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Research article

Testate amoeba functional traits and indicator taxa are important tools for tracking peatland restoration effectiveness

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ABSTRACT

Restoring degraded peatlands is vital for sustaining their capacity as carbon sinks and long-term carbon stores. Microbial assemblages serve as valuable indicators for monitoring environmental change and assessing the success of ecosystem restoration efforts. Testate amoebae are a group of unicellular shelled protists that are commonly used for Holocene palaeohydrological reconstruction in peatlands. While progress is being made, the use of testate amoebae for biomonitoring in peatland restoration is still in its early stages. The aim of this study is to assess testate amoebae response to restoration measures (drain blocking) across three lowland raised bogs in Northern Ireland. To accomplish this, *Sphagnum* samples were collected from each site using a before-after control-impact (BACI) experimental design. After peatland drainage ditches were blocked, subtle yet significant responses in testate amoebae were observed: (1) key unambiguous wet-indicator taxa became more abundant in samples adjacent to blocked dams; (2) a widespread increase in the abundance of taxa with sub-spherical tests was observed, most notably in samples near to blocked drains. The findings of this study demonstrate the reliable response of testate amoebae to wetter conditions across all sites after restoration. Functional trait analysis paired with an indicator-taxa based approach, demonstrate the value of testate amoebae as contemporary bioindicators for tracking peatland restoration success, even when detailed hydrological monitoring data is not available. However, testate amoebae should be used with some degree of caution for peatland biomonitoring until long-term assemblage-level response to restoration is better understood.

1. Introduction

Peatlands are critically at risk due to both historic and contemporary exploitation (Chapman et al., 2003; Page and Baird, 2016). Peatlands have been extensively damaged by activities such as drainage, peat cutting, burning, and land conversion for agriculture and forestry (O'Sullivan, 2007; Historic England, 2021). Peatland drainage is one of the most pervasive of these threats, and can enable large-scale mechanised peat harvesting, plantation forestry, and conversion to agricultural land (Graf and Rochefort, 2016; Turan et al., 2018). Up to half of all historic peatlands in western European have been lost due to these activities (Spiers, 1999; Andersen et al., 2017). Peat extraction on a wider scale began in Europe between the 13th – 17th century (Joosten and Clarke, 2002; Chapman et al., 2003; Deforce et al., 2007; Graf and Rochefort, 2016; Turan et al., 2018). Traditionally used as fuel, peat is also a widely used as a compost in agriculture and horticulture (Bonn et al., 2016; Turan et al., 2018). As a result of these damaging factors, particularly drainage for peat extraction and land-use change, European peatlands have become significantly drier over the past 400 years (Swindles et al., 2019), and 80–85 % of all peatlands in the UK and Ireland are in a degraded state (Connolly, 2019; Office for National Statistics, 2019; Fluet-Chouinard et al., 2023). Furthermore, the exploitation of peatlands is predicted to increase by as much as 10.3 million hectares by 2100, if climate policy with land-based mitigation measures do not provide adequate protection peatlands (Humpenöder et al., 2020).

While national measures (e.g. Department for Environment, Food and Rural Affairs, 2022; Department of the Environment, Climate and Communications, 2022) and international initiatives (e.g. Committee on Environment, Public Health and Food Safety, 2024) aim to protect

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peatlands from direct exploitation, historic threats remain relevant and recent pressures exacerbate conservation and restoration challenges. Even when direct exploitation ceases, passive pressures, such as nitrogen deposition, will continue to degrade protected sites (Eriksson et al., 2010; Payne et al., 2013; Kelleghan et al., 2021; Rowe et al., 2022). Additionally, climate change is a major threat that can alter peatland vegetation, accelerate drying, and shift the optimal ranges of critical-peatland species (Swindles et al., 2019; Antala et al., 2022; Ma et al., 2022).

An IPCC special report (Rogelj et al., 2018) states that global carbon emissions must fall to 25–30 Pg (Pg) CO_2 equivalent per year by 2030 to avoid the most harmful effects of climate change. Peatlands can act as steady sinks of atmospheric carbon, and carbon stored in peatlands exceed 600 Pg CO_2 equivalents globally (Yu et al., 2010). However, when peatlands are degraded, they can be sizeable sources of greenhouse gases (Abdalla et al., 2016; Urák et al., 2017). As a result, internationally peatland carbon emissions are estimated to exceed 1.91 Pg CO_2 equivalent per year (Leifeld and Menichetti, 2018). This means that globally, peatlands rank as the fifth highest emitter of greenhouse gasses compared against world nations (Leifeld and Menichetti, 2018; Emissions Database for Global Atmospheric Research, 2023), and are comparable to that of the United Kingdom, France, Germany, and Spain combined; together emitting 1.97 Pg CO_2 equivalents in 2022 (Emissions Database for Global Atmospheric Research, 2023). Thus, protecting peatlands is paramount to achieving international emissions targets, and reducing yearly global greenhouse gas emissions by a sizeable portion. In addition to their importance as carbon stores, healthy peatlands in the UK and Ireland improve water quality (Ritson et al., 2016), serve as natural and cultural heritage sites (Flood et al., 2021; Flint and Jennings, 2022), and are rich in biodiversity (Whitfield et al., 2011; Minayeva et al., 2016).

A range of techniques are employed in peatland restoration, including vegetation replanting, peat surface reprofiling, removal of invasive species, and rewetting through the installation of coir log bunds (González and Rochefort, 2014; Parry et al., 2014; Kamocki et al., 2017). Among these, drainage ditch blocking, which has been carried out for several decades (e.g. Fox, 1986; Meade, 1992; Siuda, 1995), remains one of the most widely applied and effective methods, having the potential to convert degraded peatlands from carbon sources to carbon sinks (Nugent et al., 2018). This is particularly important given that artificial drainage, primarily for agriculture, forestry, and peat extraction, has been one of the most widespread and damaging pressures on peatlands, leading to lowered water-tables, vegetation loss, accelerated peat decomposition, and driving greenhouse gas emissions (Chapman et al., 2003; Holden et al. 2006, 2017; Evans et al., 2017). Though currently, there is a need for restoration on a larger scale (Andersen et al., 2017), there are several factors that limit the feasibility of successful large-scale peatland restoration. For example, drain blocking is expensive and can cost >£850 per hectare in UK peatlands (Artz et al., 2019). Additionally, funding for peatland restoration often does not allow for long-term monitoring (Halme et al., 2013); thus, tracking restoration effectiveness remains challenging. Furthermore, traditional monitoring techniques (e.g. water-table depth monitoring) fail to take wider peatland ecological responses in to account (McKeown et al., 2024). It is therefore vital that future drain blocking restoration is impactful, and practitioners have access to and use suitable tools to track its effectiveness. Biomonitoring is an effective method for assessing environmental change and ecological shifts (Griffiths et al., 2016). While monitoring changes in microbial assemblages is a useful biomonitoring technique (Kitson and Bell, 2020), it is rarely incorporated into peatland monitoring programmes. Testate amoebae are a polyphyletic group of unicellular protists. In peatlands, testate amoebae are dominant microbial consumers (Gilbert et al., 2000; Smith et al., 2008; Jassey et al., 2013, 2014) that can be used to understand past environmental conditions, including water-table depth, climate, vegetation history, methane emissions and fire (Charman et al., 2000; Payne et al., 2012; Gałka et al., 2013; Amesbury et al., 2016; Frésard et al., 2023). Some testate amoeba taxa are key indicators of wetness in peatlands; for example, *Archerella flavum* is an indicator of wet conditions, while *Assulina muscorum* tends to prefer drier conditions (Tolonen, 1966, 1986). Furthermore, functional traits associated with testate amoebae survival, development, and growth have been successfully used to infer changes in peatland conditions, including hydrological change; trophic status; reproductive strategy; and food web complexity (Marcisz et al., 2020; Kuuri-Riutta et al., 2022; Violle et al., 2007; Kearney et al., 2021).

