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RESEARCH ARTICLE

Self-facilitation and negative species interactions could drive microscale vegetation mosaic in a floating fen

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Abstract

Aim: The formation of a local vegetation mosaic may be attributed to local variation in abiotic environmental conditions. Recent research, however, indicates that self-facilitating organisms and negative species interactions may be a driving factor. In this study, we explore whether heterogeneous geohydrological conditions or vegetation feedbacks and interactions could be responsible for a vegetation mosaic of rich and poor fen species.

Location: Lake Aturtaun, Roundstone Bog, Ireland.

Methods: In a floating fen, transects were set out to analyze the relation between vegetation type and rock–peat distance and porewater electrical conductivity. Furthermore, three distinct vegetation types were studied: *rich fen*, *poor fen* and *patches of poor fen within rich fen vegetation*. Biogeochemical measurements were conducted in a vertical profile to distinguish abiotic conditions of distinct vegetation types.

Results: Geohydrological conditions may drive the distribution of poor and rich fen species at a larger scale in the floating fen, due to the supply of minerotrophic groundwater. Interestingly, both rich and poor fen vegetation occurred in a mosaic, when electrical conductivity values at 50 cm depth were between 300 μS/cm and 450 μS/cm. Although environmental conditions were homogeneous at 50 cm, they differed markedly between rich and poor fen vegetation at 10 cm depth. Specifically, our measurements indicate that poor fen vegetation lowered porewater alkalinity, bicarbonate concentrations and pH. No effects of rich fen vegetation at 10 cm depth on biogeochemistry was measured. However, rich fen litter had a higher mineralization rate than poor fen litter, which increases the influence of minerotrophic water in rich fen habitat.

Conclusions: These results strengthen our hypothesis that species can drive formation of vegetation mosaics under environmentally homogeneous conditions in a floating fen. Positive intraspecific self-facilitating mechanisms and negative species interactions could be responsible for a stable coexistence of species, even leading to local ecosystem engineering by the species, explaining the local vegetation mosaic at the microscale level in a floating fen.

KEYWORDS

competition, geohydrology, mire, mutual exclusion, patterning, peatlands, poor fen, rich fen

1 | INTRODUCTION

Peatlands can be complex with large variations in structure and hydrology (Grootjans et al., 2006; Lamers et al., 2015; Rydin & Jeglum, 2006). Globally, the occurrence and characteristics of peatlands are primarily driven by climate and geomorphological processes (Joosten & Clarke, 2002). On a regional scale, peatlands often consist of large complexes that include rich fen, poor fen and bog vegetation (Joosten & Clarke, 2002; Rydin & Jeglum, 2006), which can be related to heterogeneity in environmental conditions, such as hydrology, acid buffering capacity and nutrient supply (Lamers et al., 2015). Differences in environmental conditions can result in local vegetation mosaics within one ecosystem, resulting in distinct dominating species depending on prevailing abiotic conditions (Kuhry, Nicholson, Gignac, Vitt, & Bayley, 1993). However, next to abiotic influences, biotic interactions could play an important role in the formation of a local patchy landscape (Eppinga, Rietkerk, Wassen, & De Ruiter, 2009; Rietkerk & van de Koppel, 2008), as vegetation mosaics have also been observed in environmentally homogeneous conditions. Species can on the one hand overcome adverse environmental conditions by means of self-facilitation and on the other hand can even change these environmental conditions by ecosystem engineering.

Overcoming adverse environmental conditions by means of self-facilitation can play an important role when a species invades in an ecosystem or during succession (Callaway, 1995; Holmgren, Scheffer, & Huston, 1997). Many examples of this concept have been found in a diverse range of ecosystems with plants exposed to stress, such as heat or drought (Callaway, 1995). While high plant densities can lead to competition for nutrients, space or light (Stachowicz, 2001), the establishment of new conspecific seedlings under stressful conditions will mostly take place when plants are growing in high densities and facilitate their survival. For example, the canopy of "nurse plants" facilitates establishment of seedlings in dry conditions by alleviating environmental stress (Holmgren et al., 1997). In a range of ecosystem types, such as salt marshes and seagrass ecosystems, negative species interactions and intraspecific self-facilitation processes have been identified that resulted in the coexistence of two dominating species (van der Heide et al., 2012; Van Wesenbeeck, Koppel, Herman, Bakker, & Bouma, 2007). Even

though environmental conditions were similar, both negative species interactions and intraspecific self-facilitation induced bistability of dominating species.

Another concept that can play an important role in vegetation patterning is ecosystem engineering, where organisms, either deliberately or inadvertently, modify their physical habitat (Jones, Lawton, & Shachak, 1994, 1997). Paleoecological studies have shown that peatland ecosystems can exhibit bistability, such as in hummock–hollow formation over time (Eppinga, de Ruiter, Wassen, & Rietkerk, 2009; Moore, 1977; Walker & Walker, 1961). These small-scale patterns are remarkably stable and resilient to changes in environmental conditions (Belyea & Clymo, 2001), which is often the result of habitat-modifying properties of peat mosses (Nungesser, 2003) of which a number of mechanisms have been identified (van Breemen, 1995). Many modeling studies describe bistability in peatlands (Eppinga, Rietkerk, et al., 2009; Nungesser, 2003; Rietkerk, Dekker, Wassen, Verkroost, & Bierkens, 2004). However, there are few empirical studies on this subject because of the large time scale of peat formation and patterning (Eppinga, de Ruiter, et al., 2009; Gunnarsson, Malmer, & Rydin, 2002).

In floating fens, both poor fen (e.g., certain peat mosses, *Sphagnum* spp.) and rich fen species (e.g., *Schoenus nigricans*, *Scorpidium* spp.) can occur. Peat mosses play an important role in ombrotrophication (increasing dominance of rainwater over minerotrophic water) of floating fens (Granath, Strengbom, & Rydin, 2010), due to their ability to create strong positive self-facilitating feedbacks, which are related to hydrological and biogeochemical factors (Bootsma, Van Den Broek, Barendregt, & Beltman, 2002; van Breemen, 1995). These feedbacks include acidification (Cusell et al., 2015; Soudzilovskaia et al., 2010; van den Elzen et al., 2017), low decomposition in combination with a high nutrient uptake, a high growth efficiency of peat mosses (Fritz, Lamers, Riaz, Berg, & Elzenga, 2014), peat accumulation and retention of base-poor rainwater. In this way, conditions are changed beneficially for more ombrotrophic peat mosses, enabling the perpetuation of a dominant and stable community and the exclusion of other species (Clymo & Hayward, 1982; van Breemen, 1995). Vascular plants in rich fens modify their habitat to their own advantage as well. Roots of rich fen species such as *Schoenus nigricans* leak oxygen into the rhizosphere through radial oxygen loss (Armstrong, 1967; van Bodegom, de Kanter, Bakker, & Aerts, 2005),

which enhances aerobic decomposition rates (Greenwood, 1961; Lamers et al., 2012), increasing nutrient availability (Noble, Zenneck, & Randall, 1996). Furthermore, increased evapotranspiration enhances nutrient flow, and high productivity results in light limitation for slow- and low-growing vascular plants or mosses (Berendse et al., 2001; Lamers, Bobbink, & Roelofs, 2000; Malmer, Albinsson, Svensson, & Wallén, 2003; Pouliot, Rochefort, Karofeld, & Mercier, 2011).

