


RESEARCH ARTICLE

Will they be back? A framework to guide rare macrophyte conservation decisions in lakes

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Shallow lake restoration typically focusses on the re-establishment of macrophytes. The likelihood of a species returning to a site is contingent on dispersal, proximity to propagule sources, and the on-site propagule-bank viability. We explore the potential of palaeoecological records in combination with botanical surveys and distribution maps, to ascertain the loss of three submerged macrophytes (*Littorella uniflora*, *Najas flexilis*, and *Elatine hydropiper*) from, respectively, two lakes (Barton Broad, Norfolk and Esthwaite Water, Cumbria) and one lake landscape (Greater Glasgow, Scotland). We discuss re-establishment likelihood when accounting for species' autoecology and current water-chemistry conditions. *L. uniflora* is widespread in the United Kingdom but absent locally in Norfolk without known seed bank, hence is unlikely to naturally recolonise Barton Broad. Furthermore, current conditions are unsuitable for this species suggesting that nutrient reduction is required prior to translocation. *N. flexilis* is extinct in Cumbria and the long distances involved (>100 km) for recolonisation of Esthwaite Water suggest that spatial dispersal is unlikely, rendering the seed bank the last chance of natural recovery. Alternatively, translocation may be feasible. *E. hydropiper* is a nationally scarce species in the United Kingdom yet would have only a short dispersal distance (~10 km) to recolonise Loch Libo, hence there being no requirement for translocation. In exploring the recovery possibilities for the three focal plant species, we develop a time–space integrated framework that can be employed to guide conservation decisions for other species, enabling a more rational use of translocations in the future, in line with international guidelines.

Key words: connectivity, dispersal, lakes, macrophytes, palaeoecology, recolonisation, seed bank, translocation

Implications for Practice

- A decision-making framework, informed by palaeoecological records and contemporary data, is constructed to better understand the restoration potential of three lost aquatic plant species. This can be used to inform conservation decisions at other sites and for other species, and encourage a more rational use of resources for aquatic plant species' translocations in the future.
- Suitability of current conditions and the need for improvements to water quality should be determined prior to any restoration actions.
- Full consideration of potential for dispersal through space and through time via the seed bank should be given.
- Natural dispersal and recruitment are advocated as the preferred conservation options for restoring lost aquatic plant populations where conditions allow.

Introduction

Freshwater biodiversity has seen rapid declines in recent decades linked to habitat loss and degradation, pollution, invasive species, and climate change (Collen et al. 2014; WWF 2022). Hence, there is an urgent need to protect and restore aquatic systems as part of

wider ecosystem restoration efforts under the UN Decade on Ecosystem Restoration 2021–2030 (UNGA 2019). In lakes, there have been widespread losses of aquatic plant (hereafter macrophyte) species richness and biomass and, in many cases, a complete loss of submerged macrophytes which, given the key structuring role of macrophytes in lakes, has major

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consequences for wider ecosystem health (Sand-Jensen et al. 2000; Phillips et al. 2016). Measures such as point-source control at sewage treatment works (Phillips et al. 2005), improved agricultural practices, and upstream wetland regeneration have resulted in a reduction in nutrient loading to lakes and a degree of macrophyte recovery (Jeppesen et al. 2005; Hilt et al. 2018). Nonetheless full recovery in lakes is rare (McCrackin et al. 2017).

The likelihood of a macrophyte species returning to a lake once it has been lost is contingent on a multitude of factors including suitability of conditions, dispersal capabilities, and opportunities via hydrological connectivity (Salgado et al. 2022), wind or birds (Green et al. 2002; Soons et al. 2008), seed production and the viability of seed banks (Bakker et al. 2013; Alderton et al. 2017), and proximity to source populations. The questions around whether a species can return, and what restoration strategies are appropriate, are important not only for aquatic systems but also for restoration ecology more widely (Sayer et al. 2019). There is much debate across wetland habitats concerning whether sites under restoration should be allowed to seed naturally via dispersal and remnant seed banks or whether plants should be actively introduced (Rodrigo 2021; Fenu et al. 2023). Conservation translocation (translocation, hereafter), defined as “the human-mediated movement of living organisms or propagules for conservation benefit from one area, with release in another” (World Conservation Union 2013) has shown promise for wetland plants but is not without risks and challenges (Orsenigo 2018; Rodrigo 2021). Equally, following restoration, rare macrophytes can sometimes return to lakes and ponds via long-lived seed banks and natural dispersal (Kaplan et al. 2014; Hawkins 2019; Sayer & Parmenter 2020).

Macrophytes are frequently at the heart of lake conservation assessments such as the Habitats and Species Directive (European Union 1992) and Water Framework Directive (European Union 2000) (Penning et al. 2008; Søndergaard et al. 2010), yet most monitoring programs cover periods of only years to decades, rarely extending back far enough to determine the species present prior to eutrophication. The macro-remains of macrophytes, hereafter macrofossils, preserve well in lake sediments (including seeds, fruits, oospores, turions, and vegetative fragments) and have been used successfully to inform conservation measures and restoration targets (Madgwick et al. 2011; Sayer et al. 2016; Bennion et al. 2018). However, the potential of palaeoecology to assess the likelihood of species returning to a site via spatial and temporal dispersal has only recently been explored. Alderton et al. (2017) studied historic pond sediments, demonstrating that macrophyte species were able to germinate from century-old seed banks, allowing rapid plant recovery at restored ponds. Similarly, Sayer et al. (2022) reported rapid recolonisation of diverse plant communities from exposed sediment of overgrown ponds in England where propagules display long-term viability. Salgado et al. (2019, 2022) combined present-day and palaeolimnological data on macrophyte communities in the Upper Lough Erne system, Northern Ireland, highlighting the importance of landscape connectivity in providing a continuous supply of propagules, thereby temporarily enhancing biodiversity resilience to nutrient pollution. However,

the potential for macrophytes to naturally re-colonize via dispersal through space and/or time has not been rigorously assessed and the circumstances under which intervention is required to return rare macrophytes to the landscape remain vague, with a need for a clearer framework to guide decision-making.

Here, in contrast to previous studies dealing with macrophyte recovery at the community level, we focus on specific taxa of conservation importance and ascertain the historical loss of three submerged macrophytes (shoreweed [*Littorella uniflora*] [L.] Asch., slender naiad [*Najas flexilis*] [Willd.] Rostk. & Schmidt, and eight-stamened waterwort [*Elatine hydropiper* L.]) from two UK lakes (Barton Broad, Norfolk and Esthwaite Water, Cumbria) and one UK lake landscape (Greater Glasgow), respectively, using site-specific and other relevant palaeoecological data. Combining these data with distribution maps and botanical surveys, we determine contemporary distributions for these species and, based on site environmental conditions and knowledge of plant life history traits, assess the likelihood of restoring these macrophytes to the study sites under current and future scenarios. We ask whether the species in question could recolonise if water quality is restored, where propagules would come from, and consider the implications of restoring sites which are spatially separated from source populations. Using a simple framework, we demonstrate how a time–space integrated approach of palaeoecology and maps can be employed to guide rare macrophyte conservation decisions.

