

Does the autecology of core species reflect the synecology of functional groups during the assembly of vegetation in abandoned extracted peatlands?

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SUMMARY

The combined autecology of individual species is expected to reflect the synecology of their respective functional groups and *vice versa*, but this assumption has been rarely assessed. We estimated this similarity in limiting ecological filters using vegetation survey data from 64 abandoned extracted peatlands in Estonia, which form a 50-year chronosequence of secondary succession. Partial overlap was found between filters predicting the occurrence of individual core species and richness in their respective functional groups. These overlapping filters were microtopographical form (flats, margins, ditches), time since abandonment, and various properties of peat. At the functional group level, time since abandonment and habitat properties showed clear interactions with microform type. Bog species and acidophilous bilocals successfully established on flats and ditch margins when residual peat was acidic and poorly decayed, while species of fens and mineral soils preferentially established in ditches of large extraction fields, where residual peat had higher pH and higher mineral content. We also detected some effects of landscape-level (patch area and forest neighbourhood) and regional filters (continentality); however, their limiting role was inconsistent. Many ecological filters also were shared between functional groups at the species level, but the optimal levels of these filters differed between groups. We conclude that even in species-poor habitats, both the autecology of individual species and the synecology of functional groups should be considered during habitat restoration. In peatland restoration, the following management strategies are advised to direct a faster and more successful trajectory: controlling the depth of peat extraction, partial filling of ditches, introducing plant propagules and managing mineral dust pollution.

KEY WORDS: bog restoration, ecological filtering, mire, secondary succession, species richness, substrate pH

Nomenclature: the Plant List (<http://www.theplantlist.org>) for vascular plants, Ingerpuu *et al.* (1998) for bryophytes, and Randlane & Saag (1999) for lichens.

INTRODUCTION

Restoration planning at the industrial scale should use as reference a comprehensive set of dispersal- and establishment-limiting conditions. These are called ecological filters or sometimes environmental filters (see Keddy 1992). These filters should be characterised by indicators which are robust and not sensitive to seasonal fluctuations or observer identity (Keddy 1992, Clarke & Rieley 2010, Kimmel *et al.* 2010). Limiting ecological filters can be estimated by exploring the individual adaptations of species (i.e. studying their autecology) (Boutin & Keddy 1993, Lavorel *et al.* 1997) or the combined responses of species sets (i.e. studying the synecology of ecological guilds or the whole community). The autecology of common species or core species (defined as abundant, or just frequent; Gaston 2011,

Hanski 1982) has been used in this context for estimating filters in species-poor communities (Boutin & Keddy 1993, Lavorel *et al.* 1997). The synecology of functional groups has been used for species-rich communities or when applying broad ecological generalisations and extrapolation of results to the global scale (Box 1996, Lavorel *et al.* 1997, Diaz & Cabido 2001), by assuming that species combined into functional groups share similar functional, ecophysiological and life-history traits and react similarly during community assembly (Grime *et al.* 1988, Box 1996, Blondel 2003). The strong overlap between the autecology of individual species and synecology of respective functional groups may seem to be evident, but this assumption has rarely been evaluated. The ecology of mires (*sensu lato*) has largely been described via requirements of individual species, but sometimes

species have been clustered taxonomically, functionally or by ecological response (Van der Valk 1981, Tuittila *et al.* 2000, Groeneveld & Rochefort 2002, González *et al.* 2013). Therefore, we propose that the assembly of vegetation in abandoned peat-extraction areas is a suitable system to test the similarity of ecological filters between core species and their respective functional groups.

The main contrast between these two ecological approaches is in the expectation of representativeness. In autecological studies, it is assumed that not only do core species dictate the ecological responses of the community in general, but they are also able to illustrate the ecological envelope of rare species (Wilson 1999, Diaz & Cabido 2001, Cousins & Lindborg 2004, Gaston 2011, Heegaard *et al.* 2013, Leppik *et al.* 2015). The synecology of functional groups is usually quantified using species richness in the group as a response indicator (Heegaard *et al.* 2013, Leppik *et al.* 2013); however, as species richness is sensitive to the occurrence of rare species, the identified set of ecological filters may sometimes emphasise the ecological peculiarities of these infrequent species (Markham 2014, Chung *et al.* 2015, Leppik *et al.* 2015).

The spontaneous revegetation of abandoned peat-extraction areas is slow, hindered by the stochasticity of propagule arrival and the extremely harsh conditions for establishment (Groeneveld & Rochefort 2002, Lavoie *et al.* 2003a, Triisberg *et al.* 2011, 2014; Hirata & Tsuyuzaki 2016, Karofeld *et al.* 2017). The main ecological filters affecting the assembly of a peat-forming community have been found to be the properties of residual peat, the microtopography created by peat extraction and the species composition of surrounding habitats (Girard *et al.* 2002, Triisberg *et al.* 2011, 2013, 2014; Pouliot *et al.* 2012, Konvalinková & Prach 2014). The widely-used indicator water table depth (Price *et al.* 2003, Konvalinková & Prach 2014) shows seasonal dynamics; thus, measurements taken at a single point in time cannot be used during the initial planning of extracted peatland restoration.