In this study, we empirically explored whether heterogeneous geohydrological conditions or vegetation interactions could be responsible for a vegetation mosaic of rich and poor fen species in a floating fen. For this, we studied distinct rich and poor fen vegetation in a floating mire that seemed to be bistable for at least 40 years (Figure 1; Appendix S1; Van der Maarel & Roozen, 1975; van Groenendael, Hochstenbach, Mansveld, & Roozen, 1975): poor fen vegetation dominated by *Sphagnum* spp. and rich fen vegetation dominated by *Schoenus nigricans*. We hypothesized that bistability of poor and rich fen species is caused by vegetation interactions that overcome environmental stress, increase their own density and exclude other species. Next to self-facilitation, we also hypothesized that ecosystem engineering of both poor and rich fen species could affect the local environment and contributed to the vegetation mosaic.

2 | MATERIALS AND METHODS

2.1 | Study site

Lake Aturtaun in Roundstone Bog, Connemara, Ireland (53°23′36.55″ N; 9°59′34.86″ W) comprises open water and a floating fen (Figure 1a) located on the west shore (Figure 1b). The floating fen has an average annual precipitation of 1,208 mm and an average annual temperature of 9.8°C (Grootjans et al., 2016). Vegetation patterns were studied in the floating fen of approximately 0.2 ha in June 2014 and June 2018. In 2014, a vegetation map revealed two main vegetation types: *Scorpidio-Caricetum diandrae* (rich fen) and *Erico-Sphagnetum magellanici* (poor fen, Appendix S2). In these vegetation types, relevés were constructed using the Braun-Blanquet approach (van der Maarel, 2005) in plots of 1 m × 1 m. Rich fen vegetation was particularly dominant close to the landside of the floating fen, while poor fen vegetation dominated close to the lake. In between, we found a mosaic of both vegetation types, and there we selected patches of poor fen within rich fen vegetation. Thus, three distinct vegetation plots within the floating fen were studied: *rich fen* (n = 3), *poor fen* (n = 4) and *patches of poor fen within rich fen vegetation* (n = 3) (Figure 1b, Appendix S3). Measurements were conducted in a vertical profile, measuring within hummocks (+5 cm above water table) in case of poor fen vegetation, and in all plots at 10 and 50 cm depth. In 2018, four transects consisting of 11 plots were set out to spatially analyze the floating fen vegetation related to rock–peat distance and electrical conductivity of the porewater at 10 and 50 cm below the water table.

2.2 | Geohydrology

Geohydrology of the floating fen was studied by determining the hydraulic head and electrical conductivity (EC) of the porewater throughout the mire, and by measuring rock depth below the peat surface. The calcareous rock below the peat in Roundstone Bog is known to enrich groundwater and surface water by dissolution of calcium and bicarbonate (Grootjans et al., 2016; Jenkin, Fallick, & Leake, 1992). In 2014, the hydraulic head was measured with piezometers that were placed evenly distributed throughout the floating fen (n = 10). In 2018, EC was measured at two depths (10 and 50 cm) across the fen in four transects, which consisted of 11 plots (Figure 1b), using a 2-m long EC probe calibrated with a handheld EC meter (Tetracon® 325, WTW electrode, pH/Cond 3,320 multimeter, Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). The distance between peat surface and underlying rock layer was determined using a 4-m long PVC-tube in the same transects in 2018.

2.3 | Biogeochemistry

In each vegetation plot, pore water was sampled in a vertical profile to assess the potential influence of vegetation and water below the floating mire on biogeochemical conditions, starting at +5 cm in the poor fen plots (inside *Sphagnum* hummocks); and at 10 and 50 cm depth in all plots (June 2014). Water samples were taken and filtered using vacuum syringes attached to teflon soil pore water samplers or ceramic cup samplers via a teflon tube (Rhizon SMS; Rhizosphere Research Products; Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). The sample was stored at 4°C until total dissolved phosphorus concentrations were measured by means of inductively coupled plasma emission spectrophotometry (ICP-OES; model IRIS Intrepid II XDL, Thermo Fisher Scientific, Waltham, MA, USA). A subsample of 10 ml, to which 0.1 ml 65% nitric acid (HNO_3) was added to keep metals dissolved, was kept separately. The rest of each sample, 20 ml, was stored in polyethylene bottles at −20°C prior to analyses. Nitrate (NO_3^-) and ammonium (NH_4^+) concentrations were measured colorimetrically with an auto analyzer (Auto Analyser III, Bran and Luebbe GmbH, Norderstedt, Germany) (as in Geurts, Smolders, Verhoeven, Roelofs, & Lamers, 2008).

Total Inorganic Carbon (TIC) concentration in peat soil pore water was measured using infrared gas analyses (IRGA, ABB Advance Optima, Frankfurt, Germany). Carbon dioxide levels in pore water were calculated from TIC concentrations, temperature, pH, and carbonic acid equilibrium constants (K_a) (Dickson & Millero, 1987), according to the equations below (Stumm & Morgan, 1996):

