Change to ecosystem properties through changing the dominant species: impact of *Pteridium aquilinum*-control and heathland restoration treatments on selected soil properties

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**ABSTRACT**

It is well known that soils are influenced by the plant species that grow in them. Here we consider the effects of management-induced changes to plant communities and their soils during restoration within a 20-year manipulative experiment where the aim was to change a late-successional community dominated by the weed, *Pteridium* *aquilinum*, to an earlier-successional grass-heath one. The ecological restoration treatments altered the above- and below-ground components of the community substantially. Untreated plots maintained a dense *Pteridium* cover with little understory vegetation, cutting treatments produce significant reductions of *Pteridium*, whereas herbicide (asulam) produced significant immediate reductions in *Pteridium* but regressed towards the untreated plots within 10 years. Thereafter, all asulam-treated plots were re-treated in year 11, and then were spot-sprayed annually. Both cutting and asulam treatments reduced frond density to almost zero and resulted in a grass-heath vegetation. There was also a massive change in biomass distribution, u**ntreated plots had a large above-ground biomass/necromass that was much reduced where *Pteridium* was controlled. Below-ground in treated plots, there was a replacement of the** substantive *Pteridium* rhizome mass with a much greater root mass of other species. The combined effects of *Pteridium*-control and restoration treatment, reduced soil total C and N as and available P concentrations, but increased soil pH and available N. Soil biological activity was also affected with a reduction in soil N mineralization rate, but an increased soil-root respiration. Multivariate analysis showed a clear trend along a pH/organic matter gradient, with movement along it correlated to management intensity from the untreated plots with low pH/high organic matter and treated plots with to a higher pH/lower organic matter in the sequence asulam treatment, cut once per year to cut twice per year. The role that these changed soil conditions might have in restricting *Pteridium* recovery are discussed.

*Key words:*

Conservation; Ecological restoration; Bracken control; Management-induced soil change; Long-term manipulative experiment; Soil chemistry

1. **Introduction**

Bracken *Pteridium* *aquilinum* (L.) Kuhn, hereafter referred to as *Pteridium*), originally a woodland species, invades sub-seral communities in many parts of the word (Marrs & Watt, 2006). During this invasion *Pteridium* often produces stands of dense fronds with a deep litter layer (Marrs & Watt, 2006), which combine to cause problems for agriculture and forestry where such *Pteridium* stands can inhibit crop growth (Aquilar-Dorantes et al., 2014; Levy-Tacher et al., 2015; Pakeman & Marrs, 1992; Roos et al., 2010). It also poses problems for conservation where invasion can suppress important understorey plant communities (Cox et al., 2008), leaving a much impoverished community with less conservation value than the pre-*Pteridium* state (Pakeman & Marrs, 1992). Where dense *Pteridium* occurs in long-established stands a steady-state should be reached with respect toproductivity, litter dynamics and soil processes(Pakeman & Marrs, 1996).

Given its importance as a world-wide weed, there have been many experimental attempts to control *Pteridium* and replace it with either an earlier-successional plant communities or forest cover. In Great Britain, various approaches have been tested: cutting and herbicide use (Cox et al., 2007), cutting, bruising and repeated herbicide use (Milligan et al., 2016), and in Italy initial cutting followed by ploughing or harrowing and thereafter sowing of a forage mixture (Argenti et al., 2012). For neo-tropical *Pteridium*, various approaches have been tested, for example in Mexico, repeated selective cutting (Aguilar-Dorantes et al., 2014) and initial cutting coupled with overstorey canopy competition from Balsa trees (*Ochroma pyramidale* ([Cav.](https://en.wikipedia.org/wiki/Antonio_Jos%C3%A9_Cavanilles) ex [Lam.](https://en.wikipedia.org/wiki/Jean-Baptiste_Lamarck)) [Urb.](https://en.wikipedia.org/wiki/Ignatz_Urban)), and in Ecuador, a range of mechanical and herbicidal approaches (Roos et al., 2010). Some of these studies have been of relatively short-term duration, concentrating on initial treatment responses, and this is unfortunate as *Pteridium* is well known to recover quickly, at least in northern Europe (Marrs et al., 1998). It is also important to note that there are taxonomic differences in *Pteridium* between these different geographical locations (Marrs & Watt 2006), and it is possible that the different species/sub-species react differently to control treatment as they have differing annual growth cycles (Silva Matos et al., 2014.)