The slow speed of establishment and the lack of competition during the first decades of succession allow for the expression of species' fundamental niches (see Hutchinson 1957). Therefore, established species in extracted peatlands originate from various habitat types, i.e. the community (re-)assembly is supported by the meta-pool of species harboured in various habitat types of the surrounding landscape (see Suija & Liira 2017). There are species from different mire types (swamp, fen and raised bog), species from various habitats on acidic substrates rich

in organic material, hygrophytes from low-water habitats and even generalists common from habitats on mesic mineral soils (Botch & Smagin 1993, Dierßen 2001).

Our objective in this article is to assess the general assumption that the ecological filters of the core species correspond to those of their respective functional group. We hypothesise that during the spontaneous recovery of vegetation in abandoned peat-extraction areas, the core species are limited by the same set of ecological filters as their respective functional groups. Specifically, we will compare the similarity of limiting filters as indicated by comparing significant environmental factors between two sets of prediction models: 1) autecological models on the occurrence of individual core species of the same functional group; and 2) synecological models on the accumulated species richness within each functional group. We will address five types of abiotic filters: (i) habitat microtopography; (ii) time since abandonment; (iii) properties of establishment substrate (residual peat); (iv) landscape structure; and (v) geographical positioning within the region as continentality. Several filters are characterised by multiple, partly overlapping indicators. If the hypothesis of similarity between core species and respective functional groups holds, then the extracted sets of limiting ecological filters can be used as references to optimise management methods so that the successional trajectory in extracted peatlands can be directed towards peat-forming mire communities.

METHODS

Study sites

Estonia belongs to the hemi-boreal zone, with a mean annual precipitation of 570 to 750 mm and a mean air temperature of -2.5 to -6.5 °C in February and 16.5 to 17.8 °C in July (Tarand *et al.* 2013). Natural mires cover about 5.5 % (245 000 ha) of Estonia, while the area of peatlands with ongoing peat extraction or abandoned after extraction comprises ~29,500 ha (Kimmel *et al.* 2010, Paal & Leibak 2011).

We used data from an inventory of 64 abandoned extracted peatlands in Estonia (Figure 1) carried out by the Geological Survey of Estonia (Ramst *et al.* 2005, 2006, 2007, 2008) for the Ministry of the Environment (<https://www.envir.ee/et/mahajaetud-turbatootmisalad>). These sites represent almost all the existing 5–50 year-old abandoned extracted peatlands in the country. Milling has been the main peat extraction type in the region, forming large homogeneous extraction fields. Thus, in large extraction areas, homogeneous peat fields were



Figure 1. Locations of the studied abandoned extracted peatlands in Estonia (overall centroid: 58° 41' 42", 25° 25' 59").

inventoried as separate study areas when they had been abandoned at different times or had visually different vegetation cover, e.g. because of different management treatments or fire events after abandonment. Usually, peat-extraction fields consist of three types of microtopographical habitats (microforms): flats, ditches, and ditch margins. Flats comprise the central parts of the extraction fields with widths ~16 m, ditches are usually 1 m wide and situated parallel to each other at steps of 20 m, and ditch margins are defined as 2 m wide strips of flats running alongside ditches. As all three microform types were not always present at each extraction field, the final tally of records included 101 vegetation records from flats, 58 from ditch margins and 73 from ditches. Detailed analysis of the composition and community types in these areas is presented in Triisberg *et al.* (2014).

As many extracted peatlands were sparsely vegetated and the mean vegetation cover was only 10–20 %, the occurrence list of plant species was compiled separately for each microform type in a study area (for more details see Triisberg *et al.* 2014). At each study area, the following factors were measured: the depths of slightly decomposed peat (decomposition degree <25 % or type H1–H3) and well-decomposed peat (>25 %, types H4–H10) (classification Hulme & Birnie 1997), and the total depth of the residual peat layer. The majority of the sites (85 % of studied extracted peatlands) had well-functioning drainage ditches that maintained the water level at 50–100 cm below the surface, but water levels fluctuated widely among seasons and years so that some areas were subjects to temporary flooding. Because of the large number of sites, no single index describing the hydrological conditions of the sites could be developed and used in the analysis.

Additionally, the following past or current management actions to promote the vegetation re-establishment were noted: burning, cutting of young trees, fertilisation and sowing seeds (*Vaccinium oxycoccus*, other *Vaccinium* species, *Betula* spp., *Pinus sylvestris* and *Picea abies*).