$$\frac{HCO_3}{CO_2} = \frac{K_a}{10^{-pH}} \quad (1)$$

$$HCO_3 = \frac{TIC * HCO_3/CO_2}{HCO_3 + 1} \quad (2)$$
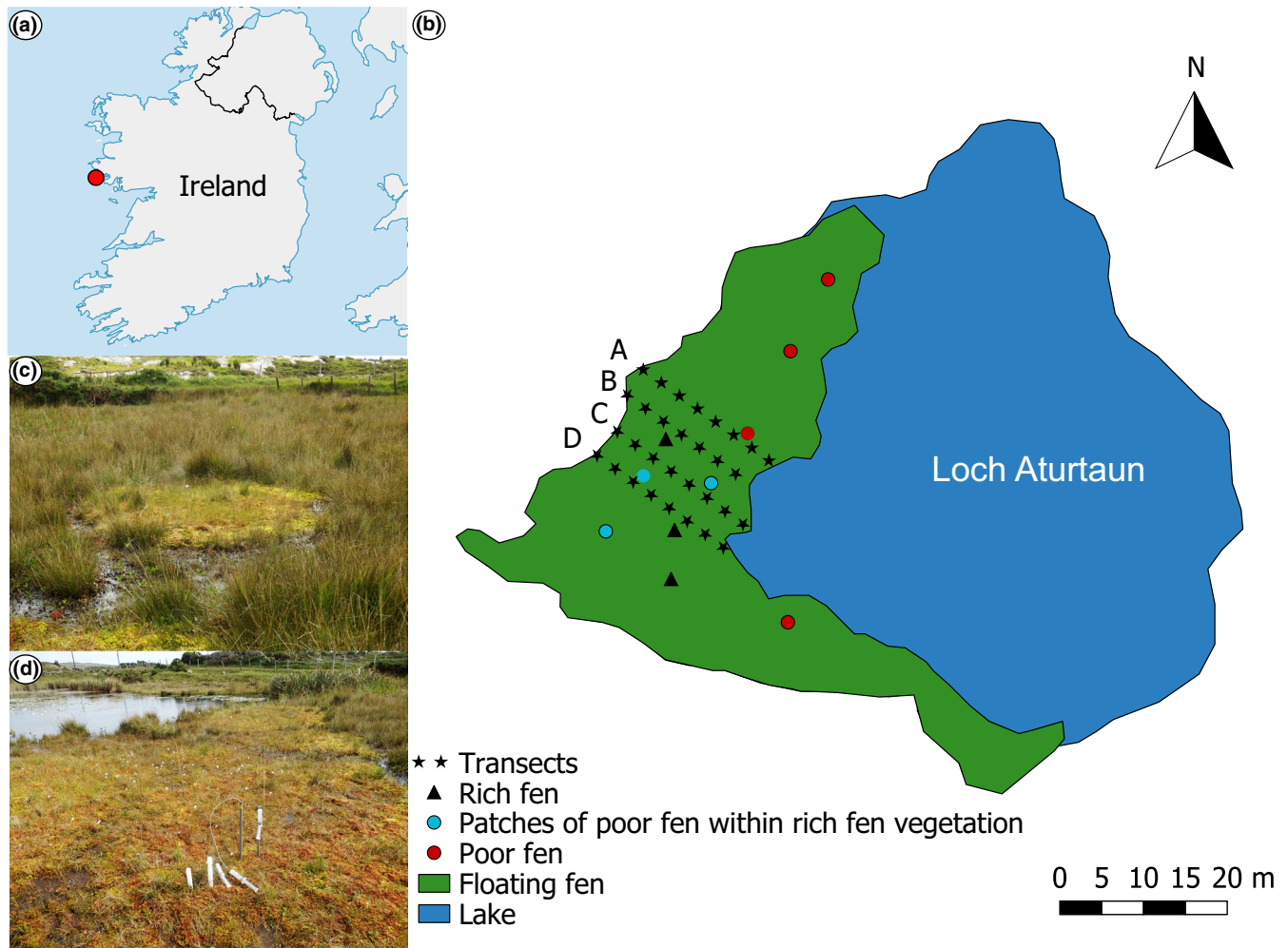
$$CO_2 = TIC - HCO_3 \quad (3)$$

FIGURE 1 (a) Location of the field site in Ireland (indicated by a red circle). (b) Schematic map of Loch Aturtaun with the floating fen (green) and open water (blue). Plots of the poor fen (red circles), patches of poor fen within rich fen vegetation (blue circles) and rich fen vegetation (black triangles) sampled in 2014. The four transects (indicated by black stars) were sampled in 2018. (c, d) Impressions of the distinct vegetation types with sharp dominating vegetation type borders, namely (c) poor fen vegetation (green-yellowish circle) surrounded by rich fen vegetation (dark green tall vegetation) and (d) large homogeneous poor fen vegetation with a sharp border of tall rich fen vegetation in the top-right corner (dark green tall vegetation). Pictures were taken in June 2014 by R.J.M. Temmink. Map (a) made with Natural Earth [Colour figure can be viewed at wileyonlinelibrary.com]

The pH and alkalinity (cf. Roelofs, 1983) were determined on the sampling day using a handheld meter (Multi 340i meter, Wissenschaftlich-Technische Werkstätten GmbH) connected to a pH probe (Orion 9156BNWP; Thermo Fisher Scientific).

In 2014, peat soil samples of a known volume were taken in every vegetation plot at approximately 10 and 50 cm depth with a half-cylinder chamber peat corer (50 cm long, Ø 5 cm). Subsamples were dried at 70°C for 48 hr to determine soil dry weight and bulk density. Bio-available phosphorus (P) (Olsen-P extract; Olsen, 1954) was determined by incubating 3 g of dried soil in 60 ml 0.5 M sodium carbonate ($NaHCO_3$) for 30 min at 105 RPM. Bio-available NH_4^+ and NO_3^- were determined by incubating 17.5 g of fresh soil in 50 ml of 0.2 M sodium chloride (NaCl) for 120 min at 105 RPM. Next, the supernatant was collected under vacuum conditions with teflon porewater samplers. Samples were measured using ICP-OES analyses (Olsen-P) and K, NH_4^+ and NO_3^- were measured with the Auto Analyser III system. In 2018, 2 g

of fresh soil of both poor fen and rich fen vegetation was placed into 12 ml incubation vials under anaerobic conditions to estimate mineralization rates. After approximately 5 days (117 hr), 0.4 ml subsamples were taken with a 1 ml syringe to determine the carbon dioxide (CO_2) and methane (CH_4) production rate with an infrared carbon analyzer (IRGA; ABB Analytical). Base saturation was estimated using NaCl extraction (see above). Concentrations of cations displaced by Na were measured by ICP (and pH measurement for H^+) and used as a proxy for base saturation (BS) (Kleijn, Bekker, Bobbink, Graaf, & Roelofs, 2008).

