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Plant community responses to experimental climate manipulation in a Welsh ombrotrophic peatland and their palaeoenvironmental context

Running title: Peatland plant responses to climate change

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Peatlands, vegetation, climate change, palaeoecology, carbon, testate amoebae, experimental climate manipulation.

Abstract

We test whether vegetation community composition from a 10-year climate manipulation experiment on a Welsh peat bog resembles vegetation communities during periods of climate change inferred from a peat core. Experimentally warmed and combined warmed and droughted treatments drove significant increases in ericaceous shrubs but *Sphagnum* was unaffected. Similarly, *Calluna vulgaris* seeds increase during inferred warmer periods in the palaeoecological record. Experimental short-term episodic drought (four 4-week drought treatments) did not affect vegetation. Plant community composition has undergone several abrupt changes throughout the past c. 1500 years, often in response to human disturbance. Only slight changes occurred during the Medieval Climate Anomaly (c. 950-1250 CE) in vegetation and hydrology, while abrupt changes occurred during the Little Ice Age (c. 1300-1850 CE) when water tables were highest, suggesting that these shifts were driven by changes in water table, modulated by climate. A period of water table drawdown c. 1800, synchronous with historical records of increased drainage, corresponds with the development of the present-day vegetation community. Modern analogues for fossil material, characterised by abundant *Rhyncospora alba* and *Sphagnum pulchrum,* are more common after this event. Vegetation changes due to climate inferred from the palaeo record differ from those observed in the experiments, possibly relating to differences in the importance of drivers of vegetation change over varying timescales. Whereas temperature is frequently identified as the dominant driver of plant community change in experiments, sustained changes in water table appear to be more important in the long-term record. We find evidence that recent climate change and other anthropogenic stressors (e.g., drainage, heavy metal, and nitrogen pollution) may promote the development of novel plant communities without analogues in the fossil record. These communities may be poorer at sequestering carbon and may respond differently to future climate change.

1. Introduction

Peatlands accumulate vegetative material over thousands of years, which preserves as peat under anaerobic and cool conditions beneath the water table (Yavitt *et al.,* 1997). As peat grows, carbon is retained, and can be stored indefinitely (Davidson and Janssens, 2006, Belyea, 2009). Peatlands contain approximately 30% of all terrestrial soil carbon, estimated at c. 500 ± 100 billion tonnes (GT) (Gorham, 1991; Yu *et al.,* 2010; Yu, 2012) despite only occupying c. 3% of global land area (Waddington *et al.,* 2015). Peatlands emit atmospheric carbon via gaseous exchange of carbon dioxide (CO_2) and methane (CH_4) whilst also losing carbon via hydrological pathways in dissolved and particulate forms (Freeman *et al.,* 2004, Blodau 2002). This constant carbon cycling produces both positive and negative climate feedbacks (Bridgham *et al.,* 1995, Gorham, 1995, Moore *et al.,* 1998). Overall, pristine peatlands are considered net carbon sinks, cooling global climate (Frolking and Roulet, 2007).

Anthropogenic climate change is projected to alter global temperatures and weather patterns, with the most pronounced changes in temperature and precipitation rates predicted for the northern hemisphere (IPCC, 2021). Temperature, water table depth and atmospheric CO_2 concentrations are important climatic variables that govern peatland resilience and functioning

(Turetsky *et al.,* 2012). Increased temperatures and lower water tables may promote vascular plant growth at the expense of *Sphagnum* mosses (e.g., Trinder *et al.,* 2008, Metcalfe *et al.,* 2011, Dieleman *et al.,* 2015). *Sphagnum* is important for maintaining peatland ecosystem functioning and resilience to climatic or anthropogenic perturbations (Bragazza *et al.,* 2013; Kuiper *et al.,*2013). By modifying the hydrology and biochemistry of the soil, *Sphagnum* creates waterlogged and acidic substrates that decay slowly (van Breemen, 1995). If *Sphagnum* cover is reduced in favour of vascular plants, decomposition may be accelerated, as the supply of readily decomposed (labile) exudates from vascular plant roots increases, coinciding with fewer inhibitory polyphenol compounds released by *Sphagnum* (Fenner and Freeman, 2011; Bragazza *et al.,* 2013). This may significantly impact peatland ecosystem functioning, decreasing its carbon sink capacity (Dieleman *et al.,* 2015). Other indirect climate change impacts, such as drought and wildfire, may also weaken or reverse peatland carbon sink functioning (Rouse *et al.,*1997, Grillakis, 2019, Blodau, 2002, Norby *et al.,* 2019). By understanding how changes in climate and hydrology will affect peatland plant communities, we can better anticipate future peatland ecosystem responses to anthropogenic climate change. A fuller understanding of these responses and their associated feedbacks may lead to future improvements in global climate models (Frolking *et al.,* 2009).

We compare changes in plant community composition following ten years of climate manipulation (warming and episodic drought) on Cors Fochno, an ombrotrophic peatland in Wales, with the long-term palaeo-vegetation history of the bog. We generate a high-resolution testate amoebae derived hydroclimatic reconstruction for the past c. 1500 years from a peat core, relating hydrological shifts with changes in plant community composition in the long-term record. We compare vegetation community composition within the experimental plots and test the hypothesis that vegetation community composition within the experimentally warmed and droughted plots resembles that of dry/warm periods over the past one and a half millennia.

Climate manipulation studies simulate climatic and hydrological changes in peatlands (e.g., Ward *et al.,* 2013, Dieleman *et al.,* 2015), allowing examination of ecosystem responses to a range of environmental stressors. However, such experiments are frequently short-lived, rarely exceeding five growing seasons and therefore become increasingly imprecise for predicting how peatlands will respond to climate change over longer timescales. Nevertheless, peatlands also record a sensitive archive of environmental and climatic change over long-term (decadal to millennial) timescales (Barber, 1993; Chambers and Charman, 2004). Changes in environmental conditions may be inferred from biological or physical proxies that record changes in precipitation, reinforced by temperature (Charman et al., 2004; 2009) and may be compared with changes in vegetation (e.g., Chambers *et al.,* 1999, Turner *et al.,* 2014, De Vleeschouwer *et al.,* 2009). Such studies can be limited by the difficulty of discerning climatic effects from anthropogenic impacts in some instances, dating uncertainties, and differential preservation of biological proxies (Kuhry and Turunen 2006, Mauquoy and Yeloff, 2008; Swindles *et al.,* 2020).

Studies incorporating both climate manipulation studies and centennial or millennial-scale proxy records are rare (Lamentowicz *et al.,* 2016). However, the methods are complementary and can be applied together to improve understanding of peatland vegetation responses to climate change (Rull 2010; Seddon *et al.,* 2014; Lamentowicz *et al.,* 2016). Interpretation of the results of long-term *in-situ* climate manipulation experiments may also be improved by considering the present state of an ecosystem in the context of its long-term history (Willis *et al.,* 2010; Lamentowicz *et al.,* 2016). Lamentowicz *et al*., (2016) considered the long-term palaeo-vegetation history for two experimental sites at Linje mire, northern Poland and Mukhrino in western Siberia, and found that the vegetation cover in both sites had changed during the past c. 200 years: due to human activities (drainage) on Linje mire and following changes in climate and bog microforms on the relatively pristine Mukhrino. They argue changes in vegetation following anthropogenic disturbances and climate changes have modified ecosystem functioning in peatlands.

For the palaeo-vegetation reconstruction at Cors Fochno we focus on the past c. 1000 years, as temperature variation during this period (c. 0.2 ° C, Mann *et al.,* 2009) likely resembled the simulated temperature differences imparted by the experiment (Bradley and Jonest, 1993; Mann *et al.,* 2009). Climatic variability during the past millennium for the Northern Hemisphere included relatively warm conditions from the mid-9th to the mid-13th century CE, followed by cooler conditions from the 14th to the mid-19th century CE (Mann, *et al.,* 1999). These events are loosely termed the Medieval Climate Anomaly (MCA) and Little Ice Age (LIA) respectively

(Lamb, 1965; Mann, 2002). The timing and magnitude of both events vary widely across regions, and neither were periods of ubiquitous warming or cooling (Matthews and Briffa., 2005; Mann, 2002; Broecker, 2001; Neukom *et al.,* 2019). The MCA was a period of generally warmer conditions over much of the Northern Hemisphere, characterised by a predominantly positive North Atlantic Oscillation (NAO) (Trouet *et al.,* 2009). The LIA was characterized by pronounced cooling over the Northern Hemisphere and a predominantly negative NOA (Matthes, 1939; Lamb, 1965; Mann *et al.,* 2009). Marine palaeoclimate reconstructions show that North Atlantic sea surface temperatures were warmer sea during the MCA and fell during the LIA (Cunningham *et al.,* 2013), corresponding with palaeoclimate data showing that conditions were generally drier throughout much of Britain during the MCA and wetter or more variable throughout the LIA (Lamb, 1965; Proctor et al., 2000; Charman and Hendon, 2000).

Previous studies have made great strides towards understanding peatland vegetation responses to climate change (e.g., Weltzin et al., 2003; Buttler et al., 2015; Malhotra et al., 2020); however, to our knowledge, no previous study has attempted to combine *in-situ* temperature and water table manipulation with palaeoecological approaches to test how well the changes in these experimental studies replicate past changes. Comparing plant community composition changes in the experimental and palaeoecological record over the past c. 1000 years provides insights on how well climate manipulation experiments reflect actual long-term ecological changes and if changes in past vegetation community composition can serve as useful analogies for future responses to anthropogenic climate change.

2. Study site, methods, and materials

2.1. Study site

Cors Fochno is a *Sphagnum*-dominated raised (ombrotrophic) bog near the Ceredigion coast, Wales, east of the town of Borth (Lat: 52.50, Long: -4.01) (Figure 1). It is the largest expanse of primary surface lowland raised bog in Wales, with a central active zone comprising c. 2 km^2 of primary surface peat, surrounded by c. 4 km^2 of degraded peatland (Poucher, 2009). The vegetation on the central dome is consistent with the UK National Vegetation Classification M18: *Erica tetralix - Sphagnum papillosum* raised and blanket mire type vegetation communities, dominated by *Sphagnum pulchrum* lawns (Rodwell, 1991). Cors Fochno overlays tidal mud flats, and the underlying geology is of Silurian Aberystwyth grits group (Howells, 2007). Peat initiation began at the site around c. 6000 BCE (Wilks, 1979). The peat attains a maximum depth above 7 m in the central raised dome, which sits c. 1m above sea level (Wilks, 1979; Hughes and Schulz, 2001; CCW 2011). Based upon local measurements, annual precipitation rates (1981-2019) were 1236 mm y^{-1}, average air temperatures (2010-2019) were 11.1 ° C and average windspeeds were 3.1 m s^{-1} (unpublished data).