In the Laboratory of the Geological Survey of Estonia, the following characteristics were estimated from the uppermost 50-cm layer of residual peat: (i) ash content, as measured by weight loss after burning at 450 °C; (ii) pH_{KCl}; and (iii) degree of decomposition (in both percentage scale and Von Post scale), as estimated by the centrifugal method (Hulme & Birnie 1997). According to the botanical composition of plant fragments in the peat, as determined under a microscope, the potential nutrient status of habitats at the time of peat accumulation was identified: (i) oligotrophic, (ii) mesotrophic, or (iii) eutrophic (method detailed in Orru *et al.* 2011).

The time of abandonment and the area of each study area were ascertained from management databases and maps. The distance from the nearest sea shore was considered as a simple combined indicator of the maritime/continental gradient or continentality (Tarand *et al.* 2013), which coincides with the base-rock gradient from limestone in the coastal region (west and north of Estonia) and sandstone inland (south-eastern Estonia). Habitats adjacent to the study site were estimated from maps and aerial photos available from the WMS-service of the Estonian Land Board (www.maaamet.ee), and the neighbourhood was classified as the following: (i) an active peat-extraction area; (ii) natural mire (*sensu lato*); (iii) forest; or (iv) a mosaic of habitats.

Data processing

Within the 181 recorded species of plants, bryophytes and lichens (for more details see Triisberg *et al.* 2014), the 27 species that occurred in at least 5 % of the records were defined as the core species (see Hanski 1982) of recovering extracted peatlands. All species were classified according to Botch & Smagin (1993) into four functional groups based on their prevailing habitat preference in stabilised communities (realised niches in Hutchinson 1957) and the abilities to form a peat-accumulating community, grow on acidic organogenic substrate or suppress organic accumulation. First, the ‘bog species’ group contains peat-forming species of raised bogs and transitional mires. Second, the ‘acidophilous bilocals’ group includes species inhabiting both raised bog and heath. Third, the ‘semi-hygrophytes’ group comprises species of fens, swamps and those growing in shallow water. Finally, ‘mesophytes’ were categorised as species growing on

mineral soils, with the exception of podzols from heathlands. Among these 27 core species, 9 species were classified as bog species, 7 as acidophilous bilocals, 7 as semi-hygrophytes and 4 as mesophytes (Table 1).

In order to compare the limiting filters of core species and their respective functional groups, we first built prediction models for both response levels and then estimated the overlap between them. Generalised linear model analysis (GLZ, Statistica version 9) with stepwise forward selection of variables was used to extract the most parsimonious and statistically significant set of conditions explaining the occurrence pattern of each core species. Because of model complexity and the occurrence of specific species sets in microforms, we were able to test only main effects. For GLZ analysis, we used the binomial error distribution and logit link-function. General linear models (GLM; implemented in the module of General regression modelling, Statistica version 9) with forward stepwise selection of variables were used to build a parsimonious prediction model explaining the variation in species richness for each functional group, and both main effects of conditions and interaction terms between habitat conditions and microforms were tested. At the final step, we estimated the similarity between filters for core species and their respective functional groups as the proportion of species within functional groups constrained by the same filters identified in their respective functional group models. The indicator conditions representing filters were pooled. In models and in the final comparisons, we addressed five ecological filters: (i) habitat microtopography (represented by microform); (ii) time since abandonment; (iii) properties of establishment substrate (various chemical and structural features of the residual peat, disturbances and treatments); (iv) landscape structure (site area and neighbourhood); and (v) continentality status within the region (represented by the log-transformed distance from the sea).

RESULTS

Core species

The results of the GLZ analyses on the occurrence of core species (Table 1) show that microtopography is the most common filter, being significant for 19 core species. The occurrence of ten core species, spread across all functional groups, was positively correlated with the flat microhabitat: *Vaccinium oxycoccus* and *Rhynchospora alba* from bog species, *Carex vulgaris* or *Empetrum nigrum* from bilocals,

Eriophorum angustifolium from semi-hygrophytes, and a common mesophyte *Epilobium angustifolium*, as well as the forest moss *Pleurozium schreberi*. Some species were negatively correlated with flats, such as the bog species *Eriophorum vaginatum* and *Sphagnum cuspidatum*, and the semi-hygrophyte *Warnstorfia fluitans*. Ditches were mostly vegetated by semi-hygrophytes such as *Typha latifolia* and various *Carex* species, while *Polytrichum strictum*, a core species on hummocks in transitional mires and raised bogs, was never recorded in ditches. Although tussocks of *E. vaginatum* can cover large areas on some extracted peatlands, we detected negative correlation between its occurrence and both flats and ditches, which indicates that *E. vaginatum* prefers ditch margins as the initial microform for establishment. Here, it must be noted that ditch margins were not included in this model to avoid over-parameterisation.

Time since the abandonment of extracted peatland was a significant predictor for nine core species (Table 1). The species accumulation over time since abandonment belonged mostly to the functional groups of bogs or bilocals, such as *E. vaginatum*, *Trichophorum alpinum*, *Calluna vulgaris*, *E. nigrum*, or the bryophytes *Aulacomnium palustre* and *P. schreberi*. *Carex rostrata* from the semi-hygrophyte functional group was the only species showing a negative correlation with time since abandonment, but the estimated slope of the relationship was low.