2.4 | Statistical analyses

Normal distribution of the residuals and homogeneity of variance of the data were tested with the Shapiro–Wilk test, Q–Q plots and Levene's test, and when necessary data were transformed

to authorize the use of parametric analyses. (a) Analyses of Variances (ANOVAs) were used to analyze biogeochemical peat soil heterogeneity at 50 cm depth [dependent value: pH, alkalinity, bicarbonate (log-transformed), base saturation and bio-available P; factor: poor fen, poor fen within rich fen and rich fen]. Differences in peat soil heterogeneity between different vegetation types were determined using Tukey HSD post-hoc tests. (b) To determine the effect of vegetation type on soil biogeochemistry at 10 cm depth, ANOVAs with post-hoc test were conducted (dependent value: pH, alkalinity, bicarbonate and bio-available P, base saturation; factor: poor fen, patches of poor fen within rich fen and rich fen). (c) Poor fen vegetation formed new habitat (*Sphagnum* lawn at 5 cm above the water table). Therefore, we determined the effect of poor fen vegetation on biogeochemical conditions at +5, 10 and 50 cm depth. ANOVAs with post-hoc tests were conducted for poor fen and poor fen within rich fen vegetation [poor fen: dependent value: pH, alkalinity ($1/x$-transformed), bicarbonate (log-transformed); factor: +5, 10 and 50 cm depth; poor fen within rich fen: dependent value: pH, alkalinity (log-transformed), bicarbonate (square-root-transformed); factor: +5, 10 and 50 cm depth]. (d) A two-sample t test was used to analyze the difference between CO_2 production rates ($1/x$-transformed) of the poor fen and rich fen litter. Bivariate interpolations were used to create heat maps of spatial EC data using the Akima and Fields packages (Akima, Gebhardt, Petzold, & Maechler, 2016; Nychka, Furrer, Paige, Sain, & Nychka, 2018). All results are shown with their standard error of the mean (±*SE*) and the significance level is at $p < 0.05$. The analyses were performed using R (version 3.5.1) statistical and programming environment (R Core Team, 2013).

3 | RESULTS

3.1 | Geohydrology

Distribution of poor fen and rich fen vegetation over the floating fen largely coincided with rock depth and EC values measured at 50 cm depth. Where rich fen vegetation dominated, the rock layer was present at less than 1 m depth and EC values were high (300–600 µS/cm). Where poor fen dominated, rock proximity to the peat layer was more than 2.5 m, coinciding with lower EC values (200–450 µS/cm; Figure 2a,b). Proximity of the rock layer to the peat surface was significantly correlated to EC (R^2 = 0.42, $p < 0.001$; Figure 2c). Nevertheless, there was considerable overlap between EC values and species occurrence. When EC values ranged between ~300 µS/cm and 450 µS/cm, both rich and poor fen vegetation occurred (Figure 2c, gray area). At 10 cm depth, conductivity was higher compared to values found at 50 cm depth, but there was less variability in the spatial EC pattern and the relationship with rock depth was less strong (Appendix S4). We quantified upward water seepage in the entire floating fen, with an average hydraulic head of 1.6 ± 0.3 cm.

3.2 | Biogeochemistry

Nutrient concentrations in the floating fen were low and we did not find any differences in the depth profile or between vegetation types. The average total dissolved phosphorus concentration was 2.6 ± 0.4 µmol/L, and NH_4^+ and NO_3^- concentrations were 16.9 ± 4.1 µmol/L and 10.7 ± 9.7 µmol/L, respectively. Bio-available P was similar in the deeper soil layer (50 cm depth) for all vegetation types, but differed significantly in the upper soil layer (10 cm depth). Highest bio-available P values were measured in the poor fen vegetation (65 ± 13 µmol/L fresh weight [FW] soil), lowest in rich fen vegetation (12 ± 4 µmol/L FW soil), and intermediate in patches of poor fen within rich fen vegetation (33 ± 20 µmol/L FW soil).

The pH, alkalinity, HCO_3^- concentrations and BS were similar in deeper soil layers (at 50 cm depth), irrespective of vegetation cover (Figure 3). Average pH and alkalinity were 5.5 ± 0.1 and 1.1 ± 0.2 mEq/L, respectively. Average bicarbonate concentration was 320 ± 105 µmol/L and we found a high BS of 88%–98% for all vegetation types. In the upper soil layer (at 10 cm depth), however, biogeochemical conditions strongly differed between vegetation types (Figure 3). The pH at 10 cm depth was lower in poor fen vegetation compared to rich fen vegetation (4.8 ± 0.06 and 5.5 ± 0.2, respectively). Patches of poor fen within rich fen vegetation did not differ significantly from other vegetation plots (average pH 4.9 ± 0.2). Alkalinity at 10 cm depth did not differ significantly between vegetation types ($p = 0.07$), but was slightly lower in poor fen vegetation (0.3 ± 0.05 mEq/L) compared to rich fen vegetation (0.8 ± 0.3 mEq/L). The HCO_3^- concentration was significantly lower in poor fen vegetation than in rich fen vegetation at 10 cm depth, with averages of 35.6 ± 9.7 µmol/L and 263.1 ± 98.0 µmol/L, respectively. Patches of poor fen within rich fen vegetation did not differ significantly from other vegetation plots with an average of 52.6 ± 20.4 µmol/L. BS was equally high in the upper soil layer of all vegetation types (>90%).

Biogeochemical conditions in the depth profile of rich fen vegetation were homogeneous, but conditions significantly differed in the depth profile of the poor fen vegetation and patches of poor fen within rich fen vegetation (Figure 3). Only BS showed equal values everywhere (>90%; Figure 3). In the poor fen vegetation, pH at 10 cm depth did not statistically differ compared to +5 cm and to 50 cm depth, but the pH was significantly lower at +5 cm compared to 50 cm depth. Alkalinity was lowest in the hummock and the upper soil layer and was significantly higher at 50 cm depth. HCO_3^- concentrations followed the same vertical pattern, with the highest values at 50 cm depth (Figure 3). In patches of poor fen within rich fen vegetation, no significant difference in pH was found compared to both other types, although the same trend was observed as in the poor fen vegetation. Alkalinity followed the same vertical pattern as in the poor fen vegetation, with a significantly higher value at 10 and 50 cm depth, compared to +5 cm. HCO_3^- concentration significantly increased with depth.

