. 2010, Priedītis 2015).

Environmental variables

For each sample plot, the following variables were recorded: (1) depth of residual peat (measured up to 100 cm using a peat corer); (2) degree of peat humification (von Post scale); (3) year of abandonment/last disturbance (after 2010, 2000–2010, 1990s, 1980s, 1970s, 1960s, and earlier; data gathered from air photos, maps and other sources); (4) substrate moisture (subjective classification: dry all year, seasonally fluctuating water table (temporarily wet), permanently wet, seasonally flooded by shallow water, permanently covered with shallow water); (5) microtopography (flat, gently sloping, gently undulating, depression, open water, hummocks); (6) soil water pH, measured once during our study in boreholes, using a portable pH tester (Hanna HI 938127–HI 98128); (7) electrical conductivity (EC) of soil water, measured in boreholes by portable tester (Hanna HI 98303); (8) cover of dead litter, visually estimated in %; (9) shading (visually estimated in the field using relative units: full light, partly shaded).

Soil water samples were taken from boreholes, the number of samples varying from two to 30 *per* site depending on the availability of water close to the peat surface. The data for water samples taken at Strēļu purvs were, regrettably, lost.

The elements sodium, magnesium, potassium and calcium were determined by atomic absorption spectrometry (Perkin Elmer *AAnalyst 200*, flame type air-C_2H_2). The concentration of phosphate was determined colorimetrically (Hach-Lange UV/Vis-spectrophotometer *DR 5000*). The measurements of phosphate concentration were performed according to the ascorbic acid method described in the *Standard Methods for the Examination of Water and Wastewater* (Eaton *et al*. 2005).

Table 1 Short description of the study sites.

Site name	Residual peat type	Humification (von Post)	Substratum	Current use	Peat extraction ceased (decade)	Number of sample plots
Praviņu purvs	Highly decomposed fen peat	H 7–8	Sand deposits	Abandoned	1970s	30
Strēļu purvs	Moderately to highly decomposed fen peat	H 5–7	Sand deposits	Partly in use	1990s	30
Labais purvs	Highly to poorly decomposed fen peat	H 3–9	Sand deposits	Abandoned	1960s	30
Umuļu purvs	Moderately to highly decomposed fen peat	H 4–6	Sand deposits, admixture of pebbles, boulders; calcareous spring deposits, small alkaline spring discharges	Abandoned	1980s	30
Ķirbas purvs	Moderately decomposed fen peat	H 5–6	Sand deposits	Abandoned	1990s	30
Elles purvs	Moderately decomposed fen peat	H 5–6	Sand deposits	Abandoned	1970s	5

Data analysis

The vegetation (155 sample plots, 222 taxa) was classified into vegetation units according to the similarity of species composition using two-way indicator species analysis (TWINSPAN; Hill 1979) with the following constraints: minimum group size = 2; maximum number of indicator species = 5; pseudo-species cut levels 0, 2, 5, 10, 20; three levels of division. The cover (%) data were used. Indirect ordination was performed using the Detrended Correspondence Analysis (DCA) method (PC-ORD 5.0; McCune & Mefford 1999), rescaling the axes but without down-weighting rare species. Down-weighting the rare species would cause loss of important ecological information, as these rare species indicate the specific conditions in a particular site (Poos & Jackson 2012). In detrending by segments the default option (26 segments) was applied. Pearson correlation coefficients between the environmental variables and DCA axes 1 and 2 were calculated and used for descriptive purposes.

RESULTS

Plant species and communities

In total, 222 taxa were recorded in the vegetation plots: 169 vascular plant taxa (68 % of the total number of taxa recorded), 63 bryophyte taxa (28.4 %), and eight lichen taxa (3.6 %). The majority of the vascular plant species were typical for mires (predominantly fens, fens/wet grasslands and bogs) or had wider ecological amplitude, being present also in mesic to dry grassland vegetation types. A fairly large proportion of species were ruderals or unspecific (occurring in different habitats, predominantly in mesic conditions) (Figure 2). Approximately 20 % of the species (mostly fen and grassland species) were typical for alkaline soils (alkaline fens and grasslands), 15 % were typical for acidic environments (bogs, heaths) and the other 65 % had fairly wide tolerance except for highly alkaline or acidic environments.

Eight plant communities were distinguished according to similarity in species composition using TWINSPAN: (1) *Agrostis canina*-*Luzula multiflora* community, (2) *Molinia caerulea* community, (3) alkaline fen pioneer community, (4) *Cladium mariscus* community, (5) *Rhynchospora alba*-*Drosera* community, (6) *Carex lasiocarpa* community, (7) *Juncus effusus*-*Sphagnum squarrosum* community, and (8) *Viola palustris*-*Sphagnum* community. The names for the communities reflect the dominant, constant species or genera. A short description of the abiotic conditions and key species (diagnostic, constant and ecologically specific and/or rare species) for each plant community is given in Table 2.

