Initiation of microtopography in re-vegetated cutover peatlands: evolution of plant species composition

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Abstract

Questions: How has plant species composition changed following initiation of microstructures in re-vegetated cutover peatlands? How many years are required for plant species composition of re-vegetated cutover peatlands to resemble natural boreal bogs?

Location: Newly formed *Sphagnum* carpets on restored, cutover peatlands (in Canada) or re-vegetated spontaneously after site abandonment (in Estonia) and on undisturbed natural bogs nearby.

Methods: Plant frequencies (point intercept method) and abundances (vegetation quadrats) were assessed along linear transects. At each assessment point, moss surface height was measured relative to a local reference point (lowest point on a given transect) to associate frequencies or abundances to a position in the gradient of microtopography. PCAs (separately for Canada and Estonia) were conducted to follow evolution of plant species frequency in the gradient of microtopography in re-vegetated sites and similarity with those of natural peatlands. In Canada, regressions were also performed to estimate relationships between moss surface height and vascular plant cover (ericaceous shrubs and Cyperaceae) as well as time required for vascular plant cover to become similar to that of natural bogs.

Results: Species composition was still dissimilar to microstructures of natural bogs 10 yr post-restoration and 70 yr post-abandonment; however, some trends were observed in re-vegetated peatlands. The greatest differences were for ericaceous species (two- to three-fold less abundant in re-vegetated peatlands), dominant Cyperaceae, and relative proportions of *Sphagnum*. In addition, hummock formation was closely related to dense (>50%) ericaceous cover.

Conclusions: All species tolerant to abiotic conditions prevailing in re-vegetated sites contributed to initiation of microtopography, although some species were found in atypical positions within the gradient of microtopography. Random events and establishment priority seemed initially to be more important in temporal evolution of microstructures than plant interactions. However, ecological restoration could effectively reduced time needed for species occurrences to approach those in natural peatlands, relative to time required for recovery of spontaneously re-vegetated peat extraction sites.

Introduction

Hummocks and hollows form an important part of microtopographical surface heterogeneity observed in almost all boreal bogs. The presence of microtopography allows an increase in biodiversity, as well as playing an important role in the carbon flux balance between peatlands and the atmosphere. The initiation and temporal resilience of microstructures can be explained in terms of factors such as water table position and meteorological conditions (Rydin 1985; Belyea 1996; Karofeld 1998), abundance of individual *Sphagnum* species, interactions between plant species (Vitt et al. 1975; Malmer et al. 1994, 2003), nutrient regimes (Damman 1978; Luken & Billings 1986) and pH (Clymo 1963). In addition, intrinsic properties and capacity to acquire water by capillarity of *Sphagnum* species affect

the thickness of the acrotelm (Nungesser 1997), and thus formation and persistence of the different microstructures that compose the hummock–hollow alternation.

The regulation of decomposition rates emerges from interactions between plant litter quality (linked in a large part by the intrinsic properties of plant species), activity of microbial communities, and a host of abiotic factors. However, peculiarities of the tissues of individual *Sphagnum* species, but not environmental conditions within the different microstructures, clearly influence the early stages of decomposition (from years to decades), as turnover rates of labile and recalcitrant organic matter pools differ between *Sphagnum* species (Turetsky et al. 2008). As studied re-vegetated cutover peatlands are relatively young (less than 30 yr, except for one site, see Table 1), intrinsic properties of *Sphagnum* mosses rather than abiotic conditions could be more important in determining decomposition rates. With depletion of the most easily degraded organic matter pools, environmental factors (temperature,

oxygen availability, water chemistry, etc.) become gradually more dominant controls on decomposition rates (Trofymow et al. 2002).

Hummock species generally have higher concentrations of decay-resistant compounds or decay inhibitors (Johnson & Damman 1993), higher cation exchange capacities (Clymo & Hayward 1982) and they invest more in structural carbohydrates (Turetsky et al. 2008) than the hollow species. In addition, a dilution effect of decay-resistant compounds in hollow species cells is associated with high growth rates (Clymo & Hayward 1982; Rydin 1993a), which are sustained by important concentrations of metabolic carbohydrates (Turetsky et al. 2008). Consequently, hummock species decompose more slowly than hollow species (Rochefort et al. 1990; Johnson & Damman 1991; Limpens & Berendse 2003).

To resist desiccation, *Sphagnum* species growing on hummocks need to transport, store and use water more efficiently than hollow species to counteract the greater

Table 1. List of the 12 peatlands investigated, showing details of the various sections, including number of points in the point intercept method and number of vegetation quadrats assessed on each part of the hummock–hollow patterning.

Site	Latitude; longitude	Type	Years since restoration or abandonment or features of natural bog	Total transect length (m)	Point intercept method			Vegetation quadrats		
					Ho	I	Hu	Ho	I	Hu
Canada										
BDB	47° 58'02″ N; 69° 25'50″ W	R	6	200	74	54	12	22	31	7
BDB	47° 58'02″ N; 69° 25'43″ W	R	7	600	199	173	49	54	86	38
CdL	47° 45'40″ N; 69° 31'11′ W	R	3	200	140	0	0	60	0	0
CdL	47° 45'52″ N; 69° 31'31″ W	R	4	200	140	0	0	60	0	0
CdL	47° 45'38″ N; 69° 31'35″ W	R	6	100	57	13	0	9	20	1
CdL	47° 45'41″ N; 69° 31'37″ W	R	7	100	41	26	3	18	10	2
CdL	47° 45'47″ N; 69° 31'33″ W	R	9	200	94	38	8	18	32	10
CdL	47° 46'06″ N; 69° 31'37″ W	R	11	200	32	21	17	6	14	10
SMM	48° 49'13″ N; 72° 10'35″ W	R	2	200	140	0	0	60	0	0
SMM	48° 49'20″ N; 72° 10'34″ W	R	3	200	140	0	0	60	0	0
SMM	48° 49'25″ N; 72° 10'40″ W	R	4	200	139	3	0	55	3	0
SMM	48° 49'28″ N; 72° 10'43″ W	R	5	200	108	31	0	28	31	1
SMM	48° 49'30″ N; 72° 10'45″ W	R	6	200	61	67	13	14	30	15
SMM	48° 49'32″ N; 72° 10'46″ W	R	7	200	57	62	21	14	31	15
Lac-St-Jean #1	48° 46'49″ N; 72° 11'02″ W	N	Without pools	100	3	19	48	4	7	19
Lac-St-Jean #2	48° 50'04″ N; 72° 10'19″ W	N	Without pools	100	2	11	57	2	1	27
Rivière-du-Loup	47° 46'59″ N; 69° 28'35″ W	N	Without pools	100	4	21	45	2	6	22
Estonia										
Rebase	59° 17'01″ N; 25° 47'48″ E	A	30	100	43	27	30	10	7	8
Viru	59° 28'44″ N; 25° 40'00″ E	A	30	100	52	42	6	10	12	3
Pilliroo	58° 37'08″ N; 25° 09'41″ E	A	70	100	32	37	31	5	10	10
Mannikjärve	58° 52'36″ N; 26° 14'52″ E	N	With pools	500	91	59	250	28	26	46
Mannikjärve	58° 52'24″ N; 26° 15'09″ E	N	Without pools	500	21	161	216	5	21	74
Nigula	58° 00'30″ N; 24° 41'36″ E	N	With pools	200	97	57	46	26	14	10
Nigula	58° 00'47″ N; 24° 42'20″ E	N	Without pools	200	36	56	108	8	14	28
Nigula	58° 00'58″ N; 24° 42'02″ E	N	With mud-bottoms	200	186	11	3	41	6	3
Ruunassoo	58° 00'38″ N; 24° 43'45″ E	N	With mud-bottoms	100	80	13	7	14	7	4