Anaerobic CO_2 production rates of the rich and poor fen litter differed significantly (Figure 4). No CH_4 was detected in the samples.
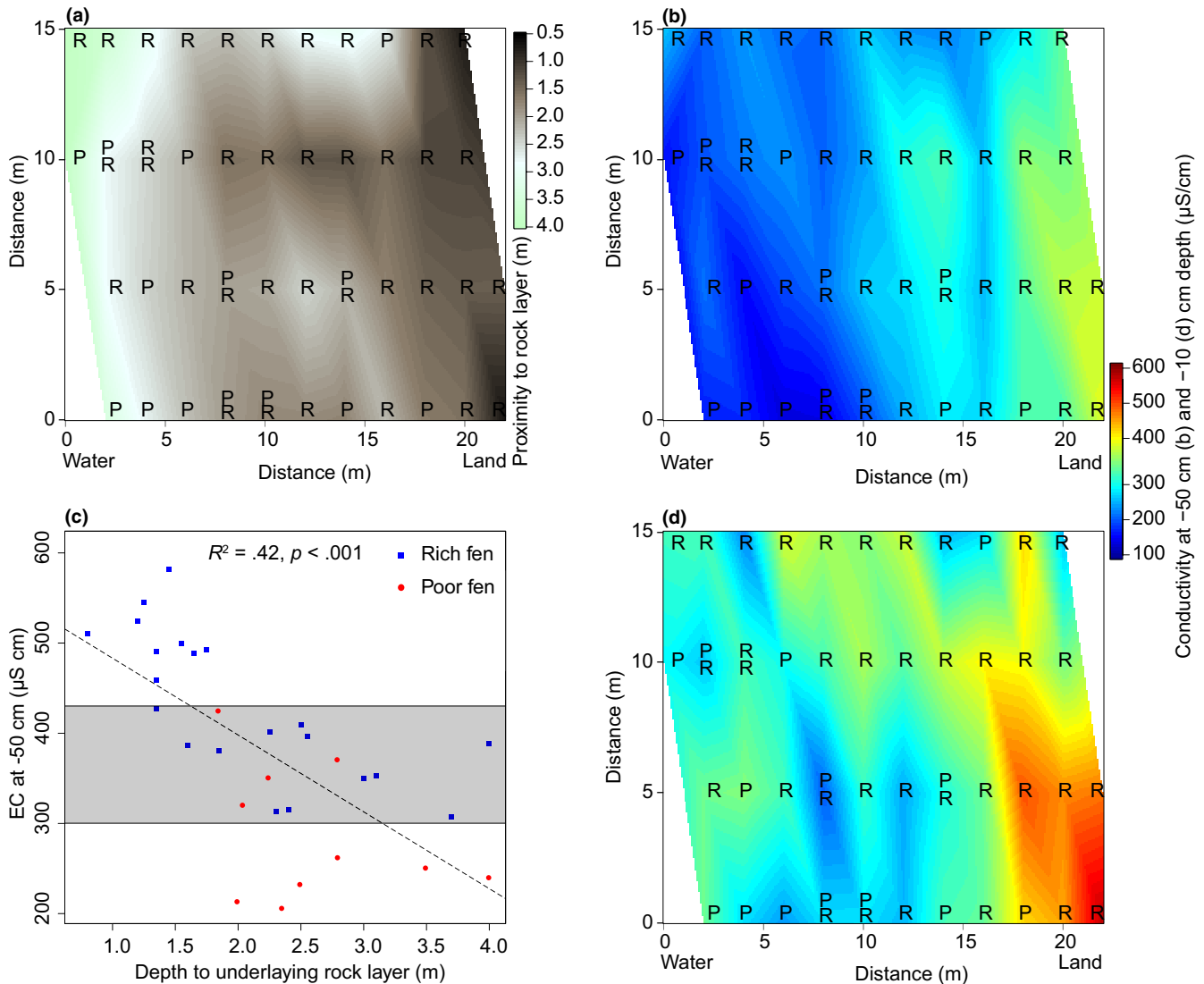
FIGURE 2 (a) Proximity of the underlying rock layer to the peat surface (m) (transect a–d, Figure 1). (b) Electrical conductivity (EC, μS/cm) values at 50 cm depth. (c) Relationship between EC and proximity of underlying rock layer to peat surface at 50 cm depth. The gray box indicates the range of EC values where both rich fen (blue squares) and poor fen vegetation (red circles) occur. The mixed vegetation types (PR) are not depicted in this graph. (d) EC (μS/cm) at 10 cm depth. Vegetation types are indicated at EC measurement points with abbreviations (R: rich fen vegetation, P: poor fen vegetation, RP: both vegetation types). *Y*-axis a-b-d: the distance corresponds to letters of the transect (A = 0 to D = 15, Figure 1) [Colour figure can be viewed at wileyonlinelibrary.com]

The rich fen litter produced 1.8 times more CO_2 compared to the poor fen litter (2.60 ± 0.27 vs. 1.40 ± 0.07 mmol CO_2/L fresh soil/day, respectively, $t = 4.98$, $p < 0.01$). The upper 10 cm of rich fen litter mainly consisted of litter and roots of *Schoenus nigricans*, while the upper 10 cm of poor fen consisted of hardly decomposed *Sphagnum* litter with *Eriophorum* spp. roots.

4 | DISCUSSION

Our results demonstrate that the distribution of poor and rich fen vegetation in this floating fen largely depends on rock proximity and correlated EC values. This indicates that geohydrology, by