A growing body of research highlights the value of using testate amoebae as a biomonitoring tool for monitoring peatlands beginning with the first published example by Buttler et al. (1996) and followed by a series of more recent studies (e.g. Swindles et al., 2016; Koenig et al., 2017; Creevy et al., 2018; 2023; Frésard et al., 2023; McKeown et al., 2024). For example, they have been used to monitor long term forest-to-bog restoration efforts, past and present methane fluxes, and their functional traits can be used to determine subtle ecological changes (Koenig et al., 2017; Creevy et al., 2018; 2023; Frésard et al., 2023; Evans et al., 2024; McKeown et al., 2024). Several studies have emphasised the need for larger-scale multi-site evaluations of testate amoebae as bioindicators of peatland restoration (Swindles et al., 2016; McKeown et al., 2024). While the use of testate amoebae as bioindicators is being increasingly established, this study provides a novel contribution by examining three concurrent, contemporary, restoration initiatives. Additionally, the use of testate amoeba functional traits, particularly test compression, as an informative tool for monitoring peatland rewetting efforts is a relatively novel aspect of this research. In this study the response of testate amoebae to rewetting across three lowland raised bogs in Northern Ireland from 2020 to 2023 was examined. A before-after control-impact (BACI) design (Green, 1979) was applied to investigate the assemblage-level change and functional traits of testate amoebae following drainage ditch damming. This research tested four key hypotheses: (1) key wet-indicator taxa increase in abundance following drain blocking; (2) changes in specific testate amoeba functional traits are observed after drain blocking; (3) testate amoeba assemblage composition changes in response to drain blocking; and (4) testate amoeba taxa diversity increases following drain blocking.

2. Methods

2.1. Field sites

This study was carried out on three lowland raised bogs across Northern Ireland: Ballynahone Bog; Garry Bog; and Peatlands Park (Fig. 1; Table 1). All three bogs are Special Areas of Conservation (SAC) that were restored through large-scale drainage ditch blocking in 2021/2022 as part of the EU INTERREG VA programme funded collaborative action for the Natura Network (CANN) project (Fig. A.6; Table 1).

2.1.1. Ballynahone Bog

Ballynahone Bog (Fig. 1B; Table 1) is predominantly owned by the Northern Ireland Environment Agency (NIEA) (98 ha). The remainder of the SAC boundary is privately owned by up-to forty individuals. Ballynahone Bog has primarily been damaged by a long history of hand cutting, and more recent industrialised peat extraction (DOENI, 2015a). All peat extraction stopped with SAC designation in 2005, through management agreements with landowners (DOENI, 2015a). Past drainage of Ballynahone Bog has been extensive, fifty large drains were dug across the bog between 1988 and 1994 (DOENI, 2015a). However, several major drains were blocked in 1994 when the site was designated as an ASSI (DOENI, 2015a). Ballynahone Bog has a history of burning, but this has not occurred following SAC designation (DOENI, 2015a). The site has a reported average nitrogen deposition rate of 25.2 kg N/ha/yr, a value well above the critical load of raised bogs (between 5 and 10 kg N/ha/yr) (DOENI, 2015a).

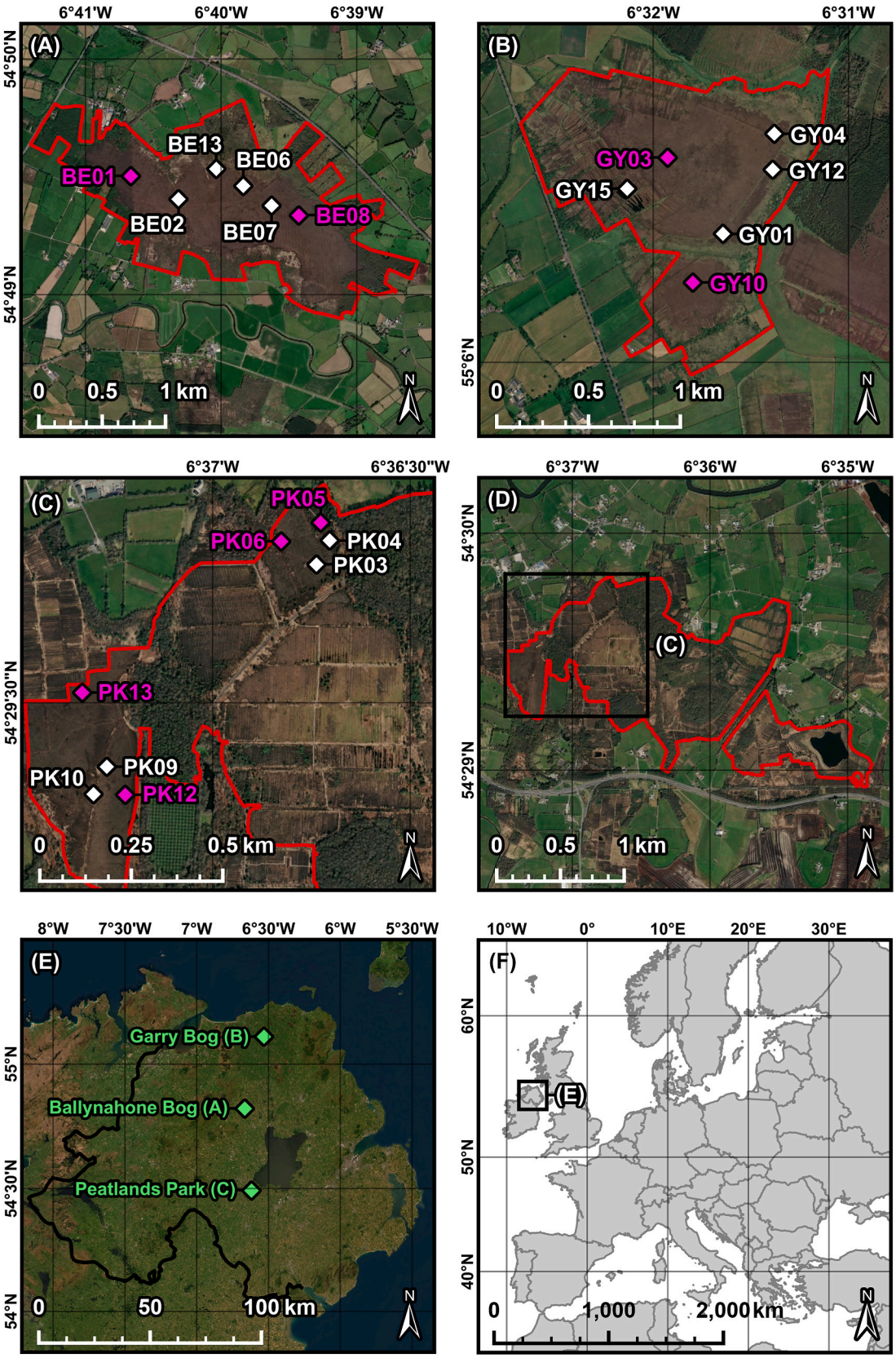

Fig. 1. The study sites – Ballynahone Bog (A), Garry Bog (B), and Peatlands Park (C; D). Shown on a wider map of Northern Ireland (E) and its position in Europe (F). Purple diamonds = control samples (e.g. GY03, BE01, & PK05); White diamonds = test samples (e.g. GY04, BE02, & PK03); Green diamonds = locations of each peatlands site in Northern Ireland; Red line = SAC boundaries. Drainage dam installation locations can be seen in Fig. A.7 (Map sources: Esri, 2024a, 2024b).