BDB, Bois-des-Bel; CdL, Chemin-du-Lac; SMM, Ste-Marguerite-Marie; R, restored peatland; A, abandoned with spontaneous re-vegetation; N, natural bog; Ho, hollows; I, intermediate habitat; Hu, hummocks.

distances from the water table (Vitt & Slack 1984; Malmer 1986; Rydin 1986) and higher evapotranspiration rates (Clymo 1973). The amplitude of hummock–hollow alternation is, therefore, dependent on the capacity of hummock species to acquire and conserve water. They show a high water retention capacity due to many intrinsic characteristics: dense capitula, spreading and hanging branches, stem leaves pointed upwards and hyaline cells to store water (Rydin & McDonald 1985). Not surprisingly, they are thus able to transport water by capillarity more effectively than hollow species (Wallén et al. 1988; Rydin 1993a). Furthermore, the higher resistance of hummock species to decomposition means that the pore network through which capillary water is acquired by the hummock as a functional unit is more persistent through time than in hollows (Rydin et al. 2006; Turetsky et al. 2008). Thus, as in the case of intrinsic properties, the variation in capacity to acquire water by capillarity between individual *Sphagnum* species plays a key role in the development of hummock–hollow microstructures.

Species in boreal bogs thus often form a particular microstructure. Dry habitats in the gradient (hummocks) are frequently created by species belonging to Section Acutifolia (e.g. *Sphagnum fuscum, Sphagnum rubellum*), whereas species from Section Cuspidata (e.g. *Sphagnum angustifolium, Sphagnum balticum* and *Sphagnum cuspidatum*) are typically restricted to wet habitats (Rydin 1997a). Despite their low decomposition rates, species from Section Sphagnum (e.g. *Sphagnum magellanicum, Sphagnum papillosum*) are unable to form the driest hummocks because their capillary water acquisition network is deficient (Limpens & Berendse 2003). However, species such as *S. angustifolium, S. magellanicum* and *S. rubellum* have fairly broad ecological amplitudes (Gignac 1992; Gauthier 2001) and occur widely within the gradient of microtopography. The majority of ericaceous shrubs (e.g. *Calluna vulgaris* in European bogs or *Kalmia angustifolia* and *Ledum groenlandicum* in Canadian bogs) prefer drier hummock conditions, whereas Cyperaceae (e.g. *Rhynchospora alba* and the majority of *Carex* spp.) are much more common in hollows, where their aerenchyma enables them to tolerate and grow in anoxic conditions. Some vascular plants also have wider ecological amplitudes; for example, *Chamaedaphne calyculata* and *Eriophorum vaginatum* can grow on more than one type of microstructure.

Even though the intrinsic properties and the capacity to more-or-less acquire water by capillarity of a number of species can determine their typical positioning within the gradient of microtopography, additional factors must also be considered as possible explanations. Random events and interactions between plants can also influence the distribution of individual species across the different microstructures and their evolution through time. First, plant establishment can be linked to random factors, such as the probability of spores or plant fragments settling on suitable habitats and distance from the nearest seed bank (Sundberg et al. 2006). Plant interactions will be most important for species distribution after establishment (Soro et al. 1999), but in some cases facilitation occurs between moss species during the establishment stage (e.g. the case of *Polytrichum strictum*, see Groeneveld & Rochefort 2005). Second, once established, pioneer *Sphagnum* species are succeeded by other species, and thus 'ecologically engineer' their own habitats (van Breemen 1995; Malmer et al. 2003). Succession within the hummock–hollow alternation of boreal bogs is primarily associated with pH and humidity gradients created by the species that are already present (Vitt et al. 1975). As the peat formed by decay-resistant species accumulates and hummock height consequently increases, species that are intolerant of drier conditions and low pH will be increasingly superseded by more tolerant hummock species. Throughout the succession, interspecific competition affects the species composition of the *Sphagnum* carpet. Finally, the life forms and architecture of vascular plants can also influence the abundance and distribution of structural units within hummock–hollow alternation by facilitating *Sphagnum* growth (Malmer et al. 1994). The usefulness of vascular plants in hummock formation and maintenance seems important, especially in drier continental climates (Pouliot et al. 2011b). Vascular plants can provide both protection and scaffolding for *Sphagnum* growth (Rydin & Jeglum 2006). Therefore, under relatively constant abiotic conditions, factors that determine species composition during the initiation of microtopography can be decisive for long-term community structure (Rydin 1997a); whereas under changing abiotic conditions, the competitive abilities of plant species are not stable and microtopography may consequently change (Limpens et al. 2003; Gunnarsson et al. 2004; Robroek et al. 2007a).

In terms of peatland time-scales, hummock–hollow alternation can develop rapidly after re-vegetation of cutover peatlands, especially in restored peatlands (in two to three decades; Pouliot et al. 2011a), but some questions remain related to species equilibrium. In this study, we aimed to determine plant species composition in the gradient of microtopography of cutover peatlands and changes during the initiation of microtopography, as well as the time needed to achieve a state comparable to that of natural boreal bogs. We hypothesized that: (1) species may occur in unusual assemblages on cutover peatlands because ample space for plant establishment is initially available and plant interactions are thus minimal; (2) all species that are able to survive can potentially contribute to the initiation of microstructures; and (3) species will gradually come to occupy their 'normal' positions for

natural peatlands as the microtopography and plant inter-actions develop. On the basis of our previous work, the expected timescale was two to three decades in restored peatlands and much more in abandoned peatlands with spontaneous re-vegetation (Pouliot et al. 2011a).