Methods

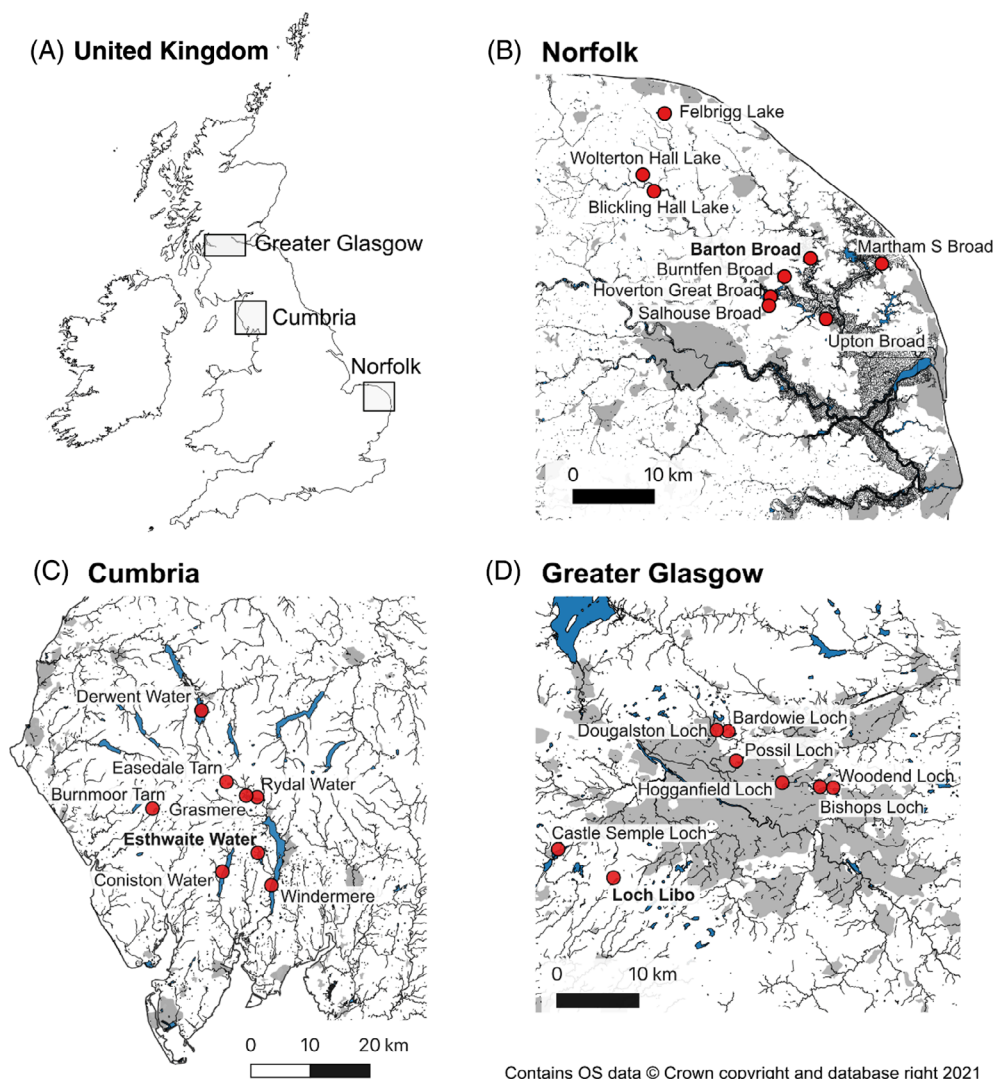
Study Sites and Species

The study sites are located in three contrasting and representative freshwater landscapes (hydrosapes) in the United Kingdom that experience varying exposure to a number of stressors and show different degrees of hydrological connectivity: lowland agricultural Norfolk in eastern England, upland Cumbria in north-west England, and urban Greater Glasgow in central Scotland (Table 1; Fig. 1). We focus on one submerged macrophyte of interest for restoration in each hydroscape.

Littorella uniflora is a low growing, isoetid plant typically of shoreline communities in nutrient-poor to mesotrophic European lakes (Vestergaard & Sand-Jensen 2000) and ponds (Preston & Croft 1997; Stroh et al. 2023). It is currently widespread across the United Kingdom and Ireland but scarce in southern and eastern England (Fig. 2A; Stroh et al. 2023), where it has declined over the last century due to eutrophication, combined with hydrological modifications which have reduced natural lake level fluctuation (Preston & Croft 1997). *L. uniflora* used to be present in Barton Broad (hereafter Barton) (52.7°N, 1.5°E), a large (0.77 km²), shallow (average depth 1.7 m) riverine lake (Fig. 1; Madgwick et al. 2011). Barton is designated for its nature conservation value at national and international levels. It is nutrient rich (mean 80 total phosphorus [TP] µg/L and 40 chlorophyll-*a* µg/L, Environment Agency unpublished data 2018–2021) and has a well-documented history of macrophyte decline with macrophytes largely absent by the 1970s (Madgwick et al. 2011). Three decades of lake restoration work followed,

Table 1. Details of all cores analyzed with key sites shown in bold italics (WBID = waterbody ID; date = date of core collection; water depth (m) = water depth at coring location; ²¹⁰Pb = Y indicates the core is dated; OSGB = Ordnance Survey National Grid reference system for Great Britain; upstream lake (Y/N) = connectivity metric from United Kingdom Lakes Portal <https://ep.ceh.ac.uk/apps/lakes>).

Site name	Core code	WBID	Date	Core length (cm) and type	Core location	Water depth (m)	Location OSGB	²¹⁰ Pb	Upstream lake (Y/N)
Cumbria									
<i>Esthwaite Water</i>									
Burmoor Tam	ESTH9	29328	01 September, 2013	109, Big Ben	Littoral	1.5	335748, 496505	Y	Y
Coniston Water	BURNMT_BB1	29215	04 July, 2016	26, Renberg	Littoral	2.7	318464, 504514	N	N
Derwent Water	CONI3	29321	01 July, 2016	94, Big Ben	Littoral	3.9	331089, 497249	N	Y
Easedale Tam	DERW3	28965	29 June, 2016	89, Big Ben	Littoral	1.15	326540, 519460	N	Y
Grasmere	EASE_BB3	29166	03 July, 2016	37, Renberg	Littoral	1.7	330712, 508614	N	Y
Rydal Water	GRAS3	29184	02 July, 2016	87, Big Ben	Littoral	2.4	333430, 506984	N	Y
Windermere	RYDA_BB2	29197	28 June, 2016	21, Renberg	Littoral	1.5	336029, 506204	N	Y
(South Basin)	WIND8	47008	30 June, 2016	23, Renberg	Littoral	3	337852, 488459	N	Y
Greater Glasgow									
<i>Loch Libo</i>									
Bardowie Loch	LIBO_D1	26535	26 July, 2016	97, Big Ben	Open	1.2	243575, 655744	Y	N
Bishop Loch	CZNS57_Litt	25866	27 July, 2016	116, Big Ben	Littoral	2	257620, 673781	N	N
Castle Semple Loch	CZNS66_D1	26163	23 July, 2016	95, Big Ben	Open	1.15	268834, 666776	Y	Y
Dougalston Loch	SEMP_Litt	26392	25 July, 2016	63, Big Ben	Littoral	1.2	235765, 658627	N	Y
Hogganfield Loch	DOUG_D1	25855	27 July, 2016	67, Livingstone	Open	0.75	256141, 673847	Y	Y
Possil Loch	HOGG_D1	26145	22 July, 2016	105 Big Ben	Open	2.2	264193, 667323	Y	Y
Woodend Loch	POSSL_INT	26001	21 July, 2016	108, Livingstone	Littoral	0.9	258534, 670008	N	N
Norfolk	WODE_D1	26167	24 July, 2016	102, Big Ben	Open	1.25	270629, 666750	Y	Y
<i>Barton Broad</i>									
Blickling Lake	BART2.3, 8,10-14	35655	1998-2008	75-136 cm, Livingstone	Littoral and Open	1-1.5	6363, 3215	N	Y
Burmfen Broad	BLIC2	35249	27 April, 2009	0-100 cm, Livingstone	Open	1	617750, 323390	Y	N
Felbrigg Lake	BURF1	35852	22 October, 2008	0-135 cm, Livingstone	Open	1.31	633835, 318774	N	N
Hoveton Great Broad	FELB6	34827	12 January, 2005	0-51 cm, Big Ben	Open	1.2	619039, 338790	Y	N
Martham South Broad	HGB01	35977	14 January, 2005	0-85 cm, Big Ben	Open	1.2	631626, 316165	Y	Y
Salhouse Great Broad	MARS1	35738	21 October, 2008	0-120 cm, Livingstone	Open	1	645950, 320206	Y	Y
Upton Great Broad	SALG1	36043	04 March, 2003	0-86 cm, Livingstone	Open	1.6	631738, 315759	Y	Y
Wolterton Hall Lake	UPTO3	36202	30 May, 2001	0-164 cm, Livingstone	Open	0.9	639034, 313376	Y	N
	WOLT1	35179	15 November, 2006	0-70 cm, Big Ben	Open	1	615979, 332500	Y	N