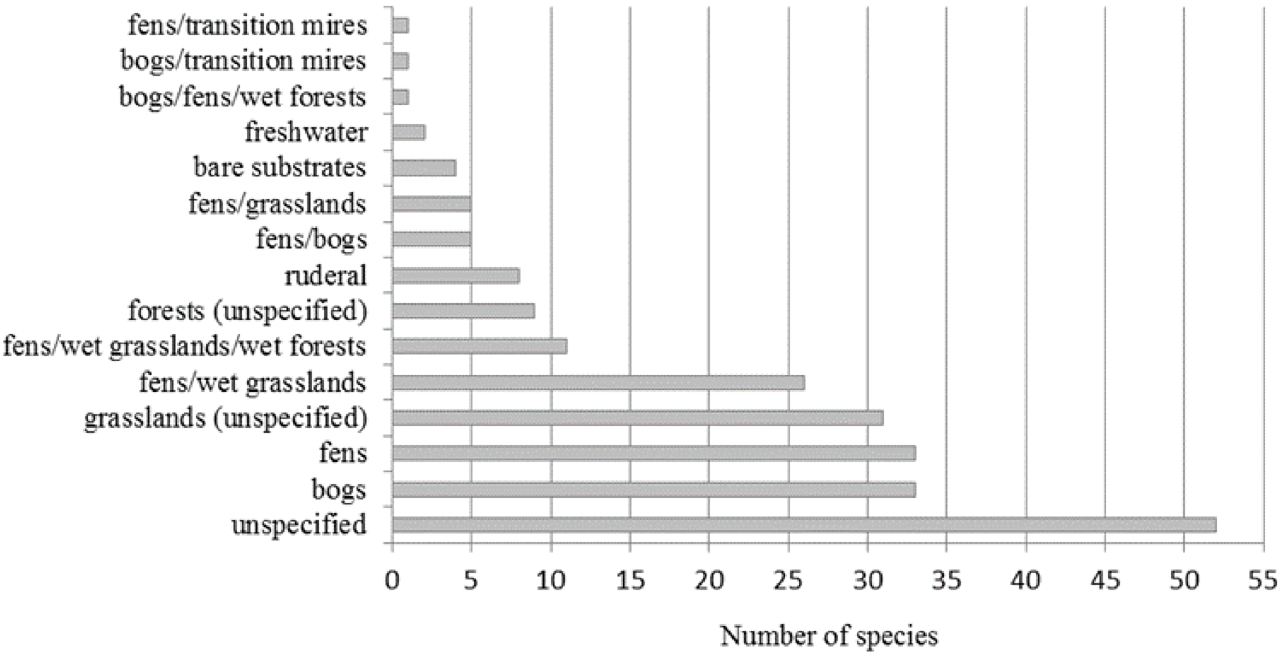

Figure 2. Summary of affiliations to certain habitat types of the plant and lichen species found in the studied cutaway fens.

Table 2. Plant communities according to TWINSPAN division.

Plant community	**Percentage of samples** (N = 155)	**Site(s)**	**Substrate conditions**	**Humification (von Post)**	**Diagnostic species**	**Constant species** Generalists* (ecologically plastic species) are underlined	**Ecologically specific and/or rare species (in the study sites and/or at country-scale)**
Agrostis canina-Luzula multiflora community (AGRLUZ)	18.7 % 29	Umuļu purvs	Dry to temporary moist, slightly to moderately well decomposed fen peat	4–6	*Agrostis canina*, *Cerastium semidecandrum*, *Cladina chlorophea*, *C. fimbriata*, *C. furcata*, *C. glauca*, *C. squamata*, *C. subulata*, *Eupatorium cannabinum*, *Holcus lanatus*, *Hypericum perforatum*, *Leontodon autumnalis*, *Luzula multiflora*, *Pilosella officinarum*, *Rumex acetosella*, *Sagina nodosa*	*Calamagrostis epigeios*, *Campylopus introflexus*, *Cladonia* spp., *Eriophorum polystachion*, *Phragmites australis*, *Polytrichum juniperinum*	
Molinia caerulea community (MOLCAE)	25.2 % 39	Praviņu purvs, Ķirbas purvs, Strēļu purvs	Dry to temporary moist (fluctuating water table), slightly to highly decomposed fen peat	5–8	*Cladina chlorophea*, *C. fimbriata*, *C. furcata*, *C. glauca*, *C. squamata*, *C. subulata*, *Festuca ovina*, *Molinia caerulea*	*Agrostis canina*, *Campylopus introflexus*, *Carex lepidocarpa* or *C. scandinavica* (*Carex flava* group), *Linum catharticum*, *Luzula multiflora*, *Pilosella officinarum*, *Phragmites australis*, *Polytrichum juniperinum*, *Trichophorum alpinum*	*Carex flacca*, *C. panicea*, *C. ornithopoda*
Alkaline fen pioneer community (ALKFEN)	33.5 % 52	Praviņu purvs Labais purvs, Ķirbas purvs, Strēļu purvs	Moist to waterlogged peat substrate, moderately to well decomposed fen peat	5–8	*Campylium stellatum*, *Carex lepidocarpa* or *C. scandinavica* (*Carex flava* group)	*Juncus articulatus*, *Linum catharticum*, *Trichophorum alpinum*, *Triglochin palustre*	*Carex panicea*, *Epipactis palustris*, *Fissidens adianthoides*, *Myrica gale*, *Pinguicula vulgaris*, *Primula farinosa*, *Schoenus ferrugineus*
Cladium mariscus community (CLAMAR)	5.8 % 9	Praviņu purvs, Labais purvs	Moist to waterlogged peat substrate, highly decomposed fen peat	7–9	*Campylium stellatum*, *Carex lepidocarpa*, *Cladium mariscus*, *Drepanocladus revolvens*, *Fissidens adianthoides*, *Scorpidium scorpioides*, *Utricularia minor*	*Comarum palustre*, *Galium palustre*, *Lycopus europaeus*, *Lysimachia vulgaris*, *Phragmites australis*, *Thelypteris palustris*, *Trichophorum alpinum*	*Carex diandra*, *Drepanocladus cossonii*, *Juncus articulatus*, *Liparis loeselii*, *Scirpus tabernaemontani*, *Taraxacum palustre*, *Triglochin palustre*

