Testate amoebae are informative bioindicators of critically high ammonia deposition on peatlands

Evans, C. R. C., Hatton, D. A., & Swindles, G. T. (2025). Testate amoebae are informative bioindicators of critically high ammonia deposition on peatlands. *European Journal of Protistology*, *99*, Article 126147. https://doi.org/10.1016/j.ejop.2025.126147

Published in:
European Journal of Protistology

Document Version:
Publisher's PDF, also known as Version of record

Queen's University Belfast - Research Portal:
Link to publication record in Queen's University Belfast Research Portal

Publisher rights
Copyright 2025 The Authors.

This is an open access article published under a Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution and reproduction in any medium, provided the author and source are cited.

General rights
Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy
The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access
This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: http://go.qub.ac.uk/oa-feedback

Download date:03. Jun. 2026

European Journal of Protistology 99 (2025) 126147

Contents lists available at ScienceDirect

European Journal of Protistology

journal homepage: www.elsevier.com/locate/ejop

Testate amoebae are informative bioindicators of critically high ammonia deposition on peatlands

Callum R.C. Evans [a,*], David A. Hatton [a], Graeme T. Swindles [a,b]

[a] Geography, School of Natural and Built Environment, Queen's University Belfast, Belfast, UK
[b] Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Canada

ARTICLE INFO

Keywords:
Peatland
Ammonia deposition
Testate amoebae
Sphagnum
Biomonitoring
Bioindicator

ABSTRACT

The global nitrogen cycle has been majorly disrupted by anthropogenic activity. While nitrogen emissions in the UK and Ireland are declining, ammonia (NH_3) remains a significant exception. NH_3 emissions are mostly agriculturally sourced and deposited on nearby habitats at high rates in both countries. Peatlands are globally important wetlands that are vulnerable to NH_3 deposition. Essential peatland restoration risks being diminished by excessive NH_3 deposition, leading to the loss of valuable ecosystem services. This study investigates testate amoebae (indicators of contemporary and historic peatland conditions) as bioindicators of seasonal NH_3 deposition on six peatlands across Northern Ireland, UK. *Sphagnum*, an NH_3-sensitive bryophyte, was sampled adjacent to NH_3 monitoring sites once per season for a year. When NH_3 deposition was critically high, multivariate analysis demonstrates a link between NH_3 and testate amoebae assemblage change. Similarly, at high NH_3 deposition sites, testate amoebae taxa diversity is observed to be significantly reduced in springtime, when it is expected to be highest. Although, in response to high NH_3 deposition large algivorous taxa do not proliferate as was anticipated, and mixotrophic taxa abundance decreases could not be linked primarily to NH_3. This research demonstrates the continued potential of testate amoebae as highly informative peatland bioindicators.

1. Introduction

Since the development of the Haber-Bosch process (industrial fixation of ammonia (NH_3) from atmospheric nitrogen) and the increasing use of manure and synthetic fertilisers in agriculture, anthropogenic activity has heavily disrupted the global nitrogen cycle (Galloway et al., 2008; Stein and Klotz, 2016). In many countries, limited access to nitrogen is contributing to acute food insecurity (Masso et al., 2017). Elsewhere, excess nitrogen can lead to reduced water quality, increases in greenhouse gas emissions, and widespread damage to biodiversity (Guo et al., 2022; Huisman et al., 2018; Midolo et al., 2019). The UK and Ireland have nitrogen in excess (Kelleghan et al., 2021; Woodward et al., 2022), although, both nations have reduced a large part of their nitrogen emissions; excluding NH_3 which has remained high for decades (Department of Agriculture, Environment and Rural Affairs, 2024a, 2024b; Environmental Protection Agency, 2024a, 2024b).

Agricultural activity produces most NH_3 emissions (> 80 % in the EU) (Leip et al., 2015), which is deposited rapidly on adjacent land and to wider areas through precipitation (Barry et al., 1993; Goss et al., 1995; Loubet et al., 2009). This has led to annual NH_3 emissions in the UK and Ireland to exceed 380 Kt, which are overwhelmingly sourced from agriculture (Department of Agriculture, Environment and Rural Affairs, 2024c; Environmental Protection Agency, 2024b; Loubet et al., 2009). A major component of this agriculturally-sourced NH_3 deposition is from the storage and field-application of livestock manure slurries (Amon et al., 2001; McGinn and Janzen, 1998). Stored manure can be an acute point-source of NH_3 emissions (Amon et al., 2001) and is often applied to agricultural land to improve productivity, replenish soils after crop harvests, and ameliorate grasslands for livestock grazing (Araji et al., 2001; Kumar et al., 2013). If NH_3 emissions are not reduced, vulnerable habitats and species could be irreparably damaged, contributing to biodiversity loss and climate change (Behera et al., 2013; Kelleghan et al., 2021).

Peatlands are internationally important habitats, that are threatened by climate change and global biodiversity loss (IPCC, 2023; WWF, 2020). These habitats account for carbon stores in excess of 600 Pg globally (Yu et al., 2010) and are uniquely biodiverse (Bullock et al., 2012; Spitzer and Danks, 2006). However, widespread drainage and industrial peat extraction threaten their carbon storage and contribute to greenhouse gas emissions as high as 1.91 Pg CO_2 equivalents per year

---

[*] Corresponding author.
E-mail address: cevans12@qub.ac.uk (C.R.C. Evans).

https://doi.org/10.1016/j.ejop.2025.126147
Received 24 October 2024; Received in revised form 23 March 2025; Accepted 24 March 2025

from peatlands (Chapman et al., 2003; Leifeld and Menichetti, 2018; Salm et al., 2012). Additionally, peatland land-use change into agriculture and forestry can severely impact peatland biodiversity (Graham et al., 2017; Heikkinen et al., 2023). Efforts to reduce the impact of these anthropogenic pressures are increasingly being pursued, and peatland restoration measures have been implemented for decades (e.g. Fox, 1986; Meade, 1992). Likewise, governments have begun to adopt country-scale peatland protection schemes (e.g. National Peatland Plan (Scotland), National Peatland Strategy (Republic of Ireland), and the Northern Ireland Peatland Strategy) (Nordbeck and Högl, 2024).

Global peatland restoration research has seen an exponential increase in recent years (Apori et al., 2022). However, peatland restoration risks being curtailed by NH_3 deposition, as these ombrotrophic and oligotrophic habitats are especially sensitive to atmospheric pollutants; receiving all their nutrients through the atmosphere (Bobbink et al., 1998; Payne et al., 2013; Levy et al., 2018). Critical levels of NH_3, defined as concentrations of NH_3 'above which direct adverse effects may occur', exist to protect vulnerable habitats like peatlands (Posthumus, 1988, cited in Cape et al., 2009, p. 1033). This is because bryophytes, such as *Sphagnum* which are integral in the formation of peat (Moore, 1987; Rydin and Jeglum, 2006), are easily damaged by NH_3 deposition (e.g. tissue/foliar damage/death) (Cape et al., 2009; Krupa, 2003; Sheppard et al., 2011). As such, the annual mean critical level of NH_3 deposition for lichens and bryophytes is 1 μg NH_3 m^{-3}, a third of the rate for more resilient higher plants (3 μg NH_3 m^{-3}) (Cape et al., 2009). Critical levels for NH_3 deposition are derived from field observations to produce ecologically relevant recommendations to protect vulnerable habitats (Cape et al., 2009). Likewise, the techniques used to define these critical levels can be adapted by practitioners in the field (e.g. Kapusta et al., 2014; Yang et al., 2017).

Testate amoebae are a polyphyletic group of unicellular amoeboid protists found in most freshwater and terrestrial habitats (Smith et al., 2008). The well-preserving shells (tests) of testate amoebae mean they have been used in palaeoenvironmental studies for over a century (e.g. Lindberg, 1899, cited in Tolonen, 1986, p. 645). More recently, palaeohydrological reconstruction techniques have been adapted to enable testate amoebae to function as contemporary bioindicators (Mitchell et al., 1999; Warner and Chmielewski, 1992). Additionally, testate amoebae functional traits and specific tolerances can be informative in determining near real-time peatland changes (e.g. Marcisz et al., 2020; McKeown et al., 2024). Specifically, large testate amoebae taxa (i.e. large pseudostome/test), which have previously been suggested as an NH_3 deposition indicator (Jassey et al., 2012; Payne et al., 2013), and mixotrophic taxa, which host endosymbiotic algae that may respond to changes in nutrient availability (Herbert et al., 2019; Marcisz et al., 2014; Payne et al., 2016), could be particularly valuable in detecting the effects of nutrient inputs like NH_3 on peatland ecosystems. Additionally, unlike surface vegetation such as *Sphagnum*, which is central to peatland functioning but may show slow or delayed responses to changes in nutrient levels (e.g. Vitt et al., 2003), testate amoebae can exhibit rapid, sensitive reactions to shifts in environmental conditions such as NH_3 deposition (e.g. Payne et al., 2016). Their quick response to subtle alterations in water chemistry, nutrient availability, and hydrological conditions makes them an ideal tool for monitoring and detecting early-stage changes in peatland ecosystems (e.g. Evans et al., 2024; Marcisz et al., 2020; Swindles et al., 2016). This sensitivity allows them to serve as valuable bioindicators in tracking the impacts of atmospheric pollutants like NH_3 on peatland health, which might not be immediately apparent through other methods, such as assessing *Sphagnum* physiology alone.

There is a growing body of research on testate amoebae as contemporary peatland bioindicators, especially concerning peatland hydrological conditions; study of other environmental factors is comparatively limited (Silva et al., 2022). Although, there have been numerous experiments considering testate amoebae responses to nitrogen input on peatlands (e.g. Gilbert et al., 1998; Jiroušek et al., 2013; Mitchell and Gilbert, 2004; Mitchell et al., 2003), and similar experiments conducted on heathland, urban/industrial areas, and arid soil crusts (Meyer et al., 2012; Payne et al., 2012; Pérez-Uz et al., 2023). However, only one study considers testate amoeba response to NH_3 deposition on peatlands specifically (Payne et al., 2013), and to date, no studies examine the response of testate amoebae to agricultural activity-linked seasonal cycles of NH_3 deposition on peatlands. In this study, the effects of NH_3 deposition on six peatlands across Northern Ireland are examined. *Sphagnum* moss was sampled adjacent to an established NH_3 monitoring program once per season for a year, coinciding with expected seasonal cycles of NH_3 deposition. The assemblage-level change and functional traits of testate amoebae were analysed to determine if testate amoebae have merit as bioindicators of critically high NH_3 deposition.

The following hypotheses were tested:

[H_1] Testate amoeba assemblage composition is altered in response to NH_3 deposition.

[H_2] Abundance of mixotrophic taxa decreases in response to NH_3 deposition.

[H_3] High NH_3 deposition causes an increase in abundances of large testate amoebae taxa.

[H_4] Testate amoebae taxa diversity decreases in response to increased NH_3 deposition.

2. Methods

2.1. Field sites

This experiment involved sampling *Sphagnum* and determining NH_3 deposition at six peatlands across Northern Ireland (Fig. 1). Samples were collected at Ballynahone Bog (54°49′21.4″ N, 6°39′45.4″ W) (Fig. 1B), Curran Bog (54°47′58.0″ N, 6°38′44.4″ W) (Fig. 1B), Garry Bog (55°06′47.0″ N, 6°31′39.1″ W) (Fig. 1A), Moneygal Bog (54°44′27.0″ N, 7°37′50.1″ W) (Fig. 1E), Peatlands Park (54°29′18.8″ N, 6°35′58.1″ W) (Fig. 1C), and Slieve Beagh (54°20′48.4″ N, 7°10'40.8″ W) (Fig. 1D). Slieve Beagh is an upland blanket bog, with all remaining sites being lowland raised bogs; and all sites are Special Areas of Conservation (SAC). As part of the EU INTERREG VA funded Collaborative Action for the Natura Network (CANN) project, all six sites in this experiment had some rewetting restoration and invasive species removal conducted between 2017 and 2022.

2.1.1. Ballynahone bog

Ballynahone Bog (Fig. 1B) has roughly equal areas of active and degraded raised bog (Table 1). The largest portion of the bog is owned by the Northern Ireland Environment Agency (NIEA) (98 ha) with more than forty individuals owning the remainder of the site. The site has been degraded by industrial peat extraction, hand cutting, burning, and significant drainage, which have not occurred since SAC designation in 2005 (Department of the Environment, 2015a). However, fifty large drains were partly blocked when the site became an ASSI (Northern Ireland Areas of Special Scientific Interest, equivalent to UK Sites of Special Scientific Interest/SSSI) in 1994 (Department of the Environment, 2015a); with many more dams installed in 2021 as part of the CANN project. NIEA and UK Centre for Ecology and Hydrology (UKCEH) NH_3 monitoring at the Ballynahone Bog identified two close-proximity farms to the site that could be sources of NH_3 (Suppl. Fig. A.1) (van Dijk et al., 2020).

2.1.2. Curran bog

Curran Bog (Fig. 1B) has mostly degraded raised bog, with a small portion of active and intact raised bog (Table 1). The site is owned by forty-three individuals, and has a history of extensive hand cutting, industrialised peat extraction, burning, and drainage (Department of the Environment, 2015b). Peat cutting and extraction have reduced since SAC designation, but it is not known if extant rights for peat cutting exist at the site (Department of the Environment, 2015b). Drainage at Curran

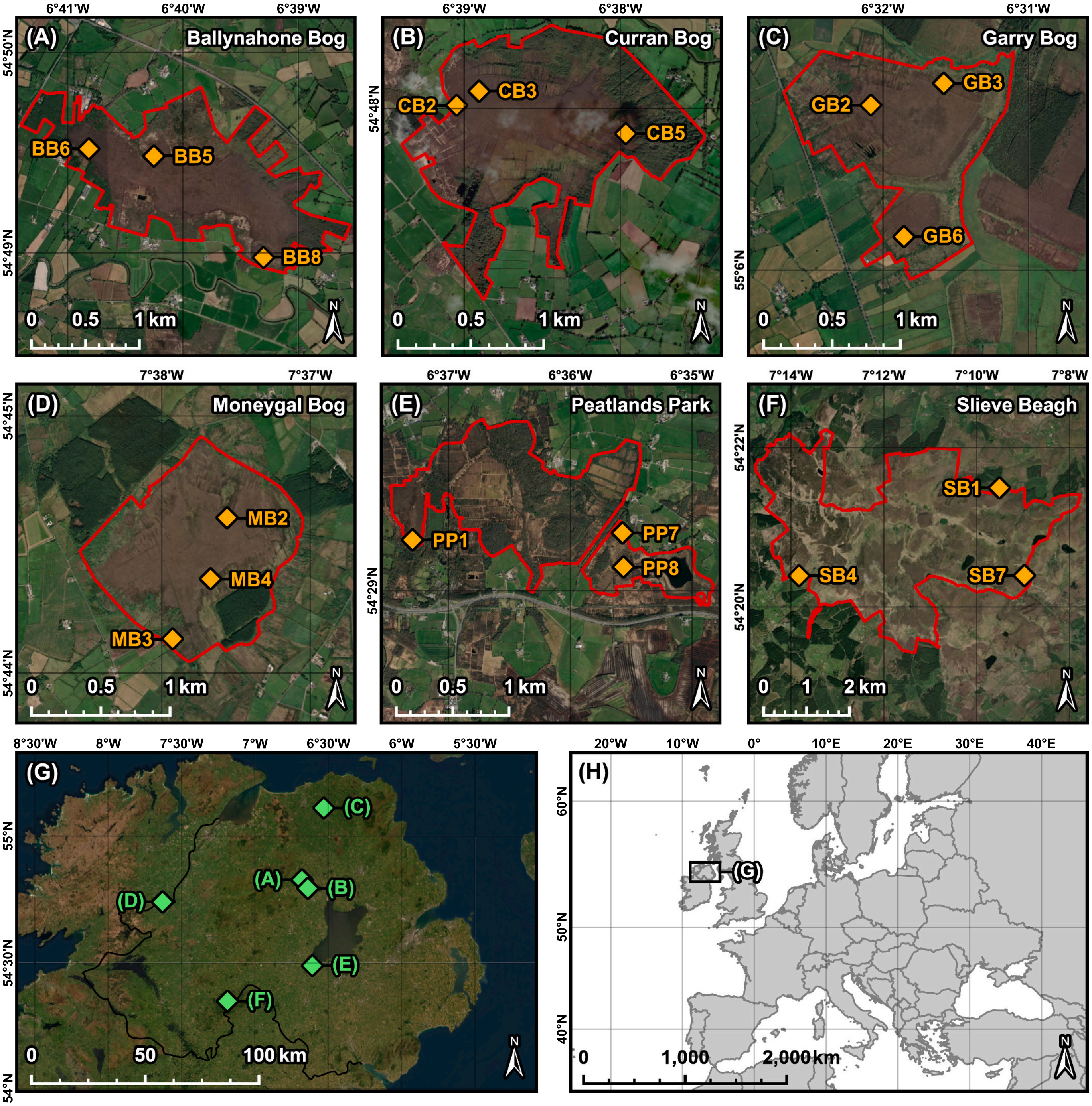

Fig. 1. The six study sites: Ballynahone Bog (**A**), Curran Bog (**B**), Garry Bog (**C**), Moneygal Bog (**D**), Peatlands Park (**E**), and Slieve Beagh (**F**). Shown on a wider map of Northern Ireland (**G**) and its position in Europe (**H**). Orange diamonds denote NH_3 monitoring and *Sphagnum* sample locations (e.g. GB2, SB1, & MB3); Green diamonds denote locations of each peatland site in Northern Ireland; Red line marks SAC boundaries (Map sources: Esri, 2024a, 2024b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Bog does not cross the intact surface at the centre of the raised bog but is extensive at the borders of the study sites. Drainage ditch dams were installed at Curran Bog as part of the CANN project, though restoration plans were never fully fulfilled due to landowner permission issues. NIEA and UKCEH NH_3 monitoring identified three large industrial farms within 5 km of the site, and twenty-four possible animal housing/slurry storage sites within 2 km, that could both represent sources of NH_3 (Suppl. Fig. A.1) (Tang et al., 2022, 2023).

