Contrasting response to mowing in two abandoned rich fen plant communities

N.M. Menichino [a,c,*], N. Fenner [a], A.S. Pullin [a], P.S. Jones [b], J. Guest [b], L. Jones [c]

[a] Bangor University, Environment Centre, Wales, Bangor, Gwynedd, North Wales LL57 2UW, UK
[b] Anglesey & Llŷn Fens LIFE Project, Natural Resources Wales, Bangor, North Wales LL57 2DW, UK
[c] Centre for Ecology and Hydrology, Environment Centre, Wales, Deiniol Road, Bangor, North Wales LL57 2UW, UK

ABSTRACT

Globally important U.K. fens are in poor condition, principally due to abandonment, following cessation of traditional mowing and grazing in recent decades. In the absence of management, rich fen flora are displaced as a result of succession. This leads to an increase in competitive species and subsequent biomass accumulation. In order to reverse this trajectory and increase species richness, management consisting of a single mowing event was employed. Mowing was conducted in two degraded fen communities in north-west Wales (U.K.) across three sites: (i) a species rich, tussock alkaline mire, dominated by *Schoenus nigricans* and *Juncus subnodulosus* (SN community) and (ii) a species poor basin mire *Cladio-Molinietum* dominated by *Cladium mariscus* (CM community). The early vegetation responses were monitored over two years. Results show a large treatment effect on species richness in the CM community, where mean species richness increased by 51% in the second year following mowing. Consequently, total species number across all sites increased to 74 in the treatment compared to 44 in the control. Mowing reduced vegetation height and litter cover and increased bare ground. These treatment effects combined with a reduction in graminoid and shrub cover collectively contributed to the initial stages of rehabilitation. Conversely, the SN community showed no increase in species richness, in spite of a reduction in litter cover and increased bare ground. Strong site heterogeneity and a sustained canopy height caused by rapid re-growth of the dominant graminoid *S. nigricans* may have impeded treatment effects. Therefore, increased mowing frequency in alternate years, switching between autumn and summer would be necessary to develop species richness in the SN community. Ongoing intervention in each fen community is needed to achieve an optimal trajectory of increased rich fen and reduction of secondary succession species.

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1. Introduction

Globally, it is estimated that fens comprise 26% of all wetlands and 42% of all peatlands, which equates to an area of 1.5 million km^2 (Joosten, 2002; Ramsar Convention and Secretariat, 2013). Fens are distributed throughout the northern hemisphere and are well represented in North America, Russia, Scandinavia and Central Europe (Lamers et al., 2014). The term 'rich' fen refers to minerotrophic peatlands which are base 'rich', due to a high concentration of base cations (calcium and magnesium) and are nutrient poor (oligo-mesotrophic) with pH values between 6.0 and 8.0, which subsequently leads to botanically diverse stress tolerant communities (Sjörs, 1950; Wheeler, 1980a; Wheeler and Proctor, 2000). Furthermore, U.K. fens are quite rare and make up just 10% of all British peatlands (JNCC, 2011b). The fens which are the focus for this study, are situated off the north-west coast of Wales (U.K.) on the island of Anglesey, are internationally significant and are designated as Ramsar sites (Jones et al., 2013). In the case of rich fens, their disjunct distribution supports their rarity, as these ground water dependent (GWD) wetlands have strict hydro-geological requirements (Joosten, 2002; Bedford and Godwin, 2003; JNCC, 2011b). It is these unique requirements which characterise the vegetation (Wheeler and Proctor, 2000) and render rich fens to be amongst the most species rich, low production wetlands in the world (Ilomets et al., 2010). Fens also support essential ecosystem services such as water purification, flood protection and climate regulation (Gorham, 1991; Zedler and Kercher, 2005; Lamers et al., 2014) in which their contribution is disproportionate to their size (Bedford and Godwin, 2003).

Historically, U.K. fens were economically important areas in the landscape, where agriculture, peat harvesting and biomass production for thatching ensured these systems experienced regular disturbance regimes. However, in the absence of management, rich fen plant communities have shifted from low competition/stress tolerant plant communities, with a complex assemblage of herbs, low stature sedges and bryophytes, to degraded plant communities which are dominated by graminoids and shrubs (Rodwell, 1992; Billeter et al., 2007; JNCC, 2011b). This change in trajectory from a low to high production community has also led to biomass accumulation from fast growing species, which is deleterious to maintaining fen species richness (Bergamini et al., 2001; White and Jentsch, 2001; Hajkova, 2003; Middleton et al., 2006b). Abandonment also leads to litter accumulation, which covers the peat surface and impedes seedling establishment (Ruprecht et al., 2010). To reverse succession to an earlier sere and increase biodiversity, partial or total removal of biomass is required, which addresses the physical barrier to restoration (Brewer et al., 1997). Mowing increases the space available for species to establish and increases light penetration to the peat surface (Schaffers, 2002; Billeter et al., 2007). Successful re-colonisation by small stature fen plant species is also dependent on the proximity of the restored plant community to a seed source, seed dispersal capability of favoured species and presence of a viable seed bank (Wheeler and Shaw, 1991; Billeter et al., 2003; Levine and Murrell, 2003; Kolos and Banaszuk, 2013). Therefore, rich fen species can only persist where traditional management has been maintained or is reinstated (Westhoff, 1971; Tilman, 1996; Middleton et al., 2006a; Šefferová et al., 2008).

This research was conducted in collaboration with the Anglesey and Llŷn fens EU LIFE project, whose main aim was to rehabilitate 751 ha of degraded fens, in support of improving habitat quality for plants and animals, as well as enhancing recreation value to the local community. The intention for this research was to examine the botanical response to mowing in these previously abandoned fens. The focus was on two European Annexe 1 plant communities, designated for their ecological importance and rarity (Saltmarsh et al., 2006). The first is *Cladio-Molinietum* (CM plant community), which is a species poor swamp community, situated within topographic depressions within valley floors and is dominated by tall sedge, *Cladium mariscus* (CM community). The second plant community is located around the fen margin, dominated by *Schoenus nigricans* and *Juncus subnodulosus* (SN plant community). *S. nigricans* is an ecologically important component as it produces elevated tussocks and consequential runnels (shaded channels around the tussock stools) that support a complex suite of fen species that include sedges, distinctive dicotyledonous herbs and an ecological group of "brown mosses" in the families of Amblystegiaceae and Calliergonaceae (Rodwell, 1992; Bedford and Godwin, 2003; Hedenas, 2003).

However due to abandonment, the CM and SN plant communities have reduced in species richness due to an increase in cover from each of the dominant graminoid species *C. mariscus* and *S. nigricans* and so machine mowing and hand cutting was selected for each plant community respectively. These methods of management were chosen due to the sensitive nature of fen habitat (Middleton et al., 2006b; Van Andel and Grootjans, 2006; Šefferová et al., 2008). In contrast to North America, burning is not common practice in U.K. fens. It is only undertaken with caution, where fire management has been used historically. This is probably due to their small areal size, which is disproportionate to high conservation value and as many species are associated with the plant litter which is being burnt (e.g. invertebrates, small mammals and amphibians) the risk to biodiversity is high (Middleton, 2002; SNH, 2011).

The aim of this study was to examine the response to mowing in two derelict rich fen communities employing a single mowing application. It was proposed that mowing would encourage colonisation by calcicole (calcium-loving) rich fen plant species, which are tolerant of a low phosphate concentration, associated with the presence of calcium carbonate found in the mineral rich groundwater (Clymo, 1962; Boyer and Wheeler, 1989; Wassen et al., 2005). It was expected that following mowing, species richness would increase due to a reduction in canopy height, standing biomass and litter cover which consequently will increase exposed peat. It was also proposed that mowing would reduce dominant vegetation components, as a reduction in graminoid and shrub cover is expected to be associated with increased herb and bryophyte cover. Therefore, it is hypothesised that due to the mechanisms described above, treatment effects would produce optimum conditions to meet the conservation aim to reduce robust late succession species and increase overall species richness in each plant community.

2. Materials and methods

2.1. Site descriptions

The study was conducted within the Anglesey fens Special Area of Conservation (SAC) which comprises 7 Sites of Special Scientific Interest (SSSI) covering 467 ha and which form part of the Anglesey and Llŷn fens Ramsar site (Jones et al., 2013). All experimental sites were situated on the island of Anglesey, which is located off the coast of mainland north-west Wales, United Kingdom. The three study sites comprise: (i) Cors Erddreiniog (53.3125 N, −4.29670 E), a valley head fen system, comprising three peat basins, and which is the largest of the three sites at 200 ha (Prosser and Wallace, 1995; Jones et al., 2013), (ii) Cors Goch (53.3075 N, −4.2575 E), a basin fen comprising 67 ha of which 25 ha are wetland and (iii) Cors Bodeilio (53.2726 N, −4.2507 E), which is the smallest site, at 39.28 ha, situated on shallow peat within a limestone valley (Jones et al., 2013). These sites are influenced by an oceanic climate with a mean annual temperature of 9.4 °C and total mean annual rainfall of 625 mm (calculated from the Cors Erddreiniog automated weather station from data collected between 2007 and 2013).