Methods

Study areas

The field studies were carried out in eastern Canada and Estonia. Both of these regions have abundant easily acces-sible peatlands and long histories of commercial peat extraction. Sites were chosen because of the availability of re-vegetated cutover areas with adjacent natural areas for comparison (Table 1). Vacuum-milled peatlands that have been restored by a *Sphagnum* moss transfer method (Rochefort et al. 2003) are ideal subjects because the peat fields are scraped and levelled to create surfaces without microtopography before a mixture of plant species typical of boreal bogs is re-introduced. Peatlands that have been spontaneously recolonized by *Sphagnum* mosses after peat extraction also offer potentially relevant information, as the abandoned surface was again relatively flat but with no active re-introduction of bog species. More explana-tions about why we used sites in eastern Canada and Estonia, as well as meteorological conditions for both regions and differences in compaction of the remaining peat, have been described in Pouliot et al. (2011a).

Plant composition measurements

Time series sequences have been used to follow the evolu-tion of plant composition within the gradient of microto-pography during the development of microtopography. Plant composition was recorded on linear transects. Tran-sects were located randomly within an area where moss cover was at least 75%. Total transect length was adjusted according to the dimensions of the section studied, and ranged from 100 to 500 m. Where the moss carpet was particularly heterogeneous (with the presence of large por-tions without mosses), several shorter transects were sur-veyed and combined to make up the total transect length and to attain our criteria of 75% moss cover. All data were recorded between Jun and Sep 2007.

Plant species frequencies were recorded using the point-intercept method (Jonasson 1988), by noting all species contacted by a small stick (diameter = less than 1 cm) low-ered vertically at 1-m intervals along each transect. The relative abundance of each species was estimated in 30 (Canada, where vegetation was more heterogeneous) or 25 (Estonia) vegetation quadrats (25 cm × 25 cm) placed randomly along each 100-m transect portion. Each point or quadrat was classified as hummock, hollow or interme-diate habitat by measuring the height (± 1 cm) of the moss surface above a local reference point. Hummocks can be defined as peat mounds whose surfaces lie at least 20 cm above the annual mean maximum level of the water table (Payette & Rochefort 2001; Weltzin et al. 2001). As the ref-erence level for each transect was either at the water table or somewhat above it (mostly in restored peatlands), points with recorded surface heights of at least 20 cm were considered to lie on hummocks. Points with heights of 10–19 cm were interpreted as falling within intermediate hab-itats, and 0–9 cm as hollows. Numbers of points recorded by the point intercept method and the numbers of vegeta-tion quadrats are summarized in Table 1.

Statistical analyses

Principal components analysis (PCA) was used to explore the similarity between re-vegetated peatlands (or restored sections) and natural bogs in terms of vegetation develop-ment along the gradient of microtopography. Particular attention was also focused on the evolution of vegetation through time since restoration or abandonment. Data from Canada and Estonia were analysed separately. For each country, PCAs were conducted for frequency values using the VEGAN library of R software (version 2.2.1, R Devel-opment Core Team, Vienna, Austria). Each part of the gra-dient of microtopography (hollows, intermediate habitats and hummocks) was considered separately. Because the data were not well adapted to the Euclidean space assumed by PCAs, they were pre-transformed using Hellinger dis-tance (Legendre & Gallagher 2001). For the restored peat-lands (Canada), linear regression was used to test the relationship between surface height and the cover of erica-ceous shrubs or Cyperaceae, as well as the effect of time since restoration on vascular plant cover. When signifi-cant, the regression equations were then used to estimate the time required for restored peatlands to become compa-rable with natural peatlands in terms of cover values for the dominant vascular plants. The regressions were con-ducted using the GLM procedure available in SAS software (version 9.1, SAS Institute Inc., Cary, NC, US), and the data were tested for homogeneity and normality (signifi-cant probability levels were set to $\alpha = 0.05$).
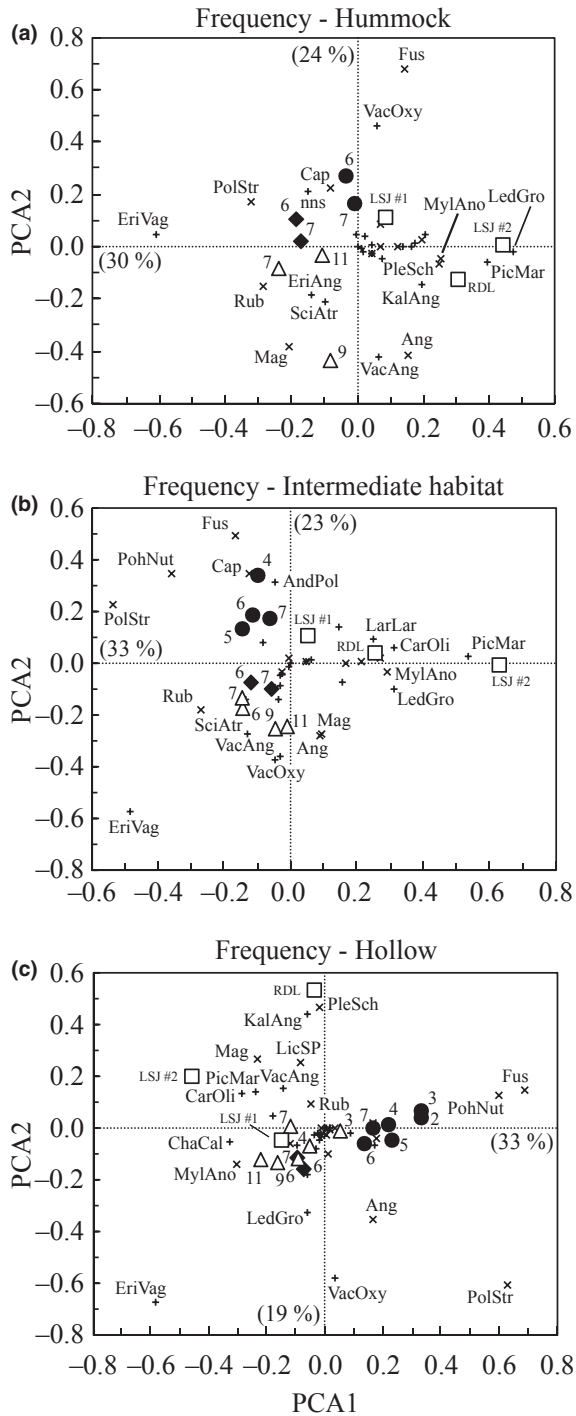
Results