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Figure 1. Site map of (A) the three hydroscapes in the United Kingdom, and sites from which sediment cores were collected in (B) Norfolk, (C) Cumbria, and (D) Greater Glasgow.

including external nutrient reduction and sediment removal, yet macrophyte communities remain sparse (Phillips et al. 2005, 2015). The lake is currently classified as “unfavorable recovering” according to the Common Standards Monitoring Scheme (CSM) (Interagency Freshwater Group 2015).

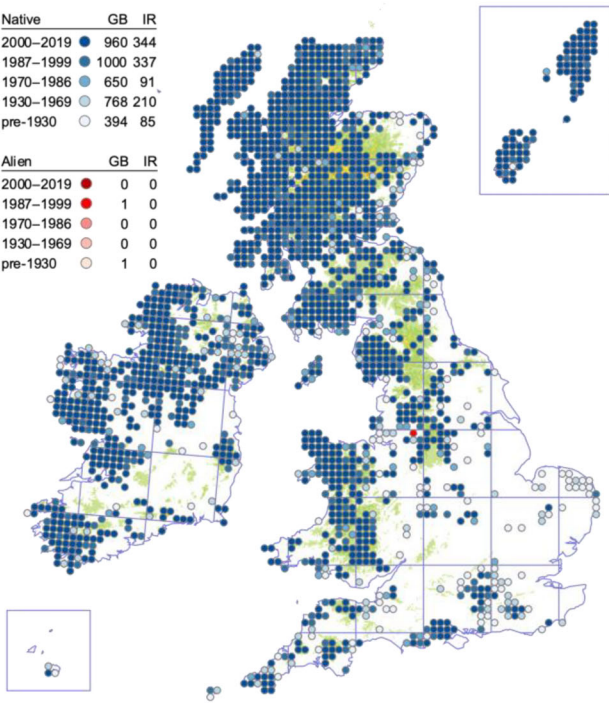
Najas flexilis is a nationally rare Schedule 8 species (Wildlife and Countryside Act 1981, <https://www.legislation.gov.uk/ukpga/1981/69/contents>) in the United Kingdom (Fig. 2B). *N. flexilis* was first discovered in Scotland in 1872 and at its only known English site, Esthwaite Water (hereafter Esthwaite), in 1914. It has, however, become extinct at many sites in eastern Scotland and at Esthwaite itself, likely due to eutrophication (Bishop et al. 2019). *N. flexilis* is currently found in Western Scotland, principally the Western Isles, and along the west coast of Ireland (Fig. 2B; Stroh et al. 2023). Esthwaite (54.4°N, 3°W) is a large (0.96 km²), shallow (average depth 6.9 m, maximum depth 15.5 m) lake in Cumbria (Fig. 1). It was designated a Site

of Special Scientific Interest (SSSI) in 1965 especially due to the occurrence of *N. flexilis*. However, *N. flexilis* has not been recorded at the site since 1982 and the current macrophyte flora is dominated by the non-native invasive *Elodea nuttallii* (Nuttall’s pondweed) with the lake classified as “unfavorable, recovering” under CSM (Bishop et al. 2019). Water chemistry (Talling & Heaney 1988) and palaeoecological data (Dong et al. 2012) document a clear history of eutrophication in Esthwaite since 1970 linked to discharges from a sewage treatment works and a fish farm (established in 1981). Winter maxima for soluble reactive P (SRP) increased from an average of 2 µg/L before 1970 to 12 µg/L after 1970. Restoration has involved P loading reduction from the sewage works since 1986, but nutrients derived from catchment run-off, fish farm operations (until 2009) and internal loading have negated reductions in lake nutrient concentrations and limited biological recovery (Maberly et al. 2011; Bennion et al. 2015).

(A)

Native		GB	IR
2000–2019	●	960	344
1987–1999	●	1000	337
1970–1986	●	650	91
1930–1969	○	768	210
pre-1930	○	394	85

Alien		GB	IR
2000–2019	●	0	0
1987–1999	●	1	0
1970–1986	●	0	0
1930–1969	●	0	0
pre-1930	○	1	0

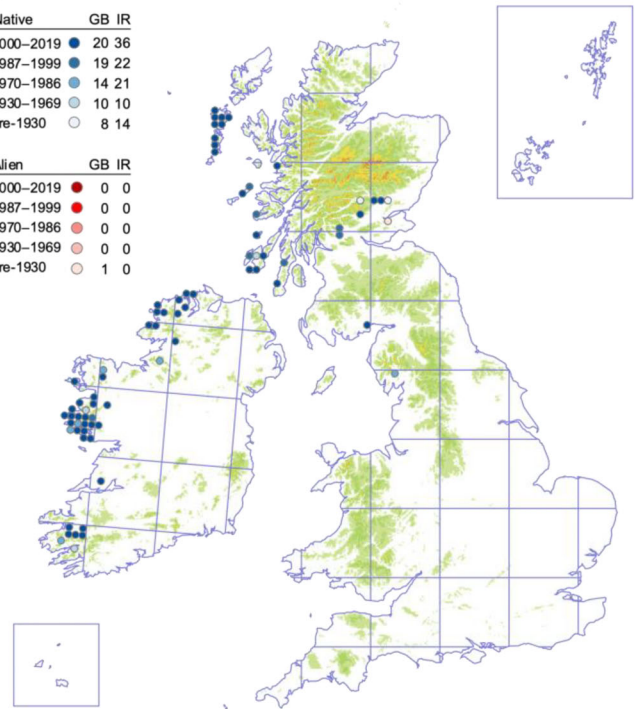


Littorella uniflora in *BSBI Online Atlas 2020*, eds P.A. Stroh, T.A. Humphrey, R.J. Burkmair, O.L. Pescott, D.B. Roy, & K.J. Walker. <https://dev-brc-plantatlas9.pantheonsite.io/atlas/2cd4p9h.818> [Accessed 16/09/2022]

(B)

Native		GB	IR
2000–2019	●	20	36
1987–1999	●	19	22
1970–1986	●	14	21
1930–1969	○	10	10
pre-1930	○	8	14

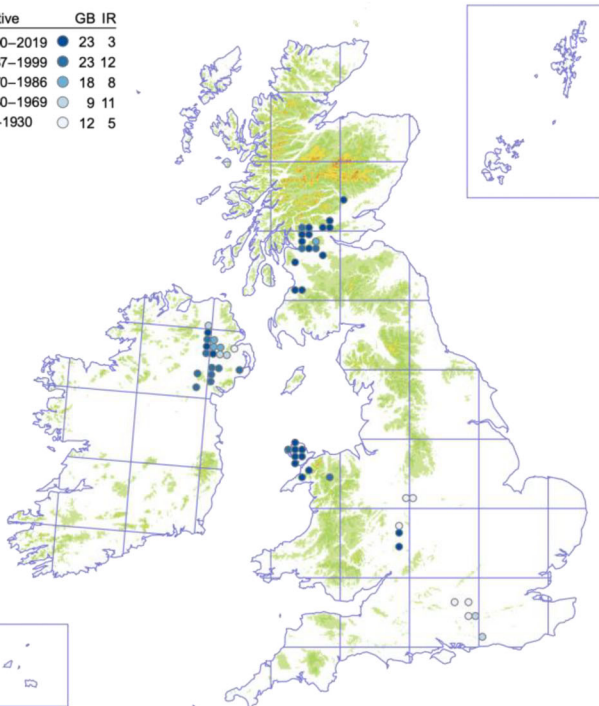
Alien		GB	IR
2000–2019	●	0	0
1987–1999	●	0	0
1970–1986	●	0	0
1930–1969	●	0	0
pre-1930	○	1	0