The site has experienced low level disturbance from human activities such as agriculture, peat cutting and mining activities throughout much of its history, which intensified at the end of the 18th century (Poucher, 2009; Page et al., 2012; Mighall et al., 2017). Population increases at this time drove demand for increased agriculture and fuel, resulting in the excavation of extensive drainage channels after 1815 and the conversion of large areas of the bog to farmland (Poucher, 2009). Annual burning of peripheral areas of the site began in the early 19th century and continued at a near annual basis until 1986 (CCW, 2011). Drainage and peat cutting continued until the 1970s, at which time restoration work began, restoring former water levels and re-establishing peat bog conditions in degraded areas (Poucher, 2009).

2.2. Experimental setup

The Cors Fochno experiment is a long-term (10-year), fully factorial *in-situ* climate manipulation experiment consisting of hydrologically isolated plots of *Sphagnum* lawn (Figure 2). The intention of the experiment is to determine the effects of climate warming and drought upon ecosystem functions in northern ombrotrophic peatlands.

The experiment was established in the spring of 2010, consisting of twelve plots, replicated in three blocks along a transect. Each plot is subjected to one of four treatments (Table 1). The treatments reflect the lower range of climate-change predictions for the UK from the present until c. 2070 (Lowe *et al*., 2018).

This project uses open top chambers (OTCs) to simulate climate warming (Figure 2); these are commonly used to moderately elevate air and soil temperatures in field experiments (Aronson and McNulty, 2009). OTCs were constructed from 2.5mm thick Perspex sheets, joined at the corners by cable ties, following designs used by the International Tundra Experiment (Marion *et al.,* 1997a; 1997b; Arft *et al.,* 1999; Shaver *et al.,* 2000). OTCs passively warm the air within the chamber like a greenhouse, with studies typically reporting a 0.35-1.0°C air temperature increase (Ward *et al.,* 2013; Walker *et al.,* 2015).

Drought in this study refers to reduced precipitation resulting in lowered groundwater levels (Loon, 2015). Drought simulation was achieved by automated groundwater pumping from within the plots. In the corner of each drought plot, we inserted a 1-metre long, 11 cm diameter perforated tube vertically into the peat and removed the peat inside. During drought simulation, plots were drained by macerator-style pumps attached to inlets (fitted with one-way valves to prevent water backflow) for each tube. Plastic piling, 1.5 m long, hydrologically separates the plots from the surrounding peat, preventing lateral flow into the drought plots. Shorter, 0.5 m piling drilled with holes were inserted into warmed and control plots to replicate this disturbance whilst still allowing for lateral water exchange to take place. Drought simulation was repeated during 2010, 2011, 2014 and 2019, each time lasting four weeks between August and September. This study tests the effects of increased drought incidence upon vegetation over ten years, rather than the effects of long-term water table drawdown.

Each plot was equipped with HOBO Onset U10 Temperature loggers (Onset Computer Corporation; Massachusetts USA) measuring air and soil (10 cm depth) temperature. These were later replaced with HOBO U23 Pro v2 temperature sensors in 2018. TruTrack WT-HR 2000 water-height data-loggers (Trutrack, Christchurch, New Zealand) record water table height. Logger values were converted to water table depth (WTD) by calibration against regular manual WTD measurements. Data gaps were filled by linear interpolation with temperatures and WTD records from neighbouring plots, as well as from an adjacent dip-well and weather station operated by Natural Resources Wales.

2.3. Vegetation survey within experimental plots

Three fixed 25 x 25 cm quadrats, each enclosing a 5 x 5 grid, were used to quantify the plant community composition and abundance in each plot. The quadrats were surveyed annually using the pin-quadrat method (Levy and Madden, 1933; Rochefort *et al*., 2013). A pin was pushed through the top-right corner of the 25 grid squares. Total touches for each species of vascular plant were tallied for each plot. *Sphagnum* (recorded to species), liverworts, and bare peat were recorded on a presence/absence basis for each segment.

2.4. Core collection and storage.

We extracted a 1.5 m-long core (BO17) from the bog in November 2017 using a 5 cm diameter Russian corer, with 5 cm of overlap between core sections (Jowsey, 1966). The coring location was proximal to the experimental site and was characterised by a *S. pulchrum* lawn. The uppermost 50 cm was extracted using a monolith tin to ensure sufficient additional material for later analysis. Extracted cores were stored in guttering, wrapped in cling film, and refrigerated at 4°C.

2.5. Chronology

Sphagnum or other above-ground plant remains were hand-picked from 1 cm-thick sub-samples in the core for Accelerator Mass Spectrometry ^{14}C dating. Rootlets were removed to avoid contamination by younger carbon (Kilian *et al.,* 1995). When insufficient identifiable plant remains were present, we analysed bulk peat. In those cases, a 1 cm thick, 1 cm^3 section of peat was washed through a 250 µm sieve and the fine particulate fraction (<250 µm) retained for analysis, following Piotowska *et al.* (2011). Samples were alkali-acid washed before oven drying at <45°C.

Recently accumulated peat was dated using Spheroidal Carbonaceous Particles (SCPs). SCPs are a component of black carbon that are only formed through fossil fuel combustion at high temperatures. SCP samples were prepared following procedures outlined by Swindles (2010). Changes in SCP concentrations throughout the soil profile are related to known ages of historical fuel combustion and can be compared with known fallout rates from other dated sedimentary sequences (Rose and Appleby, 2005; Swindles, 2010). SCP dating is a relatively rapid and low-cost alternative to radiometric methods for dating recently accumulated peat. SCPs are less mobile in peat than some radiometric isotopes such as ^{137}Cs, however some chronological accuracy may be lost compared to the absolute, continuous dating possible with ^{210}Pb (Turetsky et al., 2004).

Contiguous 1 cm^3 samples of peat were sub-sampled from the top 30 cm of the core at 1 cm resolution. SCPs were identified following criteria described by Rose (2008) using a high-powered microscope at 400x magnification. SCP concentration is reported as the number of particles per gram of dry mass (gDM^{-1}).

An additional chronostratigraphic marker is provided by a well-documented wildfire affecting the coring site during 1986 (Fowles *et al.,* 2004). Such an event would provide a clear sub-surface chrono-horizon of macrocharcoal consisting of the remains of identifiable peatland species. Macrocharcoal was sampled and analysed following procedures by Rhodes (1998) and Schlachter and Horn (2010). Contiguous 1 cm^3 sub-samples were taken at 1 cm resolution. Each sample was submerged in 6% H_2O_2 overnight before wet-sieving through a 125µm sieve, retaining the larger fraction. Charred fragments were counted under a stereo-microscope at low magnification (x10 – x100) using a Bogorov tray.

Age-depth models were generated using the package 'rBacon' (Blaauw *et al.,* 2021a), incorporating all SCPs, macrocharcoal and ^{14}C dates. This Bayesian model generates a maximum age probability at set (1 cm in this study) intervals together with maximum and minimum ages, based upon the 95% confidence interval. Dates within this study are reported as the median age probability (MAP) prefixed *circa* (*c.*) and the max-min age range is given as cal CE. Year notations are reported as Common Era (CE) dates, following the Gregorian calendar.

2.6. Palaeo-vegetation.

We used plant macrofossil analysis to determine palaeo-vegetation community change through the core. Four cm^3 of peat were sampled at contiguous 1 cm intervals. These were submerged in 10% potassium hydroxide solution for 24 hours prior to rinsing through a 125 µm sieve.

Primary peat components were assessed using a low-power stereomicroscope at 11.2x magnification following an adapted version of the quadrat and leaf count method (Barber *et al.,* 1994) by Mauquoy *et al.,* (2010). Components (e.g., total *Sphagnum*, *Rhyncospora alba* stem) were expressed as percentages of total peat components. Plant macrofossils were identified with reference to Grosse-Brauckmann (1972), Smith (2004), Souto *et al.,* (2016, 2017), Daniels and Eddy (1990) and Mauquoy *et al.,* (2007). Plant remains were identified to species level where possible. In situations where material was insufficiently preserved to facilitate species-level identification, plant types were recorded as “undifferentiated”.

Each sample was washed through a 1 mm test sieve, with both fractions retained. A Bogorov tray was used to count seeds within the <1 mm fraction, whereas material >1 mm was counted by creating a single layer of material in a petri dish underlain with numbered squares. Seeds and other objects (e.g., *Myrica gale* bud scales) were identified and counted for each square within the petri dish. Seed identification was achieved by referring to Cappers *et al.,* (2006) and Souto *et al.,* (2016). Seeds were counted under a low-power stereo-microscope at 10-200x magnification and are presented as total counts.

Sphagnum percentage counts were estimated by selecting >100 leaves from each sample for identification to species level. *Sphagnum* leaves were identified under a high-powered stereo-microscope at 100-200x magnification, with reference to Mauquoy and van Geel (2007) and Laine *et al.,* (2011) alongside reference material collected from the site. Leaf counts are expressed as percentages of the total identifiable *Sphagnum*. *Sphagnum* nomenclature follows Daniels and Eddy (1990), bryophytes follow Smith (2004), and vascular plants follow Stace (2010).

2.7. Testate amoebae

Testate amoebae are unicellular soil organisms useful as proxies for hydrological change in peatlands (Langdon *et al.,* 2012). Testate community composition changes in response to water table depth, with species distributions reflecting their ecological optima (Booth, 2008, Mitchell *et al.,* 2008). Their shells (tests) often allow identification to species level and are frequently preserved in peat (Mitchell *et al.,* 2008). Quantitative reconstruction of WTD based on fossil assemblages is possible following the development of numerical transfer function methods using present day species-environment relationships (Charman *et al.,* 2007; Payne and Mitchell, 2007).

We used the Weighted Averaging transfer function model of Amesbury *et al.,* (2016) based on a training set of 1302 samples spanning 35° of latitude and 55° of longitude. The efficacy of the model (tolerance down-weighted with inverse de-shrinking) has been rigorously tested by both statistical validation and comparison with independent test sets with associated instrumental data by Swindles et al. (2015a).

