Plant diversity and functional trait composition during mire development

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SUMMARY

During succession, plant species composition undergoes changes that may have implications for ecosystem functions. Here we aimed to study changes in plant species diversity, functional diversity and functional traits associated with mire development. We sampled vegetation from 22 mires on the eastern shore of the Gulf of Bothnia (west coast of Finland) that together represent seven different time steps along a mire chronosequence resulting from post-glacial rebound. This chronosequence spans a time period of almost 2500 years. Information about 15 traits of vascular plants and 17 traits of mosses was collected, mainly from two different databases. In addition to species richness and Shannon diversity index, we measured functional diversity and community weighted means of functional traits. We found that plant species diversity increased from the early succession stages towards the fen–bog transition. The latter stage also has the most diverse surface structure, consisting of pools and hummocks. Functional diversity increased linearly with species richness, suggesting a lack of functional redundancy during mire succession. On the other hand, Rao's quadratic entropy, another index of functional diversity, remained rather constant throughout the succession. The changes in functional traits indicate a trade-off between acquisitive and conservative strategies. The functional redundancy, _i.e._ the lack of overlap between similarly functioning species, may indicate that the resistance to environmental disturbances such as drainage or climate change does not change during mire succession. However, the trait trade-off towards conservative strategy, together with the developing microtopography of hummocks and hollows with strongly differing vegetation composition, could increase resistance during mire succession.

KEY WORDS: autogenic control, community weighted functional trait, functional diversity, primary succession, species diversity

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INTRODUCTION

Mires are peat accumulating ecosystems that store large quantities of carbon as peat, mostly since the last ice age. In the northern peatlands in Scandinavia, Russia, Siberia and Canada this peat accumulation still continues (_e.g._ Yu 2012). Generally, mires develop from ground or surface water influenced fens to more acidic bogs during several millennia following their initiation (Van Breemen 1995, Bauer _et al._ 2003, Hughes & Barber 2003). The speed of the succession appears to depend on climate and catchment hydrology: in northern boreal and arctic areas, cool climate and long periods of flooding after snowmelt have induced persistence of the fen stage, while most mires in the mid-boreal and southern boreal zones have reached the bog stage (Väliranta _et al._ 2017). However, a sudden lowering of the water table can induce ombrotrophy, _i.e._ a transition from fen to bog (e.g. Kuhry _et al._ 1993, Hughes & Barber 2003, Tahvanainen 2011).

Climate change scenarios predict increased aeration of the soil and changes in N availability (Basiliko _et al._ 2006, Bragazza _et al._ 2006). Such changes could alter vegetation production and the rate of decomposition in mires (Bridgham & Richardson 2003, Breeuwer _et al._ 2008) and consequently may threaten the functioning of mires as active carbon sinks in the future (Gong _et al._ 2013, Wu & Roulet 2014). However, if climate change accelerates autogenic succession in such a way that northern fens are overgrown by bog vegetation (Tahvanainen 2011, Väliranta _et al._ 2017), their carbon sink function may even increase as bogs

usually have a higher or, at least, more stable peat accumulation capacity than fens (Turunen *et al.* 2002, Drewer *et al.* 2010, Mathijssen *et al.* 2016).

During vegetation succession, a change in species composition occurs as one plant community is replaced by another (Miles 1987, Cortez *et al.* 2007), and both species turnover (Wheeler 1980) and environmental conditions change (Van Diggelen *et al.* 1996). The community composition depends on the stage of succession since individual species thrive best under certain types of environmental conditions (Van den Broek & Beltman 2006). During mire succession tall herbs and sedges that prevail in the early stages are gradually replaced by dwarf shrubs and *Sphagnum* mosses (Klinger & Short 1996). The shift to dominance by *Sphagnum* moss is a turning point (Magyari *et al.* 2001) as their high water absorbing capacity and resistance to decay further enhance peat accumulation under water-saturated conditions (Van Breemen 1995, Eurola 1999, Hájek *et al.* 2011). Generally, compositional changes in the vegetation are associated with changes in the functional plant traits, *i.e.* properties that determine how species respond to the abiotic and biotic environment and in turn affect the environment (Diaz & Cabido 2001, Lavorel & Garnier 2002). During succession, the availability of resources such as light, nutrients and water generally decrease. Concurrently, trait trade-offs have been observed from the 'acquisitive' (productive) strategy implemented by rapid resource acquisition towards species with slow traits and conservative strategy, which enhances survival status (Reich *et al.* 2003, Reich 2014). Logically, these trait changes affect ecosystem functioning (Weltzin *et al.* 2000).

Predictions of ecosystem responses to future disturbances like climate change require a better understanding of the processes that control community assembly during succession (Prach & Walker 2011). The reason for using functional traits and functional diversity indices in addition to taxon-based approaches is that ecosystem processes such as productivity, carbon dynamics and resilience are more directly affected by functional differences among species than by their taxonomic richness or composition (Hooper *et al.* 2002, Cadotte *et al.* 2011). While general successional changes in vegetation composition such as the increasing importance of *Sphagnum* mosses and woody species are well studied, the associated changes in functional traits in mires have not so far been addressed.

In this study we aimed to assess plant species and functional diversity during mire succession for the first time by taking advantage of ongoing post-glacial rebound. The rebound results in newly exposed land at the Finnish west coast, thus creating a primary successional series of undisturbed mires under similar climatic conditions (e.g. Tuittila *et al.* 2013). We expect species and functional diversity to increase during primary succession until the stress caused by ombrotrophication begins to filter species. We also expect changes in the functional traits of plants that reflect changes in the environmental conditions as a traits trade-off from acquisitive to conservative strategies.

METHODS

Study sites and vegetation sampling
The study area is located on the eastern shore of the Gulf of Bothnia, Baltic Sea (Siikajoki, Finland, 64° 45' N, 24° 43' E). In this area the post-glacial rebound is still in progress with a land uplift rate of 8 mm *per* year (Ekman 1996), and this provides a unique setting where sites at higher altitudes are not just older, but their ages can be estimated rather accurately. The length of the growing season in the area is approximately 150 days. The 30-year (1979–2009) average precipitation and mean annual temperature are 539 mm and 2.6 °C, respectively (Revonlahti, Siikajoki, 64° 41' N, 25° 05' E, 48 m a.s.l., Finnish Meteorological Institute).