Comparisons between restored and natural peatlands, Canada

Considering each microstructure individually, the first two axes of the PCAs accounted for 52–56% of species fre-quency variability (Fig. 1). Plant species composition was more stable relative to time in hummocks and intermedi-ate habitats than in hollows, where the relative positions

of centroids for different numbers of years post-restoration indicated an evolutionary trend. This was especially the case for one restored peatland (Ste-Marguerite-Marie),

Fig. 1. Principal components analyses (PCAs) on the first two axes (scaling focuses on inter-sample distances) for plant frequencies in the different parts of the hummock–hollow alternation in Québec peatlands: hummocks (**a**), intermediate habitats (**b**) and hollows (**c**). Numbers close to symbols of restored peatlands indicate the number of years post-restoration (some microstructures were absent according to sites, see Table 1 for site features). Abbreviations of site names are used to distinguish the natural bog sites as follows: LSJ #1: Lac-St-Jean #1; LSJ #2: Lac-St-Jean #2; RdL: Rivière-du-Loup; +: vascular plants; ×: non-vascular plants. See Table 2 for species abbreviations.

where plant species composition in hollows became much closer to that in one of the adjacent natural bogs (LSJ #1) with increasing time post-restoration (Fig. 1c). Although the vegetation in hollows at Chemin-du-Lac (where samples were also available for many different periods since restoration see Table 1), clearly changed through time, the centroid positions indicated that the hollows in restored areas still differed from the adjacent natural bog (RDL; Fig. 1c).

Total frequency and cover of *Sphagnum* mosses were comparable in restored peatlands and natural bogs regardless of microstructure; but the dominant *Sphagnum* species of hummocks, intermediate habitats and hollows differed between the two peatland types (Table 2; also centroid positions in Fig. 1). More than two-thirds of the hummock areas were covered by *Sphagnum* species belonging to Section Acutifolia (as *Sphagnum fuscum* and *Sphagnum rubellum*) no matter which peatland type was considered. These were also the main species of intermediate habitats and hollows in restored peatlands, whereas, in natural bogs, *S. rubellum* and *Sphagnum angustifolium* (in intermediate habitats) and *S. rubellum*, *S. magellanicum* and *Sphagnum fallax* (in hollows) composed a large part of the *Sphagnum* cover. Mosses other than *Sphagnum* were between four times (on hummocks) and 29 times (on hollows) more abundant in restored peatlands than in natural bogs (Table 3). *Polytrichum strictum* accounted for the majority of the cover of mosses other than *Sphagnum* in both peatland types.

Ericaceous shrubs such as *Kalmia* sp. and *Ledum groenlandicum* were more common in natural bogs than in restored peatlands (Table 2). In restored peatlands, the frequency of ericaceous shrubs increased and became closer to that prevailing in natural bogs with time post-restoration but their relative abundance remained lower in all microstructures even after 10 yr. Seven years post-restoration (the only common period for the three restored peatlands), ericaceous shrub cover was 27% compared to 54% on natural bogs. In contrast, Cyperaceae were widespread across all microstructures on restored peatlands (mean cover of 27%), but were scarcely present on the adjacent natural bog (mean cover of 8.5%; Table 2). *Eriophorum vaginatum* accounted for the majority of the area

Table 2. For Canada: mean frequencies (% – Fr) and relative abundance (% – Ab) of the principal plants used in the principal components analyses (Fig. 1) for restored peatlands (R) and natural bogs (N) in the different microstructures. + indicates less than 0.5%.

Species	Scientific name	Hummock				Intermediate				Hollow			
		R		N		R		N		R		N	
Code *		Fr	Ab	Fr	Ab	Fr	Ab	Fr	Ab	Fr	Ab	Fr	Ab
Sphagnum													
Ang	*Sphagnum angustifolium*	10	7	9	4	13	6	13	24	18	7	0	1
Cap	*Sphagnum capillifolium*	4	2	0	0	5	1	0	0	2	1	0	0
–	*Sphagnum fallax*	0	0	2	1	0	+	8	0	1	1	22	3
Fus	*Sphagnum fuscum*	50	25	56	47	45	26	27	10	29	21	8	4
Mag	*Sphagnum magellanicum*	32	5	11	4	24	4	18	2	9	2	25	15
Rub	*Sphagnum rubellum*	74	49	45	32	77	45	55	49	40	28	44	43
–	Total	100	88	96	88	99	83	86	85	70	60	67	66
Other non-vascular plants													
MylAno	*Mylia anomala*	0	+	7	0	3	1	12	1	11	3	17	13
PleSch	*Pleurozium schreberi*	0	0	8	+	0	0	11	+	0	0	17	0
PohNut	*Pohlia nutans*	26	+	32	+	40	1	23	+	37	2	28	+
PolStr	*Polytrichum strictum*	64	13	38	2	74	19	27	2	70	27	11	1
LicSp	Lichen spp.	0	0	5	+	0	0	5	0	1	+	8	5
–	Total (without lichen spp.)	66	14	61	3	82	21	50	4	74	32	36	14
Ericaceous													
AndPol	*Andromeda polifolia* var. *glaucophylla*	0	+	2	3	4	+	4	3	+	+	22	2
ChaCal	*Chamaedaphne calyculata*	46	19	51	17	32	17	40	11	23	9	36	10
KalAng	*Kalmia angustifolia*	14	2	38	17	7	3	32	12	4	1	25	12
–	*Kalmia polifolia*	10	3	7	1	6	1	10	1	2	+	17	+
LedGro	*Ledum groenlandicum*	16	6	49	16	11	4	37	17	7	2	11	14
VacAng	*Vaccinium angustifolium*	6	+	7	3	6	1	5	4	2	1	8	1
VacOxy	*Vaccinium oxycoccos*	38	2	28	1	35	1	19	1	25	1	11	1
–	Total	85	32	96	59	67	27	87	49	50	15	83	41
Cyperaceae													
CarOli	*Carex oligosperma*	0	0	6	1	0	0	18	7	0	0	28	5
EriAng	*Eriophorum angustifolium*	6	+	3	1	5	1	4	1	3	1	0	1
EriVag	*Eriophorum vaginatum*	57	25	4	2	49	26	2	2	40	21	28	5
SciAtr	*Scirpus atrocinctus*	3	1	0	0	5	1	0	0	2	1	0	0
–	Total	64	28	14	4	62	30	23	10	45	24	56	11
Tree													
LarLar	*Larix laricina*	1	1	10	1	1	+	8	1	+	0	0	0
PicMar	*Picea mariana*	0	+	15	9	1	+	29	1	+	+	17	17
–	Total	1	2	24	11	2	1	38	3	1	1	17	17
Other vascular plants													
nns	Non-native species **	5	3	0	+	3	1	0	0	2	1	0	0

*Code used in Fig. 1.

