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Holocene fen–bog transitions, current status in Finland and future perspectives

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Abstract

Minerotrophic fens and ombrotrophic bogs differ in their nutrient status, hydrology, vegetation and carbon dynamics, and their geographical distribution is linked to various climate parameters. Currently, bogs dominate the northern temperate and southern boreal zones but climate warming may cause a northwards shift in the distribution of the bog zone. To more profoundly understand the sensitivity of peatlands to changes in climate, we first used the plant macrofossil method to identify plant communities that are characteristic of past fen–bog transitions. These transitions were radiocarbon dated, to be linked to Holocene climate phases. Subsequently, palaeoecological data were combined with an extensive vegetation survey dataset collected along the current fen–bog ecotone in Finland where we studied how the distribution of the key plant species identified from peat records is currently related to the most important environmental variables. The fossil plant records revealed clear successional phases: an initial *Carex*-dominated fen phase, an *Eriophorum vaginatum*-dominated oligotrophic fen phase followed by an early bog phase with wet bog *Sphagna*. This was occasionally followed by a dry ombrotrophic bog phase. Timing of initiation and phase transitions, and duration of succession phases varied between three sites studied. However, the final ombrotrophication occurred during 2000–3000 cal. BP corresponding to the neoglacial cooling phase. Dry mid-Holocene seems to have facilitated initiation of *Eriophorum* fens. The peatlands surveyed in the fen–bog ecotone were classified into succession phases based on the key species distribution. In 33% of the studied peatlands, *Sphagnum* had taken over and we interpret they are going through a final transition from fen to bog. In addition to autogenic processes and direct climate impact, our results showed that ecosystem shifts are also driven by allogenic disturbances, such as fires, suggesting that climate change can indirectly assist the ombrotrophication process in the southern border of the fen–bog ecotone.

Keywords

Boosted Regression Trees analysis, fen–bog ecotone, fen–bog transition, Holocene, peatland, plant macrofossil analysis

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Introduction

Peatlands are essential ecosystems in the northern hemisphere because of their large areal extent and their large carbon (C) stock. Recently, this stock was estimated at 436 Gt C for peatlands above the 45°N latitude (Loisel et al., 2014), a significant amount when compared with the atmospheric C reservoir of about 750 Gt C. Therefore, the fate of peatlands currently under threat, particularly from climate change, is of vital importance (Dise, 2009; Moore, 2002). Climate warming is predicted to have the strongest influence on high-latitude ecosystems (Dise, 2009; IPCC, 2013), where warming will result in a northwards shift of vegetation zones (Walther et al., 2002). The ecotone between minerotrophic fens and raised bog zones is likely to be among the most vulnerable (Allen and Breshears, 1998; Hansen et al., 1992; Neilson, 1993). In Fennoscandia, climate change is expected to result in raised mean annual temperatures, increased winter precipitation, and increased summer evapotranspiration (IPCC, 2013), which are important climatic parameters in regulating peatland development, that is, vertical growth and related changes in trophic status (Andersen et al., 2011; Breuwer et al., 2009; Hughes and Dumayne-Peaty, 2002; Murphy and Moore, 2010). In particular, the predicted extension of the growing season, along with increased evapotranspiration rates that change the effective moisture conditions may accelerate

the ombrotrophication process where the peatland-type changes from groundwater-fed fen to atmospheric-fed bog (Roulet et al., 1992; Turetsky et al., 2014). In brief, fens are more nutrient rich, dominated by minerotrophic *Sphagna* and brown mosses and sedge vegetation, and have higher decomposition rates, while bogs are dominated by ombrotrophic *Sphagnum* mosses and dwarf shrubs, which produce highly resilient litter (Straková et al., 2011). Generally, fens support larger methane emissions and are weaker

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C sinks than bogs (Saarnio et al., 2009; Turetsky et al., 2014; Turunen et al., 2002).

