Combined palaeolimnological and ecological approach provides added value for understanding the character and drivers of recent environmental change in Flow Country lakes

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SUMMARY

The Flow Country peatlands receive national and international recognition and protection as a highly valued habitat, and also provide a number of important ecosystem services. While there has been much research on the terrestrial peatland habitat of the Flow Country, the area's many hundreds of natural water bodies have been largely unstudied. The first part of this study therefore focuses on establishing the contemporary conditions at 18 Flow Country lakes, examining between-lake heterogeneity in terms of physical structure, water chemistry and biological communities. Temporal change in these lakes is then considered by combining contemporary ecological and palaeolimnological approaches. We examine how the diatom and chironomid communities of Flow Country lakes have changed since a time prior to the mid-nineteenth century. Results show that the lake communities today are different to those present pre-1850, containing more taxa tolerant of increased acidity and nutrient availability. General linear modelling (GLM) analysis demonstrated a statistically significant association between the extent of change in diatom communities and both dissolved organic carbon (DOC) and nitrate. Community shifts, though considerable, are shown to be complex and idiosyncratic and no shift between trophic states is indicated. The extent and type of coarse-scale community change we observed points to widespread bottom-up drivers such as land management, afforestation and/or atmospheric deposition rather than more localised management practices such as fish stocking. The benefits of combining approaches is discussed and palaeolimnological methods by which land management, afforestation and atmospheric deposition could be further disentangled are identified.

KEY WORDS: diatoms, chironomids, palaeolimnology, peatland lakes, sediment cores, top-bottom analysis

INTRODUCTION

The Flow Country in north Scotland is an internationally important peatland, supporting a flora and fauna unique in Britain (Lindsay *et al.* 1988). As well as providing a range of valuable ecosystem services such as carbon storage and water regulation, peatlands are also of high conservation value (Joosten & Clarke 2002).

The extensive peatland landscape of the Flow Country is interspersed with pools and lakes which support a range of rare and specialised wetland species (Spirit *et al*. 1986, Stroud *et al*. 1988, Coulson *et al*. 1995, Downie *et al*. 1998). As a consequence the acidic, low-nutrient water bodies of the Flow Country are protected and prioritised at both national and international levels (UK Biodiversity Action Plan (BAP) habitats, Special Area of Conservation (SAC) under EU Habitats Directive Annexe 1). Priority species of Flow Country lakes include the black-throated diver (*Gavia arctica*) and European water vole (*Arvicola amphibius*), as well as the common scoter (*Melanitta nigra*) and Eurasian otter (*Lutra lutra*).

Despite their seeming remoteness, the freshwater lakes of the Flow Country have been subject to a number of anthropic pressures, all of which have the potential to perturb lake ecology via several processes, some of which are illustrated in Figure 1.

The establishment of sporting estates since the mid-19th century has resulted in Flow Country lakes being either stocked or managed to optimise brown trout (*Salmo trutta*) populations for anglers (Mark Hancock, RSPB, personal communication). Previous studies in boreal and arctic lakes have shown that fish introductions, particularly to previously fishless sites, can have significant biological effects at multiple trophic levels (Hornung & Foote 2006, Wieker *et al*. 2016, Laske *et al*. 2017,). However, the long-term (50 to 100+ years) effects of fish stocking on the

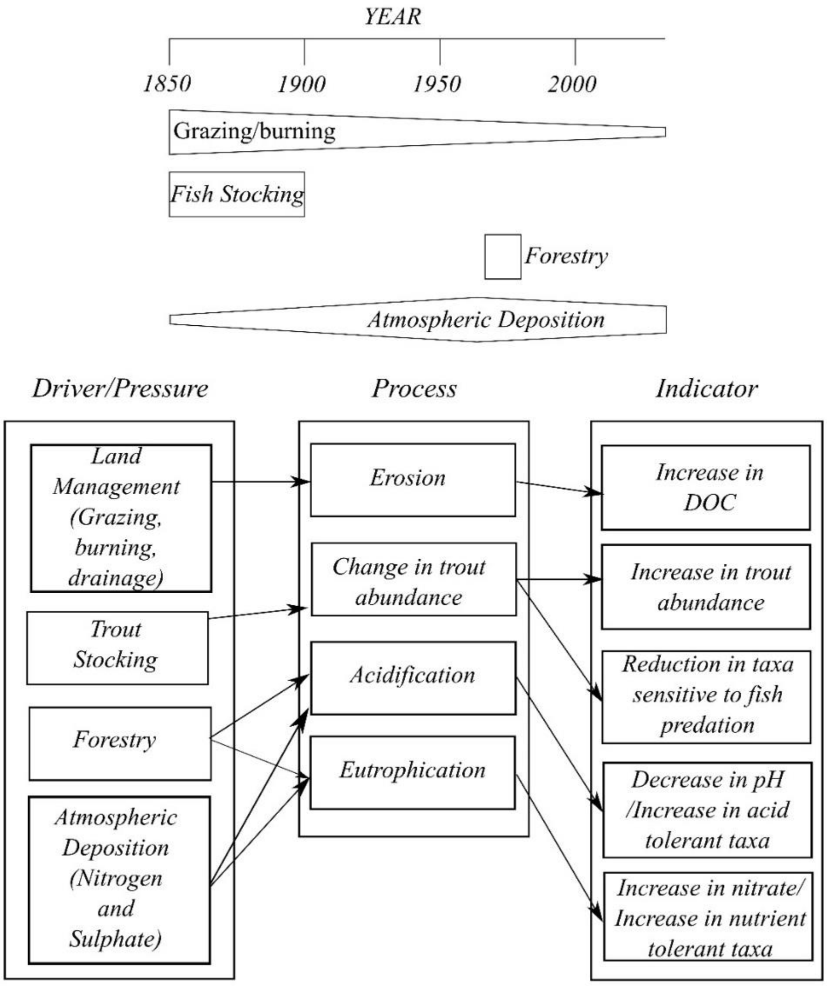

Figure 1. The putative anthropic pressures on Flow Country lakes. Top panel illustrates the timescales over which these pressures have occurred. Bottom panel illustrates some of the main processes these pressures are likely to affect and the impact this will have on key indicator variables.

communities of Flow Country lakes have not been examined.

Land management in the Flow Country peatlands has also included drainage and rotational burning of heath to encourage vegetation suitable for gamebird breeding and/or sheep grazing (Lindsay *et al*. 1988). These practices can alter the communities of nearby lakes through increased catchment erosion and/or nutrient input (Holden *et al*. 2007, Ramchunder *et al*. 2009, Holden *et al*. 2012).

In the 1970s and 1980s, highly controversial non-native coniferous forestry planting took place in the Flow Country (Stroud *et al*. 1988, Warren 2000, Stroud *et al*. 2015). Despite concerns about lake acidification (from trees capturing acid deposition) and/or eutrophication (from fertiliser application) expressed at the time (Bainbridge *et al*. 1987, Stroud *et al*. 1988), the long-term effects of the forestry on lake ecology in the Flows have not been examined.

In addition to local anthropic pressures, it is also possible that atmospheric deposition (of sulphates and nitrates) and/or climate change are affecting the lakes, as has been demonstrated for other remote lakes (Battarbee *et al*. 2002, Kernan *et al*. 2011).

Although the value of Flow Country water bodies is widely recognised, limited data are available. Routine water quality monitoring is carried out by the Scottish Environmental Protection Agency (SEPA) at only a small number of sites (< 10 of the ~ 600 lakes). Standardised macrophyte surveys were most recently carried out at around 180 lakes in the 1970s and 1980s (SNH 2018). Invertebrates and algae have been the focus of a limited number of studies (Spirit *et al*. 1986, Allott *et al*. 1994, Coulson *et al*. 1995, Downie *et al*. 1998). Chironomids, despite playing an important role in lake ecology, have not been studied at all. Without detailed survey data it is difficult to gauge current levels of heterogeneity between lakes. With a multitude of potential pressures, understanding present physico-chemical and ecological conditions is of paramount importance, particularly for conservation practitioners and land managers to prioritise sites where rare and/or sensitive species are present.

Contemporary monitoring data can establish current site condition. However, these data represent a single snapshot in time. A lack of long-term monitoring data makes it difficult to establish how Flow Country lakes may have changed in the last century. As many sites have experienced multiple pressures over this period, a temporal perspective is vital to disentangling their potential effects. There is growing evidence to support the value of complementing contemporary ecological datasets with information derived from lake sediment cores (palaeolimnology) (Davies & Bunting 2010, Gillson & Marchant 2014, Davidson *et al*. 2018). A palaeolimnological approach provides robust and standardised evidence of historical community composition and abundance (by examining biological remains deposited in lake sediment) and indirect indications of past physico-chemical conditions (by complementing direct evidence with ecological knowledge and/or using transfer functions). By adding detailed and standardised data from a period prior to major disturbance by humans it is possible to identify whether lakes which had similar fauna and flora in the past remain similar today. Additionally, the temporal perspective provided by palaeolimnology allows insights into the extent and type of change that has occurred in lakes, as well as potential drivers of change (Bennion *et al*. 2010, Sayer *et al*. 2012). The top-bottom palaeolimnological approach compares a sample from the top of a core (representing present-day conditions) with a sample from close to the bottom of the core (to represent pre-impact conditions), enabling rapid assessment of overall change at a larger number of sites (Brooks *et al*. 2005, Leira *et al*. 2006, Dalton *et al*. 2009). Findings from a multi-lake study can provide insights for oligotrophic lakes in general and enable us to explore the extent to which processes of change are systematic across a region or centred around individual lakes.

The overall aim of this study is to establish the extent and type of community change that has occurred in Flow Country lakes over the last 150 years and explore the processes driving change in the context of the anthropic pressures identified. We have two objectives; firstly to provide contemporary ecological and physico-chemical data from the Flow Country lakes, and secondly to explore the extent to which human activities may be influencing Flow Country lakes by applying a palaeolimnological top-bottom approach.

STUDY AREA

The Flow Country peatlands extend across the counties of Caithness and Sutherland in north Scotland (Figure 2 inset). It is a remote landscape in which low temperatures and high rainfall have led to the development of large areas (about 440,000 hectares) of blanket bog (Lindsay *et al.* 1988). The peat, up to several metres deep, has a high water table and is dominated by species of *Sphagnum* moss including *Sphagnum fuscum, S. rubellum, S.austinii*, heather (*Calluna vulgaris*) and cottongrass (*Eriophorum vaginatum*) (Coulson *et al.* 1995). Palaeoecological studies indicate that during the early to mid-Holocene the landscape was characterised by open woodlands of birch (*Betula* spp.), juniper (*Juniperus communis*.), hazel (*Corylus avellana*) and willow (*Salix* spp.) (Charman 1994) with a brief period of local pine (*Pinus* sp.) forest growth ca. 4,500–4,000 BP. Since then the Flow Country has been largely treeless. Charman (1994) hypothesised that the rapid decline of pine was primarily a consequence of climatic change with potentially some impact from local human populations. Significant levels of afforestation began in the Flow Country during the 1970s and 1980s. By 1986 over 30,000 hectares had been planted with the non-native coniferous species lodgepole pine (*Pinus contorta)* and Sitka spruce (*Picea sitchensis*) (Bainbridge *et al.* 1987). The controversy surrounding the afforestation of the Flow Country resulted in many of the trees being removed before reaching maturity in an attempt to restore the bog (Warren 2000).