Ca^{2+} and HCO_3^- dissolution from rock (Grootjans et al., 2016; Jenkin et al., 1992), combined with upward movement of water below the floating mire, was driving vegetation patterning at a large scale. This resulted in dominant rich fen vegetation close to the land-side and dominant poor fen vegetation close to the lakeside of the floating fen. Rich fen vegetation was found at high EC values at 50 cm depth (300–600 μS/cm) and poor fen vegetation at lower EC values (200–450 μS/cm). However, in the central zone of the floating fen, rich and poor fen species occurred when EC values in the deeper soil layer were between 300 μS/cm and 450 μS/cm. Moreover, we observed patches of poor fen vegetation within rich fen vegetation (Figure 1), thus not corresponding to rock proximity. The underlying biogeochemical conditions (pH, alkalinity,
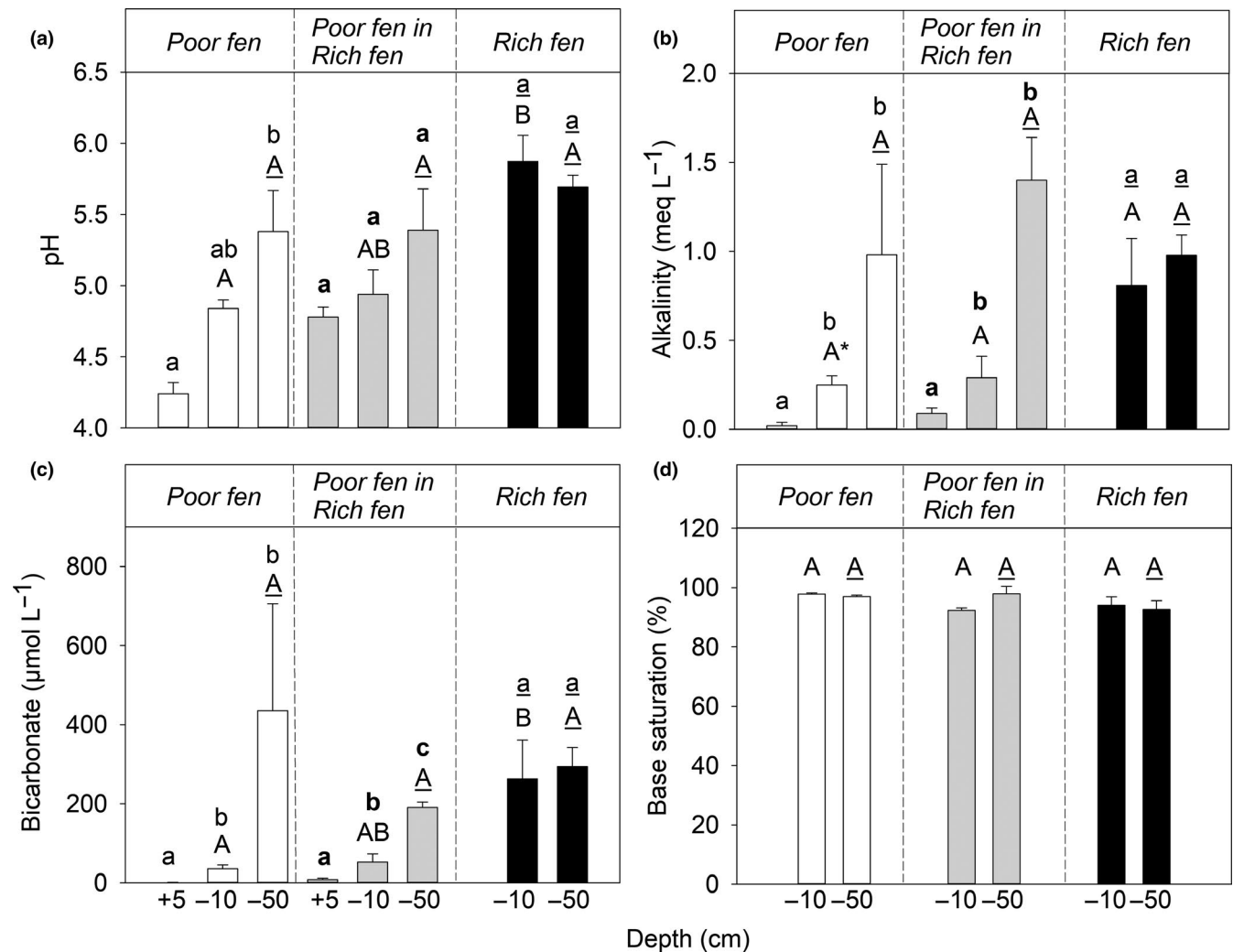
FIGURE 3 (a) Porewater pH; (b) alkalinity (mEq/L); (c) bicarbonate (μmol/L); and (d) base saturation (%) at +5 (hummock), −10 and −50 cm in poor fen (*n* = 4 ± *SE*), patches of poor fen within rich fen vegetation (*n* = 3 ± *SE*) and rich fen (*n* = 3 ± *SE*) vegetation plots. Note that the *y*-axis of the pH (a) starts at 4. Significant differences are indicated by either capitalized (between vegetation types at −10 cm), capitalized and underlined (between vegetation types at −10 cm), non-capitalized (depth within poor fen vegetation) or bold non-capitalized (depth within poor fen in rich fen vegetation) and underlined letters (depth within rich fen vegetation)
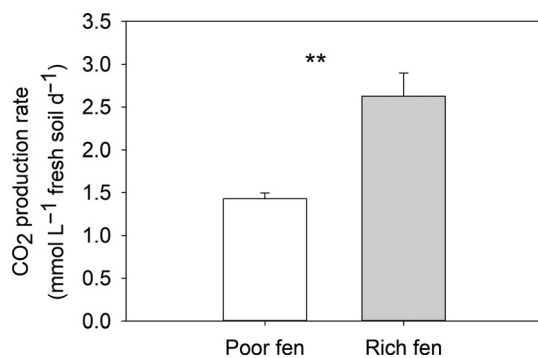

FIGURE 4 CO_2 production rates of poor fen (*n* = 4 ± *SE*) and rich fen (*n* = 4 ± *SE*) peat (mmol CO_2/L fresh soil/day) after five days of anaerobic incubation with peat collected in June 2018. No CH_4 was detected. Significance level is indicated by **<0.01

HCO_3^- concentration and bio-available P) in the deeper soil layer were similar irrespective of vegetation cover. Biogeochemical

conditions in the depth profile of rich fen vegetation were similar, but differed significantly in poor fen vegetation (Figure 3). This was the case in the poor fen vegetation near the lakeside of the floating fen, as well as in the patches of poor fen within rich fen vegetation. These results suggest that biogeochemical habitat modification by the vegetation is restricted to the upper soil layer, enabling formation of local patches of poor fen within rich fen vegetation. This strengthens our hypothesis that species interactions, self-facilitation and ecosystem engineering can drive formation of vegetation mosaics under environmentally homogeneous conditions in a floating fen.

4.1 | Habitat modification by poor fen vegetation

Poor fen species, specifically peat mosses (*Sphagnum* spp.), generate positive feedbacks enabling them to create acidic, nutrient-poor,