The border line between southern raised bogs and northern fen massifs zones in Finland roughly follows the 1100 temperature sum (degree days (d.d.)) isocline (Ruuhijärvi, 1960), although isolated raised bogs also occur inside the fen zone in the north and some large peatlands have remained as fens in the south because of terrain and local hydrology. In autogenic-driven ombrotrophication, there is a gradual increase in peat thickness, and this eventually decreases the impact of groundwater, which in turn reduces the amount of available nutrients, lowers the surface pH and slows down the decomposition process, and leads to further acceleration of the rate of peat accumulation (e.g. Pastor et al., 2002; Soudzilovskaia et al., 2010). Palaeoecological studies have shown that boreal and sub-arctic peatlands that generally initiated as minerotrophic fens (Supplementary Table 1, available online and references therein) south of the 1110 d.d. isocline evolved to ombrotrophic raised bogs over the course of time. It is not yet fully resolved as to how climate conditions determine peat accumulation processes, although it is speculated that under a warmer climate peatland plant species productivity might increase, thus leading to accelerated peat accumulation (Charman et al., 2013). Consequently, if warmer climate could trigger ombrotrophication processes in fens it may also lead to a northward movement of the raised bog zone, thereby diminishing the spatial coverage of the fen zone, especially if this zone does not shift northward at the same rate (Breeuwer et al., 2009; Moore, 2002; Parviainen and Luoto, 2007; Vitt, 2006). However, these processes are not straightforwardly linked only to climate per se but are driven by several interlinked autogenic and allogenic processes (Foster and Wright, 1990; Gignac and Vitt, 1990; Payette, 1988; Tahvanainen, 2011; Tuittila et al., 2007).

Knowledge of past peatland-type changes, that is, fen–bog transitions (FBTs), when linked to climate reconstructions, may provide valuable information on the sensitivity of peatlands to future changes in climate. As such, past FBT dynamics have been relatively widely studied, especially in Europe (Supplementary Table 1, available online and references therein). However, inconsistencies occur in terminology and in classification, which obscures the interpretations and site comparisons. In many previous studies, the bog phase is assigned to start with dominance of *Eriophorum vaginatum*, while in other studies the presence of certain *Sphagnum* species is taken as an indicator of the FBT (Supplementary Table 1, available online and references therein). Moreover, in many cases transitional phases have been determined by visual inspection of the peat content in the field or laboratory (Almquist-Jacobson and Foster, 1995; Korhola, 1992; Pajula, 2000) rather than by detailed analysis of species composition under a microscope.

This study aims to contribute to the practice of how to interpret past mire plant community shifts, most importantly the FBTs, and consequently we aim to discuss how these data can be used to recognize possible ongoing change in the fen–bog ecotone. The FBT question is approached here with two independent and complementary research strategies. First, we identify key peat plant species from the peat records, which were associated with major peatland-type shifts in the past. Then, by using an extensive vegetation survey dataset collected along the fen–bog ecotone in Finland, we study how the distribution of the key species is currently related to the environmental variables that are expected to be the major drivers in the future. Major regime shifts are radiocarbon dated to link the transitions to past regional climate phases and previous studies. We hypothesize that (1) a common indicator species of FBT can be distinguished, and (2) on the basis of the FBT indicators, the trajectories of current fens near their southern border can be predicted and linked to the regional climate. On the

basis of the results, we discuss possible future FBT dynamics in boreal peatlands and frame our findings in a broader context.

Material and methods

Palaeoecological study sites

To define the key species indicative of ombrotrophication, we studied vegetation succession from peat cores sampled from three open bog sites located in different parts of Finland within the boreal zone (Figure 1). Peat samples were cored with a Russian peat corer in the summer of 2011. The mires were selected on the basis of their location on the north–south fen–bog gradient and their differential development phase in relation to ombrotrophication. The most southern site Siikaneva (61°50'N, 24°10'E) is situated in the southern boreal vegetation zone. It is a large (1300 ha) oligotrophic fen (OF) that contains a number of isolated ombrotrophic cupola and therefore presents an interesting setting to explore the factors that trigger FBTs. The majority of Siikaneva is in a natural state. The peat core (450 cm) was taken from a *Sphagnum magellanicum* lawn. The other two sites, Honkanneva and Puohtiinsuo, are located at the fen–bog ecotone in the middle-boreal vegetation zone. Honkanneva (64°34.39'N, 25°20.35'E) is situated in western Finland (Figure 1). Despite the presence of ditches and peat mining in an adjacent area, our study area in Honkanneva has remained in its natural state (Ronkainen et al., 2013). The peat core (280 cm) was taken from a *Sphagnum balticum* dominated lawn. The Puohtiinsuo complex (62°43'N, 31°06'E) in eastern Finland contains ombrotrophic areas in the upslope parts where the sample core was taken. The coring point was an *S. magellanicum*-dominated lawn and the peat core was 480 cm long.