2.1.3. *Garry bog*

Garry Bog (Fig. 1A) is mostly active intact raised bog, with small areas of degraded bog (Table 1). The site is mostly owned by the Forest Service with remaining areas owned by two or three individuals. Garry Bog has a long-standing management agreement with the Forest Service but has previously been subject to hand cutting and mechanised extraction of peat across the fringes of the site (Department of the Environment, 2015c). No drains dissect either of the main peat domes, though old drainage is evident at the edges of the site, with many being dammed as part of the CANN project in 2022. NIEA and UKCEH NH_3

Table 1
Characterization of field sites studied.

Site	Active bog (ha)[a]	Degraded bog (ha)[a]	SAC (ha)[a]	Elevation (m)	Temperature (°C)[b]	Rainfall (mm)[c]
Ballynahone Bog	131	111	244	40–45	5.1–14.5	1233
Curran Bog	25.48	126.86	183.3	38–43	5.1–14.5	1233
Garry Bog	142.7	10.2	154.76	30–35	5.9–14.6	1016
Moneygal Bog	114.2	38	155.79	125–135	5.0–14.6	1372
Peatlands Park	21.8	117.2	207.5	15–20	5.4–15.0	1056
Slieve Beagh	1112	–	1900	200–380	5.1–14.4	1406

[a] Data obtained from Department of the Environment (2015a, 2015b, 2015c, 2015d, 2015e, 2015f).
[b] Data on temperature (mean January and July) obtained from Met Office (2024b).
[c] Data on annual rainfall obtained from Met Office (2024a).

monitoring at the site identified three large industrial farms within 5 km, and eighteen potential animal housing/slurry storage sites within 2 km, that could both be sources of NH_3 (Suppl. Fig. A.1) (Tang et al., 2022, 2023).

2.1.4. Moneygal bog

Moneygal Bog (Fig. 1E) is mostly an active raised bog, with large degraded areas (Table 1). The Forest Service owns most of the site, with a small northern parcel owned by an individual (Department of the Environment, 2015d). Moneygal Bog has been extensively hand cut for peat, with some mechanised extraction occurring (Department of the Environment, 2015d). Past burning is evident and can be clearly identified on the site (Department of the Environment, 2015d). The site has areas of forestry plantation (~ 14 ha) which have been suggested to have a drying effect on the surrounding peat surface (Department of the Environment, 2015d). Drainage is mostly at the edges of the site, with some old drains crossing the intact dome (Department of the Environment, 2015d). Some drains have since been dammed as part of the CANN project between 2020 and 2022. NIEA and UKCEH NH_3 monitoring at the site identified nine possible animal housing/slurry storage sites within 2 km, that could be sources of NH_3 (Suppl. Fig. A.1) (Tang et al., 2022, 2023).

2.1.5. Peatlands Park

Peatlands Park (Fig. 1C) is a large area of degraded raised bog, and a small area of active raised bog (Table 1), adjacent to significant Oak woodland (> 40 ha) (Department of the Environment, 2015e). The site is mostly owned by NIEA with four individuals owning small sections. Past cutting, drainage, and burning have left the site at risk of invasive species encroachment (Department of the Environment, 2015e). As part of the CANN project, many drains were dammed and invasive species (particularly *Rhododendron*) were cut-back. NIEA and UKCEH NH_3 monitoring at the site identified three large industrial farms within 5 km, and twenty potential animal housing/slurry storage sites within 2 km, that could both be sources of NH_3 (Suppl. Fig. A.1) (Tang et al., 2022, 2023).

2.1.6. Slieve Beagh

Slieve Beagh (Fig. 1D) is the third largest intact peatland in Northern Ireland and has a very large area of active blanket bog, with significant natural lakes (> 15 ha), and dry heath (80 ha) (Table 1) (Department of the Environment, 2015f). The Forest Service own approximately 600 ha of the site, with twenty individuals owning sections, and as many as sixty-five others who have turbary rights to cut peat for fuel (Department of the Environment, 2015f). Peat cutting at the perimeter of Slieve Beagh has occurred in the recent past (Department of the Environment, 2015f), and heathland management-connected burning is evident across the entire site (Department of the Environment, 2015f). Drainage is limited to the edge of the site which was dammed in 2021 as part of the CANN project. NIEA and UKCEH NH_3 monitoring at the site identified two large industrial farms within 5 km, several more within 10 km, and three possible animal housing/slurry storage sites within 2 km, that could be sources of NH_3 (Suppl. Fig. A.1) (Tang et al., 2022, 2023).

2.2. Ammonia and meteorological data

Atmospheric NH_3 gas concentrations were monitored by NIEA and the UKCEH at all six sites (Fig. 2) using adapted low-cost passive high absorption (ALPHA) samplers (Tang et al., 2001) that were installed on most sites in 2020. ALPHA samplers have been collecting atmospheric NH_3 gas concentrations at Ballynahone Bog since 2014 (van Dijk et al., 2020). ALPHA samplers were prepared using a standard UKCEH methodology that provides a representative of atmospheric NH_3 concentrations (Stephens et al., 2021; Tang et al., 2001). Additionally, plastic bird spikes were installed on top of ALPHA sampler supports to prevent bird perching and soiling, which can impact NH_3 concentrations. Atmospheric NH_3 concentrations were collected once per month, from ALPHA samplers at a range of locations across each bog and chemically analysed by UKCEH in Edinburgh. Issues surrounding data collection at Slieve Beagh led to 2023 NH_3 deposition data for this site to be incomplete. Most data for ALPHA sampler SB7 was present for 2023, whilst more than half of the planned 2023 data for SB1 and SB4 was missing. Mean NH_3 deposition data from Slieve Beagh in 2020, 2021, and 2022 was used to supplement the missing periods from 2023 data collection (Fig. 2F). At all other sites 2020–2022 data was comparable year-on-year to NH_3 deposition data collected in 2023 (Tang et al., 2022, 2023; van Dijk et al., 2020).

To compare total monthly rainfall (mm) and mean monthly temperatures (°C) at each site, the Met Office Integrated Data Archive System (MIDAS) was utilised, sourcing data from MIDAS land surface weather stations through 2023 (Fig. 3) (Met Office, 2024a, 2024b). The nearest suitable MIDAS station to each site was: Portglenone (54°51′54.0″ N, 6°27′28.8″ W) 14 km northeast of Ballynahone Bog and Curran Bog; Giant's Causeway (55°14′02.4″ N, 6°30′43.2″ W) 14 km north of Garry Bog; Castlederg (54°42′25.2″ N, 7°34′37.2″ W) 5 km southeast of Moneygal Bog; Armagh (54°21′07.2″ N, 6°39′00.0″ W) 15 km south of Peatlands Park; and Thomastown (54°19′48.0″ N, 7°35′42.0″ W) between 23 and 29 km east of Slieve Beagh (Met Office, 2024a, 2024b).

2.3. Field sampling

At each site, three ALPHA sampler locations were sampled once per season for a year (31/03/2023–13/01/2024). Three replicates of *Sphagnum capillifolium* (Ehrh.) Hedw. were collected at each ALPHA sampler in Spring 2023 (Table 2). Each replicate of *S. capillifolium* was taken within a radius of ~5 m of each ALPHA sampler. Replicates were chosen to be as far apart from one another as could be achieved, given the available *S. capillifolium* near each ALPHA sampler. Replicates were repeated in Summer, Autumn, and Winter (Table 2) from the same individual areas of *S. capillifolium*. Compass directions, distances, and handheld GPS were used to relocate the same area of *S. capillifolium* each season, in relation to permanent ALPHA samplers. Samples were selected from a single *Sphagnum* species to avoid discrepancies in sensitivity to NH_3, as differing tolerance to nitrogen deposition has been

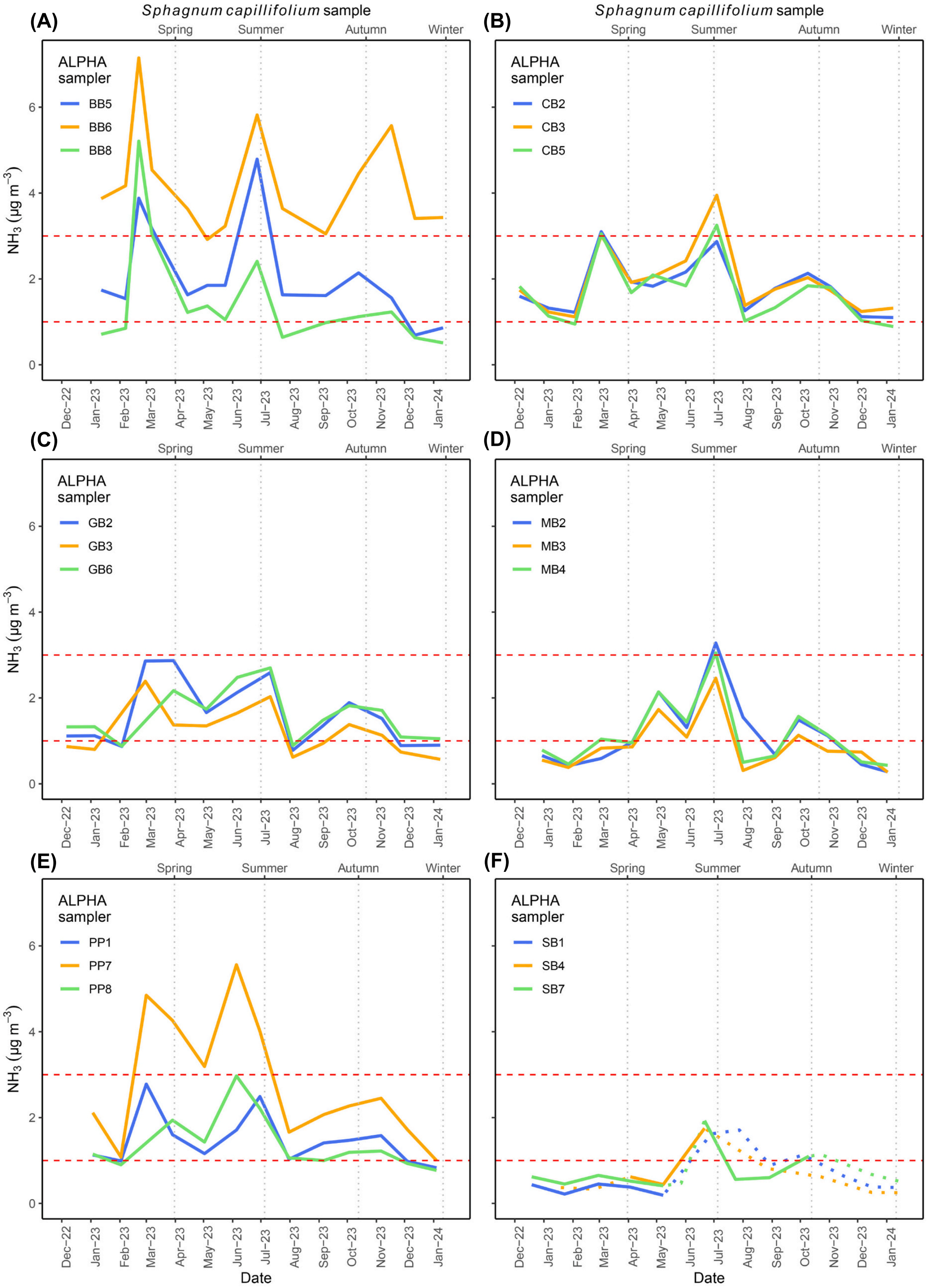

Fig. 2. NH_3 deposition rates at Garry Bog (**A**), Ballynahone Bog (**B**), Curran Bog (**C**), Moneygal Bog (**D**), Peatlands Park (**E**), and Slieve Beagh (**F**). Red dashed line denotes critical NH_3 deposition rates for bryophytes and lichens (1 NH_3 μg m^{-3}), and higher plants (3 NH_3 μg m^{-3}) (Cape et al., 2009). Grey dotted line marks *Sphagnum capillifolium* sample collection dates. ALPHA samplers SB1 (blue), SB4 (orange), and SB7 (green) for Slieve Beagh (F) have supplemented NH_3 deposition data from 2020 to 2022 (Tang et al., 2023, 2023), represented by broken lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