The occurrence of eleven core species showed significant correlations with properties of residual peat (Table 1). Acidic peat, which usually coincides with thicker residual peat layers or lower decomposition rates and nutrient status, was positively correlated to the establishment of bog species (*Drosera rotundifolia*, *V. oxycoccus*, *R. alba* and *S. cuspidatum*) and to the occurrence of some acidophilous bilocals (*E. nigrum* and *P. schreberi*). In contrast, higher peat pH facilitated establishment of the semi-hygrophytes *Erioph. angustifolium* and *Phragmites australis*. A thick residual peat layer was also correlated to the occurrence of *P. australis* and *Calamagrostis canescens*. Higher pH level also appeared to promote the establishment of the bog species *E. vaginatum*.

The management of abandoned peatlands with treatments like application of mineral fertilisers or ash, cutting young trees, sowing, or accidental fires were correlated to the establishment of seven core species. Fires promoted a bilocal bryophyte *P. strictum* and a mesophyte *Bryum caespiticum*. Various management treatments and probably also ground disturbance were positively correlated with

Table 1. Generalised linear model analysis showing slopes of the relationships between the most frequent species (core species) and environmental variables.

			Predictor variables													
			Microform		Time	Habitat							Landscape			
Fun. gr.	Species	Intercept	Flat	Ditch	Time (log)	Peat nutrient status	Peat pH	Ash (log)	Decomp. rate	Thick-ness of slightly decom-posed peat	Thick-ness of res.peat layer in total	Signs of burn	Treat-ments	Area (log)	Adja-cent forest	Dist-ance from coast (log)
1	<i>Aulacomnium palustre</i> ^B	-11.38***			6.16***											
1	<i>Drosera rotundifolia</i> ^V	0.32 ^{ns}				-1.01*	-2.0**				4.84*					
1	<i>Eriophorum vaginatum</i> ^V	-2.63*	-1.36***	-1.34***	1.60*		0.54**									
1	<i>Vaccinium oxycoccos</i> ^V	0.46 ^{ns}	2.61***				-2.01*				5.38**		1.96***		1.55**	
1	<i>Polytrichum strictum</i> ^B	-0.54**		-2.83***								2.13*				
1	<i>Rhynchospora alba</i> ^V	-5.94***	1.83**								5.39**					
1	<i>Sphagnum cuspidatum</i> ^B	19.81**	-1.80**				-	6.63***	-2.0***							
1	<i>Trichophorum alpinum</i> ^V	-19.94***			7.99***									3.76***	-1.58**	
1	<i>Vaccinium uliginosum</i> ^V	Model ns														
2	<i>Betula</i> spp. ^V	-1.25***	1.89***													
2	<i>Calluna vulgaris</i> ^V	-3.88***	1.21***		1.82*											
2	<i>Cladonia deformis</i> ^L	-3.78***	1.68**													
2	<i>Empetrum nigrum</i> ^V	-2.37 ^{ns}	0.78*		3.07**		-1.58*	1.62*								
2	<i>Ledum palustre</i> ^V	Model ns														
2	<i>Pinus sylvestris</i> ^V	-4.86**	3.62***		2.65**		-0.99**		0.07*			-2.31*				
2	<i>Pleurozium schreberi</i> ^B	-5.16 ^{ns}	1.84***		4.84***		-2.06**	1.91*							1.06*	

			Predictor variables														
			Microform		Time	Habitat							Landscape				
Fun. gr.	Species	Intercept	Flat	Ditch	Time (log)	Peat nutrient status	Peat pH	Ash (log)	Decomp. rate	Thick-ness of slightly decom-posed peat	Thick-ness of res.peat layer in total	Signs of burn	Treat-ments	Area (log)	Adja-cent forest	Dist-ance from coast (log)	
3	<i>Calamagrostis canescens</i> ^V	-1.50**															
3	<i>Carex pseudocyperus</i> ^V	-8.95***		2.25**													2.7*
3	<i>Carex rostrata</i> ^V	-3.45***		2.01***	-0.05*												
3	<i>Eriophorum angustifolium</i> ^V	-5.25***	1.44**							0.78**							-0.91*
	<i>Phragmites australis</i> ^V	-4.29**								0.58*	1.63*		-1.36*				-1.31*
3	<i>Typha latifolia</i> ^V	-3.26***		2.49***													
3	<i>Warnstorfia fluitans</i> ^B	-2.50***	-2.19**														0.79*
4	<i>Bryum caespiticum</i> ^B	-3.20***											2.91***				
4	<i>Cladonia coniocraea</i> ^L	-7.17***	1.35**		3.04*												
4	<i>Epilobium angustifolium</i> ^V	-4.20***	1.99**														
4	<i>Pohlia nutans</i> ^B	Model ns															

Fun. gr.=species functional group (1=bog species, 2=acidophilous bilocals, 3=semi-hygrophytes, 4=mesophytes).