Plant macrofossil analysis

The peat cores were subsampled into 2-cm slices and the final analysis resolution was 6 cm. A 5-cm³ subsample was taken for macrofossil analysis. The subsample was cleaned under running water using a 140-µm sieve. A stereomicroscope was used for identification and the percentage cover of different plant remains was determined on a petri dish with the aid of scale paper. We applied a modified Quadrat and Leaf Count protocol (QLC) (Mauquoy and van Geel, 2007; Väliänta et al., 2007). Seeds, leaves, charcoal particles and *E. vaginatum* spindles were counted as absolute numbers. Species-level identification was performed with a high power light microscope when the proportion of bryophytes was more than 15%.

Radiocarbon analysis

To define the timing of peatland initiation and the major plant community shifts in the studied peat profiles, a total of 10 peat samples were sent for AMS radiocarbon dating to the Finnish Museum of Natural History (LUOMUS). Dated levels were chosen based on palaeobotanical variations in the plant macrofossil record (Figure 2). Radiocarbon ages Before Present (BP) were calibrated using Intcal09-age calibration curve (Reimer et al., 2009) (Table 1) and 2-sigma range median values are used for discussion.

Palaeoecological data analysis

We applied detrended correspondence analysis (DCA) to study the main variations in historical vegetation. In order to analyse species replacement along the major gradient, we used Generalized Additive Models (GAM) (Guisan et al., 2002) to define species response to the first DCA axes.

In the GAM model, a logarithmic link function was applied assuming a Poisson distribution of errors.

Figure 1. Locations of the study sites. Three palaeoecological sites are marked by triangles, 1 = Honkanen, 2 = Siikaneva, 3 = Puotiinsuo, and 21 vegetation survey sites by circles. The dashed line indicates roughly the current border line that separates the southern bog zone from the northern fen zone. The solid lines indicate the approximate historical position of the Baltic Sea ca. 10,000 and 7,000 years ago, respectively, redrawn from Eronen et al. (2001). The current land uplift rate near the study site 1 is 7 mm yr⁻¹ (see also Tuittila et al., 2013), while in the southern coast of Finland the uplift rate is <2 mm yr⁻¹.

We applied variation partitioning (Borcard et al., 1992; Vandvik and Birks, 2002) of macrofossil data to examine the relative importance of autogenic development related to growth in peat thickness and to the disturbance succession related to fire events for the composition of peatland vegetation during its history. Explanatory variables were split into three groups: (a) peat thickness, (b) fire history (including time since fire event and occurrence of charcoal particles of >1 mm and charcoal particles of <1 mm) and (c) peatland site. The latter was included to address site-specific variations in autogenic development and fire succession. We used canonical correspondence analysis (CCA) that is suitable for data with high compositional variation

and excluded species with less than six occurrences. Data were log-transformed to stabilize the variance and to obtain a more symmetric distribution. Significance of variables ($p < 0.05$) was assessed using the Monte-Carlo permutation test before they were included. Analyses were conducted with CANOCO 5.0. (Ter Braak and Šmilauer, 2002).

Vegetation survey along the current FBT zone

To quantify the ecological niche of the key species indicative of ombrotrophication, and to estimate the current successional phases of peatlands in the fen-bog ecotone, we collected plant

Honkaneva

Siikaneva

Puohtiinsuo

Figure 2. Selected plant macrofossil taxa and chronological data for the three study sites: Honkaneva, Siikaneva and Puohtiinsuo, Finland. Macroscopic charcoal finds are counted as numbers and indicated by #; other remains are expressed as percentages proportions.

species and environmental data from 21 peatlands north of the geographical margin of bog and fen complex types in Finland (Figure 1). Quantification of the ecological niche was based on

the assumption that species have their highest abundance at their optimal conditions. Estimation of successional phase was based on the assumption that historical phases identified with

Table 1. Radiocarbon analyses results of peat profiles from the three study sites: Honkaneva, Siikaneva and Puohtiinsuo, Finland.