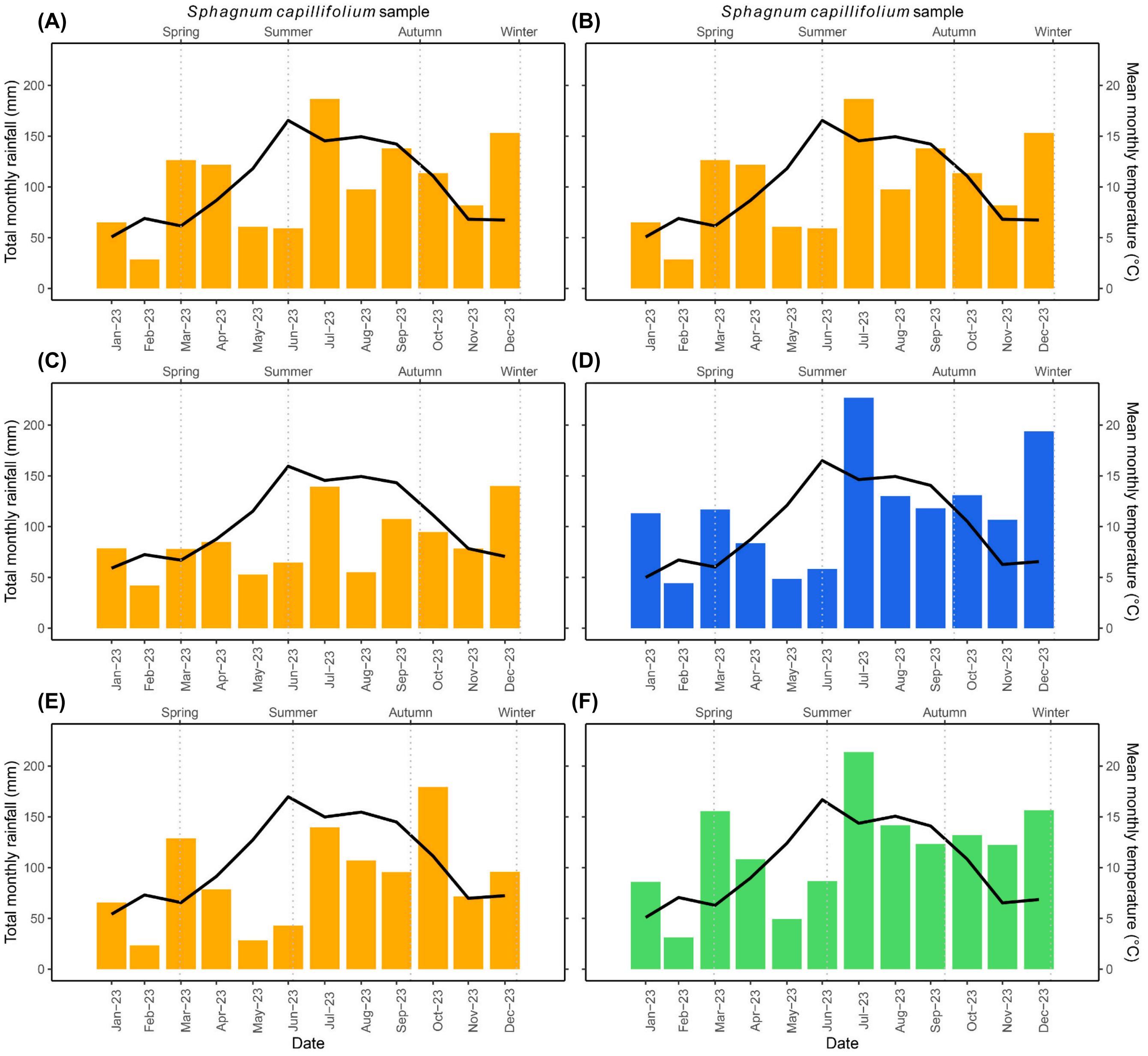

Fig. 3. Total monthly rainfall (mm) and mean monthly temperature (°C) data from the Met Office Integrated Data Archive System weather stations (Met Office, 2024a, 2024b) for Ballynahone Bog (**A**), Curran Bog (**B**), Garry Bog (**C**), Moneygal Bog (**D**), Peatlands Park (**E**), and Slieve Beagh (**F**). Site NH_3 deposition rate highlighted in orange (high; mean > 1 NH_3 µg m^{-3}); blue (intermediate; mean = 1 NH_3 µg m^{-3}); and green (low; mean < 1 NH_3 µg m^{-3}). Grey dotted line denotes *Sphagnum capillifolium* sample collection dates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

demonstrated in *Sphagnum* species (Jauhiainen et al., 1998). Additionally, *S. capillifolium* was chosen due to its abundance at each site, meaning samples were not taken at extreme distances from ALPHA samplers.

NIEA/UKCEH monitoring in previous years indicated differing NH_3 deposition rates at each peatland (Tang et al., 2022, 2023). Ballynahone Bog, Curran Bog, Garry Bog, and Peatlands Park all had high NH_3 deposition rates (mean > 1 NH_3 µg m^{-3}), often exceeding critical levels of lichens/bryophytes (1 µg NH_3 m^{-3}) and vascular plants (3 µg NH_3 m^{-3}) (Cape et al., 2009). Moneygal Bog had intermediate NH_3 deposition rates (mean 1 NH_3 µg m^{-3}), and Slieve Beagh had low NH_3 deposition rates (mean < 1 NH_3 µg m^{-3}).

Table 2
Sphagnum capillifolium replicate collection dates for spring, summer, autumn, and winter at all six sites.

Site	Spring	Summer	Autumn	Winter
Ballynahone Bog	01/04/2023	01/07/2023	21/10/2023	13/01/2024
Curran Bog	01/04/2023	01/07/2023	21/10/2023	13/01/2024
Garry Bog	01/04/2023	01/07/2023	21/10/2023	13/01/2024
Moneygal Bog	01/04/2023	01/07/2023	21/10/2023	13/01/2024
Peatlands Park	31/03/2023	05/07/2023	13/10/2023	11/01/2024
Slieve Beagh	31/03/2023	05/07/2023	13/10/2023	11/01/2024

2.4. Laboratory analysis

Three replicates of the uppermost portions (5–10 cm^3) of *S. capillifolium* capitula, stems, and branches, which have higher concentrations of live testate amoebae (Booth, 2002; Booth et al., 2010; Roe et al., 2017), were collected near three ALPHA samplers at each site. A standard method (Booth et al., 2010) involves coarse-sieving (300 µm) and back-sieving (15 µm) 2 cm^3 of *Sphagnum* in boiling water which is later refrigerated at 4 °C. It is notable that micro-sieving (15 µm back-sieve) for *Sphagnum* sample preparation has been shown to remove very small testate amoeba taxa (Avel and Pensa, 2013). However, small taxa were not the focus of this study. Larger taxa potentially respond to high NH_3 deposition rates (e.g. Jassey et al., 2012; Payne et al., 2013) and were therefore more important to this study.

Using dichotomous keys/illustrated taxonomic guides (Charman et al., 2000; Siemensma, 2024), testate amoebae species level identification was conducted at 200× under transmitted light microscopy. The status of testate amoebae was noted as 'dead' for individuals where only a test/partial test was apparent, and as 'alive/recently alive' for individuals where a clear cytoplasm was visible. To maintain ecologically relevant minor testate amoebae assemblage changes, a minimum sample size of > 150 individuals was adhered to in all replicates (Payne and Mitchell, 2009). The testate amoebae functional traits: biovolume (μm^3); mixotrophy (not-mixotrophic; mixotrophic); test material (agglutinated mineral; proteinaceous; siliceous); pseudopodia type (filose; lobose); and pseudostome size (µm), were allocated to all identified taxa after analysis was complete using taxa-specific functional trait data from published literature (Fournier et al., 2015; Krashevska et al., 2020; van Bellen et al., 2017).

2.5. Statistical analysis

Non-metric multidimensional scaling (NMDS) analysis used the Bray–Curtis dissimilarity index method to visualise the similarity of testate amoebae assemblages at all six sites for spring, summer, autumn, and winter. Additionally, environmental and experimental variables (NH_3 deposition; season; ALPHA sampler; rainfall; temperature) were fitted through envfit (999 permutations). Permutational multivariate analysis of variance (PERMANOVA) enabled significance testing between replicates, rainfall, temperature, season, ALPHA samplers, and NH_3 deposition rates. Threshold Indicator Taxa Analysis (TITAN) was performed to assess the response of testate amoebae taxa to an NH_3 deposition gradient (Baker and King, 2010). This analysis identified taxa that exhibited significant declines ('decreasers'; z-) or increases ('increasers'; z+) along an NH_3 gradient and determined community-level threshold responses. Bootstrapping (500 resamples; 500 permutations) was used to estimate uncertainty around taxon-specific thresholds, and purity and reliability scores were used to assess the consistency and significance of species responses. Peaks in sum(z-) and sum(z+) values were used to identify community-level change points along the NH_3 deposition gradient. Biovolume and pseudostome size community-weighted means were calculated for each replicate at all six sites (sum of the products of taxa functional trait values, weighted by their percentage abundance). SDI (Shannon and Weaver, 1949) values were calculated for each sample so species diversity could be understood throughout the experiment. Friedman rank sum test was performed to assess significant differences between seasons for testate amoebae functional traits and SDI values. All statistical analysis and data visualisation was carried out using R ver. 4.3.3 (R Core Team, 2024), using the R package 'vegan' ver. 2.6–4 (Oksanen et al., 2022) for all multivariate analyses, and 'TITAN2' ver. 2.4.3 (Baker and King, 2010) for TITAN analysis.

3. Results

3.1. Ammonia deposition

In this experiment, NH_3 deposition rates for all six sites (Fig. 2) broadly followed the expected trends observed in previous years (Tang et al., 2022, 2023). At sites defined to have 'high NH_3 deposition' measured NH_3 deposition for this experiment increased substantially one month before spring samples were collected (mean = 3.53 NH_3 µg m^{-3}) and again around the time of summer sample collection (mean = 3.45 NH_3 µg m^{-3}). Additionally, a third smaller increase in NH_3 deposition rates was observed at these sites approximately around the time of autumn sample collection (mean = 2.01 NH_3 µg m^{-3}). At Moneygal Bog a pre-spring peak of NH_3 deposition was not observed, though NH_3 deposition rates increase at the time of summer sampling (mean = 2.93 NH_3 µg m^{-3}) and at the time of autumn sampling (mean = 1.4 NH_3 µg m^{-3}). Moneygal Bog was the only lowland raised bog site to not experience a clear increase of NH_3 deposition just before spring sampling; however, in late April, the site was characterised by a sharp increase in NH_3 deposition rates (mean = 2 NH_3 µg m^{-3}). Finally, at Slieve Beagh a single obvious increase of NH_3 deposition occurred around the time of summer sampling (mean = 1.8 NH_3 µg m^{-3}); however, no other distinct increases in NH_3 deposition were observed at Slieve Beagh. All six sites are characterised by reduced NH_3 deposition rates at the time of winter sampling, although, mean NH_3 deposition rates were still higher in high NH_3 deposition sites (mean = 1.42 NH_3 µg m^{-3}), compared to 'low/intermediate NH_3 deposition' sites (mean = 0.49 NH_3 µg m^{-3}). Finally, for the entire experimental period, mean rates of NH_3 deposition are higher in high NH_3 deposition sites (mean = 2 NH_3 µg m^{-3}) than at low/intermediate sites (Slieve Beagh = 0.7 NH_3 µg m^{-3}; Moneygal Bog = 1.09 NH_3 µg m^{-3}).

3.2. Testate amoeba assemblages

At all six sites (Table 3), just five taxa (*Assulina muscorum*, *Nebela tincta*, *Euglypha rotunda* type, *Euglypha ciliata*, and *Euglypha strigosa*) accounted for the majority (56.9 %) of individual testate amoebae counted (Figs. A.2–A.7). Specifically, four taxa (*A. muscorum*, *N. tincta*, *E. rotunda* type, and *Archerella flavum*) accounted for more than half (51.6 %) of individuals counted at Ballynahone Bog (Suppl. Fig. A.2). Likewise, four taxa (*A. muscorum*, *N. tincta*, *E. rotunda* type, and *E. strigosa*) accounted for greater than half (58 %) of individuals counted at Curran Bog (Suppl. Fig. A.3). At Garry Bog, five taxa (*A. muscorum*, *N. tincta*, *E. rotunda* type, *E. strigosa*, and *E. ciliata*) accounted for half (50.1 %) of individuals counted (Suppl. Fig. A.4). Only three taxa (*N. tincta*, *A. muscorum*, and *E. rotunda* type) accounted for half (50.6 %) of individuals counted at Moneygal Bog (Suppl. Fig. A.5). Five taxa (*N. tincta*, *A. muscorum*, *A. flavum*, *Cryptodifflugia oviformis*, and *E. rotunda* type) accounted for half (50.6 %) of individuals counted at Peatlands Park (Suppl. Fig. A.6). Finally, at Slieve Beagh, four taxa (*N. tincta*, *A. muscorum*, *E. ciliata*, and *E. rotunda* type) accounted for over half (52.7 %) of individuals counted (Suppl. Fig. A.7). On average, SDI values (Figs. A.8 and A.9; Table 3) were lower in spring samples at bogs with high NH_3 deposition (Ballynahone Bog, Curran Bog, Garry Bog, and Peatlands Park), when compared to summer ($p = 0.034$); where at sites with low/intermediate NH_3 deposition (Slieve Beagh and Moneygal Bog) there was no statistically significant difference in SDI values between seasons.

3.3. Multivariate analysis

NMDS ordination of testate amoebae assemblages and key environmental variables from all six sites were plotted using the Bray–Curtis dissimilarity index on two dimensions (Fig. 4); resulting in varying 'stress' at each site; wherein stress < 0.2 is a good fit, and stress > 0.2 is a poor fit and means NMDS ordination is harder to interpret (Ballynahone Bog = 0.28; Curran Bog = 0.26; Garry Bog = 0.21; Moneygal Bog = 0.2; Peatlands Park = 0.16; Slieve Beagh = 0.24). Replicates from different seasons at Ballynahone Bog (Fig. 4A), Curran Bog (Fig. 4B), and Garry Bog (Fig. 4C) are clustered separately in the NMDS ordination space. Whereas Moneygal Bog (Fig. 4D), Peatlands Park (Fig. 4E), and Slieve Beagh (Fig. 4F) seasonal replicates are not clearly distinct and are clustered together in the centre of each biplot. Environmental variables

Table 3
Summary of total samples, individual counted testate amoebae, identified taxa, and Shannon–Wiener diversity index (SDI) values at all six sites.

Site	Samples	Individuals	Taxa	Spring SDI	Summer SDI	Autumn SDI	Winter SDI
Ballynahone Bog	36	7923	32	2.0782	2.1963	2.1343	2.1382
Curran Bog	36	7800	33	2.1992	2.4111	2.2223	2.1646
Garry Bog	36	7680	42	2.1249	2.257	2.5082	2.3341
Moneygal Bog	36	7944	39	1.9321	1.996	2.0754	1.9079
Peatlands Park	36	7849	41	2.0908	2.2095	2.1221	2.125
Slieve Beagh	36	8032	35	2.116	2.3202	2.0572	1.9962
All sites	216	47,228	51	2.0902	2.2317	2.1866	2.111

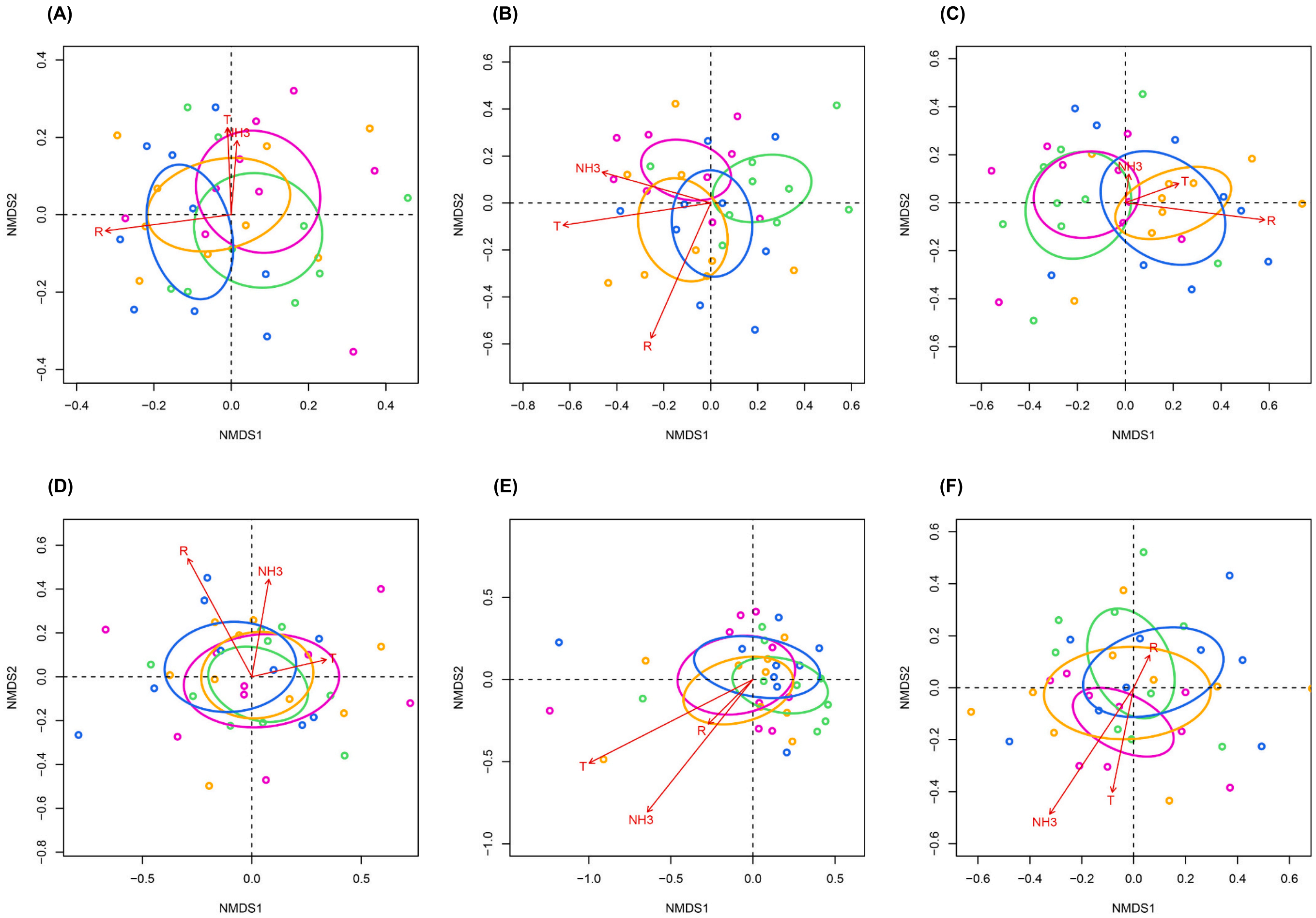

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination biplots for testate amoebae assemblages at Ballynahone Bog (**A**), Curran Bog (**B**), Garry Bog (**C**), Moneygal Bog (**D**), Peatlands Park (**E**), and Slieve Beagh (**F**). Centroids are plotted as coloured ellipses for replicates from each season: spring (green); summer (purple); autumn (orange); and winter (blue). Red arrows represent 'envfit' environmental variables for NH_3 deposition, rainfall (R), and temperature (T). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fitted through 'envfit' to the assemblage dataset (Fig. 4; Table 4) show that NH_3 deposition significantly explained the ordination results with a low goodness of fit in half of the high NH_3 deposition sites (Table 4). ALPHA samplers (three locations across each site where replicates and NH_3 were sampled) significantly explain the ordination with a more moderate goodness of fit in five out of six sites (Table 4). Season and temperature each only significantly explained the ordination of Curran Bog with a low goodness of fit (Table 4), and rainfall significantly explained the ordination of Curran Bog and Garry Bog with a similarly low goodness of fit (Table 4). Increasing NH_3 deposition was most closely associated with spring and summer replicates at Ballynahone Bog (Fig. 4A), Curran Bog (Fig. 4B), and Garry Bog (Fig. 4C). Due to being clustered around 0 on both NMDS axes 1 and 2, it was not possible to discern the relationship between NH_3 deposition and particular seasonal replicates at Moneygal Bog (Fig. 4D), Peatlands Park (Fig. 4E), and Slieve Beagh (Fig. 4F).