Interspersed throughout the blanket bog of the Flow Country are many streams, rivers and lakes. The lakes vary greatly in size (1–3,371 ha, mean area 40 ha) and altitude (from sea level to 543 m a.s.l.), with 29 % of the total area of standing water occurring within Sites of Special Scientific Interest (SSSIs) (SNH 2002).

Eighteen lakes were selected as the focus of this study (Figure 2, Table 1). When using palaeolimnology to examine recent environmental change, a thorough understanding of contemporary conditions is vital as this provides the baseline from which change can be assessed. There is little contemporary ecological information for Flow Country lakes, so this was an important consideration in site selection. The eighteen lakes selected were those that were both broadly representative of Flow Country lakes (based on their geology, area, depth and landscape setting) and those for which there was a good level of contemporary baseline data, including the only standardised brown trout survey data for Flow Country lakes (see later).

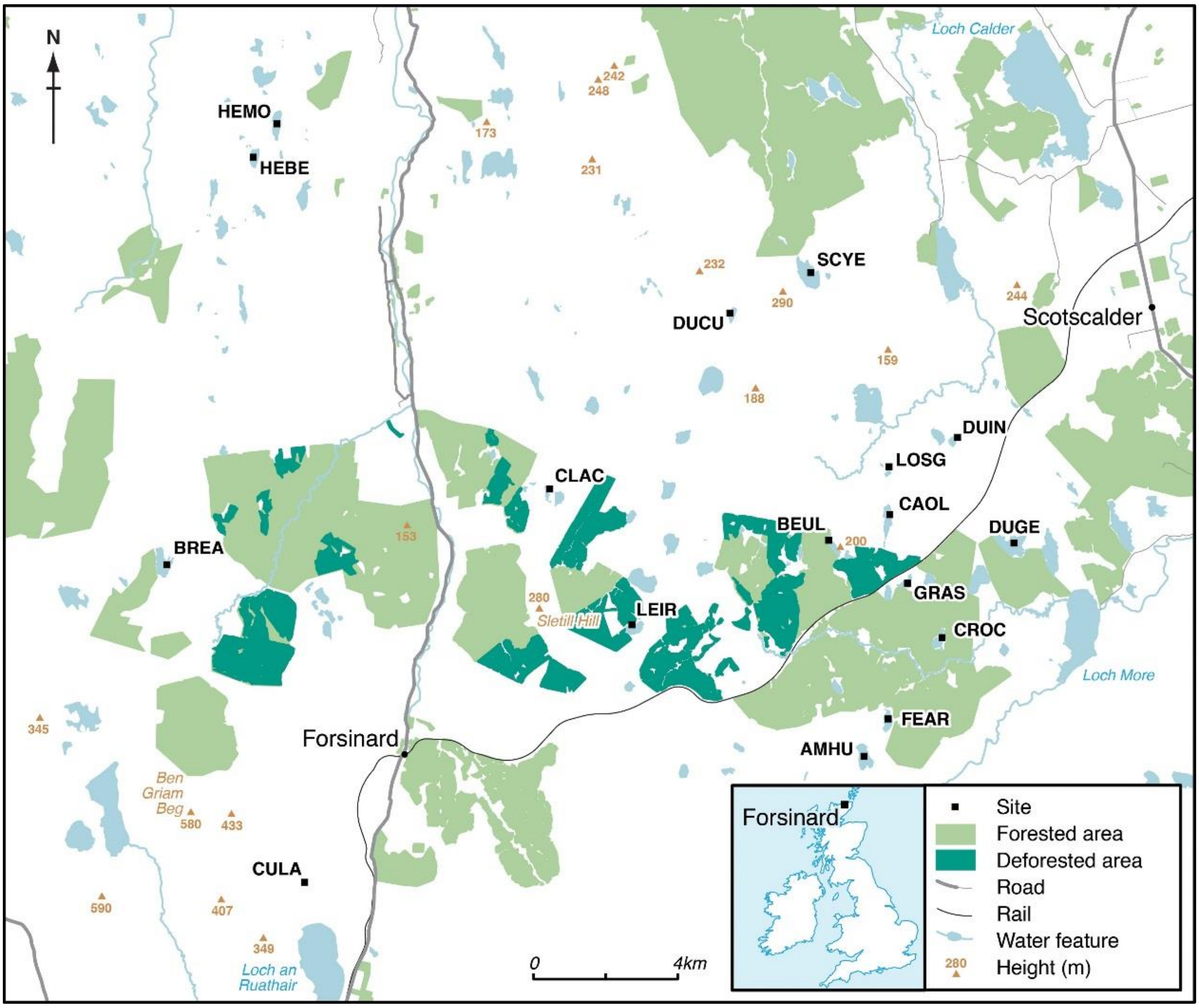

Figure 2. Map showing the locations of the 18 study lakes (lochs) and Forsinard railway station. The lakes are: Loch a'Mhuillinn (AMHU), Lochan Beag Beul na Faire (BEUL), Loch nam Breac (BREA), Caol Loch (CAOL), Loch nan Clach Geala-west (CLAC), Lochan Croc nan Lair (CROC), Loch Culaidh (CULA), Lochan Dubh Cul na Beinne (DUCU), Lochan Dubh Nan Geodh (DUGE), Loch an Duine (DUIN), Loch nam Fear (FEAR), Grassie Loch (GRAS), Loch na h-Eaglaise Beag (HEBE), Loch na h-Eaglaise Mor (HEMO), Loch Leir (LEIR), Loch Losgann (LOSG), Loch Scye (SCYE) and Loch Talaheel (TALA).

METHODS

The two objectives of this study were implemented using different methods, which are described separately below.

Objective 1: contemporary ecological and physico-chemical surveys

The first objective involved undertaking detailed contemporary surveys at a representative sample of Flow Country lakes to establish current physico-chemical and ecological conditions. Multivariate analysis was used to explore current patterns and heterogeneity among sites.

Field and laboratory methods

Aquatic macrophyte surveys were carried out at all 18 study lakes between 17 August and 05 September 2014. Sixteen of the lakes were surveyed by boat and the remaining two, Loch an Duine (DUIN) and Loch Losgann (LOSG) (Figure 2), which are small and remote, by wading from the shoreline. Boat surveys traversed the whole lake by parallel transects (3–5 m apart) with sample points positioned every 5–20 m along the transects, depending on lake size.

At each sample point, water depth (using an Echotest 2 depth sounder), sediment depth (the depth to which a metal pole could be inserted into the sediment) and presence of different sediment types

Table 1. List of study sites: full name of lake, lake code, lake size, catchment area and dominant land cover types as % of catchment area, from CEH (2018). NGR = UK National Grid Reference.

NGR	Lake name	Lake code	Area (ha)		Catchment land cover (%)		
			lake	catchment	bog	forestry	deforested
ND018422	Loch a'Mhuillinn	AMHU	22	470	94	6	
ND015476	Lochan Beag Beul na Faire	BEUL	3	6	100		
NC827479	Loch nam Breac	BREA	29	942	86	14	
ND025486	Caol Loch	CAOL	17	87	100		
NC932496	Loch nan Clach Geala-west	CLAC	4	20	100		
ND039452	Lochan Croc nan Lair	CROC	12.5	6	47	53	
NC863390	Loch Culaidh	CULA	11	25	100		
NC984544	Lochan Dubh Cul na Beinne	DUCU	7	96	100		
ND060478	Lochan Dubh Nan Geodh	DUGE	34	71	91	9	
ND044507	Loch an Duine	DUIN	4	30	100		
ND025431	Loch nam Fear	FEAR	9.5	22	68		
ND030469	Grassie Loch	GRAS	7	38	75		25
NC854590	Loch na h-Eaglaise Beag	HEBE	11	155	100		
NC861599	Loch na h-Eaglaise Mor	HEMO	15	437	100		
NC955458	Loch Leir	LEIR	9.4	96	91		9
ND026500	Loch Losgann	LOSG	3	37	100		
ND006554	Loch Scye	SCYE	35	166	100		
NC955489	Loch Talaheel	TALA	6	25	100		

were recorded. Sediment was characterised according to Lake Habitat Survey classification (Rowan *et al*. 2006) and each category was assigned a number between 1 and 6 (from boulders to fine sediments including peat), representing decreasing particle size and changing sediment composition.

Macrophyte percentage cover and macrophyte species percentage composition were estimated at each point (on an estimated 1 m^2 area) based on plant material brought up by a double-headed rake or viewed through a bathyscope. Plants were identified to genus or species in the field except for charophytes and mosses which were collected for identification using a microscope. Percentage volume infested (PVI) was calculated as percentage macrophyte cover multiplied by mean macrophyte height, divided by water depth (Canfield *et al*. 1984)

pH and conductivity (EC) were measured in the field using a Hach HQ40d multiprobe. Water samples were collected and analysed at the University of Nottingham for nitrate, dissolved organic carbon (DOC) and chlorophyll-a.

Existing datasets

No electrofishing data were available for any of the study sites. However, the fish communities of all 18 lakes were surveyed in 2010 and 2011 (between April and August) using standardised rod and line surveys (Hancock *et al*. 2015). Each lake was fished by the same individual for a total of ten hours. Abundance of brown trout (standardised per rod hour) and mean brown trout weight were calculated for each lake.

Statistical analysis

Indirect ordinations were used to explore and visualise patterns and groupings of lakes based on contemporary physico-chemical and biological variables. Ordinations were carried out in Canoco v.5

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(ter Braak & Šmilauer 2012). Principal component analysis (PCA) was used in preference to detrended correspondence analysis (DCA) based on results of initial DCA gradient length analysis (ter Braak & Šmilauer 2012, Šmilauer & Lepš 2014). Variables were centred by species and log transformed.

Objective 2: palaeolimnological top-bottom analysis

The second objective was addressed by taking sediment cores. Core stratigraphies and chronologies were established by analysis of core samples. Community composition was examined for key indicator taxa (chironomids and diatoms) in sediments from the top of the core (present-day communities) and from the base of the core (communities in existence prior to significant human influences, i.e. pre-1850).

Field and laboratory methods

A short (< 0.4 m) sediment core was collected from the littoral zone of each of the 18 lakes using a Glew corer (7.4 cm internal diameter; Glew 1991). Sixteen sites were cored in October 2013 and the remaining two (Loch nam Fear (FEAR) and Loch a'Mhuillinn (AMHU)) in August 2014. The cores were sliced in the field at 1 cm intervals.

Lithostratigraphic (% loss on ignition) and geochemical (heavy metals by x-ray fluorescence) analyses were carried out on each slice of the 18 cores following the methods outlined in Appendix 1 and by Dean (1974), Rose (1994) and Rose *et al*. (2004). These analyses were used to establish the stratigraphical integrity of the cores and to confirm that the sample from the base of the core represented a time prior to 1850. The dates indicated by x-ray fluorescence were validated by radiometric dating of two cores (GRAS and CAOL). This analysis was carried out by the Bloomsbury Environmental Isotope Facility (BEIF) at University College London following methods described in Appendix 1 and Appleby (1997).

Samples from the top (1–2 cm) and base (between 5 and 27 cm) of each Glew core were prepared for diatom and chironomid analysis. Methods for preparation of diatom slides followed Battarbee *et al*. (2001), and identification (of about 300 valves per sample) was based on Krammer & Lange-Bertalot (1986–1991) and Camburn & Charles (2000). Diatom species abundances were calculated as percentages of total diatom valves counted. Chironomid slide samples were prepared following Brooks *et al*. (2007), and at least 50 larval heads per sample were picked and identified from a known volume of sediment. Identification followed Brooks *et al*. (2007) and Anderson *et al*. (2013).