The sites were located along a 10 km transect and were selected to represent different successional stages in primary paludification after exposure of the land from beneath the sea. The sites began their development towards mire vegetation after exposure, as is seen in a palaeological investigation of their peat profiles (Merilä *et al.* 2006, Tuittila *et al.* 2013). The subsoil beneath the peat at all sites was sand. The study included 22 mires, which we assigned to seven different groups based on their estimated age: SJ 0 (less than 100 years), SJ 1 (~180 years), SJ 2 (~200 years), SJ 3 (~700 years), SJ 4 (~1000 years), SJ 5 (~2500 years) and SJ 6 (~3000 years). Each time step had four replicates, except for SJ 0 and SJ 6 which had only one site each. The replicate sites were as similar as possible in age and development history. The first three groups had no soil or a very shallow organic soil layer and can be regarded as primary mires, since they are not yet real mires (*sensu* Joosten *et al.* 2017). Site SJ 0 was a seashore, exposed some decades ago and characterised by the absence of an organic soil layer. The vegetation at this site was dominated by graminoids (e.g. *Festuca rubra, Calamagrostis stricta, Carex glareosa* and *Juncus gerardii*) and it had a very poorly developed bryophyte layer. Group SJ 1 included wet meadows with a patchy cover of mainly brown mosses such as

Warnstorfia spp. In group SJ 2 the bryophyte layer was better developed and *Sphagnum* mosses occurred as patches among the brown mosses. Otherwise, both groups were dominated by sedges and grasses such as *Carex nigra* and *Agrostis canina*, while the forbs *Comarum palustre* and *Lysimachia thyrsiflora* were also common. The organic layer was only a few centimetres thick in both groups. Groups SJ 3 and SJ 4 were characterised by mesotrophic and oligotrophic fen vegetation, respectively. The vegetation consisted mainly of sedges (e.g. *Carex chordorrhiza*, *Carex rostrata* and *Carex limosa*). Dominant forbs in SJ 3 and SJ 4 were *C. palustre* and *Menyanthes trifoliata,* respectively. Hummock formation with very dense *Sphagnum* carpets had already started at the edges of the fens, while the middle parts of the fens were strongly impacted by spring and autumn floods. These sites were located 7 m and 12 m above sea level and the peat layer was 0.4 m and 0.9 m thick in SJ 3 and SJ 4, respectively. Group SJ 5 was at the fen–bog transition stage with a mosaic of clearly ombrotrophic hummock surfaces with *Rubus chamaemorus*, *Empetrum nigrum,* *Vaccinium oxycoccos* and *Sphagnum fuscum*, and wetter surfaces dominated by *Scheuchzeria palustris*, *Carex livida, Carex limosa* and *C. chordorhiza*. *Sphagnum* species accustomed to different water table depths formed a continuous moss layer. The sites were located 25 m above sea level and the peat layer was 1.9 m thick on average. Site SJ 6 was a bog, characterised by *S. fuscum, Sphagnum angustifolium* and dwarf shrubs such as *E. nigrum* and *Rhododendron tomentosum* at the hummock surfaces and *Sphagnum balticum* and *Eriophorum vaginatum* in wetter depressions. The peat layer in SJ 6 was up to 2.3 m thick, with a terrestrial age of 3000 years. See Tuittila *et al*. (2013) for further details of the study sites.

To cover the characteristic variation in moisture and vegetation at each site, we placed six 50 × 50 cm sample plots along a 10 m transect from the centre to the edge of the mire. We surveyed the projection cover of different vascular plant and moss species on a percentage scale in a total of 132 sample plots. The survey was conducted in July 2003, except in sites SJ 0 and SJ 6 where it was carried out in July 2007. The nomenclature follows http://theplantlist.org/.

Diversity measures
As a measure of species diversity, we calculated the species richness and the Shannon diversity index (Tuomisto 2012) for each study site based on the species occurrences. We also calculated the indices separately for vascular plants and mosses to facilitate comparison with functional diversity indices.

To study functional diversity, we extracted plant trait information from two databases, namely BIOLFLOR (Klotz *et al*. 2002) and LEDA (Kleyer *et al*. 2008), and from literature sources (Dierssen 2001, Ulvinen *et al*. 2002, Smith 2004). Specific leaf area (SLA) for the most common species was measured by collecting samples of leaves from vascular species at each site. Leaf area was measured from scanned leaves with the ImageJ program and the dry weight of each leaf was measured after drying at 40 ºC for 72 hours. The data consisted of leaf traits, reproductive and dispersion traits, morphological traits, life history strategy, indicator values, environmental requirements, and flowering phenology traits. Altogether, 15 traits for vascular plants (Table A1, see Appendix) and 17 traits for mosses (Table A2) were included.

We calculated two different functional diversity indices, namely functional diversity (FD) by Petchey & Gaston (2002) which is a measure of functional richness, and Rao's quadratic entropy (RaoQ) which combines functional richness (*i.e*. the range of trait values) and functional divergence (*i.e*. the position of dominant species relative to centre of the trait range) (e.g. Botta-Dukát 2005). In addition, we calculated the community weighted means of functional traits (CWM traits) (Villéger *et al*. 2008, Laliberté & Legendre 2010). RaoQ (Botta-Dukát & Czúcz 2016) and CWM traits were calculated using the ''FD'' package (Laliberté *et al*. 2014) in the R environment (R Development Core Team 2011). As functional traits were both categorical and numerical variables, we applied Gower's distance coefficient (Podani & Schmera 2006) to prepare a matrix of dissimilarity, which was used for calculations of functional diversity components. We used the dendrogram-based method with Gower distances following Petchey & Gaston (2002) to calculate FD (Figure A1). The non-randomness in FD along the mire chronosequence was tested using three null community models, R0 (Patterson & Atmar 1986), C0 (Jonsson 2001), and quasi-swap method (Miklós & Podani 2004). We created 9999 simulations with all three methods and compared the observed FD to the density distribution of the simulated FD for the null communities. The models differ: the R0 method holds the species number and all species have the same sampling probability; while the C0 method holds original species frequencies although their locations are random and, unlike R0, it does not retain the observed species richness. The non-sequential quasi-swap method uses fixed species frequencies and numbers of species. In the C0 and quasi-swap methods, the original commonness and rarity of species are retained, while in the R0 method all

species are equal. Functional diversity (FD) and tree-based dissimilarities were calculated with the vegan package (Oksanen *et al.* 2011) in the R environment (R Development Core Team 2011).

To test for differences between successional steps in each diversity metric, we carried out ANOVA analysis with Tukey post hoc tests. We included only the replicated successional steps SJ 1–5. In addition, we calculated Pearson's correlation coefficients between species richness and other diversity indices, separately for vascular plants and mosses.

RESULTS

Plant species diversity

The species richness and Shannon diversity index increased evenly towards the fen–bog transition stage (SJ 5) (Figure 1). Both indices varied significantly between successional steps (Table 1), so that SJ 5 had higher Shannon index than all other groups, while SJ 3 and SJ 4 had higher Shannon index than SJ 2 (Figure 1a). Similarly, SJ 5 had higher species richness than all other groups, and SJ 4 had higher species richness than SJ 2 (Tukey post hoc $p < 0.05$) (Figure 1b). Vascular plant and moss diversity developed in rather similar manner during succession, being lowest in wet meadows (SJ 1 and SJ 2) and highest in fen–bog transition (SJ 5) (Figure 2a,b).