Lab. code	Sample	¹⁴ C BP age	Calibrated 2-sigma range and the median
Hela-2857	Honkaneva 118–120 cm	1115 ± 30	1120–935, 1015
Hela-2858	Honkaneva 142–144 cm	3144 ± 31	3445–3270, 3375
Hela-2859	Honkaneva 262–264 cm	4099 ± 36	4815–4445, 4615
Hela-2860	Honkaneva 276–278	4133 ± 36	4825–4530, 4675
Hela-2868	Siikaneva 272–274 cm	3197 ± 32	3470–3360, 3415
Hela-2869	Siikaneva 406–408 cm	6858 ± 46	7795–7590, 7690
Hela-2870	Siikaneva 446–448 cm	8481 ± 54	9550–9420, 9495
Hela-2865	Puohtiinsuo 122–123 cm	2072 ± 32	2130–1945, 2040
Hela-2866	Puohtiinsuo 284–286 cm	5966 ± 43	6900–6675, 6800
Hela-2867	Puohtiinsuo 476–478	9005 ± 58	10,255–9915, 10,180

palaeoecological data analysis from peat cores could also be seen in current vegetation. From aerial photographs, we selected basins or sub-basins that appeared as typical fens. The vegetation data were collected along transects that crossed the peatlands with a study point interval of 20 m. At each study point, pH, peat thickness and water table (WT) levels were measured and vegetation coverage (%) surveyed from three replicates using circular relevés of 30 cm in diameter. A total of 272 transect points with 673 vegetation relevés were surveyed in August 2011.

The western part of the ecotone is characterized by more enhanced post-glacial rebound that continuously exposes new land and enables primary paludification (Ekman and Mäkinen, 1996). Topographically, western Finland is lowland and the topography in the eastern part of the ecotone is more variable with some supra-aquatic high areas that were never inundated by any of the post-glacial Baltic Sea phases (Figure 1; Tikkanen and Oksanen, 2002). Accordingly, eastern peatlands are on average older than the western peatlands at the same latitude.

Mean annual precipitation (P) in the western and eastern parts of the study area is on average 563 and 650 mm, respectively. The mean annual temperature is 1.6°C throughout the studied transition areas. The January mean temperature is slightly lower in the east (−11.1°C) than in the west (−10.7°C), although the July mean temperatures are similar (15.5 and 15.6°C). Temperature sum in d.d. is 1000 to 1200 and the annual potential evapotranspiration (PET) is about 287 mm. In the west, the difference between annual precipitation and annual potential evapotranspiration (P–PET) is smaller (286 mm) than in the east (362 mm) (Finnish Meteorological Institute, 1961–1990 measurement period). In the west, the climate is slightly more oceanic and the growing season longer (Karlsen et al., 2006).

Analysis of the relationship between living plant species and environmental parameters

The key plant species indicative of ombrotrophication based on palaeobotanical data were selected for environmental response analyses. We used Boosted Regression Trees (BRTs) to model the species response to WT, peat thickness, pH, and the 30-year means of climate parameters (T and P) (Finnish Meteorological Institute, 1961–1990 measurement period). BRTs have been proven to perform well in studies on species responses to environmental variables (De'ath, 2007; Elith et al., 2006; Leathwick et al., 2006; Moisen et al., 2006). BRTs rely on numerical optimization that minimizes residuals and consist of two algorithms: regression trees based on binary splits, and boosting that connect the regression trees into a final model (Elith et al., 2008). As a result, BRT assigns relative importance of each model parameter to the response variable based on how many times each of the parameters was allocated to the regression trees. The possible interactions are automatically counted (Elith et al., 2008) and each tree is made from a random subset. Generalized Boosted

Regression Models were made with libraries *gbm* (Ridgeway, 2012) and *dismo* (Elith et al., 2008) in R software (R Development Core Team, 2010). Interaction depth was set to 3, learning rate to 0.001, and Gaussian distribution was used. Multicollinearity was taken into account by choosing only parameters that did not correlate strongly $|r| < 0.70$. In BRTs, a number of simple regression-tree models are combined for each of the key species to produce a final predictive model. The final models were selected by cross-validating the deviance explained (Elith and Leathwick, 2015).

The current succession phase of each studied peatland was defined by relating the current vegetation composition to the vegetation composition in successional sequences defined from the peat cores. We calculated the proportion of key species and plant groups for the succession phases, identified from palaeobotanical data, from the total coverage of the current vegetation. The determination was based only on the vegetation data collected from the centres of the study basins (defined as central 50% of the transect length, $n = 371$ vegetation plots) because the edge vegetation in fen massifs is typically formed by bog species.