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Table 2 continued

Plant community	**Percentage of samples** (N = 155)	**Site(s)**	**Substrate conditions**	**Humification (von Post)**	**Diagnostic species**	**Constant species** Generalists* (ecologically plastic species) are underlined	**Ecologically specific and/or rare species (in the study sites and/or at country-scale)**
Rhynchospora alba-Drosera community (RHYDRO)	6.5 % 10	Labais purvs	Moist to waterlogged peat substrate, highly decomposed fen peat	7–9	*Drosera anglica, D. rotundifolia, Oxycoccus palustris, Rhynchospora alba, Sphagnum cuspidatum, Warnstorfia fluitans*	*Calluna vulgaris, Carex cinerea, Comarum palustre, <u>Eriophorum polystachion</u>, <u>Phragmites australis</u>, <u>Polytrichum juniperinum</u>, Sphagnum magellanicum, S. palustre*	*Lycopodiella inundata, Riccardia latifrons*
Carex lasiocarpa community (CARLAS)	3.9 % 6	Labais purvs	Waterlogged peat substrate, slightly decomposed fen peat, newly developed acrotelm	4	*Carex lasiocarpa*	*Carex rostrata, <u>Phragmites australis</u>, <u>Eriophorum polystachion</u>, Sphagnum squarrosum, S. fallax,* other *Sphagnum* spp.	
Juncus effusus-Sphagnum squarrosum community (JUNSPH)	3.2 % 5	Labais purvs	Waterlogged peat substrate, moderately decomposed fen peat, newly developed acrotelm	5	*Carex cinerea, C. rostrata, Juncus effusus, Naumburgia thyrsiflora, Sphagnum squarrosum, S. palustre, Viola palustris*	*Agrostis canina, Calliergon gigantea, Calliergonella cuspidata, Galium palustre, Lysimachia vulgaris, <u>Phragmites australis</u>, Salix myrsinifolia*	
Viola palustris-Sphagnum community (VIOSPH)	3.2 % 5	Elles purvs	Waterlogged peat substrate, slightly decomposed fen peat, newly developed acrotelm	4	*Aulacomnium palustre, Calliergonella cuspidata, Climacium dendroides, Deschampsia cespitosa, Festuca rubra, Filipendula ulmaria, Galium palustre, Galium uliginosum, Lycopus europaeus, Lysimachia vulgaris, Peucedanum palustre, Sphagnum warnstorfii, S. rubellum, S. russowii, S. teres, S. warnstorfii, Viola palustris*	*Agrostis canina, Calamagrostis canescens, Calliergonella cuspidata, Carex cinerea, C. rostrata, Comarum palustre, Dryopteris cristata, Epilobium adenocaulon, <u>Polytrichum juniperinum</u>, Potentilla erecta, Rumex acetosa*	

* Generalists - in cutaway peatlands, often present at different moisture conditions and on different peat substrates, on both *Sphagnum* peat and fen peat.