It is well known that ecosystem function including soil processes can be influenced by the plant species that grow in them (Connell & Slatyer, 1977; Jenny, 1980) and *Pteridium* should be no exception. Recent research in this area has focused on the mechanisms involved in this process, where plant species diversity is the major control (Dybrinski, et al., 2008; Fornara & Tilman, 2008) or whether the majority of processes are controlled primarily by the traits of the dominant species, the “mass-ratio effect” (McLaren & Turkington, 2010). The transition between dense *Pteridium* and an earlier-successional community is an in ideal model system to investigate whether (a) changes in soil processes occur, and (b) they are likely to assist or hinder ecological restoration efforts. In Great Britain, the ideal conservation management\restoration objective is to reduce *Pteridium,* a perennial geophyte, to a low level and then create an alternative stable state (ASS) dominated by perennial species with a mixture of life-histories/traits, that might include: dwarf shrubs (chamaephytes; *Calluna vulgaris (*L.) Hull, *Vaccinium myrtillus L.*), grasses (geo-cryptophytes; *Agrostis capillaris*, L., *Deschampsia flexuosa* (L.) Trin.) and forbs (hemi-cryptophytes; *Galium saxatile*, L. *Potentilla erecta* (L.) Räusch) (Alday et al., 2013). This new ASS would maintain itself and prevent *Pteridium* re-invasion. This change in the balance of traits would be predicted to modify ecosystem function including soil processes (Diaz et al., 2007; Cortois et al., 2016), although soil processes have also been shown to be affected by soil microbial community composition (Wubs et al., 2016), interacting with climatic factors such as drought (Kaisermann et al., 2017). Here, we hoped that management action that created and maintained the stable state would enforce soil change.

In this paper, therefore, we report the results of such an enforced change within a former *Pteridium*-dominated community under experimental conditions over a twenty-year period. In this experiment, previous analyses over a ten-year period showed that *Pteridium* was reduced and a grass-heath developed. Alday et al. (2013) described this as an Alternative State (AS) because it was achieved by continuous application of a pulse treatment and hence there could be no guarantee of stability in the absence of treatment application. The early-successional grass-heath community is preferred from a conservation viewpoint because it has a greater value than the later-successional, *Pteridium*-dominated one (Pakeman & Marrs, 1992), meeting local and national Habitat Action Plan targets (Anon, 2016). Grass-heath communities tend to occur on nutrient-poor soils (Marrs, 1993; Mitchell et al., 1996) and it was hoped that soil changes induced by this newly-created community would maintain itself and prevent *Pteridium* re-invasion. Such modified soil regimes, brought about through a changed community structure, have been demonstrated elsewhere (Diaz et al., 2007).

To investigate this, the effects of a series of *Pteridium*-control and grass-heath ecological restoration treatments on soil properties were measured over a 20-year period (1993-2013). We hypothesized that the management applied would reduce *Pteridium* cover and create a more diverse community made up of species with markedly different traits and this transformation would modify some soil properties, reduce total soil carbon and nitrogen and increase in soil pH, available nutrients and soil biological activity.

**2. Methods**

The experiment is located at Hordron Edge site in the Peak District, Derbyshire, UK (Latitude and Longitude: 53°23’N, 1°41’W). The starting condition was a community with a dense *Pteridium* fronds (1-2 tall) anda deep litter layer (ca. 30 cm) and an extremely species-poor understory vegetation. *Pteridium* has been present for at least 100 years (N. Taylor, pers. comm.). Currently, the site is grazed by sheep at a low stocking density, ca. 0.5 sheep ha-1 (Pakeman et al., 2000).

The experiment was set up in 1993 using a randomized block, split-split-plot design with three blocks (60 m x 40 m) each with six main plots (10 m x 36 m) initially (1993-2003) receiving one of six *Pteridium*-control treatments: no treatment (experimental control, Untr), cut once yearly (Cutx1), cut twice yearly (Cutx2) and three treatments using the herbicide asulam applied by knapsack at 4.4 kg ai ha-1, 11 litres Asulox in 400 litres water ha-1 (Manufacturers, Bayer CropScience Ltd, Cambridge, UK and United Phosphorus Ltd, Warrington, UK). The three herbicide treatments were: a single treatment in 1993 (Asulam), a single treatment in 1993 followed by a single cut in 1994 (AsuCut), and a single cut in 1993 followed by a single spray in 1994 (CutAsu). Restoration treatments were applied to sub-plots (10 m x 18 m) and sub-sub-plots (10 m x 5 m). The sub-plot treatments tested sheep-grazing *versus* no sheep-grazing (grazed *versus* ungrazed) and the sub-sub-plot treatments received one of three *Calluna vulgaris* (L.) Hull seeding treatments (no seeding, seed applied in brash, and seed applied in litter). All treatments were applied randomly within each experimental stratum.