Paired plots were used to ensure that hydrological and topographical conditions were as comparable as possible. One half of each paired plot (10 m²) was randomly assigned as treatment, the other as control. Within each control and treatment plot, a set of 5 quadrats (2 m by 2 m) were established. Co-ordinates for each randomly assigned quadrat were generated, utilising an online random number generator (Random.org) and quadrats were positioned within each 10 m² plot. The locations of the paired 10 m² plots were permanently marked by placing steel marker pegs in the peat at each corner of the plot, to allow for re-location with a metal detector after cutting. A Leica 1200 RTK digital global positioning system (dGPS) was employed to permanently locate plots and quadrat centroids and post processing was undertaken using Leica Geo Office together with RINEX data and Holyhead reference station, downloaded from the Ordinance survey GPS website (http://www.ordnancesurvey.co.uk/gps/os-net-rinex-data/). Bamboo canes were also used for ease of re-location of quadrats and plots, but were temporarily removed or pushed into the peat during mowing. Treatment and control conditions included a 5 m buffer zone beyond the perimeter of each paired plot to allow for edge effects.

2.2. Plant communities

The *Cladio-Molinietum* (CM community) is a tall herb community found in base-rich (pH 6.0–7.5) peatlands, and characterised as topogenous due to its location on valley floors, where water

flow is low and vertical and in summer can move below the peat surface (Wheeler, 1980b; Saltmarsh et al., 2006; JNCC, 2011a; SNH, 2011). The total U.K. extent is estimated at 5 km². Its specialised hydro-geological requirements have contributed to its rapid decline (Buczek and Buczek, 1996; JNCC, 2007). Wheeler (1980b) describes the CM community as a swamp community owing to its location within inundated areas of the fen. The CM community is dominated by *C. mariscus*, a dominant perennial, sedge, which can reach a canopy height of 2 m (Saltmarsh et al., 2006). In the absence of management, dense species poor communities are common, which have promoted a closed canopy. Although not monotypic, accompanying species are few and commonly include: *Phragmites australis*, *Menyanthes trifoliata* and *Myrica gale* (Wheeler, 1980b).

The second fen community occurs on peat and mineral soils and is characterised as soligenous, encountering seasonal lateral water movement. This is due to its association with springs along the fen margin, where water can be running, standing or soil remains moist, and the pH range in this community is slightly higher (pH 6.5–8.0) (Wheeler, 1980a; SNH, 2011). This community can also occur within the fen basin, where contact is maintained with calcium rich nutrient poor ground water (Rodwell, 1992; SNH, 2011).

The SN community is a tussock community dominated by *S. nigricans* and *J. subnodulosus* and is composed of a complex and rich assemblage of rich fen species; some of which are rare and the mean number of species is 27 derived from 2 m × 2 m quadrats (Rodwell, 1992). Currently, the U.K. extent is estimated at 16.32 km² and 18–48% of all alkaline fens are not being managed effectively, under statutory protection (JNCC, 2007). Losses in this tussock community are due to agricultural gain and eutrophication (Criodain and Doyle, 1997). It is the physical characteristics that make this community so diverse as tussocks (optimal height 40 cm) and surrounding runnels can support a host of low growing sedges, herbs and bryophytes (Rodwell, 1992).

2.3. Treatments

Management intervention in both habitats involved a single mowing event and biomass removal in both plant communities. Mowing was undertaken once in the CM community plots using a Pistenbully 100 Allseason soft tracked vehicle, modified with a 10 m³ aluminium hopper and Mera Rabbeler forage harvester as hand cutting was not possible due to decades of biomass and litter accumulation. Harvesting was undertaken between 3 February 2012 and 28 March 2012. Vegetation was cut and collected in the hopper and removed from site. The target mowing height was 5–10 cm, although this varied slightly depending on water table depth (WTD), peat structure and woody root density. In the SN community, one application of hand cutting was undertaken between 7 February 2012 and 29 March 2012. Due to the nature of the sensitive tussock vegetation and historical management the SN community was hand cut using strimmers (Stihl FS460C (Baden-Württemberg, Stuttgart, Germany)), fitted with 3 mm nylon wire and hand raked the same day as cutting so that biomass could be removed from site. This method was chosen, as fens throughout Europe were historically mown by hand, using a scythe (cutting tool with a long curved blade) (Rowell, 1986; Bartoszuk and Kotowski, 2009).

2.4. Botanical surveys

Baseline plant surveys were undertaken between 26 June 2011 and 28 October 2011, and quadrats were re-surveyed post-treatment between 30 July 2012 and 20 August 2012 and 17 July 2013 and 8 August 2013. Plant surveys were undertaken by assigning all rooted taxa a percentage cover estimate, as assessed by eye. Canopy height was measured using a marked 2 m cane and

5 measurements of maximum plant height were taken to the nearest 5 cm for each vegetation component of total drooping vegetation height (the point at which the plant is no longer erect). Measurements were undertaken by placing a 2 m marking stick at the centre and 30 cm in from each quadrat corner to calculate mean heights.

2.5. Biomass and nutrient content

A measurement of biomass was undertaken in December 2013 to provide an estimate of the total amount of biomass removed from the system during harvesting. Further calculations could then be undertaken to estimate the quantity of accumulated N and P tissue concentration removed in the biomass. A 1 m² quadrat was randomly sampled from the control and treatment for each paired plot and plant community. The biomass was collected using secateurs, cutting to a sward height of 10 cm to ensure comparability with the mowing regime. Measurements included live and dead plant biomass combined. In the treatment plots, this included re-growth since cutting in 2011. Vegetation biomass was oven dried at 65 °C for 48 h to remove water content, in a Riley 1250 litre HDH-OV-1250-F-250-DIG oven (West Midlands, UK). Samples were weighed immediately after drying using a Sartorius Universal balance (GMBH, Gottingen, Germany). The percentage of tissue nitrogen (N) and phosphorus (P) was derived from graminoid tissue chemistry concentrations found in the literature for rich fens (Bombonato et al., 2010). Calculations were only applied to control quadrat biomass weights for each plant community and further calculated to determine kg N ha^{-1}. Atmospheric N deposition loads were derived for fen habitat and the site locations from the UK Air Pollution Information System web page (www.apis.ac.uk).

2.6. Statistical analysis

Statistical package 'R' (R-Core-Team, 2014) was employed to undertake statistical analysis of all data. Each plant community was analysed separately, using a linear mixed effect (LME) model in 'R' using the lmer function and lme4 package (Bates et al., 2014). The null model comprised response plus random effects ("site", "plot" and "quadrat") and the full model tested response as a function of treatment plus random effects. Analysis of variance (ANOVA) was then employed to compare differences between the variance in the null and full models to determine significance values. Treatment effects on vegetation component percentage cover, species richness, vegetation height and biomass weight. Individual species cover data (2013) were also tested.

Firstly, the models examined whether there were underlying baseline differences for the pre-treatment and control plots in 2011, to ensure the paired plots were botanically comparable prior to treatment. Percentage cover and height data were analysed using the difference between the current and base year (2012–2011, 2013–2011) to test for treatment effects in subsequent years with exception of species richness and biomass weight, which were tested using raw data. To test the significance of total number of species present in all control plots versus treatment plots in 2013; a general linear model was performed with a binomial distribution.

Multivariate analysis was undertaken to examine the relationship between plant species composition and environmental variables. Mean Ellenberg indicator values were calculated and combined with botanical data, to undertake a multivariate analysis using CANOCO (ter Braak and Šmilauer, 2002). Initially, a de-trended correspondence analysis (DCA) using an indirect gradient analysis was undertaken to assess linearity of the primary axis. As the gradient lengths were short, a linear ordination method was adopted. Indirect analysis of species data was undertaken,

using principal component analysis (PCA), as a means to summarise each plant community's variation in response to treatment. Meaned Ellenberg values were used to create environmental ordination plots. The PCA ordination plots were examined to interpret results, which were best described using axes 1 and 2 for CM community and axes 2 and 3 for SN community. Axis 1 was not used for the SN community as it only showed broad site differences, not within and between environmental heterogeneity. Finally, in order to extract patterns from the explained variation and to test significance of environmental variations, a redundancy direct analysis (RDA) was performed. To test significance of environmental variables in response to treatment, Monte Carlo methods within CANOCO (ter Braak and Šmilauer, 2002) were employed. This calculated the total explained variation and also assigned a percentage value to each environmental variable to indicate what proportion of explained variation was due to the species-environment relationship.

3. Results

3.1. Percentage cover of vegetation components

There were no significant differences observed in the baseline vegetation survey for each plant community for vegetation components and species richness. This confirmed that control and pre-treatment plots were botanically comparable. There were also no significant differences in DGPS elevations between treatments for the CM community (P, 0.14) and SN community (P, 0.67), suggesting topography was also equivalent.