Factors affecting the plant communities

The plant communities were ordinated using the DCA method, and the first two axes were used to depict the distribution of the plots in the ordination space. The percent variance in the distance matrix represented determination coefficients, which show correlations between ordination distances and distances in the original space (McCune & Grace 2002) for the ordination axes as follows: $r^2 = 0.282$ for Axis 1, $r^2 = 0.130$ for Axis 2. DCA ordination helped to identify the factors that potentially affect species composition. The communities were differentiated mostly by three factors: substrate moisture, soil water pH, and time since peat extraction ceased (Table 3, Figure 3 and Figure 4). Other environmental variables used in the study were of minor importance.

The ordination using the affiliation to plant community and site as separate grouping variables shows that the vegetation composition is strongly related to site-specific factors as suggested by DCA ordination results (Figure 3 and Figure 4). This means that, in terms of species composition, the sample plots at the same site are more similar to each other than to plots with more or less similar environmental conditions (moisture, age, pH *etc*.) in the other sites.

Table 3. Correlation of environmental variables with DCA Axes 1 and 2 (N = 155).

Environmental variables	DCA Axis 1	DCA Axis 2
Age since abandonment	0.47	0.35
Moisture	0.47	0.49
Peat decomposition rate	0.08	0.44
Soil water pH	-0.57	0.01
EC of soil water	-0.24	0.36
Depth of residual peat layer	-0.33	-0.01
Microtopography	0.32	-0.02
Shading	-0.149	-0.24
Cover of dead litter	-0.06	0.44

Physical and chemical properties of soil water

The physical and chemical properties of soil water were summarised for each study site except Praviņu purvs and Strēļu purvs (where some data were missing) and each community (Table 4). The properties were highly variable among sites, among similar plant communities at different sites and, in most cases, also at the same site and in the same plant community.

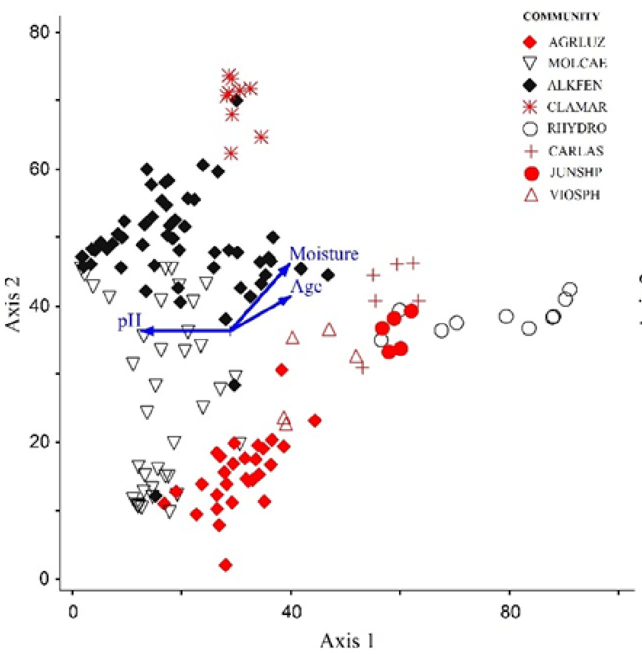

Figure 3. DCA ordination of vegetation plots, grouped according to their affiliations to plant communities (TWINSPAN division, see Table 2). For abbreviations used in the Figure, see Table 2.

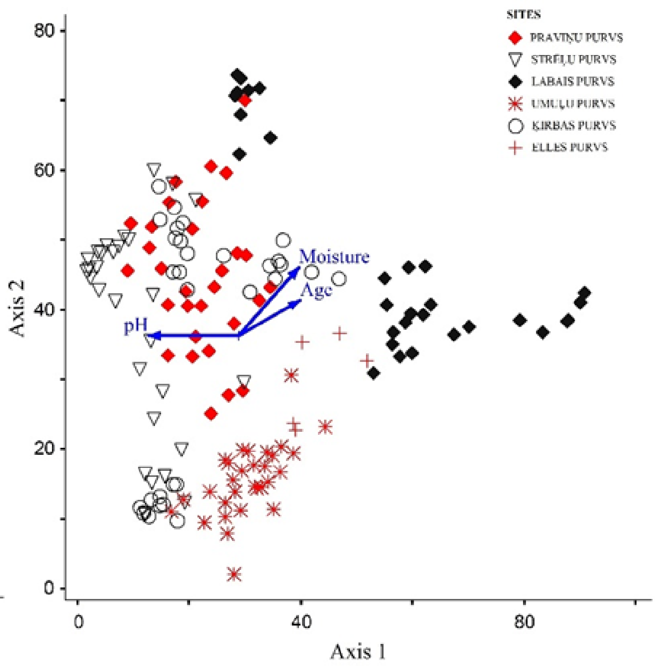

Figure 4. DCA ordination of vegetation plots using the sites (geographical location) as the grouping variable.