Taxonomic groups: ^B – bryophytes, ^V – vascular plants, ^L – lichens.

Significance levels: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

V. oxycoccus. Increased ash content in residual peat favoured the colonisation of bilocals *E. nigrum* and *P. schreberi* and the semi-hygrophyte *P. australis*.

The landscape properties of extracted peatlands influenced the establishment success of six core species. A larger area of abandoned peatland predicted the occurrence of *Trichophorum alpinum*, *Carex pseudocyperus* and *Warnstorffia fluitans*. Being in the neighbourhood of forests increased the occurrence of a forest species *P. schreberi* and also a bog species *V. oxycoccus*. At the same time, forest neighbourhood was negatively correlated with the occurrence of fen species (the semi-hygrophyte group) *T. alpinum* and *Erioph. angustifolium*. Increased distance of the extracted peatland from the sea was negatively correlated with the occurrence of *P. australis*, showing that reed is enhanced by maritime climate conditions.

Functional groups

The results of the GLM analyses show the increase of species richness over time in three functional groups, most frequently on flats and most infrequently in ditches (Table 2, Figure 2). Among them, bog species showed the most uniform levels of accumulation over all three microforms (Figure 2A). Bilocals and mesophytes accumulated mostly in flats and ditch

margins. Semi-hygrophytes were not constrained by time, and they were equally represented in flats and ditches, but less in ditch margins (Figure 2C).

The effects of residual peat properties varied among functional groups. The most common substrate indicator was peat pH. On very acidic residual peat, bog species established uniformly across all microforms (Figure 2A), and that was supported by the higher thickness of the slightly decayed residual peat layer. Bilocals were positively correlated with low pH-levels only in flats and ditch margins (Figure 2B). In contrast, semi-hygrophytes were facilitated by high peat pH, but mostly in ditches, and they preferred thin layers of slightly decayed peat in flats (Figure 2C). Mesophytes had mixed reactions to pH, as they preferred high pH on flats and low pH in ditch margins (Figure 2D). However, they showed clear preferences for higher ash content in peat (Table 2, Figure 2D).

The positive effect of the forest neighbourhood around the extraction area was only observed in bilocals (Table 2, Fig 2B). Bilocals and semi-hygrophytes were also correlated to proximity to the sea, but this effect was microform-specific: under maritime conditions, the richness of bilocals increased in ditch margins and the richness of semi-hygrophytes increased in ditches (Table 2, Figure 2B, C).

Table 2. GLM analysis showing significance levels (p-values) of environmental conditions affecting the species richness of functional groups. For descriptions of functional groups, see legend to Figure 2. Model effects are illustrated in Figure 2. Significant p-values are shown in bold font.

Factor	Functional group of species			
	Bog species	Acidophilous bilocals	Semi-hygrophytes	Mesophytes
AdjR ²	17.4	48.3	26.0	31.9
Intercept	0.1465	0.2027	0.1062	0.1985
Microform	0.0144	0.7110	0.1527	0.0208
Time (log)	0.0068	0.0008		0.0035
Microform *Time		0.0389		0.0041
Slightly decayed peat	0.0002		0.1288	
Microform*Sl.Decayed p.			0.0156	
Peat pH	0.0013	0.0008	0.0001	0.7682
Microform*pH		0.0279	0.0316	0.0220
Ash content (log)				0.0192
Neighbourhood forest		0.0038		
Distance from coast (log)		0.0467	0.1226	
Microform*Distance		0.0217	0.0263	

Similarity in ecological filters

Core species and their functional groups had only partial similarity in limiting filters (Table 3). The strongest agreement between core species and functional groups was in the effect of microform filters on bilocals, as 86 % of the core species models shared indicators of the same filter type with their respective functional group models. The reaction of other functional groups to microform type was supported by half of their core species (44–57 % of species models). The filtering effect of time since abandonment and substrate properties found in functional groups was partially supported from respective core species, with agreement between models varying from 25 % to

57 %. In addition, the importance of time since abandonment was reflected in semi-hygrophytes by only a single core species within this group. The importance of landscape filters, such as the effect of site area and neighbourhood habitats, was partially corroborated in the case of bilocals with agreement by a single species. The importance of spatial effects was also suggested by core species of bog specialists and semi-hygrophytes, but uncorroborated at functional group levels. The suppressing effect of continentality found in bilocals at the functional group level was not supported by any individual core species, while the effect on the semi-hygrophyte group was supported by only one core species.