Najas flexilis in *BSBI Online Atlas 2020*, eds P.A. Stroh, T.A. Humphrey, R.J. Burkmair, O.L. Pescott, D.B. Roy, & K.J. Walker. <https://dev-brc-plantatlas9.pantheonsite.io/atlas/2cd4p9h.1hc> [Accessed 16/09/2022]

(C)

Native		GB	IR
2000–2019	●	23	3
1987–1999	●	23	12
1970–1986	●	18	8
1930–1969	○	9	11
pre-1930	○	12	5



Elatine hydropiper in *BSBI Online Atlas 2020*, eds P.A. Stroh, T.A. Humphrey, R.J. Burkmair, O.L. Pescott, D.B. Roy, & K.J. Walker. <https://dev-brc-plantatlas9.pantheonsite.io/atlas/2cd4p9h.ywq> [Accessed 16/09/2022]

Figure 2. Distribution map for presence in the United Kingdom of (A) *Littorella uniflora*, (B) *Najas flexilis*, and (C) *Elatine hydropiper* (Source: Stroh et al. 2023) (GB, Great Britain; IR, Ireland; numbers, number of 10×10 km grid squares [hectads] in which the species was found in each time period).

Elatine hydropiper is nationally scarce in the United Kingdom (Stewart et al. 1994; Stroh et al. 2023) and is classed as vulnerable or endangered in parts of central and northern Europe (Taura et al. 2022). It disappeared from former historical strongholds in southern England during the twentieth century (last recorded 1944) (Fig. 2C). It was first recorded in Scotland in 1968 and has expanded within Central Scotland since this time (Idle et al. 1970; Stroh et al. 2023). It is possible, however, that like the equally inconspicuous six-stamened waterwort (*Elatine hexandra*), it may have been under-recorded historically. There are currently populations in Southern and Central Scotland, North Wales and Anglesey, Gloucestershire, and Northern Ireland (Fig. 2C). The principal threat to this plant is eutrophication and linked changes in lakebed substrates from firm to less cohesive silt, as well as water level alteration. Eight lakes in the Greater Glasgow area were subject to palaeoecological investigation to ascertain the historical occurrence of *E. hydropiper* (Table 1). Of key significance was Loch Libo (hereafter Libo) (55.77°N, 4.5°W), a small (0.09 km²), shallow (average depth 0.8 m, maximum depth 1.2 m) lake located in East Renfrewshire, designated as a SSSI in 1972 (Fig. 1). This lake had diverse biota in the past with extensive macrophytes including *E. hexandra* (EnviroCentre Ltd. 2015), but *E. hydropiper* has never been reported from it. Libo has one main inflow and a single outflow, but no direct hydrological connections to any upstream lakes. It is currently nutrient-rich (annual mean SRP of 20 µg/L, Natural Environment Research Council hydroscape project unpublished data 2016–2017) and has been classified as “unfavorable” under CSM owing to the presence of non-native *Elodea canadensis* (Canadian pondweed) (EnviroCentre Ltd. 2015).

Core Collection and Dating

The sediment core from Esthwaite (ESTH9), 109 cm in length, was collected from the littoral zone of the lake at a depth of 1.5 m on 1 September, 2013 (Bishop et al. 2019). The core from Libo (LIBO-D1), 97 cm in length, was collected from an open water location at a depth of 1.2 m on 26 July, 2016. Both cores were taken with a “Big Ben” wide-diameter piston corer (Patmore et al. 2014). Studies have shown that plant macrofossils tend to accumulate close to source plants (Birks 1980; Zhao et al. 2006) and thus, for the relatively deep Esthwaite, a core from the littoral zone was thought optimal. For Libo, where macrophytes may potentially grow across the whole lake bed, an open water core was deemed appropriate. For Barton, bulk basal samples from eight cores were collected at a range of locations within the lake from 1998 to 2008, using a Livingstone corer to provide information on “pre-disturbance” macrophyte communities (Madgwick et al. 2011). The layer representative of pre-1850 conditions was identified by observing the uppermost limit of the peat (constituting the lake bed prior to sediment deposition) and the first 10-cm slice above this level was sampled for each core. For each site, a number of cores (21–164 cm in length) from lakes in the surrounding area were also collected for macrofossil analysis to determine whether the species of interest had been present in, and subsequently lost

from, other lakes within the respective hydroscape (Table 1). Sediment cores were collected from seven more lakes in each of the Cumbrian and Greater Glasgow hydroscares in 2016, and archived core material was available for eight additional lakes in Norfolk collected from 2001 to 2009 (Table 1; Fig. 1).

The Esthwaite (ESTH9) and Libo (LIBO-D1) cores were dated radiometrically in the Environmental Radiometric Facility at University College London with ²¹⁰Pb, ²²⁶Ra, ¹³⁷Cs, and ²⁴¹Am measured by direct gamma assay (Appleby et al. 1986) (Supplement S1). The other cores were either dated radiometrically (as above) or cross-correlated with radiometrically dated cores from the same site (Table 1), and the samples approximating to 1850 AD were selected to represent the “reference samples.” For the United Kingdom, it is generally agreed that 1850 AD is a suitable date against which to assess impacts for lakes as this represents a period prior to major industrialization and agricultural intensification (Bennion & Simpson 2011). The surface (uppermost 0.5 or 1 cm) sample of each core was used to provide information on the current macrofossil assemblages in the lakes, representing the last few years’ accumulation of sediment.

Macrofossil Analysis

Plant macrofossils were identified from selected samples in the cores from Esthwaite ($n = 35$, Bishop et al. 2019) and Libo ($n = 6$), in the Barton bulk samples ($n = 8$, Madgwick et al. 2011), and in the surface sediment and reference samples of the additional lakes within each hydroscape ($n = 22$) (Table 1). For all samples, with the exception of the Barton bulk samples, an accurately measured volume of sediment (range 30–75 cm³) was analyzed as determined by water displacement. For the Barton bulk samples, approximately 300 cm³ of sediment was analyzed. All samples were sieved at 355 µm and, with the exception of the Barton bulk samples, also at 125 µm following Birks (2001). The entire residue from the 355 µm sieve was examined under a stereomicroscope at ×10–40 magnification and plant macrofossils were identified by comparison with reference material at the Environmental Change Research Centre, University College London. A quantitative sub-sample, typically one-fifth of the sample from the 125 µm sieve retent, was analyzed for smaller remains such as Nymphaeaceae scleroids and charophyte oospores. The macrofossil data were taken from three separate studies, thus accounting for the slightly different methodologies used, but all provided good species representation. It was not possible to ascribe all macrofossils to species level and in some cases aggregate groups were employed. Macrofossil data are presented as the number of remains per 100 cm³ of wet sediment. Sub-samples for pollen analysis from the Barton bulk samples were processed following standard methods (Berglund & Ralska-Jasiewiczowa 1986).

