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The impact of alternating drainage and inundation cycles on geochemistry and microbiology of intact peat cores

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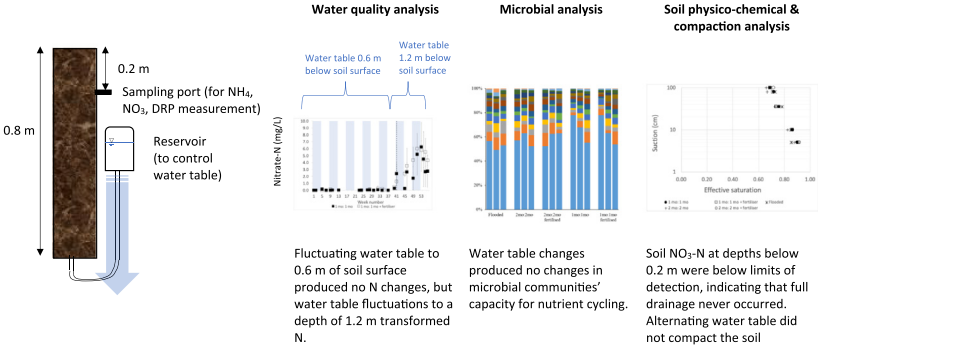
HIGHLIGHTS

- Release of nitrate in pore water may be an issue of concern in rewetted peatlands.
- Prolonged drainage and inundation periods did not compact the soil structure.
- Depth of water table may be significant in releasing nitrate after inundation.
- Longer and shorter periods of draining/inundation did not impact water quality.

GRAPHICAL ABSTRACT



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ABSTRACT

The rewetting of degraded peatlands has been adopted as a method to address climate change. Concerns have been raised about the effects of peat inundation and drying cycles, in more extreme climate events, on the potential release of nitrogen (N) species, in particular ammonium (NH_4-N), once rewetted, as well as the physico-chemical and biological properties of the peat. This study used intact peat cores to measure the impact of two different cycles of peat inundation and drying (1 month and 2 month) over a total study duration of 56 weeks on the (1) NH_4-N, nitrate-N (NO_3-N) and dissolved reactive phosphorus (DRP) in the soil pore water; (2) microbial community structure; (3) physico-chemical properties of the peat; and (4) the structure of the peat, and therefore its ability to mitigate flood risks and storm surges. The study found that rewetted cores released NO_3-N in the pore water up to a concentration of 6.25 mg L^{-1}, but had no appreciable impact on NH_4-N, which remained below 1.7 mg L^{-1} over the study duration. DRP moved quickly though the upper layers of the cores, but physico-chemical analysis suggested it was adsorbed to more iron-rich soil, which was present at depths below 0.4 m in the cores. Time intervals between inundation produced no significant difference on the forms of inorganic N released, nor did it compact the soil or change the microbial community structure. The depth of the water table, however, had a significant impact on inorganic N release, particularly NO_3-N, which indicates that this N species, and not NH_4-N, may be problematic in rewetted peatlands.

1. Introduction

Peatlands only cover between 1.2 and 2.8 % (185–423 million hectares) of the Earth's surface (Ribeiro et al., 2021), but provide a range of ecosystem

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functions including pollutant retention, water storage and flow regulation (Leifeld and Menichetti, 2018). In Europe, peatlands cover about 10 % of the total surface area (241,812 km^2) (Tanneberger et al., 2021a). The total proportion of degraded peatlands in Europe is 25 % (Tanneberger et al., 2021b). Degradation is caused mainly by artificial drainage for agriculture, peat extraction or forestry, and can lead to emissions of carbon dioxide (CO_2) and nitrous oxide (N_2O) to the atmosphere (Harris et al., 2021), biodiversity loss (Krejcová et al., 2021), and nitrate (NO_3-N) leaching to surface and groundwater (Rodriguez et al., 2021). As peatlands have been identified as potentially playing a significant role in addressing existential challenges, in particular climate change (Hompenöder et al., 2020), rewetting of peatlands has been adopted as a policy in many countries. While there is evidence of the positive impact of peatland rewetting on ecosystem services, there are also concerns over the potential negative impacts, such as methane (CH_4) emissions (which may result in net greenhouse gas emissions), phosphorus (P) and nitrogen (N) release (Forsmann and Kjaergaard, 2014; Nieminen et al., 2020).

Guidelines for the after-use rewetting of peatlands are confounded by the variable functions of the ecosystems, geochemical variability and anthropogenic activity (Monteverde et al., 2022). This makes the implementation of a universal management practice difficult. Furthermore, predicted increasing evapotranspiration, drought and more intense rainfall events due to climate change (Seneviratne et al, 2012), will change the hydrological cycle of peatlands, meaning that even if rewetted, the soil will be subject to an intensified hydrological cycle. The duration and frequency of these hydrological cycles, with their alternating aerobic and anaerobic conditions, will impact the physico-chemical properties and microbiological structure of the peat: Rewetting of peatlands quickly converts the soil environment from aerobic to anaerobic, causing denitrification or dissimilatory nitrate reduction to ammonium (DNRA), likely in a carbon-rich environment, ammonium (NH_4) release and P release (if the soil has been fertilised), and enhanced CH_4 emissions (Harpenslager et al., 2015). Drying (mainly by evapotranspiration in drought conditions) would make the soil aerobic, meaning that mineralisation and therefore N_2O release is likely (Hu et al., 2017). In addition, soil properties and water retention may be altered (Word et al., 2022) and CO_2 may be emitted.

The resilience and adaptation of the microbial community to changes in peatland management also has a significant effect on the N cycle (Van Groenigen et al., 2015), potentially increasing the N pool in peatlands, resulting in more N release to freshwater bodies. To date, N cycling has been mainly examined in tropical (Espenberg et al., 2018), baltic (Truu et al., 2020) or sub-artic (Weedon et al., 2011; Jiang et al., 2021) peatlands drained for agriculture or subject to yearly temperature fluctuations, or with N fertiliser additions (Ma et al., 2021). However, the internal cycling of N, in controlled laboratory experiments under permanently flooded, prolonged drought, and more frequent inundation and drying events is infrequently examined in the literature (Wang et al., 2016; Hu et al., 2017), as is the impact of these scenarios on the peat microbial community.

The impact of multiple rewetting and drying cycles on the soil carbon and N dynamics, microbiology and physico-chemical profile are very difficult to quantify in the field, particularly as there is often complex hydrology in field sites, variations in climatic parameters and variable geochemistry. Therefore, implementation of policy on peatland management, particularly policy relating to rewetting in a potentially changing environment, needs to be guided by empirical evidence collected in controlled experiments. Intact soil cores have been frequently used to conduct such experiments (Wang et al., 2016; Hu et al., 2017; Wen et al., 2020).