Significant reductions were observed in the percentage cover of vegetation components for mown plots, compared with the control plots in the CM community for each year following mowing, Fig. 1(a). Reductions were evident following comparisons between the treatment and control mean percentage cover for each vegetation component, reported here with ±1 s.e.: (i) graminoid cover in the treatment plots reduced by 46% in 2012 (50.2 ± 2.7) compared to the control (93.5 ± 2.8) and by 28% in the treatment (51.3 ± 2.5)

in the following year, compared to the control (71.48 ± 3.9), (ii) ericoid/sub-shrub cover also reduced by 45% in the treatment (15.3 ± 1.4) compared to the control (27.6 ± 2.8) in 2012 and by 33% in the treatment (24 ± 2) compared to the control in the following year (36 ± 3.1) and (iii) litter cover was significantly reduced by 46% in treatment plots in 2012 (50.3 ± 5.5) compared to the control (93.3 ± 2.7) and by 50% in treatment plots in the following year (47.9 ± 5.9) compared to the control (95.3 ± 3.1). Bare ground was absent in both control and treatment plots in 2011 (0). However, in 2012 bare ground was 14% higher in treatment plots in 2012 (14.2 ± 2.1) compared to the control (0), and treatment plots further increased by 16% in 2013 (16.2 ± 2.4) compared to control plots (0.2 ± 0.2).

Herb cover showed no difference (P, 0.64) between treatment (1.1 ± 0.3) and control plots (2.7 ± 0.9) in the first year, however by the second year, herb cover increased by 79% in treatment plots (3.9 ± 0.7) compared to the control plots (2.2 ± 0.5). In addition, a reduction in the dominant sedge was also observed; $C.$ $mariscus$ cover decreased by 63% ($P < 0.001$) in treatment plots in 2012 (30.4 ± 3) compared to the control plots which remained high (81.9 ± 4.1). A smaller reduction, 55% was observed in the treatment plots in the following year ($P < 0.001$, 25.8 ± 2) compared to the control (57.6 ± 4.2). Bryophyte cover was the only vegetation component to be unaffected by treatment in the CM plant community.

The SN plant community, Fig. 1(b) did not show a reduction in the majority of vegetation components which is in contrast to the CM community. Graminoid cover reduced by 28% in 2012 in treatment plots (55.7 ± 3.3) compared to control plots (77.7 ± 4.6); however this reduction was not sustained in 2013. A temporary reduction was also reflected in the percentage cover of dominant graminoid $S.$ $nigricans$, which reduced by 49% in treatment plots (18.83 ± 2.146) in the first year following mowing, compared to the control (40.65 ± 4.717), only to become comparable to the control plots once again in the subsequent year.

Ericoid/sub-shrub cover showed no treatment reduction following mowing in the first year, but did show a 39% reduction
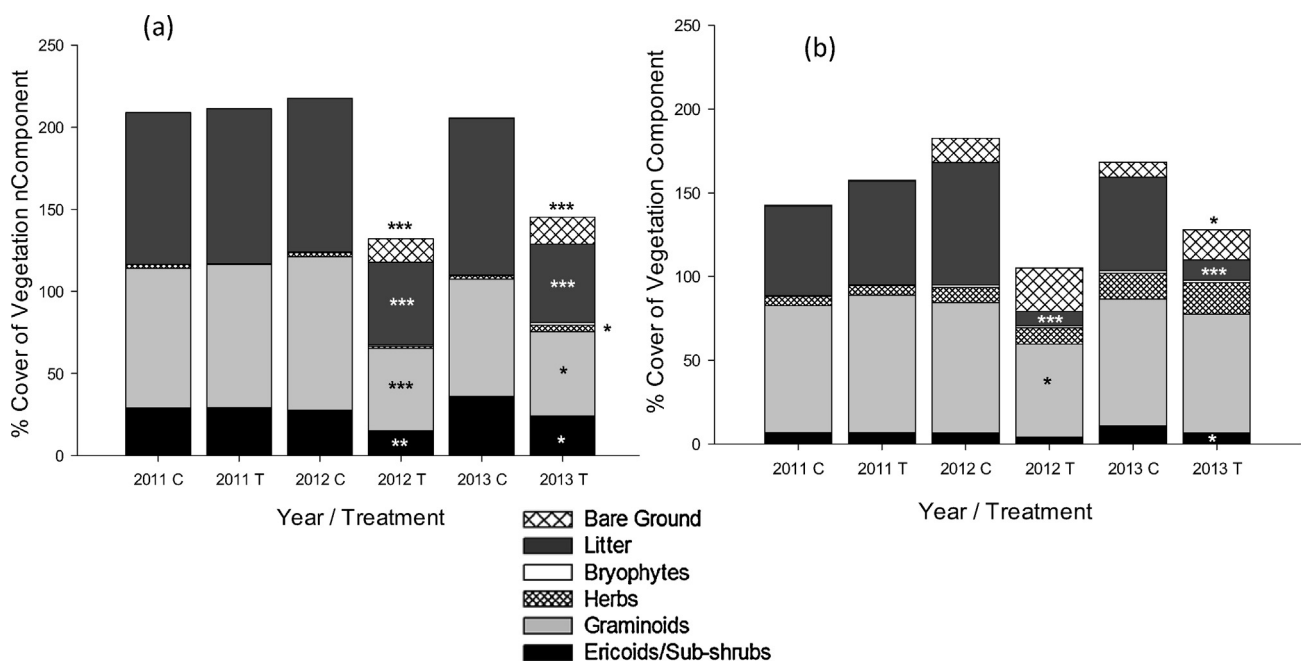

Fig. 1. CM community (a) ($n = 9$) and SN community (b) ($n = 8$) show mean percentage cover for each vegetation component across all sites for the paired plots control (C) and treatment (T) for each year. Statistical analysis of treatment effects was undertaken on differenced data (T/C year minus T/C baseline) for each vegetation component and applied to LME model to test significant differences between the control and treatment for each year. Statistical codes used: '***' $P < 0.001$, '**' $P < 0.01$, '*' $P < 0.05$ and no symbol, $P > 0.05$.
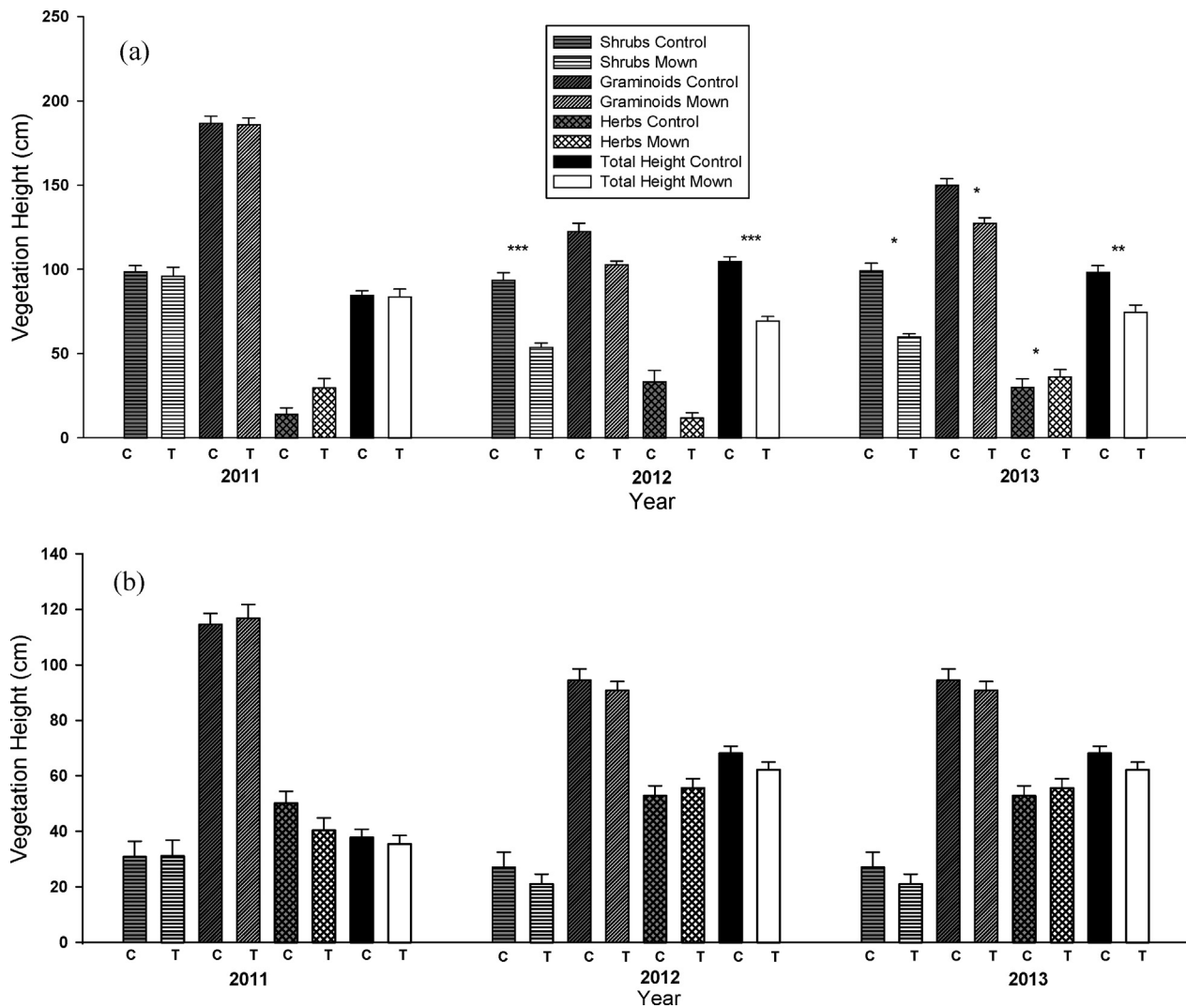
Fig. 2. Vegetation height for CM community (a) (n = 9) and SN community (b) (n = 8) across all sites for the paired plots control (C) and treatment (T). Mean maximum for each vegetation components and overall mean maximum for all sites is illustrated. Statistical analysis of treatment effects was undertaken on differenced data (T/C year minus T/C baseline) for each vegetation height component and applied to LME model to test significant differences between the control and treatment for each year. Statistical codes used: '***' $P < 0.001$, '**' $P < 0.01$, '*' $P < 0.05$ and no symbol, $P > 0.05$.