Two cm^3 samples (1 cm thick) were sub-sampled at 2 cm intervals. Tests were extracted following an adaptation of protocols by Hendon and Charman (1997). Each sample was submerged in water with a lycopodium tablet (Batch: 3862) then washed through a 355µm test-sieve, retaining the smaller fraction. These were then centrifuged at 3000 rpm for 10 minutes before mounting in glycerol. Tests were counted at 250 x magnification using a high-powered stereo-microscope, with minimum counts of 100 individuals achieved following Payne and Mitchell (2009). Testate amoebae are identified with reference to Charman *et al.* (2000), Clarke (2003), Mazei and Tsyganov (2006), and Siemensma (2019).

2.8. Statistical analyses.

All analyses were carried out using the statistical package 'R' (R core team, 2021). Further details (fixed effects, accounting for hierarchical and repeated measure design of the experiment) of the statistical methods used are provided in the supplementary materials. Statistical differences in temperature and water table between treatments were tested for using mixed effects linear models using the 'lme4' package in R (Bates *et al.,* 2012), and significant differences tested for using likelihood ratio tests (LRT). These tests assesses the goodness of fit of two statistical models, one with and another without the fixed effect of treatment against time, based on the ratio of their likelihoods.

Changes in vegetation (by species and functional type) over time across all combinations of treatments were tested by generalised linear models (GLMs) using the 'mvabund' package (Wang *et al.,* 2012; Wang *et al.,* 2020). GLMs are an extension of linear regression, relating linear models to their response variable via link functions.

Functional type data were compared by removing vegetation from the modern data with no analogy in the palaeoecological record. The remaining counts were summed into taxonomic groups of *Sphagnum* (sub-genera), shrubs, sedges, and liverworts.

Stratigraphically constrained incremental sum of squares cluster analysis (CONISS; Grimm, 1987) was used to identify groups of stratigraphically adjacent plant community assemblages, indicating changes have occurred between identified clusters throughout core BO17. Since CONISS is unable to deal with the different data-types (Relative % abundance and counts) in the plant macrofossil data (Birks, 2014), only the percentage peat component data were used to partition palaeo-vegetation zones.

To compare palaeoecological plant community composition with modern experimental vegetation communities, we used analogue matching (AM) using the 'analogue' package (Simpson, 2007). This is a technique used to identify close modern analogues (CMAs) for fossil datasets (Overpeck *et al.,* 1985; Simpson *et al.,* 2007). Similarity coefficients were calculated between experimental and fossil communities using methods described by Bray & Curtis (1957). A number between 0 and 1 is assigned for each pair of samples based on the statistical (dis)similarity between communities, with 0 indicating that samples are identical, while a coefficient of 1 indicates samples are completely unalike. A Monte-Carlo simulation with 10,000 permutations was employed as described by Simpson (2007) to define a critical value for dissimilarity to categorise CMAs at the 95% confidence interval. Data were square-root transformed prior to analysis to reduce possible differences between the two methods.

3. Results

3.1. Air temperature

To determine if the experimental treatments affected soil and air temperature or water table depth, we analysed temperature data from 2019 as a representative year and WTD measurements from the 2019 drought manipulation experiment. OTCs have a significant warming effect on air temperature (LRT: X2 (1) = 11.64, p = <0.001), increasing it by an average of 0.47 °C throughout 2019 (Figure 3a). Temperature differences were greatest during summer months, differing by as much as c. 7.4 °C, with mean temperature differences greatest between

12 noon and 6pm (Figure 3a-c). During winter months, mean temperatures are often slightly cooler within the OTCs than in controls (Figure 3c), with a maximum cooling of 3.4 °C. This is likely due to sheltering by the OTCs, restricting heat transport by wind passing over the vegetation canopy (Samson *et al.,* 2018).

3.2 Soil temperature

The OTCs significantly increased soil temperature (10 cm depth) by an average of 0.45 °C (95% CI: 0.09–0.80 °C) throughout 2019 (Figure 3b). Soil warming in plots with OTCs was slightly higher during the winter months, indicative of a lag between air and soil temperatures (Figure 3b-d).

3.3. Water table depth

Significant differences occurred in water table depth due to pumping during the 2019 water table drawdown experiment (LRT: X2 (1) = 1835.3, p = <0.001) (Figure 4). Pumping reduced water table depths by an average of 16.1 cm (95% CI: 13.7-18.4 cm) during the pumping period, comparable to the average water table depths within the plots during a drought that affected much of the Northern Hemisphere between June – August 2018 (16.4 cm).

3.4. Vegetation changes in the 10-year experimental study.

A total of 21 plant taxa occurs within the experimental plots. The most abundant species, *Rhyncospora alba*, constitutes 30.2±12.6% (1σ) of mean vegetation coverage in the plots. The second most abundant species recorded was *Sphagnum pulchrum,* at 28.4±11.1%. Supplementary Figures S1 to S6 illustrate changes in functional type and species differences between various treatments. The results of the Wald tests between each treatment are given in Table 2.

Shrub abundance significantly increased under both warmed and combined treatments relative to controls. However, this effect only significantly affected overall plant community composition in the plots with OTCs, which increased by >200% (rising from 4 % of total cover within the plots to 29 %) between 2010 and 2020, relative to >90% (increase in cover 14 to 26 %) in the combined treatment plots and a >7% decrease in the control plots during this time. Shrub taxa were less abundant in the warmed and combined treatment plots at the beginning of the experiment, which is in part a consequence of the small number of experimental plots (three for each treatment), a practical limitation of this study. However, in both cases the 95% CIs overlapped with controls at the start, and in both cases the increase in shrubs was logarithmic, reaching a plateau in 2016, six years after the start of treatments (Figure 5). Drought had no significant effect upon vegetation abundance, indicating that the significant increase in shrubs in the combined treatments was due to warming alone. Presence of OTCs had a significant effect upon the plant community at the species level relative to controls. This was mostly driven by increases in *Calluna vulgaris*, which doubled in abundance between 2010 and 2020, and increased significantly in the warmed plots. *Calluna vulgaris* is relatively uncommon in the plots, achieving a mean relative abundance of 5.6% of the entire community by 2020.

3.5. Core chronology

The results of the radiocarbon analyses are shown in Table 3. Dates are in stratigraphic order, except for the 44 and 50 cm depths, where the median date for the overlying sample is older than that of the underlying sample. The age ranges for these two depths overlap completely, indicating that their ages are statistically indistinguishable. This is the same for 75 and 80 cm depths. All other ages are significantly different from each other.

SCP concentrations in the core (Figure 6) were relatively low compared to other studies within the UK (e.g., Rose and Appleby, 2005), probably due to the predominantly westerly winds blowing relatively clean air from the Irish and Atlantic seas. The SCP profile is bimodal, with peaks at 13 and 20 cm. Such a double peak has been identified in previous SCP profiles from Cors Fochno and nearby sites (Rose, 1995; Schulz, 2004). The upper profile is consistent with typical SCP profiles for Britain and Northern Ireland (Rose *et al*., 1995), with the sharp decline above 10 cm reflecting the success of air pollution legislation in the last decades of the 20th century. The age distribution of a calibrated radiocarbon date of 1922-1690 CE at 29 cm makes it difficult to ascertain whether the SCPs within the deeper part of the profile were deposited *in-situ*, or relate to downward mobility of SCPs resulting from water table fluctuations. Because of this, only a single date could be tentatively ascribed: 1976±3 for the sub-surface peak at 13 cm based upon comparison of SCP profiles from Lakes in north and central Wales with corresponding ^{210}Pb age-depth profiles (Rose and Appleby, 2005).

At 12cm, a macrocharcoal layer containing >10mm fragments of charred peatland vegetation is considered to reflect the position within the core relating to the 1986 fire (see Figure 8).

The age-depth model for BO17 (Figure 7) has a mean 95% confidence range of 185 years and a maximum range of 287 years between 35 and 65 cm. All dates used overlap with the model, producing a relatively linear trend as is commonly observed in peat (Belyea and Clymo, 2001). A maximum sampling depth of 100 cm was chosen for all palaeoecological analyses based on the age-depth model, capturing the past c. 1000 years within the mean 95% CI of the model whilst providing sufficient prior environmental context.

3.6. Plant macrofossils

Sphagnum is the principal plant macrofossil, accounting for 31.6±17.6% of peat components (Figure 8). Other abundant components include monocotyledon radicells (22.0±12.4%), ericaceous rootlets (21.1±12.4%), and unidentified organic matter (UOM: 20.8±13.8%). Above-ground remains (e.g., identifiable leaves, stems and flowers) of vascular plants are poorly represented. Nine phases of significant vegetation development were identified

3.7. Testate amoebae

The stratigraphic profile of core BO17 is mainly characterised by the species *Amphitrema wrightianum, Archerella flavum, Arcella discoides,* and *Phryganella arcopodia.* These are indicators of wet conditions (Charman *et al.,* 2000) and occur throughout the profile. Dry periods are indicated by abundant *Difflugia pulex* and *Cryptodifflugia oviformis* types. The former typically prefers slightly wetter to intermediate conditions (e.g., Charman *et al.,* 2007), although these are rare in modern samples and thus have poorly constrained optima (Swindles *et al.,* 2015). The latter prefers deeper water tables (Lamentowicz and Mitchell, 2005; Amesbury *et al.,* 2012). The relative abundance of testate amoebae throughout the stratigraphy of core BO17 is provided in the supplementary figures (S8). The water-table reconstruction for core BO17 is shown in Figure 9. The reconstruction indicates that water tables gradually increased from c. 600

to c. 1800 CE, with a slight period of increasing water table depth between c. 1000 – 1300 CE. Mean values were above the peat surface from c. 1550 to 1750, suggesting the coring location underwent an aquatic phase at this time. This is followed by significant increase in water table depth from c. 1800 – 1970 CE, where the highest water table depths are attained, until water tables abruptly increase to their prior levels until the end of the profile.

3.8. Comparing experimental vegetation composition and palaeoecological data

The methods used to quantify plant populations differ between the experimental (pin-touch and quadrat) and palaeoecological (leaf-count) studies; both have limitations of their own (Goodall, 1952; Birks, 2007 Mauquoy and Yeloff, 2008) in addition to the sources of error when comparing between them. For example, certain taxa (e.g., *Rhyncospora alba*) may have elevated counts from the pin-touch method due to their wide, tall, spreading shape and the density in which they can grow together (Heslehurst, 1971), whereas the representation of certain taxa in the palaeoecological record may be biased by taphonomic effects favouring more recalcitrant remains (e.g., *Sphagnum* leaves) over more labile remains (e.g., ericaceous woody remains) (Mauquoy and Yeloff, 2008). Even within *Sphagnum,* certain species are more robust than others (Bengtsson *et al.,* 2016) and are therefore likely to be preserved better and be more readily identified, falsely inflating their apparent abundance (Johnson and Damman, 1991). Some *Sphagnum* species also lose their leaves more readily from their branches, and therefore contribute leaves to the palaeoecological record in differing quantities (Barber, 1981). These differences and limitations hinder our ability to make quantitative comparisons between palaeoecological and modern vegetation communities from peatlands. However, comparisons can still be made on a qualitative basis.