**Species with a common habitat that is not peatlands.

covered by Cyperaceae in restored peatlands (see centroid position in Fig. 1).

Comparison between abandoned peatlands with spontaneous re-vegetation and natural bogs, Estonia

Considering each microstructure individually, the first two axes of the PCAs accounted for 54–63% of species frequency variability (Fig. 2). The centroid positions indicate that plant species compositions of re-vegetated and natural peatlands were dissimilar regardless of position within the gradient of microtopography. The only exception was for hummocks at the re-vegetated Viru site in northern Estonia, whose vegetation was similar to that of local natural bogs (Fig. 2a).

Sphagnum covered more than 75% of all of the sites studied, but the dominant *Sphagnum* Section for the different parts of the gradient of microtopography varied according to peatland type (Table 3). On hummocks, abundance of *Sphagnum* species belonging to Section Acutifolia (as
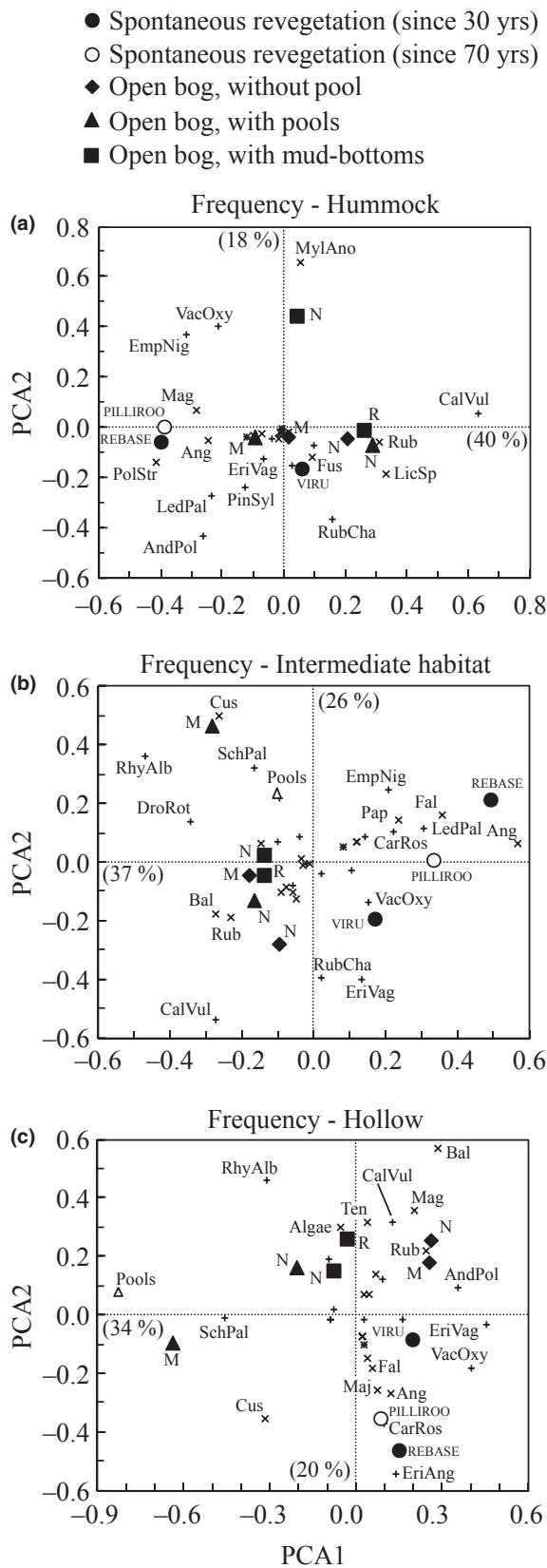
Table 3. For Estonia: mean frequencies (% – Fr) and relative abundance (% – Ab) of the most abundant plants used in the principal components analyses (Fig. 2) for abandoned peatlands with spontaneous re-vegetation (A) and natural bogs (N) in the different microstructures. + indicates less than 0.5%.