The objectives of the study were to (1) investigate the impacts of water table changes and fertiliser addition to peat soils on nutrient release and microbial activity, and (2) quantify the impact of a climate change scenario, comprising longer periods of peat inundation (through extreme flooding) and drying on water quality and physico-chemical parameters, and microbial community structure.

2. Materials and methods

2.1. Site description

The site chosen for investigation was within the Garryduff peatland in Co. Offaly (53.250245, −8.051519), in the Republic of Ireland. The site was drained and was used for industrial peat production since the 1960s. At the time of the core collection in 2020, production had ceased for one year. The water table in Garryduff was controlled by a pump, so its water table at the time of collection was significantly lower than the surrounding area. The underlying geology is dark limestone and shale, and the soils and sub-soils are classified as 'raised bog cutover peat' (Bord na Móna, 2021).

2.2. Collection of peat cores

Ground and airborne geophysical techniques (Beamish, 2014; Binley et al., 2015) were used to identify sites suitable for core extraction. Airborne radiometric data, which measures naturally occurring gamma ray intensity (Minty, 1997), can be useful at identifying intra-peat variation of physical properties (Beamish, 2014; Minasny et al, 2019). For this study radiometric data acquired over the study site were grouped together using self-organizing maps clustering (Kohonen, 2013). These groups were projected to the data spatial coordinates, which identified the study site. A ground geophysics survey, using the electromagnetic method (Boaga et al., 2020), was used to verify the thickness of the peat, prior to core extraction.

Using an Usinger piston corer (to mitigate against peat compression), with a core tube diameter of 0.08 m, a total of 18 cores were taken. Cores, each approximately 0.8 m in length, were extruded on site into PVC pipes, sealed in an airtight covering, and transported back to the laboratory, where they were stored in a temperature (10 °C) and humidity (75 %) controlled room. This is representative of the average temperature and humidity in Ireland (Walsh, 2012). Of the 18 cores, three were destructively sampled for initial physico-chemical characterisation of the peat (hereafter referred to as 'virgin' cores) and 15 were used in the experiments.

2.3. Laboratory column preparation and experimental configuration

The sides of the peat cores were fully sealed (full information at: https://youtu.be/58BzVQZZrPI). Briefly, each extruded peat core was covered in an impermeable polymer-based sealant (Bostik Waterstop, Bostik Industries Ltd., Ireland), overlain with a scrim material (to ensure structural integrity), before finally being overlaid, for a second time, with the sealant and placed in a vertical position. Headspace above each core was provided by 0.05 m deep open-ended plastic containers, sealed to the top of the cores. Each peat core was instrumented with a ceramic sampling port, located at a distance of 0.2 m from the surface, to allow pore water extraction. Drainage and rewetting of each peat core was controlled by the vertical movement of a plastic bottle, acting as a reservoir, which allowed the water table to be controlled. This replicated water table movement that might be instigated on a field site by the construction of dams and drainage blocks (Buschmann et al., 2020).

The experiment was conducted over a period of 56 weeks. The temperature and humidity were maintained at 10 °C and 75 %, respectively. Five scenarios were examined: wetting and drying cycles of one-month or two-month durations, each operated with and without the addition of a natural alkaline P fertiliser (11 % P), applied at the start of the experiment in one dose at a rate equivalent to 250 kg P ha^{-1} (commonly applied in Ireland to encourage *Sphagnum* growth in peatlands; DAFM, 2015); and continuously flooded. In the cores subject to wetting and drying cycles of 1 month durations, the total period over which the cores were saturated was 196 days, whereas in the cores subject to a wetting and drying cycles of 2 months' durations, the total duration of saturation was 224 days. Continuously flooded cores were saturated for the entire study duration (392 days). All peat cores were replicated at n = 3. The two-month cycling duration was examined to investigate what changes would occur to the

Table 1
Experimental design of peat core study.

Treatment	No. of days saturated	No. of days drained	No. of flooded cycles	No. of drained cycles
1 month: 1 month	196	196	7	7
1 month: 1 month + fertiliser	196	196	7	7
2 month: 2 month	224	168	4	3
2 month: 2 month + fertiliser	224	168	4	3
Flooded	392		–	–

physico-chemical and microbial properties of a peat core in a climate change scenario, with longer periods of flooding and drought. The experimental design is shown in Table 1.

Before the start of the experiment, all peat cores were flooded with deionized water to minimize core heterogeneity (after Hu et al., 2017). The continuously flooded cores were maintained under a flooded condition over the study duration and the remaining cores were subjected to drainage and inundation scenarios. To simulate rainfall on the columns, 80 ml of deionized water was applied weekly in two 40 ml doses over 2 h (equivalent to 829 mm of rainfall yr^{-1}, which is in the mid-range of annual rainfall amounts in Ireland) (after Troy et al., 2013). The water collected in the headspace above each core, before draining naturally over time.

For the first 40 weeks of the study, the water table in each peat core was cycled between flooded (the reservoir outlet was at the same height as the surface of the core) to drained conditions. The reservoir controlled the water table to a depth of 0.6 m below the soil surface. This was in line with typical water level fluctuations reported in Irish bogs, which reported ranges of between 0.3 and 1 m (Gill and Keegan, 2020). However, as no transformations in N species were observed, likely due to the fact that the soil remained fully saturated even under suctions of around 0.6 m, the reservoir was dropped to a distance of 1.2 m below the surface from Week 41 until the end of the experiment (Week 56) in order to desaturate the soil and facilitate air entry. Although the depth of the soil core was 0.8 m, lowering the reservoir to a depth of 1.2 m below the soil surface placed the core under tension, and therefore allowed controlled drainage to occur.

2.4. Water quality

Water samples were extracted using a syringe weekly from the pore water sampler in each core. The water samples were immediately filtered through a 0.45 μm filter membrane and tested for NH_4-N, NO_3-N and dissolved reactive P (DRP) using a nutrient analyser (Aquakem 600A/Konelab 60, Thermo Clinical Labsystems, Vantaa, Finland). All water quality parameters were tested in accordance with the standard methods (APHA, 2005).

2.5. Microbial analysis

At the end of the study, each of the peat cores were aseptically cut at 0.2 m from the top, and approximately 5 g of peat was removed for analysis of the microbial community structure. Total genomic DNA was extracted from a 0.25 g sample using the DNeasy PowerSoil Pro Kit (QIAGEN, Germantown, Maryland, US), in line with the manufacturer's guidelines. Extracted DNA was shipped on ice to NovoGene Ltd. (Cambridge, UK) for amplicon library preparation, sequencing and bioinformatics analysis. Amplicon library preparation was performed using 515F (GTGCCAGC MGCCGCGG) and 806R (GGACTACHVGGGTWTCTAAT) primers to target the V4 hypervariable region of the 16S rRNA gene. The polymerase chain reaction (PCR) reactions were conducted with a Phusion® High-Fidelity PCR

Table 2
Average (± standard deviation) soil physico-chemical properties at depth increments of 0–0.2 m, 0.2–0.4 m, and 0.4–0.8 m from the surface at the start ('Virgin cores') and at the end of the experiment for each treatment (flooded, 2 mo inundated: 2 mo drained [with and without fertiliser addition], 1 mo inundated: 1 mo drained [with and without fertiliser addition]).