Table 1
Ballynahone Bog, Garry Bog, and Peatlands Park site information and meteorological conditions during the study period (Department of the Environment (DOENI) 2015a; 2015b; 2015c; Met Office 2024a; 2024b).

	Ballynahone Bog	Garry Bog	Peatlands Park
Active bog area (ha)	131	142.7	21.8
Degraded bog area (ha)	111	10.2	117.2
SAC area (ha)	244	154.76	207.5
Restoration completion date	30/11/2021	31/03/2022	28/02/2022
Latitude	54°49′21.4″ N	55°06′47.0″ N	54°29′18.8″ N
Longitude	6°39′45.4″ W	6°31′39.1″ W	6°35′58.1″ W
Elevation (m)	40–45	30–35	15–20
Annual rainfall (mm)	899–1073	846–1126	794–862
Mean January temperature (°C)	4.7	5.5	5
Mean July temperature (°C)	15.4	14.6	16.1

2.1.2. Garry Bog

Garry Bog (Fig. 1A; Table 1) is primarily owned by the Forest Service with the remaining sections privately owned by two or three individuals. Hand cutting around the edges of the intact bog, and later industrialised peat extraction have occurred at Garry bog; with old areas of peat cutting showing positive signs of regeneration (DOENI, 2015b). Additionally, there is evidence of recent peat cutting, though this has been limited since SAC designation in 2005 (DOENI, 2015b). Drainage at Garry Bog is limited to the site margins in associated with hand cutting and industrialised peat extraction (DOENI, 2015b). Historic burning is known to have occurred (DOENI, 2015b). Nitrogen deposition rates on Garry Bog average 22.6 kg N/ha/yr; above the sites estimated critical load (DOENI, 2015b).

2.1.3. Peatlands Park

Peatlands Park (Fig. 1C; Table 1) is mostly owned by the NIEA, with four private individuals owning the remainder of the site. Peat cutting and extensive drainage have damaged the raised bog areas within Peatlands Park, unlike the other sites this has encouraged major encroachment of invasive species including Sycamore (*Acer pseudoplatanus*); Dogwood (*Cornus sanguinea*); and Rhododendron (*Rhododendron ponticum*) (DOENI, 2015c). Burning has been used for vegetation management in the past across the site (DOENI, 2015c). Peatlands Park has an average nitrogen deposition rate of 20.5 kg N/ha/yr, which are above the critical load for lowland raised bogs; and higher rates of nitrogen deposition averaging 37 kg N/ha/yr are reported in the bog woodland areas of the site (DOENI, 2015c).

2.2. Field sampling

During the sampling period (28/08/2020–07/12/2023) (Table A.2) live *Sphagnum* samples were collected from twenty locations across Ballynahone Bog, Garry Bog, and Peatlands Park (Fig. 1). Approximately 5–10 cm^3 of *Sphagnum* (capitula, stems, and branches) were sampled in the field and were frozen until further preparation. The upper-most aerobic portions of *Sphagnum* stems have higher concentrations of live testate amoebae (Booth, 2002; Booth et al., 2010; Roe et al., 2017). At each site, five replicate samples were taken pre-restoration ($t_{-5} - t_{-1}$), one replicate was taken during extended drain blocking work (t_0), and five replicates were collected post-restoration ($t_1 - t_5$). At Ballynahone Bog, it was not possible to collect a replicate at the time of drain blocking; however, six replicates were collected post-restoration ($t_1 - t_6$). Replicate sample codes (e.g. $t_{-5} - t_6$) refer to the replicate (t), and order in which replicates were collected pre- and post-restoration ($_{-5} - _6$); negative numbers represent replicates taken pre-restoration, with positive numbers for post-restoration replicates. Each replicate was collected approximately 1 m away from hydrological monitoring stations (piezometer) present at each site. Following a before-after control-impact approach (Green, 1979) replicates were collected next to piezometers categorised as 'test' and 'controls'. Test samples (n = 12) were replicates taken next to piezometers positioned near drains. Control samples (n = 8) were replicates taken next to piezometers situated away from drains. Areas close to drains should experience more immediate and pronounced changes post-restoration, with the restoration impact taking longer to manifest in areas far from blocked drains. Ballynahone Bog and Garry Bog each had four test and two control samples, Peatlands Park had four test and four control samples, reflecting the complexity of human impacts at the site.

2.3. Meteorological and hydrological data

Meteorological data on total monthly rainfall (mm) and mean monthly air temperature (°C) was sourced from Met Office Integrated Data Archive System (MIDAS) land surface weather stations (Fig. 2) (Met Office 2024a; 2024b). The closest stations available for each bog were: Portglenone (54°51′54.0″N, 6°27′28.8″W) (Met Office 2024a; 2024b), located 14.1 km north-east of Ballynahone Bog; Giant's Causeway (55°14′02.4"N, 6°30′43.2"W) (Met Office 2024a; 2024b), located 13.9 km north of Garry Bog; and Armagh (54°21′07.2"N, 6°39′00.0"W) (Met Office 2024a; 2024b), located 15.7 km south of Peatlands Park. Monthly hydrological monitoring was carried out by Ulster Wildlife as part of the CANN project (Fig. A.1). Forty-four piezometers were installed across all three sites in 2019 (Ballynahone Bog = 15; Garry Bog = 15; Peatlands Park = 14) to monitor water-table depth across each site prior to rewetting. Piezometers were installed either in locations near drains (n = 19), or in 'control' locations far from drains (n = 10). Remaining piezometers were installed in mixture of areas, including cutover peatland and areas where presence/absence of drainage was not certain (n = 15). Water-table depth data was available from January 2020 at Garry Bog and Peatlands Park and slightly earlier, in June 2019, at Ballynahone Bog due to active Ulster Wildlife management at this site. Hydrological monitoring ended around the time restoration completion at all three sites (Table 1).

2.4. Laboratory analysis

A standard method was adapted for use in preparing modern testate amoebae samples (Booth et al., 2010). One *Lycopodium* spore tablet and 2 cm^3 of *Sphagnum* were boiled in water, coarse-sieved (at 300 μm), and back-sieved (at 15 μm); the remaining sieved material was stored at 4 °C. Testate amoeba species level identification was conducted under transmitted light microscopy at x200 using taxonomic guides (Charman et al., 2000; Siemensma, 2025). Individuals were tallied as 'dead' where only the test/partial test were present and 'alive/recently alive' when a clearly visible cytoplasm was observed. A minimum count of 100 individuals is recommended by Payne and Mitchell (2009) for peatland testate amoebae studies, with counts of 150 being suggested to maintain 'ecologically relevant' minor assemblage changes. In this study, a minimum of 200 testate amoebae were counted per sample (mean = 231) to resemble the methods of our previous study (mean = 197) (Evans et al., 2024); and to exceed a recommended minimum 150 individuals, a count which improves minor but 'ecologically relevant' assemblage changes (Payne and Mitchell, 2009). Test concentrations were calculated using an established formula (Stockmarr, 1971) that compared *Lycopodium* spore counts against total testate amoebae per sample, as recommended by the standard method (Booth et al., 2010). The use of micro-sieving (15 μm back-sieve) for *Sphagnum* sample preparation can remove very small testate amoeba taxa (Payne, 2009; Avel and Pensa, 2013; McKeown et al., 2019). However, due to on a focus on wet-indicator taxa, and broad testate amoeba functional traits in this study, micro-sieving was considered appropriate and greatly improved the quality and useability of final testate amoebae samples. Testate amoeba functional traits were assigned to all taxa identified during the study period after all data collection was complete, using taxa-specific