Results

Variation in palaeoecological records

The palaeobotanical records from the three peatlands revealed distinct succession phases (Figure 2), which were also clearly seen in the groupings of species response curves along the main gradient in the historical vegetation (Figure 3). These were (1) an initial *Carex*-dominated fen (CF) phase that was characterized by key minerotrophic species such as *Carex* spp., *Scheuchzeria palustris*, *Equisetum* spp. and *Menyanthes trifoliata* (right end of axis 1 in Figure 3). The CF phase was followed by (2) an OF phase, where *E. vaginatum* clearly dominated the plant assemblages (middle of axis 1 in Figure 3), and (3) a *Sphagnum*-dominated bog (SB) phase that typically initiated as a wetter *Sphagnum* phase with species such as *S. balticum*, *S. angustifolium* and *S. magellanicum* (SB I). In some cases, SB I was replaced by hummock communities that included for instance *S. fuscum* and *S. rubellum* (SB II) (left end of axis 1 in Figure 3). The dry phase (SB II) was not always clearly visible in the palaeo-communities as the coring took place in a lawn surface. Our records suggest that the FBT is characterized by replacement of *Eriophorum* by ombrotrophic *Sphagnum*: *S. balticum*, *S. angustifolium* and *S. magellanicum*. Accordingly, these four species are identified as key FBT species. In Honkaneva, the transition from CF to OF occurred at 4615 cal. BP. The change from OF to SB was gradual but can be assigned to around 3300 cal. BP, when the amount of *S. angustifolium* started to increase. The minerotrophic and *Eriophorum* phases lasted 60 and 1240 years, respectively. In Siikaneva, the transition from CF to OF occurred at 7690 cal. BP and the change from OF to SB, when the amount of *E. vaginatum* clearly decreases, occurred at 3415 cal. BP (Figure 2). The CF and OF

phases lasted 1800 and 4280 years, respectively (Table 2). In Puohtiinsuo, the transition from CF to OF occurred at 6800 cal. BP, and the transition from OF to SB occurred at 2040 cal. BP. The CF and OF phases lasted 3335 years and 4760 years, respectively.

Variation partitioning indicated that peat thickness, time since fire event and peatland initiation together explained 43.4% of the variation in the palaeobotanical records of the three Finnish mires (Supplementary Figure 1, available online). Autogenic succession driven by peat thickness was site-specific while peat thickness alone explained only 2.6% of the variation in palaeovegetation composition, when combined with site-specific succession it explained 11.4% of the variation. Species succession following fire was more common between the sites; time since fire alone explained 3.6% of the variation and when combined with site-specific fire succession it explained 6.3%. Differences in the palaeobotanical records between the three Finnish peatlands were responsible for 15.3% of the variation.

Current vegetation: Key species' relationship to environmental factors

According to BRT analysis, WT, pH and peat thickness were clearly the most powerful factors (relative contribution of the variables typically over 10%) that determine species distribution in the studied fens (Figure 4a and b). Grouping of individual climate variables was found to have a less powerful impact on WT than when the variables were inspected separately. The key species had different WT optima, pH and peat thickness values, and

the level of significance of the environmental variables also varied (Table 3). *E. vaginatum* and *S. balticum* were more abundant on sites with lower pH and a thicker peat layer, whereas *S. angustifolium* and *S. magellanicum* thrived on sites with higher pH (Figure 4a and b). Less important environmental factors were PET for *E. vaginatum*, P for *S. balticum* and the water balance for *S. magellanicum*. The Spearman rank correlations between the observed and predicted values were good for the *E. vaginatum* and *S. balticum* models; however, the *S. magellanicum* model performed very poorly (Table 3).

Current succession phases along the fen–bog gradient and their environmental characteristics

The key species for the different succession phases were defined from the palaeobotanical data, namely *E. vaginatum*, *S. angustifolium*, *S. balticum* and *S. magellanicum* (Figures 2 and 3). The current succession phase of each peatland along the ecotone was defined based on the proportional abundance of those species. All defined succession phases based on palaeobotanical data were represented in our plant community inventory. From the study sites located in the recent FBT zone, 57% were categorized as a minerotrophic fen phase based on the dominance of *Carex* spp. in the field layer, five peatlands in the western study area and six peatlands in the eastern study area (Figure 5). Only 10% of the surveyed sites were currently in the OF phase that precedes the FBT, while 33% were currently in the middle of a transition from fen to bog. This phase is characterized by a proportional increase in *Sphagnum*. Median pH for CF, OF and FBT sites was 4.17, 3.92 and 3.89, respectively. Mean peat thickness was 2.2, 2.1 and 2.8 m for the CF, OF and FBT sites, respectively.

Figure 3. Generalized Additive Models (GAM) response patterns of the identified key species illustrate the different succession stages. In axis 1, early succession fen species occur on the right while bog species become more abundant on the left side of the axis. *Eriophorum vaginatum* occurs in the middle of the succession where it acts as an ecosystem engineer.