Existing datasets

Data from the Centre for Ecology and Hydrology (CEH) Lake Portal database were used to determine the dominant land cover types within the catchment of each study lake (CEH 2018).

Statistical analysis

The extent of community change in each lake relative to the variation between sites was examined using Procrustes rotation and formalised by the associated procrustean randomisation test (PROTEST). Procrustes rotation analysis is an effective tool for comparing two or more ordinations by determining the deviation between corresponding points from two (or more) datasets (Legendre & Legendre 2012). In a top-bottom context the Procrustes residual (distance between the top and bottom point in ordination space) represents the relative magnitude of community change that has occurred at a site. The communities of sites with small residual scores are considered more similar than those with large residual scores. The Procrustes sum of squares value and root mean square error (RMSE) scores are measures of the degree of rotation necessary to match one ordination to another, with low values indicating high concordance between ordinations.

The PROTEST is an analysis of congruence and is conducted to formalise the results of the Procrustes rotation by determining the likelihood that similarities between ordinations are not due to chance. A correlation score (known as m12) and an associated p-value are produced. A significant PROTEST score therefore indicates that the correlation between top and bottom ordinations is significant and not due to chance. Conversely a non-significant PROTEST score demonstrates that the top and bottom ordinations are no more similar than might have been expected by chance, i.e. the communities of the sites are considerably different between the tops and bottoms of the cores. All Procrustes and PROTEST analyses were carried out in R (R Core Team 2016).

To explore the extent to which environmental variables are driving community change, general linear models (GLMs) were implemented in R (R Core Team 2016). The response variable was the length of residual from the Procrustes analysis (for either chironomids or diatoms), i.e. a measure of the magnitude of community change. The environmental explanatory variables used were those that are indicative of the pressures faced by Flow Country lakes, namely: DOC to represent erosion associated with grazing/burning/drainage; nitrate to represent eutrophication associated with forestry; pH to represent acidification associated with forestry; and fish abundance to represent brown trout introductions and/or management (Figure 1).

Whilst Procrustes and PROTEST are useful in establishing the extent of change that has taken place at a site, constrained ordinations provide a means for understanding the type of change that has occurred. Therefore, canonical correspondence analysis (CCA) and redundancy analysis (RDA) were carried out on the diatom and chironomid community data, in Canoco v.5 (ter Braak & Smilauer 2012). Contemporary environmental variables relevant to the hypothesised drivers of change were used as explanatory variables in the ordinations of the top samples, and the bottom samples were passively plotted onto the same ordination space. Direct ordination of surface samples with the bottom samples plotted passively is useful in a top-bottom context as sites 'move' in the ordination space relative to environmental variables. As for the GLMs, the environmental variables used were DOC, fish abundance, pH and nitrate (Figure 1). Environmental and community datasets were transformed prior to analysis (Appendix 1).

RESULTS

Objective 1: contemporary ecological and physico-chemical surveys

An ecological overview of each lake is provided in the appendices and supplementary material, including: bathymetry and percentage vegetation cover maps for each lake (Supplement 1); biological (chironomids, diatoms, mosses and macrophytes) data (Supplement 2); and sediment composition (Figure A2.4 in Appendix 2). A summary of the physico-chemical and biological lake data is presented in Table 2 and Figure 3.

The lakes are small and shallow, and have predominantly fine, soft sediment. Surface area ranges from 3 to 35 hectares and maximum depth from 1.1 to 3.8 m. The most commonly recorded sediment types were peat, silt and sand, which were present at all sites. Boulders were recorded at ten of the sites, and gravel in only seven lakes. Sediment depth ranged from 0 m to > 3 m (Figure A2.4).

The physico-chemical attributes of the sites were typical of lakes located in ombrotrophic blanket bog, with low to neutral pH (5.06–7.72) and low nitrate (0–0.037 mg L^{-1}). OC ranged from 4.33 to 15.11 ppm and conductivity from 54.3 to 87.3 µS cm^{-1}.

The fish populations were a mixture of brown trout (*Salmo trutta*) and three-spined stickleback (*Gasterosteus aculeatus*) (Hancock *et al*. 2015). Brown trout were caught at 13 sites, where their abundance was between 0.1 and 5.2 individuals per rod hour and mean fish weight by lake was between 58 and 1,986 g (RSPB/WWT unpublished data).

In total, 72 chironomid morphotypes were identified in the surface sediments, giving an average of 21 taxa per site (range 13–31) (Supplement 2). Chironomids associated with low-nutrient acidic conditions were common, as were eurytopic morphotypes such as *Tanytarsus mendax*. However, at most of the sites, taxa tolerant of less acidic and more mesotrophic conditions, such as *Polypedilum nebeculosum* and *Psectrocladius* spp., were also present.

The total number of diatom species recorded in the surface sediment samples from the 18 lakes was 94, with an average of 24 species per lake (range 19–34) (Supplement 2). Benthic species dominated the communities. Two cosmopolitan species of *Fragilaria* sensu lato, namely *Stauroforma exiguiformis* (typical of low nutrient, acidic sites) and *Staurosira construens* var. *venter*, were dominant. Centric, possibly planktonic, species of *Aulacoseira*

Table 2. Water chemistry for the study sites, sampled in 2014. Lake codes as in Table 1.

Lake code	pH	EC (µs cm^{-1})	DOC (ppm)	Nitrate (mg L^{-1})
AMHU	6.06	54.3	6.52	0.009
BEUL	5.29	61.7	5.33	0.097
BREA	7.14	59.1	10.78	0
CAOL	7.54	77.8	6.20	0.026
CLAC	5.66	56	4.33	0.014
CROC	5.06	76.2	4.97	0.016
CULA	7.44	69.5	4.57	0.015
DUCU	7.56	57.6	15.10	0.015
DUGE	5.51	87.2	5.10	0.020
DUIN	5.43	82.2	6.89	0.009
FEAR	6.79	72.3	6.38	0.028
GRAS	7.19	87.3	9.41	0.008
HEBE	6.99	64.4	14.72	0
HEMO	7.20	71.9	14.10	0
LEIR	7.72	62.2	9.37	0
LOSG	5.92	56.5	8.87	0.037
SCYE	7.19	73.7	5.99	0.027
TALA	6.86	55.2	9.97	0.040

were absent from several lakes (BEUL, LEIR and LOSG), and when present did not form a large fraction of the diatom community. At six sites the more nutrient-tolerant planktonic taxon *Asterionella formosa* was recorded.

Mosses made up an average of 30 % of the aquatic plant community (range 1–84 %) and the mean number of species recorded per site was 3 (range 1–5) (Supplement 2). The most frequently recorded moss species were *Sphagnum denticulatum* (8 sites), *Fontinalis antipyretica* (7 sites) and *Fontinalis squamosa* (6 sites).

Twenty species of aquatic macrophyte where recorded across the sites (mean 7, range 1–13) (Supplement 2). Frequently occurring species were those typical of low-nutrient acidic lakes such as *Lobelia dortmanna*, *Littorella uniflora*, *Isoetes lacustris*, *Myriophyllum alterniflorum* and *Juncus bulbosus*. Three species of *Potamogeton* (*P. natans*, *P. perfoliatus*, *P. polygonifolius*) were identified. The two charophyte species *Chara virgata* and *Nitella flexilis* agg. were also recorded, with *N. flexilis* agg. dominating in FEAR.

The PCA of environmental variables indicates heterogeneity across the sites, as they are distributed widely across the ordination space (Figure 4). Groupings of sites are not immediately apparent, although four of the larger, deeper and less productive lakes (CAOL, CROC, DUGE and SCYE) are placed together in the upper left quadrant while five of the more-vegetated and productive sites (BEUL, CLAC, CULA, FEAR and LOSG) are grouped in the lower left quadrant. The remaining sites are spread across the right-hand side of PCA Axis 1. DUCU is an outlier and strongly associated with high fish abundance.

Lake code	PVI	Fish Abundance per rod hour	Chironomid head capsule abundance per gram of wet sediment
AMHU	1	2.7	31
BEUL	3.46	0	115
BREA	0.09	1.6	25
CAOL	3.76	0.4	123
CLAC	5.33	0	137
CROC	1.98	0.1	51
CULA	11.91	0.5	80
DUCU	4.25	5.2	25
DUGE	0.08	0	48
DUIN	2.37	0	86
FEAR	10.87	0.3	51
GRAS	5.18	0.7	92
HEBE	0.08	1.3	101
HEMO	0.45	0.8	73
LEIR	4.23	2	68
LOSG	10.1	0	35
SCYE	2.06	0.4	60
TALA	4.24	1.6	52

Figure 3. Summary of biological variables including plant volume inhabited (PVI), fish abundance, chironomid abundance (in surface sediments) and Shannon's diversity of chironomids and diatoms (in surface sediments).

Objective 2: palaeolimnological top-bottom analysis
Lithostratigraphical and geochemical analysis of the sediment cores showed that the sediments of these shallow, potentially wind-stressed lakes have not been substantially disturbed. Every core had a visible stratigraphy, and analyses of both heavy metals (18 cores) and ^{210}Pb (2 cores) were used to establish core integrities and chronologies (Figures A2.1–3 in Appendix 2 and Robson 2017). All of the bottom samples represented pre-1850 conditions.

The extent of recent environmental change and potential drivers
Procrustes rotations of chironomid and diatom community composition in the tops and bottoms of the cores were used to explore the extent of community change that had taken place between pre-1850 times and the present (Figure 5). There is good concordance for core bottoms, with most sites located towards the centre of the ordination space.

In contrast, the tops of the cores show divergence, with surface samples being more widely spread across the ordination space for both chironomid and diatom communities, indicating that the communities of these two biological groups are less similar now than they were historically. The Procrustes residuals (Figure 6) and the high Procrustes sum of squares and root mean sum of squares (RMSE) scores (Figure 5) confirm this initial observation. Although the m12 values of the PROTEST analysis are relatively close to unity (0.78 for chironomids, 0.80 for diatoms) and thus indicate a degree of similarity between the top-bottom ordinations, the similarity is non-significant ($p = 0.242$ for chironomids, $p = 0.066$ for diatoms), showing that the top and bottom communities are different.

GLM analysis indicates no significant relationship between magnitude of chironomid community change and DOC, fish abundance, nitrate or pH ($p = 0.8$, df = 4, 13) (Table 3). However, for diatoms there is a significant positive relationship between magnitude of community change and both DOC ($P < 0.01$, df = 4, 13) and nitrate ($p < 0.05$, df = 4, 13) Table 4), meaning that diatom community change is greatest at sites with highest contemporary DOC and lowest nitrate.