in treatment plots (6.6 ± 1.5) in the second year compared to the control (10.7 ± 2.8). Litter cover reduced by 88% in treatment plots (8.5 ± 1.7) in 2012 compared to control plots (73.1 ± 4.6) and sustained a 78% reduction by 2013 in treatment plots (12.4 ± 1.9) compared to control plots (55.9 ± 4.7). Furthermore, no difference in bare ground was observed in the first year, although in the following year, treatment plots (8.9 ± 2) increased compared to control plots (17.7 ± 1.5). In spite of the sustained reduction in litter cover; the temporary reduction in graminoid cover is likely to be attributable to the unaffected cover of herbs and bryophytes.

3.2. Vegetation height

In the CM community, Fig. 2(a), mowing reduced the overall mean vegetation height between the treatment and the control in 2012 and 2013 by 34% and 24% respectively. Ericoid/sub-shrub cover reduced by 66%, and 67% and graminoid cover reduced by 35% and 41% with no observed difference in herb height. No treatment effect was observed for the mire vegetation heights, Fig. 2(b).

3.3. Biomass and nutrient removal

Standing biomass and litter in the CM community, Fig. 3(a) was reduced by 75% compared to the control, which was comparable across all sites. Mean biomass weight removed was calculated as 1396.4 g m^2. N removal was calculated as 240.18 kg N ha^{-1} and equated to 15 years of N in annual atmospheric deposition, which is 16.1 kg ha^{-1} year^{-1} for fen habitat at these sites (APIS, 2014) and P removal was calculated as 13.27 kg P ha^{-1}.

In contrast, Fig. 3(b) illustrates that the overall amount of biomass removed in the SN community was much lower (41%) and it was not comparable across sites, owing to large error bars caused by site heterogeneity. Cors Goch was the only site with a significant reduction. However, biomass contained 57.04 ha^{-1} N, which equates to 3.5 years of N being removed and 3.15 kg ha^{-1} P.

3.4. Species richness

In the CM community, following the initial disturbance caused by mowing in 2012, a 51% increase in species richness was observed in 2013, Fig. 4(a). The positive change in species richness was driven by an increase in the number of herbs. By 2013 the mean
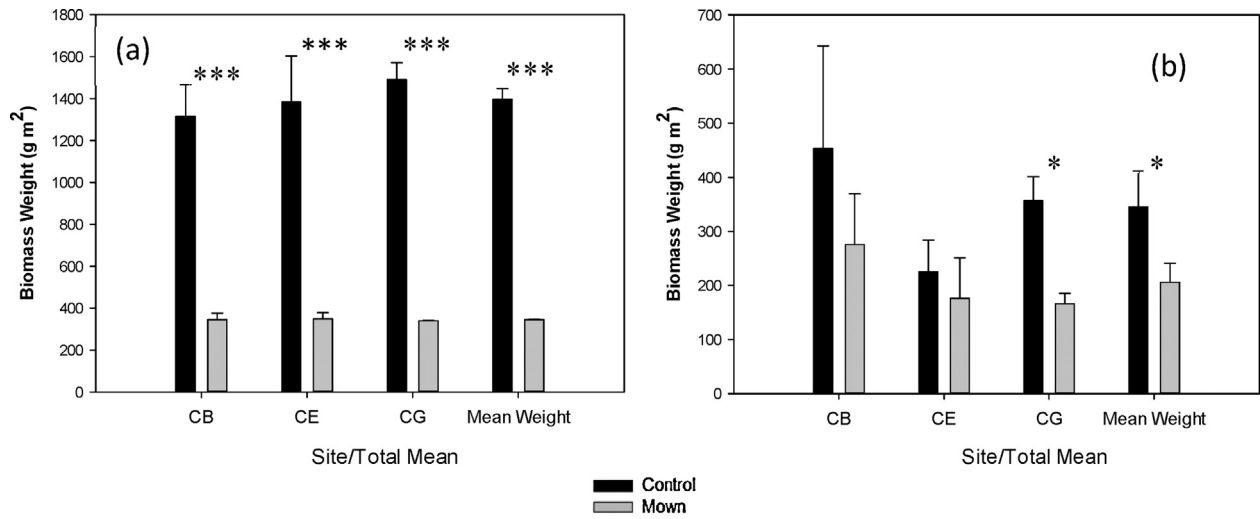
Fig. 3. Biomass weight for CM community (a) and SN community (b) showing mean weight for all control and treatment plots for each site and overall mean biomass weight for all sites: Cors Bodeilio (CB), Cors Erddreiniog (CE) and Cors Goch (CG). Black bars indicate the control plots and grey bars indicate the mown plots. Each bar shows ±1 standard error and statistical codes used are: '***' $P < 0.001$, '**' $P < 0.01$, '*' $P < 0.05$, no symbol, $P > 0.05$.
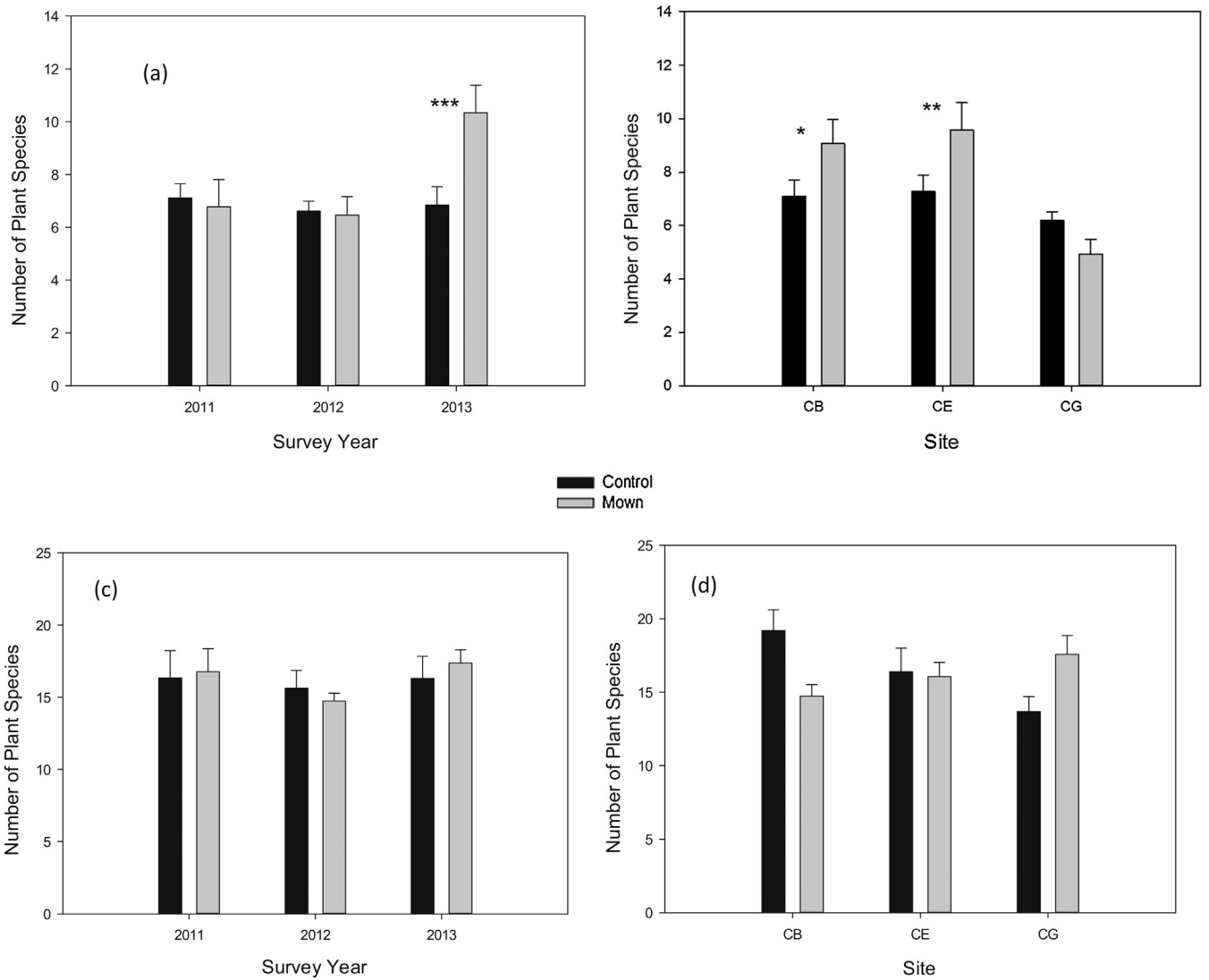