The result of the close modern analogue (CMA) analysis is presented in Figure 10. From the experimental communities, 237 samples counted as CMAs for 52 fossil samples using a Bray-Curtis (dis)similarity cut-off of 0.1106. These were only 1.8% of the total number of comparisons made, indicating that the current vegetation composition in all the plots (control and treatments) is unlike nearly all the inferred plant communities in the bog over the last 1500 years. Close modern analogues appear to relate to the abundance of the two most common functional groups within the modern datasets: sedges and *Sphagnum* sect. *sphagnum,* whilst showing little correspondence with periods of hydroclimatic change (Figure 10). Most of the CMAs were from control (77) and combined treatment communities (71), with warmed and drought plots less likely to be CMAs (47 and 42 respectively). The dominant vegetation within the experimental plots is *S. pulchrum* and *R. alba*, members of these functional groups. Most (70.5%) of the CMAs occurred within the top 28 cm of the core, between c. 1822 to 2012 cal CE. This period is dominated by ericaceous roots, *S. pulchrum* and *S. tenellum*. The depth with the most CMAs occurred at 26 cm, which matched with 36 experimental vegetation communities. This sampling interval represents c.1840 cal CE and is characterised by high *Sphagnum* sect. *cuspidatum* (50%) and sedge abundance (35%), with shrubs representing a further 11 % and *Sphagnum* sect. *sphagnum* representing only 4 % of the total assemblage. Most of the CMAs for this depth were from control (14) and combined (13) plots.

Groupings of CMAs also occur between c. 815 to 940 cal CE, c. 975 to 1280 cal CE, c. 1510 to 1525 cal CE, and c. 1570 to 1615 cal CE (Figure 10). Climatic conditions and species composition vary between these periods. Between c. 815 to 940 cal CE, the vegetation community composition composed predominantly of sedges (c. 40 %) and the formerly abundant *S. austinii* (c. 27%), a species within the *Sphagnum* section *sphagnum*. The period c. 970 to 1280 cal CE covers the timing of the MCA, where shrubs (c. 31%), sedges (30%) and *Sphagnum* sect. *sphagnum* (25%) type taxa dominated, mainly *S. austinii*. Groupings between c. 1510 to 1525 cal CE and c. 1570 to 1615 cal CE occur during the LIA and are characterised by high abundances of sedge (c. 50%) and *Sphagnum* section *sphagnum* (30%), the latter represented by *S. papillosum*.

4. Discussion

4.1. Effect of experimental warming and drought upon peatland vegetation

Ericaceous shrubs became more abundant in response to warming over ten years. Increased ericaceous shrub cover is commonly reported with warming in climate manipulation experiments in peatlands. For example, Weltzin *et al.,* (2003) reported a 50% increase in shrub cover in a bog mesocosm experiment following summer temperature increases between 1.6-4.1°C over five years, comparable to the temperature changes in this study. Buttler *et al.,* (2015) conducted an *in-situ* climate warming experiment using OTCs on an ombrotrophic bog in the Jura mountains, finding that *Andromeda polifolia* increased over five years due to increased rooting depth. Malhotra *et al.,* (2020) found similar results in an entire ecosystem manipulation experiment on a forested ombrotrophic bog in northern Minnesota. Increased soil temperatures expanded the below-ground growing season, increasing root density.

This finding has several implications for peatland ecosystem functions including the peatland carbon sink. Increased ericaceous shrub dominance due to warming may initially increase the rate of CO_2 sequestration due to their high productivity, although this may be offset by increased carbon respiration resulting from increased root exudates and a reduction in the quality of plant litter (Weltzin *et al.,* 2000; Fenner *et al.,* 2007; Ward *et al.,* 2013; Bell *et al.,* 2018). Other vegetation types, particularly *Sphagnum*, may be suppressed by shrubs due to shading and enhanced water use, increasing the depth to the water table (Norby *et al.,* 2019). Loss or decline of *Sphagnum* is an important indicator of the future direction of peatland functioning under climate change due to its importance as a peat-former and ecosystem engineer (van Breemen, 1995).

No significant changes occurred for *Sphagnum* due to increases in air temperature of 0.3–0.7°C over ten years (Figure 3), which is in-line with low range UK temperature projections until c. 2070 (Lowe *et al*., 2018). Weltzin *et al.,* (2000; 2003) found no significant change in Sphagnum cover in bog mesocosms with increased summer soil temperatures of 1.6-4.1°C. Similarly, Walker *et al.,* (2006) found that *Sphagnum* cover did not significantly change with 1-3°C of warming across multiple sites in Arctic regions. Some studies even suggest that modest warming may increase the production of certain *Sphagnum* species (Dorrepaal *et al.,* 2004; Robroek *et al.,* 2007). However, a critical temperature for *Sphagnum* decline appears to exist. Dieleman *et al.,* (2015) found that *Sphagnum* from a poor (nutrient deficient) fen in Ontario, Canada declined significantly following temperature increases of 8°C in a mesocosm experiment. A transplantation study by Bragazza *et al*., (2016) of peat mesocosms from a Swiss ombrotrophic bog to a warmer location (+5°C) reduced the productivity of *S. fallax* by 60%. Norby *et al.,* (2019) found that *Sphagnum* productivity in an ombrotrophic bog in northern Minnesota initially increased with warming but declined at temperature increases above 5°C, declining by nearly 100% with warming of 9°C.

The experiment therefore showed that the expected change in climate by the mid-century for this region does not reach the critical temperature threshold for *Sphagnum* decline over a ten-year period. However, it does not rule out a change in Sphagnum over the longer term, either in direct response to a sustained temperature/water table change, or indirectly through a community shift driven by the influx of shrubs. Projections for temperature increases in Northern Hemispheric regions by 2100 range from 2 °C to above 8 °C relative to 1850-1900 baselines, based on predictions by the IPCC (IPCC, 2021). The negative effect of experimental warming to such a rapid and dramatic increase in temperature upon *Sphagnum* is commonly achieved using infrared heat-lamps, which may scorch *the Sphagnum* and unrealistically increase soil drying (Harte and Shaw, 1995; Johnson *et al.,* 2013). Whether the effects of high temperatures on *Sphagnum* cover using infrared heat lamps should be considered realistic responses to warming or experimental artefacts depends on how rapidly we expect temperatures to increase in these regions.

Our results suggest that increased drought frequency does not significantly influence peatland vegetation, at least over a ten-year period. This disagrees with the results of other water table drawdown experiments (e.g., Strack *et al*., 2006; Murphy *et al.,* 2009; Bragazza *et al*., 2013). However, ours differs from previous studies since we simulate repeated episodes of temporary seasonal drought, rather than inducing a permanent step-change in the water table.

4.2. Vegetation changes in the palaeoecological record

Vegetation and inferred water tables were stable for much of the palaeo-vegetation record of Cors Fochno. For example, between c. 850 to 1300 cal CE, during the warmer MCA, there were few changes in vegetation community composition, and only slight changes in hydrology towards drier conditions (Figure 10). The stability of peatland flora and hydrology during the MCA is typical of many peatland palaeoecological studies (e.g., Magnan *et al.,* 2018). Plant communities and their functional diversity often exhibit remarkable stability due to several autogenic feedback mechanisms that result in a degree of homeostasis in peatland hydrology (Belyea, 2009). These have moderated peatland responses to past changes in climate (Dise, 2009; Swindles *et al*., 2012; Churchill *et al*., 2015). Peatland feedback mechanisms are known to operate over a range of timescales (Belyea, 2009), and it may be that peatland vegetation is resilient to short-term changes in water table but may rapidly shift to a new composition in response to long-term shifts.

This stability in the Cors Fochno palaeovegetation record is punctuated by relatively abrupt changes in vegetation which occur without obvious changes in water table depth. These seem to occur either because of anthropogenic disturbances (burning) or may be mediated by hydro-climatic changes, reflecting interspecific competition between *Sphagnum* and other plant species in response to long term, gradual changes in water table depth (Robroek *et al.,* 2007). For example, between c. 1300 and 1500 CE, *Sphagnum austinii* disappears and *E. tetralix* reach a peak following a burning event at c. 1400 CE. *Sphagnum austinii* was a formerly common and important peat-forming species in northern peatlands until its pronounced decline in the past 2000 years (Swindles *et al.,* 2015b). Many environmental and anthropogenic causes for this decline have been suggested (Swindles *et al.,* 2015b). In core BO17, it is virtually absent by c. 1300 CE, later than the formerly established date of its extinction from this site of 1100 cal CE by Hughes and Schulz (2001). While it is beyond the scope of this paper to identify the cause of the *S. austinii* extinction, its timing in the core following a fire event suggests possible anthropogenic influence.

During the c. 1200-year period between the start of the record until c. 1800 CE, water table depth is relatively stable, exhibiting a general monotonic trend towards wetter conditions. A sudden shift towards more aquatic vegetation occurred around c. 1500 CE and lasted until c. 1800 CE. This shift is indicative of the development of a bog-pool, reflected in the palaeo-hydrology of the site, where average reconstructed water tables rise above the peatland surface (Figure 9). Other studies also document dramatic shifts in vegetation following the onset of the LIA (Mauquoy *et al*., 2002; Magnan *et al.,* 2018). The correspondence of this shift with increasingly wet, cool conditions suggests it was climatically mediated, with thresholds for compositional change defined by the position of the water table. These changes in water table depth agree with several studies which often show generally wetter conditions in Britain during the MCA and drier conditions during the LIA (Lamb, 1965; Charman and Hendon, 2000; Turner et al., 2016), although other records disagree, likely due to a lack of spatial coherence proxy precipitation records across Britain (Proctor et al., 2000).