In 2004, it was apparent that *Pteridium* was recovering in the three herbicide treatments (Cox et al., 2007). Accordingly the Asulam, AsuCut and CutAsu treatments were resprayed with asulam (as above) in August 2004, followed up annually with spot-spraying until 2012, with the asulam applied individually by knapsack sprayer to all emergent fronds at a rate of 1 ml solution/frond of 6% vol:vol Asulox:water (Robinson, 2000). Both cutting treatments were continued. For clarity, the original treatment codes have been retained.

## *2.1. Assessing trends in vegetation*

In 1993, species composition was measured in five sub-samples within each of three selected sub-plots in each block to ensure that the “visually uniform” vegetation and *Pteridium* variables were similar at the start (Cox et al., 2007). Thereafter, vegetation composition was then monitored in all experiments in June (i.e. before the application of the first cutting treatment) from 1994 to 2008 and 2013. Each year, two quadrats (1 m x 1 m) were placed at random co-ordinates on 1 m x 1 m grids within each sub-sub-plot and the cover (%) of all vascular plant, bryophyte and lichen species recorded visually as well as an estimate of *Pteridium* litter cover. Within the central 0.5 m x 0.5 m of the quadrats all fronds were counted and their length measured. Mean frond length and frond density (number m-2) were then calculated.

In late-July 2013, at frond peak biomass (Lowday et al.,1983; Williams & Foley, 1976), the biomass of above- and below-ground biomass was harvested in randomly-selected 0.5 m x 0.5 m quadrats in both grazing treatments (grazed *versus* ungrazed) in three of the main-plot treatments (Untr, Cutx2, Asulam). Sampling was confined to the un-seeded sub-sub-plots to avoid any differential effects of the *C. vulgaris-*seeding treatments. All above-ground vegetation was collected and sorted into component species-groups. At the same time a soil core (6 m diameter x 21 cm depth) was collected. The roots and rhizomes were extracted carefully by washing over a 1 mm mesh sieve. All vegetation samples were over-dried at 800C for 48 h and weighed.

## *2.2. Assessing the effects of treatment on soil properties*

In early June 2013, random positions were located in each of the 108 sub-sub-plots. At each location, the surface vegetation was removed from a small area and a surface soil core removed using an Eijkelkamp auger (7 cm diameter, 20 cm depth). Initially the fresh weight of the entire core was measured to estimate bulk density. Thereafter the core was split into two, one was used for analyses carried out on fresh soils, and the other was air-dried and sieved to pass a 2 mm mesh. Soil pH and soil available N nitrogen (NH4-N and NO3-N) and P were measured on fresh soils, whereas total N and C and soil exchangeable K, Ca, Mg were measured on dried soils. Total C and N was measured using a CE Instruments NC2500 Elemental Analyzer machine, available N was extracted in 2M KCL, and available P and exchangeable cations were extracted in 2.5% vol:vol acetic acid. Analytical methods followed Allen (1989).

At the same time, soil-root respiration was measured in both of the grazing treatments (grazed *versus* ungrazed) in the Untr, Cutx2, Asulam main-treatments. To avoid interference form effects of the seeding sub-sub-treatments only un-seeded sub-sub-plots were sampled (n = 18, 3 Blocks x 3 *Pteridium*-control treatments x 2 grazing treatments). In early July 2013, soil-root respiration was measured using an LCi-portable photosynthesis system (ADC BioScientific Ltd Hoddesdon, UK). The surface vegetation was removed and collars (enclosed soil volume is 97.5cm2) inserted into the ground. The soil-root respiration hood was then placed on the collar and CO2 efflux measured over a 20 minute period using a flow rate of 200 µmol s-1. Within blocks, individual sampling was carried out randomly through the day to minimize any diurnal effects. In early July 2014, soil samples were collected in a similar manner as above from the same sub-plots and soil nitrogen mineralization rates determined using the method of Allen (1989) but with incubation at 25oC for 21 days.

## *2.3. Statistical analysis*

All statistical analyses were performed in R v.3.1.1 (R Development Core Team, 2014). As the aim here was to describe the broad vegetation trends that had occurred in the different treatments over time only *Pteridium* variables (mean frond length, frond density, *and Pteridium* cover) and aggregated vegetation variables (species richness, Shannon-Weiner diversity, and cover of graminoids and dwarf-shrubs) are considered here. The graminoids included grasses, sedges and rushes and the dwarf shrubs included *C. vulgaris*, *Erica tetralix* L*.,* *Vaccinium myrtillus* L., *V. oxycoccus* L.and *V. vitis-idaea* L.Two analyses were performed: (1) calculation of means and standard errors for each variable to compare the vegetation at the start (1993) and the year after treatment stopped (2013). Second, a description of the changing response of each variable was assessed using Generalized Additive Modelling (GAM), fitted using the ‘gam’ function (‘s’ option) within the ‘mgcv’ package (Crawley, 2013). A selection of these GAM outputs are presented to give an overview of vegetation change (Figs S1-S3). Only one of the asulam-treatments are presented as they all showed similar responses.