Species	Scientific name	Hummock				Intermediate				Hollow			
		A		N		A		N		A		N	
Code *		Fr	Ab	Fr	Ab	Fr	Ab	Fr	Ab	Fr	Ab	Fr	Ab
Sphagnum													
Ang	*Sphagnum angustifolium*	7	3	+	+	36	30	0	0	12	10	0	0
Bal	*Sphagnum balticum*	0	0	2	2	0	1	13	6	2	2	28	19
Cus	*Sphagnum cuspidatum*	0	0	+	0	0	1	10	3	52	57	19	19
Fal	*Sphagnum fallax*	1	1	+	+	26	16	5	+	12	4	4	1
Fus	*Sphagnum fuscum*	35	26	30	25	2	0	4	8	0	0	0	1
Mag	*Sphagnum magellanicum*	48	39	20	9	37	21	51	32	11	4	31	26
Maj	*Sphagnum majus*	0	0	0	0	0	1	0	0	9	6	0	0
Pap	*Sphagnum papillosum*	2	0	0	0	10	3	0	0	1	3	0	0
–	*Sphagnum riparium*	0	0	0	0	2	4	0	0	3	1	0	0
Rub	*Sphagnum rubellum*	40	29	68	47	32	22	53	40	11	8	11	4
Ten	*Sphagnum tennelum*	0	0	0	0	0	0	2	+	0	0	9	2
–	Total	100	98	92	83	100	99	95	89	98	95	77	72
Other non-vascular plants													
MylAno	*Mylia anomala*	0	0	12	2	0	0	3	1	0	0	2	+
PolStr	*Polytrichum strictum*	24	2	1	1	2	+	0	0	1	0	0	0
LicSp	Lichen spp.	0	0	11	6	0	0	3	1	0	0	1	1
Algae	Algae	0	0	0	0	0	0	+	1	0	0	0	12
–	Total (without lichen spp. and algae)	24	3	2	5	2	+	+	2	0	3	10	1
Ericaceous													
AndPol	*Andromeda polifolia* var. *polifolia*	33	4	20	2	36	3	45	4	26	2	22	2
CalVul	*Calluna vulgaris*	29	4	83	24	15	1	45	13	1	+	8	2
EmpNig	*Empetrum nigrum*	14	1	9	2	14	+	1	+	0	0	0	0
LedPal	*Ledum palustre*	20	1	2	+	16	2	+	+	2	+	0	0
VacOxy	*Vaccinium oxycoccos*	37	2	37	1	53	3	34	1	48	2	15	1
–	Total	86	12	96	29	83	10	84	19	61	5	37	5
Cyperaceae													
CarRos	*Carex rostrata*	3	1	0	0	6	+	0	0	14	2	0	0
EriAng	*Eriophorum angustifolium*	0	0	0	0	4	+	0	0	26	2	0	0
EriVag	*Eriophorum vaginatum*	53	5	33	5	57	9	30	6	42	4	17	2
RhyAlb	*Rhynchospora alba*	0	0	3	+	0	0	24	4	6	1	36	7
SchPal	*Scheuchzeria palustris*	0	0	+	0	0	0	4	+	0	0	5	1
–	Total	57	6	36	5	65	10	55	11	82	9	55	10
Tree													
BetNan	*Betula nana*	6	2	0	0	1	0	0	0	0	0	0	0
PinSyl	*Pinus sylvestris*	9	1	3	1	5	+	1	+	1	0	0	0
–	Total	14	2	3	1	6	+	1	+	1	0	0	0
Other vascular plants													
DroRot	*Drosera rotundifolia*	0	0	5	1	0	0	14	1	0	+	5	+
RubCha	*Rubus chamaemorus*	8	0	10	2	19	0	4	1	19	0	+	+

*Code used in Fig. 2.

S. rubellum and *S. fuscum*) was 1.3 times higher in natural bogs than in re-vegetated peatlands (mean cover of 72% vs 55%). Species belonging to Section Sphagnum (mainly *Sphagnum magellanicum*) made up the difference on hummocks of re-vegetated peatlands (mean cover of 39%). When considering species individually, four *Sphagnum* species were co-dominant in intermediate habitats of re-vegetated peatlands (in decreasing order: *S. angustifolium*, *S. rubellum*, *S. magellanicum* and *Sphagnum fallax*; Table 3).

Sphagnum rubellum were still dominant in intermediate habitats of natural bogs (with *S. magellanicum*). *Sphagnum* species from Section Cuspidata were common in hollows everywhere, but were around twice as abundant in re-vegetated peatlands than in natural bogs (mainly *Sphagnum cuspidatum* with *Sphagnum balticum* in natural bogs; Table 3). *Sphagnum magellanicum* made up the difference on hollows of natural bogs (mainly where mud-bottoms were present). The same trends were indicated by the PCA

Fig. 2. Principal components analyses (PCAs) on the first two axes (scaling focuses on inter-sample distances) for plant frequencies in the different parts of the hummock–hollow alternation at spontaneous re-vegetated and natural bogs, Estonia: hummocks (**a**), intermediate habitats (**b**) and hollows (**c**). Abbreviations used for the site names of natural bogs are: M, Mannikjärve; N, Nigula and R, Ruunasso. See Table 1 for site features and Table 3 for species abbreviations.
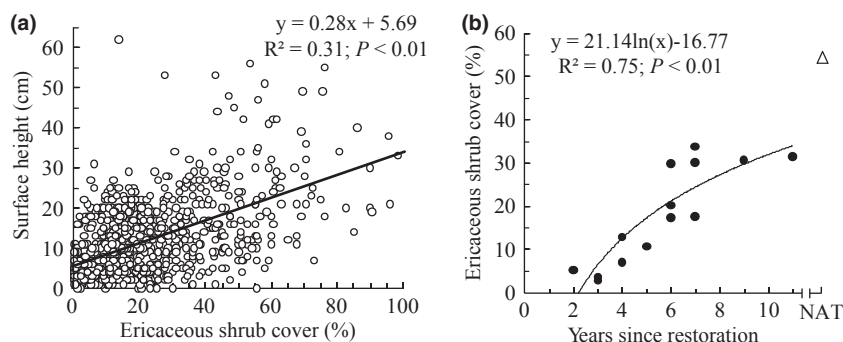
centroid positions (Fig. 2). Mosses other than *Sphagnum* were sparse throughout (Table 3).

Mean cover of ericaceous shrubs (mainly *Calluna vulgaris*) on hummocks and intermediate habitats was higher in natural bogs than in re-vegetated peatlands, even though frequencies were relatively similar; whereas the occurrence of Cyperaceae on hummocks (mean cover 6%) did not differ between peatland types (Table 3). Vascular plants were sparse (mean cover of 14%) in hollows of both peatland types, and occurrences of ericaceous shrubs and Cyperaceae were similar (Table 3). However, the dominant Cyperaceae species differed between peatland types. *Rhynchospora alba* was the most abundant vascular species of hollows in natural bogs but was almost absent from re-vegetated peatlands, where it was replaced by *E. vaginatum* and *Eriophorum angustifolium* (Table 3; also centroid positions in Fig. 2). Furthermore, around 30% of the hollow area was covered by open water in natural bogs with pools and by algae in those with mud-bottoms (no open water or mud-bottoms in re-vegetated peatlands).

Relationship between vascular plant cover and moss surface height

Around 31% of the data variability was explained by the relationship between ericaceous shrub cover and moss surface height (Fig. 3a). A significant positive relationship of ericaceous shrub cover to moss surface height was found ($P < 0.01$). According to the regression equation, an ericaceous shrub cover of at least 15% was associated with a moss surface similar to the height of intermediate habitats (10–19 cm, as defined in the previous section). More than 50% cover of ericaceous shrubs was associated with a surface height corresponding to hummocks (≥ 20 cm), and this could take around 24 yr to develop in restored peatlands ($R^2 = 0.75$; $P < 0.01$; Fig. 3b). No relationship was found between moss surface height and Cyperaceae cover ($R^2 \leq 0.01$; $P = 0.47$).