Fig. 4. CM community species richness for (a) all sites over time and species richness for (b) each site in 2013. SN community species richness for (c) all sites over time and species richness for (d) for each site in 2013. Site codes: Cors Bodeilio (CB), Cors Erddreiniog (CE), Cors Goch (CG). Black bars indicate the control plots and grey bars indicate the mown plots. Each bar shows ±1 standard error and statistical codes used are: '***' $P < 0.001$, '**' $P < 0.01$, '*' $P < 0.05$, no symbol, $P > 0.05$.

Table 1

List of CM community environmental variables (EV) and associated abbreviations shown in the following environmental ordination plot, Fig. 5(c), which depicts percentage of total species variation explained within RDA and significance tested for each variable independently.

Environmental variables [EV]	Variance (%)
Site	12.6%***
EllenbergN – nitrogen [EN]	12.2%***
EllenbergR – acidity [ER]	10%***
C. mariscus cover [Cl]	7.7%***
Species richness [Spp]	7.6%***
Litter cover [L]	6%***
EllenbergF – moisture [EF]	5.8%***
Bare ground [B]	3%***
EllenbergL – light [EL]	2.6%***
Year [Y]	2.2%***
Vegetation Height [H]	2.3%***
Treatment [T]	1.8%***

*** $P < 0.001$.

number of herbs were 2.31 (±0.328) in the treatment plots versus 0.95 (±0.174, $P < 0.05$) in the control plots. Also, by 2013 there were 2.16 (±0.208) bryophyte species per treatment plot versus 0.56 (±0.148, $P < 0.001$) per control plot. Differences between sites were also apparent, Fig. 4(b), where Cors Erddreiniog and Cors Bodeilio both increased in species richness and Cors Goch showed no response to treatment (P, 0.55).

Overall the SN community showed no change in species richness, Fig. 4(c) in response to treatment. However, Cors Goch, which was the least species rich site, exhibited a weak positive response to treatment (P, 0.06) which was not significant, Fig. 4(d). In 2013, it was observed that the mean number of species remained low at 17.38 (±0.532) species per treatment plot and 16.30 (±0.710) species per control plot. This is 36% lower than the constant mean number of species for this community (Rodwell, 1992).

3.5. Multivariate analysis for CM plant community

All environmental variables (EV), Table 1, tested highly significant ($P < 0.001$) using the Monte Carlo permutation test, which showed that EN, ER, and *C. mariscus* cover made a considerable contribution to total species variation.

In the CM community, the PCA showed that the first 4 axes explained 78.3% of the species environment relationships and explained 52.3% of percentage variance for species data for axes 1 and 2 is 36.6% and the largest effect size was derived from site.

This is evident from the distinct spatial heterogeneity in species distribution, Fig. 5(a). In the CM community, the PCA showed that the first 4 axes explained 78.3% of the species environment relationships and explained 52.3% of the total species variance. The cumulative percentage variance for species data for axes 1 and 2 is 36.6% and the largest effect size was derived from site. This is evident from the distinct spatial heterogeneity in species distribution, Fig. 5(b).

The ordination plot for the CM community, Fig. 5(a) clearly illustrates that Cors Goch (CG), (diamonds) differs from the other two sites based on environmental gradients. This is a possible cause for the unaltered change in species richness [Spp] (as reported earlier), shown by the low position on axis 1, which is associated with higher moisture, Fig. 5(c). Species impoverishment is also evident by the low position on axis 1 in Fig. 5(b) and close association with *C. mariscus*, *Salix cinerea* and aquatic specie *Equisetum palustre*, suggesting that these species' requirements for N and moisture are higher here, Fig. 5(c). CG has higher levels of moisture, and nitrogen, as evident from its position on the Ellenberg N – nitrogen [EN]/Ellenberg F – moisture [EF] gradient. CG is also associated with increased vegetation height [H], litter cover [L] and *C. mariscus*

cover [Cl]. At Cors Bodeilio [CB], (circles), Fig. 5(a), samples move from left to right across axis 1 over time, consistent with an increase in species richness. This trajectory is negatively associated with increased moisture, EllenbergL – light [EL] and vegetation height, as indicated by the opposing gradient of [EN], EllenbergR – pH [ER], moisture, light and vegetation height.

There is also a divergence along axis 2, suggesting within site heterogeneity is high. This site also demonstrates more acidic conditions and reduced light as demonstrated by species (*Calluna vulgaris*, *S. subnitens* and *Erica tetralix*) present in bottom right axes in Fig. 5(b). Finally, Cors Erddreiniog (CE), (triangles) is moving up axis 2 and across axis 1, demonstrating a strong positive response to treatment in regard to species richness. This site's trajectory is more progressed than CB and CG as this is the most species rich of all three sites as a result of treatment. This site is also associated with less litter, lower canopy height and lower cover of *C. mariscus* which are negatively associated with treatment, Fig. 5(c).

By 2013 in the CM community, a total of 74 species were recorded in treatment plots across all sites versus 44 in the control ($P < 0.001$). Treatment effect was evident in 13 species with the majority increasing in percentage-abundance; in particular, *P. australis*, which increased by 78% in mown plots. However, notable reductions were observed in other graminoids and sub-shrubs such as: *C. mariscus*, *C. vulgaris* and *M. gale*. Two new species colonised: *Hypericum pulchrum* and *Campylopus flexuosus*, refer to Fig. 5(b) for other significantly affected species.

3.6. Multivariate analysis for SN plant community

The percentage variance for species data for axes 2 and 3 is 20.9% and the largest effect size was derived from EllenbergF – moisture [EF], site, *C. mariscus* cover [Cl] and EllenbergN – nitrogen [EN]. All environmental variables (EV) tested highly significant ($P < 0.001$) using the Monte Carlo permutation test, Table 2. In the SN community, the PCA showed that the first 4 axes explained 74.4% of the species environment relationships and explained 46.5% of the total species variance. Axes 2 and 3 are presented for the SN community which best describes the species environment relationships as axis 1 mainly illustrated site differences.

The PCA shows a clear divergence between sites' individual trajectory in response to treatment, Fig. 6(a). Axis 3 displays a species richness [Spp], year [Y] and treatment [T] gradient, which is negatively associated with [EF], litter [L] and vegetation height [H]. Axis 2 exhibits increasing EllenbergR – acidity [ER], EN, *C. mariscus* cover and bare ground, which is negatively associated with EL.

CG (diamonds) is the only site that exhibits a positive shift up axis 3, Fig. 6(a), which is consistent with species richness (P, 0.06) data reported earlier and appears to be associated with increased bare ground, reduced litter cover and negative association with nitrogen. CB (circles) is moving across axis 2 and up axis 3 towards increased bare ground [B] and acidity [ER], with a more gradual shift towards species richness. Finally, CE (triangles) demonstrates a strong divergence between plots which appear to be distributed based on a moisture/litter/canopy height gradient which is negatively associated with species richness. Species in wetter samples included *Menyanthes trifoliata*, *P. australis* and *E. tetralix*, Fig. 6(b). Overall, species richness at this site remained constant and exhibited no treatment effect.