Table 4. Physical and chemical properties (mean values (± SD)) of soil water samples collected from the study sites. N = number of samples.

	Rich fen communities										*Poor fen communities*		
	MOLCAE*	ALKFEN	MOLCAE	ALKFEN	AGRLUZ	MOLCAE	MOLCAE	ALKFEN	VIOSPH	CLAMAR	RHYDRO	CARLAS	JUNSPH
Site	Praviņu purvs	Praviņu purvs	Strēļu purvs	Strēļu purvs	Umuļu purvs	Umuļu purvs	Ķirbas purvs	Ķirbas purvs	Elles purvs	Labais purvs	Labais purvs	Labais purvs	Labais purvs
pH	6.98 (±0.78)	7.18 (±0.56)	6.30 (±0.25)	6.68 (±0.33)	6.72 (±0.37)	6.11 (±0.00)	6.79 (±0.02)	7.19 (±0.36)	6.34 (±0.38)	6.11 (±0.51)	4.76 (±0.32)	5.29 (±0.12)	5.13 (±0.14)
N	9	21	16	14	29	1	12	18	5	9	10	5	5
EC (µS cm^{-1})	572.36 (±123.63)	664.09 (±186.01)	283.56 (±84.20)	312.21 (±154.21)	482.23 (±131.17)	167 (±0.00)	182.25 (±0.87)	353.11 (±157.48)	130.80 (±70.56)	1048.78 (±734.60)	92.80 (±79.33)	31.17 (±12.89)	53.60 (±9.07)
N	9	21	16	14	29	1	12	18	5	9	10	5	5
PO_4^{3-} (mg dm^{-3})	-	-	-	-	0.192 (±0.358)	0.002 (±0.00)	0.015 (±0.0009)	0.006 (±0.003)	0.049 (±0.031)	0.798 (±2.339)	0.020 (±0.024)	0.005 (±0.006)	0.204 (±0.256)
N	-	-	-	-	29	1	2	4	5	9	7	6	5
Na (mg L^{-1})	-	4.08 (±2.22)	-	-	3.44 (±0.87)	3.26 (±0.00)	2.97 (±0.09)	2.49 (±0.60)	0.85 (±0.41)	2.47 (±1.21)	1.63 (±1.03)	0.91 (±0.25)	1.65 (±0.36)
N	-	2	-	-	29	1	2	4	5	9	7	6	5
Mg (mg L^{-1})	-	22.63 (±14.31)	-	-	8.34 (±3.61)	4.23 (±0.00)	3.13 (±0.02)	12.79 (±1.06)	2.14 (±0.67)	13.72 (±6.50)	2.79 (±2.46)	1.58 (±0.52)	1.59 (±0.22)
N	-	2	-	-	29	1	2	4	5	9	7	6	5
K (mg L^{-1})	-	1.35 (±0.91)	-	-	1.06 (±2.05)	0.14 (±0.00)	1.00 (±0.04)	0.71 (±0.35)	1.69 (±2.24)	1.04 (±0.87)	2.50 (±3.69)	1.09 (±1.13)	1.16 (±0.29)
N	-	2	-	-	29	1	2	4	5	9	7	6	5
Ca (mg L^{-1})	-	101.78 (±61.26)	-	-	87.15 (±38.26)	28.40 (±0.00)	39.91 (±0.83)	129.04 (±13.35)	31.10 (±7.57)	276.95 (±219.41)	13.96 (±9.67)	12.37 (±8.26)	10.33 (±1.56)
N	-	2	-	-	29	1	2	4	5	9	7	6	5

* Abbreviations for plant community names (see also Table 2): AGRLUZ = *Agrostis canina-Luzula multiflora* community, ALKFEN = alkaline fen pioneer community, CARLAS = *Carex lasiocarpa* community, CLAMAR = *Cladium mariscus* community, JUNSPH = *Juncus effusus-Squagnum squarrosum* community, MOLCAE = *Molinia caerulea* community, RHYDRO = *Rhynchospora alba-Drosera* community, VIOSPH = *Viola palustris-Sphagnum* community.

According to the water properties, the young fens formed on cutaway peatlands could be classified into two conditional groups by using EC values as a robust borderline: *rich fens* (EC > 100 μS cm^{-1}) and *poor fens* (EC < 100 μS cm^{-1}). The greatest variation was found within one area in Labais purvs, where both rich and poor fen conditions were present. However, in most cases, the variation within a single site was rather unimportant.

Rich fen communities were associated with relatively high pH value (generally > 6) and a wide range of EC (generally 130 to >1000 μS cm^{-1}), being richer in macroelements, especially calcium. The plant communities that occurred in conditions characteristic for *rich fens* were as follows: *Agrostis canina*-*Luzula multiflora* community, *Molinia caerulea* community, alkaline fen pioneer community, *Cladium mariscus* community, *Viola palustris*-*Sphagnum* community.