Distribution Maps and Site-Specific Botanical Surveys

Stroh et al. (2023) provide expert-checked, data-driven distribution maps for the three focal plant species. The underpinning data contain all confirmed occurrences of the species, as curated

by the Botanical Society of Britain and Ireland (BSBI). These distribution maps enabled calculation of the distance between the study lakes and nearest locations for each focal species. In addition, the BSBI database was accessed (URL: <https://database.bsbi.org/>) to identify the recorded occurrences of the focal species prior to 1900. To confirm presence or absence of the focal species at waterbodies within the immediate landscapes surrounding Barton, Esthwaite, and Libo, macrophyte surveys were undertaken using standard methods at 158 lake and pond sites as described by Law et al. (2019). These surveys used a grapnel, waders, and/or a boat, as appropriate, to capture all macrophyte species. This approach is complementary to the current BSBI distribution maps which cannot always confirm whether absence of a record is due to actual absence of the species or lower survey effort. This is particularly critical for species such as *E. hydropiper*, which are inconspicuous, can grow fully submerged and have been historically less well recorded.

Data Analysis and Visualization

The plant macrofossil stratigraphies were plotted using C2 (Juggins 2003) to visualize ecological change over time. Maps were plotted using QGIS (QGIS.org 2023) to include presence and absence of the focal species as recorded in the BSBI database, in the palaeoecological records, and at the waterbody specific surveys (Law et al. 2019).

Results

Littorella uniflora was found by pollen analysis in one pre-1850 bulk sample collected from Barton (Fig. 3A; Madgwick et al. 2011). BSBI-derived plant records for Norfolk from the 1700 to 1900s show *L. uniflora* as present at Filby Broad (1805, 1840—13 km from Barton), Martham Broads (1866—10 km from Barton), Upton Fen (1866—9 km from Barton), Belton Common (1889—25 km from Barton) and Sutton Broad (1914—2.5 km from Barton), and several other sites in the wider East Anglian region (Fig. 3B). The Flora of Norfolk of 1914 (Nicholson 1914) describes it as “overlooked” and in “several of the broads abundant”. However, post-1900 it had declined, being present at perhaps 10 sites in Norfolk and Suffolk, and by the 1990s it was restricted to three sites, none being close to Barton: Perch Lake, Westwick (1991—11 km from Barton), reservoirs in Lound (1996—25 km from Barton), and Home Mere, East Wretham (1991—60 km from Barton), the latter being its last extant Norfolk site where it was found in 2015 (Figs. 2A & 3C).

The macrofossil record of Esthwaite indicates that *Najas flexilis* was relatively abundant in the lake until the early to mid-1900s, after which the number of seeds declined, with only intermittent presence from that time (Fig. 4A; Bishop et al. 2019). Accordingly, a vegetation survey undertaken in 1914 (Pearsall 1920), reported *N. flexilis* as relatively abundant at Esthwaite, growing alongside a plant community typical of a mildly alkaline lake including charophytes and greater bladderwort (*Utricularia vulgaris*). Between approximately 1915 and 1978, the macrofossil

record reveals a community shift toward a vegetation tolerant of eutrophic conditions including perfoliate pondweed (*Potamogeton perfoliatus*) and blunt-leaved pondweed (*Potamogeton obtusifolius*) (Fig. 4A; Bishop et al. 2019). *N. flexilis* remains were absent from the macrofossil records in both the reference and surface samples of the other seven lakes in the Cumbrian hydroscape suggesting that this species has never been present at these sites (Fig. 4B & 4C). *N. flexilis* has not been recorded in plant surveys at Esthwaite since 1982 and BSBI data suggest it has never been recorded for other Cumbrian sites (Fig. 4B & 4C), with the closest recent record at Loch Kindar, southwest Scotland (60 km from Esthwaite) (Fig. 2B).

The macrofossil data indicate that *Elatine hydropiper* was present in Libo in the past alongside *Sphagnum* spp. and charophyte spp. (Fig. 5A). A community shift toward eutrophic conditions, dated to the mid-1900s (Supplement S1; Tables S1–S3; Figs. S1 & S2), saw the appearance of fine-leaved *Potamogeton* spp. and ivy-leaved duckweed (*Lemna trisulca*) (Fig. 5A). Diatom assemblage shifts in Libo, indicative of nutrient-enrichment, were coincident with these changes (Fig. S3). *E. hydropiper* remains were found in the reference samples of four of the eight Glasgow cores, but present in surface samples of only two of these cores: Bardowie Loch (20 km from Libo) and Castle Semple Loch (7 km from Libo) (Fig. 5B & 5C). At Libo and Possil Loch, remains of *E. hydropiper* were found only in reference samples with complete absence from other core samples, suggesting that it was lost from these two lochs during the nineteenth century (Fig. 5B & 5C). Historically, *E. hydropiper* was first recorded in Scotland in 1968, so the macrofossil records provide new information on the past presence of the species. Macrophyte surveys of 22 lochs and 26 ponds in the region found *E. hydropiper* restricted to Bardowie Loch and Lochend Loch (28 km from Libo). There are further records from the southeastern tip of Loch Lomond and at four smaller nearby sites near Lochwinnoch, southwest Glasgow (Fig. 5C).

A simple decision-making framework to guide practical conservation decisions for our focal plants, and more widely, is proposed (Fig. 6).

Discussion

Many freshwater macrophytes have undergone major declines during the last century leading to a strong desire for species conservation (Sand-Jensen et al. 2000; Zhang et al. 2017). Various approaches aimed at recovering rare and extinct species can be taken, including water quality improvement, habitat restoration, and changes in management, sometimes combined with species translocation (Orsenigo 2018). The decision-making basis for employing ecological restoration and/or species translocation as tools for increasing the range of threatened macrophytes needs to be informed by good evidence so that appropriate decisions are made. There has been a marked increase in plant translocations globally since around 2010, despite there being a relatively poor understanding of what governs the success of such interventions (Fenu et al. 2023). In combining