Mixotrophic taxa appeared to be commonly associated with increasing NH_3 deposition on one or both NMDS ordination axes (Suppl. Fig. A10). Specifically, *Amphitrema stenostoma* was associated with increasing NH_3 deposition at three of the four sites this taxon was observed to occur at, *Amphitrema wrightianum* at two of three sites, *Heleopera sphagni* at four of six sites, and *Placocista spinosa* type at all five sites it was observed to occur at. However, *Hyalosphenia papilio* was only associated with increasing NH_3 deposition at two of four sites. Furthermore, *A. flavum*, which constituted the vast majority of individual mixotrophic taxa occurrences across all six sites (87 %), was only associated with increasing NH_3 deposition in three of the total six sites. Only half of the mixotrophic taxa observed at Moneygal Bog (2/4) and

Table 4

NMDS ordination environmental variable goodness of fit results at all six sites. Significant *p*-values (< 0.05) are marked by an asterisk (*). ALPHA samplers represent three locations at each site where *S. capillifolium* replicates and NH_3 were sampled.

Site	Variable	*p*	R^2
Ballynahone Bog	ALPHA sampler	0.007 *	0.1821
	Season	0.139	0.1315
	NH_3	0.253	0.081
	Rainfall	0.094	0.1384
	Temperature	0.183	0.1011
Curran Bog	ALPHA sampler	0.241	0.0761
	Season	0.002 *	0.2577
	NH_3	0.069	0.1394
	Rainfall	0.007 *	0.2519
	Temperature	0.008 *	0.2379
Garry Bog	ALPHA sampler	0.04 *	0.1348
	Season	0.051	0.1828
	NH_3	0.017 *	0.2264
	Rainfall	0.006 *	0.2516
	Temperature	0.404	0.0551
Moneygal Bog	ALPHA sampler	0.001 *	0.4446
	Season	0.941	0.0246
	NH_3	0.821	0.0117
	Rainfall	0.744	0.017
	Temperature	0.921	0.0046
Peatlands Park	ALPHA sampler	0.001 *	0.3513
	Season	0.617	0.0642
	NH_3	0.029 *	0.1997
	Rainfall	0.995	0.0006
	Temperature	0.319	0.0705
Slieve Beagh	ALPHA sampler	0.002 *	0.2554
	Season	0.314	0.1041
	NH_3	0.018 *	0.2074
	Rainfall	0.82	0.0118
	Temperature	0.169	0.1026

Table 5

PERMANOVA results for environmental variables at all six sites. Significant *p*-values (< 0.05) are marked by an asterisk (*). ALPHA samplers represent three locations at each site where *S. capillifolium* replicates and NH_3 were sampled.

Site	Variable	*p*	*F*
Ballynahone Bog	ALPHA sampler	0.011 *	2.6576
	Season	0.019 *	2.8154
	NH_3	0.019 *	2.6738
	Rainfall	0.468	0.8989
	Temperature	0.19	1.3638
Curran Bog	ALPHA sampler	0.011 *	2.05
	Season	0.539	0.9011
	NH_3	0.083	1.8107
	Rainfall	0.004 *	3.3432
	Temperature	0.028 *	2.26
Garry Bog	ALPHA sampler	0.001 *	2.7791
	Season	0.121	1.5672
	NH_3	0.004 *	3.012
	Rainfall	0.026 *	2.0533
	Temperature	0.375	1.0416
Moneygal Bog	ALPHA sampler	0.001 *	3.5058
	Season	0.002 *	2.8951
	NH_3	0.195	1.3317
	Rainfall	0.001 *	3.5886
	Temperature	0.012 *	2.7747
Peatlands Park	ALPHA sampler	0.001 *	4.507
	Season	0.329	1.1426
	NH_3	0.004 *	3.9505
	Rainfall	0.067	2.0507
	Temperature	0.009 *	3.3233
Slieve Beagh	ALPHA sampler	0.001 *	3.001
	Season	0.538	0.8874
	NH_3	0.057	1.7965
	Rainfall	0.002 *	3.0978
	Temperature	0.125	1.5057

Peatlands Park (3/6) were associated with increasing NH_3 deposition. More than half of each mixotrophic taxa observed at Ballynahone Bog (2/3), Garry Bog (3/5), and Slieve Beagh (5/6) were associated with increasing NH_3 deposition. Finally, all mixotrophic taxa observed at Curran Bog (4/4) were found to be associated with increasing NH_3 deposition along one or both NMDS axes.

PERMANOVA analysis (Table 5) showed that NH_3 deposition explained a statistically significant amount of the variance in the testate amoebae assemblages of the majority of the high NH_3 deposition sites, although not at Curran Bog, or either of the low/intermediate sites (Table 5). PERMANOVA analysis also indicated that testate amoebae replicates were significantly different between each ALPHA samplers at all six sites (Table 5), rainfall explained a moderate degree of the variance in testate amoebae assemblages at four of the total six sites (Table 5), and temperature explained a similar degree of the variance at three sites (Table 5).

3.4. *TITAN analysis*

TITAN analysis was conducted on a combined dataset of all six sites to identify significant thresholds in the response of testate amoeba taxa in relation to NH_3 deposition gradients. Rare ($<$ 3 total occurrences) and ubiquitous (appearing in all samples) taxa were filtered prior to analysis, which included the rare taxa *Arcella hemispherica*, *Centropyxis aerophile*, *Centropyxis platystoma* type, *Difflugia bacillariarum*, *Galeripora artocrea*, *Nebela carinata*, *Plagiopyxis callida*, and *Quadrulella symmetrica*, and the ubiquitous taxon *A. muscorum*.

TITAN analysis identified eleven taxa with robust responses to NH_3 deposition, comprising five taxa that significantly declined (decreasers; z-) and six taxa that significantly increased (increasers; z+) along the gradient. The decreasers included *Centropyxis aculeata*, *Corythion–Trinema type*, *C. oviformis*, *Galeripora catinus*, and *N. tincta*, while the increasers consisted of *Assulina seminulum*, *Cryptodifflugia* sp. 1, *E. rotunda*, *Euglypha tuberculata*, *Nebela flabellulum*, and *Pseudodifflugia fulva* (Fig. 5). These taxa exhibited strong indicator responses with high purity ($>$ 0.95) and reliability ($>$ 0.95) scores, signifying clear ecological thresholds in relation to NH_3 deposition.

Peak sum(z-) (decreasers) and sum(z+) (increasers) for all eleven identified taxa occurred above the critical level for lichens and bryophytes (1 μg NH_3 m^{-3}) but below that of higher plants (3 μg NH_3 m^{-3}) (Fig. 6). However, the 95 % confidence interval for decreasers does span the lichen and bryophyte critical level threshold, whereas the 95 % confidence interval for increasers clearly falls above the same critical level threshold (Fig. 6). Specific decreaser and increaser taxa vary in the strength of their response (z-score) to increasing NH_3 deposition, with *G. catinus* being the most responsive decreaser, while *A. seminulum* is the most responsive increaser (Fig. 5). Additionally, of the eleven identified taxa, most decreasers have lobose pseudopodia (4 of 5), whereas the majority of the increasers have filose pseudopodia (4 of 6) (Fig. 5).

3.5. *Functional traits*

Community-weighted mean (CWM) biovolume and pseudostome size were not found to change significantly through seasons at most ALPHA samplers at all six sites. However, across all sites combined, CWM biovolume was found to be significantly lower in winter when compared to summer ($p = 0.008$) and autumn ($p = 0.02$), but to not be significantly different between seasons when high or low/intermediate NH_3 deposition sites were grouped. CWM pseudostome was not found to be significantly different between any season, or when grouping sites by NH_3 deposition levels.

Test material construction at all six sites had no immediately obvious trends between seasons. However, testate amoeba taxa with silicious tests were the most abundant at all six sites, with a mean abundance of 83.9 % across the entire study. Additionally, mean abundances of taxa with siliceous tests were relatively stable across seasons at all sites

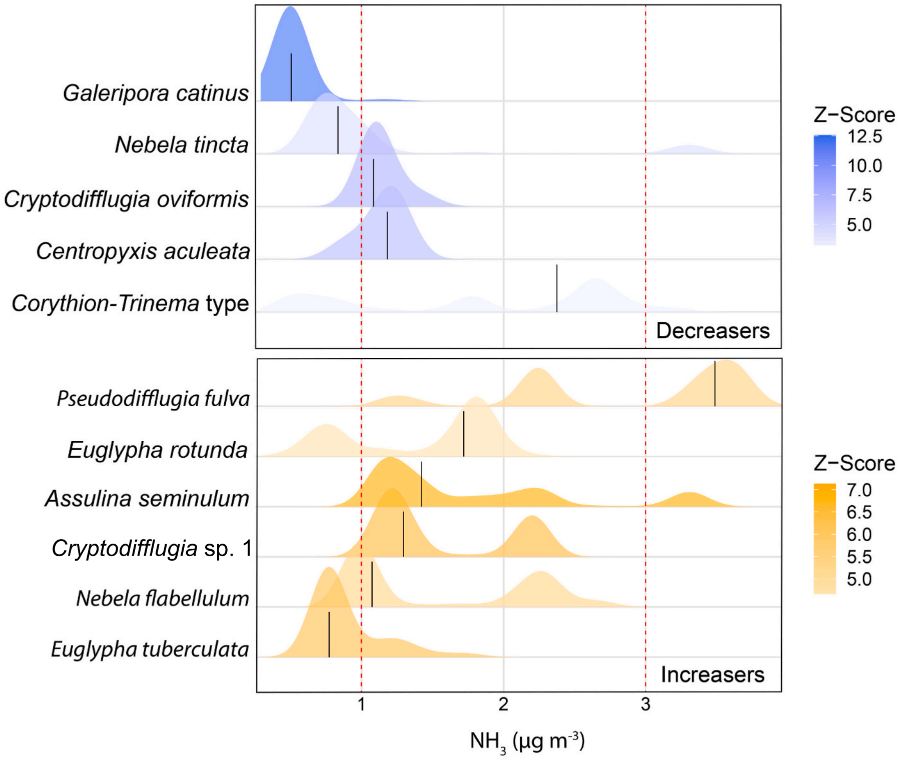

Fig. 5. TITAN analysis ‘ridge plot’ showing the response of testate amoebae taxa to increasing NH_3 deposition (µg m^{-3}). Each density curve represents the distribution of NH_3 values associated with a specific taxon, coloured by z-score values indicating the strength of response. Taxa responding negatively to NH_3 are shown in blue (top panel), while those responding positively are in orange (bottom panel). Black vertical lines indicate the NH_3 deposition at which each taxon shows a significant change in response. Red dashed lines denote NH_3 deposition critical levels for lichens/bryophytes (1 µg m^{-3}) and higher plants (3 µg m^{-3}). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(spring = 85.2 %; summer = 88.1 %; autumn = 81.9 %; winter = 80.3 %). Taxa with proteinaceous tests were the next most common (mean abundance = 14.1 %), and taxa with agglutinated mineral tests were the least common (mean abundance = 2 %). Most sites had relatively similar taxa abundances of different test materials at samples taken near each ALPHA sampler; a notable exception was all 3 ALPHA samplers at Curran Bog, which had much lower mean abundances of taxa with proteinaceous tests (mean = 4.5 %). However, sites with high NH_3 deposition had notably lower mean proteinaceous test taxa abundances in summer (9.86 %) when compared with all other seasons (mean = 15.61 %) (Fig. 7B). Sites with low/intermediate NH_3 deposition proteinaceous test taxa abundances increased throughout the year, peaking in winter (Fig. 7B).

Mixotrophic testate amoebae taxa varied considerably between sites and samples in this experiment, and 7 of the 18 total ALPHA samplers had very low abundances of mixotrophic taxa across all seasons (maximum abundance < 2 %). Across all replicates at all six sites, the mean abundance of mixotrophic taxa was 93 % in spring, 4.42 % in summer, 9.03 % in autumn, and 8.91 % in winter (Fig. 7A). In total, six mixotrophic taxa were identified across all six sites (*A. stenostoma*, *A. wrightianum*, *A. flavum*, *H. sphagni*, *H. papilio*, and *P. spinosa* type). The overwhelming majority of the mixotrophic taxa occurrences observed throughout this experiment, were *A. flavum*, at 87 %. All other mixotrophic taxa abundances were roughly equal (2–4 %), with *A. wrightianum* being the least abundant mixotrophic taxa observed at all six sites (0.52 %). Curran Bog was observed to have by far the lowest overall mean mixotrophic taxa abundances (mean = 1.13 %). Per season, high NH_3 deposition rate sites had similar mixotrophic taxa abundances in all seasons; except summer which was notably lower (Fig. 7A). In low/intermediate NH_3 deposition rate sites, mean mixotrophic taxa abundances increase season-on-season to a peak abundance in autumn (Fig. 7A).

The ratio of testate amoebae with lobose or filose pseudopodia (L/F ratio) was not characterised by any obvious trends during the study period. The mean L/F ratio of all six sites for each season was stable (spring = 0.36; summer = 0.35; autumn = 0.35; winter = 0.33). Likewise, between sites, the mean L/F ratio was relatively similar (Ballynahone Bog = 0.32; Curran Bog = 0.27; Garry Bog = 0.3; Moneygal Bog = 0.4; Peatlands Park = 0.39; Slieve Beagh = 0.4). In all replicates at all six sites, the L/F ratio rarely exceeded 0.5 (taxa with lobose pseudopodia outnumbering taxa with filose pseudopodia), only occurring 31 times in the 216 total replicates of this experiment (Ballynahone Bog = 3; Curran Bog = 0; Garry Bog = 1; Moneygal Bog = 12; Peatlands Park = 7; Slieve Beagh = 8).