Species response across all SN community sites showed that in the first year following mowing *M. gale* reduced ($P < 0.05$) and *Angelica sylvestris* ($P < 0.05$) increased, although neither species sustained this treatment effect. In 2013 *Oenanthe lachenalii* ($P < 0.01$) reduced and there was an increase in *Carex flacca* (P, 0.055) and *Lythrum salicaria* (P, 0.053), as observed by a weak positive treatment effect. However no new species colonised following treatment. Across all sites, total number of species were 103 in the control and 98 in the
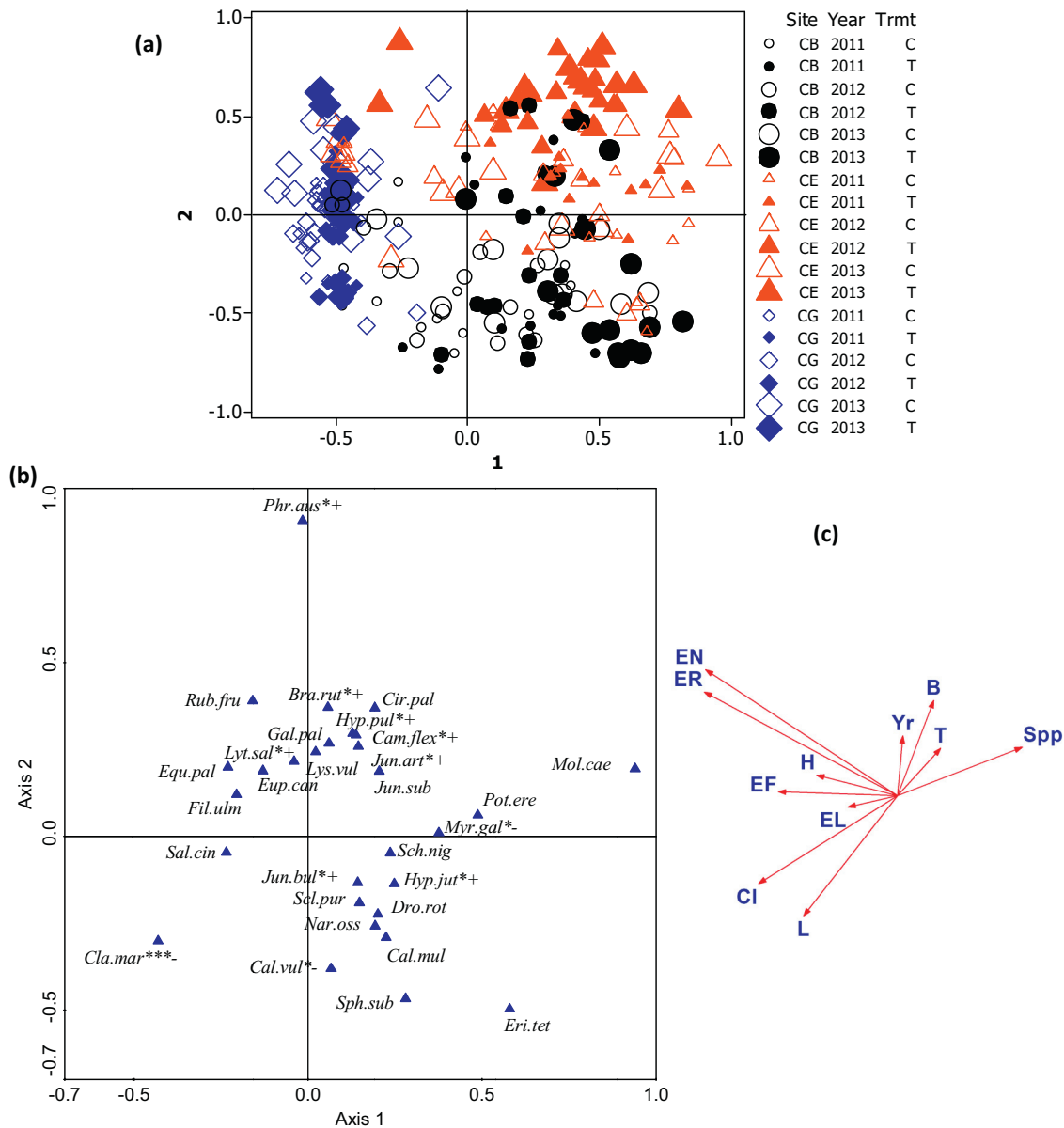
Fig. 5. PCA sample ordination plot for CM community (a) for all sites and all years. Site abbreviations are: Cors Bodeilio (CB), Cors Erddreiniog (CE) and Cors Goch (CG). Open symbols represent control (C) and solid symbols represent treatment (T) and symbol size depicts time (years), (b) Species ordination plot (PCA) for all years depicts species weighting >0.05 as well as enforced significant species shown below this threshold. Statistical codes for species indicate treatment effect in 2013: '***' $P<0.001$, '**' $P<0.01$, '*' $P<0.05$ where + indicates a significant increase in cover and − indicates a significant reduction in cover as a result of treatment, (c) the environmental ordination plot (c) is applicable to both diagrams and also derived from the PCA.

treatment in the baseline year. By 2013, total number of species were recorded as 97 in both the control and treatment.

4. Discussion

This research demonstrates how a single mowing event can have contrasting effects on two botanically different vegetation communities and that the disparity observed is complex. Variation in response to restoration is complicated by ecological gradients between and within sites, which include historical management and plant community dynamics (Turner et al., 1998; Wheeler and Proctor, 2000; White and Jentsch, 2001). Inherent conditions such as nutrient availability, hydrology, peat depth and buffering capacity (Cusell et al., 2014; Lamers et al., 2014) (not examined here) are also likely to be mechanisms which are driving the positive and negative response to restoration.

In the CM community, a large increase in species richness was achieved through mechanised mowing, due to a modification to vegetation structure and peat disturbance. This has led to botanical recovery in the short term. Hypotheses were confirmed due to biomass and litter removal, disturbance to the soil and subsequent peat exposure. This resulted in a reduced canopy and reduction in graminoid and shrub cover, which collectively contributed to the strong treatment response observed. Biomass removal changed the physical structure in the CM community, causing subsequent changes which have eliminated pre-existing ecological barriers (created by secondary succession) and supported rehabilitation for early succession species to colonise. Conversely, although the SN community vegetation components responded to treatment initially; this was short lived. However, species richness remained constant throughout.

Table 2

List of SN community environmental variables (EV) and associated abbreviations shown in following environmental ordination plot, Fig. 6(c), which depicts percentage of total species variation explained within RDA and significance tested for each variable independently.

Environmental variables [EV]	Variance (%)
EllenbergF – moisture [EF]	10%[***]
Site	9.6%[***]
C. mariscus cover [Cl]	7.6%[***]
EllenbergN – nitrogen [EN]	7.2%[***]
EllenbergR – acidity [ER]	6.7%[***]
EllenbergL – light [EL]	5%[***]
Species richness [Spp]	3%[***]
Year [Y]	2.2%[***]
Litter cover [L]	2.1%[***]
Vegetation Height [H]	1.3%[***]
Bare ground [B]	1.3%[***]
Treatment [T]	2%[***]

[***] $P < 0.001$.

Biomass removal has the potential to reduce available N and P from each plant community in the long term, which would be a beneficial treatment response at these co-limited sites (Venterink et al., 2003; Bombonato et al., 2010). If biomass is not removed, 50–60% of N and 80–90% of P is resorbed from decaying above-ground biomass, in which graminoids are particularly efficient at resorbing P (Aerts, 1996; Aerts and Chapin, 2000). Therefore, if nutrient cycling can be inhibited following routine biomass removal over time; this will be benefit the low nutrient requirements of target fen species, which subsequently will support target fen community rehabilitation. Limiting the availability of N and P in a fen is an important component in restoration but nutrient recovery will need repeated intervention (Grime et al., 1988; Venterink et al., 2009; Bombonato et al., 2010).

4.1. CM community

In the short term, the CM community has responded rapidly to intervention, where moisture and nitrogen levels are low. Therefore, this community has achieved the conservation aim of increasing species richness. Removal of physical barriers (biomass and litter) and peat exposure, combined with a reduction in graminoid and ericoid/sub-shrub cover are likely to be the principle causes for species recovery. In particular, mowing reduced the cover of dominant graminoid and woody species: *C. mariscus*, *M. gale* and *C. vulgaris*. Prior to mowing, these species dominated the canopy and outcompeted small stature species for all available resources. Reduced cover from these species and optimised environmental conditions has permitted new herbs and bryophytes to colonise. However, due to coppiced shrubs such as *M. gale* and clonal growth of late succession graminoids such as *C. mariscus*; these two vegetation components began to recover, in spite of sustaining a significant reduction overall. Therefore, for this community to progress along a trajectory of increased herbs and reduced graminoids and shrubs, ongoing management is needed to control dominant species expansion, biomass accumulation and vegetation height (Middleton et al., 2006b; Rasran et al., 2007).