Parameter	Units	Depth increment (m)	Virgin cores[a]	Flooded	2 mo: 2 mo	2 mo: 2 mo + fertiliser	1 mo: 1 mo	1 mo: 1 mo + fertiliser
		0–0.2	91.4 ± 5.2	87.2 ± 2.9	82.7 ± 6.6	86.9 ± 1.8	87.3 ± 0.2	87.3 ± 1.5
Organic matter	% w/w	0.2–0.4	87.4 ± 5.9	84.4 ± 2.8	86.1 ± 0.4	86.3 ± 0.5	84.0 ± 3.8	85.6 ± 1.0
		0.4–0.8	87.8 ± 9.5	71.9 ± 2.1	78.6 ± 7.2	72.4 ± 0.7	73.6 ± 1.0	73.2 ± 0.7
		0–0.2	1.7 ± 0.7	2.1 ± 0.1	1.7 ± 0.2	1.8 ± 0.3	2.4 ± 0.1	2.2 ± 0.1
Total nitrogen	% w/w	0.2–0.4	1.6 ± 0.2	1.5 ± 0.1	1.7 ± 0.3	1.6 ± 0.3	2.2 ± 0.2	2.1 ± 0.1
		0.4–0.8	2.5 ± 0.7	2.9 ± 0.3	2.8 ± 0.2	3.1 ± 0.0	3.0 ± 0.1	3.0 ± 0.1
		0–0.2	57.8 ± 25.0	39.9 ± 25.1	22.4 ± 9.4	6.3 ± 0.4	16.9 ± 19.9	7.1 ± 0.4
Ammonium	mg kg^{-1}	0.2–0.4	137.1 ± 98.9	57.7 ± 8.8	50.9 ± 6.6	46.5 ± 14.2	71.7 ± 14.4	61.2 ± 6.9
		0.4–0.8	385.0 ± 127.2	61.2 ± 32.1	89.3 ± 9.2	57.9 ± 40.3	92.2 ± 7.0	73.7 ± 33.0
		0–0.2	<1	<1	32.2 ± 10.2	18.9 ± 8.1	31.7 ± 5.2	17.4 ± 5.9
Nitrate	mg kg^{-1}	0.2–0.4	<1	<1	<1	<1	<1	<1
		0.4–0.8	<1	<1	<1	<1	<1	<1
		0–0.2	8.9 ± 9.4	2.9 ± 0.8	3.6 ± 0.9	3.6 ± 0.8	3.1 ± 0.5	3.2 ± 0.45
Total iron	g kg^{-1}	0.2–0.4	2.6 ± 1.5	9.2 ± 3.0	6.1 ± 0.2	5.7 ± 0.3	7.6 ± 2.7	7.5 ± 2.9
		0.4–0.8	2.7 ± 2.1	13.9 ± 2.0	12.9 ± 2.4	14.3 ± 1.0	13.0 ± 0.5	13.9 ± 0.9
		0–0.2	17.8 ± 6,2	26.1 ± 0.9	26.4 ± 2.0	25.6 ± 2.3	25.6 ± 1.0	24.2 ± 1.1
Total calcium	g kg^{-1}	0.2–0.4	16.6 ± 1.6	26.3 ± 1.6	28.4 ± 0.2	27.4 ± 1.9	25.8 ± 4.2	26.5 ± 3.1
		0.4–0.8	17.7 ± 7.5	15.8 ± 0.5	17.1 ± 0.2	15.7 ± 1.0	16.9 ± 0.2	17.7 ± 1.5
		0–0.2	0.90 ± 0.77	0.52 ± 0.1	0.46 ± 0.0	0.5 ± 0.0	0.46 ± 0.0	0.43 ± 0.0
Total magnesium	g kg^{-1}	0.2–0.4	0.53 ± 0.07	0.42 ± 0.1	0.40 ± 0.0	0.41 ± 0.0	0.4 ± 0.1	0.4 ± 0.0
		0.4–0.8	0.46 ± 0.05	0.58 ± 0.0	0.53 ± 0.0	0.56 ± 0.0	0.53 ± 0.0	0.54 ± 0.0
		0–0.2	0.29 ± 0.16	0.15 ± 0.0	0.16 ± 0.0	0.17 ± 0.0	0.16 ± 0.0	0.15 ± 0.0
Total phosphorus	g kg^{-1}	0.2–0.4	0.19 ± 0.02	0.16 ± 0.0	0.16 ± 0.0	0.16 ± 0.0	0.17 ± 0.0	0.17 ± 0.0
		0.4–0.8	0.23 ± 0.05	0.27 ± 0.0	0.25 ± 0.0	0.26 ± 0.0	0.26 ± 0.0	0.27 ± 0.0
		0–0.2	0.24 ± 0.19	0.07 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.07 ± 0.0
Total potassium	g kg^{-1}	0.2–0.4	0.11 ± 0.03	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
		0.4–0.8	0.15 ± 0.06	0.36 ± 0.0	0.4 ± 0.0	0.38 ± 0.0	0.37 ± 0.0	0.4 ± 0.0
		0–0.2	44.4 ± 5.2	47.1 ± 1.0	46.7 ± 0.3	46.3 ± 1.7	46.6 ± 0.6	47.3 ± 0.5
Total carbon	mg kg^{-1}	0.2–0.4	47.8 ± 0.8	47.4 ± 3.3	46.2 ± 2.5	46.8 ± 0.6	48.6 ± 6.4	45.9 ± 0.2
		0.4–0.8	45.8 ± 5.7	42.2 ± 3.7	40.7 ± 0.2	39.2 ± 0.5	39.6 ± 0.2	39.5 ± 1.4
		0–0.2	27.7 ± 8.3	22.6 ± 1.3	27.6 ± 2.7	26.3 ± 3.9	19.7 ± 0.6	20.9 ± 1.2
Carbon:nitrogen	:1	0.2–0.4	29.4 ± 3.6	30.3 ± 0.4	28.7 ± 5.7	28.9 ± 6.1	17.5 ± 4.5	21.3 ± 1.1
		0.4–0.8	18.3 ± 6.1	14.2 ± 1.8	14.3 ± 1.1	12.8 ± 0.0	13.1 ± 0.4	13.1 ± 0.7

[a] Virgin cores refer to peat cores that were destructively sampled at the start of the experiment for physico-chemical analysis.