4. Discussion

4.1. Ammonia deposition

At Ballynahone Bog, Curran Bog, Garry Bog, and Peatlands Park NH_3 deposition was on average much higher than the critical level of bryophytes and lichens (1 µg NH_3 m^{-3}) (Cape et al., 2009) (Fig. 2). Whereas Moneygal Bog was unique among lowland raised bog sites in not having an increase of NH_3 deposition just before spring sampling, and overall having lower mean NH_3 deposition rates for the year (equal to the critical level of bryophytes and lichens) (Fig. 2D). Finally, at Slieve Beagh, rates of NH_3 deposition only exceeded the critical level of bryophytes and lichens in a summer spike of deposition, with a mean NH_3 deposition rate lower than this critical level throughout the year (Fig. 2F). Observing testate amoeba assemblage dynamics in relation to changing and often critically high NH_3 deposition onto peatlands, appears to have merit in the biomonitoring of this pollutant; although their

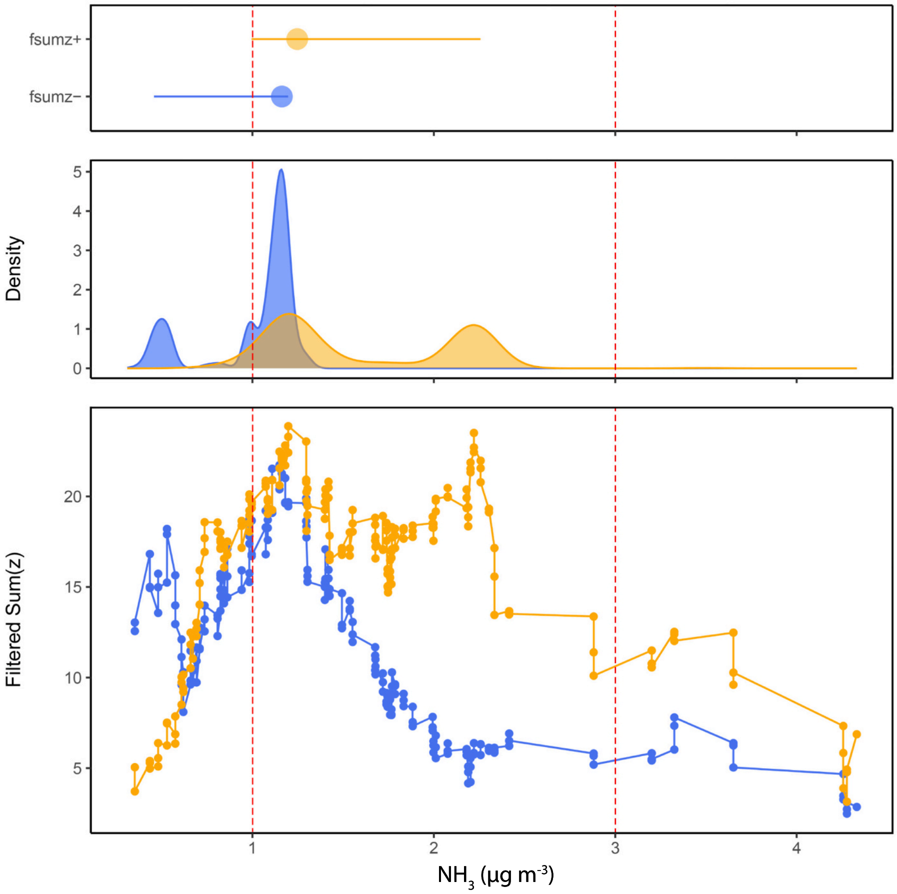

Fig. 6. TITAN summary plot showing community-level responses of testate amoebae to increasing NH_3 deposition (µg m^{-3}). The top panel displays the reliability and strength of change points for negatively (blue; decreasers; fsumz−) and positively (orange; increasers; fsumz+) responding taxa. The middle panel shows kernel density estimates of NH_3 deposition rates associated with each response group. The bottom panel presents filtered sum(z) scores for decreaser (blue) and increaser (orange) taxa. Red dashed lines denote NH_3 deposition critical levels for lichens/bryophytes (1 µg m^{-3}) and higher plants (3 µg m^{-3}). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

response at each site was variable, and more research is required to further elucidate this.

Observed increases in NH_3 deposition throughout the year were likely related to agricultural activity. At Ballynahone Bog, Curran Bog, Garry Bog, and Peatlands Park, dramatic increases in NH_3 deposition were measured in spring, summer, and autumn (Fig. 2). At Moneygal Bog a spike of NH_3 deposition was detected in late April, in summer, and autumn (Fig. 2D). Slieve Beagh alone had only one obvious NH_3 deposition spike, in mid-June before summer samples were collected (Fig. 2F). In previous years, similar increases of NH_3 deposition at these sites were suggested to be the result of nearby application of agricultural manure as slurry (Tang et al., 2022, 2023). Furthermore, other studies have reported that this agricultural practice increases NH_3 deposition rates (Jordan et al., 2007; Pedersen et al., 2024; Uwizeye et al., 2020). Low rates of NH_3 deposition across-the-board in winter during this experiment are related to the Nutrients Action Programme, which prohibits slurry spreading during a 'closed period' in Northern Ireland, beginning in autumn (15th September – 31st October), ending in mid-winter (31st January) (Department of Agriculture, Environment and Rural Affairs, 2024c; The Nutrient Action Programme Regulations (Northern Ireland), 2019). Outside of this period spreading is likely to occur in early spring, summer, and sometimes autumn (Lewis et al., 2003; Tang et al., 2022, 2023; Webb et al., 2010); which aligns closely with observed trends in this study.

Deposition rates at each site are likely a direct result of agricultural activity near each site (Suppl. Fig. A.1) (Tang et al., 2022, 2023; van Dijk et al., 2020). Likewise, though exact information on local animal housing/slurry store or large industrial farming activity was not available for Ballynahone Bog; two large farms directly border the site, which could account for its very high mean NH_3 deposition levels (Suppl. Fig. A.1) (van Dijk et al., 2020). Slieve Beagh was observed in previous years (and in the intermittent data collected for this experiment) to have very low NH_3 deposition rates; related to the size of this large upland blanket bog. Distance from deposition sources is known to strongly control NH_3 deposition (Leith et al., 2004; Zapletal and Mikuška, 2019), and due to the site characteristics of Slieve Beagh most agricultural activity was more distant from the sites ALPHA samplers, compared to all other sites of this study.

4.2. Multivariate analysis

Multivariate results suggest that higher rates of NH_3 deposition have detectable effects on testate amoebae assemblages. Particularly, PERMANOVA analysis showed that testate amoebae assemblage variance could be explained by NH_3 deposition at a majority of high NH_3 deposition sites, but not at sites with low/intermediate rates of NH_3 deposition. Likewise, NMDS ordination biplots (Fig. 4) only showed seasonality between replicates in high NH_3 deposition sites, which often appeared to be associated with increasing NH_3 deposition (Fig. 4A–C). However, this analysis alone only identifies that known high NH_3 deposition significantly controlled testate amoebae assemblage variance in this experiment; further analysis is needed if this method can be used as a bioindication tool for monitoring peatlands for this pollutant, wherein measurements of NH_3 would not be taken.

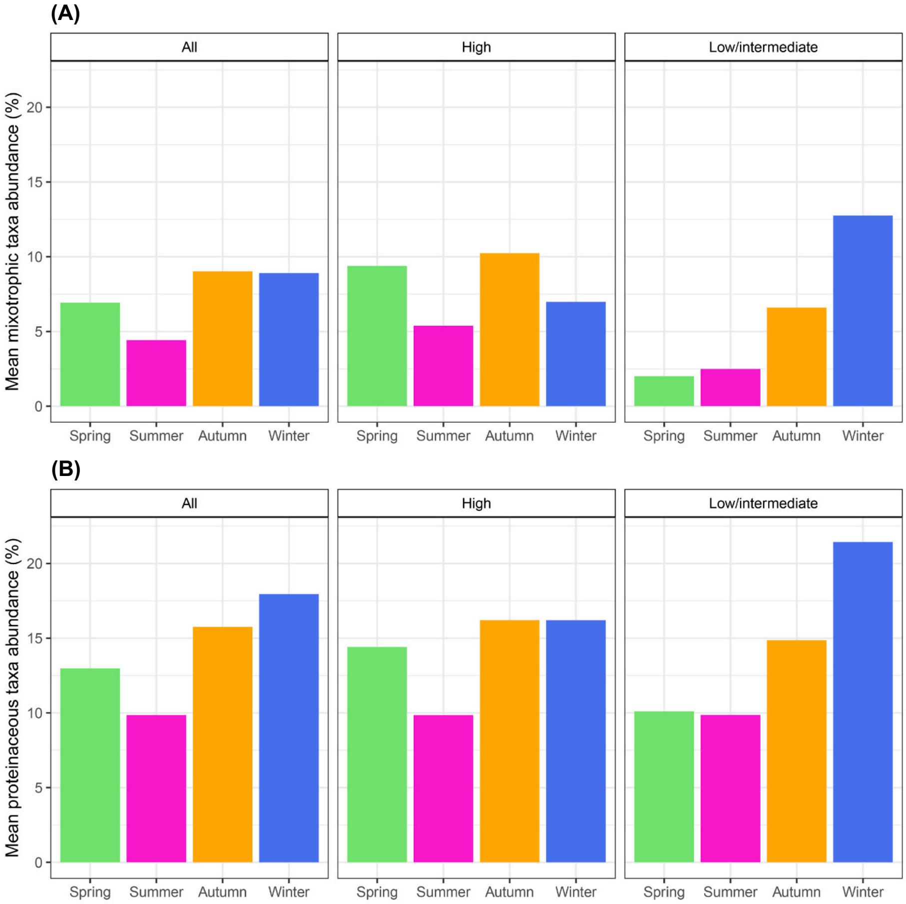

Fig. 7. Mean abundances (%) of mixotrophic testate amoebae taxa (**A**) and taxa with proteinaceous test material construction (**B**) at all six sites, at high NH_3 deposition sites (Ballynahone Bog, Curran Bog, Garry Bog, and Peatlands Park) (mean > 1 NH_3 µg m^{-3}), and low/intermediate NH_3 deposition rates (Slieve Beagh/ Moneygal Bog) (mean ≤ 1 NH_3 µg m^{-3}).

4.3. TITAN analysis

Our findings highlight a clear ecological threshold in the responses of certain testate amoeba taxa to NH_3 deposition, with decreasers peaking around the important lichen and bryophyte critical level (1 µg NH_3 m^{-3}) and increasers showing significant changes above this level (Figs. 5 and 6). While these thresholds align with critical NH_3 levels for lichens and bryophytes, the confidence intervals suggest some overlap, indicating potential variability in species sensitivity, particularly for decreasers (taxa that respond negatively to increasing NH_3 deposition). The strong indicator responses of taxa (Fig. 5) reinforce the utility of TITAN analysis in identifying NH_3-sensitive bioindicators.

Although we observed a distinction in pseudopodium type, with most decreasers having lobose pseudopodia and most increasers possessing filose pseudopodia (Fig. 5), our broader functional trait analysis suggests this pattern is not conclusive. Further study is needed to determine whether pseudopodium type could serve as a meaningful indicator of NH_3 deposition severity on peatlands.

Overall, our results demonstrate that TITAN analysis, particularly when integrated with NMDS and other multivariate techniques, provides a powerful approach for assessing testate amoebae responses to NH_3 deposition. Further research incorporating additional environmental gradients and functional trait-based analyses will be essential to refining our understanding of these relationships.

4.4. Community-weighted functional traits

NH_3 deposition in peatlands may promote algal biomass increases that affect testate amoeba assemblage dynamics (Payne et al., 2013). This study suggested larger testate amoebae may increase in abundance when NH_3 deposition is critically high, potentially a response to increased algal food availability for these dominant microbial predators (Jassey et al., 2012; Payne et al., 2013). In this experiment, it was expected that the abundance of larger (potentially algivorous) testate amoebae taxa would increase in line with NH_3 deposition rates. Additionally, it was anticipated that these taxa would be more abundant in sites with generally higher rates of NH_3 deposition. To evaluate this, testate amoeba CWM biovolumes and pseudostome sizes were examined. It was found that a detectable change in CWM biovolume occurred when all six sites were grouped; wherein winter CWM biovolumes were found to be ~17 % smaller than that of the previous sampling period. Grouped in the same way, no CWM pseudostome size difference was found. The mean reduction of CWM biovolumes during winter at all sites of this study could have been evidence that increased NH_3 deposition in the other periods of this experiment equated to increased abundances of larger testate amoebae taxa. Although having not detected a statistically significant change in CWM pseudostome size for the same period, suggests this size disparity may not be related to large algivorous taxa. Furthermore, a change in CWM biovolume was not observed specifically in high NH_3 deposition sites; suggesting CWM biovolumes were on average smaller in winter at all sites for some other reason. Testate amoebae biovolume and pseudostome size have been linked to changing hydrological conditions, trophic status, and type of vegetation (Fournier et al., 2012; Marcisz et al., 2020; Zhang et al., 2020a); any which could have caused a reduction in CWM biovolumes observed in this experiment.

4.5. Taxa diversity

Overall SDI values did not change much in the study period, although SDI values from all sites combined were lower in spring than the next sampling period (Suppl. Fig. A.8). However, no difference was observed for low/intermediate NH_3 deposition rate, and when high NH_3 deposition sites were grouped, lower spring SDI values were still evident (Suppl. Fig. A.8). Reduced taxa diversity in spring, specifically in sites with high NH_3 deposition rates, directly contrasts with previous research, where testate amoebae taxa diversity is expected to be highest in spring, and little evidence exists for nitrogen pollutants influencing diversity (Lamentowicz et al., 2013; Marcisz et al., 2014; Mitchell, 2004; Mitchell and Gilbert, 2004). A possible explanation for the reduced SDI values observed in spring during this study could be due to a dominant few taxa having greater success during this period. Payne et al. (2013) suggest that algivorous taxa may have greater success in peatlands with higher NH_3 deposition. However, in this study, it was not clear whether algivorous taxa were more successful at times of higher NH_3 deposition, with no taxa responding consistently to changes in NH_3 deposition throughout the year. Additionally, without a longer study period, it is not possible to eliminate the possibility that SDI values were lower in the previous months/years and some other effect is driving the increase in SDI values observed after spring in this study (i.e. CANN project rewetting restoration).

4.6. Mixotrophic taxa

Mixotrophic taxa and their endosymbiotic algae should be more abundant in the summer period due to increased light availability (Herbert et al., 2019; Marcisz et al., 2014; Payne et al., 2016). However, mixotrophic taxa abundances have been shown to reduce in abundance with increasing nitrogen (Mitchell, 2004). In this experiment, mixotrophic taxa had a complicated response to different NH_3 deposition rates (Suppl. Fig. A.11). Broadly, in high NH_3 deposition rate sites, mean mixotrophic taxa abundances were relatively similar across seasons, with a clear overall reduction in mixotrophs in summer and winter (Fig. 7A). Conversely, in low/intermediate NH_3 deposition rate sites mean mixotrophic taxa abundance was lowest in spring and summer, higher in autumn, and highest in winter (Fig. 7A). Across-the-board increases of summer NH_3 deposition observed in this study could explain reduced mixotrophic taxa abundance during this period (Fig. 2). However, NMDS ordination (Suppl. Fig. A.10) showed most individual mixotrophic taxa being associated with increasing NH_3 deposition; with *P. spinosa* type observed to always be associated with increasing NH_3 deposition in this study. Most other mixotrophic taxa had opposite responses to NH_3 deposition at some sites compared to others; overall being associated with increasing NH_3 deposition in most sites they appeared in. These results are difficult to interpret, particularly the response of specific mixotrophic taxa to often critically high NH_3.