Functional diversity

We observed a similar successional trend in FD to that in plant species diversity but Rao's quadratic entropy remained rather stable throughout the chronosequence (Figure 2c,d; Table 1). The vascular plant FD was highest at the fen–bog transition (SJ 5) (Figure 2c) and we found significant differences
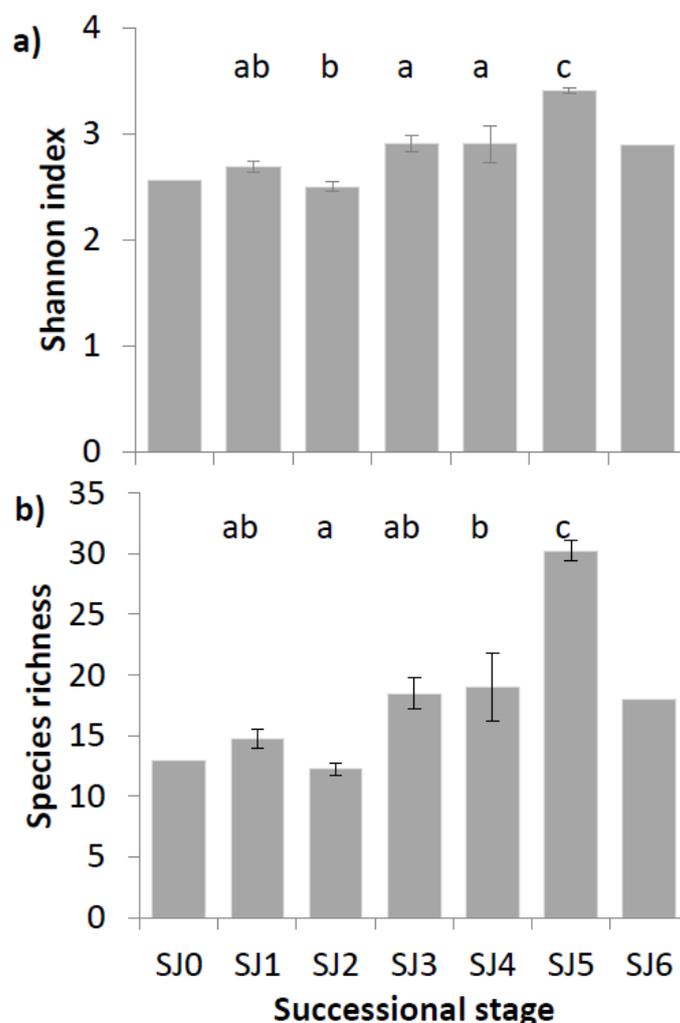

Figure 1. Changes in a) Shannon diversity index and b) species richness during the mire chronosequence. Significant differences based on Tukey's post hoc tests are indicated by different letters. SJ 0 and SJ 6 were not included in the tests because they did not have replicate sites.

between early and late successional steps (Table 1): SJ 5 had higher FD than SJ 1 and SJ 2, and SJ 4 higher FD than SJ 2 (Figure 2c). Of the null models, only the C0 model, which allows species number to vary, showed a notable pattern for the vascular plants ($0.05 \leq p \leq 0.08$), with FD smaller than random for SJ 0, SJ 2_1, SJ 2_3 and higher than random for SJ 4_2 (the abbreviation SJx_y, denotes a particular site y and successional step x). The null model results are not shown.

Similarly to vascular plants, FD of mosses increased during succession until SJ 5. SJ 5 had higher FD than the younger groups but there were no significant differences between the other groups (Figure 2c). The C0 null model gives strength to this increasing successional trend in FD, as FD was smaller than random in the early successional steps (SJ 0 ($p = 0.057$) and SJ 1_1, 2, 3 ($p < 0.05$)) and higher than random in the fen–bog transition (SJ 5, $0.008 \leq p \leq 0.0001$). However, the R0 and quasi-swap models, which take into account species number, did not recognise the unimodal pattern. This indicates that the increase in FD was directly due to an increase in taxonomic diversity.

There was a positive linear relationship between FD and species richness for vascular plants and mosses (Figure 3a), but RaoQ showed no relationship with species richness (Figure 3b).

Table 1. One way ANOVA results for different diversity indices and community weighted mean (CWM) plant traits. Successional steps SJ 1 to SJ 5 are included in the analysis; df is 4.

			F	p-value
Diversity indices	Whole community	Shannon	14.34	<0.001
		species richness	21.44	<0.001
	Vascular plants	Shannon	8.886	<0.001
		species richness	9.989	<0.001
		functional diversity (FD)	7.764	0.001
		Rao's quadratic entropy (RaoQ)	1.045	0.417
	Mosses	Shannon	5.151	0.008
		species richness	16.19	<0.001
		functional diversity (FD)	7.202	<0.001
		Rao's quadratic entropy (RaoQ)	0.572	0.687
CWM traits	Vascular plants	specific leaf area (SLA)	10.61	<0.001
		leaf persistence	13.34	<0.001
		stem specific density (SSD)	3.63	0.029
		reproductive type	15.23	<0.001
		terminal velocity (TV)	8.79	<0.001
		germinula height	47.75	<0.001
		germinula length	7.63	0.001
	Mosses	life form	17.65	<0.001
		life strategy	10.00	<0.001
		sexuality	3.08	0.052
		commonness of sporophytes	3.06	0.052
		spore size (µm)	27.36	<0.001

Changes in functional plant traits

The community weighted mean (CWM) of vascular plant specific leaf area (SLA) had a unimodal pattern with high values for forb-rich wet meadows (SJ 1 and SJ 2) and low values at both ends of the gradient, *i.e.*, for bog communities with shrub dominance and for sandy beach, where vegetation was largely composed of narrow-leaved grasses (Figure 4a, Table 1). During succession, deciduous species were replaced by evergreens and simultaneously the stem specific density (SSD) increased (Figure 4b). SJ 1, SJ 2 and SJ 3 had significantly more deciduous species than SJ 4 and SJ 5, while stem specific density was significantly higher at SJ 5 compared to wet meadows. The reproduction strategy changed so that vegetative reproduction traits became more common as succession proceeded. We found significant differences between wet meadows and older sites

(Figure A2 in Appendix). Terminal velocity (TV) - that is, the maximum rate at which a seed with its appendages can fall in still air - showed a unimodal pattern, being significantly higher for fens than for wet meadows and lower in SJ 5 than in SJ 4 (Figure A2a). The shapes of the seeds changed so that they were significantly shorter in wet meadows than in older sites, and narrower in SJ 1 than in SJ 4 and in SJ 2 compared to older sites (Figure A2b).