4.3. Comparing past and future vegetation responses to climate change

This study demonstrates that ericaceous shrubs increased in abundance with warming in both experimental and palaeoecological studies from the same site. This correspondence suggests that where ericaceous cover has increased in response to warming in peatlands in the past, it may continue to do so with future climate change**.** The lack of a significant effect of increased drought in our experimental study can neither be supported or refuted by the palaeo record because the experimental droughts simulate short, episodic water table drawdown, rather than prolonged periods of water-table drawdown as are recorded by the long-term palaeo record (e.g., between c. 1800 to 1970 CE). We see that during that time there is a shift in vegetation, with bog pool vegetation (particularly *S. denticulatum*) making way for more terrestrial species, including hummock-forming *Sphagnum* species such as *S. medium* and *S. capillifolium.* During this time, ericaceous rootlets increase after having previously declined during the very wet preceding conditions. This event corresponds to a period of intensive drainage at Cors Fochno (Poucher, 2009). The palaeo record suggests that water tables returned to pre-drainage levels by c. 1970 CE, likely in response to drainage blocking and peatland restoration taking place around this time (Poucher, 2009). No large changes in peatland vegetation occurred following this restoration (Figures 7 and 9). These findings suggest that while sustained water-table drawdown may have a dramatic effect upon vegetation communities, increased hydrological droughts at the frequency, magnitude and timescale imparted by our study (four x 4-week simulated droughts over ten years) are unlikely to result in significant changes in vegetation, although we cannot be sure that this will remain the case over longer timescales. Manipulation experiments are unlikely to capture changes resulting from slow, long-term changes in climate which can be seen in the paleorecord. Conversely, the palaeo record may not be sufficiently fine-scaled to identify annual to decadal-scale changes in vegetation that may respond more to temperature change than to water table fluctuations.

We find that the current vegetation composition of Cors Fochno, including the species within the experimental plots, has few analogues in the palaeo record as far back as 600 CE. We find most CMAs are from control or combined treatments, rather than warmed or droughted plots. This suggests that these treatments produce fewer analogues since periods of warming typically coincide with periods of drying. Most close analogues occur near the top of the profile, following the development of the modern-day vegetation community in the central dome of the site, around c. 1800 CE (Poucher, 2009). This is contemporaneous with a period of enhanced human activity and peatland drainage, as indicated by the macrocharcoal and palaeohydrological reconstructions (Figures 7 and 8). This suggests that changes in the modern-day plant communities are a consequence of human activity during recent centuries.

The later development of the modern-day vegetation community is likely to have resulted in a change in carbon sequestration, with the dominant *S. pulchrum* being a member of the sub-genera *Sphagnum* sect. *cuspidatum* that produces more readily decomposed litter, meaning more carbon is lost to the atmosphere by decay (as CO_2) then is retained in the soil (Bentsson *et al.,* 2016); however, the waterlogged lawn environments that this species occupies delays their decomposition. *Sphagnum* sect. *sphagnum* type species (e.g., *S. austinii*) have similar productivity rates but are less prone to decomposition and, like *S. pulchrum*, used to occupy lawns (Mauquoy and van Geel, 2002; Bentsson *et al*., 2016). Therefore, this change in dominant species is likely to have resulted in a net decline in carbon sequestration rates.

The intensification of anthropogenic impacts on peatlands over the past c. 300 years may have driven threshold shifts in plant communities (Swindles *et al.,* 2019). Even where apparently pristine conditions have been maintained or restored, peatlands may still be affected by climate change, past disturbance, or atmospheric pollution (e.g., Berendse *et al.,* 2001; Talbot *et al.,* 2014; Swindles *et al.,* 2016). In palaeoecological studies, anthropogenic effects are the dominant drivers of many palaeoecological proxies (Turner *et al*., 2014; Gauthier *et al.,* 2019). Differences in the relative importance of the drivers of vegetation change over time represents an important distinction between the results of palaeoecological and experimental studies. Whereas temperature is frequently identified as the dominant driver of change in experiments (Weltzin *et al.,* 2000; Breeuwer *et al.,* 2008; Heijmans *et al.,* 2013; Dieleman *et al.,* 2015), in palaeoecological studies, hydrological conditions are often of greater importance (Charman *et al.,* 2009). This suggests that the importance of the main drivers of vegetation change differ between short (sub-decadal) and longer (multidecadal to millennial) timescales, although this may also be a consequence of the low temperature sensitivity of peatland palaeo records (Payne, 2014). This study supports the notion that peatlands are less resistant to direct anthropogenic disturbances such as burning or drainage than they are to climate change. This agrees with Swindles *et al.,* (2016) who found that multiple anthropogenic disturbances at Helwith Moss over 50 years overcame the site's capacity to resist vegetation succession.

Approximately 15% of the world's peatlands are in a state of degradation (Joosten, 2012) and many of Europe's peatlands have undergone substantial drying throughout the past c.300 years on account of human activity (Swindles *et al.,* 2019). Species turnover and functional diversity affect peatland ecosystem service provision (Ward *et al.,* 2009; Dieleman *et al.,* 2015), and these are, in turn, impacted by anthropogenic disturbance (Gatis *et al*., 2015). The combined effects of anthropogenic climate change, drainage, burning and environmental pollution may result in the development of novel vegetation communities (Alexander *et al.,* 2015; Ordonez *et al*., 2016). Woody plant encroachment and the establishment of generalists and exotic species has been related to the effects of climate change (Gunnarsson *et al*., 2002; Pellerin and Lavoie, 2003).

Changes in vegetation are likely to impact ecosystem functions (Johnson and Damman, 1991; Hájek, 2009; Swindles *et al.,* 2019). Consequently, past peatland responses to climate changes may differ from future responses, and may not be accurately represented within the palaeo record. It is for this reason that we recommend long-term experimental climate manipulation studies continue, since these can provide clues as to the direction of future changes under post-disturbance baselines. Palaeoecological records may still provide an important source of information on how peatlands have responded to climate change under pre-disturbance conditions, improving our understanding by documenting responses to environmental and climatic changes beyond those that can be obtained from experimental studies alone (Graumlich, 1994). They are also useful, as in the case of this study, for contextualising experimental studies against the long-term history of a site, elucidating past vegetational changes and disturbances.

5. Conclusions

Our study compares the peatland vegetation response to a ten-year climate manipulation experiment with those inferred over the last 1500 years from the palaeo record in response to climate and habitat change. The results of our experimental study showed that warming increased the abundance of shrub-type vegetation over ten years, a result supported by most warming experiments in peatland ecosystems. This result is corroborated by increases in *Calluna vulgaris* seeds during apparently warmer periods in the long-term vegetation record, supporting the likelihood of increased shrub dominance in peatlands with warming. We see no evidence for a significant change in *Sphagnum*, likely since the c.0.5°C warming imparted by this study, in line with changes expected over the next 70 years for the UK, does not appear to exceed a critical threshold for *Sphagnum* decline. An increase in ericaceous shrub dominance may result in changes in the carbon balance of peatlands, potentially resulting in increased carbon losses due to enhanced root exudates and a reduction in litter quality. The persistence of *Sphagnum,* at least over the short term, may ameliorate this change. However, we cannot rule out that *Sphagnum* may eventually decline in response to either sustained warming or to ecological changes, particularly increases in shrub cover.

Vegetation community composition in ombrotrophic bogs is resilient to increases in short-term episodic droughts at the severity imparted by our manipulations (four additional 4-week droughts over a ten-year period). The long-term palaeoecological record does not record individual drought events but rather periods of long-term water table drawdown, therefore this result could not be corroborated by the palaeoecological record. The results of the experimental study suggest that the predicted increase in short-term episodic droughts may not compound the effects of warming upon peatland vegetation in the near future. Our palaeoecological study, on the other hand, suggests vegetation composition may change in response to long-term sustained water-table drawdown, which agrees with experimental studies that replicate such a scenario.

Based on this study, we suggest that studying the response of modern peatlands to climate change, either through experiments, resurveys, or targeted gradient studies, provides the best way to predict peatland responses to climate change over the next few decades or more. Since all such studies benefit from understanding the long-term environmental and disturbance context of a site, peatland palaeoecological studies are still highly valuable in our understanding of peatland ecosystem dynamics. To better predict future climate change responses, long-term studies have the capacity to identify long-term drivers of changes in vegetation, possibly allowing for the identification of tipping-points that drive the large magnitude changes in vegetation communities frequently observed in palaeoecological studies. Responses in vegetation community composition to climate change inferred from the peatland palaeoecological record may be unreliable as an analogue for future change because many peatlands, even seemingly 'pristine' ones, have been influenced by anthropogenic drivers such as drainage or air pollution. Such anthropogenic impacts have become stronger drivers of change in peatland plant community composition than climate, and peatland autogenic feedbacks do not confer the same level of resistance to these impacts.

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Tables

Table 1. Experimental treatments in the Cors Fochno climate manipulation experiment. The two experimental levels are denoted by shading of the table rows. Presence of open top chambers (OTCs) and groundwater pumping treatments (Pumped) are denoted by an x. Combined warming and drought plots are referred to as ‘combined’.

Treatment	OTC	Pumping	Number of plots	Plot ID
OTC	x		6	1, 3, 5, 8, 10, 12
Pumped		X	6	1, 4, 6, 8, 9, 12
Control			3	2, 7, 11
Warmed	x		3	3, 5, 10
Drought		X	3	4, 6, 9
Combined	x	X	3	1, 8, 12

Table 2. Results of the statistical tests for vegetation differences between plots. Each plot with OTCs (OTC in table) and each pumped plot (Pumped in table) are compared against the plots without OTCs and plots that are not pumped as controls. The results of these tests are shaded white in the table. All other comparisons are made between individual treatments: control, warmed, drought, and combined (combined warming and drought), these tests are shaded in light blue.

Control						
Functional Types		Res.DF	DF.diff	Wald	p. val	Functional types
OTC		110	10	7.493	0.055	Shrubs (Wald: 7.493; p=0.035)
Pumped		110	10	7.828	0.359	NA
Warmed		44	10	12.892	**0.001***	Shrubs (Wald: 10.897; p=0.001)
Drought		44	10	10.636	0.10	NA
Combined		44	10	9.579	0.20	Shrubs (Wald: 7.744; p=0.033)
Individual taxa		Res.DF	DF.diff	Wald	p. val	Species
OTC		110	10	16.70	**0.039***	No single species
Pumped		110	10	12.871	0.324	NA
Warmed		44	10	13.825	0.35	*Calluna vulgaris* (Wald: 7.108; p=0.013)
Drought		44	10	13.291	0.20	NA
Combined		44	10	13.088	0.60	NA
Warmed						
Functional Types		Res.DF	DF.diff	Wald	p. val	Functional types
Drought		44	10	8.145	**0.05***	No single species
Combined		44	10	6.168	0.75	NA
Individual taxa		Res.DF	DF.diff	Wald	p. val	Species
Drought		44	10	12.524	0.35	NA
Combined		44	10	11.455	0.60	NA
Drought						
Functional Types		Res.DF	DF.diff	Wald	p. val	Functional types
Combined		44	10	8.145	0.35	NA
Individual taxa		Res.DF	DF.diff	Wald	p. val	Species
Combined		44	10	11.900	0.20	NA

Table 3. Table of AMS ^{14}C dates from BO17 core, Cors Fochno. Dates were calibrated using the IntCal20 calibration curve (Reimer *et al.,* 2020) in OxCal version 4.4 (Ramsey, 1995).