Poor fens had acidic to slightly acidic waters (pH generally 4.7–5.3) with EC generally 30–93 μS cm^{-1}. In comparison to rich fens, they were poorer in macroelements. In our study, these conditions were found to be suitable for the *Rhynchospora alba*-*Drosera*, *Carex lasiocarpa* and *Juncus effusus*-*Sphagnum squarrosum* communities.

DISCUSSION

Vegetation patterns

Studies of, and restoration plans for, spontaneously recovering cutaway peatlands in fen-like and especially alkaline conditions are scarce in Europe (e.g. Tratt 1997, Anon. 2008, Anon. 2010). Perhaps one of the reasons is the rarity of examples of cutaway peatlands with residual layers of fen peat which have not been transformed into water bodies, agricultural land or woodlands. This means that it is hardly possible to compare our results with those of other studies, making any generalisation difficult. However, the results of spontaneous re-vegetation and plant species composition observed in our study sites are similar to those at some other cutaway sites in Europe, although the abiotic conditions are highly variable and cannot be generalised. For example, Kreshtapova *et al*. (2003) mentioned similar species composition in recently abandoned cutaway peatlands in European Russia with different water table levels from those observed in our study sites: predominantly grasses (e.g. *Calamagrostis* spp., *Festuca ovina*, *Molinia* spp.) at sites with low water table (> 0.9 m below the peat surface) and sedges (e.g. *Carex rostrata*, *C. lasiocarpa*, *C. diandra*) and willows at sites with higher water table (within 0.4 m of the peat surface). In patches with stagnant water, *Phragmites australis* and *Sphagnum* prevailed. A study of spontaneous succession in peat milling areas by Konvalinková & Prach (2010) revealed similar vegetation patterns to those observed in our study. Hochegger *et al*. (2013) suggested that, in Austria, a cutaway peatland can turn into a valuable alkaline fen, though of secondary origin and different from the original by being less stable and more vulnerable to tree invasion. Notes from Irish sites suggest that some cutaway peatlands are suitable for establishment of fen vegetation, including alkaline fen communities, if the peat is extracted down to the bottom (Anon. 2010). Tratt (1997) studied the vegetation development of fens, including cutover fens, in the Scottish Borders and her results show that the cutover peatlands can be well recovered in terms of vegetation development, although her study sites were abandoned a long time ago and were extracted using traditional peat cutting methods, which caused different impacts from those of the vacuum harvesting method that was applied in our study sites.

Our results are hardly comparable to fen restoration trials on cutaway peatlands in North America (e.g. Graf *et al*. 2008, Graf & Rochefort 2008) because the climate, bedrock and site-specific conditions are different. In most of our sites the substrate is richer and more alkaline than in Canadian sites with residual fen peat, where *Sphagnum*-dominated poor fen vegetation tends to dominate (e.g. Cobbaert *et al*. 2004).

The character of spontaneous vegetation in cutaway fens can, to some extent, be predicted according to the properties of residual peat, moisture conditions and other factors. But at the same time, generalisations are difficult. The results of our study in six cutaway fens show that the plant communities are highly variable among sites, many of them being strongly related to abiotic conditions at the site. An alkaline fen pioneer community with similar species composition formed by calciphilous sedges and brown mosses was found in several sites (Praviņu purvs, Strēļu purvs, Labais purvs). A *Molinia caerulea* community with similar species composition was found both in Ķirbas purvs and Strēļu purvs. The rest of the communities were more site-specific and occurred only within a single fen where conditions differed from those at other sites (Figure 3–4).

The key factors determining the succession of vegetation and vegetation types in cutaway fens are water table and soil water pH. The third most significant variable, age, is closely (but not always) related to moisture conditions. The site often becomes wetter through time, as the drainage system stops functioning due to lack of maintenance. Most probably, the current vegetation patterns do not result from unidirectional succession. The hydrological conditions may have changed gradually, or even have changed several times, in the post-abandonment period. The shallow-water areas were probably colonised by plants when they were drier, and were gradually becoming wetter as the sub-surface drainage system became clogged.

The roles of remnants of the mire vegetation, and of surrounding landscapes with distinct floristic composition, were not taken into account when analysing the data. Nevertheless, these might be crucial in determining plant species composition (Tratt 1997, Konvalinková & Prach 2010, Lamers *et al*. 2015). In our study the richest communities, which included numerous rare species, were found on Labais purvs in Ķemeri National Park (alkaline fen pioneer community, *Cladium mariscus* community, *Rhynchospora alba-Drosera* community; Table 2), one of the most species-rich areas in Latvia in terms of alkaline fens. It might be that natural succession leads from a secondary alkaline fen community to a *Cladium mariscus* community as was observed in two of the study sites (Labais purvs and Praviņu purvs). However, *Cladium mariscus* is a rare species so it is probable that it can occur only on cutaway sites where it was present before peat extraction or is abundant in the surrounding landscape. Thus, we cannot generalise that the *Cladium mariscus* community can develop naturally in all areas even if the conditions are similar to those in our study sites.