cold and anoxic conditions. These conditions positively affect peat accumulation (leading to ombrotrophication) and stimulate peat moss dominance (van Breemen, 1995). We clearly observed acidification of the upper soil layer in peat moss plots in the floating fen, which has been observed in many studies and habitats (Clymo, 1964; Cusell et al., 2015; Hájek & Adamec, 2009; Harpenslager, van Dijk, et al., 2015; Soudzilovskaia et al., 2010; van den Elzen et al., 2017). Although we observed upward seepage of water from below the floating mire in the entire floating fen (average hydraulic head of 1.6 ± 0.3 cm), together with a high base saturation in all vegetation types and soil layers (>90%), poor fen vegetation still had a significantly lower pH, alkalinity and HCO_3^- concentration in the hummock and at 10 cm depth (Figure 3). Only in patches of poor fen within rich fen vegetation, no significant differences were found in the vertical pH profile, but they showed the same trend as the poor fen vegetation (Figure 3), indicating patches of poor fen within rich fen vegetation had more difficulties with acidifying their environment. Soudzilovskaia et al. (2010) suggested that active release of protons by *Sphagnum* species was not an important mechanism of peat acidification during the shift from fen to bog. However, peat mosses in poor fens form a hummock, because they produce high amounts of secondary metabolites (e.g., phenolic compounds), which result in slower decomposition rates compared to rich fen species (Clymo, 1964; Clymo & Hayward, 1982; Mettrop, Cusell, Kooijman, & Lamers, 2014; Verhoeven & Liefveld, 1997). We did not identify a significant difference in seepage of HCO_3^--rich groundwater throughout the fen, but likely the hummock formed a groundwater mound that limited the supply of acid-neutralizing HCO_3^--rich groundwater. The slower decomposition in poor fen was indeed confirmed by the low CO_2 production in poor fen litter, mainly consisting of peat moss biomass (1.40 ± 0.07 mmol CO_2/L fresh soil/day). Low poor fen decomposition rates together with relatively high production rates result in a high net peat production leading to ombrotrophication. With increasing distance from buffered conditions combined with the ability of peat mosses to retain rainwater, the influence of nutrient-poor and less buffered rainwater increases, and acids produced are less easily neutralized (Bootsma et al., 2002; Granath et al., 2010; Soudzilovskaia et al., 2010; van Breemen, 1995). Nevertheless, we still found the highest bio-available P concentration in poor fen vegetation in the upper soil layer, which may be explained by either the fact that sphagnum lacks roots able to mobilize this P fraction or by self-facilitating feedbacks of poor fen species that cause a buoyancy-driven upward flow of underlying water with an extra supply of nutrients (Adema et al., 2006; Rappoldt et al., 2003).

4.2 | Habitat modification by rich fen vegetation

Rich fen litter, mainly consisting of *Schoenus nigricans* litter, showed a 1.8 times higher potential CO_2 production rate than poor fen litter. Additionally, we observed no biogeochemical trends in pH, alkalinity, HCO_3^- concentrations and BS along the vertical depth profile. We expect this to be caused by self-facilitating feedbacks of rich fen vegetation. High anaerobic decomposition rates generate alkalinity

(Mettrop, Cusell, Kooijman, & Lamers, 2015) and mineralization will result in a relatively high nutrient availability. This high nutrient availability will stimulate the growth rate and height of the rich fen vegetation, making it a strong competitor (e.g., for light), specifically for the generally short-growing poor fen vegetation. Furthermore, fast decomposition rates result in a low organic matter accumulation rate (Bragazza, Buttler, Siegenthaler, & Mitchell, 2009; Lamers et al., 2000; Scheffer, Van Logtestijn, & Verhoeven, 2001; Verhoeven & Toth, 1995) and in this way, a habitat with close proximity to base-rich groundwater is maintained with environmental conditions favoring rich fen vegetation growth (Tyler, 1979).

4.3 | Competition for light: mutual exclusion

The spatially segregated occurrence of rich and poor fen vegetation in dense tussocks and hummocks indicates that next to self-facilitating feedbacks, competitive strategies are preventing invasion of the contrasting vegetation. For example, peat mosses form acidic rainwater lenses, which diminishes the influence of base-rich groundwater. The rich fen vegetation does not prefer these abiotic conditions (Tyler, 1979). It has been shown that acidic conditions decrease germination of rich fen vegetation, specifically *Schoenus nigricans*, though the exact mechanism remains unclear (Boatman, 1962; Clymo & Hayward, 1982). Inversely, abiotic conditions that favor rich fen vegetation growth, such as a high pH, high alkalinity and high HCO_3^- concentrations (Tyler, 1979), negatively affect poor fen vegetation performance (Harpenslager, van den Elzen, et al., 2015; Vicherová, Hájek, & Hájek, 2015; Vicherová, Hájek, Šmilauer, & Hájek, 2017). Additionally, dense rich fen vegetation tussocks reduce light and water accessibility to the moss layer, thereby impeding generally sparsely and lower growing poor fen vegetation growth (Berendse et al., 2001; Lamers et al., 2000; Malmer et al., 2003; Pouliot et al., 2011).

4.4 | Overcoming mutual exclusion

Within an EC range of ~300–450 mEq/L, patches of poor fen within rich fen vegetation (e.g., peat mosses) were able to survive negative effects from upward mineral-rich water seepage on density, as judged from the intermediate pH, alkalinity and bicarbonate concentration compared to the other vegetation plots (either poor or rich fen, Figure 3). However, no clear succession from rich fen vegetation into a *Sphagnum*-dominated bog took place in this floating fen (Appendix S1; this study; Van der Maarel & Roozen, 1975; van Groenendael et al., 1975). Thus, during the last 40 years poor fen vegetation was unable to outcompete rich fen vegetation on the ecosystem scale, because of restricting geohydrological conditions (constant upward movement of HCO_3^--rich water) combined with positive vegetation feedbacks maintaining dense rich fen vegetation tussocks. Base-rich conditions originating from the influence of calcareous groundwater in upper fen layers previously explained the occurrence of *Schoenus nigricans* in a similar

peatland ecosystem (Grootjans et al., 2016). The observed mosaic of rich and poor fen vegetation could originate from a short period of alleviating environmental stressors: a window of opportunity (sensu Balke, Herman, & Bouma, 2014), as generally poor fen vegetation is unable to establish in areas influenced by upwelling and inundation of HCO_3^--rich groundwater (Lamers, Smolders, & Roelofs, 2002; Vicherová et al., 2015, 2017). Therefore, we expect that a period of drought resulted in lower groundwater levels, which temporarily alleviated stress enabling establishment of poor fen vegetation inside rich fen vegetation. Simultaneously, reduced groundwater pressure likely lowered alkalinity and bicarbonate concentrations in the porewater. During drought, peat mosses are less affected by HCO_3^- toxicity, which can enable the poor fen vegetation to become locally dominant (Granath et al., 2010). After having reached a critical density and size, feedbacks created by the peat moss vegetation itself (acidification, rainwater retention and peat accumulation), further reduce the negative impact of HCO_3^- on the poor fen vegetation (Cusell et al., 2015).