Depth (CM)	Lab code	Material dated	^{14}C Age	^{14}C error	Calibrated age range (years CE) 95.4%	Median age (Years CE)
29	D-AMS 034826	*Sphagnum* stems and leaves	94	26	1690-1922	1837
44	D-AMS 029938	*Sphagnum* stems and leaves	427	26	1426-1613	1455
50	D-AMS 034971	*Sphagnum* stems and leaves	379	24	1449-1630	1498
60	D-AMS 034827	*Sphagnum* stems and leaves	724	29	1230-1381	1281
70	D-AMS 034972	*Sphagnum* stems and leaves	1129	25	775-994	933
75	D-AMS 029939	*Sphagnum* stems and leaves	1016	31	979-1153	1022
80	D-AMS 034828	*Sphagnum* stems and leaves	1052	27	897-1032	1002
100	D-AMS 034973	Fine fraction of bulk peat	1514	27	400-638	569
135	D-AMS 029940	*Racomitrium lanuginosum* stem and leaves	1729	33	247-408	334

Figure 1. Satellite image of Cors Fochno, Ceredigion, west Wales. The red dot denotes the location of the experimental plots and core. The inset map shows the location of Cors Fochno within Wales (blue dot). Satellite image sourced from Bing maps.

Figure 2. Cors Fochno Experiment climate manipulation plots: a. plot with open top chamber (OTC); b: Control plot; c: Drought plot undergoing drought manipulation and d: Schematic of plot design (Kay, 2019).

Figure 3. Temperature variations between treatments for the year 2019. Temperatures for plots without OTCs are shown in purple; plots with OTCs are in yellow. a-b: loess curves showing the differences in a. air and b. soil temperatures throughout the year. c-d: Differences in monthly mean air (c) and soil (d) temperatures during different time periods for different times of year. Periods= midnight c.12 am; morning c.6 am; midday c.12pm, early evening c. 6pm.

Figure 4. Difference in water table depths (WTD) between pumped (blue) and not pumped (black) plots during the 2019 drought manipulation experiment. Six weeks of daily WTD measurements are shown, including week-long measurements post and pre drought manipulation. Dashed vertical lines indicate the start (12th August) and end (6th September) of the drought manipulation for this year.

Figure 5. Responses of shrubs to treatments relative to controls over the ten-year experiment. The y-axis abundance is total summed counts for each plot +1, plotted on a log-linear scale. Shading indicates the 95% confidence interval.

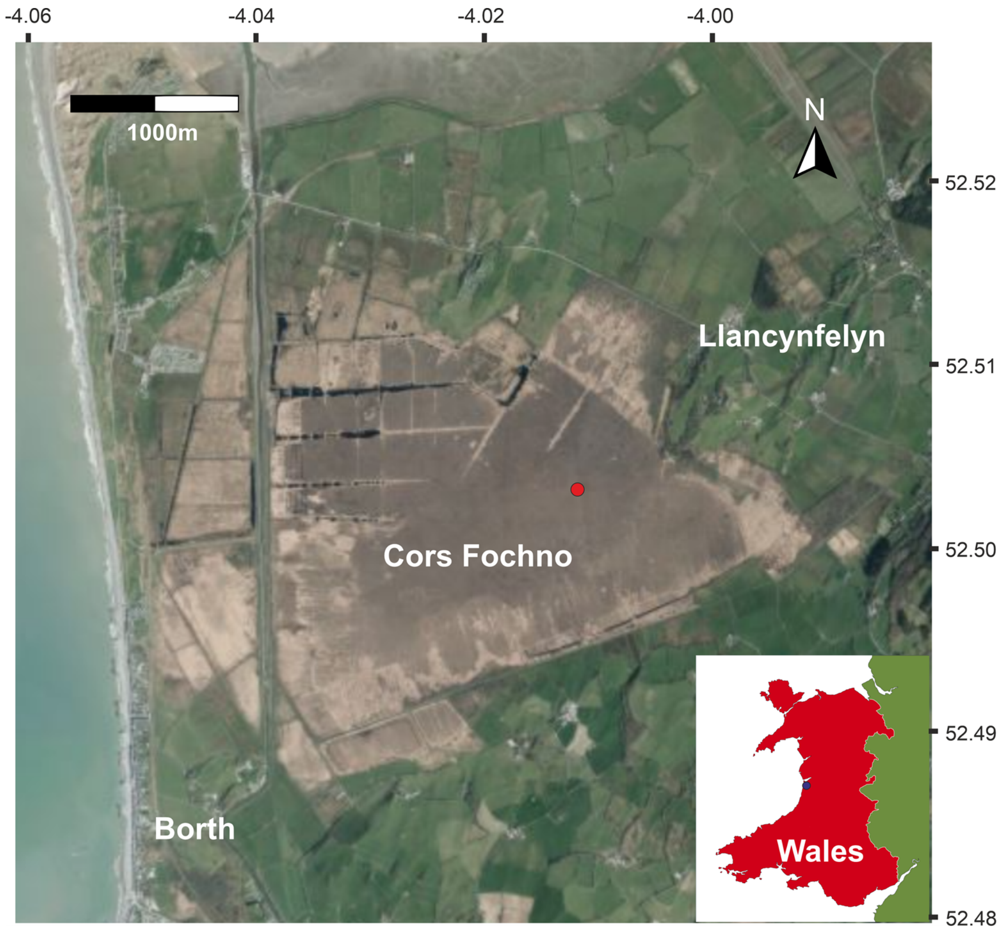
Figure 6. Spheroidal carbonaceous particles (SCP) concentration (gDM^{-1}) profile for Cors Fochno core (BO17). The radiocarbon date given for 29cm is the calibrated date for the sample.

Figure 7. Age depth model for core BO17, based on integrated radiocarbon, macrocharcoal and spheroidal carbonaceous particles (SCPs). The model was generated using rBacon (Blaauw and Christen, 2011; 2013; Blaauw *et al.,* 2021b). Probability distribution functions (PDFs) for ^{14}C dates are shown in blue, PDFs for calendar dates (SCPs and macrocharcoal) are shown in green. Black shading denotes interpolated age distributions for all depths. 95% confidence intervals are denoted by dashed lines. Plots for model performance are presented in supplementary figure S7.

Figure 8. Plant macrofossil diagram for core BO17. CONISS illustrates the hierarchical clustering upon which the diagram zonation is based, red horizontal lines indicate zone boundaries. A broken stick model was used to determine the number of significant zones (Bennett, 1996). Peat components accounting for less than 5% of the overall percentage abundance and seeds with count numbers less than 5 in all levels are omitted although these data are included in all other analyses.

Figure 9. Testate amoebae inferred water-table depth reconstruction generated using the pan-European training set developed by Amesbury *et al.* (2016). Age is given as the median age probability (MAP). Shaded areas denote sample-specific errors, based on 1000 bootstrapping cycles.

Figure 10. Relative changes in plant functional types and total number of close modern analogues of vegetation community composition (CMAs) for each sampling interval from core BO17. Horizontal coral-coloured bars denote periods of lower water table (drier/warmer periods), blue bars denote periods of higher water table (wetter/cooler periods), as inferred from the testate amoebae based palaeohydrological reconstruction. Age cal BP is given as the median age probability (MAP).



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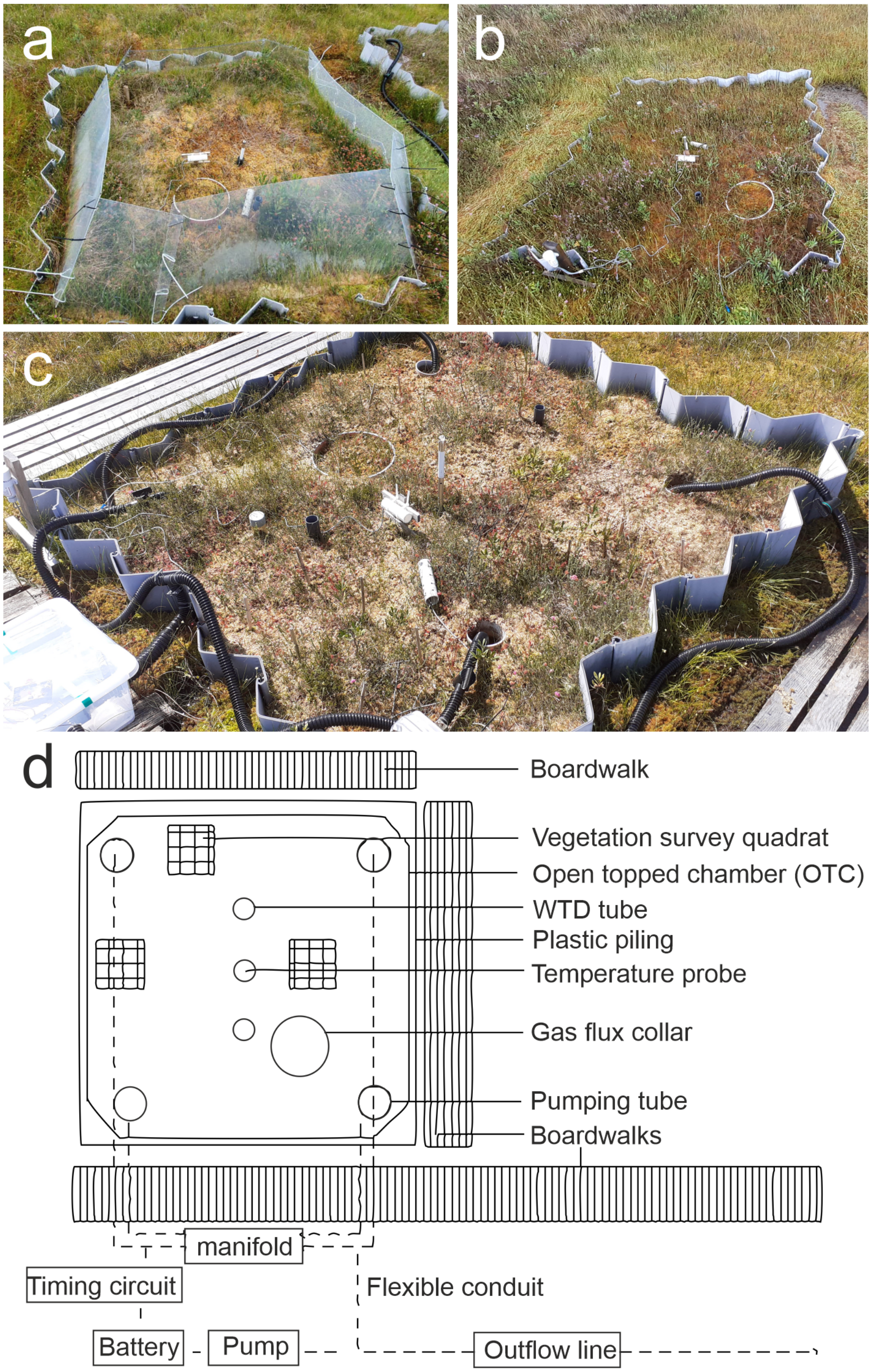