Master Mix (New England Biolabs). Amplicon Sequencing using the Illumina NovaSeq PE250 platform (Illumina Inc. USA), was utilized to sequence the extracted DNA to a depth of 30 K tags of raw data per sample. Sequence analysis was performed using Uparse software (Uparse v7.0.1001). Sequences with ≥97 % similarity were given the same Operational Taxonomic Units (OTUs). OTU abundance information was normalized using the sample with the least sequences (93,313). Analysis of alpha and beta diversity was conducted using these normalized data in order to assess diversity within and between individual samples, respectively. Alpha Diversity Indices were calculated with QIIME (Version 1.7.0). Although ACE and Chao1 both relate to community richness, ACE estimates the total number of species using the sum of probability of observed species, while Chao1 gives more weight to low abundance species (Kim et al., 2017). Shannon and Simpson both assess community diversity, which is based on species richness and evenness, although Shannon places greater emphasis on richness, while Simpson places greater emphasis on evenness (Kim et al., 2017). Finally, Goods coverage was included to assess for sequencing depth, and ensure that the dataset sufficiently represents the true diversity of the microbial community (Kim et al., 2017).

2.6. Soil physico-chemical analysis

At the end of the study, all 15 peat cores were split into three depth increments (0 to 0.2 m from the soil surface, 0.2–0.4 m, and 0.4 m to 0.8 m) and destructively sampled for organic matter (OM) content by loss on ignition at 500 °C (BSI, 1990). Total phosphorus (TP), potassium (K), magnesium (Mg) and calcium (Ca) were measured using an inductively coupled plasma optical emission spectrometer (Agilent 5100 ICP-OES) and total carbon and nitrogen were measured using a high temperature combustion analyser (LECO TruSpec CN analyser). Plant available N (NO_3-N and NH_4-N) was measured colourimetrically on a potassium extract using an Aquakem 600 Discrete Analyser. The P absorbency of each depth increment in the virgin cores was measured using the methodology described in Callery et al. (2015).

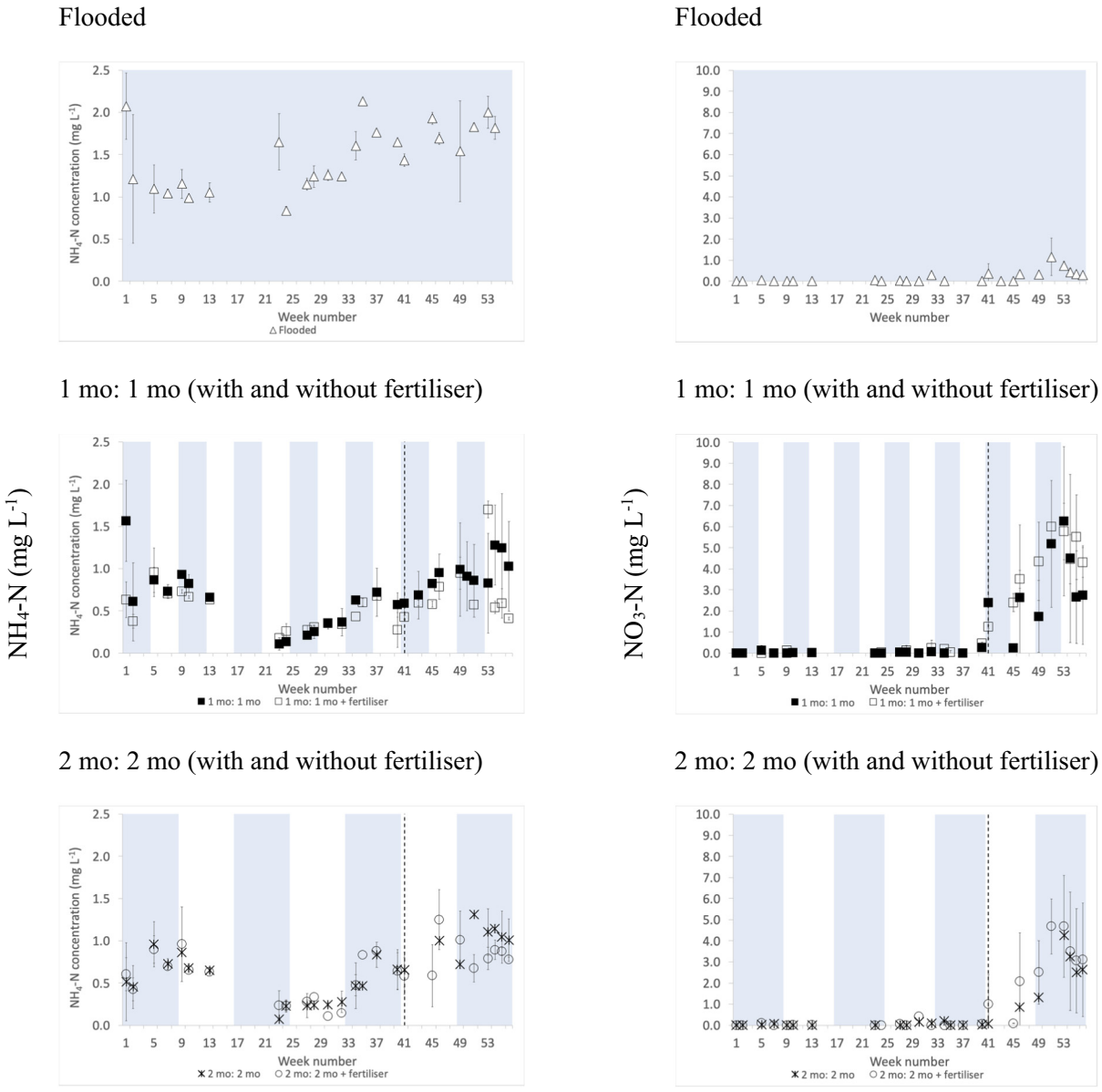

Fig. 1. Variation in mean ammonium (NH_4-N) and nitrate-N (NO_3-N) for each treatment (flooded, 2 months inundated: 2 months drained [with and without fertiliser addition], 1 month inundated: 1 month drained [with and without fertiliser addition]) at a depth of 0.2 m below the soil surface over the 56-week study duration. DRP omitted as concentrations were below LOD. Periods of inundation indicated by shaded area. Hatched vertical line at week 41 indicates time that water table was lowered from a depth of 0.6 m below the soil surface to 1.2 m below the soil surface.

2.7. Soil compaction

The impact of the draining and inundation cycles on water retention (and therefore compaction) was measured by developing a soil water characteristic curve (a graph of volumetric water content, θs, versus soil suction) at approximately the mid-point in each peat core replicate. Briefly, stainless steel tubes, each measuring 23 mm (diameter) × 70 mm high, were used to obtain intact soil cores from each treatment. The samples were then saturated and suctions were applied using a SIGMA 4-16KS centrifuge, from which a relationship could be developed between centrifugation velocity, suction and volumetric water content (Vero et al., 2016). To account for small differences in initial volumetric content, the volumetric water contents were expressed as fractions of the θs.