The life form of mosses changed quite early in the succession (SJ 3) from other bryophyte species to dominant *Sphagnum* mosses (Figure 5a). This change in bryophyte type was accompanied by a change in life strategy from colonists and pioneers towards perennial stayers (Figure 5b). The trends in reproduction traits were less uniform: spore size increased during succession (Figure A2c) but there were no differences in the commonness of sporophytes (results not shown).
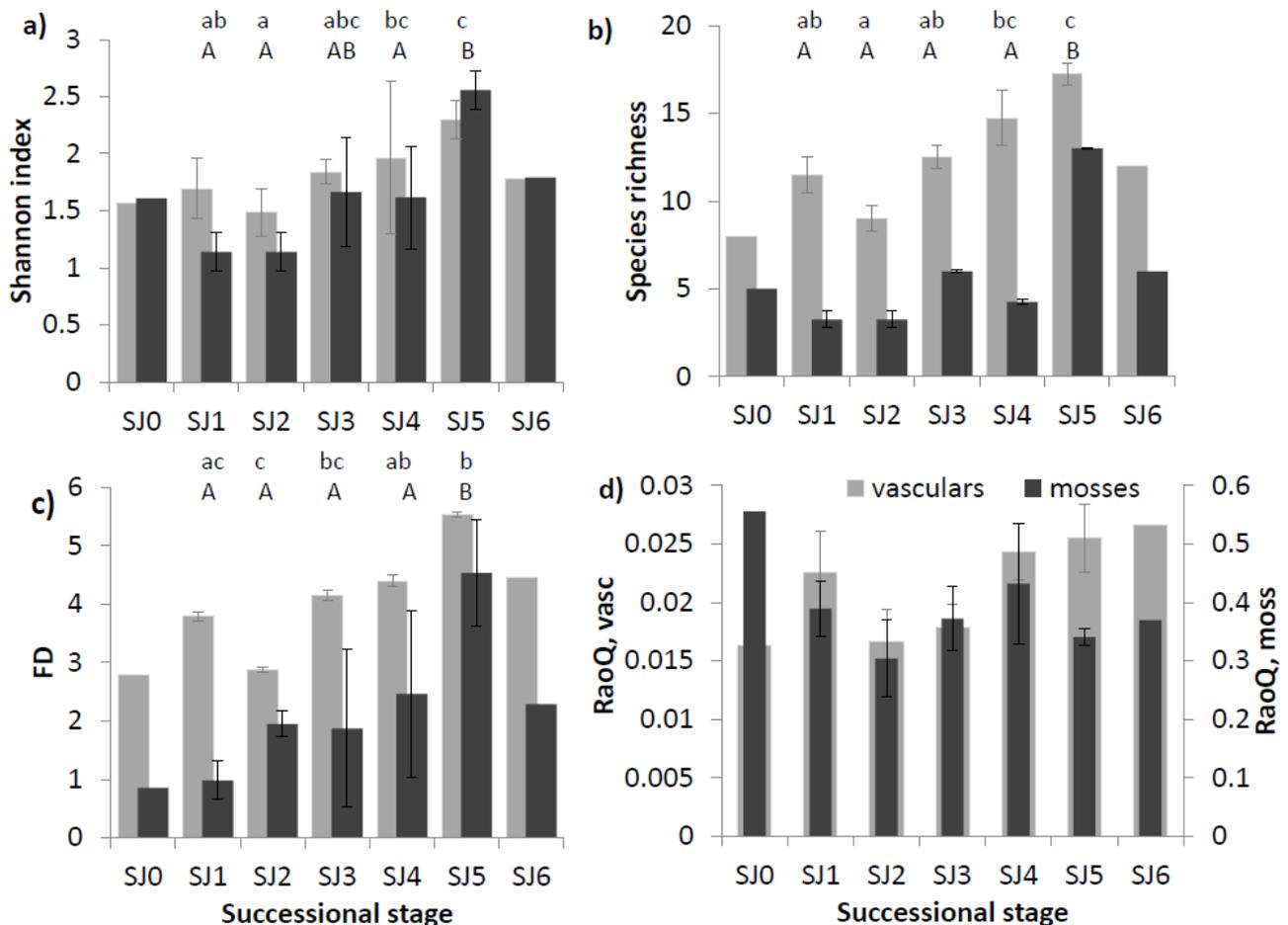

Figure 2. Changes in a) Shannon index ± SE, b) species richness ± SE, c) functional diversity (FD) ± SE and d) Rao's quadratic entropy (RaoQ) ± SE during mire succession. Separately for vascular plants (lighter shading) and mosses (darker shading). Significant differences based on Tukey's post hoc test are indicated by different letters; lowercase for vascular plants and uppercase for mosses. SJ 0 and SJ 6 were not included in the tests because they did not have replicate sites.
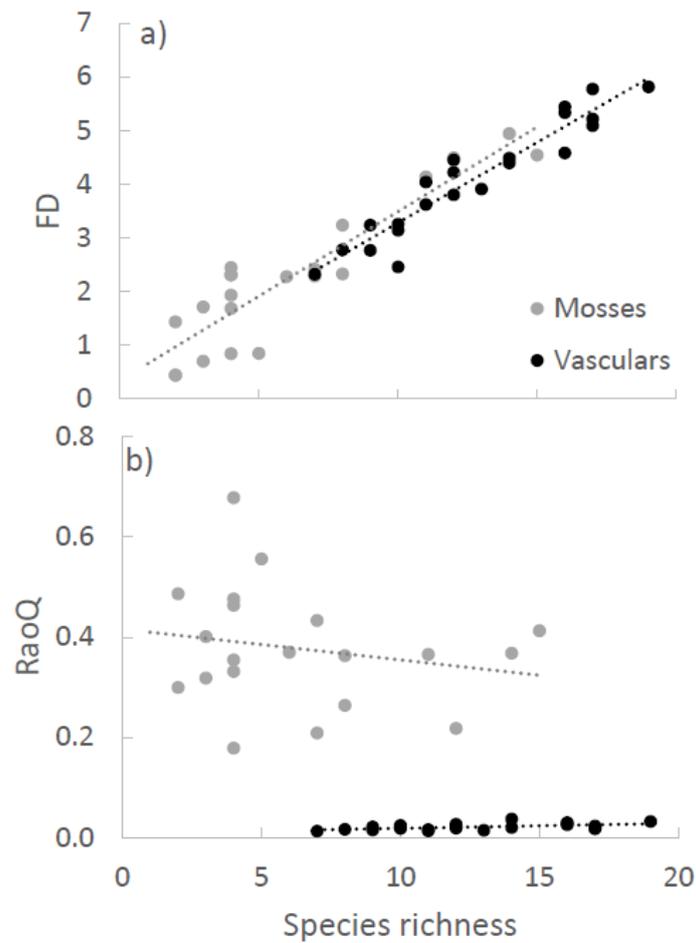
Figure 3. Relationships between species richness of vascular plants and mosses, and a) functional diversity (FD), b) Rao's quadratic entropy (RaoQ). Pearson's correlation coefficients between vascular plant species richness and FD and RaoQ were 0.95 and 0.55, respectively. Pearson's correlation coefficients between moss species richness and FD and RaoQ were 0.92 and -0.20, respectively.
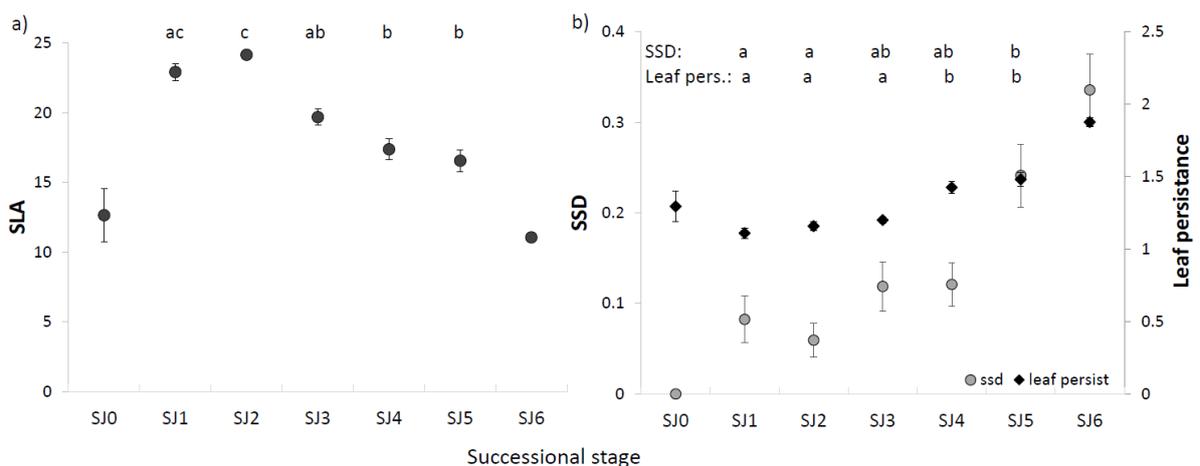