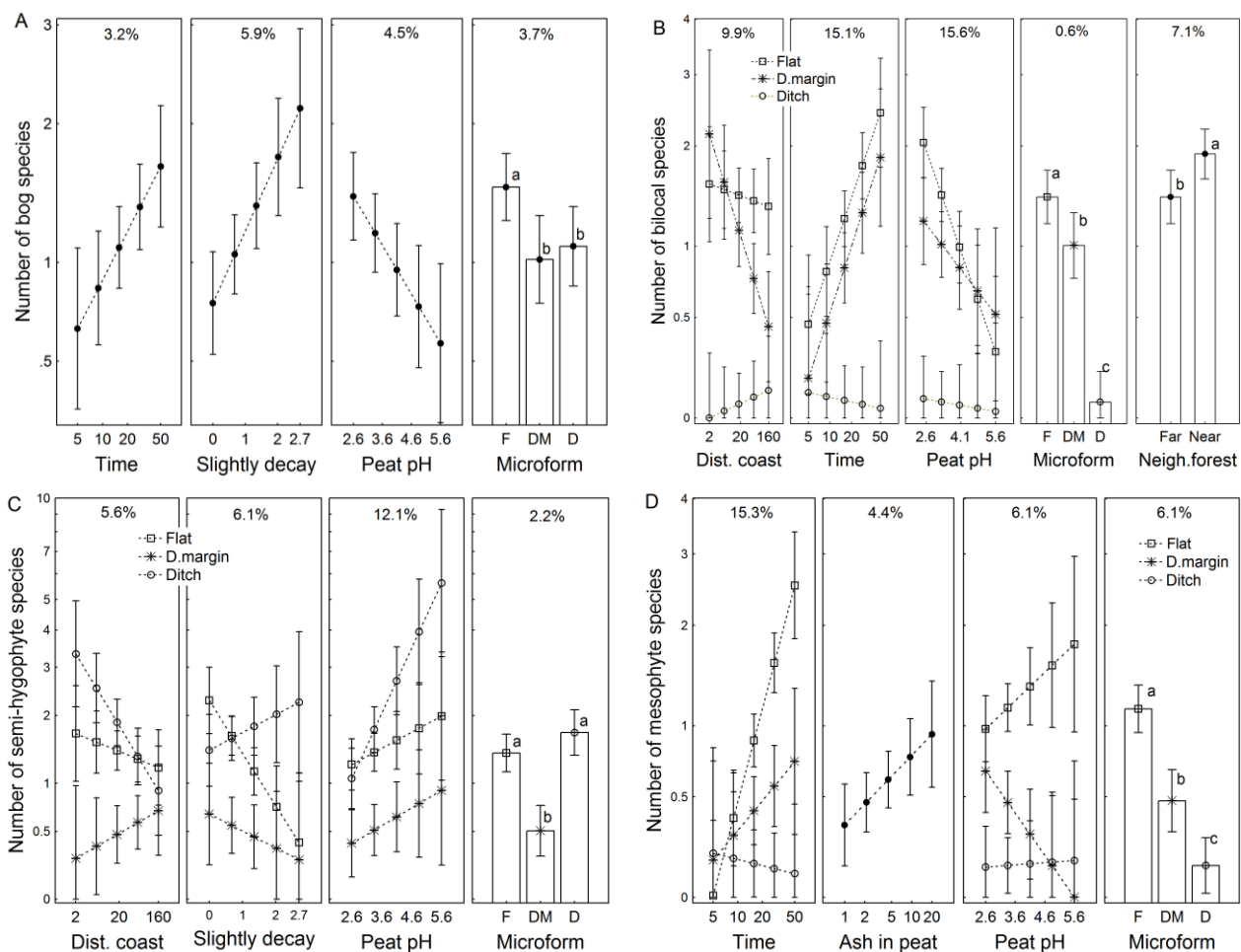


Figure 2. General linear model (GLM) predictions of species richness for four functional groups: A) bog species (raised bogs and transitional mires); B) acidophilous bilocals (raised bogs and heaths); C) semi-hygrophytes (early successional bogs including fens, swamps and some drier habitats); and D) mesophytes (mineral soils). Accompanying statistics are given in Table 2. Percentages at the top of each graph denote the variability accounted by each indicator factor in the GLM models. Time = log-transformed time (years) since peatland abandonment; Slightly decayed = thickness of slightly decomposed peat (m); Peat pH = pH of the upper-layer peat (0–0.5 m); Microform = microtopographical form type; Dist. coast = distance from the sea (log-transformed, km); Ash in peat = the log-transformed ash content of upper-layer peat (0–0.5 m).

Table 3. Percent of core species models (Table 1) identifying the same filter effects as found in respective functional group models (Table 2). Additional filters only found in species models are labelled with “+”.