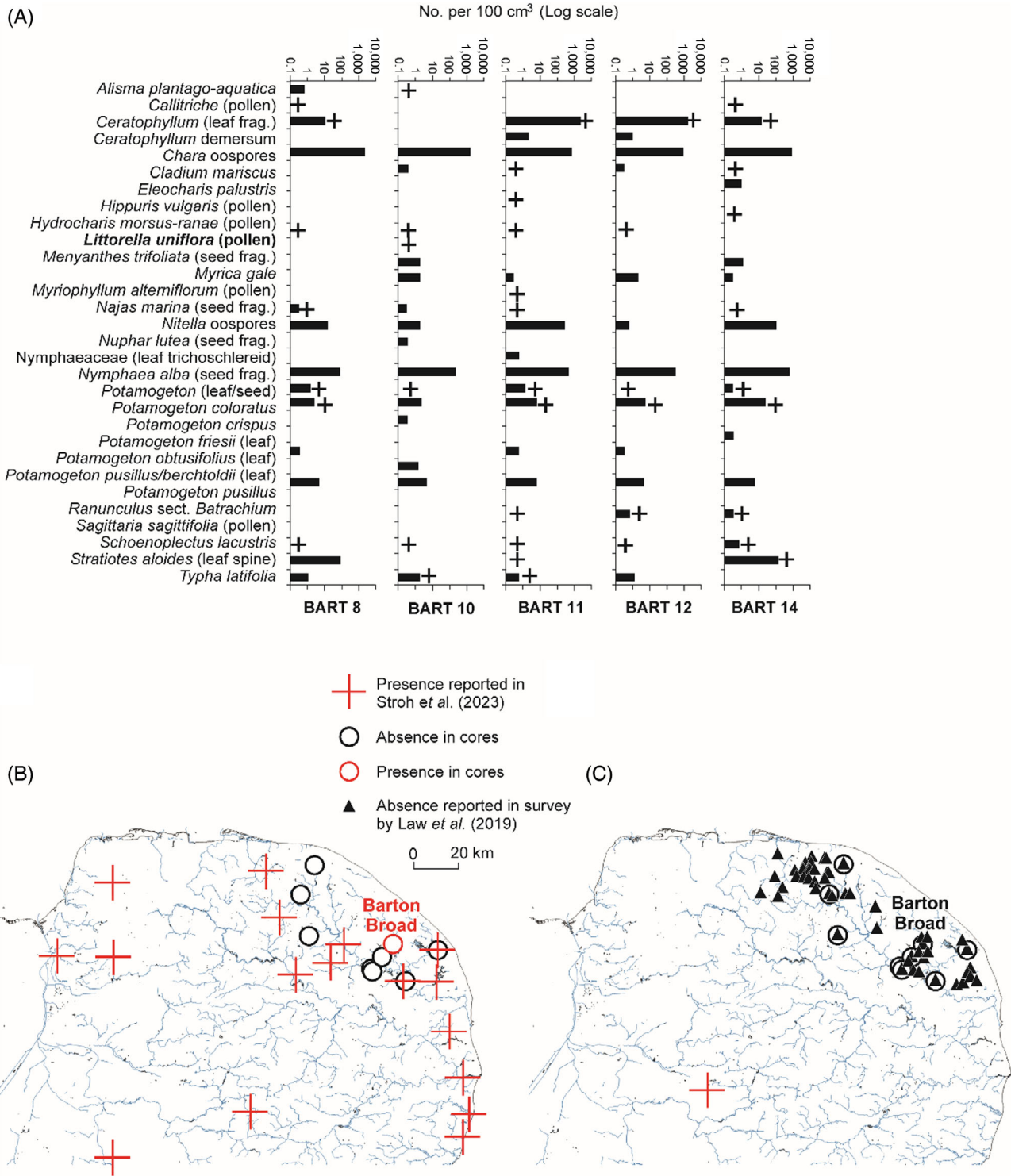
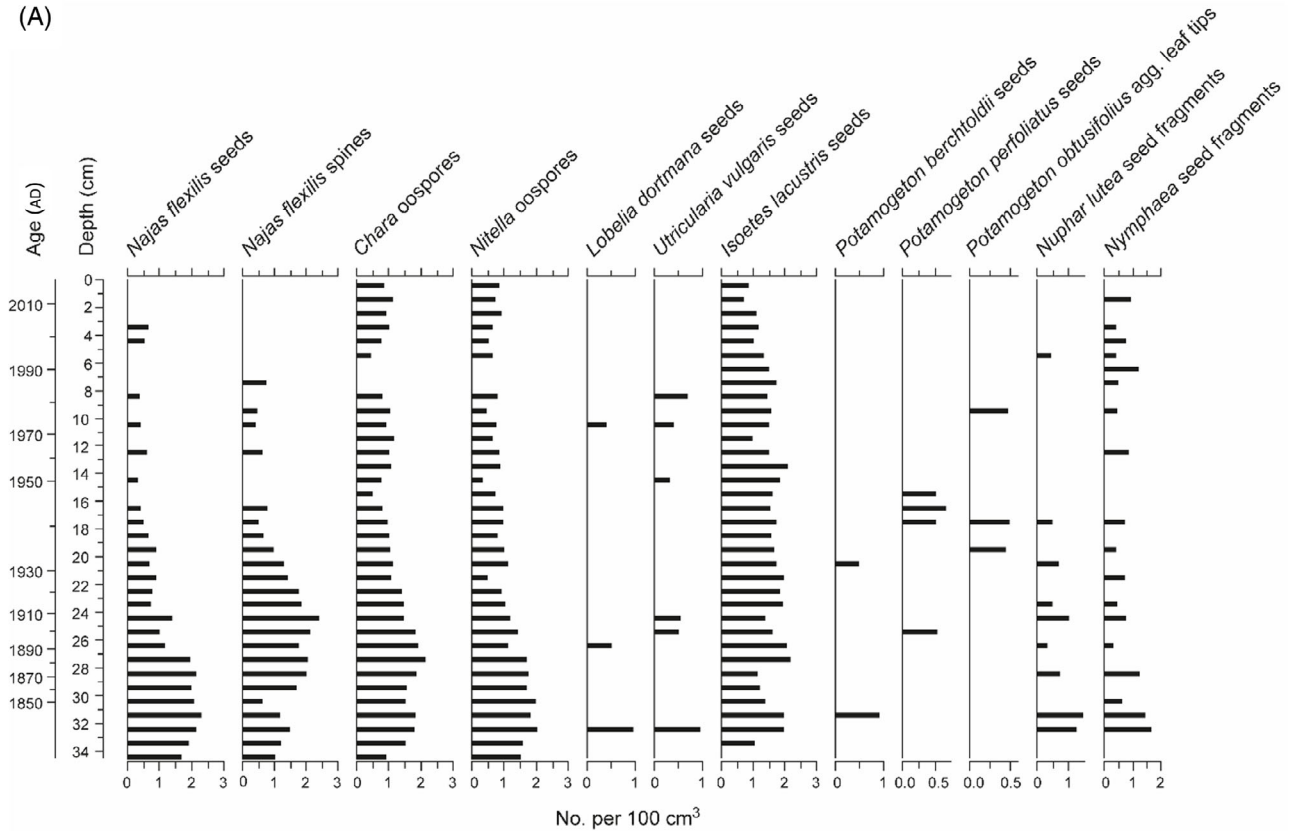


Figure 3. *Littorella uniflora*: (A) plant macrofossil and pollen remains in pre-1850 bulk samples from selected cores of Barton Broad, modified from Madgwick et al. (2011) (+ represents plants recorded by pollen analysis); (B) distribution prior to 1900 in Norfolk based on historical and palaeoecological data, and (C) distribution since 2000 in Norfolk based on recent survey and palaeoecological data.

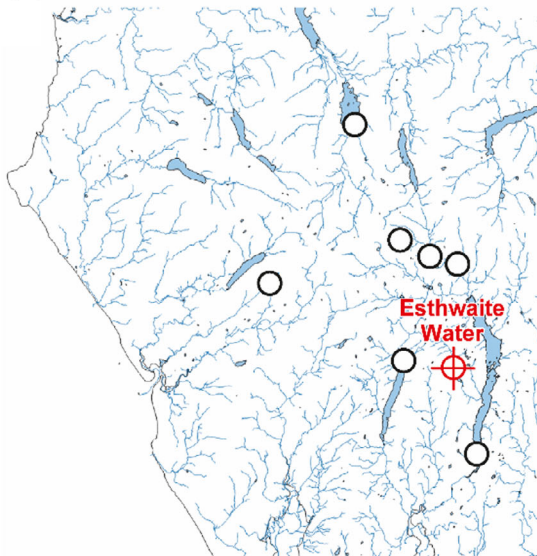
palaeoecology with historical and current data on species occurrence in three United Kingdom regions, we discuss the appropriateness of translocation in each case. The proposed

decision-making framework firstly considers suitability of local conditions, followed by potential for dispersal through space and finally dispersal through time via the seed bank.

(A)



(B)



(C)

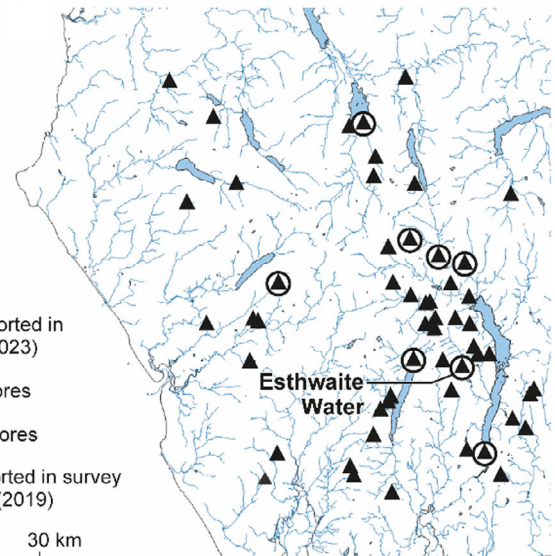


Figure 4. *Najas flexilis*: (A) plant macrofossil stratigraphy of Esthwaite Water (numbers per 100 cm³); (B) distribution prior to 1900 in Cumbria based on historical and palaeoecological data, and (C) distribution since 2000 in Cumbria based on recent survey and palaeoecological data.