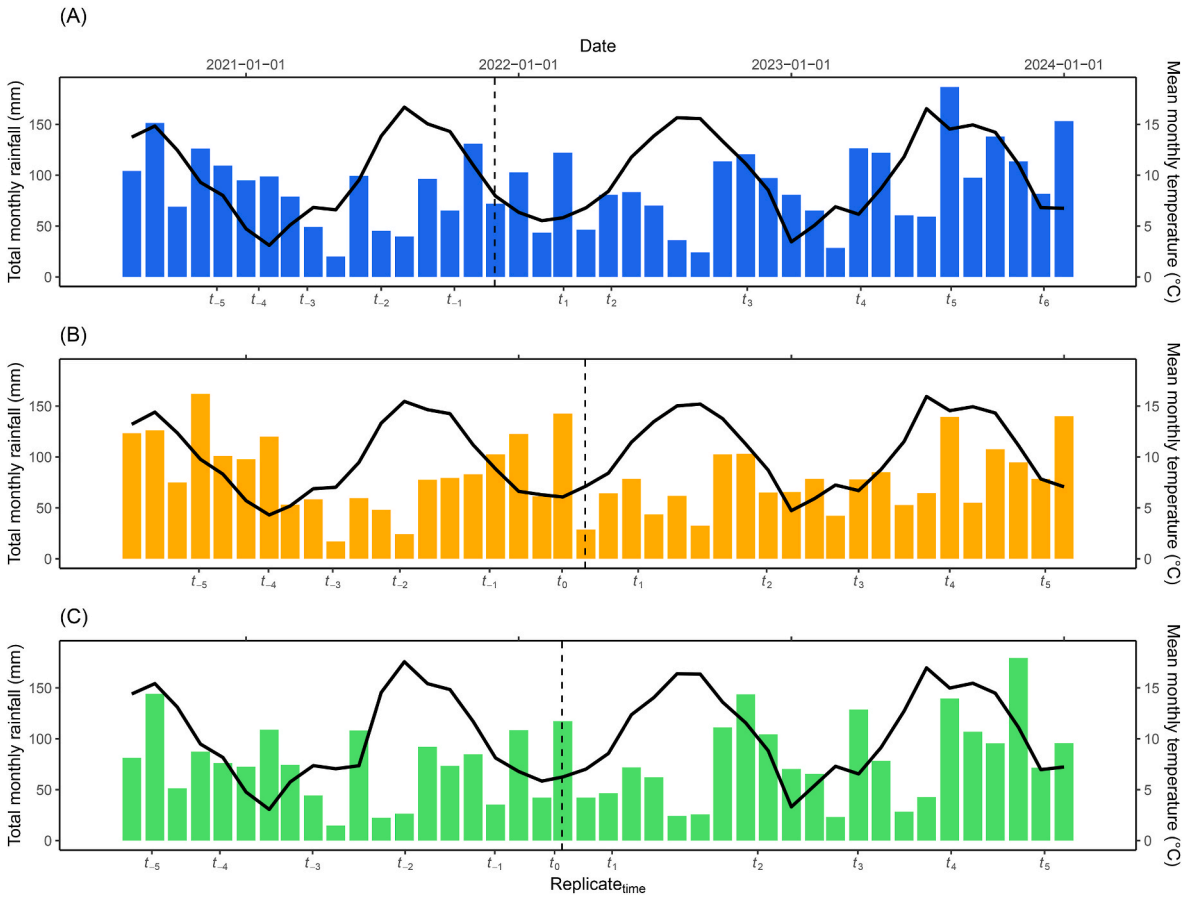

Fig. 2. Total monthly rainfall (mm) and mean monthly temperature (°C) data from the Met Office Integrated Data Archive System weather stations (Met Office 2024a; 2024b) for Ballynahone Bog (A), Garry Bog (B), and Peatlands Park (C).

functional trait data from previous publications (van Bellen et al., 2017; Fournier et al., 2015; Krashevska et al., 2020); including: biovolume (μm3); mixotrophy (mixotrophic, or not mixotrophic); pseudopodia type (filose, or lobose); aperture position (central, cryptic, sub-terminal, or terminal); pseudostome size (μm); test compression (spherical, sub-spherical, compressed, or very compressed) (Fig. 3); and test material (proteinaceous, siliceous, or agglutinated mineral).

2.5. Statistical analysis

Shannon-Wiener diversity index (SDI) (Shannon and Weaver, 1949) values were calculated for individual replicates to examine species diversity throughout the experiment. Non-metric Multidimensional Scaling (NMDS) analysis was carried out using a Bray–Curtis dissimilarity index technique, to display and explore similarities in the testate amoebae assemblage pre- and post-restoration (stress = ~0.25). Environmental and experimental variables (test/control replicate, rainfall, temperature, and time) were fitted through envfit (999 permutations). Analysis of similarities (ANOSIM) and permutational MANOVA (PERMANOVA) were used to determine the significance of test/control replicates, rainfall, temperature, and time. Testate amoebae community-weighted means were calculated for each numerical functional traits (biovolume and pseudostome size); calculated for each replicate as the sum of the products of taxa functional trait values weighted by their percentage abundance. Changepoint analysis was performed to identify major changes in the functional trait dataset throughout the experiment. Bayesian, 'at most one change' (AMOC), and 'pruned exact linear time' (PELT) methods were compared to gain a robust understanding of likely changepoints. R version 4.3.2 (R Core Team, 2023) was used for all statistical analysis and data visualisation.

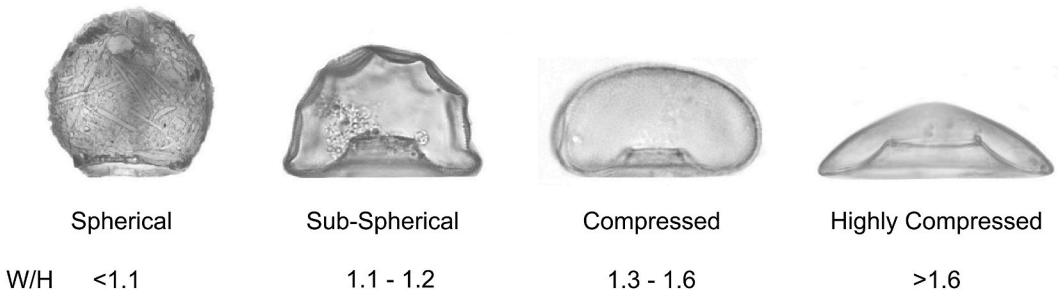

Fig. 3. Diagram of testate amoebae test shape categories: spherical (*Difflugia globulosa*), sub-spherical (*Arcella gibbosa*), compressed (*Arcella rotundata*), and highly compressed (*Galeopora discoides*). Width-to-height ratio (W/H) classifications, as adapted from van Bellen et al. (2017), Fournier et al. (2015) and Krashevska et al. (2020), are shown in the lower portion of the figure (Test image source: Siemensma, 2025).

Multivariate analysis used the R package 'vegan' (version 2.6–4) (Oksanen et al., 2022), and changepoint analysis was carried out with the R packages 'changepoint' (version 2.2.4) and 'bcp' (version 4.0.3) (Erdman and Emerson, 2007; Killick and Eckley, 2014).