2.8. Statistical analysis

Data for the elemental analysis of TP were tested for normality using a Shapiro-Wilk test and homogeneity of variance using Levine's test. Following confirmation of normality and homogeneity, the data were analysed using one-way analysis of variance (ANOVA). For the microbial analysis, Unweighted Pair-group Method with Arithmetic Mean Clustering was used for the interpretation of the distance matrix using QIIME software (Version 1.7.0). Significant differences between samples based on alpha or beta diversity were assessed using the pairwise Mann-Whitney Wilcoxon rank-sum test (Mann and Whitney, 1947; Wilcoxon, 1943).

3. Results and discussion

3.1. Elemental content

The Ca, Mg, K, and TP contents of the cores were similar across all depth increments (Table 2) and were consistent with those recorded in drained minerogenic peatlands across Europe (Haapalehto et al., 2015; Raudina and Loiko, 2019; Negassa et al., 2020). There was no significant difference in TP in the upper 0.4 m of the cores ($p < 0.05$), including those to which the P fertiliser was applied. Iron, an element associated with the physical adsorption of P (Harpenslager et al., 2015), was also low in this depth increment, ranging from 2.9 to 9.2 g kg^{-1}, as was the P adsorption capacity (0.5–6.2 mg P kg^{-1} dry weight). The high Fe:P ratio in the 0.4–0.8 m depth increment, ranging from 50:1 to 54:1, indicated that P would not be released under anoxic conditions (Gu et al., 2019).

Inorganic N measurements indicated that NH_4-N was more abundant than NO_3-N at all depth increments in the virgin cores (Table 2). This was attributable to the fact that these cores were drained, meaning that mineralisation of organic N had already occurred by the start of the experiment. At the end of the study, the NO_3-N content at depths below 0.2 m in all cores that were subject to intermittent drainage was below the limits of detection (<1 mg kg^{-1}). This indicated that despite attempts to fully drain the columns by lowering the water table to 1.2 m below the soil surface from week 41 onwards, full drainage of the columns never occurred.

3.2. Pore water nitrogen

Ammonium-N and NO_3-N pore water concentrations, collected at a depth of 0.2 m below the peat surface, are shown in Fig. 1. Before week 41 alternating inundation and draining periods had no impact on the N species examined: NH_4-N varied between the limits of detection (LoD) and 1.7 mg L^{-1}, and NO_3-N varied between the LoD and 2.4 mg L^{-1} (just below the guideline limit of 2.6 mg NO_3-N L^{-1} for discharge to estuaries; EPA, 2021). This may have been due to the capillary fringe of the peat, which may have maintained sufficient moisture in the peat such that oxygen transfer may have been inadequate for the occurrence of significant ammonification or nitrification (Fig. 2). The peatland from which the intact cores were extracted was drained, which likely resulted in the mineralisation of organic matter (Zak et al., 2021), so the initial flooding of the laboratory columns caused a washout (to a limited extent) of NH_4-N in all peat cores at the start of the study. Despite this, the NH_4-N concentration in the continuously flooded cores remained consistently higher than the other cores over the study duration, indicating that net N mineralisation rates may have persisted after rewetting – a characteristic that has been observed in other studies (Venterink et al., 2002).

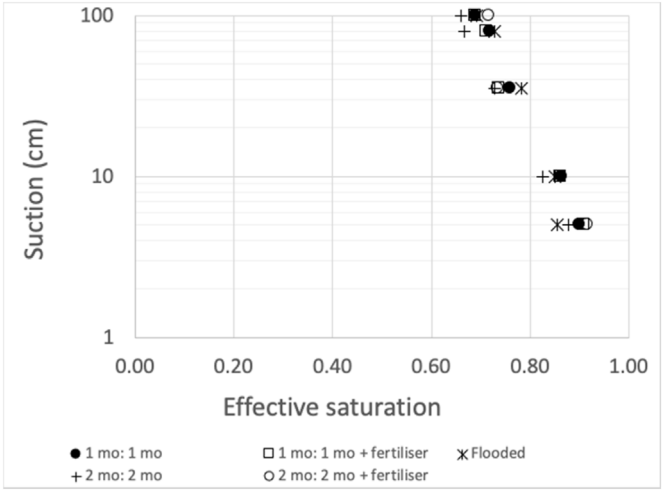

Fig. 2. Soil water characteristic curve, presented a plot of average effective saturation versus suction (cm) for the each treatment (flooded, 2 months inundated: 2 months drained [with and without fertiliser addition], 1 month inundated: 1 month drained [with and without fertiliser addition]).

Nitrogen transformations during the longer (2 month) and shorter (1 month) periods of inundation and drainage were of the same order of magnitude, but the depth of the drainage channels, normally used to control the water table in peatlands, may have an impact on inorganic N loss in peatlands: Lowering of the water table to a depth of 1.2 m of the peat surface drained the uppermost layers such that adequate oxygen entered the peat (Fig. 2). This had no impact on NH_4-N concentration, but produced a moderate increase in the concentration of NO_3-N (maxima before the water table change was just above the LOD, but was 6.25 mg L^{-1} after the change). The pore water sampling depth was 0.2 m below the peat surface, so the NO_3-N concentrations in the pore water may have been lower at depths below 0.2 m. The periods of drainage and inundation were relatively short in this study, but other studies have suggested that longer periods of drought may cause NH_4-N to build up in the peat, before it is released under inundated conditions (Wang et al., 2016). Indeed, inorganic N release, primarily as NH_4-N, has been observed in the rewetting and restoration of peatlands (Wen et al., 2020), but the current study indicated that the issue of environmental concern, certainly in the first 56 week of re-wetting, may be potentially NO_3-N release instead. This is supported by the NO_3-N content in the upper 0.2 m of the peat of the drained cores, which ranged from 17 to 32 mg kg^{-1} (Table 2). Macrae et al. (2013) also found low mineralisation rates and only modest increases in KCl-extractable NO_3 in peat with an artificially lowered water table position in a bog and fen in Canada and speculated that this may be due to an increased microbial demand for N, a process known as microbial immobilisation, which normally occurs in soils with C:N ratios >15–20 (Weintraub and Schimel, 2003). This may have occurred in the current study, as the C:N ratio of the peat was >19 in the upper layers of the column (Table 2).

3.3. Changes in physical and microbiological characteristics

A hypothesis of the current work was that prolonged periods of flooding and varying periods of drainage and inundation alters the compaction of the soil and therefore its ability to transform N. The soil water characteristic curve, which as well as characterising the water holding capacity of the soil, may also be used to indicate whether compaction has occurred. The results indicated that the hydrological conditions pertaining in this study had no

Table 3
Alpha diversity indices (mean ± SE, n = 3).