The type of recent environmental change and potential drivers of change
The explanatory variables account for 27 % (CCA) and 28 % (RDA) of the variation in the ordinations. Constrained ordinations show no dominant or consistent pattern of change in the chironomid and diatom communities with respect to environmental variables and some lakes show greater change than others (Figure 7). The communities of the lakes initially appear to be ‘moving’ to different extents and in different directions within the ordination space. However, communities in both the tops and the bottoms of the cores from FEAR, DUGE, CROC, CLAC and LOSG occupy a different part of the ordination space from the other sites. This indicates

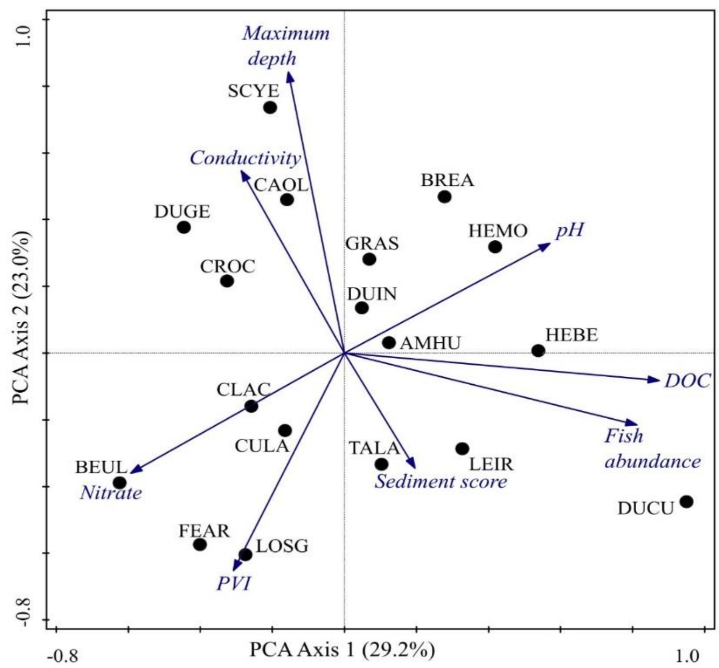

Figure 4. Principal component analysis (PCA) of the 18 study sites by environmental variables, PVI = percentage infested volume and DOC= dissolved organic carbon. Lake codes as in Table 1.

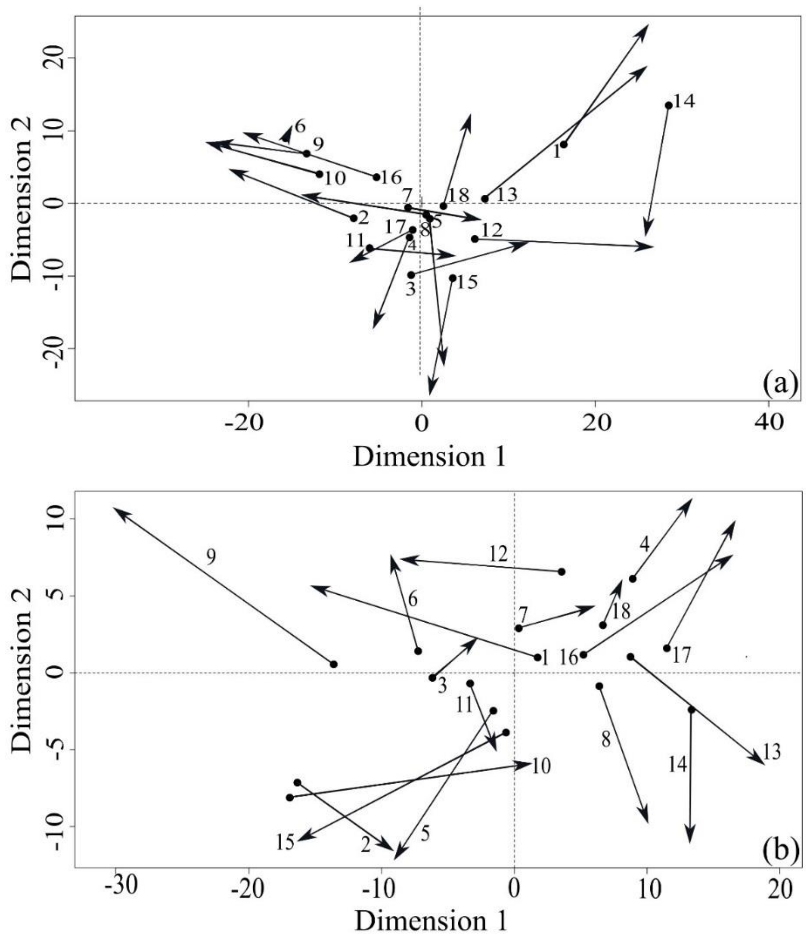

Figure 5. Procrustes residuals in two-dimensional ordination space for (A) chironomids and (B) diatoms. Procrustes sum of squares value and root mean square error (RMSE) for chironomids = 2.99 and for diatoms = 3.34; correlation score (m12) for chironomids = 0.78 and for diatoms = 0.80; p-value for chironomids = 0.24 and for diatoms = 0.07.

Lake code	Procrustes Residuals: Chironomids (0 3 6)	Procrustes Residuals: Diatoms (0 3 6)	pH	DOC ppm	Nitrate mg l $^{-1}$	Fish per rod hour
AMHU			6.06	6.52	0.009	2.7
BEUL			5.29	5.33	0.000	0.0
BREA			7.14	10.78	0.097	1.6
CAOL			7.54	6.20	0.026	0.4
CLAC			5.66	4.33	0.014	0.0
CROC			5.06	4.97	0.016	0.1
CULA			7.44	4.57	0.015	0.5
DUCU			7.56	15.11	0.015	5.2
DUGE			5.51	5.10	0.020	0.0
DUIN			5.43	6.89	0.009	0.0
FEAR			6.79	6.38	0.028	0.3
GRAS			7.19	9.41	0.008	0.7
HEBE			6.99	14.72	0.000	1.3
HEMO			7.20	14.10	0.000	0.8
LEIR			7.72	9.37	0.000	2.0
LOSG			5.92	8.87	0.037	0.0
SCYE			7.19	5.99	0.027	0.4
TALA			6.86	9.97	0.040	1.6

Figure 6. Procrustes residual length with the indicator variables for each of the hypothesised drivers of decline.

Table 3. Output of the general linear model (GLM) analysis testing the relationship between magnitude of chironomid community change and DOC, fish abundance, nitrate and pH. SE = standard error.

variable	estimate	SE	test statistic	p-value
intercept	7.31	3.73	1.96	0.072
DOC	-0.56	2.31	-0.24	0.813
fish abundance	-0.01	0.31	-0.01	1.00
nitrate	-4.79	16.72	-0.29	0.78
pH	-0.65	0.61	-1.07	0.305

model statistics

residual standard error:
1.37 on 13 degrees of freedom

multiple R-squared: 0.11

adjusted R-squared: -0.16

F-statistic: 0.41 on 4 and 13 degrees of freedom

p-value: 0.8013

AIC = 68.54

Table 4. Output of the general linear model (GLM) analysis testing the relationship between magnitude of diatom community change and DOC, fish abundance, nitrate and pH. SE = standard error.

variable	estimate	SE	test statistic	p-value
intercept	2.29088	2.49383	0.919	0.37502
DOC	5.02843	1.54462	3.255	0.00626
fish abundance	0.09212	0.20493	0.450	0.66045
nitrate	-24.28945	11.16750	-2.175	0.04868
pH	-0.52683	0.40851	-1.290	0.21965

model statistics

residual standard error:
0.91 on 13 degrees of freedom

multiple R-squared: 0.60

adjusted R-squared: 0.48

F-statistic: 4.89 on 4 and 13 degrees of freedom

p-value: 0.01257

AIC = 54.00

that, although community change has taken place, these sites have remained dissimilar to the other lakes. Additionally, there is evidence that for some sites both diatom and chironomid communities are being strongly influenced by the same drivers. In both diatom and chironomid plots DUCU shows a change towards a community associated with high fish abundance, while the diatom and chironomid assemblages at BEUL indicate a response to increasing nitrates. Diatom and chironomid assemblages at FEAR show a change associated with lowering DOC and pH, while the diatom and chironomid communities of SCYE and CAOL move towards a community associated with decreasing fish abundance and DOC.

DISCUSSION

Assessing recent change in Flow Country lakes

This study has built upon and extended the scope of existing contemporary survey data (Spirit *et al*. 1986, Coulson *et al*. 1995, Downie *et al*. 1998, Hancock *et al*. 2015) to provide new lake-based ecological and physico-chemical data for Flow Country lakes. Characterisation of 18 superficially similar Flow Country lakes has demonstrated that whilst they are chemically, biologically and physically broadly similar to other peatland lakes in Scotland and northern Europe (Maitland *et al.* 1994, Rydin & Jeglum 2013), there is substantial between-lake variability in diatoms, chironomids and aquatic plants, even at sites that are located close together.

Furthermore, this study has demonstrated the benefit of combining contemporary and top-bottom palaeolimnological approaches to explore community change. By examining the extent of change at a relatively large number of lakes, geographically spread across the core area of the Flow Country peatlands, we were able to show that change is not limited to a single or small number of sites. This suggests that observed ecological changes are due to landscape-scale drivers such as afforestation, land management and/or atmospheric deposition rather than site-specific changes such as the introduction of trout. However, while all sites demonstrated a degree of community change, the amount of change was shown to vary between sites, as did the direction of change observed. While this could be indicative of multiple drivers acting at each site, it could equally indicate that the response of Flow Country lakes to these putative anthropic pressures is complex and idiosyncratic. The latter hypothesis is supported by the fact that although all

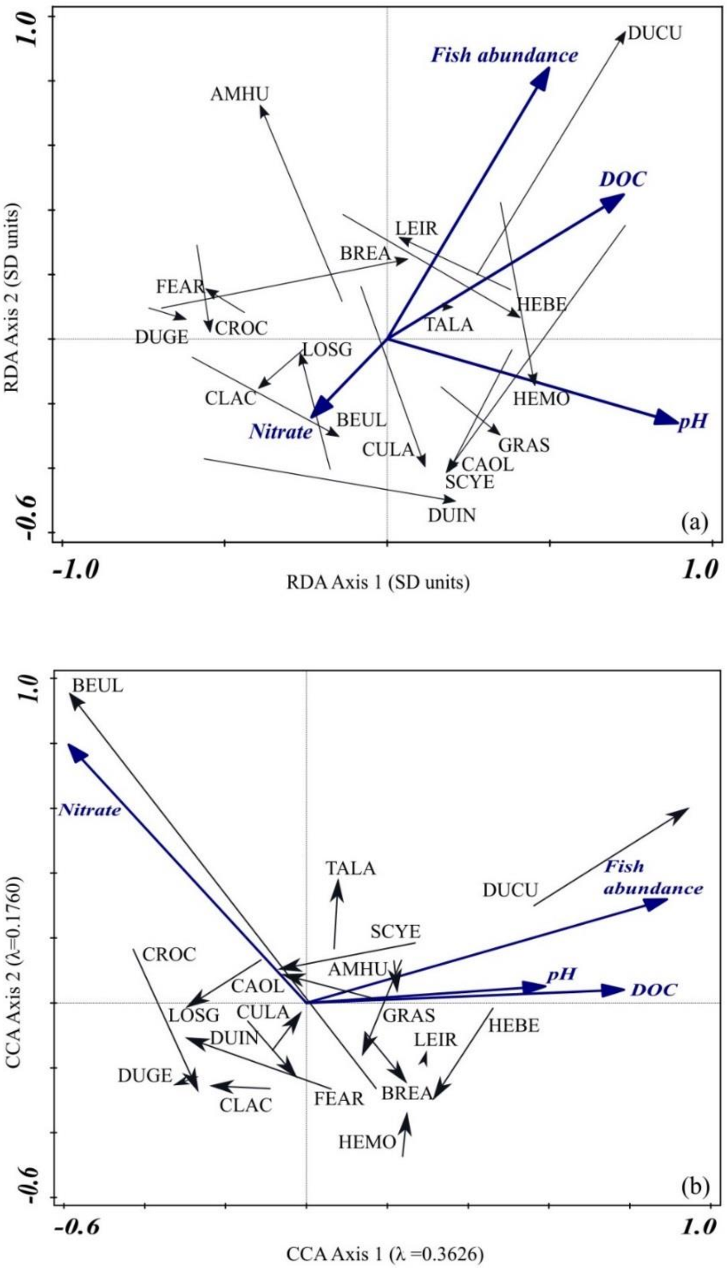

Figure 7. Constrained ordinations of the tops of the cores by key environmental indicator variables. The bottom samples are passively plotted onto the same ordination space. Arrows indicate the surface sample and the end of the line the bottom sample. (a) RDA of chironomid community and (b) CCA of diatom community - selection based on gradient length.

lake communities have changed, some lakes have remained consistently different from others, pointing to a degree of persistent dissimilarity between the lakes since a time prior to significant human influence.