3. Results

3.1. Overview

In total, 47,778 individual testate amoebae were counted across the three study sites (mean = 29.6 % alive/recently alive). During the study period 206 samples were collected (Ballynahone Bog = 59; Garry Bog = 61; Peatlands Park = 86) Altogether 49 taxa were identified, with four taxa accounting for >50 % of individuals counted (*Assulina muscorum*, *Euglypha ciliata*, *Euglypha rotunda* type, and *Nebela tincta*) (Fig. A.2 – A.4). SDI values ranged from 1.15 to 2.72. None of the selected variables for PERMANOVA and ANOSIM analyses were found to have a statistically significant effect on the testate amoeba assemblages from Ballynahone Bog, Garry Bog, or Peatlands Park (95 % level). Furthermore, NMDS ordination did not illustrate any changes in testate amoebae assemblages at any of the three sites pre- or post-restoration (Fig. A.5). Wet-indicator taxa (e.g. *Archerella flavum*, *Amphitrema stenostoma, Amphitrema wrightianum*, and *Centropyxis aculeata* type) (Fig. 4) appear infrequently in low abundances in test samples pre-restoration ($t_{-5} - t_{-1}$); but appear in isolated higher abundances post-restoration (t_0 onwards). The presence of higher abundances of wet-indicator testate amoeba in the controls reflects the generally wetter conditions of these locations on each peatland, away from the influence of drains. In the control samples, wet-indicator taxa are more abundant than the samples closer to drains pre-restoration but sharply decline after the drains are blocked. The functional traits test biovolume, pseudopodia type, pseudostome size, and aperture position did not notably change over the course of the study. However, the wet-indicator taxa *A. flavum*, *A, stenostoma,* and *A. wrightianum* are mixotrophic (taxa that can access photosynthetically derived food resources via an endosymbiotic algae). This means the abundance of mixotrophic taxa decreased post-restoration in control samples, but increased post-restoration in test samples in-line with what was observed with wet-indicator taxa. Additionally, a change in test compression was observed across all sites and was particularly apparent in test samples (Fig. 5). In particular, changepoint analysis showed the single most likely changepoint (AMOC) in sub-spherical test abundance occurred post-restoration in all three sites in both control and test samples (Fig. 6); this coinciding with moderate increases in the mean abundance (%) of taxa with sub-spherical tests (Fig. 5). A Bayesian changepoint analysis method indicated that this across-the-board 'most likely' changepoint had a higher probability in test samples (mean posterior probability = 0.77) than in control samples (mean posterior probability = 0.4) (Fig. 6). No obvious trends or across-the-board changepoints were apparent in taxa with compressed, or highly compressed test; and no taxa where categorised as spherical in any of the three sites.

3.2. Ballynahone Bog

A total of 13,356 testate amoebae were counted (mean = 33.5 % alive/recently alive); and 41 taxa were identified at Ballynahone Bog. Four taxa account for almost half (45 %) of counted individuals (*A. muscorum*, *E. ciliata*, *E. rotunda* type, and *N. tincta*) (Fig. A.2). The SDI values between test and control samples ranged from 1.34 to 2.72. Mean SDI values marginally increased towards the end of the study period in test and control samples, though SDI values in the controls was notably variable before restoration ($t_{-5} - t_{-1}$). Wet-indicator taxa abundance (Fig. 4) peaked (60.7 %) in a control sample (BE01) less than two months before restoration (t_{-1}). The abundance of wet-indicator taxa fell to between 2.2 % and 7 % by the end of the study period (t_6). However, the abundance of wet-indicator taxa was variable in the test samples throughout the experiment. *A. flavum* increased in abundance after restoration (t_1 onwards) in test samples. However, less than two months prior to the completion of restoration (t_{-1}) the wet-indicator taxon *C. aculeata* type represented the highest abundance (17.3 %) for test samples. Testate amoebae with proteinaceous tests declined after restoration in the controls. Test samples also showed a muted decline in siliceous test construction in the final replicates of the study period, and proteinaceous tests increased.

3.3. Garry Bog

In total 13,979 testate amoebae were counted at Garry Bog (mean = 31.5 % alive/recently alive). Four taxa accounted for 53.7 % of all individuals counted (*A. muscorum*, *E. ciliata*, *E. rotunda* type, and *N. tincta)*; with 42 taxa being identified (Fig. A.3). SDI values ranged between 1.17 and 2.65. Wet-indicator taxa declined in the control samples and increased in test samples following restoration (Fig. 4). *A. stenostoma* and *A. wrightianum* had a combined peak in abundance (4 %) prior to restoration in control samples. After restoration *A. wrightianum* never reappeared, and *A. stenostoma* has a single, individual occurrence (0.35 %). In test samples, *A. stenostoma* accounted for the sole (0.43 %) wet-indicator taxon occurrence pre-restoration ($t_{-5} - t_{-1}$). Wet-indicator taxa increased to a maximum of 5.37 % after restoration (t_4). Taxa with sub-spherical tests increased in abundance post-restoration (t_0 onwards) in test samples, increasing from a peak of 9.73 % pre-restoration (t_{-5}) to 28.98 % post-restoration (t_5). Additionally, a very clear changepoint was identified in all methods of changepoint analysis post-restoration (t_1; posterior probability = 0.88) (Fig. 6). A decline in siliceous test construction was observed in the test samples ($t_3 - t_5$); replaced by taxa with proteinaceous and agglutinated mineral test construction.

3.4. Peatlands Park

Altogether 20,443 testate amoebae were counted (mean = 25.6 % alive/recently alive); accounting for 40 taxa at Peatlands Park. Four taxa represent over half (51.4 %) of all counted individuals (*A. muscorum*, *E. ciliata*, *E. rotunda* type, and *N. tincta*) (Fig. A.4). SDI values ranged between 1.15 and 2.56. SDI values appear to increase in test samples prior to restoration ($t_{-5} - t_{-1}$), followed by a sharp decrease after restoration (t_0); generally increasing to a similar pre-restoration mean by the end of the experiment. Wet-indicator abundances at Peatlands Park declined in the controls and increased in test samples (Fig. 4). The wet-indicator taxon *A. flavum* peaked at 37.5 % abundance in the controls before restoration (t_{-3}); declining to a maximum of 2.06 % post-restoration (t_2). In test samples, there were two singular occurrences (0.42 % & 0.45 %) of *A. flavum* before restoration (t_{-5}). The maximum peak abundance of a wet-indicator taxa (36.54 %) was observed post-restoration (t_3) in test samples. Abundance of taxa with sub-spherical tests increased in both control and test samples. A mean abundance peak of 6.45 % was observed pre-restoration (t_{-4}) in test samples, rising to 12.12 % post-restoration (t_5). In control samples a pre-restoration (t_{-4}) peak mean abundance of 11.18 % increased to 15.9 % post-restoration (t_5). Changepoint analysis of sub-spherical tests indicated the most likely changepoint (AMOC) occurred post-restoration (t_3) in test and control samples. Furthermore, other methods of changepoint analysis (PELT; Bayesian) indicated a highly probable changepoint post-restoration in test samples (posterior probability = 0.99) (Fig. 6).

4. Discussion

Restoration led to a varied testate amoeba assemblage response across the three sites. Wet-indicator taxa abundances increased across all test samples, and changes in specific functional traits were observed; although, increases in wet-indicator taxa in control samples mean the first hypothesis can be partially accepted, while the second hypothesis