	Raw reads	Processed reads	OTUs	Goods coverage
Flooded	106,599 ± 3584	81,708 ± 245,124	2418 ± 135	99.2 ± 0.06
1 month:1 month	113,340 ± 2663	91,399 ± 274,198	2591 ± 170	99.2 ± 0.06
1 month:1 month fertilised	109,919 ± 3884	89,073 ± 267,220	2661 ± 274	99.1 ± 0.06
2 months:2 months	102,994 ± 6225	77,225 ± 231,676	2542 ± 173	99.4 ± 0.06
2 months:2 months fertilised	114,091 ± 2932	92,350 ± 277,050	2458 ± 219	99.2 ± 0.06

impact on compaction (Fig. 2). This implies that flow paths in a peatland, subject to drainage and inundation conditions similar to the current study, may remain unchanged. Compaction of peat due to drainage is well reported in the literature (Motorin et al., 2017; Liu et al., 2020), but to the best of our knowledge the impacts of alternating drainage and inundation cycles have not been explored to date. The methodology used in this study to measure the soil water characteristic curve is one of many laboratory approaches used in the literature (ASTM, 2016; Dexter et al., 2012; Smagin, 2011). This curve is a function of soil texture and is dependent on the conditions to which the soil has been subjected (Table 1).

Following trimming and quality control, a total of 1,295,268 sequences (79 % of the 1,640,828 total raw sequences) were obtained from the fifteen individual samples, which corresponded to between 72,504 and 97,299 sequences per sample (mean ± SE [n = 15] = 86,351 ± 1891; Table 3). Sequences represented between 2090 and 3038 OTUs per sample (2534 ± 79; Table 3), with an average length of 253 bp. Although the number of sequences were lower than that reported in other studies using similar sequencing approaches (2.5 and 3.4 million; Chroňáková et al., 2019 and Emsens et al., 2020, respectively), goods coverage (> 99.1 %; Table 3) and rarefaction curves (Fig. S1, Supplementary Information) confirmed that the sampling depth and sequence coverage were sufficient to describe the diversity of the microbial communities present in the samples from the peat cores. No significant differences ($p > 0.05$) in alpha diversity measures, including species richness (ACE and Chao1), Simpsons evenness and Shannon diversity, were observed within samples from different treatments (Fig. 3 A-D, respectively). Furthermore, the richness and diversity, as measured by Chao1 and Shannon indices, respectively, were similar to other studies reporting microbial communities in peatlands (Chroňáková et al., 2019).

Unweighted UniFrac analysis showed no significant differences ($p > 0.05$) in Beta diversity between treatments (Fig. 4A). As unweighted UniFrac distance only considers the presence/absence of taxa within a sample, this metric gives greater emphasis to the impact of less abundant

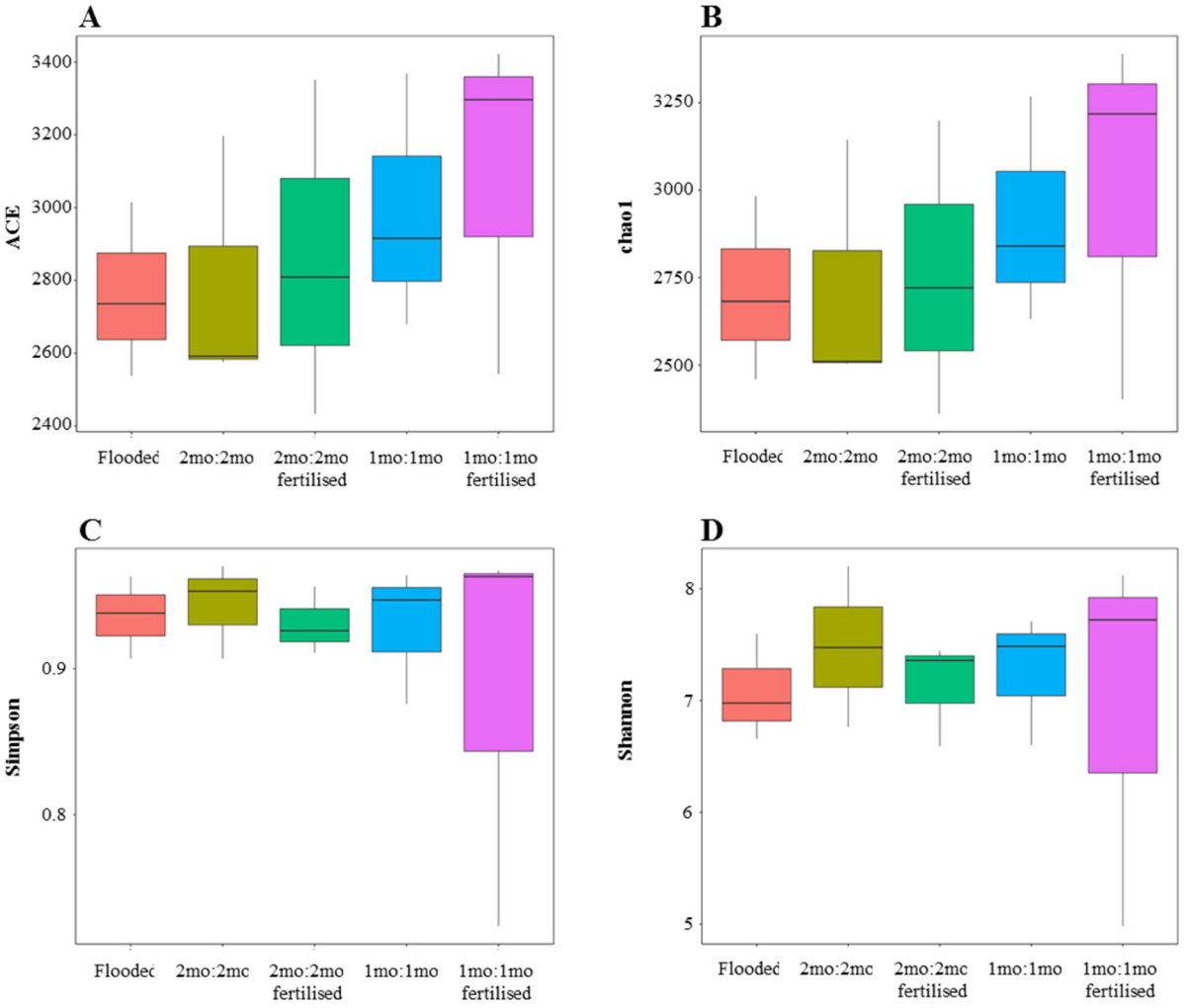

Fig. 3. Alpha diversity measures for richness and diversity, where high ACE (A) and high Chao1 (B) are indicative of high richness, and low Simpson (C) and high Shannon index (D) are indicative of high diversity within samples.