Functional group	Ecological filters				
	Microform	Time	Substrate properties	Landscape	Continentality
Bog species	44	33	44	+	
Acidophilous bilocals	86	57	43	14	0
Semi-hygrophytes	57	+	43	+	14
Mesophytes	50	25	25		

DISCUSSION

Similar ecology of core species and functional groups

The slow vegetation recovery of extracted peatlands allowed us to quantify the establishment of species with contrasting ecological profiles and to identify the ecological filters directing community assembly. The hypothesised similarity between the autecology of individual core species and the synecology of respective functional groups was partly confirmed. This similarity was found for around half of the core species. When considering the similarity in the effects of insignificant ecological filters on core species and their respective functional groups, this hypothesis received even greater support. Many ecological filters were found to influence different functional groups and core species of different groups; however, there were differences in optimal filter levels (as represented by contrasting slope estimates) for species of different groups. Some of the disagreement between core species and functional groups can be explained by the effect of rare species.

We conclude that core species poorly represent the ecological envelope of each other within their own functional groups, and for infrequent species the situation is even more problematic (Wilson 1999, Diaz & Cabido 2001, Cousins & Lindborg 2004, Gaston 2011). Also, species richness within a functional group might be too strongly affected by occasionally occurring species to be a truly representative response indicator of the functional group (Markham 2014, Chung *et al.* 2015, Leppik *et al.* 2015).

Microform as an ecological filter

Microform type was the most common significant ecological filter for both core species and functional groups. Microtopography is a complex factor, as it integrates the effects of a whole set of specific

limiting conditions, such as exposure to wind and other disturbance, moisture level and peat properties, and it delimits contrasting plant synusia or micro-communities (Lindsay 1995, Triisberg *et al.* 2014). Flats were important microhabitats for the establishment of all species groups, but this was not as evident at the individual species level. Ditch margins were suitable only for bilocals and somewhat suitable for mesophytes (but only at the group level). Ditches were suitable microhabitats only for semi-hygrophytes as a group, as well as for individual species in this group, showing that ditches direct successional assembly towards swamps. The importance of ditch margins and ditches should be emphasised as these linear microhabitats host relatively many species given their small area relative to flats. However, as these species are mostly non-bog specialists, these linear microhabitats should be reduced through management.

The effect of microform type per se, however, was more complicated. This was shown by the importance of interaction terms between microform and other environmental indicators in the models for functional groups. The low frequency or deterministic occurrence of core species on various microforms did not allow for the inclusion of interaction terms in the species models. The microform-dependent autecological peculiarities of core species should be quantified in the future using more detailed small-scale surveys.

Time as an ecological filter

The immigration of species, which combines the steps of dispersal and establishment, is slow in these systems, as indicated by the importance of time passed since abandonment for both core species and functional groups. Several decades are needed to detect the accumulation patterns of species at early stages of community assembly, as other studies with shorter chronosequences have shown time-

independent patterns of species accumulation during the recovery of extracted peatlands (Lavoie *et al.* 2005, Konvalinková & Prach 2014). The deliberate introduction of species has been rarely practiced in this region. Its positive effect was detected only in a bog species *V. oxycoccus*, a species that has been tested for cultivation suitability in some of these areas.

At the core species level, successional accumulation over time was confirmed for some well-known early arrival species, such as bog species *E. vaginatum* and bilocal *P. sylvestris* (Tuittila *et al.* 2000, Campbell *et al.* 2003). However, we detected even more evident time-dependence for some other species, such as bog species *T. alpinum* and *Aulacomnium palustre*, and bilocals *E. nigrum* and *P. schreberi*. Their values as indicator species for successional stages are probably underestimated as they are less conspicuous to observers than *E. vaginatum* and *P. sylvestris*. At the functional group level, the mostly uniform accumulation of species across microforms was observed for bog species, while acidophilous bilocals accumulated only on flats and ditch margins, and mesophytes only on flats. Thus, immigration rate for functional groups was microform-specific.

The vegetation of ditches was less dynamic, as the time effect was insignificant for semi-hygrophytes, the main functional group found in ditches. Apparently, semi-hygrophytes are either very efficient dispersers or they were already present before site abandonment because ditches are less managed just before peat extraction is terminated. This is supported by a weak negative effect revealed for the semi-hygrophyte *C. rostrata*, which seems to disappear during late stages of succession. According to the field experience of managers, ditches start to collapse about 50 years after site abandonment.

Substrate as an ecological filter

In general, we found similarities between core species and functional groups in their responses to the properties of the uppermost layer of residual peat. Various substrate properties have been used to explain the establishment and persistence of plant species on extracted peatlands (Salonen 1994, Beleya 2004, Triisberg *et al.* 2011, 2013). Indeed, various individual indicators were identified as significant drivers by core species and functional group models, but few of the same indicators were identified for both core species and their respective functional groups. This variability in the importance of specific substrate indicators can be explained by the microform-specific effects revealed at the functional group level (represented by interaction terms in models), except for bog specialists. Generally, peat

layer conditions, such as peat pH-level or decay level, are inter-correlated with the thickness of the residual peat layer (Laine & Vasander 1996). Specifically, at both levels (core species and functional group), a slightly-decomposed acidic peat favours the establishment of bog species and acidophilous bilocals. Other substrate properties were less consistent at both levels. For instance, higher ash content of peat promoted only mesophytes as a functional group and some other groups only at the core species level, such as bilocals (*E. nigrum* and *P. schreberi*) and semi-hygrophytes (*Erioph. angustifolium* and *P. australis*). The actual mineral content probably also reflected the inflow of dust particles from the gravel used in the paved service road network rather than naturally accumulated ash content. The act of burning itself enhanced the establishment of only one bog bryophyte *Polytrichum strictum* and one mesophyte bryophyte *Bryum caespiticum*, which are also typical post-fire species in other habitats rich in organic material. The long-term ecological consequences of suppressing pine through fire might be positive, as it reduces shading on light-demanding bog species.