According to our results, the time since peat extraction ceased is one of the most significant factors affecting the plant communities. Age differentiates the composition of plant communities. However, the plant communities in secondary fens are not stable, and are still under development for up to 50–60 years after abandonment. Their dynamics might be related to both age and abiotic conditions that change along with age. According to our observations, in most cases the water table fluctuates more widely, and the peat surface is drier, in recently abandoned cutaway peatlands than in older sites. This is related to the functionality of drainage systems, which become clogged through time. Thus, the vegetation of younger sites was composed predominantly of grassland and ruderal species (e.g. *Agrostis canina-Luzula multiflora* community at Umuļu purvs, *Molinia caerulea* community at Strēļu purvs and Ķirbas purvs) with a small proportion of mosses (or sometimes dominance of *Campylopus introflexus*) and presence of lichens, whereas older sites had fen and bog species, higher moss richness, and no lichens.

The variation of communities within a single site with relatively uniform abiotic conditions (pH, EC, nutrients) suggests that the early successional stage with dry grassland species might turn into a secondary alkaline fen community if the water table rises. The effect of age is such that in young secondary alkaline fen communities (e.g. Strēļu purvs, Ķirbas purvs) brown mosses (*Drepanocladus* spp., *Scorpidium scorpioides*, *Fissidens adianthoides*) are rare or absent. In older cutaway fens with alkaline conditions (in our study, Labais purvs and Praviņu purvs), which are often wetter, the bryophyte cover can be rich in brown mosses, and the structure of the vegetation can be similar to that in natural alkaline fens with communities belonging to associations of *Schoenetum ferruginei*, *Cladietum marisci* and *Caricetum lasiocarpae* (Tabaka 1960, Salmiņa 2009). Similarly, the variation along the moisture gradient within a single site suggests that the species-poor *Molinia caerulea* community also turns into the secondary alkaline fen community, which is richer in species, when the peat surface becomes wetter. Along with succession, the secondary alkaline fen community might turn into a *Cladium mariscus* community similar to those found in natural conditions in Latvia (Tabaka 1960, Salmiņa 2009) if propagule sources are available. If the water table does not rise, the dry grassland-like communities might turn into dry secondary birch or mixed *Pinus sylvestris-Betula pubescens* stands with the ground layer dominated by *Molinia caerulea* and/or *Campylopus introflexus*, *Polytrichum* spp. and/or lichens (*Cladonia* spp.).

The succession of cutaway fen communities naturally leads to diversification of microtopography and other structures (formation of hummocks, accumulation of dead litter, especially in the *Cladium mariscus* community), modifies the growing conditions and causes gradual turnover of species. The accumulation of dead litter provides a kind of shelter in terms of microclimate for fen and bog mosses, but perhaps causes decline of some light-demanding small plants with pioneer strategy, e.g. *Liparis loeselii*, *Carex scandinavica* and *Lycopodiella inundata*.

Factors limiting recovery of fen vegetation

Studies in cutaway bogs and fens demonstrate that successful regeneration of mire vegetation is defined mostly by high water table, properties of residual peat and depth of residual peat layer (e.g. Graf *et al*. 2008, Triisberg *et al*. 2013). Basically, the potential vegetation type is defined by peat and soil water properties (botanical composition, decomposition rate, moisture, pH and other). For example, in a study of cutaway and cutover peatlands in the Czech Republic, Konvalinková & Prach (2010) concluded that abiotic site factors (soil pH, water table, nitrates) and geographical location are more important in determining species composition than successional age. Triisberg *et al*. (2013) found that microtopography is the main factor distinguishing the composition of the first plant communities.

The success of revegetation in vacuum harvested fen peatlands is predominantly influenced by water table (Tratt 1997, Konvalinková & Prach 2010, Malloy & Price 2014). Fen vegetation can develop only if the water table reaches the peat surface. Fluctuations of the water table occur in all cases, but in sites where the drainage system is no longer functional, the amplitude of fluctuations is smaller than in sites with well-functioning drainage systems. Also in our study sites, we found substrate moisture to be among the most significant environmental variables (Table 2, Figure 3 and Figure 4).