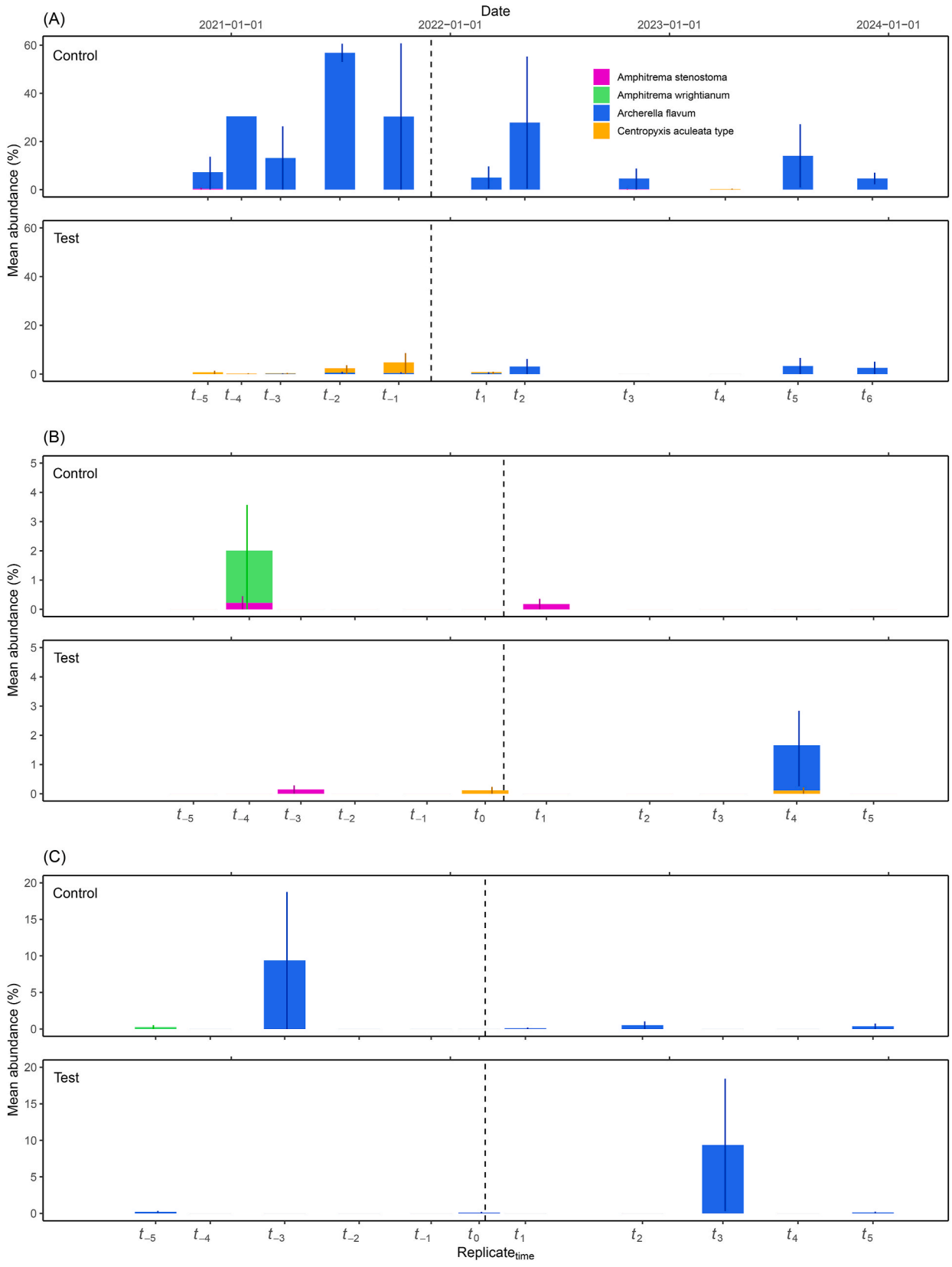

Fig. 4. Mean abundance (%) of unambiguous wet-indicator taxa before (t_{-5} – t_{-1}) and after restoration (t_0 – t_6) at Ballynahone Bog (A), Garry Bog (B), and Peatlands Park (C). Standard error bars are included (coloured lines). Total monthly rainfall (mm) is displayed for each site (grey bars) (Met office 2024a; 2024b). Black dashed line = restoration completion date. Y-axis (mean abundance of wet-indicator taxa) ranges differ between sites: 0–60 % (A), 0–5 % (B), and 0–20 % (C) in order to best visualise the available data of each peatland site.

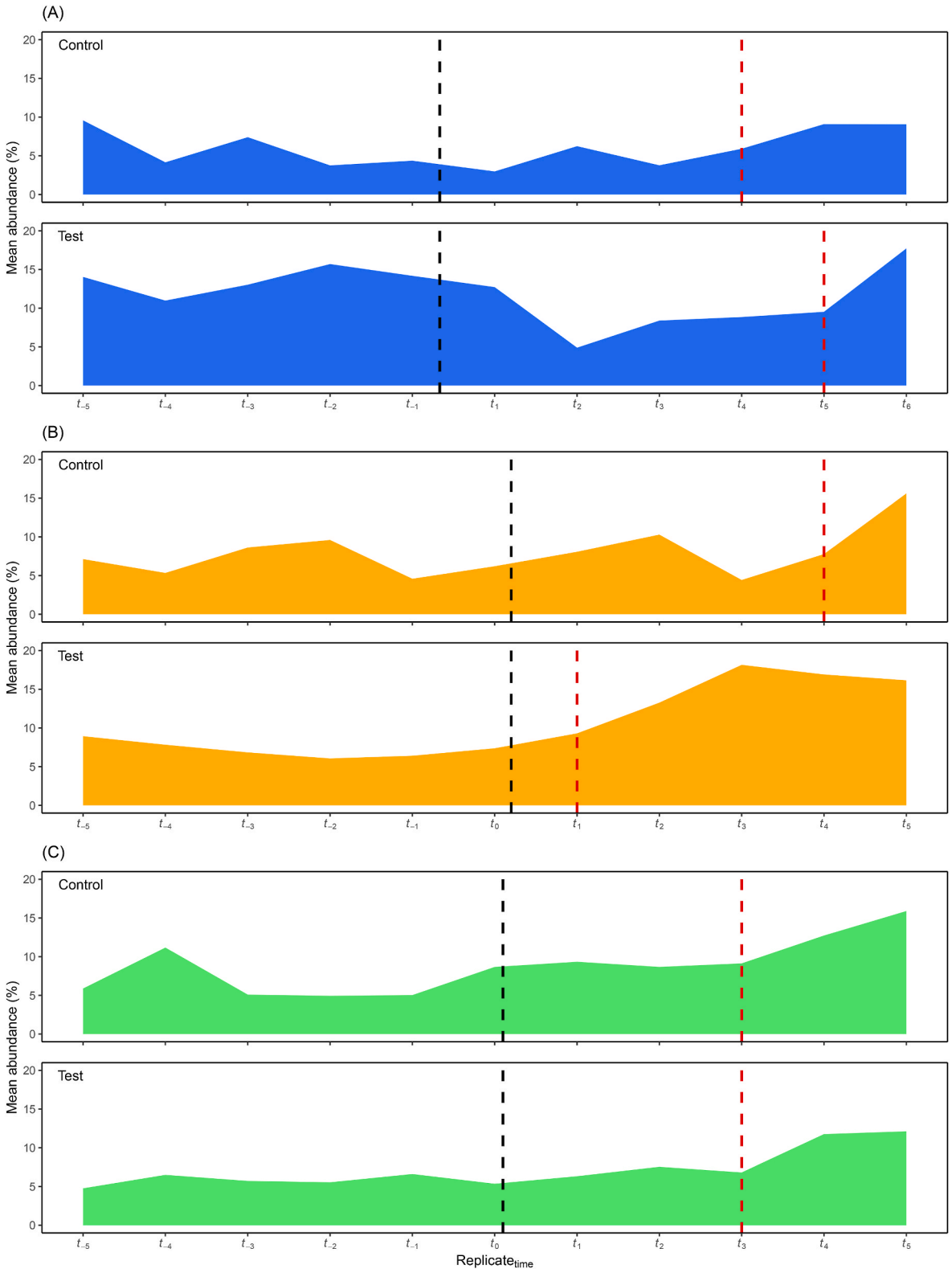

Fig. 5. Mean abundance (%) of testate amoebae taxa with sub-spherical tests before ($t_{-5} - t_{-1}$) and after restoration ($t_0 - t_6$) at Ballynahone Bog (A), Garry Bog (B), and Peatlands Park (C). Black dashed line = restoration completion date. Red dashed line = position of 'at most one change' changepoint analysis results (Fig. A.6).

can be fully accepted (H1 – Key wet-indicator taxa abundances increase in response to drain blocking; H2 – Changes in testate amoeba functional traits are observed after drain blocking). Some changes to testate amoeba assemblage and diversity were observed, but it was not possible to demonstrate this statistically with SDI or multivariate analysis and the remaining two hypotheses must be rejected (H3 – Testate amoebae assemblage composition changes in response to drain blocking; H4 – Testate amoeba taxa diversity increases after drain blocking).