Discussion

Past succession phases, timing of transitions and climate implications

OF phase. In all our palaeobotanical study sites, an OF phase dominated by *E. vaginatum* preceded the FBT, that is, emergence of bog *Sphagnum* species in all peat cores. This corresponds to what has been reported by previous studies (e.g. Dudová et al., 2013; Hughes, 2000; Hughes and Barber, 2004; Hughes and Dumayne-Peaty, 2002) (Supplementary Table 1, available online). *E. vaginatum* has been identified as an ‘ecosystem engineer’ that changes the habitat conditions so that they are more suitable for the establishment of oligotrophic–ombrotrophic *Sphagnum* mosses (Hughes and Dumayne-Peaty, 2002). The long and aerenchymatous roots that are a characteristic feature of *E. vaginatum* allow large WT fluctuations to be tolerated. Moreover, the highly resistant remains of *E. vaginatum* promote peat accumulation and consequent ombrotrophication (Coulson and Butterfield, 1978; Wein, 1973).

In Siikaneva and Puohtiinsuo, the *Eriophorum*-phase corresponds to the dry and warm mid-Holocene period between ca. 8500 and 5000 cal. BP (Seppä et al., 2005; Snowball et al., 2004). Low effective moisture likely resulted in lowered WT levels (Korhola et al., 2005; Mathijssen et al., 2014; Välranta et al., 2005), and this would have benefited tolerant plant species, such

Table 2. Duration of different peatland succession phases and the timing of the fen–bog transition in the three study sites: Honkaneva, Puohtiinsuo and Siikaneva, Finland.

Site	Mire initiation cal. BP	Duration of minerotrophic fen phase	Timing of minerotrophic fen– <i>Eriophorum</i> fen transition	Duration of <i>Eriophorum</i> fen phase	Timing of fen–bog transition
Honkaneva	4675	60	4615	1240	3375
Siikaneva	9495	1800	7690	4280	3415
Puohtiinsuo	10,180	3335	6800	4760	2040

(a)

(Continued)

Figure 4. Response of living key plant species; *Eriophorum vaginatum* and *S. balticum* (4a), and *Sphagnum angustifolium* and *S. magellanicum* (4b), to the various environmental factors based on Boosted Regression Tree model (BRT). Columns present the relative influences of each variable. The most important factors are peat thickness, pH and water table level. Partial dependence plots for each parameter in the BRT models. Predictors are centered and are on a standard deviation scale. Partial dependency functions (Friedman 2001) visualize the dependency between fitted response (vertical axis) and each predictor. The vertical axes in partial dependency plots are not comparable with the range of the response variable. Nevertheless, the shape of the partial dependency function reflects the effect shape and the range is proportional to the relative contribution of the predictor (Friedman 2001). Note the different vertical axes ranges in plots. Note that the response curves to parameters with low relative influence (< 5%) are unlikely to contain much relevant information.

Table 3. Correlations between pH, water table level and peat thickness and key species coverage (%). Values in bold are statistically significant ($p < 0.01$).

	<i>E. vaginatum</i>	<i>S. angustifolium</i>	<i>S. balticum</i>	<i>S. magellanicum</i>
pH	-0.31	0.14	-0.48	0.00
Peat thickness	0.11	-0.17	0.38	-0.02
Water table level	-0.13	-0.27	0.10	-0.12

Figure 5. Inferred current succession stages of the studied peatlands along the fen–bog ecotone based on the vegetation survey. White dots indicate minerotrophic fens, the grey dots represent sites that are in an *Eriophorum*-phase preceding the final fen–bog transition, and black dots indicate peatlands where the amount of bog *Sphagnum* was notable, that is, bogs.

as *E. vaginatum*. In contrast to the other sites, the initiation of the *Eriophorum*-dominated OF phase at the youngest site Honkanen only seems to start long after the large-scale climate shift towards cool and moist conditions around 5000 cal. BP. This suggests that post-glacial rebound has been an important driving factor in changing peatland hydrology. Previous data, for instance from Ireland and England, show that the duration of the *Eriophorum*-dominated OF phase varied considerably (380 to 1800 years) between sites (Supplementary Table 1, available online).