Figure 4. Development of community weighted mean trait values ± SE during mire succession: a) specific leaf area (SLA, mm^2 mg^{-1}); b) stem specific density (SSD, g cm^{-3}) and leaf persistence (1 = deciduous, 2 = evergreen) for vascular plants. The different letters indicate Tukey post hoc test results, so that successional steps that do not share a common letter differ from each other with $p < 0.05$. SJ 0 and SJ 6 were not included in the tests because they did not have replicate sites.
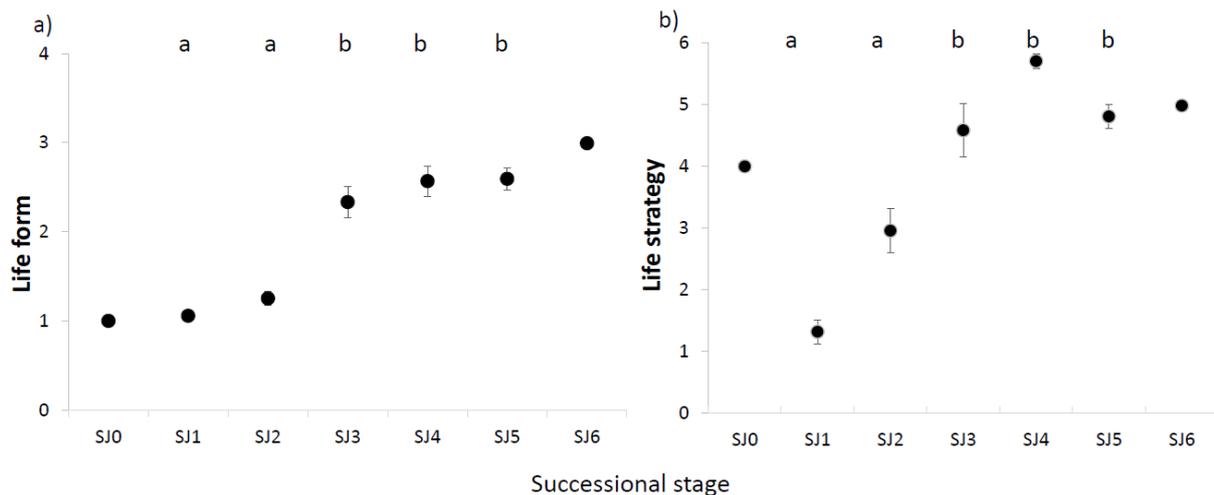
Figure 5. Development of community weighted mean trait values ± SE of moss a) life form (1 = bryophyte, 2 = liverwort, 3 = *Sphagnum*) and b) life cycle strategy (annual shuttle, colonist, ephemeral colonist, pioneer colonist, short-lived shuttle, geophyte, perennial, competitive perennial, stress-tolerant perennial, long-lived shuttle). The different letters indicate Tukey post hoc test results, so that successional steps which do not share a common letter differ from each other with p < 0.05. SJ 0 and SJ 6 were not included in the tests because they did not have replicate sites.

DISCUSSION

Plant species diversity

Mire succession, during which the vegetation develops from herbaceous dominated towards *Sphagnum* and shrub dominated due to decreasing influence of mineral-enriched groundwater, has been well described in the literature (Kuhry *et al*. 1993, Klinger & Short 1996, Glaser *et al*. 2004). Here we use a 'space-for-time' approach to connect this development with plant species and functional diversity. Similarly to studies carried out in ecosystems that started to develop after glacial retreat (primary succession; Reiners *et al*. 1971) and in abandoned arable fields or forests (secondary succession; Eggeling 1947, Auclair & Goff 1971, Reiners *et al*. 1971, Shafi & Yarranton 1973, Bazzaz, 1975, Sheil 2001, Purschke *et al*. 2013) we observed a unimodal diversity pattern during mire succession. The successional pattern of species diversity varies, however, according to ecosystem type and the intensity of the disturbance that starts the succession. In Californian shrublands, for instance, the diversity was highest during the first years after fire disturbance (Keeley *et al*. 2005). In our study the species richness and the Shannon diversity index increased as we moved inland from the coastal sandy shore, peaked at the fen–bog transition stage (SJ 5), then decreased again at the bog stage (SJ 6) where fen species had disappeared due to increased ombrotrophication. The fen–bog transition stage has the most diverse surface mosaic of wetter fen lawns

and hollows alternating with drier ombrotrophic hummocks, which offers different types of habitats and thus causes high environmental heterogeneity (Leppälä *et al*. 2011a). Environmental heterogeneity increases species diversity (Schwilk & Ackerly 2005, Zelený *et al*. 2010) and in mires it offers suitable niches particularly for several *Sphagnum* species that have ecological optima at different water levels (e.g. Andrus *et al*. 1983). In contrast to forests, where light is a strong filter for diversity because the canopy closes during the later stages of succession (Sheil 2001), the decreased diversity in late-succession open mire (bog) communities is likely to be caused by decreasing pH and reduced availability of nutrients causing increased stress for plants.