There are indications that lake community change is being driven by changes in water chemistry. This also strongly supports the theory that land management, afforestation and/or atmospheric deposition are the ultimate drivers of community change within Flow Country lakes rather than top-down processes such as fish predation pressure. The increases in particular taxa such as *Asterionella formosa*, *Tabellaria flocculosa* and *Psectrocladius sordidellus* along with concurrent declines in taxa such as *Polypedilum nebeculosum* suggest a shift towards higher-nutrient and/or more acidic conditions (Camburn & Charles 2000, Pillot 2009, Pillot 2014). Both acidification and eutrophication have been shown to be associated with land management practices (such as afforestation, grazing and burning) on peatlands (Miller *et al*. 1996, Tierney *et al*. 1998, Cummins & Farrell 2003, Drinan *et al*. 2013) but also to result from atmospheric deposition of sulphur (leading to acidification) and nitrogen (leading to eutrophication) (Flower *et al*. 1987, Bergstrom & Jansson 2006, Leira *et al*. 2007). In the Flow Country, Allot & Rose (1993) also observed increases in nutrient and acid tolerant species of diatom from cores taken in the 1990s. They attributed this to a combination of forestry and commercial fish farming within the lakes. No recent commercial fish farming has taken place at any of the lakes in this study and, to our knowledge, neither has it taken place historically.

Whilst top-bottom analysis can establish whether patterns of community change are consistent across a relatively large number of sites and can identify the most probable drivers of change, it is not without its limitations. While land management, atmospheric deposition and afforestation are theoretically temporally separable (because we know the management history of the area), it is not possible to separate the different management practices with the coarse resolution of a top-bottom analysis. Therefore, finer-scale multiproxy analysis of Flow Country lakes is now vital. Despite the limitations of a top-bottom analysis, our findings are clearly inconsistent with fish management and/or stocking being the primary driver of community change. Our findings contrast with those of Hancock *et al*. (2015) who theorised that the presence of fish and, particularly, the size of fish within the population were dominant drivers of freshwater invertebrate populations in Flow Country lakes. In our study, constrained ordinations of both diatoms and chironomid communities indicated increases in fish abundance at only one site (DUCU). However, it is acknowledged that inferences about fish as drivers of community change are of limited value because the fish data are not especially robust. The information about trout populations obtained by semi-quantitative methods conflicts with that from other sources in the angling community which suggest that some of the lakes with zero fish catches contained large numbers of trout in recent times (Crawford 1991, Sandison 2015). A robust and standardisable palaeolimnological method for assessing the effect of fish introductions and/or changes in fish management over the last ca. 150 years would involve looking at changes in invertebrate indicator taxa (such as *Chaoborus* and large *Daphnia*) or the abundance of fish scales in sediment cores (Jeppesen *et al*. 1996, Jeppesen *et al*. 2001, Davidson *et al*. 2003, Johansson *et al*. 2005). However, these analyses would require larger volume coring equipment than we used here (e.g. Patmore *et al*. 2014).

Few studies to date have used palaeolimnology to examine recent environmental change in multiple peatland lakes (Allott & Rose 1993, Turkia *et al*. 1998). However, findings from these studies accord with those we have presented here, with results indicating patterns of increased nutrients and/or acidification but no consistency in the extent and direction of community change observed or in the apparent drivers. Instead it appears that the response of peatland lakes, although driven by large-scale drivers such as land management, afforestation and/or atmospheric deposition, is somewhat idiosyncratic. This finding is particularly important for conservation practitioners and peatland managers because it suggests that sites which may be assumed to be similar because of their proximity to one another may, in fact, be different ecologically and physico-chemically, and their response to ecological management may be equally heterogeneous.

The value of a combined approach

Substantial value can be added to contemporary surveys by repeating them over time to assess environmental change at a site (or group of sites). The addition of a temporal perspective enables hypotheses for change to be explored more robustly, as spatially correlated hypotheses can be temporally separated. However, the repeated survey approach has numerous limitations. Frequently, repeated surveys are not comparable to one another due to changes in methodology and require long-term investment (of both time and money) to maintain. Even where repeated survey data exist, they rarely cover timescales longer than 3–10 years. There is now a growing body of evidence that demonstrates the value of complementing contemporary surveys with long-term palaeolimnological data derived from lake sediment cores (Davies & Bunting 2010, Sayer *et al*. 2012, Gillson & Marchant 2014, Davidson *et al*. 2018). This combined approach has many advantages including being able to generate robust standardised data for sites covering a range of taxa, and timescales ranging from tens to hundreds or even thousands of years. Typically, the main limitation of a palaeolimnological approach is the time involved in sample processing, particularly for multiple indicators, which commonly results in a small number of sites (one or two) being the primary focus of any study. Whilst palaeolimnological studies that focus on single systems can provide a wealth of data, the generalisability of the outcomes can be limited. Therefore, in the current study a top-bottom approach was used to enable assessment of environmental change at a larger number of sites but at coarser temporal scale. The trade-off between number of sites and temporal resolution does itself have limitations, particularly when working with a limited number of taxa. Here we were unable to conclusively separate all the hypothesised drivers of change.

Overall, the current study has provided unique insights into recent change in Flow Country lakes, demonstrating that substantial change has taken place resulting in the lake ecosystems being more different now than they were in the past. While we were able to refine the list of hypothesised drivers of change, further work is required to definitively identify the ultimate drivers of the ecosystem changes. This could be achieved by adopting a broader multi-proxy approach and analysis of cores from Flow Country sites at a finer temporal resolution.

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AUTHOR CONTRIBUTIONS

All of the authors jointly conceived the idea and generated funding for the project from their respective institutions. HJR led the fieldwork with VJJ, SB, CDS and GMH. HJR carried out the laboratory analysis and identification of chironomid and diatom taxa with support from SB and VJJ. HJR wrote most of the manuscript with significant contributions from VJJ, GMH and SB. All authors have contributed to amendments and revisions.

REFERENCES

Allott, T.E.H. & Rose, N.L. (1993) *A Palaeolimnological Study of Recent Water Quality Changes in Lochs with Black-Throated Diver Populations. Report to the RSPB*. Research Report 5, Environmental Change Research Centre (ECRC), Department of Geography, University College London (UCL), 62 pp.

Allott, T.E.H., Golding, P.G. & Appleby, P.G. (1994) *Studies of Water Quality Change at Black-throated Diver Sites: Progress Report to the RSPB.* Research Report 10, Environmental Change Research Centre (ECRC), Department of Geography, University College London (UCL), 39 pp.

Anderson, T., Cranston, P.S. & Epler, J.H. (eds.) (2013) *The Larvae of Chironomidae (Diptera) of the Holarctic Region - Keys and Diagnoses*. Insect Systematics & Evolution, Supplement No. 66, Scandinavian Entomology Ltd., Lund, Sweden, 573 pp.

Appleby, P. (1997) Dating recent sediments by ^{210}Pb: problems and solutions. In: Ilus, E. (ed.) *Dating of Sediments and Determination of Sedimentation Rate: Proceedings of a Seminar held in Helsinki 2–3 April 1997*, STUK-A145, Radiation and Nuclear Safety Authority, Helsinki, 7–24. ISBN: 951-712-226-8. Online at: https://inis.iaea.org/collection/NCLCollectionStore/_Public/29/040/29040425.pdf?r=1&r=1, accessed 31 Jly 2019.

Appleby, P.G., Nolan, P.J., Gifford, D.W., Godfrey, M.J., Oldfield, F., Anderson, N.J. & Battarbee, R.W. (1986) ^{210}Pb dating by low background gamma counting. *Hydrobiologia*, 141, 21–27.

Appleby, P.G., Richardson, N. & Nolan, P.J. (1992) Self-absorption corrections for well-type germanium detectors. *Nuclear Instruments and Methods in Physics Research B*, 71, 228–233.

Bainbridge, I.P., Housden, S.D., Minns, D.W. & Lance, A.N. (1987) *Forestry in the Flows of Caithness and Sutherland*. Conservation Topic Paper 18, Royal Society for the Protection of Birds, Edinburgh, UK, 24 pp.

Battarbee, R., Carvalho, L., Jones, V.J., Flower, R.J., Cameron, N.G. & Bennion, H. (2001) Diatoms. In: Smol, J.P., Last, W.M. & Birks, H.J.B. (eds.) *Tracking Environmental Change Using Lake Sediments Volume 3: Terrestrial, Algal, and Siliceous Indicators*, Kluwer Academic Publishers, Dordrecht, Germany, 105–202.

Battarbee, R.W., Grytnes, J.A., Thompson, R., Appleby, P.G., Catalan, J., Korhola, A., Birks, H.J.B., Heegaard, E. & Lami, A. (2002) Comparing palaeolimnological and instrumental evidence of climate change for remote mountain lakes over the last 200 years. *Journal of Paleolimnology*, 28, 161–179.

Bennion, H., Battarbee, R.W., Sayer, C.D., Simpson, G.L. & Davidson, T.A. (2010) Defining reference conditions and restoration targets for lake ecosystems using palaeolimnology: a synthesis. *Journal of Paleolimnology*, 45, 533–544.

Bergstrom, A. & Jansson, M. (2006) Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. *Global Change Biology*, 12, 635–643.

Brooks, S.J., Udachin, V. & Williamson, B.J. (2005) Impact of copper smelting on lakes in the southern Ural Mountains, Russia, inferred from chironomids. *Journal of Paleolimnology*, 33, 229–241.

Brooks, S.J., Langdon, P.G. & Heiri, O. (2007) *The Identification and Use of Palaearctic Chironomidae Larvae in Paleoecology*. QRA Technical Guide No. 10, Quaternary Research Association, London, UK, 276 pp.

Camburn, K.E. & Charles, D.F. (2000) *Diatoms of Low-Alkalinity Lakes in the Northeastern United States*. Special Publication, Academy of Natural Sciences of Philadelphia, Philadelphia, USA, 152 pp.

Canfield, D.E.Jr., Shireman, J.V., Colle, D.E., Haller, W.T., Watkins, C.E.II & Maceina, M.J. (1984) Prediction of chlorophyll *a* concentrations in Florida lakes: Importance of aquatic macrophytes. *The Canadian Journal of Fisheries and Aquatic Sciences*, 41, 497–501.