Fen–bog transition. The key transitional *Sphagnum* species in our study, *S. angustifolium*, *S. balticum* and *S. magellanicum*, have also been identified by earlier studies as important early-stage bog species (e.g. Bohlin, 1993; Hughes, 2000; Loisel and Garneau, 2010; Robichaud and Bégin, 2009; Sillasoo et al., 2007; Tuittila et al., 2007). Hummock communities with *S. fuscum*, *S. rubellum* and dwarf shrubs are seen as climax bog communities (Klinger, 1996). These species are commonly found in hummock microforms in our study sites, and more generally in the region of

this study. Our results taken in conjunction with others would suggest that bog development can proceed either through a wet or a dry *Sphagnum* phase (Almqvist-Jacobson and Foster, 1995; Hughes, 2000; Pajula, 2000).

In our study sites, FBT occurred during the period 3375–2040 cal. BP (Table 2) when the cool moist climate had already prevailed for millennia. Many, but not all, previous studies have reported that initiation of the ombrotrophication process occurred during the late-Holocene period (Bohlin, 1993; Hughes and Dumayne-Peaty, 2002; Janssen, 1992; Korhola, 1992) (Supplementary Table 1, available online). In some southern Finnish peatlands, the FBT already occurred in the early Holocene (Tolonen, 1966). As a general rule, in Europe, towards north the ombrotrophic peat layer is typically younger than in the south (Tolonen, 1987). Moreover, *Eriophorum*- and bog *Sphagnum*-dominated peat layers alternate and co-occur throughout peatland history often as a result of fire events and no clear FBT may be visible (Mathijssen et al., 2016; Tuittila et al., 2007). Such discrepancies highlight the fact that peatland

succession patterns are also regulated by factors other than climate or autogenic succession.

Initiation of bog development in moist conditions is in slight contradiction to the view that low moisture availability, for instance as a result of autogenic vertical peat growth or catchment processes, such as drainage (Tahvanainen, 2011), is an essential factor triggering the ombrotrophication process (Hughes, 1997, 2000; Leah et al., 1998). An alternative hypothesis proposes that increased precipitation may wash the nutrients from the already slightly convex peatland surface thereby creating suitable ombrotrophic habitats for bog *Sphagnum* establishment (Hughes, 2000). A cool and humid climate can also slow down decomposition rates thus accelerating peat accumulation (Andersson and Schoning, 2010), and consequently promote ombrotrophication. This fundamental process is also included in the peatland development model of Frolking et al. (2010).

Even though the late-Holocene has been characterized as a moist climate phase, macroscopic charcoal records from boreal bogs, which indicate repeated intensive fire frequency periods, suggest that prolonged summer droughts have synchronously occurred during the last 5000 years (Morris et al., 2015; Sillasoo et al., 2011; see also Ronkainen et al., 2013). The importance of fire events was also observed in the variation partitioning where fire succession explained 6% of the compositional variation during the history of the peatlands. The presence of macroscopic charcoal particles in the Siikaneva record during the *Eriophorum*-phase suggests local fires. Severe fires may actually have a two-fold influence: the burning may result in temporary wet conditions when burning lowers the surface level close to the WT (Sillasoo et al., 2011), and/or the reduction in vegetation may decrease evapotranspiration rates (Tuittila et al., 2007). In any case, *E. vaginatum* has been found to benefit from fires (Tuittila et al., 2007) and other disturbances: it is an early colonizer where resources become rapidly available (Komulainen et al., 1999; Tuittila et al., 2000). Its appearance may further assist the ombrotrophication process.

Future trajectory of succession at the Finnish fen–bog ecotone

The succession phases that were defined from the palaeoecological data were also detectable in the plant survey data. Peatland succession towards the bog phase seems to have proceeded further in the east than in the west of the country (Figure 5). This may be partly linked to landscape evolution and land uplift so that the peatlands are younger in western Finland (Figure 1; Huttunen and Tolonen, 2006; Tikkanen and Oksanen, 2002). It should be noted, however, that age is not a very strong succession phase determinant; peatlands in Lapland had already initiated during the early Holocene period, but have remained as fens since mainly because of climate (e.g. Mäkilä and Moisanen, 2007; Väiliranta et al., 2014). Climate envelope models suggest that temperature is the most important individual climate parameter to define the current distribution of bogs and fens (Parviainen and Luoto, 2007). Moreover, strong spring floods caused by snow melt, are considered to be essential for the maintenance of fens as they restrict *Sphagnum* growth (Granath et al., 2010).