The responses of all soil variables to *Pteridium*-control and grazing treatments were modelled using linear mixed-effects models, with plot nested in block as random effects to account for plot- and/or block-level effects resulting from the split-split plot experimental design (Pinheiro & Bates, 2000). All models were implemented in a Bayesian framework using the MCMCglmm v.2.16 package (Hadfield, 2010), incorporating parameter-expanded priors and run with sampling of every 50th iteration for 1.0 x 106 iterations after a 1.0 x 104 burn-in, resulting in an effective sample size of approximately 2.0 x 104 for each predictor from the posterior distribution. Convergence of all models was assessed through trace plots inspection.

To assess the relative impacts of treatment on all soil variables a Principal Components Analysis (PCA) was performed using (function ‘rda’) within the ‘vegan’ package (function ‘rda’) (Oksanen et al., 2011), The PCA included all soil variables (pH, bulk density, available concentrations and total concentrations), standardized to zero mean and unit standard deviation (function ‘decostand’). Environmental treatments were then correlated with the PCA axes using the ‘envfit’ function, significance being assessed using a randomization test with 9999 permutations. Finally, the relative *Pteridium*-treatment positions were displayed on the PCA biplots as bivariate-standard-deviational ellipses using the ‘ordiellipse’ function.

**3.Results**

*3.1. Vegetation change over the course of the study*

The Untr plots showed little difference in mean frond length between the start of the study and 2013, although there was a slight increase in the ungrazed plots compared to the grazed ones in 2013 (Fig.1a). Mean frond density and *Pteridium* litter cover showed broadly similar patterns except there was an increase in 2013 compared to the start. Grazing had little effect on these two variables (Fig. 1b,c).All *Pteridium*-control treatments reduced the three *Pteridium* variables by 2013. The three treatments involving asulam were most effective, followed by Cutx2 and then Cutx1 (Fig. 1a-c). Species richness did not change in the untreated plots over the course of the study, but the cover of graminoids and dwarf-shrubs declined (Fig. 1d-f). Species richness and graminoid cover increased where *Pteridium* was controlled,with few differences between *Pteridium-control* treatments where grazed. Removal of grazing brought about a reduction in species richness and graminoid cover (Fig. 1d,e). Dwarf-shrubs (Fig. 1d) showed a more idiosyncratic response being greater in the CutAsu treatment than the others, but with high variability (Fig. 1e).

The modelled time courses for the three *Pteridium* performance variables are illustrated graphically along with summary statistics in Supplementary Materials: frond density to describe change in live summerbiomass (Fig. S1), litter to describe changes in year-round *Pteridium* necromass present (Fig. S.2) and graminoid cover to describe improvement restored vegetation (Fig. S.3). These fitted relationships were all highly significant (P<0.001)

Frond density showed large fluctuations throughout the study period in the untreated plots (Fig. S1), with the grazed plots showed an increasing trend through time and the ungrazed plots being more stable. The Cutx2 plots showed the most rapid decline and this was faster where ungrazed. The Cutx1 treatment showed a similar decline but there was a marked increase in frond density in the early years with large fluctuations. All three asulam-treatments showed a good initial reduction in frond density, but this was followed by gradual recovery until the treatments were repeated when there was good reduction in frond density which continued with the repeat spot-treatments. The *Pteridium* litter cover responses were similar (Fig. S2), with increasing cover in the untreated plots, fastest reductions in the Cutx2 plots, with a slower reduction the in Cutx1 treatment. The herbicide treatments had the slowest reduction in litter cover, followed by recovery until reapplication, after which *Pteridium* cover declined and this continued with each annual spot-treatments. Graminoid cover remained very low throughout in the untreated plots (Fig. S3), but increased in all plots where *Pteridium* was controlled. The largest and fastest increases were in the sheep-grazed Cutx1 and Cutx2 treatments, and slower responses in the three asulam-treated plots which also had a smaller cover.



**Fig. 1.** Comparison of some of changes in vegetation between the start of the study in 1993 (pre-treatment) and after the final application of *Pteridium*-control and sheep grazing treatments in 2013. (a) *Pteridium* frond length, (b) *Pteridium* frond density, (c) *Pteridium* litter cover, (d) species richness, (e) graminoid cover, (f) dwarf-shrub cover. *Pteridium*-control treatments are coded: Untreated (Untr), Cut once/yr (Cutx1), Cut twice/yr (Cutx2), Asulam (Asulam), Asulam + Cutting (AsuCut), Cutting plus Asulam (CutAsu) – note all asulam treatments were retreated with asulam in 2004 and followed up annually with spot-spraying thereafter until 2012; sheep grazing (□), ungrazed =no sheep-grazing (■). Mean values ± SE are presented.