The species composition and potential vegetation are strongly influenced by pH and water chemistry (as suggested by the example of Labais purvs, they can vary from poor fen to extremely rich fen within a single area). The content of calcium is of particular importance, being strongly linked to pH. Thus, the water properties (especially pH, EC and calcium) can be used as the basic factors for predicting the directions of spontaneous vegetation development before raising the water table in recently abandoned peat milling fields. In sites with high pH and high calcium content it is highly probable that calciphilous vegetation will develop. High calcium content can be influenced by local peculiarities, e.g. alkaline groundwater discharges (Tratt 1997) or dolomite bedrock close to the residual peat layer having a positive effect on the formation of calciphilous vegetation.

In our study sites we did not find the thickness of the residual peat layer to be an important variable as found, for example, by Triisberg *et al*. (2013). These authors suggested that milled peat fields with thin (< 2.3 m) and well-decomposed residual peat should be restored toward fen vegetation types, whereas sites with thick (> 2.3 m) and less-decomposed residual peat should be restored toward transitional mires or raised bogs. In our opinion, the thickness of the peat layer cannot be used in a generalised way because the fen peat layer can be of different thicknesses or sometimes the acidic *Sphagnum* peat lies directly on mineral ground.

The role of mineral subsoil might be crucial, especially when the layer of residual peat is thin (Picken 2006). Mineral subsoil was not studied in our case (predominantly sand deposits, with admixture of calcareous spring deposits or still-active spring discharges in a couple of sites). But, as observed in our study sites and also noted by Price *et al*. (2003), fen vegetation may also develop in cases when the peat layer has been completely removed from part of the cutaway peatland. Also in such cases the basic variables predicting the outcome are pH and EC (Picken 2006).

However, natural alkaline fens are poor in phosphorus and soluble phosphorus is sparingly formed (El-Kahloun *et al*. 2003, Rydin & Jeglum 2013). In peat milling fields that have been abandoned for a long time without any restoration measures, after rewetting the mineralised peat can release soluble phosphorus and other substances leading to less desirable directions of vegetation development (Meissner *et al*. 2008, Zak *et al*. 2010). This can increase the availability of soluble phosphate, elevating primary productivity and promoting eutrophication and associated problems (Cabezas *et al*. 2013). Our results show high variability of phosphate, which was most probably influenced by sampling (higher concentrations in wetter sites with surface water, and lower concentrations in subsurface water at sites with lower water table). Therefore, at least in this study, it cannot be used as an indicator. This must be taken into account, but further studies are necessary to clarify the intricate biogeochemistry of fens.

Criteria to define successful recovery of fen vegetation

Vegetation is the major indicator of success or failure of fen recovery in cutaway peatlands. The presence of typical species for alkaline fens/wet grasslands as opposed to the generalist species of degraded peatlands and their assemblages indicate successful recovery. We suggest that the species listed in Table 2 (constant, diagnostic, ecologically specific, rare species) can be used as indicators for revegetation success or failure. The first two communities listed in Table 2 (*Agrostis canina*-*Luzula multiflora* and *Molinia caerulea* communities) could be regarded as indicators of failure in terms of fen recovery. They do not represent typical communities for fens and are not able to contribute to the recovery of fen or bog functions (peat formation, accumulation of water and organic matter).

As suggested by our results, the plant communities are highly site-specific, therefore the indicators cannot be generalised, e. g. for a monitoring scheme. The diagnostic species of communities (Table 2) could be used as indicators; but the constant species, especially the generalists, could not. Without a context (community) the presence of certain species might be misleading because, due to a relatively wide tolerance to abiotic conditions (especially water table), they can indicate both successful fen recovery and continuous degradation. For example we do not recommend the use of *Molinia caerulea*, *Trichophorum alpinum*, *Eriophorum polystachion* or *Phragmites australis* as indicators of fen recovery, even though they are frequent fen species with wide distributions.

Can secondary fens be valuable habitats?

Secondary fens in cutaway peatlands can develop species-rich plant communities that include specialists of fens, transition mires and bogs as well as rare species (Table 2). In our study, at least three sites – Labais purvs, Praviņu purvs and Elles purvs, abandoned in the 1960s and 1970s, represent excellent examples of rich alkaline fen communities sheltering rare plant species (e.g. *Carex scandinavica*, *Cladium mariscus*, *Liparis loeselii*, *Pinguicula vulgaris*, *Primula farinosa*, *Schoenus ferrugineus*, *Taraxacum palustre*).

Using solely the presence of certain species as indicators is somewhat risky, since many species are unspecific, have relatively wide ecological tolerance, or might occur by accident. The presence of rare (or protected, or threatened) plant species is often a good sign, but presence alone is not always sufficient to judge the site ‘valuable’. Therefore, it should be combined with species communities, which provide deeper insights about the processes of further fen degradation or recovery. If we use rare, threatened species as indicators, we should be sure *what* they indicate.

Cutaway peatlands with residual fen peat still remain a poorly studied topic, particularly in Europe. Therefore, more studies will be necessary to discover which factors affect spontaneous vegetation under different conditions and the restorability of these sites.

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