During drought, oxygen can penetrate the soil and potentially decrease the acid-neutralizing capacity and pH as a result of acid production by aerobic microbial redox processes (Stumm & Morgan, 1996). Peat mosses are able to retain rain water during drought via the ability to store water in their hyaline cells in order to regulate capillary pressure that transports water from below and to reduce hydraulic conductivity of the peat layer, preventing lateral and vertical water losses (Clymo & Hayward, 1982; Päivänen, 1973; Rydin & Jeglum, 2006; Schipperges & Rydin, 1998). Rich fen species are much more prone to drought, because they lack these mechanisms

(Bakker, van Bodegom, Nelissen, Aerts, & Ernst, 2007; Mettrop et al., 2015), which gives them a competitive disadvantage in periods with reduced groundwater pressure.

4.5 | Conceptual model

Here, based on empirical data, we present a conceptual model for a window of opportunity due to a short period of drought for the rise of a stable vegetation mosaic of rich and poor fen vegetation. When peat mosses are well-established, they are able to overcome HCO_3^- stress by means of density-dependent feedbacks, including acidification and the formation of hummocks that retain poorly buffered rainwater (Granath et al., 2010; Hájková et al., 2012). Similarly, this situation would occur when HCO_3^--rich groundwater pressure increases again after a period of drought that temporarily alleviated stress for peat mosses so their density could increase. At the same time, when HCO_3^--rich groundwater pressure increases, rich fen vegetation gains a competitive advantage and the ability to outcompete poor fen vegetation (Granath et al., 2010; Hájková et al., 2012). Succession from rich to poor fen species likely stagnates and instead of reaching a climax stage of succession, a vegetation mosaic could emerge in the floating fen (Figure 5). We expect that as conditions remain within certain boundaries (e.g., EC values of ~300–450 mEq/L in the deeper soil layer), coexistence of poor and rich fen vegetation is possible and maintained due to self-facilitating feedbacks and mutual
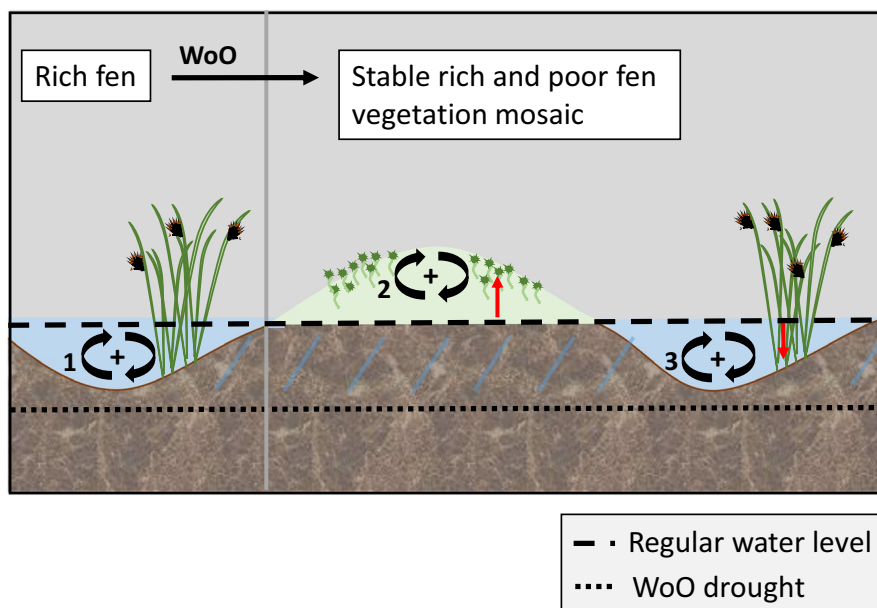

FIGURE 5 Conceptual model of a floating fen showing the development of a rich fen vegetation-dominated state (1: left situation) towards a stable mosaic of rich and poor fen vegetation (2 and 3: right situation). During drought as a window of opportunity (WoO), the influence of HCO_3^--rich groundwater is reduced (from dashed to dotted line) and poor fen vegetation colonizes the floating fen (2). When poor fen vegetation density increases, self-facilitating feedbacks cause ombrotrophication and poor fen vegetation is able to overcome HCO_3^- stress when groundwater pressure increases (red arrow). Simultaneously, when groundwater pressure is high again, rich fen vegetation (3) is able to outcompete poor fen vegetation again with self-facilitating feedbacks such as fast decomposition, resulting in close proximity to HCO_3^--rich groundwater (brown arrow). A stable system arises due to intraspecific self-facilitating feedbacks and negative species interactions as explained [Colour figure can be viewed at wileyonlinelibrary.com]

exclusion. Currently, causal relationships are lacking and further experiments should focus on elucidating this mechanism.

4.6 | Conclusion

Our findings strengthen our hypothesis that multiple vegetation feedbacks, leading to engineered environmental conditions in the upper soil layer, combined with stochastic events, are likely responsible for the vegetation patchiness of characteristic rich and poor fen vegetation in the floating fen. This occurred on a local scale with homogeneous EC values, of 300–450 µS/cm in the deeper soil layer, and the vegetation mosaic is thus not only driven by abiotic conditions, in contrast to large-scale patterns driven by geohydrological conditions. Positive feedbacks are known to play a key role in ecosystem organization (DeAngelis & Post, 1991) and with additional negative species interactions this leads to mutual exclusion and spatially segregated coexistence, as has been shown for other ecosystems, such as salt marshes and seagrass ecosystems (van der Heide et al., 2012; Van Wesenbeeck et al., 2007). Other studies of fen ecosystems previously showed that differences in environmental conditions were related to vegetation mosaics at a microscale (Hájek, Hekera, & Hájková, 2002). Here, we provide a possible explanation for the mosaic of poor and rich fen species in a floating fen based on empirical data. Interestingly, self-facilitation of species not only helps them to cope with environmental stress, but also engineers their direct environment (upper soil layer) and likely results in a stable coexistence. We expect this principle to play an important role in the resilience of fen ecosystems and therefore further research should elucidate the mechanism underlying vegetation mosaics in similar environmental conditions.

AUTHOR CONTRIBUTIONS
JR, AG, TH and LL initiated the project; TB, RT, LT, WB, KR, AD, AW conducted the fieldwork and data analyses. LL, TH, TB and RT developed the conceptual framework. TB and RT did the majority of manuscript writing and all authors contributed to improved versions of the manuscript.

DATA AVAILABILITY STATEMENT
Data are available via the Data Archiving and Networked Services (DANS) EASY https://doi.org/10.17026/dans-xx9-gzz5 (Van Bergen et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Vegetation maps of lake Aturtaun of 1975 and 2014

Appendix S2. Braun-Blanquet relevés of vegetation plots of 2014

Appendix S3. Coordinates of the plots in Loch Aturtaun

Appendix S4. Relationship between electric conductivity at 10 cm depth