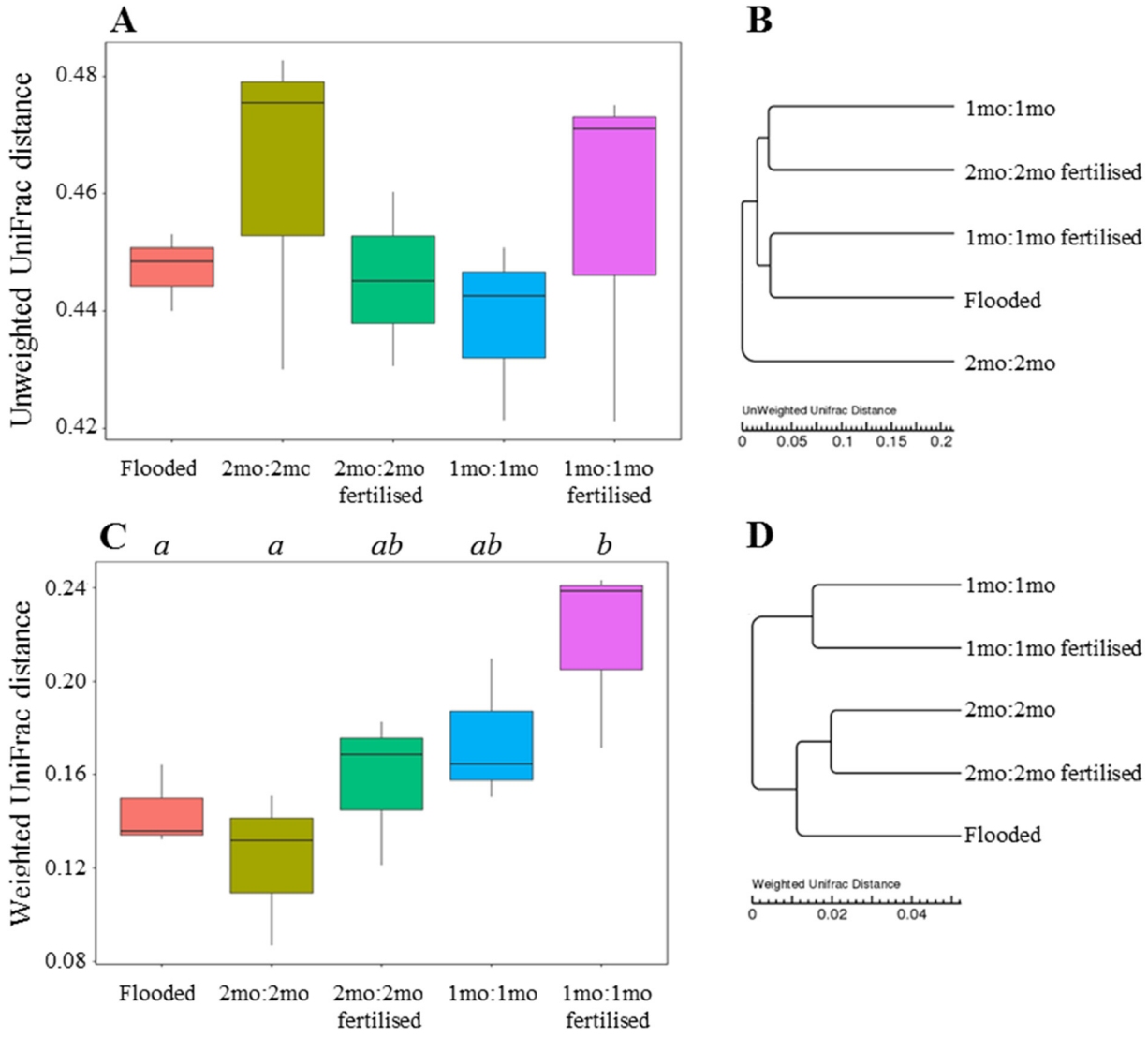

Fig. 4. Unweighted and weighted UniFrac distance (A and C, respectively) and UPGMA clustering at phylum level (B and D, respectively) for microbial communities from peat cores with different flooding treatments. The lower case (a, ab, b) over 4C denote statistical significance between samples. No significant differences were observed for Unweighted Unifrac distance (Section 4A).

organisms, which are more likely to be removed from a community as a result of changes in environmental conditions (Lozupone and Knight, 2005). However, this was not the case in our study and low abundance taxa were not significantly impacted by either the flooding regime or fertiliser application, as confirmed by UPGMA clustering of treatments (Fig. 4B). On the contrary, weighted UniFrac distance considers the relative abundance of taxa in addition to presence/absence, and is thereby more heavily influenced by the higher abundance taxa within a sample that are likely to change in abundance but persist in the community regardless of varying environmental conditions (Lozupone et al., 2007). Using the weighted UniFrac distance (Fig. 4C), significant differences were observed in the overall microbial community structures between the continuously flooded and 1mo:1mo fertilised treatments ($p = 0.0205$), and also between the 1mo:1mo fertilised and 2mo:2mo treatments ($p = 0.0061$). UPGMA analysis demonstrated that by using weighted UniFrac distance, samples clustered by flooding cycle length rather than fertiliser application, due to the response of the more abundant taxa in the peat microbial communities to the experimental conditions (Fig. 4D). Consequently, further discussion of the structure of the microbial communities focusses on the top 10 dominant taxa within any phylogeny level.

The samples were dominated by bacteria at kingdom level, representing between 86 % and 97 % of the microbial communities, while archaea represented 3–13 %, with a small proportion of OTUs (< 0.05 %) unassigned at kingdom level. Phylum level taxonomic assignments revealed the dominance of Proteobacteria, representing 45–54 % of the microbial community in all samples, as well as ca. 5 % each of Bacteroidota, Plantomycetota, Acidobacteriota, Crenarchaeota, Firmicutes, Spirochaetota and Chloroflexi (Fig. 5). Both Proteobacteria and Bacteroidota are fast growing phyla, that favour the presence of highly available carbon and organic matter sources (Wang et al., 2019; Bai et al., 2017). Organic matter was abundant in all of the peat columns in our study, at between 83 and 87 % of the wet weight content (Table 2), which is well above the 70 % threshold for peat soils (Kazemian, 2018).

Within the dominant Proteobacteria phylum, bacteria were primarily members of the Burkholderiales order (Fig. 6; data in Supplementary Material), which are associated with degradation of dead and decaying organic matter (Coenye, 2014). Interestingly, Burkholderiales are obligate aerobes (Coenye, 2014), indicating that dissolved oxygen was available at 0.2 m depth in all cores regardless of flooding treatment. Within the Burkholderiales order, all samples contained multiple autotrophic ammonia and nitrite oxidising bacterial genera, specifically GOUTA6, IS-44, MND1, Ellin6067 and Nitrosospira (all ammonia oxidisers) and Candidatus Nitrotoga (nitrite oxidiser), which collectively represented between 3.5 and 4.8 % of the microbial communities of each sample (data not shown). This indicates the microbial