CEH (2018) *The UK Lakes Portal*. Online at: https://eip.ceh.ac.uk/apps/lakes/, accessed 15 Dec 2017.

Charman, D.J. (1994) Late-glacial and Holocene vegetation history of the Flow Country, northern Scotland. *New Phytologist*, 127, 155–168.

Coulson, J., Bauer, L., Butterfield, J., Downie, I., Cranna, L. & Smith, C. (1995) The invertebrates of the northern Scottish Flows, and a comparison with other peatland habitats, 74–94 pp. In: *Heaths and Moorland. A Cultural Landscape*. Her Majesty's Stationery Office (HMSO), Edinburgh, UK, 400 pp.

Crawford, L. (1991) *Caithness & Sutherland, Trout Loch Country*. North of Scotland Newspapers, Wick, UK, 65 pp.

Cummins, T. & Farrell, E.P. (2003) Biogeochemical impacts of clearfelling and reforestation on blanket-peatland streams II. Major ions and dissolved organic carbon. *Forest Ecology and Management*, 180, 557–570.

Dalton, C., Taylor, D. & Jennings, E. (2009) The role of palaeolimnology in implementing the Water Framework Directive in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy*, 109B, 161–174.

Davidson, T.A., Sayer, C.D., Perrow, M.R. & Tomlinson, M.L. (2003) Representation of fish communities by scale sub-fossils in shallow lakes: implications for inferring percid–cyprinid shifts. *Journal of Paleolimnology*, 30, 441–449.

Davidson, T.A., Bennion, H., Reid, M., Sayer, C.D. & Whitmore, T.J. (2018) Towards better integration of ecology in palaeoecology: from proxies to indicators, from inference to understanding. *Journal of Paleolimnology*, 60, 109–116.

Davies, A. & Bunting, M. (2010) Applications of palaeoecology in conservation. *Open Journal of Ecology*, 3, 54–67.

Dean, W.E. (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Research*, 44, 242–248.

Downie, I., Coulson, J., Foster, G. & Whitfield, D. (1998) Distribution of aquatic macroinvertebrates within peatland pool complexes in the Flow Country, Scotland. *Hydrobiologia*, 377, 95–105.

Drinan, T.J., Graham, C.T., O'Halloran, J. & Harrison, S.S.C. (2013) The impact of catchment conifer plantation forestry on the hydrochemistry of peatland lakes. *Science of the Total Environment*, 443, 608–620.

Flower, R.J., Battarbee, R.W. & Appleby, P.G. (1987) The recent palaeolimnology of acid lakes in Galloway, South-West Scotland: diatom analysis, pH trends, and the role of afforestation. *Journal of Ecology*, 75, 797–823.

Gillson, L. & Marchant, R. (2014) From myopia to clarity: sharpening the focus of ecosystem management through the lens of palaeoecology. *Trends Ecology and Evoloution*, 29, 317–325.

Glew, J. (1991) Miniature gravity corer for recovering short sediment cores. *Journal of Paleolimnology*, 5, 285–287.

Hancock, M., Robson, H.J. & Smith, T. (2015) Correlates of lake use by breeding common scoters in Scotland. *Aquatic Conservation*: *Marine and Freshwater Ecosystems*, 26, 749–767.

Holden, J., Shotbolt, L., Bonn, A., Burt, T.P., Chapman, P.J., Dougill, A.J., Fraser, E.D.G., Hubacek, K., Irvine, B., Kirkby, M.J., Reed, M.S., Prell, C., Stagl, S., Stringer, L.C., Turner, A. & Worrall, F. (2007) Environmental change in moorland landscapes. *Earth-Science Reviews*, 82, 75–100.

Holden, J., Chapman, P., Palmer, S. & Kay, P. (2012) The impacts of prescribed moorland burning on water colour and dissolved organic carbon: a critical synthesis. *Journal of Environmental Management*, 101, 92–103.

Hornung, J.P. & Foote, A.L (2006) Aquatic invertebrate responses to fish presence and vegetation complexity in Western Boreal wetlands with implications for waterbird productivity. *Wetlands*, 26, 1–12.

Jeppesen, E., Madsen, E. & Jensen, J. (1996) Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface sediment calibration data set from shallow. *Freshwater*, 36, 115–127.

Jeppesen, E., Leavitt, P., De Meester, L. & Jensen, J.P. (2001) Functional ecology and palaeolimnology: using cladoceran remains to reconstruct anthropogenic impact. *Trends in Ecology and Evolution*, 16, 191–198.

Johansson, L.S., Amsinck, S.L., Bjerring, R. & Jeppesen, E. (2005) Mid- to late-Holocene land-use change and lake development at Dallund Sø, Denmark: trophic structure inferred from cladoceran subfossils. *The Holocene*, 15, 1143–1151.

Joosten, H. & Clarke, D. (2002) *Wise Use of Mires and Peatlands: Background and Principles Including a Framework for Decision-Making*. International Mire Conservation Group and International Peat Society, Saarijarvi, Finland, 304 pp.

Kernan, M., Battarbee, R. & Moss, B. (2011) *Climate Change Impacts on Freshwater Ecosystems*. John Wiley & Sons, London, 314 pp.

Krammer, K. & Lange-Bertalot, H. (1986–1991) *Bacillariophyceae*. Volumes 1–5, Gustav Fischer Verlag, Stuttgart, Germany.

Laske, S.M., Rosenberger, A.E., Kane, W.J., Wipfli, M.S. & Zimmerman, C.E. (2017) Top-down control of invertebrates by Ninespine Stickleback in Arctic ponds. *Freshwater Science*, 36, 124–137.

Le Roux, G. & Marshall, W.A. (2011) Constructing recent peat accumulation chronologies using atmospheric fall-out radionuclides. *Mires and Peat*, 7(08), 1–14.

Legendre, P. & Legendre, L. (2012) *Numerical Ecology*. Third edition, Elsevier, Amsterdam, The Netherlands, 990 pp.

Leira, M, Jordan, P., Taylor, D., Dalton, C., Bennion, H., Rose, N. & Irvine, K. (2006) Assessing the ecological status of candidate reference lakes in Ireland using palaeolimnology. *Journal of Applied Ecology*, 43, 816–827.

Leira, M., Cole, E.E. & Mitchell, F.J.G. (2007) Peat erosion and atmospheric deposition impacts on an oligotrophic lake in eastern Ireland. *Journal of Paleolimnology*, 38, 49–71.

Lindsay, R., Charman, D.J., Everingham, F., O'Reilly, R.M., Palmer, M.A., Rowell, T.A. & Stroud, D.A. (1988) *The Flow Country: The Peatlands of Caithness and Sutherland*. Joint Nature Conservation Committee, Peterborough, 174 pp.

Maitland, P.S., Boon, P.J. & McLusky, D.S. (1994) *The Fresh Waters of Scotland. A National Resource of International Significance*. John Wiley and Sons Inc., New York, USA, 639 pp.

Miller, J.D., Anderson, H., Ray, D. & Anderson, A., (1996). Impact of some initial forestry practices on the drainage waters from blanket peatlands. *Forestry*, 69, 193–203.

Patmore, I.R., Sayer, C.D., Goldsmith, B., Davidson, T.A., Rawcliffe, R. & Salgado, J. (2014) Big Ben: A new wide-bore piston corer for multi-proxy palaeolimnology. *Journal of Paleolimnology*, 51, 79–86.

Pillot, H. (2009) *Chironomidae Larvae, Volume 2: Biology and Ecology of the Chironomini*. KNNV Publishing, Zeist, The Netherlands, 312 pp.

Pillot, H. (2014) *Chironomidae Larvae, Volume 3: Biology and Ecology of the Aquatic Orthocladiinae*. KNNV Publishing, Zeist, The Netherlands, 370 pp.

R Core Team (2016) *R: A Language and Environment for Statistical Computing*. The R Foundation, Vienna, Austria. Online at: https://www.R-project.org/, accessed 15 Mar 2016.

Ramchunder, S.J., Brown, L.E. & Holden, J. (2009) Environmental effects of drainage, drain-blocking and prescribed vegetation burning in UK upland peatlands. *Progress in Physical Geography*, 33, 49–79.

Robson, H.J. (2017) *Causes of Decline of Common Scoter* (Melanitta nigra) *in North Scotland: Evidence from Palaeolimnology*. PhD thesis, University College London, 367 pp.

Rose, N.L. (1994) A note on further refinements to a procedure for the extraction of carbonaceous fly-ash particles from sediments. *Journal of Paleolimnology*, 11, 201–204.

Rose, N.L., Harlock, S., Appleby, P.G. & Battarbee, R.W. (1995) Dating of recent lake sediments in the United Kingdom and Ireland using spheroidal carbonaceous particle (SCP) concentration profiles. *The Holocene*, 5, 328–335.

Rose, N.L., Rose, C.L., Boyle, J.F. & Appleby, P.G. (2004) Lake-sediment evidence for local and remote sources of atmospherically deposited pollutants on Svalbard. *Journal of Paleolimnology*, 31, 499–513.

Rowan, J.S., Carwardine, J., Duck, R.W., Bragg, O.M., Black, A.R., Cutler, M.E.J., Soutar, I. & Boon, P.J. (2006) Development of a technique for Lake Habitat Survey (LHS) with applications for the European Union Water Framework Directive. *Aquatic Conservation*: *Marine and Freshwater Ecosystems*, 16, 637–657.

Rydin, H. & Jeglum, J. (2013) *Biology of Peatlands*. Second Edition, Biology of Habitats series, Oxford University Press, Oxford, UK, 382 pp.

Sandison, B. (2015) *Secret Lochs and Special Places*. Black and White Publishing, Edinburgh, UK, 256 pp.

Sayer, C., Bennion, H. & Davidson, T. (2012) The application of palaeolimnology to evidence-based lake management and conservation: examples from UK lakes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22(2), 165–180.

Šmilauer, P. & Lepš, J. (2014) *Multivariate Analysis of Ecological Data using Canoco 5.* Cambridge University Press, Cambridge, UK, 362 pp.

Smol, J.P. (2008) *Pollution of Lakes and Rivers: A Paleoenvironmental Perspective*. Second edition, Blackwell Publishing, Oxford, 396 pp.

SNH (2002) *Natural Hertitage Zones: A National Assessment of Scotland's Freshwaters*. Report, Scottish Natural Heritage, 445 pp. Online at: https://www.nature.scot/sites/default/files/2017-06/B464892%20-%20National%20Assessment%20of%20Scotland%27s%20landscapes%20%28from%20NHF%29.pdf, accessed 01 Apr 2016.

SNH (2018) *Standing Waters Database*. Scottish Natural Heritage (SNH). Online at: https://gateway.snh.gov.uk/pls/apex_cagdb2/f?p=111:12:::NO:::, accessed 01 Dec 2017.

SNIFFER (2008) *Lake Habitat Survey in the United Kingdom: Field Survey Guidance Manual, Version 4*. Project WFD 99, Scotland and Northern Ireland Forum for Environmental Research (SNIFFER) & Scottish Natural Heritage (SNH), Edinburgh, 78 pp.

Spirit, M.G., Jackie, R., McCann, A.G., Muir, D., Doull, N., Locke-Scobae, S., Davies, I., Mackay, A. & Allan, L. (1986) *Freshwater Invertebrates of Caithness*. Caithness and Sutherland District Councils Community Programmes Agency, Wick, UK, 169 pp.