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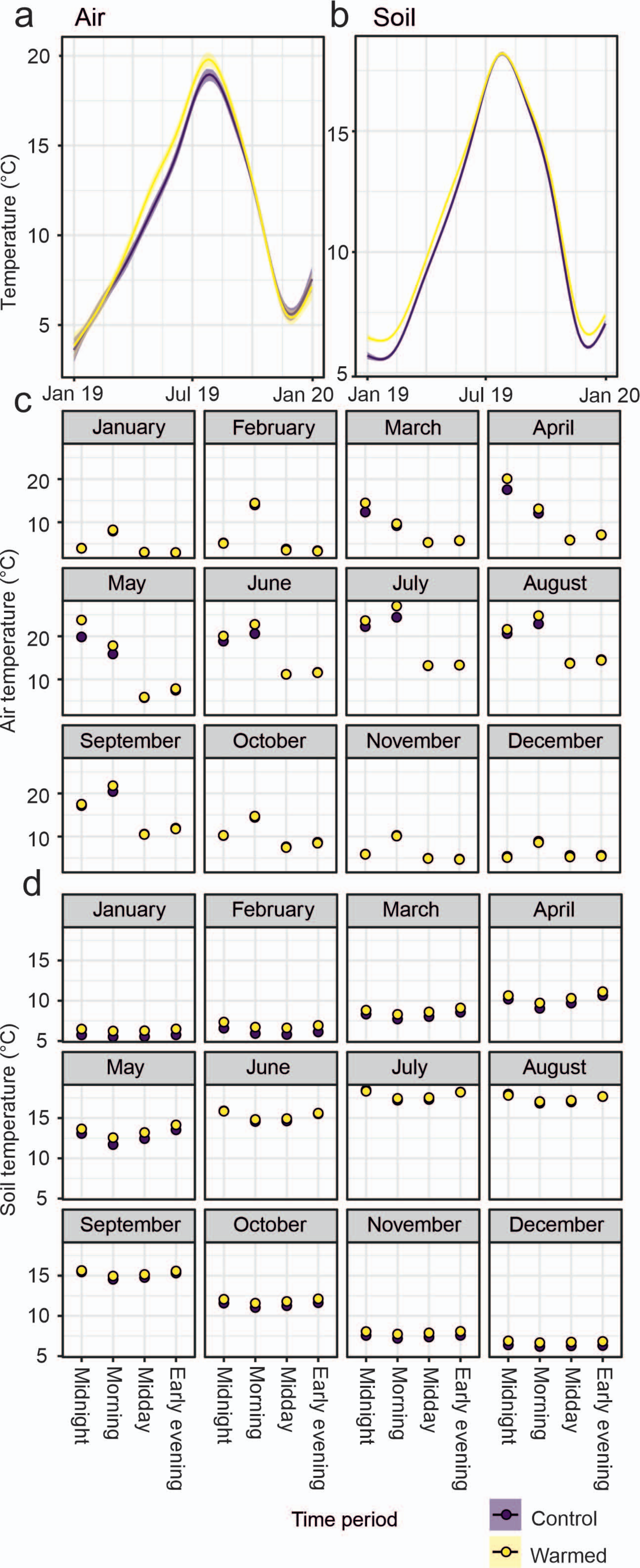
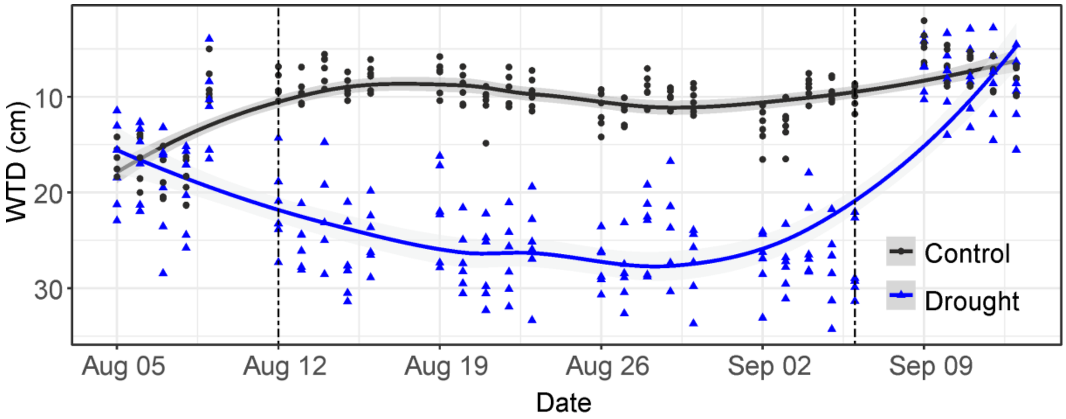

a
Air
b
Soil
Temperature (°C)
20
15
10
5
Jan 19
Jul 19
Jan 20
c
January
February
March
April
May
June
July
August
September
October
November
December
Air temperature (°C)
d
Soil temperature (°C)
Midnight
Morning
Midday
Early evening
Time period
Control
Warmed



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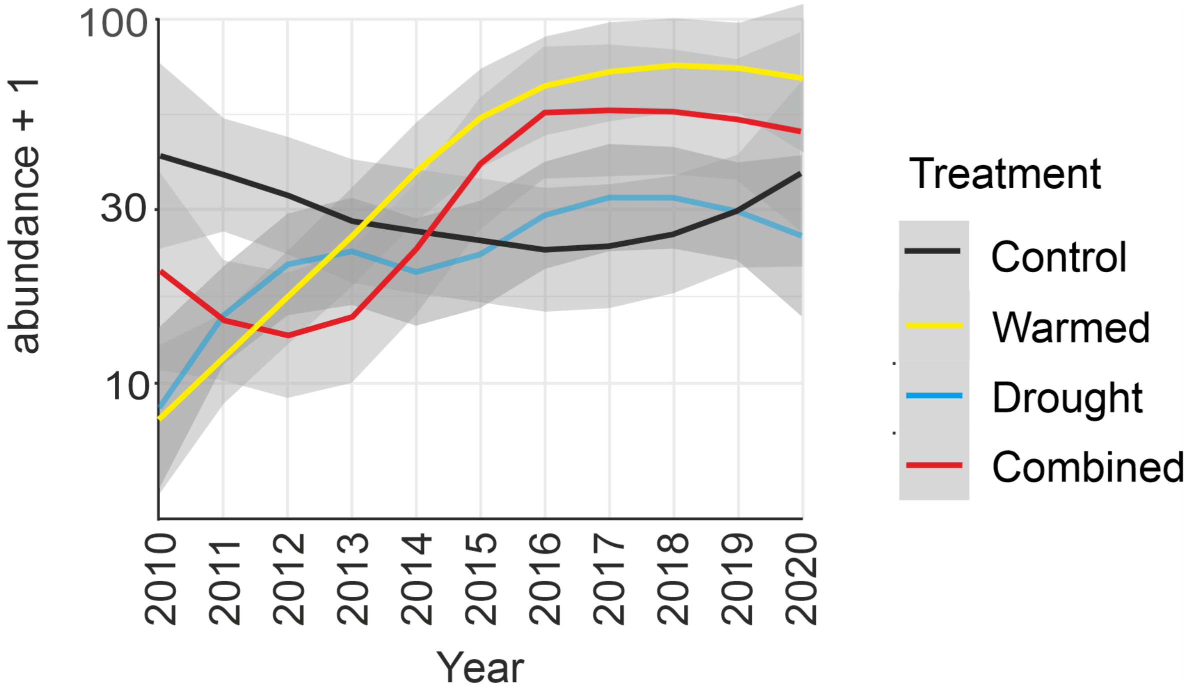

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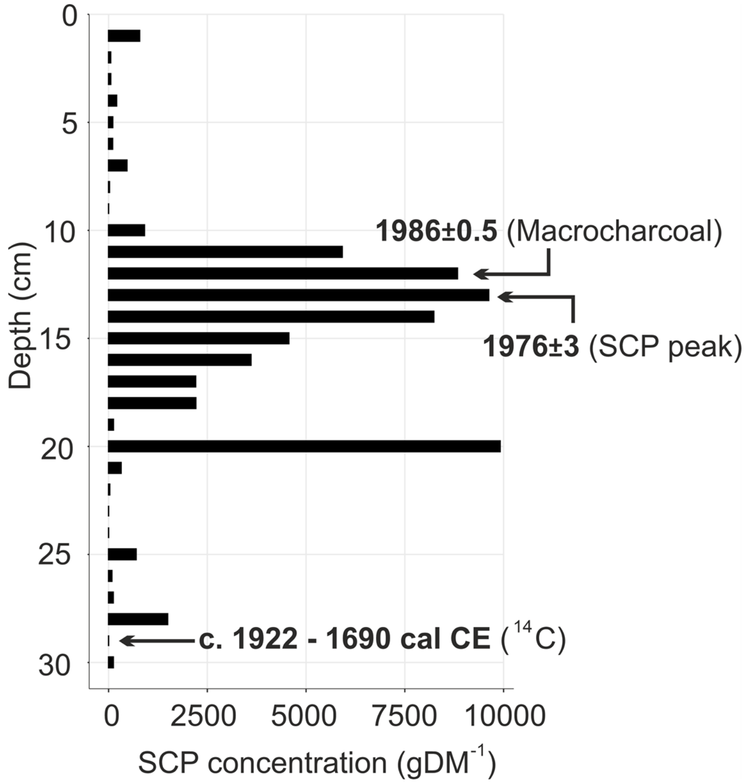