Spatial context as an ecological filter

Spatial context may be important in community assembly because the intensity of seed rain depends on the proximity of propagule sources to target sites (Salonen & Setälä 1992, Houlahan *et al.* 2006, Konvalinková & Prach 2014). However, the lack of similarity between significant filters for core species and respective functional groups appeared most clearly in the role of landscape properties and regional positioning of these study sites. We detected a neighbourhood or site area effect for only six core species spread across three functional groups (the bog species, bilocals and semi-hygrophytes), while at the functional group level, only acidophilous bilocals showed evidence of this effect.

A bog species *T. alpinum* and two semi-hygrophytes *C. pseudocyperus* and *W. fluitans* were promoted by greater area of the extraction site. These species require seasonally or constantly wet microhabitats for colonisation, which appeared to be present in large-area flats where runoff efficiency is low and the probability of ditch network clogging is higher (Triisberg *et al.* 2011). Being in the vicinity of a forest suppressed the occurrence of *T. alpinum* and *Erioph. angustifolium*, which may reflect the limited availability of suitable source habitats because of neighbouring forests. Being in the neighbourhood of a forest positively affected the establishment of bilocals as a functional group, but this pattern was only supported by a single core species *P. schreberi*.

The positive effect of forest vicinity on a bog species *V. oxycoccus* can have multiple causes, such as enhanced dispersal by birds or the fact that various site treatments are performed more commonly near the margins of extraction sites for logistical reasons. We had expected positive correlations with spatial factors in mesophytes (Lavoie *et al.* 2003b), but distance from the edge and size of extraction area were not found to be important for their establishment, probably because many of them are adapted for long-distance dispersal, e.g. *Epil. angustifolium* by wind.

Estonia is a small country, but it has strong regional contrasts in climate (from maritime to continental) and geology (from limestone bedrock to sandstone bedrock). The regional specificity of species immigration success was demonstrated in two functional groups (bilocals and semi-hygrophytes) as the positive effect of being closer to the sea. At the species-level, however, this effect was found only in the semi-hygrophite *P. australis*. A milder maritime climate has been shown to enhance seed set of *P. australis*, as well as increase overwintering survival of its seedlings (McKee & Richards 1996, Egawa & Tsuyuzaki 2011). An alternative interpretation — the effect of calcium-rich bedrock in the coastal region on peat properties — is already covered by the positive effect of ash content in the model. In addition, the greater richness of bilocals near the coast indicates the sufficient acidity level of the residual peat. Therefore, we interpret the revealed effect of the maritime–continental gradient to emphasise the general harshness of establishment conditions on open peat for these species in Estonia.

CONCLUSION

The prevalence of each core species or functional group is predicted to depend on the status of ecological filters. Each of these filters may result in different successional trajectories during habitat recovery and many of these successional pathways will delay the eventual formation of peat-forming communities. We found partial evidence for the hypothesis of similar limiting factors during assembly processes between core species and their respective functional groups. This shows that even in species-poor habitats where core species are evident indicators of the community, the ecological requirements of both core species and functional groups should be considered for directing succession towards a desired state. This is because functional groups also represent the limiting ecological filters of infrequent species.

We suggest that a comprehensive list of strategies required in the restoration planning of extracted peatlands to initiate processes of natural peat formation should consist of four principles:

- (1) In general, the properties of the residual peat layer will constrain the optimal set of species to be used for restoring vegetation. However, when the restoration of a peat-forming bog community is the main target, then extraction should be stopped before exhaustion of the acidic, slightly decayed peat layer.
- (2) As ditches support mostly semi-hygrophytes, some of which are very aggressive colonisers (e.g. common reed or some sedges), partial filling of ditches is advised, and the resulting heterogeneous flats will more closely mimic the hummock-ridge-hollow microtopography which is suitable for bog and bilocal species.
- (3) The slow, stochastic arrival of species can be reversed by aided introduction of species or their propagules from neighbouring bogs or transitional mires, as well as from (heath) forests with soils rich in organic material, where the properties of organic layers resemble peat in raised bogs.
- (4) The inflow of mineral dust particles from the service road network, which may be an important filter in directing succession away from peat-forming vegetation, should be avoided.

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