Suitability of Current Conditions

A foremost requirement for species recovery is suitable environmental conditions, an assessment of the drivers that led to extinction in the first place and confirmation that the driver of

extinction is no longer operating (World Conservation Union 2013; Guo et al. 2019). For macrophytes, the following aspects are crucial: alkalinity, light, nutrients, substrate, water level fluctuation, grazing pressure, and competition with other

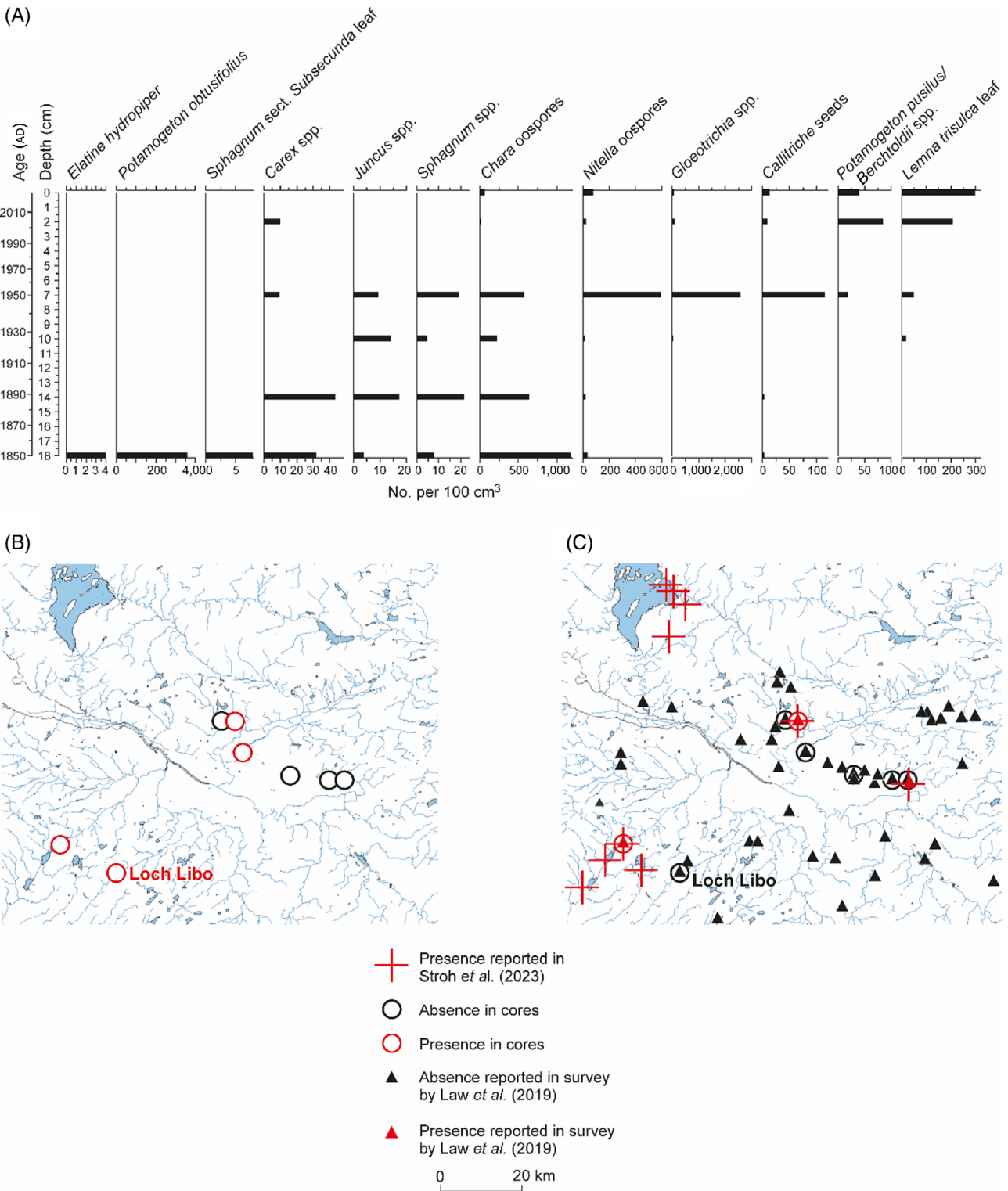


Figure 5. *Elatine hydropiper*: (A) plant macrofossil stratigraphy of Loch Libo (numbers per 100 cm³); (B) distribution prior to 1900 in Greater Glasgow based on historical and palaeoecological data, and (C) distribution since 2000 in Greater Glasgow based on recent survey and palaeoecological data.

plants, notably invasive species (Barko *et al.* 1986; Bakker *et al.* 2013). Palaeoecological data can provide valuable information on when focal plant species decline and why

(Bishop *et al.* 2019). When this information is coupled with contemporary data and knowledge on species ecology, it provides a sound basis for assessing the possibility of a species

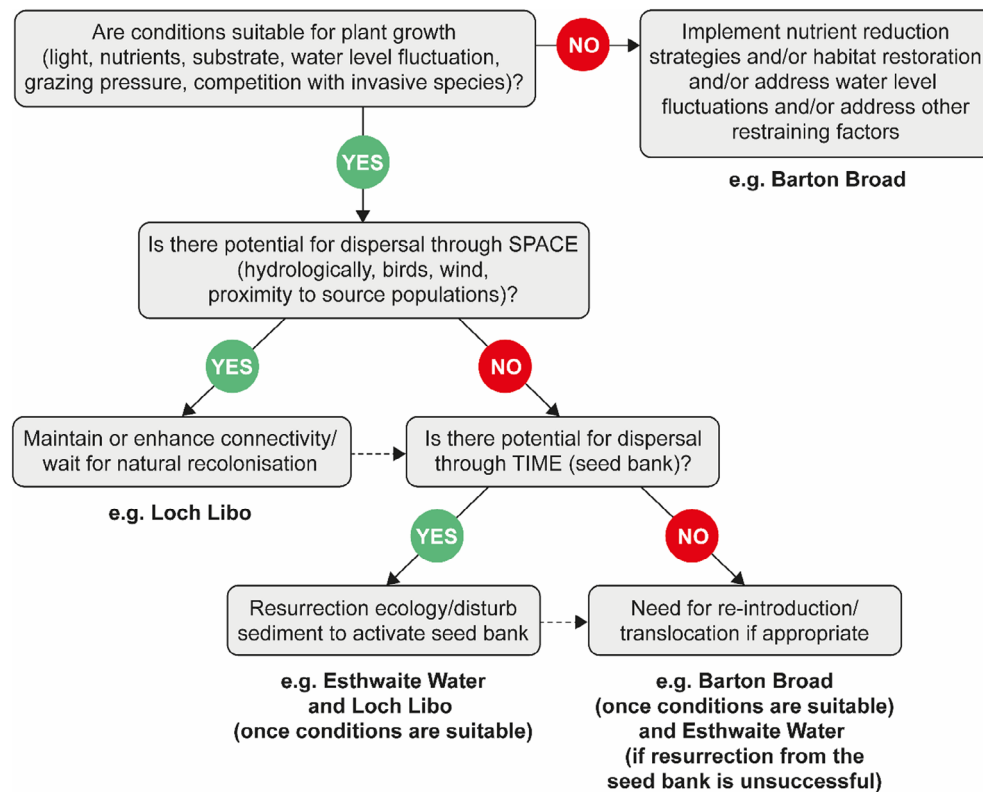


Figure 6. Flowchart showing a framework to guide conservation decisions for restoration of macrophytes in lakes (dashed arrows indicate further options).

returning under current and potentially future conditions via restoration work.