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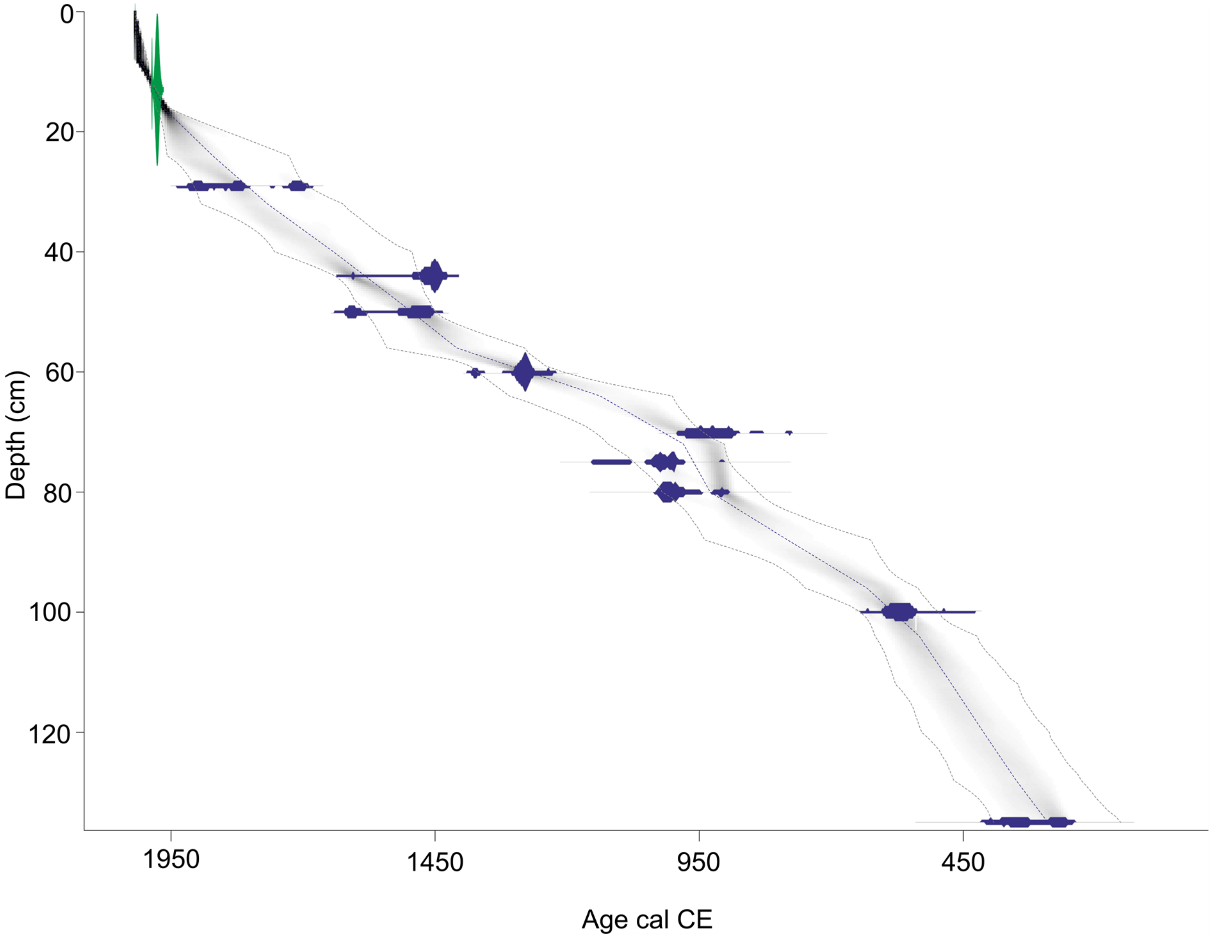

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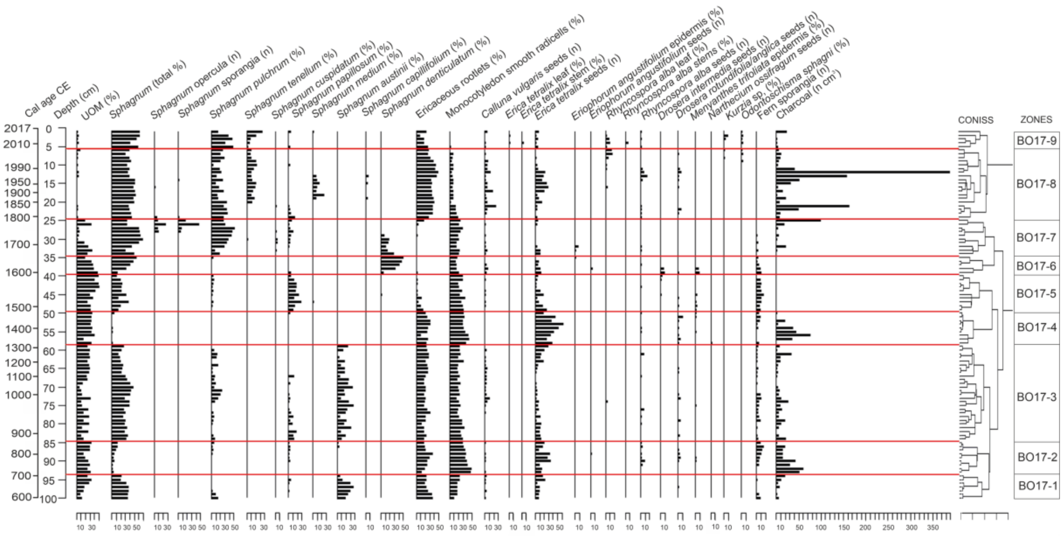

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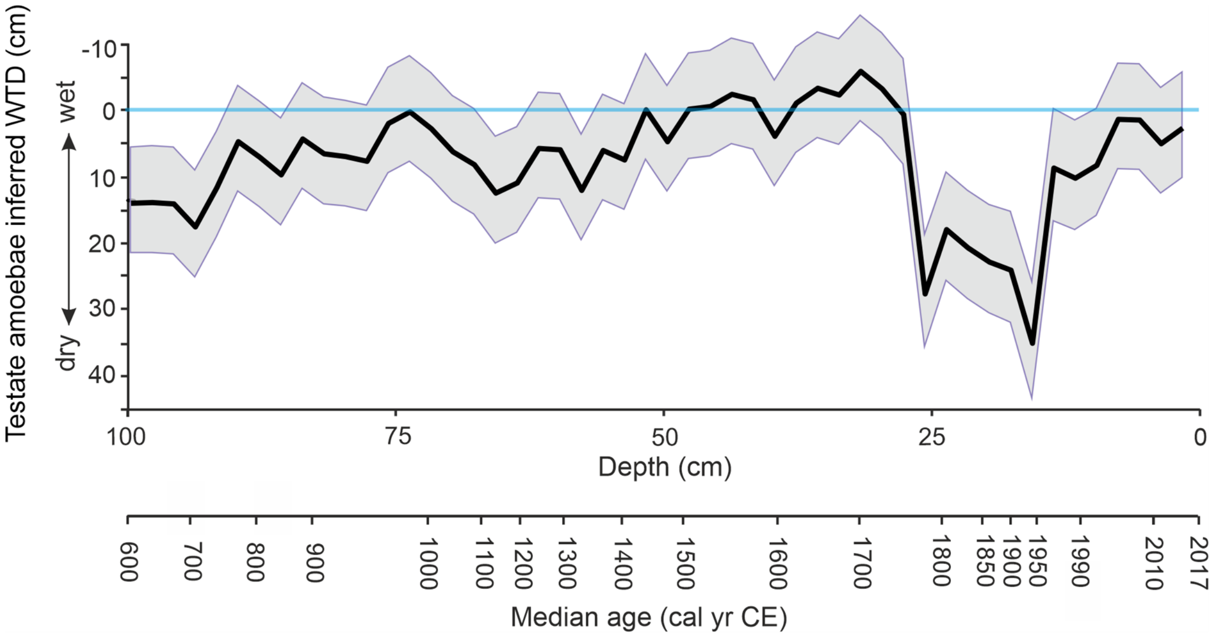

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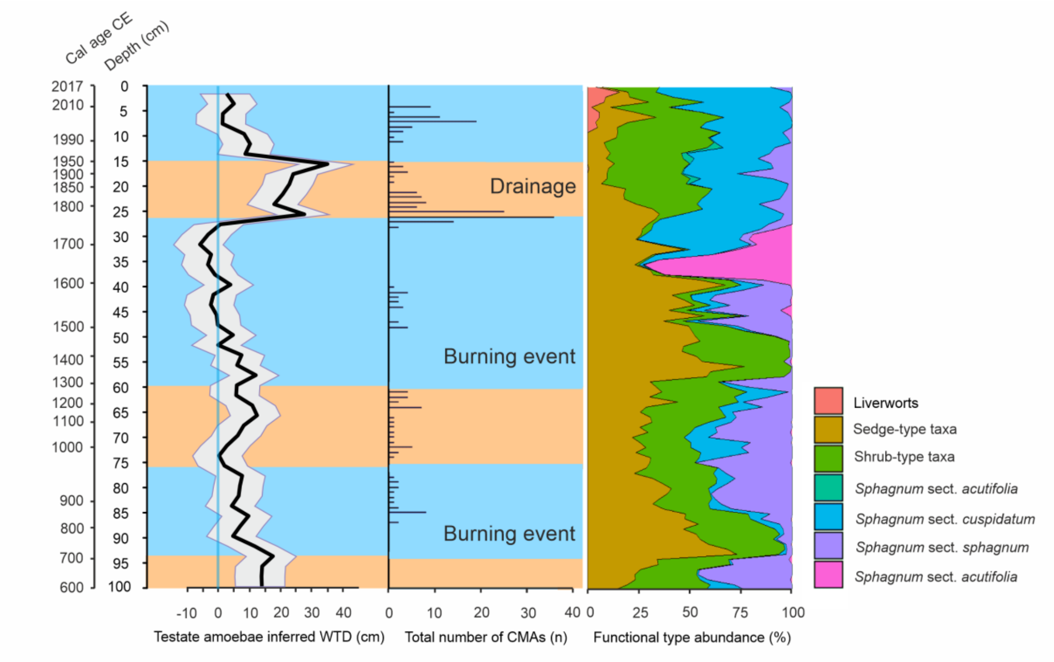

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