The low moss diversity in the "initial mires", *i.e.* wet meadows, was probably connected to the difficult moisture conditions, ranging from flooding to drought, due to poor water-holding capacity of the underlying mineral soil (Leppälä *et al*. 2008, Rehell & Heikkilä 2009). This is particularly harmful for *Sphagnum* mosses (Laitinen *et al*. 2008). During mire development the developing peat layer increases autogenic control of the water level and stabilises growth conditions, making them suitable for *Sphagnum* species.

Functional diversity

Our study partly confirmed our expectation that functional diversity increases during mire development until the ombrotrophication process starts to limit it. The controls on community

assembly change during succession, from abiotic to biotic filtering (e.g. Leibold *et al.* 2004, Purschke *et al.* 2013), which increases functional diversity (Weiher & Keddy 1995). In general, abiotic filtering selects for species with shared adaptations to a particular habitat and, therefore, similar traits (Diaz *et al.* 1998, Cornwell *et al.* 2006). On the other hand, biotic filtering increases functional diversity through processes that select for functionally different species, such as competitive exclusion and resource partitioning (Weiher & Keddy 1995, Weiher *et al.* 2011). In our study the functional complexity index (FD) confirmed this hypothesis, as it increased until the fen–bog transition stage and decreased again in the ombrotrophic bog where abiotic filtering is likely to play an important role. The same trend has been observed in other ecosystems (Mason *et al.* 2011, Lohbeck *et al.* 2012, Purschke *et al.* 2013). On the other hand, the Rao's quadratic entropy did not confirm the same pattern, but remained rather constant throughout the chronosequence. Unlike FD, Rao's quadratic entropy combines functional richness with functional divergence (Mouchet *et al.* 2010). High functional divergence indicates a high degree of niche differentiation and, thus, low resource competition (Mason *et al.* 2005). The reason we did not observe changes in functional divergence may be that, during mire succession, the habitats remain open and there is little change in light competition, while below-ground competition for soil nutrients and water dominates. Compared to size-asymmetric light competition, the size-symmetric below-ground competition does not enhance niche differentiation in a similar manner (Mason *et al.* 2013).

We found a clear positive correlation between species richness and FD for both vascular plants and mosses. A similar relationship has been found during secondary forest succession (Lochbeck *et al.* 2012). This could imply a lack of functional redundancy during mire succession so that each added species will equally increase the functional diversity and the traits of species do not overlap strongly (Petchey & Gaston 2002). Then again, the correlation with species richness is built into the parameter FD, which is the summed branch lengths of the dendrogram of species based on functional differences. Therefore, entering a new species into the community increases the number of branches and consequently increases FD (Botta-Dukát 2005). A disadvantage of our analysis of functional diversity is that it was not possible to include vascular plants and mosses in the same analysis because they have very different functional traits. For many mire functions, the shift of dominance from vascular plants to *Sphagnum* is

the most notable change during succession (e.g. Van Breemen 1995). In our chronosequence, *Sphagnum* species were already starting to dominate the moss layer in mesotrophic fens (SJ 3), and at the fen–bog transition stage the total cover of *Sphagnum* exceeded that of vascular plants (Figure A3).

Trait change

We found an expected trait trade-off from acquisitive species to conservative species during hydroseral mire development. The community weighted mean of SLA clearly decreased after ombrotrophication had started. SLA is positively correlated with growth rate and resource richness and negatively correlated with investment into leaf protection (Schierenbeck *et al.* 1994, Westoby 1998). Therefore, decreasing SLA during succession is a common phenomenon (Schleicher *et al.* 2011, Purschke *et al.* 2013). In addition, an increase in the stem specific density (SSD) and a shift from deciduous to evergreen plants supports the trade-off towards conservative strategy. As for mosses, the dominance of *Sphagnum* species had already begun in the 700-year-old fens. The development of *Sphagnum* cover is seen as a turning point in mire succession as it creates more stable moisture conditions and accelerates autogenic development towards ombrotrophication (Van Breemen 1995). Reproductive traits changed along the succession gradient in accordance with traditional succession theory, in that there was more effective colonisation by vascular plants at younger successional stages than at later successional stages. At younger sites, reproduction occurred mostly *via* seeds that were smaller in size and had higher terminal velocity, allowing better wind dispersal. The reproductive traits of mosses followed the same trajectory as those of vascular plants, with spore size increasing during succession, but we found no differences in the commonness of sporophytes. In general, our observations on the changes in traits are very similar to those found by Navas *et al.* (2010) in abandoned Mediterranean fields.

Consequences for ecosystem functions

The shift from acquisitive to conservative strategy during succession influences several ecosystem processes such as productivity and decomposition (e.g. Kazakou *et al.* 2006). Furthermore, increasing diversity is linked not only with increased rates of productivity but also with ecosystem resilience (*e.g.* Zak *et al.* 2003). In our study, increasing diversity and trait shift occurred hand-in-hand. In our chronosequence, the water table regime, carbon dioxide (CO_2) dynamics and methane (CH_4) emissions were more stable at the most diverse

successional stage (namely the fen–bog transition) than in the early stages (Leppälä *et al.* 2011a,b). At the young stages, ecosystem functions seemed extremely sensitive to catchment hydrology and changes in precipitation, as the buffering capacity of the peat layer was as yet poorly developed. We do not have data on the inter-annual variability of gas fluxes and water table from our bog site, but Korrensalo *et al.* (2017) recently showed that the diverse plant communities in a bog can stabilise carbon sequestration because different plant species meet their optimal conditions at different times. This indicates that resistance to water level fluctuations and the associated stabilisation of peat accumulation increase during mire succession. The acquisitive strategy makes species most productive and competitive under their optimal growing conditions (Reich 2014). Therefore, when the conditions change to suboptimal due to *e.g.* change in land use or climate, they are likely to suffer. Soudzilovskaia *et al.* (2013) noticed that conservative species with high resource input into structural traits such as thick leaves and low SLA and, at the same time, high C content in roots, increase in abundance under warmer climate conditions. An artificial warming experiment in tundra increased leaf size and plant height, and decreased specific leaf area (SLA) and leaf C concentration (Hudson *et al.* 2011). Experimental warming and water table manipulations at ecosystem/community level have shown that fens are more sensitive than bogs to increased temperature and drying (Weltzin *et al.* 2003, Bridgham *et al.* 2008). While the functional redundancy during mire succession, indicated by the correlation between FD and species richness, suggests that resistance to environmental disturbance does not change during mire succession, the trait trade-off from acquisitive strategy to conservative strategy, together with the development of hummock-hollow microtopography with strongly differing vegetation composition, indicates increasing resistance during succession.

These counteracting processes create a highly valuable setting for further investigations on changes in plant functional traits during natural mire development and environmental disturbances such as climate change or land use change. While the use of traits data from databases is practical for many situations, it does support the investigation of intraspecific variability in traits between different mire types or land uses. This raises a need for further investigations and highlights the need to measure traits from a variety of peatland types (see also Moor *et al.* 2017). In mires and other ecosystems where mosses play an important role, the use of functional diversity indices is complicated by the fact that it is not practical to use the same traits for mosses and vascular plants. Therefore, the indices need to be calculated separately for these two components.