The displacement of robust species and reduced competition has led to the total number of species in the control and treatment significantly increasing from 44 to 74 respectively. Reduced competition has supported the colonisation of previously absent small stature species such as *H. pulchrum* and *C. flexuosus*. However, in spite of these species' contribution to increased species richness, their ecology suggests they are not target rich fen species (Stace, 2010). Their presence may be more indicative of the presence of non-target species within the seed bank (Kiehl et al., 2010). However, some target species did increase by the second year,

as demonstrated by a significant increase in target brown moss *Campylium stellatum var. stellatum*. Bryophytes are an important component of rich fens and an increase in the number of species from this vegetation group will further facilitate vascular plant recovery. This is due to their influence on biogeochemical processes, such as P acquisition (Crowley and Bedford, 2011). Other species which have increased due to mowing include: *L. salicaria*, *J. articulatus* and *J. bulbosus* which are pioneers, owing to their high light requirements (Hill et al., 2004). New species colonisation suggests propagule availability is not limited for these species and seed/spore bank viability is good, as ameliorated conditions have supported seedling establishment (Stroh et al., 2012). However, if target wetland species do not increase in subsequent years through natural re-colonisation, species re-introduction should be considered via hay, plant or bryophyte fragment transfer from botanically characteristic sites (Van Groenendael et al., 1998; Cobbaert et al, 2004; Graf, 2010; Hedberg et al., 2012). Ho and Richardson (2013) suggest that *Juncus* and *Carex* spp. seed reintroduction can facilitate restoration, as these native perennials are considered to protect against invasions from more competitive species.

Although litter cover was reduced, it remained higher than expected. During harvesting, shredded litter was blown from the Pistenbully's open auger, adhering to the inundated peat surface. Therefore, harvesting should not be undertaken when the wetland is heavily inundated or during high winds, as this appears to inhibit litter removal rates. Litter cover has been shown (in both plant communities) to be negatively associated with species richness and is a known barrier to low growing species establishment (Jensen and Meyer, 2001).

Although mowing has been beneficial for the CM community, mowing in the winter has exposed some deleterious effects to species composition. *P. australis* exhibited stimulated growth and increased in cover as a result of mowing. This is due to winter mowing, which allows translocation and storage of resources to rhizomes at the end of the growth season (Asaeda et al., 2006). Carbon translocation and vigorous expansion can be minimised if mowing takes place in late summer (Fogli et al., 2014).

4.2. CM community sites response

CG was the only site in which the CM community did not increase in species richness, which is considered to be caused by inherent site conditions. For this site, higher nitrogen [EN] and moisture [EF] values were observed, which are negatively associated with species richness. Wetter sites favour dominant graminoid species, such as *C. mariscus* and *P. australis*; the former thrives on a high water table year round (Saltmarsh et al., 2006), which limits species richness. If the wetland is too wet, limited species can germinate (Kennedy et al., 1992) and target species may be precluded. Bryophyte distribution is also deleteriously affected by a high water table, becoming less frequent in inundated areas of the fen (Ilomets et al., 2010). Wetter conditions and higher nitrogen availability are thought to have contributed to the poor treatment response at this site. Therefore, further attempts of restoration at this site are less likely to be successful, until the water level and nitrogen availability is reduced.

Conversely, CE exhibited better conditions for fen restoration, which is evident from increased species richness and a good ecological trajectory in response to mowing. This site's trajectory is positively directed towards increased species richness, which is associated with increased bare ground and a lower canopy height. CB also demonstrated an increase in species richness, however its trajectory is not as strong as CE. However, due to this site's strong association with *C. mariscus* and litter cover; it is suggested that these ecological barriers will prevent continuing increased species richness, unless a mowing regime is established.
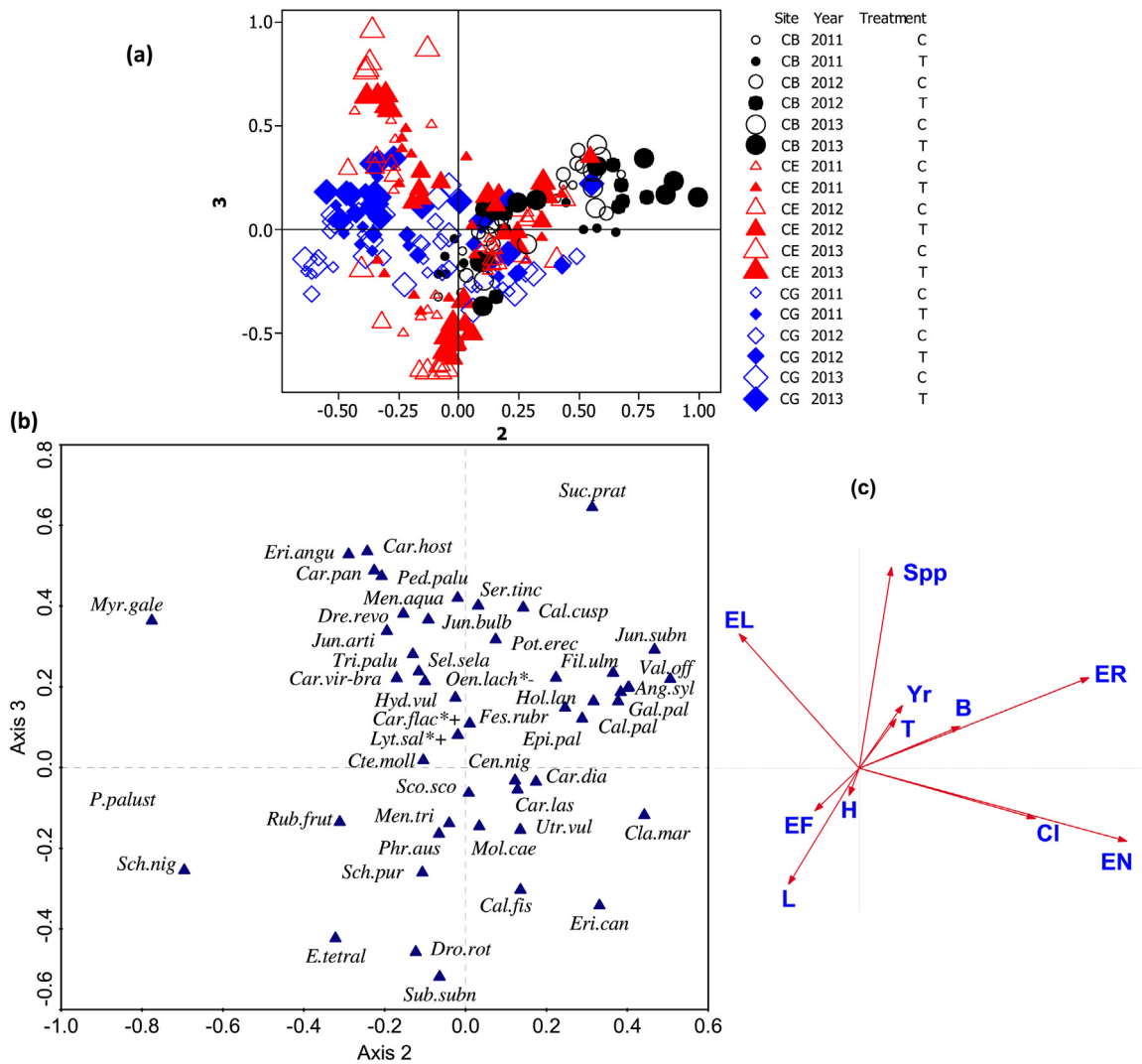
Fig. 6. PCA sample ordination plot for SN community (a) for all sites and all years. Site abbreviations are: Cors Bodeilio (CB), Cors Erddreiniog (CE) and Cors Goch (CG). Open symbols represent control (C) and solid symbols represent treatment (T) and symbol size depicts time (years), (b) species ordination plot (PCA) for all years depicts species weighting >0.05 as well as enforced significant species shown below this threshold. Statistical codes for species indicate treatment effect in 2013: '***' $P < 0.001$, '**' $P < 0.01$, '*' $P < 0.05$ where + indicates a significant increase in cover and − indicates a significant reduction in cover, as a result of treatment. The environmental ordination plot (c) is applicable to both diagrams and also derived from the PCA.

Finally, ongoing monitoring is needed to determine when species richness stops increasing and begins to decline, to ensure timely and cost-effective mowing can be reinstated on rotation. Modern fen management follows a 3–5 year rotation as tracked machines can cause large scale disturbance, such as pooling on the peat surface; furthermore a flexible mowing date will support the conservation of wetland fauna (McDougall, 1972; SNH, 2011; Kotowski et al., 2013). Mowing on rotation will manage biomass and litter accumulation (Diemer et al., 2001; Valko et al., 2012) which are the primary physical inhibitors for small stature herbs (Kolos and Banaszuk, 2013). Furthermore, timing and frequency should be site dependent. Autumn mowing is optimum in this community, as this can alleviate internal eutrophication, inhibit *P. australis* expansion and maintain a low shrub cover; however this would need to be repeated routinely (Aerts and Chapin, 2000; Hovd and Skogen, 2005; Sundberg, 2011).