*3.2. Effect of treatment on biomass distribution*

In the untreated plots there were no significant differences (P<0.05) between grazed and ungrazed treatments for any of the four *Pteridium* parameters measured (overall mean values ± SE (n = 6) for loge transformed data of the *Pteridium* biomass were calculated with back-transformed means in parentheses: frond biomass = 6.564±0.111 (708 g m-2); *Pteridium* litter = 7.945±0.111 (2385 g m-2); rhizome biomass = 7.122±0.096 (1239 g m-2)). There was no graminoid biomass in the untreated plots and there were no significant differences between *Pteridium*-control treatment and their interaction with grazing. Significant effects were found between grazing treatments (F1,4 = 9.78, P<0.05), where above-ground biomass in the ungrazed treatment was double the grazedone, 7.1300±0.076 (1249g m-2) compared to 6.455±0.297 (635 g m-2).

For both root and rhizome biomass the untreated plots were significantly different from the treated ones, but there was no significant difference between the two *Pteridium*-control treatments tested: Roots (F2,4 = 10.25, P<0.03, LSD0.05= 1.042: untreated= 6.290±0.341, asulam=7.205±0.366, cut twice yearly =7.652±0.287) with back-transformed values of 539, 1346 and 2104 g m-2; Rhizomes (F2,4 = 162.71, P<0.0001, LSD0.05= 2.390: untreated= 7.146±0.274, asulam=0.914±0.914, cut twice yearly =0±0), with back-transformed values of 394, 40 and 0 g m-2.

*3.3. Effects of treatment on soil properties*

The results of the statistical analyses of soil properties are presented in Supplementary materials (Tables S.1, S.2), the intercept is the untreated grazed plot, and an interaction graph is presented for all soil variables.

All *Pteridium*-control treatments increased soil pH significantly from < 4 in the untreated control to a maximum of ~4.6 in the Cutx2 treatment (Fig. 2a). Removal of grazing had no significant additional effect on soil pH. Soil C:N showed no significant differences throughout. Soil moisture was greatest in the untreated control than where any of the *Pteridium*-control treatments had been applied, with the two cutting treatments resulting in the greatest reductions (Fig. 2b). Only the Cutx2 treatment showed an additional effect of grazing removal, with soil moisture content showing a significant increase compared to the grazed comparator.

Soil mineralization were significantly reduced in the Cutx2 and Asulam treatments compared to the untreated control (mineralization rates = ~20 vs 60 µg Ng-1 21d-1) (Fig. 2c).There were no significant effects of any other treatment on nitrification rates (mean values = ~10 g N 21d-1). In contrast, soil-root respiration rates were much greater in all *Pteridium*-control treatments than in the untreated plots (>3 vs <1 M CO2 s-1 m-2) (Fig. 2d). There were no significant additional effects of grazing removal on soil mineralization or respiration rates.

Total N was significantly lower under all *Pteridium*-control treatments in the grazed plots compared to the untreated control (< 0.4% vs 0.6%), and there was no additional effect of grazing-removal on the asulam or either of the cutting treatments (Fig. 3a). However, there was a significant reduction in total soil N in the untreated plots after grazing-removal (to 0.4%), whereas there were significant increases



**Fig. 2.** Effects of twenty-years of *Pteridium*-control treatments and release from sheep-grazing on selected soil properties: (a) soil pH, (b) moisture content, (c) soil N mineralization rate, and (d) soil-root respiration rate. Modelled responses are shown, the intercept (untreated grazed, the control) is denoted in red. Grazed treatments that are significantly different from the intercept are grouped using the bracket, and ungrazed treatments that differ significantly from their grazed comparator are identified by the arrows. Statistical information is presented in Table S.1.