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Appendix

Table A1. Traits of vascular plants used in the study. Number of species indicates how many species received a value for the particular trait. In total, 60 vascular plant species were found at our study sites.

Trait	Level of measurement	Number of classes	classes	Number of species
Life form	Nominal	9	hydrophytic, gamephytic, geophytic, hemicryptophytic, macrophanerophytic, nanerophytic, heminarenophytic, pseudonanerophytic, terophytic	43
Leaf persistence	Nominal	2	deciduous, evergreen	43
SLA	Nominal	1	relationship between area of a leaf and its weight, mm^2 mg^{-1}	43
Leaf anatomy	Nominal	5	succulent, xeromorph, hydromorph, mesomorph, hygromorph	27
Guild	Nominal	4	grasses, sedges, woody plants, herbs	42
Symphenological groups	Ordinal	10	unavailable, end of winter, start of early spring, end of early spring, start of mid-spring, end of mid-sping, start of early summer, end of early summer, mid-summer	39
Reproductive organ	Nominal	7	fruit, achene, fruitlet, seed, aggregate fruit, spore, mericarp	37
R_weight	Ratio	1	weight, mg	21
R_length	Ratio	1	length, mm	36
R_width	Ratio	1	width, mm	34
R_height	Ratio	1	height, mm	32
Reproduction type	Nominal	4	seed/spore, mostly seed, seed/vegetative reproduction, mostly vegetative reproduction	43
Pollen vector	Nominal	4	geitogamy, insects, self-pollination, wind	42
TV	Ratio	1	maximal velocity at which the seed moves in standing air, $m\ s^{-2}$	26
SSD	Ratio	1	relationship between dry mass and fresh mass of stem, $g\ cm^{-3}$	37
CSR strategy	Nominal	4	competitors, competitor stress-tolerants, competitor stress-tolerant ruderals, stress-tolerants	38

Table A2. Traits of mosses used in the study. Number of species indicates how many species received a value for the particular trait. In total, 37 moss species were found at our study sites.

| Trait	Level of measurement	Number of classes	classes	Number of species
Life form	Nominal	4	liverworts, howrnworts, *Sphagna*, other Bryophyta	23
Sexuality	Nominal	2	monoecious, dioecious	22
Commonness of sporophytes	Ordinal	5	common, ordinary, occassional, rare, very rare	22
Size of spores	Ordinal	5	small, rather small, smallish–rather large, rather large, large	22
Acidity		6	e acidophyte (pH < 3,3), h acidophyte (pH 3.4–4.0), c acidophyte (pH 4.1–4.8), m acidophyte (pH 4.9–5.6), subneutrophyte (pH 5.7–7.0 (7.5)), basiphyte (pH > 7)	
average	Ratio	1	average of classes the species belongs to	20
number of classes	Ordinal		number of classes the species belongs to	20
Moisture			extremely wet, wet, wet–relatively dry, dry, tolerates flooding	
average	Ratio	1	average of classes the species belongs to	20
number of classes	Ordinal		number of classes the species belongs to	20
Light			shaded, relatively shaded, relatively exposed, exposed, full light	
average	Ratio	1	average of classes the species belongs to	20
number of classes	Ordinal		number of classes the species belongs to	20
life cycle strategy	Nominal	11	refugee, annual shuttle, colonist, ephemeric colonist, pioneer colonist, short-lived shuttle, geophyte, perennial, competitive perennial, stress-tolerant perennial, long-lived shuttle	20
Spores	Ratio	1	size µm	10
Stem leaf width	Ratio	1	size mm	11
Stem leaf length	Ratio	1	size mm	11
Branch leaf width	Ratio	1	size mm	11
Branch leaf length	Ratio	1	size mm	9
Commonness of capsules	Nominal	5	common, common–occassional, occassional, rare, very rare	15
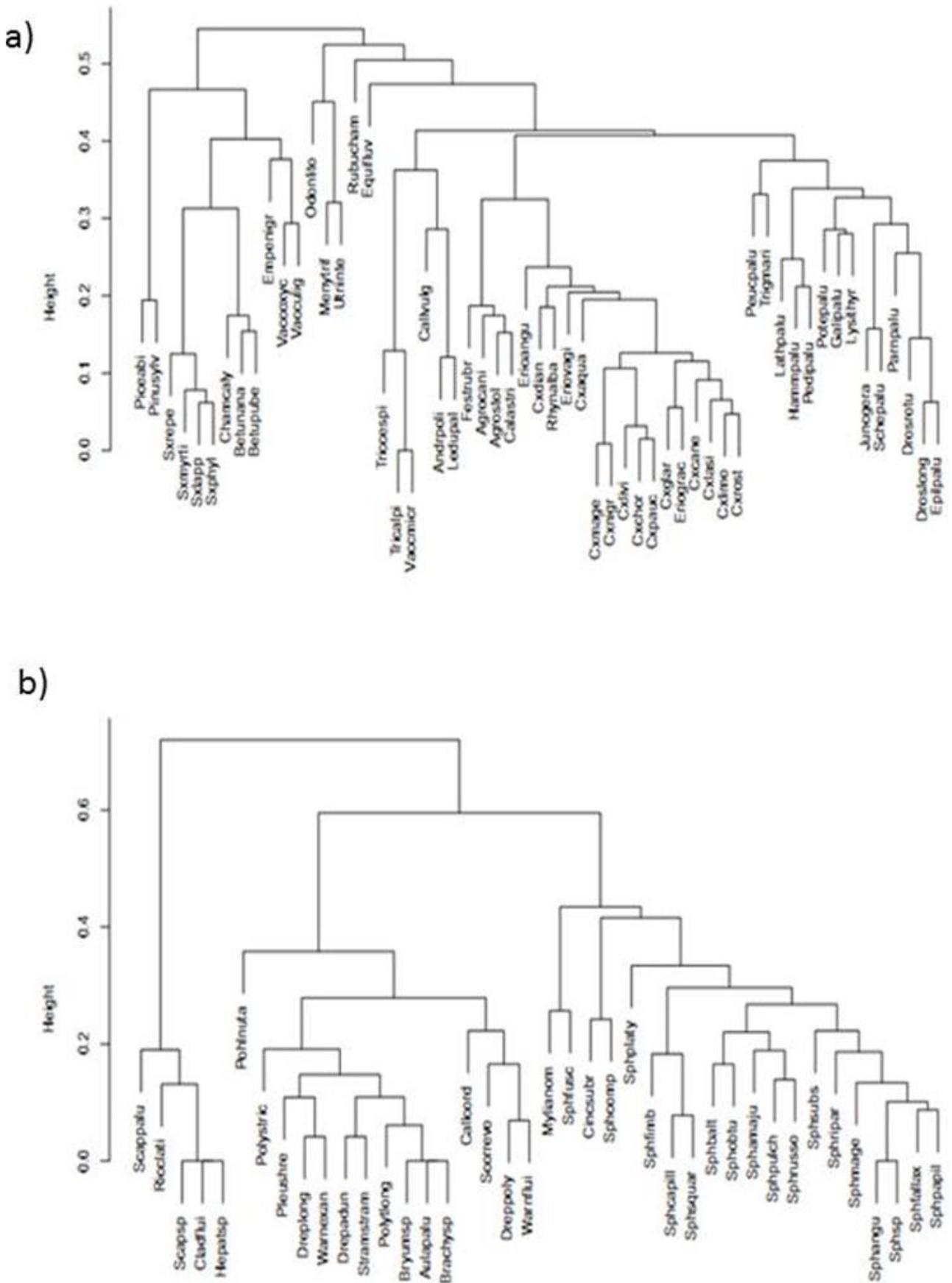
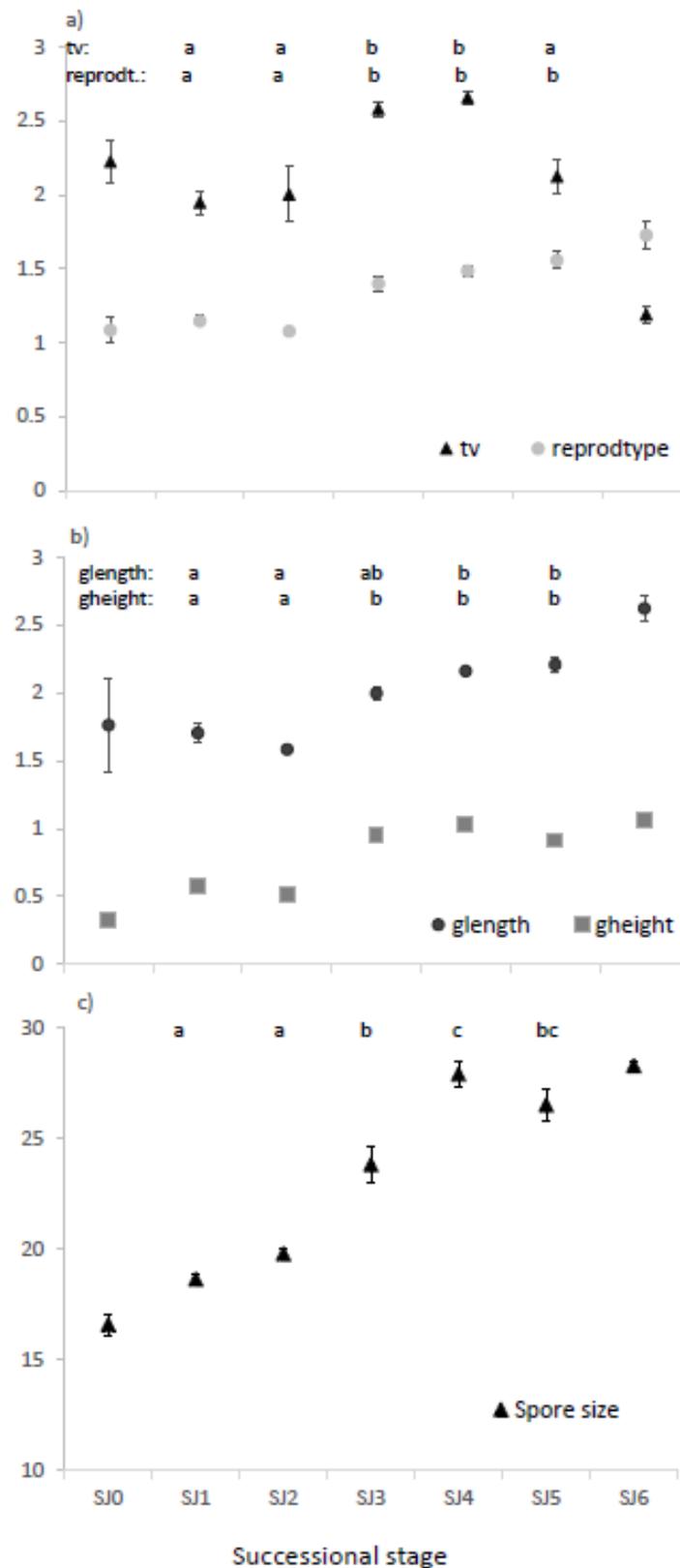Figure. A1. Cluster dendrogram for a) vascular and b) bryophyte species, based on Gower distances between species.