4.3. SN community

The response to a single treatment in the SN community did not confirm all the hypotheses, in terms of increasing species richness, reducing dominant species and reducing canopy height. In spite of this, positive treatment effects included a reduction in litter cover and biomass and an increase in bare ground.

Overall, fewer treatment effects were evident in this plant community, owing to the inhibitory physical constraints imposed by graminoids and high within and between site spatial heterogeneity, evident by differing species richness and biomass weights (Valko et al., 2012; Lamers et al., 2014). Therefore, the SN plant community would benefit from a more intense, frequent mowing regime that is also site specific.

Mowing reduced graminoid cover initially, however graminoids regained their pre-treatment cover in the second year, reinstating competition against smaller herbs for nutrients and space. Other studies have shown that seed banks become depleted exponentially with succession, which may have contributed to the absence of new species following management (Jensen, 1998; Bakker and Berendse, 1999; Hald, 2000; Donath et al., 2007). The mean number of species in the control (16.3) and treatment (17.3) was constant two years after treatment. However, a reference SN plant community has 27 constant species present (Rodwell, 1992). This indicates that the SN plant community remains degraded following a single mowing application.

The fast re-establishment of graminoid cover is probably due to the dominant sedge, *S. nigricans*; its cover reduced temporarily in year one, but was comparable to the control in year two. It is not known to be clonal; although the semi-evergreen foliage produces large quantities of persistent biomass each growth season, which contributed to the unchanged canopy height, two years following mowing (Wheeler and Shaw, 1991; Rodwell, 1992). High percentage cover of *S. nigricans* was also negatively associated with species richness. This is because it is tolerant of low nutrients, as well as forming drier microhabitats (tussocks) which are raised from waterlogged conditions (Rodwell, 1992). However, this graminoid provides essential physical structure to this plant community, contributing to the species richness. Future management needs to control biomass accumulation so that runnels remain open and a light canopy is provided for low stature herbs and bryophytes to colonise.

Furthermore, shrubs exhibited a delayed response to mowing, reducing only by the second year. Reduced shrub cover in 2013 was not being driven by dominant shrub *M. gale* as presumed, as this species renewed its cover in the same year. Therefore the overall change in shrub cover was driven by Ericoids which are less likely to pose a threat to herb colonisation as they support a smaller canopy, located in the understorey. Tall herbs also responded to treatment, where *A. sylvestris* initially increased in cover, but was not sustained. Similarly, *O. lachenalii* also decreased in cover in the second year; both effects are probably owing to the renewed growth from graminoids, also observed in the subsequent year. Wetland pioneer species *L. salicaria* and target fen species *C. flacca* also increased; the latter species is usually present in high frequency (Rodwell, 1992), which suggests some target fen species can persist.

Biomass reduction was only shown at one site (CG), although an overall treatment effect was observed. This is possibly associated to within and between site heterogeneity, which has driven change in productivity (Wheeler and Proctor, 2000), imposing control on restoration outcomes. There is a clear environmental gradient, where high moisture, high litter cover, low bare ground and increased canopy height are collectively negatively associated with species richness.

Conversely, species that have increased in response to treatment are associated with low moisture, high bare ground cover, low litter cover and low canopy height. Therefore, secondary succession species are present in wetter conditions, support a taller canopy and higher litter cover. These species were evident in the species ordination plot and include *P. australis* and *S. nigricans*. These robust graminoids inflict strong competitive vigour and impose change within the community's micro-climate and canopy height, typically imposed by fast growing rhizomatous species (Rosenthal, 2010).

4.4. SN community sites response

High spatial heterogeneity is evident across and within all sites and it is these inherent diverse conditions (Cusell et al., 2014; Lamers et al., 2014) which are likely to be contributing to the varied response to treatment. Species richness is negatively associated with increased moisture [EF] and reduced bare ground [B]. Therefore, those sites experiencing prolonged hydro-periods will have reduced bare peat, due to inundation. As discussed earlier, this can inhibit plant colonisation (Kennedy et al., 1992). Overall, CG appears to be on the best trajectory, as it is the only site which demonstrated increased species richness. This may be driven by the biomass reduction, solely observed at this site and an apparent shift towards drier conditions following treatment. CE demonstrated a strong species richness divergence, which did not appear to be associated with treatment, where a large number of samples were

located in wetter conditions. Furthermore, this site did not show a reduction in biomass, which in addition to high moisture has impeded species recovery. CB did not respond well to treatment, which does not appear to be related to high moisture, rather this site has exhibited no change in biomass.

A higher mowing frequency is needed in the SN community to combat graminoid and sub-shrub cover. This should be undertaken on alternate years to sustain herb diversity (Wheeler, 1980b; Bissels et al., 2006; Leng et al., 2011; Valko et al., 2012) and switch between autumn and summer to favour overall plant diversity (Valko et al., 2012; Kolos and Banaszuk, 2013). Autumn mowing impedes shrub encroachment (Sundberg, 2011) and inhibits internal eutrophication (Aerts and Chapin, 2000; Hovd and Skogen, 2005).

5. Conclusion

This short term study has demonstrated that both communities have exhibited varying degrees of restoration success. The CM community experienced rapid rehabilitation, which resulted in an increase in species richness, although the same progress was not achieved in the SN community. As Bradshaw (1996) and later others (Pfadenhauer and Grootjans, 1999) have stated; restoration is gradual and projecting target community composition is very difficult, given the contrasting influence of abiotic, biotic and historical management activities between sites (Lamers et al., 2014).

Principally, rehabilitation is driven by increased bare ground, reduced vegetation height, litter and graminoid cover, which was achieved in the CM community, primarily because mowing reduced cover of the dominant graminoid, *C. mariscus*. Conversely, the SN community's species richness remained constant, due to sustained graminoid cover, imposed by *S. nigricans*, which is also likely to have caused the sustained vegetation height. A finer control on the dominant sedge, *S. nigricans* is needed, so that runnels remain clear; however, light shade is important for target fen herbs and bryophytes to colonise.

In the CM community, winter mowing has also caused *P. australis* to expand. Summer mowing may be necessary to reduce *P. australis* cover as the removal of shoots during the growth season intercepts the carbohydrate translocation to rhizomes (Asaeda et al., 2006; Fogli et al., 2014).

Although success has been achieved in the short term, the trajectory for each plant community is not optimal. The SN community supports indicative species but falls below the mean number of species for a characteristic SN community (Rodwell, 1992) and the CM community is increasing in species but early indications suggest these are not target fen species that are colonising. However, it is expected that with ongoing mowing, more target species will colonise through natural processes, although seed banks will need investigation at these sites prior to further investment and management intervention. If evidence suggests the species pool is in poor condition, species reintroduction would be needed to increase species richness along an alkaline fen trajectory. This is more likely to be a possible barrier to species recovery in the impoverished CM plant community, which is located further away from a seed source and most sites are inundated year round which may affect seed viability. Finally, optimum mowing frequency will facilitate sustained control over graminoid and sub-shrub cover, as succession towards these vegetation components, as shown here, is very strong (Shea et al., 2004).

6. Recommendations

Future restoration intervention should include extensive baseline surveys to record environmental variables such as water table depth, N and P inputs (groundwater, surface water) as well as

biological surveys. Pre-determining hydro-chemical and/or biological barriers to restoration will provide an insight in to pre-restoration site conditions (Bakker and Berendse, 1999; Holzel et al., 2012; Lamers et al., 2014). Fen systems which are free from deleterious environmental issues should be targeted first and other sites may require additional management to ensure any environmental barriers are removed prior to mowing (Lamers et al., 2014). This will ensure restoration is efficient and a higher rate of success is secured.

Furthermore, seed/spore bank viability and availability of diaspores (Holzel et al., 2012) needs investigating for each plant community, as little work has been undertaken on abandoned rich fens and seed bank viability, which may be limiting target species establishment (Bakker and Berendse, 1999; Bart et al., 2015). It is likely both communities will require further intervention by way of seed re-introduction and or hay transfers, in order to maintain a positive rich fen trajectory. Site and plant community specific interpretations to restoration must also be examined carefully so that individual management plans can be established (Schmitz, 2012). Careful monitoring will also avoid further investment in sites which support inhibitory conditions.

Restoration success should not be based on species presence alone; improvements in ecological function and interaction must also be examined to ensure natural ecological processes initiate for the system to be considered restored (Mitsch and Gosselink, 2007). Ecosystem function affects plant diversity and vice versa, so belowground processes such as microbial interactions, soil condition and resource availability should also be examined in addition to phenotypic plasticity of plant traits (within and between sites) which collectively affect ecological function (Loreau and Hector, 2001; Zak et al., 2003; Sutton-Grier et al., 2011).

Finally, the majority of restoration has been undertaken on degraded wetlands and so more research into the biogeochemical functioning of pristine systems is needed to better understand how to restore degraded systems back to a reference state (Zak et al, 2011). It is suggested future research should focus on rich fen trajectory to predict end point communities and set targets based on varying starting points.

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