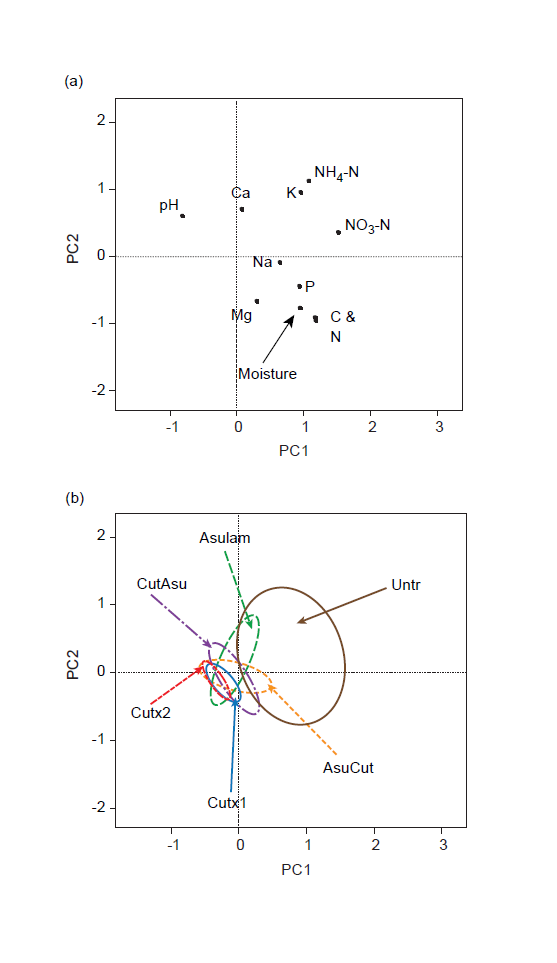


**Fig. 3.** Effects of twenty-years of *Pteridium*-control treatments and release from sheep-grazing on selected soil properties: (a) total N, (b) total C, (c) extractable P, (d) extractable NH4-N, (e) extractable NO3-N. Modelled responses are shown, the intercept (untreated grazed, the control) is denoted in red. Grazed treatments that are significantly different from the intercept are grouped using the blue bracket, and ungrazed treatments that differ significantly from their grazed comparator are identified by the arrows. Statistical information is presented in Table S.2.

found in the both combination treatments (AsuCut and CutAsu) after grazing removal. Total soil C was found to be significantly lower than the untreated plots for all *Pteridium-*control treatments in the grazed plots (>10% vs <7%, Fig. 3b). Removal of grazing pressure resulted in a significant increase in soil C only in the AsuCut treatment. There were no significant effects found in any of the other treatments, although the untreated, ungrazed plots showed a reduction that was close to significance.

Soil extractable P was significantly lower in the three *Pteridium*-control treatments, asulam, Cutx1 and Cutx2 compared the untreated control (Fig. 3c), and there as a significant additional increase only in the AsuCut treatment when grazing was removal There were significant reductions in available soil NH4-N availability in three treatments (CutAsu, Cutx1 and Cutx2) compared to the untreated control under grazing (Fig. 3d). Grazing-removal resulted in an additional significant reduction in NH4-N only in the asulam treatment. Compared to the untreated grazed control, soil available NO3-N was significantly reduced in all *Pteridium*-control treatments in the grazed plots (Fig. 3e), and the only additional effect of grazing-removal was found in the untreated plots.

The PCA produced eigenvalues of 3.931 and 2.398 for the first two axes explaining 33% and 20% of the total variation in the data. The soil variables produced a gradient along axis 1 from soils with a higher pH at the negative end through to soils with a higher organic matter content (total N and C) at the positive end, available concentrations of Ca, Mg and Na were intermediate and available P and N fractions were associated with high organic matter on this axis (Fig. 4a). The soils were separated on axis 2 on the basis of high organic matter and moisture content at the negative end and high concentrations of available N, Ca and K and higher pH at the positive end (Fig. 4a). Only the *Pteridium*-control treatments were correlated significantly with the PCA scores (r2=0.23, P<0.001), There was no significant effect of grazing or restoration treatments. The standard-deviational ellipses for the *Pteridium*-control treatments indicate a major shift along the first axis with the untreated plots located where the soils have greatest organic matter (total C and N) and greatest concentrations of available P and N, and the plots where *Pteridium* was controlled being located at the negative end on soil with larger pH and exchangeable Ca and Mg concentrations (Fig. 4b). The order of treatments from positive to negative on axis 1 is Untr > AsuCut and asulam > CutAsu and Cutx1 > Cutx2. However, it was not just the position of the treatments that was affected by treatment, the standard-deviational ellipses reduced in area, reflecting a reduction in soil variability in chemical composition. The sizes of the ellipses were: untreated=2.51, asulam=0.50, AsuCut=0.35, CutAsu=0.39, Cutx1 = 0.17, and Cutx2=0.11. The reduction in ellipse area was greater with an increasing number of cuts.

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**Fig. 4.** PCA biplots of soil properties within the *Pteridium*-control experiment at Hordron Edge, Derbyshire: (a) soil chemical variables (b) individual quadrats and the distribution of the *Pteridium-control* treatments bivariate-standard-deviational ellipses. Key to soil variables:C & N are total concentrations, other elements are available concentrations, and Moisture is the soil moisture content. Key to *Pteridium*-control treatments: Untr = untreated, Asulam = asulam only, AsuCut = asulam + cutting, CutAsu = cutting plus asulam, Cutx1 = cutting once per year, Cutx2= cut twice per year.