Our results also reveal the importance of pH and WT level for peatland vegetation and are in agreement with several earlier studies (e.g. Bubier, 1995; Gignac, 1992; Hughes and Barber, 2004; Jeglum, 1971; Lemly and Cooper, 2011; Økland et al., 2001; Vitt and Slack, 1984) (Figure 4a and b). Peat thickness, pH and WT are local factors that have a direct effect on plants. However, these factors are strongly linked to temperature, precipitation and evapotranspiration, and this complicates the interpretation.

According to recent climate scenarios, the climate is unlikely to change unanimously all over Fennoscandia for instance (Gong et al., 2012), and consequently, assessment of the implications for

ecosystem functioning is a challenge. WT levels in peatlands correlate strongly with the precipitation–evapotranspiration ratio, in particularly with the summer moisture deficit (Charman et al., 2006). While evapotranspiration models differ from region to region, higher temperatures generally lead to increased evapotranspiration rates and a lowering of WT levels (Heijmans et al., 2013). A recent model prediction for Finland based on ACCLIM climate change scenarios (Gong et al., 2012) showed that average water levels over the period 2000–2099 would decrease by 2–4 cm, and by up to 11 cm in the south-western parts of the fen region. Water level draw-down is predicted to be most pronounced in late spring (Gong et al., 2012) thereby diminishing surface water flow and the spring flood effect, and this may stimulate *Sphagnum* production and thus bog development (Bauer et al., 2003). Lowered WT levels can also promote tree establishment on peatlands (Päivänen, 1999; Päivänen and Hännell, 2012). This may increase evapotranspiration and lower the WT even further (Sarkkola et al., 2010), which again benefits the establishment of dry bog species, such as *S. rubellum* and *S. fuscum*. Under suitable conditions, the FBT can happen quickly, even within years if bog *Sphagnum* invade the peatland (Granath et al., 2010; Kuhry et al., 1993; Loisel and Yu, 2013; Tahvanainen, 2011; Tuittila et al., 2013). Once established, *Sphagnum* mosses have the ability to change the ecosystem to their advantage by acidifying the habitat and creating after their death a water logged, anoxic, nutrient poor environment that impedes other species.

There is evidence from Finnish Lapland to show that the dry mid-Holocene climate, which can be used as an approximate analogue for a future climate, and associated lowering of the fen WT did not trigger bog development, but instead produced a dramatic slow-down in peat accumulation (Mathijssen et al., 2014). It may be that spring flood patterns did not change in this region and thus pH levels remained high, which prevented bog *Sphagnum* establishment (Granath et al., 2010).

According to the peatland habitat theory, the concave shape of fens should mean that the centres of fens support mainly minerotrophic lawn or flark species, vascular plants and bryophytes. Thus, in this study those fens where the key FBT species, *E. vaginatum*, *S. angustifolium*, *S. balticum* and *S. magellanicum*, were abundant in the centre, were classified as FBT sites. It can be speculated that the abundant presence of various bog *Sphagnum* species may result in increased peat accumulation rates in the near future (Breeuwer et al., 2009; Gorham, 1991).

Conclusion

The palaeobotanical analyses clearly revealed some key species that have been involved in past FBTs after the initial fen phase (hypothesis 1). These were *E. vaginatum*, *S. angustifolium*, *S. balticum* and *S. magellanicum*. The following succession phases were detected from the peat records: a CF phase, an *E. vaginatum*-dominated OF phase and a true bog phase, where wet bog *Sphagnum* replaced *Eriophorum*. Bog succession may continue and eventually wet bog communities could be replaced by dry bog species. The duration of these phases varied but the FBT mainly occurred during the late-Holocene. Based on our knowledge of how nutrient levels and hydrological functioning differ between oligotrophic fens and raised bogs, we suggest that in the future only the transition that separates the *Eriophorum*-dominated phase from the phase dominated by ombrotrophic *Sphagnum*, wet or dry, be called an FBT, even though we acknowledge that this transition is not always clearly definable.

All succession phases identified from our palaeobotanical data were also detected in the current fen–bog ecotone. Our analysis confirmed our second hypothesis whereby on the basis of the FBT indicators the trajectories of current fens located near the 1100 d.d. isocline border can be predicted and linked to regional climate. Our results also showed that 43% of the ecotonal peatlands

surveyed in this study are currently undergoing a change towards more ombrotrophic conditions. Climate change accompanied by autogenic succession may drastically alter the spatial proportions of fens and bogs by increasing the amount of bog area. Our study provides the basis for future studies to investigate if and how peatland succession proceeds.

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