If NH_3 deposition was driving mixotrophic taxa abundance declines in this study, it would stand to reason that these taxa would also be less successful in spring and autumn; particularly at high NH_3 sites, where spring, summer, and autumn deposition rates were similar (Fig. 2). Furthermore, summer should be the single most affected sampling period at low/intermediate NH_3 sites, because NH_3 deposition rates were not as high in spring and autumn at these sites. Instead, spring had the lowest abundance of mixotrophic taxa at these sites (Fig. 7A). Moreover, mean mixotrophic taxa abundance was highest in winter at low/intermediate NH_3 sites, directly countering the most favourable conditions of these taxa (Fig. 7A). Increased temperature and reduced rainfall have been demonstrated to decrease mixotrophic testate amoebae taxa abundances and biomass (Basińska et al., 2020; Jassey et al., 2015; Zhang et al., 2020b), and the warmest mean temperatures and some of the lowest total monthly rainfalls were recorded in the months preceding summer sampling at all six sites (Fig. 2). Furthermore, global climate records were consistently broken, month-on-month, throughout 2023 (e.g. global land and sea surface temperatures) (Ripple et al., 2023). Though not simple to determine outright given the study parameters, observed low rainfall and high temperatures at the time of summer sampling at all six sites could be driving mixotrophic taxa declines (Fig. 3); potentially adding to the negative pressure of NH_3 deposition at this time. PERMANOVA analysis supports this, as Ballynahone Bog alone was the only site where either rainfall, temperature, or a combination of the two was not found to significantly explain some of the testate amoebae assemblage variance alongside NH_3 deposition. The methods of this study expanded over multiple years, with on-site measured meteorological conditions, might be able to better separate temperature, rainfall, and NH_3 deposition effects on mixotrophic taxa abundances.

A trend of increasing abundance of taxa with proteinaceous tests was observed in low/intermediate NH_3 deposition sites over the course of the experiment, with the highest abundance of these taxa being from winter replicates at these sites (Fig. 7B). Of the six mixotrophic taxa observed across the six sites, only two do not have proteinaceous tests (*H. sphagni* and *P. spinosa*). Furthermore, these two taxa, which have a siliceous plate test construction, account for only 5.56 % of all mixotrophic taxa occurrences overall. Therefore, changes in test material appear to be overwhelmingly driven by increasing mixotrophic taxa abundances in this experiment (Fig. 7).

4.7. Other environmental influences

Testate amoebae have often been shown to be affected directly or indirectly by rainfall and temperature, particularly in degraded peatlands (Lamentowicz et al., 2013; Marcisz et al., 2014; Swindles et al., 2016), with these being important climatic variables on ombrotrophic bogs (Rydin and Jeglum, 2006; Siegel and Glaser, 2006; Tsyganov et al., 2013). Ballynahone Bog was the only site where both rainfall and temperature did not appear to have some statistically significant effect on the testate amoebae assemblage (Table 5). Despite their proximity to one another (< 3 km) (Fig. 1B), testate amoebae assemblages at Ballynahone Bog appear resilient to changing rainfall and temperature, where these meteorological variables impacted the testate amoebae assemblages at Curran Bog significantly (Table 5). Although both sites have a history of extensive drainage, fire, and peat extraction (Department of the Environment, 2015a, 2015b), Ballynahone Bog remains a large area of active raised bog (Table 1); a counterpoint to the majority degraded raised bog area of Curran Bog (Table 1). The disparity in their overall condition may have led to this evident diverging response in testate amoebae assemblages. Likewise, the poor condition of Curran Bog may have influenced why high NH_3 deposition rates were not found to significantly explain testate amoebae assemblage variation at this site (Table 5). Peatlands Park also has significant areas of degraded raised bog (Table 1); however, only temperature, and not rainfall, was found to explain a degree of the testate amoebae assemblage variance for this site ($p = 0.009$; $F = 3.23$) (Table 5). However, the weather station near Curran Bog recorded almost 200 mm more annual rainfall than the station near Peatlands Park (Fig. 3; Table 1). It is not clear if higher rainfall at Curran Bog or comparatively low rainfall at Peatlands Park led to differences in the effect of NH_3 deposition at these sites; a longer study might aid in interpreting the complex interactions of these environmental variables.

4.8. Limitations

It was not possible to select a lowland raised bog site with low NH_3 deposition rates in place of Slieve Beagh. If possible, this would have ensured all sites were lowland raised bogs eliminating additional considerations when comparing sites. As an upland blanket bog, Slieve Beagh has key differences to all other sites in this experiment, including peat depth and age, land area, annual rainfall, and elevation (Joosten, 2016; Minayeva et al., 2016; Rydin and Jeglum, 2006). Furthermore, as an upland site, Slieve Beagh will receive more wet nitrogen deposition than all other sites of this study (Fowler et al., 1995); which may negatively influence the site's intended role as a low NH_3 deposition comparison to the intermediate and high NH_3 deposition rates of the other sites. Nevertheless, upland blanket bogs and lowland raised bogs are both ombrotrophic, oligotrophic, and share much of the same vegetation making both types of peatlands similarly vulnerable to atmospheric deposition (Bobbink et al., 1998; Levy et al., 2018; Rydin and Jeglum, 2006).

NH_3 data for Slieve Beagh had to be supplemented with data from previous years (Fig. 2F) (Tang et al., 2022, 2023). While this measure was deemed appropriate based on data from most other sites in this study, it includes NH_3 data from during the height of the COVID-19 pandemic. COVID-19 has widely been linked to disrupted agricultural activity (Gruère and Brooks, 2021; Kuttippurath et al., 2024; Tang et al., 2022, 2023), which could have affected the applicability of these previous years as substitutes for missing 2023 data; however, no other data was available for NH_3 deposition at Slieve Beagh. Nevertheless, as the only monitored peatland in Northern Ireland with low NH_3 deposition year-on-year, Slieve Beagh is likely still useful as a counterpoint to the moderate or critically high NH_3 deposition rates of all other sites; although, comparisons and conclusions drawn from the site need to be taken with caution.

In this study, nearby landowners were not contacted to determine the exact timing and location of agricultural slurry spreading or storage near each study site, as NH_3 deposition data collection and land access rights were facilitated by NIEA and UKCEH. As a result, there was limited direct dialogue with landowners regarding NH_3 data or land access rights. Future research should engage with landowners to better identify the timing and location of NH_3 point sources, which would improve the interpretation of NH_3 deposition data, help validate seasonal measurements and provide a clearer understanding of the relationship between agricultural activity, peatland pollution, and the response of testate amoebae.

4.9. Implications

Agricultural activity-linked seasonal NH_3 deposition at Ballynahone Bog, Curran Bog, Garry Bog, Moneygal Bog, Peatlands Park, and Slieve Beagh was characterised by a varied testate amoebae assemblage response. Multivariate analysis was leveraged to demonstrate complex testate amoebae assemblage-level changes, specifically at sites where NH_3 deposition was on average critically high; allowing the first hypothesis of this study to be accepted (H_1 – Testate amoebae assemblage dynamics are altered in response to NH_3 deposition). The fourth hypothesis is accepted (H_4 – Testate amoebae taxa diversity changes in response to increased NH_3 deposition) due to observing SDI values that were statistically significantly lower in the spring at sites with high NH_3 deposition rates. Conversely, the final two hypotheses must be rejected (H_2 – Mixotrophic testate amoebae abundances decrease in response to NH_3 deposition; H_3 – High NH_3 deposition causes increases in abundances of large testate amoebae taxa). No compelling evidence of increased abundance of larger testate amoebae taxa was found, and while mixotrophic taxa abundances did decrease at most ALPHA samplers in summer, it was apparent that low rainfall and high temperatures at this time were likely involved in this decline. Further study will be needed to untangle broad environmental factors and the specific effects of NH_3 deposition, particularly in regard to the abundances of mixotrophic taxa.

This experiment was designed to aid peatland restoration efforts by illuminating the potentially substantial impact of anthropogenic NH_3 deposition on these habitats through testate amoebae analysis. Failing to consider NH_3 deposition when managing peatlands could lead to ineffectual restoration (Krupa, 2003; Zhou et al., 2021). In Northern Ireland, where NH_3 deposition is particularly acute and increasing (Dore et al., 2020; Garland et al., 2023; Jordan et al., 2007; Tang et al., 2018) its consideration is vitally important. However, future research must focus on expanding the methods of this experiment over multiple years to ensure these effects are consistent over longer timescales; especially as this might allow for separating the complex effects of relevant environmental variables. Furthermore, it would be beneficial to test these methods with a wider range of environmental variables, such as: water-table depth; pH; vegetation abundance; light availability; and conductivity, to ensure NH_3 deposition affects testate amoebae to the degree reported here. Notwithstanding these considerations, this study presents testate amoebae assemblages as a promising bioindicator of NH_3 deposition and highlights the widespread nature of this pollutant on peatlands in Northern Ireland.

5. Conclusions

This study investigated the response of testate amoebae assemblages to seasonally variable NH_3 deposition across six peatlands across Northern Ireland. The key findings are as follows:

1. Seasonal peaks in NH_3 deposition, linked to agricultural activity, frequently exceeded critical thresholds for bryophytes and lichens at most study sites.
2. Multivariate analysis revealed distinct seasonal shifts in testate amoebae assemblages at sites experiencing critically high NH_3 deposition, demonstrating their potential as indicators of this peatland pollutant.
3. TITAN analysis identified key NH_3-sensitive testate amoebae taxa, suggesting their potential use in biomonitoring NH_3 pollution in peatlands.
4. Contrary to expectations, large testate amoebae taxa did not show increased abundance in response to elevated NH_3 deposition. Further research is needed to assess this hypothesized response.
5. Sites with critically high NH_3 deposition exhibited lower abundances of mixotrophic testate amoebae taxa during typically favourable months, indicating the potential of this functional trait as a bioindicator of NH_3 pollution.
6. Testate amoebae diversity was lowest in spring at high NH_3 deposition sites, diverging from previous findings that nitrogen deposition does not affect diversity and that taxa richness should peak in spring. While NH_3 may contribute to this decline, further experimental studies are needed to disentangle its effects from other environmental factors.

These findings highlight the value of testate amoebae as bioindicators of NH_3 pollution and suggest further research is needed to refine their application in peatland monitoring and conservation efforts.

CRediT authorship contribution statement

Callum R.C. Evans: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **David A. Hatton:** Writing – review & editing, Project administration, Investigation. **Graeme T. Swindles:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Funding sources

This study was undertaken as part of a PhD project at Queen's University Belfast, Northern Ireland, UK. A PhD stipend and research training support grant were provided by the Department for the Economy Collaborative Awards in Science and Technology (DfE CAST) to CRCE. The Northern Ireland Environment Agency, an executive agency within the Department of Agriculture, Environment and Rural Affairs, funds the atmospheric ammonia monitoring, analysis, and reporting used in this study in partnership with the UK Centre for Ecology and

Hydrology, Ulster Wildlife, and Monaghan County Council. GTS acknowledges financial support from the Dutch Foundation for the Conservation of Irish Bogs, the Quaternary Research Association and the Leverhulme Trust (RPG-2021-354). GTS was employed by Queen's University Belfast during the study period. All authors have no other relevant financial or non-financial interests to disclose.

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.

Acknowledgments

The authors would like to thank staff at the Department of Agriculture, Environment and Rural Affairs, Northern Ireland Environment Agency (NIEA), including Anne McCourt and Áine O'Reilly, for providing the data for this study under NIEA's programme of work to evaluate nitrogen deposition impacts on NI's natural ecosystems, and for their help in accessing all six peatland sites. Likewise, our thanks to their project partners Dr. Ulli Dragosits and staff at the UK Centre for Ecology and Hydrology, Ulster Wildlife, and Monaghan County Council. Additionally, thanks to Adrien Craig, David Evans, Keith Moore, and Route Gun Club for ensuring safe access to Curran Bog, Garry Bog, and Slieve Beagh was possible. Finally, thanks also to Helen Essell and Matthew Hunt for extensive fieldwork assistance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ejop.2025.126147.

Data availability

Data will be made available on request.

References

Amon, B., Amon, T., Boxberger, J., Alt, C., 2001. Emissions of NH_3, N_2O and CH_4 from dairy cows housed in a farmyard manure tying stall (housing, manure storage, manure spreading). Nutr. Cycl. Agroecosyst. 60, 103–113. https://doi.org/10.1023/A:1012649028772.

Apori, S.O., Mcmillan, D., Giltrap, M., Tian, F., 2022. Mapping the restoration of degraded peatland as a research area: a scientometric review. Front. Environ. Sci. 10, e942788. https://doi.org/10.3389/fenvs.2022.942788.

Araji, A.A., Abdo, Z.O., Joyce, P., 2001. Efficient use of animal manure on cropland – economic analysis. Bioresour. Technol. 79, 179–191. https://doi.org/10.1016/S0960-8524(01)00042-6.

Avel, E., Pensa, M., 2013. Preparation of testate amoebae samples affects water table depth reconstructions in peatland palaeoecological studies. Est. J. Earth Sci. 62, 113–119. https://doi.org/10.3176/earth.2013.09.

Baker, M.E., King, R.S., 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds. Methods Ecol. Evol. 1, 25–37. https://doi.org/10.1111/j.2041-210X.2009.00007.x.

Barry, D.A.J., Goorahoo, D., Goss, M.J., 1993. Estimation of nitrate concentrations in groundwater using a whole farm nitrogen budget. J. Environ. Qual. 22, 767–775. https://doi.org/10.2134/jeq1993.00472425002200040019x.

Basińska, A.M., Reczuga, M.K., Gąbka, M., Stróżecki, M., Łuców, D., Samson, M., Urbaniak, M., Leśny, J., Chojnicki, B.H., Gilbert, D., Sobczyński, T., Olejnik, J., Silvennoinen, H., Juszczak, R., Lamentowicz, M., 2020. Experimental warming and precipitation reduction affect the biomass of microbial communities in a *Sphagnum* peatland. Ecol. Indic. 112, e106059. https://doi.org/10.1016/j.ecolind.2019.106059.

Behera, S.N., Sharma, M., Aneja, V.P., Balasubramanian, R., 2013. Ammonia in the atmosphere: a review on emission sources, atmospheric chemistry and deposition on terrestrial bodies. Environ. Sci. Pollut. Res. 20, 8092–8131. https://doi.org/10.1007/s11356-013-2051-9.

Bobbink, R., Hornung, M., Roelofs, J., 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J. Ecol. 86, 717–738. https://doi.org/10.1046/j.1365-2745.1998.8650717.x.

Booth, R.K., 2002. Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: modern ecology and hydrological calibration. J. Paleolimnol. 28, 329–348. https://doi.org/10.1023/A:1021675225099.

Booth, R.K., Lamentowicz, M., Charman, D.J., 2010. Preparation and analysis of testate amoebae in peatland palaeoenvironmental studies. Mires Peat 7, 1–7.

Bullock, C.H., Collier, M.J., Convery, F., 2012. Peatlands, their economic value and priorities for their future management – the example of Ireland. Land Use Policy 29, 921–928. https://doi.org/10.1016/j.landusepol.2012.01.010.

Cape, J.N., van der Eerden, L.J., Sheppard, L.J., Leith, I.D., Sutton, M.A., 2009. Evidence for changing the critical level for ammonia. Environ. Pollut. 157, 1033–1037. https://doi.org/10.1016/j.envpol.2008.09.049.

Chapman, S., Buttler, A., Francez, A.-J., Laggoun-Défarge, F., Vasander, H., Schloter, M., Combe, J., Grosvernier, P., Harms, H., Epron, D., Gilbert, D., Mitchell, E.A.D., 2003. Exploitation of northern peatlands and biodiversity maintenance: a conflict between economy and ecology. Front. Ecol. Environ. 1, 525–532. https://doi.org/10.1890/1540-9295(2003)001[0525:EONPAB]2.0.CO;2.

Charman, D.J., Hendon, D., Woodland, W.A., 2000. The identification of testate amoebae (Protozoa: Rhizopoda) in peats. QRA technical guide no. 9. Quaternary research association, London, pp. 1–147.

Department of Agriculture, Environment and Rural Affairs, 2024a. Emissions of air pollutants in the UK – Summary. https://www.gov.uk/government/statistics/emissions-of-air-pollutants/emissions-of-air-pollutants-in-the-uk-summary (accessed 27 August 2024a).

Department of Agriculture, Environment and Rural Affairs, 2024b. Emission of air pollutants in the UK – Ammonia (NH_3). https://www.gov.uk/government/statistics/emissions-of-air-pollutants/emissions-of-air-pollutants-in-the-uk-ammonia-nh3 (accessed 11 June 2024b).

Department of Agriculture, Environment and Rural Affairs, 2024c. Nutrients Action Programme Implementation Report for 2020–2023. https://www.daera-ni.gov.uk/nutrients-action-programme-implementation-report-2020-2023 (accessed 23 August 2024c).