**4. Discussion**

The aim of this paper was to test the hypothesis that the *Pteridium*-control treatments coupled with grass-heath restoration would induce a shift from a *Pteridium*-dominated community to one dominated by graminoids and dwarf shrubs, resulting in a more diverse community made up of species with markedly different traits and this would induce change in soil properties. However, there are two steps needed to test this overall hypothesis. First, to describe the changes in the plant community brought about by direct and indirect effects of management, and second to test for differential impacts on soil processes.

*4.1. Management-induced change in the plant community*

Previous analysis of the vegetation response in this experiment has shown four major results in the first 10 years (Alday et al., 2013). First, the untreated plots maintained a dense *Pteridium* cover with little understory vegetation. Second, a single asulam application (± a single cut applied before or after the herbicide) all produced significant immediate reductions in *Pteridium* after treatment and improved grass-heath vegetation but regressed towards the untreated plots thereafter. Third, the two cutting treatments applied continuously produced significant effects on *Pteridium* and the underlying vegetation. Finally, sheep-grazing interacting with bracken control treatments produced more diverse plant communities with a greater complement of grass-heath species than where sheep-grazing was excluded.

In the period 2004-2012, a different approach to *Pteridium-*control was introduced. The three herbicide treatments (asulam, asulam + cutting and cutting + asulam) where *Pteridium* was recovering were blanket-resprayed with asulam in 2004 and then every year thereafter each emergent bracken frond was spot-sprayed with asulam until 2012 in accordance with developing good-practice (Robinson, 2000). Here, this approach was demonstrated to be very successful in reducing *Pteridium* frond density and litter and increasing graminoid cover, confirming Milligan et al. (2016). The two cutting treatments maintained a low *Pteridium* cover. Removal of sheep-grazing had some impact on both *Pteridium* and graminoid responses. All *Pteridium* treatments would now be considered as having achieved an AS.

These changes also resulted in a shift in biomass distribution. **The untreated plots had a large above-ground biomass and necromass (fronds and litter) and this was much reduced in the plots where *Pteridium* was controlled.** Below-ground biomass has also been changed, in the untreated plots, there was a substantive *Pteridium* rhizome mass but this declined in the Asulam treatment and was undetectable in Cutx2 treatments. Root biomass of the vegetation showed an opposite response with low values in the untreated plots and greater amounts in all treated plots with the greatest mass in the Cutx2 treatment.

*4.2. Effects of Pteridium-control and restoration treatments on measured soil variables*

The combined effects of *Pteridium*-control and restoration treatment and associated changes in plant community structure and function has significantly changed some soil properties; a reduction in total soil C and N and available P, and an increased soil pH and extractable N. Soil biological activity was also affected with a reduction in soil N mineralization rate, but increased soil-root respiration. This result for soil N mineralization suggests a relationship with total soil N concentration (mainly N in organic matter). This is in keeping with the conclusions of DeLuca et al. (2013), who showed that *Pteridium* created a N-rich environment relative to a *C. vulgaris*-dominated ecosystem with much greater nitrification rates, essentially *Pteridium* produces a N-rich organic-rich soil with relatively high N turnover. This is different from most increases in organic matter in upland British soils where N is sequestered in developing peat organic matter (Tallis, 1998). The greater N turnover under *Pteridium* is presumably the cause of the enhanced N leaching reported by Smart et al. (2007).

In the restored grass-heath communities there was a greater root mass and soil-root respiration than under *Pteridium*, a change also described in grasslands by Tavares et al. (2010). The multivariate analyses demonstrated a shift along a pH/organic matter gradient from the untreated soils (higher total N and C concentrations and lower pH) to grass-heath soils (lower C and N concentrations and higher pH). The increased soil pH might reflect Ca and Mg release from the *Pteridium* rhizome system into the soil-available pool; both these elements are present in high concentrations in the rhizomes (Marrs et al., 2007).

These effects on soil processes can only have been brought about by the *Pteridium*-control treatments and effect size was dependent on the intensity of application, the sheep grazing treatments had a much lesser effect. The order of effectiveness, summarized by the multivariate analysis, was from the Untr (untreated control), Asucut, Asulam, CutAsu, and Cutx1 through to Cutx2, the most successful treatment. It is unfortunate that the asulam-treated plots were not treated continuously from the start as this might have moved them further along the gradient and closer to the cutting treatments. Two important questions can be derived from these results. What are the mechanisms that have brought about these changes? What is the potential role of the induced soil change in influencing future *Pteridium* recovery?