Wet-indicator taxa increased (Fig. 4) in test samples across all three bogs post-restoration (t_0 and t_1 onwards), although this was somewhat

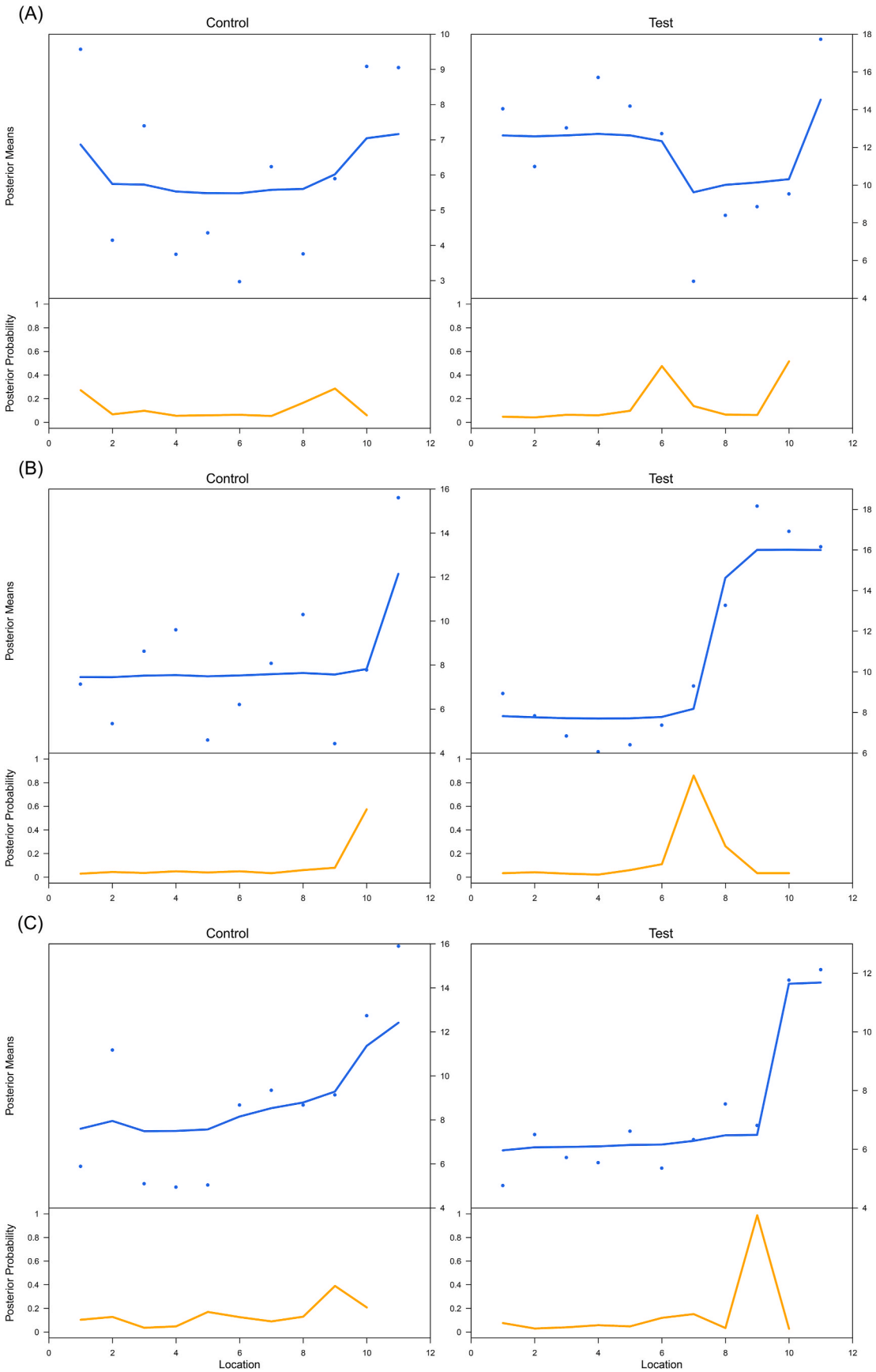

Fig. 6. Bayesian changepoint analysis results for Ballynahone Bog (A), Garry Bog (B), and Peatlands Park (C). Each panel shows posterior means (blue) and posterior probabilities (orange) of a changepoint across control and test samples.

less pronounced than in similar studies (e.g. Swindles et al., 2016; Evans et al., 2024). This observation was contrasted by decreasing abundance of wet-indicator taxa in controls after restoration. It is not clear what mechanism led to this reduction, though it could be linked to improved condition near the dammed drains. Similarly, Swindles et al. (2016) reported no wet-indicator taxa in control treatments prior to restoration work on a Welsh blanket bog. Swindles et al. (2016) found a proliferation of wet-indicator taxa 771 days post-restoration. In this study, only Ballynahone Bog had a replicate taken so long post-restoration (Table A.2; 735 days post-restoration; t_6). It has been shown that restoration effects can take great deal of time to meaningfully manifest (e.g. Creevy et al., 2018; 2023; Schaller et al., 2022), meaning sample collection at all three sites may have ceased before a significant testate amoebae response occurred in response to rewetting restoration efforts.

After restoration, testate amoebae with sub-spherical tests increased most in test samples at Garry Bog and Peatlands Park (Fig. 5). Test compression in testate amoebae is an adaptation to dry conditions and living in thinner water films (van Bellen et al., 2017; Fournier et al., 2012, 2015). Testate amoebae with compressed tests have been shown to decline in only the wettest conditions (Fournier et al., 2015; Koenig et al., 2018a,b). In this experiment test compression was defined on a semi-continuous scale (spherical, sub-spherical, compressed, and highly compressed) after the methods of previous studies (van Bellen et al., 2017; Fournier et al., 2015; Krashevska et al., 2020) (Fig. 3). The clear proliferation of taxa with sub-spherical tests in test samples at Garry Bog and Peatlands Park is a positive signal of wetter conditions post-restoration.

Across all three bogs mixotrophic taxa abundance was largely explained by *A. flavum*. Mixotrophic taxa were observed to follow similar trends to wet-indicator taxa due to significant overlap between the taxa representing these two categories in this experiment. Reductions in mixotrophic taxa is commonly associated with drying conditions and disturbance (Marcisz et al., 2016; Zhang et al., 2020). Increased abundance of *A. flavum* and other mixotrophic taxa in test samples may indicate wetter conditions across all three bogs. Notably, proteinaceous test construction is associated with mixotrophic taxa (Koenig et al., 2018a,b); and most proteinaceous taxa were observed in Ballynahone Bog control samples pre-restoration, where higher abundances of *A. flavum* are also observed. Additionally, increasing mixotrophic taxa abundance in test samples was countered by a decline in mixotrophic taxa abundance in the control samples post-restoration. The community-weighted mean biovolume and pseudostome size did not meaningfully change after restoration. Pseudostome size is closely associated with prey size in testate amoebae (Kuuri-Riutta et al., 2022). Testate amoebae taxa with large pseudostomes are considered dominant microbial consumers and potentially indicate complex food webs (Marcisz et al., 2020). Additionally, pseudostome size has been shown to be an adaptation to peatland hydrological conditions; small pseudostomes being an adaptation to dry conditions (van Bellen et al., 2017). Test biovolume and test size is related to peatland hydrological conditions. Larger taxa are more successful in wet peatlands, and small taxa are adapted to dry peatlands (Koenig et al., 2018a,b; Marcisz et al., 2020); though small test size might also be indicative of highly fluctuating water-tables (Sullivan and Booth, 2011; McKeown et al., 2019, 2024).