Department of the Environment, 2015a. Ballynahone Bog SAC, UK0016599, conservation objectives. https://www.daera-ni.gov.uk/sites/default/files/publications/doe/land-information-ballynahone-bog-conservation-objectives-2015a.pdf (accessed 3 June 2024).

Department of the Environment, 2015b. Curran Bog SAC, UK0030322, conservation objectives. https://www.daera-ni.gov.uk/sites/default/files/publications/doe/land-information-curran-bog-conservation-objectives-2015b.pdf (accessed 3 June 2024).

Department of the Environment, 2015c. Garry Bog SAC, UK0016610, conservation objectives. https://www.daera-ni.gov.uk/sites/default/files/publications/doe/land-information-garry-bog-conservation-objectives-2015c.pdf (accessed 3 June 2024).

Department of the Environment, 2015d. Moneygal Bog SAC, UK0030211, conservation objectives. https://www.daera-ni.gov.uk/sites/default/files/publications/doe/land-information-moneygal-bog-conservation-objectives-2015d.pdf (accessed 3 June 2024).

Department of the Environment, 2015e. Peatlands Park SAC, UK0030236, conservation objectives. https://www.daera-ni.gov.uk/sites/default/files/publications/doe/land-information-peatlands-park-conservation-objectives-2015e.pdf (accessed 3 June 2024).

Department of the Environment, 2015f. Slieve Beagh SAC, UK0016622, conservation objectives. https://www.daera-ni.gov.uk/sites/default/files/publications/doe/Conservation%20Objectives%20%282017%29.%20%20Slieve%20Beagh%20SAC.%20%20Version%202.1%20-%20amendment%2010.10.2017.%20PDF.PDF accessed 3 June 2024).

Dore, A., Hall, J., Rowe, E., Pescott, O., Carnell, E., Tomlinson, S., Dragosits, U., Tang, S., Simkin, J., Stephens, A., Braban, C., Bealey, W., Sutton, M., 2020. Modelling the concentration of ammonia and exceedance of the critical level in the UK. In: Mensink, C., Gong, W., Hakami, A. (Eds.), Air Pollution Modeling and its Application XXVI. ITM 2018. Springer Proceedings in Complexity. Springer, Cham, pp. 59–64. https://doi.org/10.1007/978-3-030-22055-6_10.

Environmental Protection Agency, 2024a. Ireland's provisional greenhouse gas emissions 1990–2023. https://www.epa.ie/publications/monitoring–assessment/climate-change/air-emissions/irelands-provisional-greenhouse-gas-emissions-1990-2023.php (accessed 27 August 2024a).

Environmental Protection Agency, 2024b. Ireland's air pollutant emissions 2022 (1990–2030). https://www.epa.ie/publications/monitoring–assessment/climate-change/air-emissions/irelands-air-pollutant-emissions-2022-1990-2030.php (accessed 27 August 2024b).

Esri, 2024a. Imagery (WGS84). https://www.arcgis.com/home/item.html?id=52bdc7ab7fb044d98add148764eaa30a (accessed 16 September 2024).

Esri, 2024b. Light gray canvas. https://www.arcgis.com/home/item.html?id=979c6cc89af9449cbeb5342a439c6a76 (accessed 16 September 2024).

Evans, C.R.C., Mullan, D.J., Roe, H.M., Fox, T.M., Gray, S., Swindles, G.T., 2024. Response of testate amoeba assemblages to peatland drain blocking. Wetlands Ecol. Manag. 32, 1–18. https://doi.org/10.1007/s11273-023-09949-w.

Fournier, B., Malysheva, E., Mazei, Y., Moretti, M., Mitchell, E.A.D., 2012. Toward the use of testate amoeba functional traits as indicator of floodplain restoration success. Eur. J. Soil Biol. 49, 85–91. https://doi.org/10.1016/j.ejsobi.2011.05.008.

Fournier, B., Lara, E., Jassey, V.E., Mitchell, E.A., 2015. Functional traits as a new approach for interpreting testate amoeba palaeo-records in peatlands and assessing the causes and consequences of past changes in species composition. Holocene 25, 1375–1383. https://doi.org/10.1177/0959683615585842.

Fowler, D., Leith, I.D., Binnie, J., Crossley, A., Inglis, D.W.F., Choularton, T.W., Gay, M., Longhurst, J.W.S., Conland, D.E., 1995. Orographic enhancement of wet deposition in the United Kingdom: continuous monitoring. Water Air Soil Pollut. 85, 2107–2112. https://doi.org/10.1007/BF01186145.

Fox, A.D., 1986. Effects of ditch-blockage on adult Odonata at a coastal raised mire site in central West Wales, United Kingdom. Odonatologica 15 (3), 327–334.

Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320, 889–892. https://doi.org/10.1126/science.1136674.

Garland, L., Gleeson, L., Blannin, L., Mitchell, J., Batchelor, A., Szanto, C., Hampshire, K., King, K., Richmond, B., Thistlethwaite, G., 2023. Air pollutant inventories for England. Scotland, Wales, and Northern Ireland 2005–2021. https://uk-air.defra.gov.uk/reports/cat07/2310261138_DA_Air_Pollutant_Inventories_2005-2021_Final_v1.2.pdf. (Accessed 21 August 2024).

Gilbert, D., Amblard, C., Bourdier, G., Francez, A.-J., 1998. The microbial loop at the surface of a peatland: structure, function, and impact of nutrient input. Microb. Ecol. 35, 83–93. https://doi.org/10.1007/s002489900062.

Goss, M.J., Beauchamp, E.G., Miller, M.H., 1995. Can a farming systems approach help minimize nitrogen losses to the environment? J. Contam. Hydrol. 20, 285–297. https://doi.org/10.1016/0169-7722(95)00074-7.

Graham, C.T., Wilson, M.W., Gittings, T., Kelly, T.C., Irwin, S., Quinn, J.L., O'Halloran, J., 2017. Implications of afforestation for bird communities: the importance of preceding land-use type. Biodivers. Conserv. 26, 3051–3071. https://doi.org/10.1007/s10531-015-0987-4.

Gruère, G., Brooks, J., 2021. Viewpoint: Characterising early agricultural and food policy responses to the outbreak of COVID-19. Food Policy 100, e102017. https://doi.org/10.1016/j.foodpol.2020.102017.

Guo, C., Liu, X., He, X., 2022. A global meta-analysis of crop yield and agricultural greenhouse gas emissions under nitrogen fertilizer application. Sci. Total Environ. 831, e154982. https://doi.org/10.1016/j.scitotenv.2022.154982.

Heikkinen, R.K., Aapala, K., Määttänen, A.-M., Leikola, N., Kartano, L., Aalto, J., 2023. Climate change and land use threats to species of aapa mires, an EU priority habitat. J. Nat. Conserv. 73, e126390. https://doi.org/10.1016/j.jnc.2023.126390.

Herbert, R.P., Peters, S.C., Nelson, D.M., Booth, R.K., 2019. Light variability and mixotrophy: responses of testate amoeba communities and shell δ^{13} C values to a peatland shading experiment. Eur. J. Protistol. 67, 15–26. https://doi.org/10.1016/j.ejop.2018.10.005.

Huisman, J., Codd, G.A., Paerl, H.W., Ibelings, B.W., Verspagen, J.M.H., Visser, P.M., 2018. Cyanobacterial blooms. Nat. Rev. Microbiol. 16, 471–483. https://doi.org/10.1038/s41579-018-0040-1.

IPCC, 2023. Climate Change 2023: Synthesis Report. https://www.ipcc.ch/report/ar6/syr/downloads/report/IPCC_AR6_SYR_FullVolume.pdf (accessed 7 June 2024).

Jassey, V.E.J., Shimano, S., Dupuy, C., Toussainta, M.-L., Gilbert, D., 2012. Characterizing the feeding habits of the testate amoebae *Hyalosphenia papilio* and *Nebela tincta* along a narrow "fen-bog" gradient using digestive vacuole content and ^{13}C and ^{15}N isotopic analyses. Protist 163, 451–464. https://doi.org/10.1016/j.protis.2011.07.006.

Jassey, V.E.J., Signarbieux, C., Hättenschwiler, S., Bragazza, L., Buttler, A., Delarue, F., Fournier, B., Gilbert, D., Laggoun-Défarge, F., Lara, E., Mills, R.T.E., Mitchell, E.A.D., Payne, R.J., Robroek, B.J.M., 2015. An unexpected role for mixotrophs in the response of peatland carbon cycling to climate warming. Sci. Rep. 5, e16931. https://doi.org/10.1038/srep16931.

Jauhiainen, J., Wallén, B., Malmer, N., 1998. Potential NH_4^+ and NO_3^- uptake in seven *Sphagnum* species. New Phytol. 138, 287–293. https://doi.org/10.1046/j.1469-8137.1998.00110.x.

Jiroušek, M., Poulíčková, A., Kintrová, K., Opravilová, V., Hájková, P., Rybníček, K., Kočí, M., Bergová, K., Hnilica, R., Mikulášková, E., Králová, Š., Hájek, M., 2013. Long-term and contemporary environmental conditions as determinants of the species composition of bog organisms. Freshw. Biol. 58, 2196–2207. https://doi.org/10.1111/fwb.12201.

Joosten, H., 2016. Peatlands across the globe. In: Bonn, A., Allott, T., Evans, M., Joosten, H., Stoneman, R. (Eds.), Peatland Restoration and Ecosystem Services: Science, Policy and Practice. Cambridge University Press, Cambridge, pp. 19–43.

Jordan, C., Higgins, A., Wright, P., 2007. Slurry acceptance mapping of Northern Ireland for run-off risk assessment. Soil Use Manage. 23, 145–253. https://doi.org/10.1111/j.1475-2743.2007.00089.x.

Kapusta, P., Szarek-Łukaszewska, G., Godzik, B., Łopata, B., 2014. Recent nitrogen deposition in Poland monitored with the moss *Pleurozium schreberi*. Pol. Bot. J. 59, 131–135. https://doi.org/10.2478/pbj-2014-0018.

Kelleghan, D.B., Hayes, E.T., Everard, M., Keating, P., Lesniak-Podsiadlo, A., Curran, T. P., 2021. Atmospheric ammonia and nitrogen deposition on Irish Natura 2000 sites: implications for Irish agriculture. Atmos. Environ. 261, e118611. https://doi.org/10.1016/j.atmosenv.2021.118611.

Krashevska, V., Tsyganov, A.N., Esaulov, A.S., Mazei, Y.A., Hapsari, K.A., Saad, A., Sabiham, S., Behling, H., Biagioni, S., 2020. Testate amoeba species- and trait-based transfer functions for reconstruction of hydrological regime in tropical peatland of Central Sumatra, Indonesia. Front. Ecol. Evol. 8, e225. https://doi.org/10.3389/fevo.2020.00225.

Krupa, S.V., 2003. Effects of atmospheric ammonia (NH_3) on terrestrial vegetation: a review. Environ. Pollut. 124, 179–221. https://doi.org/10.1016/S0269-7491(02)00434-7.

Kumar, R.R., Park, B.J., Cho, J.Y., 2013. Application and environmental risks of livestock manure. J. Korean Soc. Appl. Biol. Chem. 56, 497–503. https://doi.org/10.1007/s13765-013-3184-8.

Kuttippurath, J., Patel, V.K., Kashyap, R., Singh, A., Clerbaux, C., 2024. Anomalous increase in global atmospheric ammonia during COVID-19 lockdown: need policies to curb agricultural emissions. J. Clean. Prod. 434, e140424. https://doi.org/10.1016/j.jclepro.2023.140424.

Lamentowicz, M., Bragazza, L., Buttler, A., Jassey, V.E.J., Mitchell, E.A.D., 2013. Seasonal patterns of testate amoeba diversity, community structure and species–environment relationships in four *Sphagnum*-dominated peatlands along a 1300 m altitudinal gradient in Switzerland. Soil Biol. Biochem. 67, 1–11. https://doi.org/10.1016/j.soilbio.2013.08.002.

Leifeld, J., Menichetti, L., 2018. The underappreciated potential of peatlands in global climate change mitigation strategies. Nat. Commun. 9, e1071. https://doi.org/10.1038/s41467-018-03406-6.

Leip, A., Billen, G., Garnier, J., Grizzetti, B., Lassaletta, L., Stefan Reis, S., Simpson, D., Sutton, M.A., de Vries, W., Weiss, F., Westhoek, H., 2015. Impacts of European livestock production: nitrogen, Sulphur, phosphorus and greenhouse gas emissions, land-use, water eutrophication and biodiversity. Environ. Res. Lett. 10, e115004. https://doi.org/10.1088/1748-9326/10/11/115004.

Leith, I.D., Sheppard, L.J., Fowler, D., Cape, J.N., Jones, M., Crossley, A., Hargreaves, K. J., Tang, Y.S., Mark Theobald, M., Sutton, M.R., 2004. Quantifying dry NH_3 deposition to an ombrotrophic bog from an automated NH_3 field release system. Water Air Soil Pollut. Focus 4, 207–218. https://doi.org/10.1007/s11267-004-3031-3.

Levy, P., van Dijk, N., Gray, A., Sutton, M., Jones, M., Leeson, S., Dise, N., Leith, I., Sheppard, L., 2018. Response of a peat bog vegetation community to long-term experimental addition of nitrogen. J. Ecol. 107 (3), 1167–1186. https://doi.org/10.1111/1365-2745.13107.

Lewis, D.R., McGechan, M.B., McTaggart, I.P., 2003. Simulating field-scale nitrogen management scenarios involving fertiliser and slurry applications. Agr. Syst. 76, 159–180. https://doi.org/10.1016/S0308-521X(02)00032-X.

Lindberg, H., 1899. En rik torffyndighet i Jorvis-socken Savolaks (A rich peat deposit in the Jorvis parish of Savolaks). Finska Mosskulturföreningens Årsbok 1899, 178–213.

Loubet, B., Asman, W.A.H., Theobald, M.R., Hertel, O., Tang, S.Y., Robin, P., Hassouna, M., Dämmgen, U., Genermont, S., Cellier, P., Sutton, M.A., 2009. Ammonia deposition near hot spots: Processes, models and monitoring methods. In: Sutton, M.A., Reis, S., Baker, S.M.H. (Eds.), Atmospheric Ammonia. Springer, Dordrecht, pp. 205–267.

Marcisz, K., Lamentowicz, Ł., Słowińska, S., Słowiński, M., Muszak, W., Lamentowicz, M., 2014. Seasonal changes in *Sphagnum* peatland testate amoeba communities along a hydrological gradient. Eur. J. Protistol. 50, 445–455. https://doi.org/10.1016/j.ejop.2014.07.001.

Marcisz, K., Jassey, V.E.J., Kosakyan, A., Krashevska, V., Lahr, D.J.G., Enrique Lara, E., Lamentowicz, Ł., Lamentowicz, M., Macumber, A., Mazei, Y., Mitchell, E.A.D., Nasser, N.A., Patterson, R.T., Roe, H.M., Singer, D., Tsyganov, A.N., Fournier, B., 2020. Testate amoeba functional traits and their use in paleoecology. Front. Ecol. Evol. 8, e575966. https://doi.org/10.3389/fevo.2020.575966.

Masso, C., Baijukya, F., Ebanyat, P., Bouaziz, S., Wendt, J., Bekunda, M., Vanlauwe, B., 2017. Dilemma of nitrogen management for future food security in sub-Saharan Africa – a review. Soil Res. 55, 425–434. https://doi.org/10.1071/SR16332.

McGinn, S.M., Janzen, H.H., 1998. Ammonia sources in agriculture and their measurement. Can. J. Soil Sci. 78, 139–148. https://doi.org/10.4141/S96-059.

McKeown, M.M., Burge, O.R., Richardson, S.J., Wood, J.R., Mitchell, E.A.D., Wilmshurst, J.M., 2024. Biomonitoring tool for New Zealand peatlands: testate amoebae and vascular plants as promising bioindicators. J. Environ. Manage. 354, e120243. https://doi.org/10.1016/j.jenvman.2024.120243.

Meade, R., 1992. Some early changes following the rewetting of a vegetated cutover peatland surface at Danes Moss, Cheshire, UK, and their relevance to conservation management. Biol. Conserv. 61, 31–40. https://doi.org/10.1016/0006-3207(92)91205-7.