*4.3. Mechanisms bringing about change in soil properties?*

The only way the soil can have changed is through the impact of a process that is manipulated through application of the *Pteridium*-control/grass-heath restoration treatments (visualized, Fig. 5), i.e. reducing the *Pteridium* components and increasing the grass-heath components. *Pteridium*-control reduced both above-ground frond production and the litter through time, increasing the light getting through to the ground-layer and reducing the importance of the litter as a physical barrier to plant colonization (Ghorbani et al. 2006). There is also some evidence that the litter can produce allelopathic chemicals that interfere with seedling establishment (Marrs & Watt, 2006). Two likely candidate chemicals include Selligueain A detected recently in litter from South American *Pteridium* (Jatoba et al., 2016), and Ptaquiloside, a carcinogen, detected in stream water from *Pteridium* catchments (Clauson-Kaas, et al., 2016). The relative importance of physical and chemical factors within the litter in reducing species colonization remains to be determined. Nevertheless, here management reduced accumulated litter mass, but the speed of this reduction was treatment dependent, quickly where cutting comminutes the litter by the cutting action (Lowday & Marrs, 1992), or slowly on herbicide-treated plots where litter



**Fig. 5.** Hypothetical diagram of potential ways the *Pteridium*-control and vegetation restoration treatments could impinge on soil processes (modified from Marrs et al.,2007).

reduction must be a function of reduced inputs coupled with slowed decomposition (Marrs et al., 2007). Although the speed at which the litter layer reduces varied between treatments over the 20 years, it reached very low values in all treated plots. The changing composition of the litter during the course of the experiment might also have affected decomposition rates, either because it has been derived from a more species-diverse vegetation (Vos et al., 2013) or because the dominant species have different leaf traits which determine decomposability (Fortunel et al., 2007). Further experimental research is needed to elucidate the exact explanation.

As the above-ground *Pteridium* mass declines there was also a reduction in the below-ground *Pteridium* rhizomes and roots (Le Duc et al., 2003), but the reduction is controlled by different processes. Mechanical treatment reduces rhizome reserves by influencing the balance between carbohydrate removal to fuel frond growth (rhizome = source; frond = sink) and replenishment as fronds become self-sufficient and carbohydrate flow is reversed (frond = source; rhizome = sink) (Williams & Foley, 1976). Mechanical control actively interrupts this flow, maximizing resource removal and minimizing rhizome replenishment. With herbicidal use, the active ingredient is translocated to the meristematically-active rhizome buds, where it prevents their development. Here rhizome mass reduction must occur passively through respiration loss and eventual decomposition. Irrespective of the process involved, *Pteridium*-control treatments have reduced rhizome mass within this experiment.

With the reduction of *Pteridium* above-ground mass, grass-heath has established through a reduction in competition and the increased availability of safe sites for germination and establishment (Harper, 1977). The grass-heath species will compete for space, water and nutrients and as it develops will provide an increased root biomass, rhizosphere and associated microbial activity. This was evident here from the increased root biomass and the increased soil-root respiration rates in the *Pteridium*-treated plots relative to the untreated controls. The changing soil microbial community is almost certainly important in determining the restoration outcome (Kaiserman et al., 2017; Wubs et al., 2016), but this remains to be investigated.

*4.4. Role of soil change in influencing future Pteridium recovery*

The *Pteridium*-management and restoration treatments have affected both vegetation and soil properties substantially. Essentially, the ecosystems have been pushed from one dominated by a single species to a more diverse community composed of graminoids and shrubs and a soil system that has much less C and N, much greater root biomass and soil-root respiration and a lower N and P availability. There are two lessons to be learned from this. *Pteridium*, a species with a reputation as an indicator of relatively-fertile soils (Marrs & Watt, 2006) appears to sequester nutrients and produce an ecosystem with a deep litter layer and a substantive C and N concentration in the surface layers. The greater concentrations of available N and P and mineralizable N in the *Pteridium*-dominated plots suggests rapid N and P turnover, presumably an essential requirement for such a productive species. That these soil properties are reduced in the grass-heath communities suggests that these “more infertile” ecosystems will be harder for *Pteridium* to re-colonize as a result of both increased competition and reduced soil resources. We would predict that it will take some time for *Pteridium* re-colonization to re-accumulate the C and N to values typical of the untreated controls. This positive management-induced feedback might give improved long-term *Pteridium*-control, in that it slows down recovery, but this remains to be verified in much longer-term studies that the 20 years reported here.

**Acknowledgements**

We thank DEFRA (Project BD1226), the Heather Trust and the Centre for Global Eco-Innovation (Project 241) for financial support, Jeremy Archdale for access to his land and Neil Taylor for helpful logistic support.

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