Stroud, D.A., Reed, T.M., Pienkowski, M.W. & Lindsay, R.A. (1988) *Birds, Bogs and Forestry - The Peatlands of Caithness and Sutherland.* Joint Nature Conservation Committee, Peterborough, UK, 121 pp.

Stroud, D., Reed, T., Pienkowski, M. & Lindsay, R. (2015) The Flow Country: battles fought, war won, organisation lost. In: *Nature's Conscience. The Life and Legacy of Derek Ratcliffe*. Langford Press, Norfolk, UK, 401–439.

ter Braak, C.J.F. & Šmilauer, P. (2012) *CANOCO Reference Manual and User's Guide: Software for Ordination (Version 5.0)*. Microcomputer Power, Ithaca, New York, USA, 496 pp.

Tierney, D., Kelly-Quinn, M. & Bracken, J.J. (1998) The faunal communities of upland streams in the eastern region of Ireland with reference to afforestation impacts. *Hydrobiologia*, 389, 115–130.

Turkia, J., Sandman, O. & Huttunen, P. (1998) Palaeolimnological evidence of forestry practices disturbing small lakes in Finland. *Boreal Environment Research*, 3, 45–61.

UCL (2019) *Loss on Ignition*. Department of Geography, University College London. Online at: https://www.geog.ucl.ac.uk/resources/laboratory/laboratory-methods/lake-sediment-analysis/loss-on-ignition, accessed 07 Oct 2019.

Warren, C. (2000) 'Birds, bogs and forestry' revisited: the significance of the Flow Country controversy. *Scottish Geography Journal*, 116, 315–337.

Wieker, J.E., Schoonover, C.M., Gaines, R.K., Jones, A., Mattes, C., Moses, K., Perry, J., Prior, K., Smith, S., Swilling, B., Rule, M. & Joyner-Matos, J. (2016) Effects of introduced Brook Stickleback (*Culaea inconstans*) on benthic macroinvertebrate communities in the nearshore area of lentic systems in Turnbull National Wildlife Refuge, Washington. *Northwest Science*, 90, 278–289.

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Supplementary material (available for separate download):
Supplement 1 (S1): Bathymetry and percentage vegetation cover maps (two PNG images per lake).
Supplement 2 (S2): Data (chironomids, diatoms, mosses, macrophytes) (Microsoft Excel Worksheet)

Appendix 1: Laboratory and statistical methods

Loss on ignition

The percentage weight lost on ignition is a measure of the organic content of the sediment. Generally, percentage loss on ignition values show an inverse relationship with percentage dry weight values. The method followed UCL (2019), which is based on Dean (1974).

Sediment samples (1–2 g) were weighed out (balance precision 4 decimal places) into clean, dry porcelain crucibles and dried overnight at 105 °C. The crucibles were then transferred to a furnace set at 550 °C where they remained for 2 hours (preheated furnace) or 2 hours 45 minutes (furnace heated from cold). They were then retrieved using long-handled tongs and allowed to cool slightly on an asbestos mat before placing in a desiccator. After full cooling the crucibles were re-weighed and the percentage of dry weight lost on ignition calculated.

Radiometric dating

Lead-210 (half-life 22.3 years) is a naturally-produced radionuclide derived from atmospheric fallout (termed unsupported ^{210}Pb). Cesium-137 (^{137}Cs; half-life 30 years) and Americium-241 (^{241}Am) are artificially produced radionuclides arriving at the study area by atmospheric fallout from nuclear weapons testing and nuclear reactor accidents. All three of these radionuclides have been used extensively in (radiometric) dating of recent sediments (Le Roux & Marshall 2011).

Dried sediment samples from three of the sediment cores were analysed for ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am by direct gamma assay at the Bloomsbury Environmental Isotope Facility (BEIF) at University College London, using an ORTEC HPGe GWL series well-type coaxial low background intrinsic germanium detector. Lead-210 was determined via its gamma emissions at 46.5keV, and ^{226}Ra by the 295keV and 352keV gamma rays emitted by its daughter isotope ^{214}Pb following storage for 3 weeks in sealed containers to allow radioactive equilibration. Cesium-137 and ^{241}Am were measured by their emissions at 662 kev and 59.5 kev (Appleby *et al*. 1986). The absolute efficiencies of the detector were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self absorption of low energy gamma rays within the sample (Appleby *et al*. 1992).

X-ray fluorescence analysis

X-ray florescence (XRF) analysis is a type of elemental analysis that allows quantitative determination of the geochemical composition of sediments. A sample of known weight (between 0.5 and 3 grams) is bombarded with X-rays which displace electrons from the inner orbital shells of atoms in the sample. This causes electrons to move from outer to inner shells to fill the gap, releasing energy in the process (known as fluorescence). The energy released by electrons moving in this way is uniquely characteristic for each element, allowing the elemental concentration of the sample to be determined (typically Si, Ti, Ca, K, Fe, Mn Cl, S, Nb, Ni, Pb, Rb, Sr, Zn and Zr).

The heavy metal profiles from XRF analysis can be used to provide a rough estimate of the timescale covered by recent (1850–present) sediments in the core. Anthropogenic atmospheric pollutants (such as heavy metals Zn, Pb and Cu) deposited at lakes are rapidly taken up by sediments (Smol 2008). Therefore, heavy metal analysis of samples along the length of sediment cores can provide a historical record of atmospheric pollution experienced by a lake and its catchment. The profile of heavy metal pollutants in recently deposited lake sediment shows a pattern similar to the schematic profile for spherical carbonaceous particles (SCPs) shown in Figure A1.1. Concentrations typically increase from the period of the industrial revolution (ca.1850) until the 1970s,

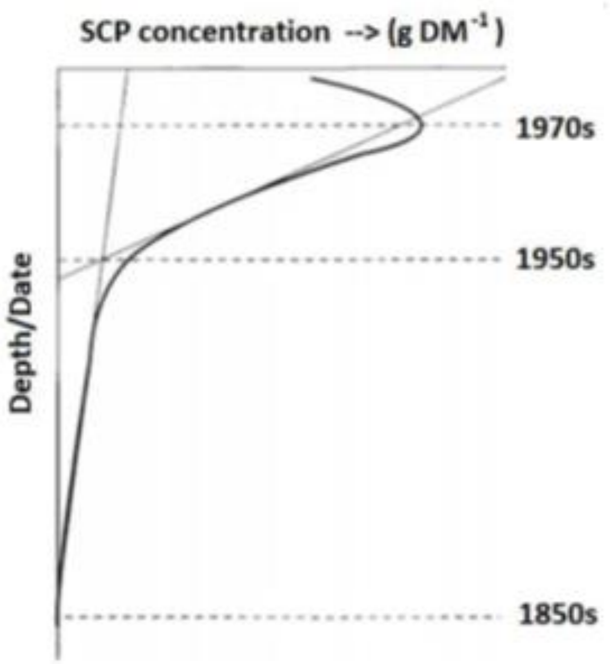

Figure A1.1. Schematic profile of spherical carbonaceous particles (SCPs) in a sediment core, adapted from Rose *et al.* (1995).

when pollution legislation was introduced. A reduction in atmospheric metal pollution followed and this can be observed in the profile, subsequent to the '1970–1980' subsurface peak.

In this study, samples of each 1 cm slice of all 18 cores were frozen, freeze dried and ground into a fine powder prior to XRF analysis using a XLAB2000 X-ray fluorescence spectrometer (SPECTRO Analytical Instruments GmbH, Kleve, Germany).

Data transformations

Prior to statistical analysis, the normality of data distributions was tested and where necessary data were transformed to provide the closest approximation of a normal distribution. For each environmental variable normality was determined using the Shapiro-Wilks test in R (R Core Team 2016), and multivariate community datasets were assessed in Canoco 5 (ter Braak & Smilauer 2012). The transformations applied are shown in Table A1.1.

Table A1.1. The data transformations carried out on the environmental and community datasets prior to analysis.

<table>
<tr><th colspan="2">Variable</th><th>Transformation</th></tr>
<tr><td rowspan="4">Environmental</td><td>DOC</td><td>natural log</td></tr>
<tr><td>fish abundance</td><td>square root</td></tr>
<tr><td>nitrate</td><td>square root</td></tr>
<tr><td>pH</td><td>none</td></tr>
<tr><td rowspan="2">Community</td><td>diatom</td><td>log (x+1)</td></tr>
<tr><td>chironomid</td><td>log (x+1)</td></tr>
</table>

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Appendix 2: Results of sediment analyses

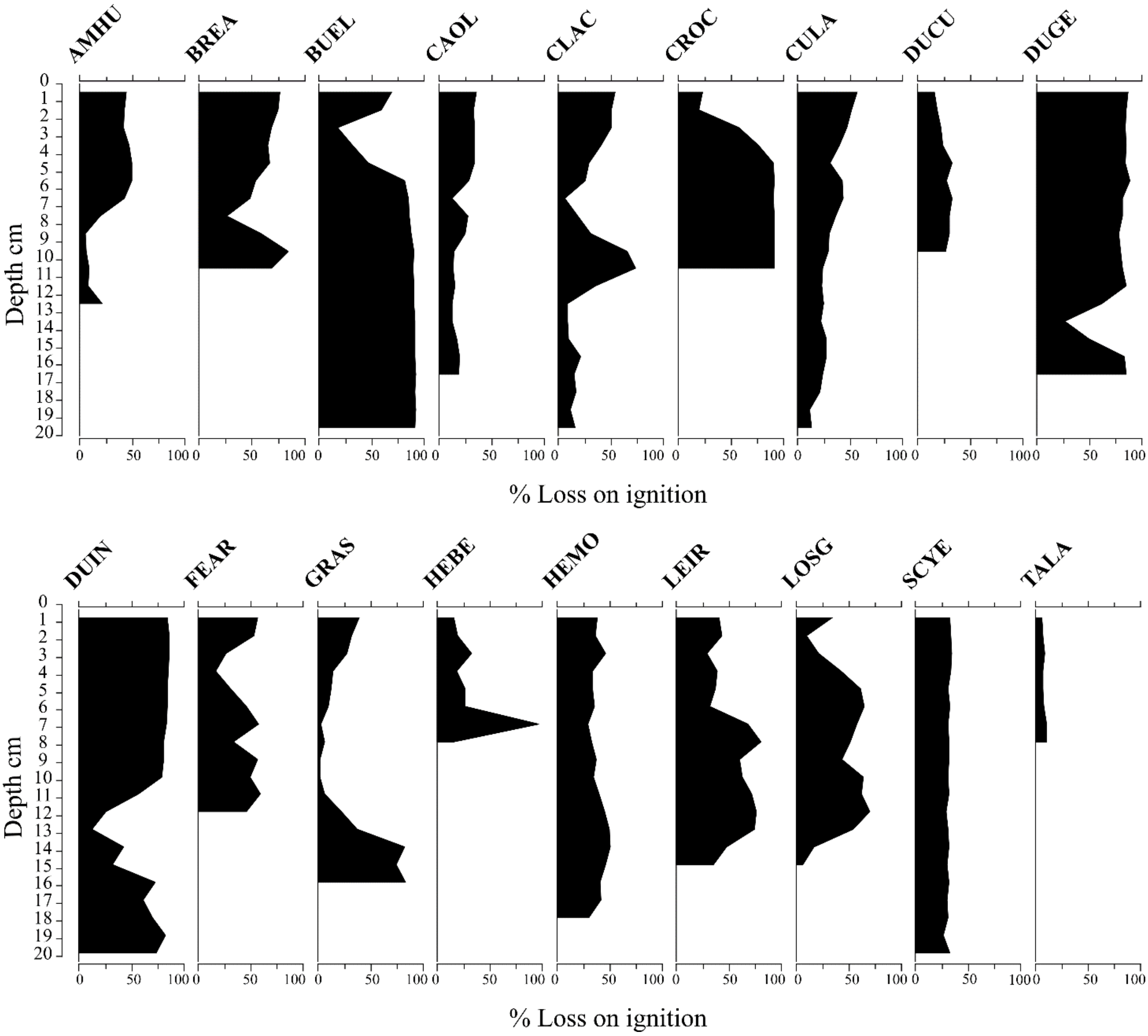

Figure A2.1. Loss on ignition profiles for the 18 study sites. Lake codes as in Table 1.