Discussion

Comparisons between restored and natural peatlands

In the restored peatlands, initiation of the microstructures of hummock–hollow alternation and their subsequent

Fig. 3. Relationships between (**a**) moss surface height and ericaceous shrub cover, and (**b**) ericaceous shrub cover and years after restoration.

evolution towards the microtopographical patterns found in natural bogs was clearly apparent during the first few decades post-restoration (Pouliot et al. 2011a). However, although plant species have changed visibly through time, the species composition (frequency and cover) of different microstructures did not evolve directly towards that of natural bogs within the time series of post-restoration sites examined. Vegetation also changed in different ways between microstructures.

This discrepancy may lie with the ecological restoration process. Using the peat moss transfer approach (Rochefort & Lode 2006), drier peatlands are chosen as donor sites as they can support the tractors used to harvest plant material, with the consequence that most of the moss mix used for reintroduction consists of species such as *Sphagnum rubellum*, *Sphagnum fuscum* and *Polytrichum strictum*. This material is then spread onto bare peat, giving Acutifolia moss species a short-term advantage ahead of others to colonise most of the available space. As meteorological conditions during the restoration year have a considerable effect on moss carpet development (Chirino et al. 2006), these species can also have an advantage over others when peat moss transfer occurred during a dry year due to a higher capacity to transport water by capillarity (Wallén et al. 1988; Rydin 1993a). Nevertheless, a small proportion of hollow species will colonise the sites. With time, the hummock species, with slower decomposition rates (Rochefort et al. 1990; Johnson & Damman 1991; Limpens & Berendse 2003), accumulate peat and form increasingly tall hummocks. With the prevalence of bigger hummocks, hollow species can become established in spots not colonized by species actively reintroduced or between hummocks in possibility wetter zones, and thus form new hollows. Hollow species abundance will then be able to increase and reach composition similar to natural bogs.

Another factor explaining the discrepancy of the faster return of hummock–hollow structure compared to specific composition is, for some sites, the use of a phosphorus fertilizer in the peatland restoration process when frost heaving could be a prevalent problem. Phosphorus fertilization enhances the establishment of *P. strictum* during the early post-restoration period (Sottocornalo et al. 2007). Carpets of *P. strictum* in turn enhance *Sphagnum* establishment by stabilizing the peat surface and thus reducing the severity of frost heave events (Groeneveld & Rochefort 2005). Small *Sphagnum* fragments added during restoration will thus be able to survive in a higher proportion. With time, *P. strictum* is replaced (lower competitive ability compared to *Sphagnum* mosses) but retards the expected species composition found in natural peatlands since that moss was more abundant during the first years following restoration.

The abundance of both ericaceous shrubs and Cyperaceae at the different microstructure levels seems to change gradually towards that seen in natural bogs, but growth characteristics of both types of vascular plant slow down the return of hummock–hollow structures. The small fragments of ericaceous shrubs that are reintroduced with the moss mix grow slowly and, even if their frequency and abundance increase progressively, are still less abundant in restored peatlands than in natural bogs a decade post-restoration. Moreover, *Eriophorum vaginatum* readily colonizes the harsh environments of abandoned (Lavoie et al. 2005) and newly restored peatlands (this research; Peatland Ecology Research Group, unpublished data), but is not particularly abundant in natural peatlands where specialist Cyperaceae (e.g. some *Carex* spp.) are the most frequent representatives of the group.

Thus, two steps of the peatland restoration process linked with meteorological conditions, namely the composition of the reintroduced plant matrix and phosphorus fertilisation, when applied, and growth features of vascular plants can be major factors influencing temporal changes in plant species composition within the microtopographical gradients of restored peatlands.

Comparisons between spontaneously re-vegetated and natural peatlands

Plant species composition within the hummock–hollow alternation of abandoned peatlands with spontaneous re-vegetation was dissimilar from that found in any of the natural bogs studied. As in the case of structural pattern development (see Pouliot et al. 2011a), probably many more than 70 yr will be required to attain similar plant frequencies and abundances in spontaneously re-vegetated and natural peatlands. Plant species abundances in abandoned peatlands can be linked with distance from the nearest natural bog edge (Campbell et al. 2003) and the depth of residual peat deposit (changes in growth parameters; Poulin et al. 2005). Mosses (spores via wind) and ericaceous shrubs (seeds via animal, water and wind) generally have high immigration potential (Campbell et al. 2003) and probably have no difficulty in recolonizing abandoned peatland due to their proximity to natural bogs. According to Campbell & Rochefort (2001), studied abandoned peatlands still maintain abiotic conditions of peatlands dominated by *Sphagnum* (also demonstrated by chemical analyses from water samples coming from sampled abandoned peatlands; R. Pouliot, unpublished data). Consequently, differences in plant species composition between abandoned peatlands and bogs have to be explained by factors other than distance from bog edge or depth of residual peat.

The prevalence of *Sphagnum* species from Section Cuspidata, such as *Sphagnum cuspidatum*, in re-vegetated peatlands explains the dissimilarity between plant species composition of re-vegetated and natural bogs. These species are usually better colonizers than typical hummock builders due to their rapid growth rates (Rydin 1993a; Grosvernier et al. 1997), especially if the water table is high, as in the re-vegetated peatlands studied here. Smolders et al. (2003) argue that the lower occurrence of hummock species in European bog remnants with blocked ditches is related to colonization impediments rather than a lack of suitable growing conditions. The optimal habitat for all *Sphagnum* species is humid hollows (Rydin 1993a), but hollow species are better competitors than hummock species so that the latter are pushed towards the hummock tops (Andrus et al. 1983; Titus & Wagner 1984; Rydin 1997a). Hummock species cannot become well established on re-vegetated peatlands if the water table is high and hummocks are poorly developed. On the dates of sampling visits, water tables at the re-vegetated peatlands were closer to the surface than at the natural bogs with or without pools (−13 cm vs −19 cm; R. Pouliot, unpublished data). If this reflects the relative water table throughout the growing season, this would explain the difference in plant species composition between re-vegetated peatlands and natural bogs.

Again, growth features of ericaceous shrubs and Cyperaceae explain a part of the differences between plant species compositions in re-vegetated and natural bogs. In re-vegetated peatlands without active restoration, ericaceous shrubs can establish only from seed. Because their growth is a slow process, it is unsurprising that their abundance is lower in re-vegetated peatlands than in natural bogs. *Eriophorum* species generally grow in a wide range of peatland microhabitats (Gignac et al. 2004), and *Eriophorum angustifolium* and *E. vaginatum* can establish more readily in re-vegetating peatland than Cyperaceae with narrower ecological niches, such as *Rhynchospora alba*. With the development of microtopography, generalist species become less common and the establishment of non-generalist species is fostered, as expected through niche differentiation (Moser et al. 2007).