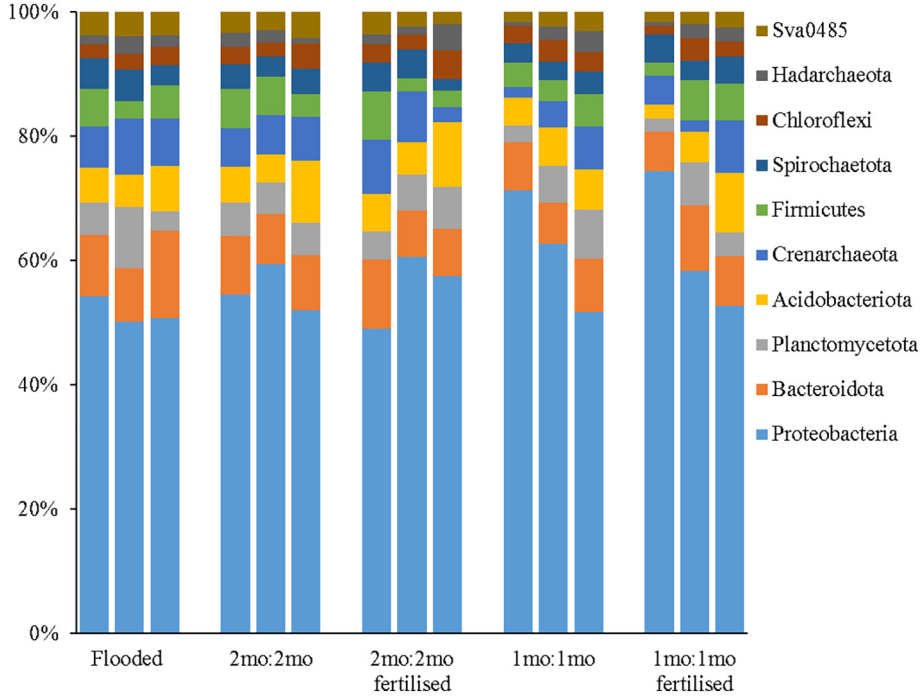

Fig. 5. Microbial community structure of ten dominant bacterial phyla.

communities within each of the peat cores maintained the ability to carry out nitrification regardless of the flooding regime applied by retaining key taxa within the system. The retention of nitrifiying species during anoxic/oxic cycling has previously been demonstrated in wastewater treatment (Ge et al., 2014; Yang and Yang, 2011), which showed that nitrite oxidation is slower to recover than ammonium oxidation when transitioning from anoxic to oxic conditions.

Samples consistently contained 7–10 % of the Bacteroidota phylum (Fig. 5), regardless of treatment, although the structure at lower phylogenic levels demonstrated some variances that may have been related to the applied flooding regimes. Specifically, the order Ignavibacteriales dominated the Bacteroidota within the continuously flooded cores (Fig. 6), representing 46–58 % of the total Bacteroidota phylum. The 2mo:2mo treatment, irrespective of fertiliser application, resulted in a decrease in Ignavibacteriales to 25–51 % with a corresponding increase in the order Bacteroidales (Fig. 6). The proportion of Ignavibacteriales decreased further (24–32 %) in the 1mo:1mo treatments, again irrespective of fertiliser application (Fig. 6). Ignavibacteriales are obligate anaerobes, while Bacteroidales were represented by a highly diverse range of genera representing both aerobic and anaerobic respiration preferences. The decrease in, but not loss of, Ignavibacteriales from cores where drainage would have induced oxidative stress, indicates that the microbial community was highly resilient to the impact of the treatments, and could recover once favourable conditions were restored.

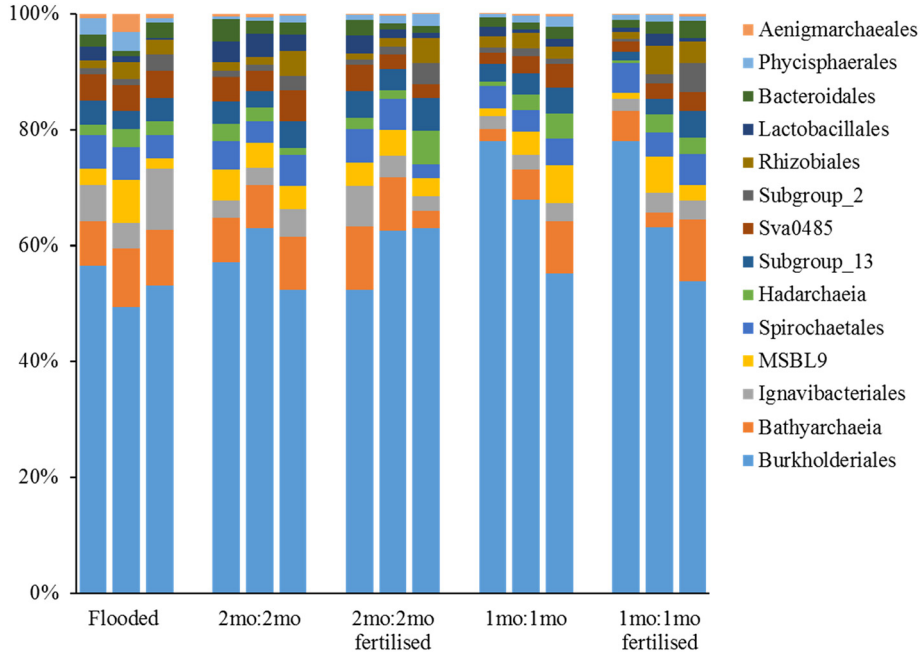

Fig. 6. Microbial Community Structure at Order level, including all orders representing >1 % of the total microbial community within any given sample.

Overall, the changes in microbial community structure associated with the treatments were not sufficient to impact on the communities' capacity for nutrient cycling once the required metabolic conditions were restored.

4. Conclusions

Peatland management requires careful land and water management to reduce the negative impacts on water resources. Management practices such as water table control and controlled flooding are commonly used methods, but any potential benefits may be confounded by existential pressures such as prolonged periods of drought and flooding, which may produce elevated levels of inorganic nitrogen in pore (and surface) water and compact the peat. This study found that there was no significant difference in inorganic N release between longer and shorter periods of inundation and drainage, but found that the depth of the water table may be significant releasing NO_3-N in the pore water, once inundation occurs. Alternating water table fluctuations between the surface and 60 cm of the surface produced no change in pore water N, but fluctuations to a depth of 1.2 m of the surface transformed N. Release of NH_4-N is often cited as an environmental concern once peatland is inundated, but this study indicates that the main issue of concern may be NO_3-N.

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CRediT authorship contribution statement

M.G. Healy: Conceptualization; Funding acquisition; Investigation; Methodology; Validation; Visualization; Writing – review & editing. **A. Siggins:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Roles/Writing – original draft; Writing – review & editing. **K. Molloy:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Roles/Writing – original draft; Writing – review & editing. **A.P. Polito:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Roles/Writing – original draft; Writing – review & editing. **E. Daly:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Roles/Writing – original draft; Writing – review & editing. **D. O'Leary:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Validation; Visualization; Roles/Writing – original draft; Writing – review & editing. **O. Callery:** Conceptualization; Funding acquisition; Investigation; Methodology; Validation; Visualization; Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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