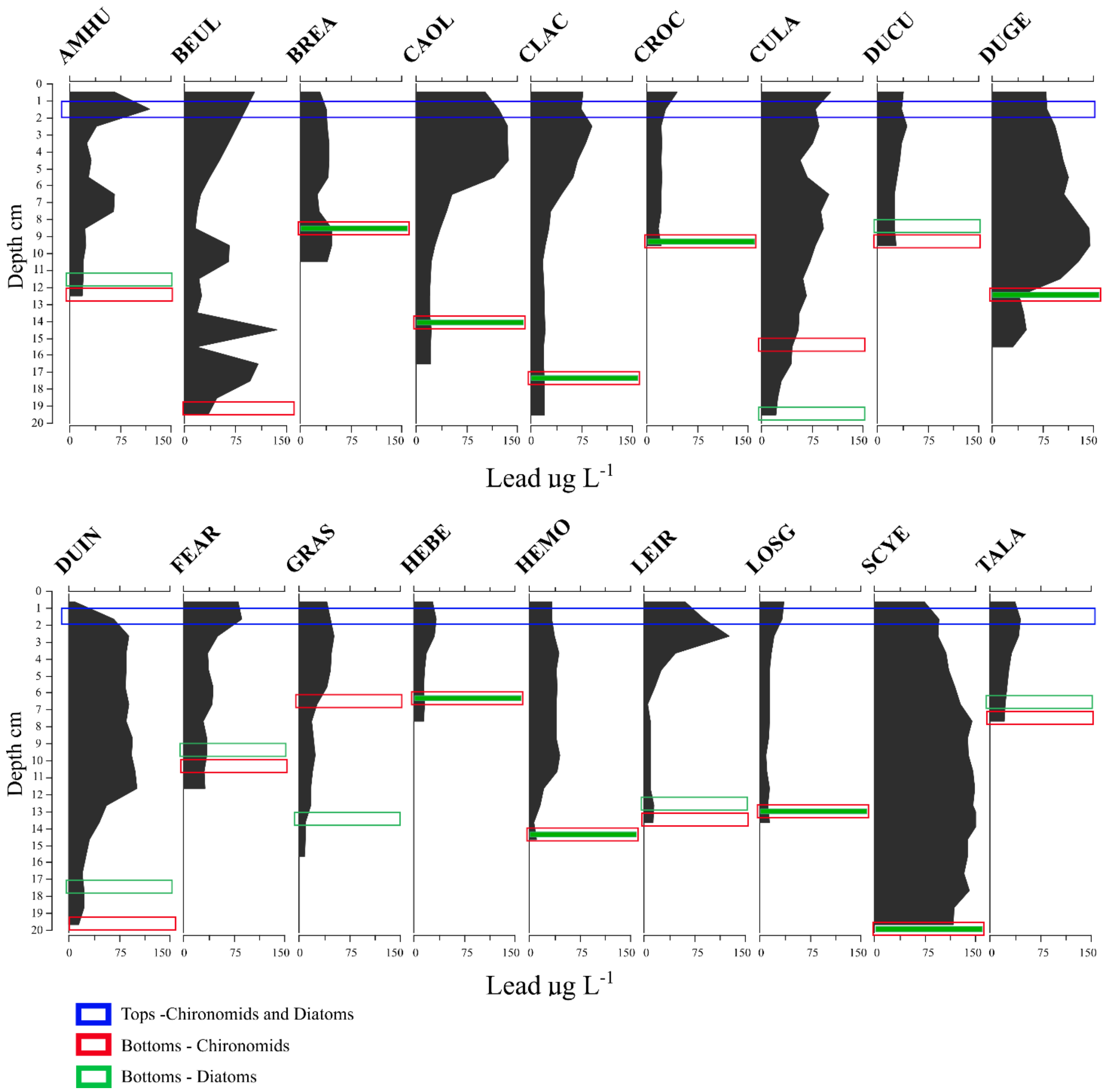

Figure A2.2. Lead concentrations measured by x-ray fluorescence (XRF) plotted against depth. The top and bottom slices used for chironomid and diatom analysis are highlighted. Lake codes as in Table 1.

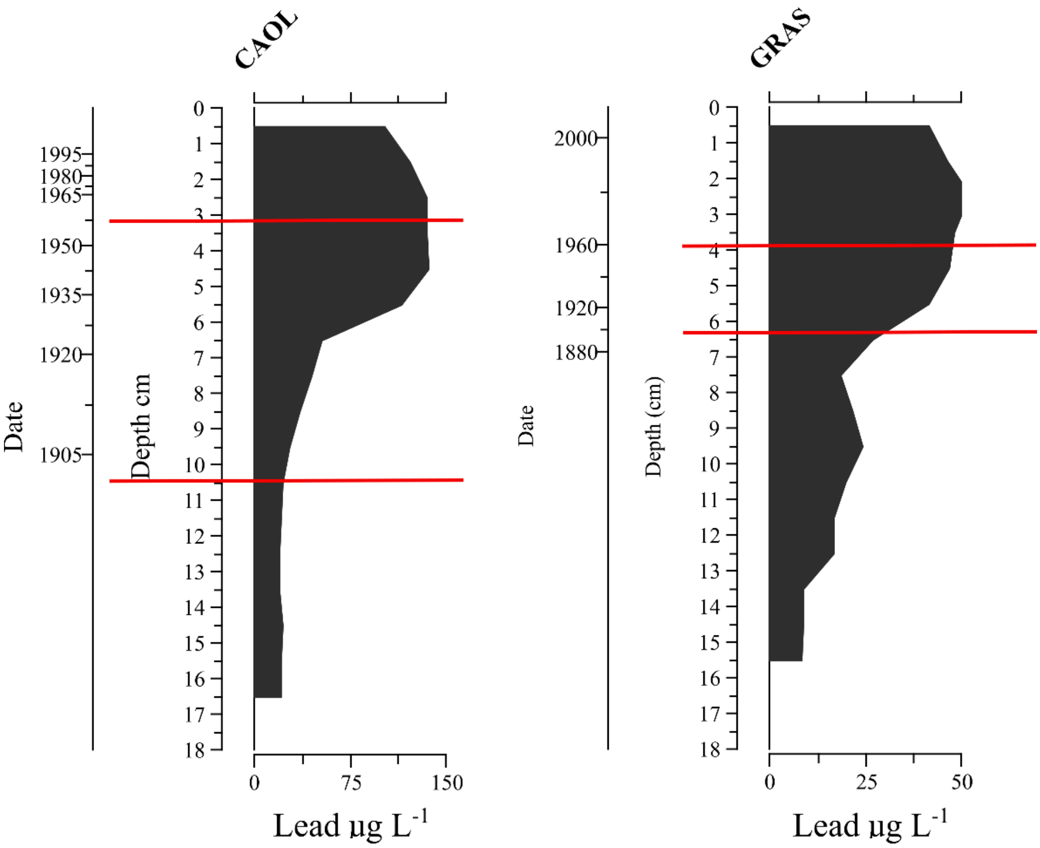

Figure A2.3. Lead concentrations measured by x-ray fluorescence (XRF) plotted against depth. Red line indicates 1900 and 1960 as determined by radiometric dating using ^{210}Pb. Lake codes as in Table 1.

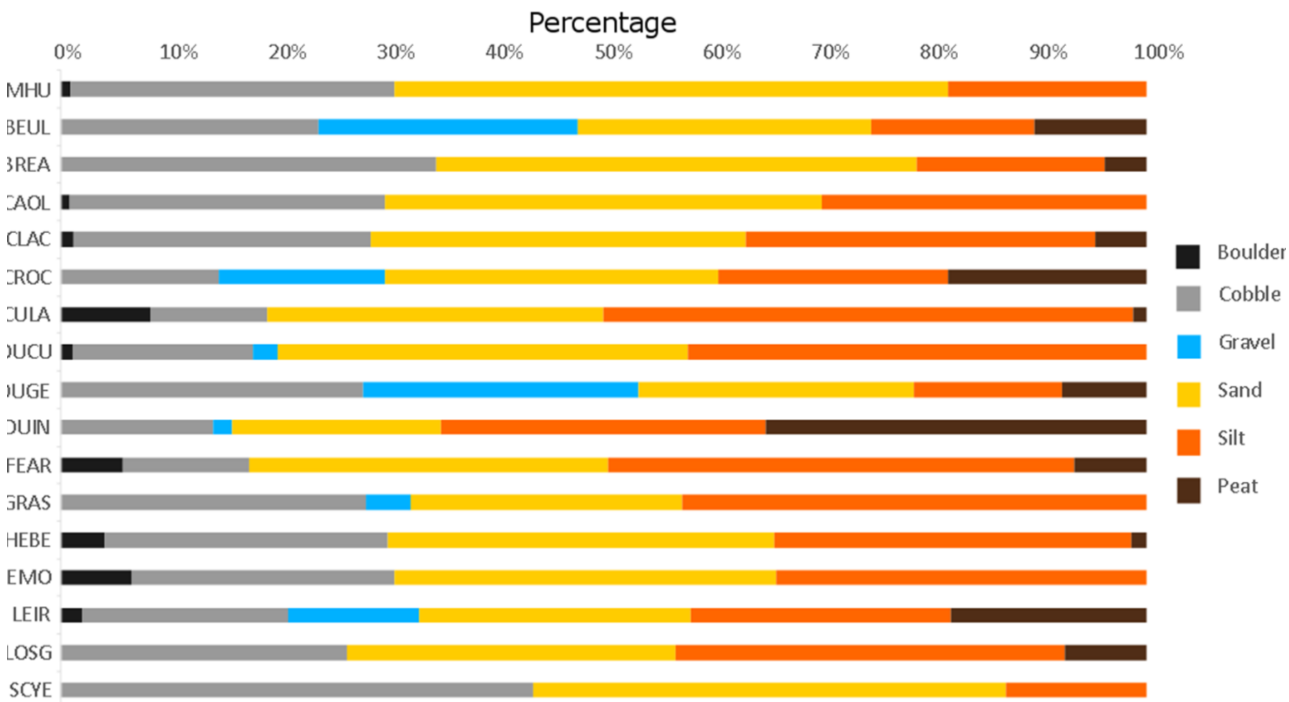

Figure A2.4. Sediment characterisation for the 18 study sites. The horizontal bar for each lake shows the percentages of different sediment types recorded (in 2014), classified by field estimation of particle size according to SNIFFER (2008). Site (lake) codes as in Table 1.