Met Office, 2024a. MIDAS open: UK hourly rainfall data, v202407. NERC EDS Centre for environmental data analysis, 06 august 2024. https://doi.org/10.5285/6c619c67138843b8839a5788ac749e12. Accessed 15 August 2024.

Met Office, 2024b. MIDAS open: UK daily temperature data, v202407. NERC EDS Centre for environmental data analysis, 06 august 2024. https://doi.org/10.5285/b7c6295b72c54fa9bcd8308fea2727e7. Accessed 15 August 2024.

Meyer, C., Gilbert, D., Gillet, F., Moskura, M., Franchi, M., Bernard, N., 2012. Using "bryophytes and their associated testate amoeba" microsystems as indicators of atmospheric pollution. Ecol. Indic. 13, 144–151. https://doi.org/10.1016/j.ecolind.2011.05.020.

Midolo, G., Alkemade, R., Schipper, A.M., Benítez-López, A., Perring, M.P., de Vries, W., 2019. Impacts of nitrogen addition on plant species richness and abundance: a global meta-analysis. Glob. Ecol. Biogeogr. 28, 398–413. https://doi.org/10.1111/geb.12856.

Minayeva, T., Bragg, O., Sirin, A., 2016. Peatland biodiversity and its restoration. In: Bonn, A., Allott, T., Evans, M., Joosten, H., Stoneman, R. (Eds.), Peatland Restoration and Ecosystem Services: Science, Policy and Practice. Cambridge University Press, Cambridge, pp. 44–62.

Mitchell, E.A.D., 2004. Response of testate amoebae (Protozoa) to N and P fertilization in an Arctic wet sedge tundra. Arct. Antarct. Alp. Res. 36, 78–83. https://doi.org/10.1657/1523-0430(2004)036[0078,ROTAPT]2.0.CO;2.

Mitchell, E.A.D., Gilbert, D., 2004. Vertical micro-distribution and response to nitrogen deposition of testate amoebae in *Sphagnum*. J. Eukaryot. Microbiol. 51, 480–490. https://doi.org/10.1111/j.1550-7408.2004.tb00400.x.

Mitchell, E.A.D., Buttler, A.J., Warner, B.G., Gobat, J.-M., 1999. Ecology of testate amoebae (Protozoa: Rhizopoda) in *Sphagnum* peatlands in the Jura mountains, Switzerland and France. Écoscience 6, 565–576. https://doi.org/10.1080/11956860199911682555.

Mitchell, E.A.D., Gilbert, D., Buttler, A., Amblard, C., Grosvernier, P., Gobat, J.-M., 2003. Structure of microbial communities in *Sphagnum* peatlands and effect of atmospheric carbon dioxide enrichment. Microb. Ecol. 46, 187–199. https://doi.org/10.1007/BF03036882.

Moore, P.D., 1987. Ecological and hydrological aspects of peat formation. Spec. Publ. 32, 7–15. https://doi.org/10.1144/GSLSP.1987.032.01.02.

Nordbeck, R., Högl, K., 2024. National peatland strategies in Europe: current status, key themes, and challenges. Regul. Environ. Change 24, e5. https://doi.org/10.1007/s10113-023-02166-4.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. Vegan: community ecology package. R package version 2.6-4. https://cran.r-project.org/web/packages/vegan/vegan.pdf (accessed 18 April 2024).

Payne, R.J., Mitchell, E.A.D., 2009. How many is enough? Determining optimal count totals for ecological and palaeoecological studies of testate amoebae. J. Paleolimnol. 42, 483–495. https://doi.org/10.1007/s10933-008-9299-y.

Payne, R.J., Thompson, A.M., Standen, V., Field, C.D., Caporn, S.J.M., 2012. Impact of simulated nitrogen pollution on heathland microfauna, mesofauna and plants. Eur. J. Soil Biol. 49, 73–79. https://doi.org/10.1016/j.ejsobi.2011.08.003.

Payne, R.J., Jassey, V.E.J., Leith, I.D., Sheppard, L.J., Dise, N.B., Gilbert, D., 2013. Ammonia exposure promotes algal biomass in an ombrotrophic peatland. Soil Biol. Biochem. 57, 936–938. https://doi.org/10.1016/j.soilbio.2012.09.012.

Payne, R.J., Creevy, A., Malysheva, E., Ratcliffe, J., Andersen, R., Tsyganov, A.N., Rowson, J.G., Marcisz, K., Zielińska, M., Lamentowicz, M., Lapshina, E.D., Mazei, Y., 2016. Tree encroachment may lead to functionally-significant changes in peatland testate amoeba communities. Soil Biol. Biochem. 98, 18–21. https://doi.org/10.1016/j.soilbio.2016.04.002.

Pedersen, J., Hafner, S.D., Pacholski, A., Karlsson, V.I., Rong, L., Labouriau, R., Kamp, J. N., 2024. Evaluation of optimized flux chamber design for measurement of ammonia emission after field application of slurry with full-scale farm machinery. Atmos. Meas. Tech. 17, 4493–4505. https://doi.org/10.5194/amt-17-4493-2024.

Pérez-Uz, B., Galfione, V.C., Ochoa-Hueso, R., Martín-Cereceda, M., 2023. Protist diversity responses to experimental N deposition in biological crusts of a semiarid Mediterranean ecosystem. Protist 174, e125929. https://doi.org/10.1016/j.protis.2022.125929.

Posthumus, A.C., 1988. Critical Levels for Effects of ammonia and Ammonium. Proceedings of the Bad Harzburg Workshop, UBA, Berlin, pp. 117–127.

R Core Team, 2024. R: A Language and Environment for Statistical Computing. Austria, Vienna. https://www.r-project.org/ (accessed 15 July 2024).

Ripple, W.J., Wolf, C., Gregg, J.W., Rockström, J., Newsome, T.M., Law, B.E., Marques, L., Lenton, T.M., Xu, C., Huq, S., Simons, L., King, D.A., 2023. The 2023 state of the climate report: entering uncharted territory. BioScience 73, 841–850. https://doi.org/10.1093/biosci/biad080.

Roe, H.M., Elliott, S.M., Patterson, R.T., 2017. Re-assessing the vertical distribution of testate amoeba communities in surface peats: implications for palaeohydrological studies. Eur. J. Protistol. 60, 13–27. https://doi.org/10.1016/j.ejop.2017.03.006.

Rydin, H., Jeglum, J., 2006. The Biology of Peatlands. Oxford University Press, Oxford.

Salm, J.-O., Maddison, M., Tammik, S., Soosaar, K., Truu, J., Mander, Ü., 2012. Emissions of CO_2, CH_4, and N_2O from undisturbed, drained and mined peatlands in Estonia. Hydrobiologia 692, 41–55. https://doi.org/10.1007/s10750-011-0934-7.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, IL.

Sheppard, L.J., Leith, I.D., Mizunuma, T., Cape, J.N., Crossley, A., Leeson, S., Sutton, M. A., van Dijk, N., Fowler, D., 2011. Dry deposition of ammonia gas drives species change faster than wet deposition of ammonium ions: evidence from a long-term field manipulation. Glob. Change Biol. 17, 3589–3607. https://doi.org/10.1111/j.1365-2486.2011.02478.x.

Siegel, D.I., Glaser, P., 2006. The hydrology of peatlands. In: Wieder, R.K., Vitt, D.H. (Eds.), Boreal Peatland Ecosystems, Ecological Studies, vol. 1988. Springer, Heidelberg, pp. 289–311.

Siemensma, F.J., 2024. Microworld, world of amoeboid organisms. https://arcella.nl/ (accessed 5 June 2024).

Silva, Y.G.D., Sampaio, G.S., Ramos, B.R.D., Freitas, Y.G.C., Nascimento, L., Branco, C.W.C., Miranda, V.B.S., 2022. Testate amoebae (Amorphea, Amoebozoa, Cercozoa) as bioindicators: a scientometric review. Acta Limnol. Bras. 34, e20. https://doi.org/10.1590/s2179-975x0722.

Smith, H.G., Bobrov, A., Lara, E., 2008. Diversity and biogeography of testate amoebae. Biodivers. Conserv. 17, 329–343. https://doi.org/10.1007/s10531-007-9260-9.

Spitzer, K., Danks, H.V., 2006. Insect biodiversity of boreal peat bogs. Annu. Rev. Entomol. 51, 137–161. https://doi.org/10.1146/annurev.ento.51.101041.150036.

Stein, L.Y., Klotz, M.G., 2016. The nitrogen cycle. Curr. Biol. 26, R94–R98. https://doi.org/10.1016/j.cub.2015.12.021.

Stephens, A., Iwanicka, A., Tang, S., 2021. Ammonia Measurements from Passive Samplers at Four UK Eutrophying and Acidifying Pollutants (UKEAP) Network Sites, 2020. https://doi.org/10.5285/1766eb32-1878-47e6-8dc8-d434957d1e32 (accessed 27 August 2024).

Swindles, G.T., Green, S.M., Brown, L., Holden, J., Raby, C.L., Turner, T.E., Smart, R., Peacock, M., Baird, A.J., 2016. Evaluating the use of dominant microbial consumers (testate amoebae) as indicators of blanket peatland restoration. Ecol. Indic. 69, 318–330. https://doi.org/10.1016/j.ecolind.2016.04.038.

Tang, Y.S., Cape, J.N., Sutton, M.A., 2001. Development and types of passive samplers for monitoring atmospheric NO_2 and NH_3 concentrations. Sci. World J. 1, 513–529. https://doi.org/10.1100/tsw.2001.82.

Tang, Y.S., Braban, C.F., Dragosits, U., Dore, A.J., Simmons, I., van Dijk, N., Poskitt, J., Pereira, G.B.S., Keenan, P.O., Conolly, C., Vincent, K., Smith, R.I., Heal, M.R., Sutton, M.A., 2018. Drivers for spatial, temporal and long-term trends in atmospheric ammonia and ammonium in the UK. Atmos. Chem. Phys. 18, 705–733. https://doi.org/10.5194/acp-18-705-2018.

Tang, Y.S., Williams, M.R., Carnell, E.J., Stephens, A.C.M., Iwanicka, A.K., Duarte, F., van Dijk, N., O'Reilly, Á., McCourt, A., McHardy, F., Fox, T., Dragosits, U., 2022. Atmospheric ammonia assessments on six designated sites in Northern Ireland year 1: June 2020 – May 2021 (UKCEH Project no 07102). https://nora.nerc.ac.uk/id/eprint/533585 (accessed 20 August 2024).

Tang, Y.S., Williams, M.R., Carnell, E.J., Stephens, A.C.M., Iwanicka, A.K., Duarte, F., van Dijk, N., Espina-Martin, P., Pearson, C., O'Reilly, Á., McCourt, A., Fox, T., Dragosits, U., 2023. Atmospheric ammonia assessments on six designated sites in Northern Ireland report 2: June 2020 – May 2022 (UKCEH Project no 07102). https://nora.nerc.ac.uk/id/eprint/535652 (accessed 20 August 2024).

The Nutrient Action Programme Regulations (Northern Ireland), 2019. https://www.legislation.gov.uk/nisr/2019/81/contents. (Accessed 23 August 2024).

Tolonen, K., 1986. Rhizopod analysis. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Paleohydrology. John Wiley, Chichester, pp. 645–666.

Tsyganov, A.N., Keuper, F., Aerts, R., Beyens, L., 2013. Flourish or flush: effects of simulated extreme rainfall events on *Sphagnum*-dwelling testate amoebae in a subarctic bog (Abisko, Sweden). Microb. Ecol. 65, 101–110. https://doi.org/10.1007/s00248-012-0115-x.

Uwizeye, A., de Boer, I.J.M., Opio, C.I., Schulte, R.P.O., Falcucci, A., Tempio, G., Teillard, F., Casu, F., Rulli, M., Galloway, J.N., Leip, A., Erisman, J.W., Robinson, T. P., Steinfeld, H., Gerber, P.J., 2020. Nitrogen emissions along global livestock supply chains. Nat. Food 1, 437–446. https://doi.org/10.1038/s43016-020-0113-y.

van Bellen, S., Mauquoy, D., Payne, R.J., Roland, T.P., Hughes, P.D.M., Daley, T.J., Loader, N.J., Street-Perrott, F.A., Rice, E.M., Pancotto, V.A., 2017. An alternative approach to transfer functions? Testing the performance of a functional trait-based model for testate amoebae. Palaeogeogr. Palaeoclimatol. Palaeoecol. 468, 173–183. https://doi.org/10.1016/j.palaeo.2016.12.005.

van Dijk, N., Thomas, I.N., Iwanicka, A.K., Harvey, D., Stephens, A.C.M., Tang, Y.S., Sutton, M., Dragosits, U., 2020. Vegetation analysis and bioindicator checks at Ballynahone Bog SAC (UKCEH Project no 07102, Issue 1, Number 1, Task 5). https://nora.nerc.ac.uk/id/eprint/533587 (accessed 20 August 2024).

Vitt, D.H., Wieder, K., Halsey, L.A., Turetsky, M., 2003. Response of *Sphagnum fuscum* to nitrogen deposition: a case study of ombrogenous peatlands in Alberta, Canada. Bryologist 106 (2), 235–245. https://doi.org/10.1639/0007-2745(2003)106[0235,ROSFTN]2.0.CO;2.

Warner, B.G., Chmielewski, J.G., 1992. Testate amoebae (Protozoa) as indicators of drainage in a forested mire, northern Ontario, Canada. Arch. Protistenkd. 141 (3), 179–183. https://doi.org/10.1016/S0003-9365(11)80067-9.

Webb, J., Pain, B., Bittman, S., Morgan, J., 2010. The impacts of manure application methods on emissions of ammonia, nitrous oxide and on crop response – a review. Agric. Ecosyst. Environ. 137, 39–46. https://doi.org/10.1016/j.agee.2010.01.001.

Woodward, H., Oxley, T., Rowe, E.C., Dore, A.J., ApSimon, H., 2022. An exceedance score for the assessment of the impact of nitrogen deposition on habitats in the UK. Environ. Model. Software 150, e105355. https://doi.org/10.1016/j.envsoft.2022.10.5355.

WWF, 2020. Living Planet Report 2020 - Bending the curve of biodiversity loss. https://www.wwf.org.uk/sites/default/files/2020-09/LPR20_Full_report.pdf (accessed 7 June 2024).

Yang, J., Zhang, X., Xie, Y., Song, C., Sun, J., Zhang, Y., Giesy, J.P., Yu, H., 2017. Ecogenomics of zooplankton community reveals ecological threshold of ammonia nitrogen. Environ. Sci. Technol. 51, 3057–3064. https://doi.org/10.1021/acs.est.6b05606.

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J., 2010. Global peatland dynamics since the last glacial maximum. Geophys. Res. Lett. 37, 2010GL043584. https://doi.org/10.1029/2010GL043584.

Zapletal, M., Mikuška, P., 2019. Ammonia emissions and dry deposition in the vicinity of dairy farms. Atmósfera 32, 337–350. https://doi.org/10.20937/ATM.2019.32.04.06.

Zhang, H., Amesbury, M.J., Piilo, S.R., Garneau, M., Gallego-Sala, A., Väliranta, M.M., 2020a. Recent changes in peatland testate amoeba functional traits and hydrology within a replicated site network in northwestern Québec, Canada. Front. Ecol. Evol. 8, e228. https://doi.org/10.3389/fevo.2020.00228.

Zhang, H., Väliranta, M., Piilo, S., Amesbury, M.J., Aquino-López, M.A., Roland, T.P., Salminen-Paatero, S., Paatero, J., Lohila, A., Tuittila, E.-S., 2020b. Decreased carbon accumulation feedback driven by climate-induced drying of two southern boreal bogs over recent centuries. Glob. Change Biol. 26, 2435–2448. https://doi.org/10.1111/gcb.15005.

Zhou, Y., Huang, Y., Peng, X., Xu, J., Hu, Y., 2021. *Sphagnum* response to nitrogen deposition and nitrogen critical load: a meta-analysis. Glob. Ecol. Conserv. 30, e01791. https://doi.org/10.1016/j.gecco.2021.e01791.