The functional trait analysis in this study was carried out after taxa counting was complete. Test biovolume and pseudostome size were not measured for the specific sampled taxa of this study; instead, were sourced from supplementary material of previous studies (van Bellen et al., 2017; Fournier et al., 2015; Krashevska et al., 2020). Traits and dimensions of testate amoebae can vary within and between species, and many commonly recorded taxa actually represent 'species complexes' (i.e. groups of morphologically similar but distinct forms that may differ subtly in test shape and size) (Kosakyan et al., 2013; Soler-Zamora et al., 2023). For example, the *N. tincta-collaris-bohemica* group has been shown to consist of several genetically and morphologically distinct species (Kosakyan et al., 2013), and *E. rotunda* may similarly encompass a complex of cryptic taxa with overlapping morphologies (Lara et al., 2007; Soler-Zamora et al., 2023). Published examples of morphotypes within described species further illustrate this variability (Yu et al., 2014; Roland et al., 2017). This 'cryptic' variation means that the published trait measurements used here (van Bellen et al., 2017; Fournier et al., 2015; Krashevska et al., 2020) may not capture the range of morphotypes present in our samples. This could introduce uncertainty in trait-based analyses, as differences between morphotypes within a species complex may influence functional interpretations, meaning this study could have been strengthened by directly measuring biovolume and pseudostome size. However, mixotrophy, pseudopodia type, aperture position, test compression, and test material are well defined in the literature and suitable for post-hoc analysis. Additionally, sample collection at all three sites was opportunistic and reflected hydrological monitoring (Fig. A.1) associated with a peatland restoration campaign (CANN project). Total monthly rainfall (mm) and mean monthly temperature (°C) (Met Office 2024a; 2024b) aided in identifying any seasonal effect on testate amoebae, in the absence of post-restoration hydrological monitoring data. However, no clear link was found between meteorological conditions and the testate amoebae assemblage dynamics over the course of the experiment (Fig. 4). Key wet-indicator taxa may have been minimally impacted by seasonal rainfall and temperature. Additionally, this study used a standard method of testate amoebae preparation (Booth et al., 2010) that involves micro-sieving Sphagnum samples. Cryptodifflugia oviformis is often reduced through micro-sieving (Avel and Pensa, 2013), and in all three bogs C. oviformis makes up only a small percentage of the overall assemblage, which may be a micro-sieving induced loss. The suppression of this taxon, and other small taxa, from this studies samples could have affected community-weighted mean calculations. However, micro-sieving should not have impacted observations of wet-indicator taxa which are too large (>45 μm) to be omitted by this testate amoebae preparation method.

This study built on the methodologies of our previous work (Evans et al., 2024), extending the focus to multiple larger lowland raised bogs. Ballynahone Bog, Garry Bog, and Peatlands Park each have a more complex history of exploitation and restoration compared to our earlier study site (Evans et al., 2024), and lacked post-restoration hydrological monitoring data. While this limited clarity on restoration success at these sites, it also highlights real-world challenges in peatland restoration and monitoring. These complexities likely contributed to the more subtle wet-indicator responses observed, offering important insight into the range of ecological outcomes following restoration. Furthermore, this study highlights an important deficit of long-term monitoring in ecosystem restoration, and how it can limit practitioners from understanding the effectiveness of restoration efforts (e.g. Andersen et al., 2017). Nonetheless, functional traits and the response of wet-indicator taxa suggest restoration may have led to wetter conditions on all three bogs. Functional traits were a critical asset for examining the response of testate amoebae to peatland restoration. Although previous studies have shown strong responses of wet-indicator taxa in assessing peatland restoration (e.g. Swindles et al., 2016; Evans et al., 2024), this study found a more subtle response, which is important in highlighting the variability in testate amoebae as bioindicators. Importantly, this underscores the value of including functional trait analysis alongside taxa-based approaches, which can enhance detection of early-stage rewetting effects and provide a more nuanced understanding of restoration outcomes. Additionally, testate amoebae taxa and functional traits can be used to indicate anthropogenic pollutants on peatlands. Taxa abundances can be altered after anthropogenic depositions due to anthropogenic particle availability (Fiałkiewicz-Kozieł et al., 2015). Larger algivorous taxa abundances increase on peatlands with high ammonia deposition (Payne et al., 2013). Future research should focus on understanding how to apply functional traits and taxa-based approaches to biomonitoring anthropogenic pollution on peatlands.

While this study focused on three bogs within a specific small geographical context, the observed functional trait and key indicator taxa responses provide valuable insights into testate amoebae as sensitive bioindicators of hydrological restoration more widely. The findings contribute to a growing body of evidence indicating that ecological responses to peatland rewetting are often site-specific in their timing and magnitude yet display consistent trends in functional traits and key indicator taxa associated with wetness and ecological recovery. These results offer transferable lessons for environmental managers seeking to monitor restoration success, particularly regarding the utility of functional trait-based approaches alongside taxa-level analyses. By demonstrating the practical application of testate amoebae data in a real-world restoration programme, this study helps to advance broader understanding of how bioindicators can be effectively integrated into peatland management and monitoring frameworks beyond these three sites.

5. Conclusions

The response of testate amoebae to drain blocking on three lowland raised bogs in Northern Ireland was explored. This study found that wet-indicator taxa increased in abundance in test samples across all three sites. Functional traits indicative of wetter conditions, specifically taxa with sub-spherical tests, became more abundant at Garry Bog and Peatlands Park. However, taxa diversity did not increase following restoration, and multivariate analysis did not reveal clear trends in the dynamics of testate amoeba assemblages. These findings suggest that a combined analysis of key wet-indicator taxa and functional traits provides a valuable approach for monitoring the effectiveness of peatland restoration.

Echoing our previous study (Evans et al., 2024), some caution remains warranted when using testate amoebae as bioindicators of peatland restoration. Future research should prioritize long-term, multi-site studies that integrate hydrological monitoring to better track testate amoebae responses over time. Where hydrological data are limited or unavailable, functional trait analysis – particularly test shape (i.e. spherical and sub-spherical tests) – offers a promising alternative for assessing restoration impacts. Overall, this study underscores the practical value of combining wet-indicator taxa and functional traits to effectively monitor early restoration stages, especially when conventional hydrological monitoring is not feasible.

CRediT authorship contribution statement

Callum R.C. Evans: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michelle M. McKeown:** Writing – review & editing, Validation, Methodology. **Graeme T. Swindles:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Callum Robert Clifford Evans reports financial support was provided by Northern Ireland Department for the Economy. Graeme T Swindles reports financial support was provided by Dutch Foundation for the Conservation of Irish Bogs. Graeme T Swindles reports financial support was provided by Quaternary Research Association. Graeme T Swindles reports financial support was provided by Leverhulme Trust. Graeme T Swindles reports a relationship with Queen's University Belfast that includes: employment. Michelle M McKeown reports a relationship with University College Cork that includes: employment. Sphagnum samples were collected by Ulster Wildlife staff working on the Collaborative Action for the Natura Network (CANN) project, an Interreg Europe project managed by the Special European Union's Programme Body - CRCE. If there are other authors, they 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.126406.

Data availability

Data will be made available on request.

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