Figure A2. Development of community weighted mean values ($\pm$ SE) for reproduction-related traits during mire succession. For vascular plants: a) terminal velocity of seeds (TV, m s^{-2}) and reproductive type (from seeds (1) to mostly vegetative (4)); b) germinula height (mm) and germinula length (mm). For mosses: c) spore size (μm). The different letters indicate Tukey post hoc test results; successional steps that do not share a common letter differ from each other with $p < 0.05$. SJ 0 and SJ 6 were not included in the tests because they did not have replicate sites.
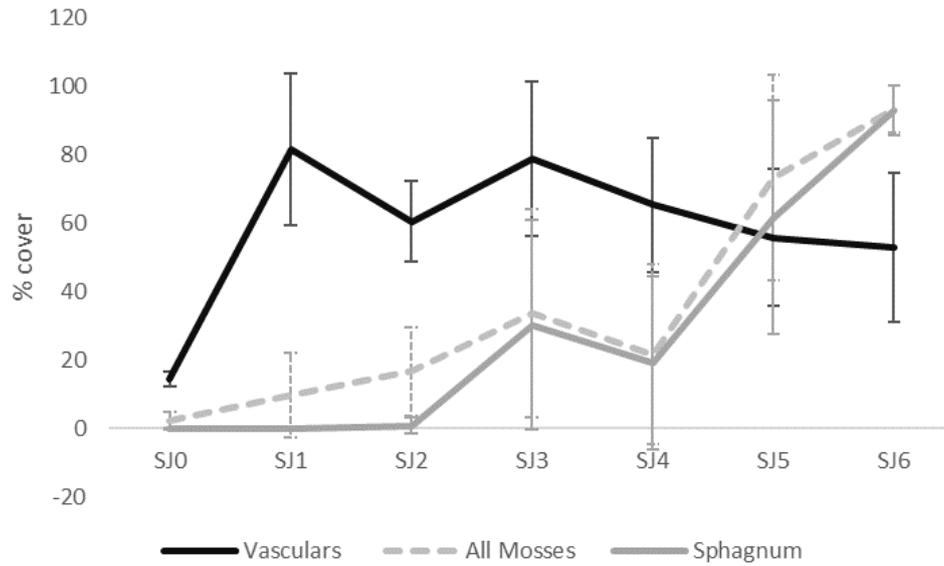
Figure A3. Development of vascular plant, moss and *Sphagnum* cover (± SD) during mire succession.