Thus, initial high water table of after-use sites, stronger competition by hollow species and growth characteristics of vascular plants can be identified as three reasons for departure of the plant species composition in re-vegetated peatlands from that found on corresponding microstructures within the hummock–hollow alternation of natural bogs.

Plant interactions

Closely-related *Sphagnum* species generally co-exist in the long term (Rydin & Barber 2001) and competitive exclusion is uncommon in moss carpets (Slack 1977). In this situation, seasonal changes in the relative abundance of different *Sphagnum* species are frequent even under abiotic conditions that are physiologically tolerable for all of them (Rydin 1993b), but no species is able to entirely replace the others within a year (Rydin 1997b). However, *Sphagnum magellanicum* could partially impede *S. fuscum* (and probably other hummock species) from occupying its fundamental niche in lower parts of the gradient of microtopography (Mulligan & Gignac 2002). For example, on one restored peatland (Ste-Marguerite-Marie), *S. fuscum* grew well (mean cover 59%) in the hollows of five restored sections where *S. magellanicum* was almost absent (cover < 1%), but in one restored section where *S. magellanicum* cover was slightly higher (7%) the mean cover of *S. fuscum* was only 17%. Plant mix used for reintroduction came from the same donor site, but differences between initial plant species composition cannot be totally excluded. Alternatively, the low occurrence of *Sphagnum* species typical of hollows during the early post-restoration years might be partly explained by the fact

that water levels in restored peatlands are lower than in spontaneously re-vegetated peatlands. Under recurrent drought conditions, the competitive balance shifts towards hummock species, as they are able to retain moisture most efficiency than hollow species (for example: Clymo & Hayward 1982; Andrus 1986), and this could modify the course of pattern development (Robroek et al. 2007b). Because the species are closely related, priority of colonization or establishment is probably more important for the development of hummock–hollow alternation (Rydin 1986).

Early environmental events may also be significant in determining species abundances and thus influence the development of microstructures, and this could explain the atypical assemblages of *Sphagnum* species that are found in restored and spontaneously re-vegetated peatlands. For example, variations in weather (Chirino et al. 2006) and nitrogen availability (Li & Vitt 1994) between growing seasons differentially influence the establishment rates of individual moss species and thus the overall species distribution. Therefore, the species composition of the *Sphagnum* carpet could be governed initially by stochastic processes such as environmental events, and only later during the development of patterning is influenced by species interactions (Fenton et al. 2007).

The relationship between cover of ericaceous shrubs and moss surface height (Fig. 3) suggests a link between the growth of these species and the accentuation of hummock–hollow alternation. The cover of ericaceous shrubs associated with hummocks (defined as $\geq$ 20 cm in height) points to a requirement for 24 yr to develop. This coincides with the time needed for the initiation of microstructures on restored peat extraction sites (~ two decades, Pouliot et al. 2011b). A positive association between *Sphagnum* mosses and ericaceous shrubs in hummocks is often evoked (Vitt et al. 1975; Clymo & Hayward 1982; Andrus 1986; Kenkel 1988) but seldom substantiated. Upward growth of the moss surface could favour the establishment of ericaceous shrubs by raising their roots above the water table; and the enhancement of ericaceous shrub cover in turn promotes peat accumulation (and thus hummock formation) by providing appropriate structures to support upward-growing *Sphagnum* shoots (Malmer et al. 1994; Pouliot et al. 2011b). Moreover, an increase in the frequency and/or duration of low water table periods may cause a shift in the dominant species of both *Sphagnum* and vascular plants (e.g. Cyperaceae to ericaceous shrubs), thus triggering a change from hollow to hummock vegetation (Breewer et al. 2009). The same phenomenon may arise during the development of hummock–hollow patterning; the species shift occurring as the hummocks become drier simply on account of their increasing height. *Eriophorum*

shoots and tussocks can act as establishment centres for *Sphagnum* mosses (Soro et al. 1999), but we did not find any relationship between Cyperaceae cover and moss surface height. This is probably due to the low luminosity beneath dense Cyperaceae canopies, as mosses prefer microhabitats with intermediate levels of light availability where the combination of radiation and moisture is optimal for their growth (Bergamini et al. 2001). Also, although sparse *Eriophorum* cover promotes the extension of *Sphagnum* shoots, the resulting moss carpet is insufficiently dense to form tall hummocks (Pouliot et al. 2011b). In brief, a well-developed ericaceous shrub layer could be a prerequisite for the formation of clear hummock–hollow patterns.

Conclusions

In active peatland restoration or within the natural regeneration process of an industrial peat-extracted site, we conclude that the surface structure (hummocks and hollows) of the ecosystem returns more rapidly than species composition forming the typical hummock–hollow alternation. After peat extraction, the vegetation is still dissimilar to the species composition of natural patterned bogs 10 yr post-restoration and 70 yr post-abandonment, although a trajectory towards typical species composition is observed. Active restoration clearly reduces the time required for the occurrence of plant species in restored peatlands to resemble the composition of natural peatlands, but the process is influenced by both the choice of species re-introduced and their specific success in establishing moss carpets. Moreover, increases in moss surface height could be associated with the presence of ericaceous shrub cover. The time needed for re-establishment of an ericaceous shrub layer sufficient to promote hummock formation, could retard the development of microstructures. A well-developed cover of *Sphagnum* mosses is present in abandoned peatlands with spontaneous re-vegetation, but some hydrological works (as blocking drainage ditches) are needed to accelerate this process (Soro et al. 1999). We suggest that all species able to tolerate the conditions prevailing on cutover peatland post-restoration or post-abandonment can contribute to the initiation of hummock–hollow patterning, but they could form atypical assemblages. Random events and the establishment priority are initially more important than plant interactions for the evolution of patterning. Another possibility is that the plant species compositions observed in re-vegetated peatlands could be as stable as that observed in natural bogs, but with different species dominances. Harvesting, drainage ditches or other factors could have sufficiently altered the trajectory of

vegetation in re-vegetated peatlands so that natural plant composition in the different microstructures could be not regained. We suggest that restored peatlands are good subjects for long-term monitoring to follow the development of hummock–hollow patterning and, potentially later, of macrostructures through the initiation of pools or string-and-flark alignment.

Acknowledgements

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