Barton undoubtedly remains too eutrophic and turbid to permit a return of *Littorella uniflora*. Even after 20 years of restoration, macrophytes are sparse in the lake (Phillips et al. 2015). Palaeoecological and historical data for Barton suggest that, as eutrophication progressed from around 1900, a taller canopy-forming community displaced the low growing macrophytes including *L. uniflora* (Madgwick et al. 2011). A lack of suitable substrate for *L. uniflora* is also a concern as the peat ridges and gravel-shorelines thought to have provided the chief habitat for *L. uniflora* in the past (Preston & Croft 1997) are no longer present in Barton and have been replaced by highly organic, unconsolidated sediments unfavorable to its growth (Madgwick et al. 2011).

There is little evidence for ecological recovery in palaeoecological or long-term monitoring data for Esthwaite (Dong et al. 2012; Bishop et al. 2019; this study) with P release from lake sediments and the effects of climate change on phytoplankton community structure appearing to confound recovery (Maberly et al. 2011). *Najas flexilis* is usually found in clearwater, mesotrophic lowland lakes, and the Esthwaite macrofossil record concurs with this, providing evidence for its association with a typical oligo-mesotrophic, mildly alkaline lake pre-loss. It is possible that competition with non-native *Elodea nuttallii*, which expanded during the period of advanced eutrophication, may have contributed to *N. flexilis* decline and might prevent

N. flexilis return even if nutrient concentrations are much reduced. On balance, lake conditions seem not to be sufficiently improved to support the return of *N. flexilis*.

Libo is eutrophic and as *Elatine hydropiper* is generally found in mesotrophic or eutrophic lowland lakes, it is possible that current water quality conditions could support it. However, as a self-fertilizing annual which requires bare cohesive lake sediments, it may be adversely affected by fluid sediments arising from eutrophication (Schutten & Davy 2000), and competition with non-native, typically canopy-forming, *Elodea canadensis*, which is currently present, due to a shading-out effect (Zehnsdorf et al. 2015). Libo is a club-owned coarse fishery and attracts high numbers of waterbirds during the winter, hence sediment disturbance and herbivory may present further difficulties for macrophyte establishment. Thus, like the other two sites, conditions are currently unfavorable to the return of the focal species.

Dispersal Through Space

While the answer to the question “Are conditions suitable for plant growth?” is currently “No” for our focal sites, we consider the next steps should the answer become “Yes” in the future, and ask whether there is potential for propagule dispersal into each site. One of the obstacles to the recovery of macrophytes is a lack of local extant populations in the landscape (Bakker et al. 2013). For example, plant recovery was delayed in Lake

Fure, Denmark (Sand-Jensen et al. 2017) and limited in a set of German lakes (Hilt et al. 2010) because many species were regionally rare or even extinct and hence reassembly of previous macrophyte communities did not occur. Macrophytes have several possible dispersal vectors: water (hydrochory), wind (anemochory), and animals (zoochory). Hydrological connectivity and seed buoyancy have a major influence on the distribution of macrophytes where surface waters connect to propagule sources (Nilsson et al. 2010; Fergus et al. 2017). Several reviews highlight the role of waterbirds in dispersing macrophytes either externally (ectozoochory) by adhering to their feathers, feet, or bill, or internally (endozoochory) via the digestive tract (Figuerola & Green 2002; Green et al. 2002). Relative to hydrochory, there is greater potential for medium to long-distance dispersal events (10s of kilometers) because many waterbirds move over considerable distances (Green et al. 2002). For example, the duck Pintail (*Anas acuta*) can travel up to 1,000 km in 72 hours during migration (Miller et al. 2005). However, propagule distribution tends to be highly patchy and patterns are species-specific, with variable chances of propagule survival in transit (Beltman & Allegrini 1997). Viability is greatest where the diaspores are small and thick-walled and can pass quickly through the bird's digestive tract (Figuerola & Green 2002; Weyembergh et al. 2004; Soons et al. 2008), which hence limits dispersal distance.

In the case of *E. hydropiper* and its return to Libo, there is potential for dispersal spatially. While the site is not hydrologically connected to neighboring lakes, the closest source populations are less than 10 km away at Castle Semple Loch, with two additional *E. hydropiper* sites within approximately 30 km at Bardowie and Lochend Lochs. *E. hydropiper* is a self-fertile annual and a prolific seed producer (Taura et al. 2022). Migratory waterbirds such as Eurasian Teal (*Anas crecca*) and Greylag Geese (*Anser anser*) are known vectors for *Elatine* species (Molodovsky 1971; Takács et al. 2017) and passerine birds such as Barn Swallow (*Hirundo rustica*), which gather wet mud for nests, can also transport seeds of *E. hydropiper* (Kerner von Marilaun & Hansen 1916). In contrast, for *L. uniflora* at Barton and *N. flexilis* at Esthwaite, large distances to source populations suggest little potential for spatial dispersal. *L. uniflora* is widespread in the United Kingdom yet there is only one site with a recent record of *L. uniflora* within 60 km of Barton, with other sites greater than 100 km distance. Thus, it is unlikely that *L. uniflora* would recolonise Barton via contemporary dispersal. *N. flexilis* is dependent on seeds for its dispersal (Gunn & Carvalho 2020) and is a prolific seed producer giving good scope for movement by birds. This is especially true of Mute Swan (*Cygnus olor*) (Clausen et al. 2002) and seeds of *Najas*, albeit holly-leaved naiad (*N. marina*), can be retained in the guts of Mallard Duck (*Anas platyrhynchos*) for 10–12 hours (Figuerola & Green 2002). Despite its high potential dispersibility, all recent occurrences of *N. flexilis*, with the exception of one site (Loch Kindar, south-west Scotland), are at a minimum of 200 km away from Esthwaite. Therefore, natural spatial recolonisation of *N. flexilis* would be possible only if long-range dispersal occurred.

In answering “Yes” to the question of “Is there potential for seed dispersal through space?”, we propose the required action to be either maintain connectivity where it already exists or enhance connectivity if necessary, and then wait for recolonisation to occur naturally. Should the answer to the question be “No,” we then ask if there is potential for dispersal through time via long-lived seed banks.

Dispersal Through Time

Temporal dispersal is a known mechanism for the long-term persistence of organisms in aquatic habitats (Beltman & Allegrini 1997; Weyembergh et al. 2004). A key factor to consider in macrophyte restoration is whether a focal species is present in the propagule bank and, crucially, whether propagules are viable (Hilt et al. 2010; Bakker et al. 2013). Although seed banks can become depleted over time, research has shown decadal to multi-centennial seed persistence for a number of macrophytes in pond, lake, and ditch sediments (Van der Valk et al. 1992; Stobbe et al. 2014; Alderton et al. 2017). Hence, if the goal of a restoration project is to bring about the return of a species then propagule banks hold enormous potential, particularly where a species is locally and/or regionally rare, or where the landscape has become fragmented.

Our palaeoecological data show *N. flexilis* seeds to be abundant in the sediments of Esthwaite, but laboratory studies have thus far failed to germinate its seeds from Esthwaite core samples (Gunn & Carvalho 2020). In theory, there is potential for dispersal through time at Esthwaite, but there is no certainty of success. In practice, translocation from sites in Scotland may be necessary, raising the issue of using nonlocal genetic stock and broader consideration of following good reintroduction practice which would advocate use of local seeds (Gunn & Carvalho 2020).

L. uniflora reproduces by seed and vegetatively by rooting stolons and has a persistent seed bank shown to remain viable for at least two or three decades in the sediments of eutrophic, softwater lakes (Arts & van der Heijden 1990; Roelofs 1996). Seed bank experiments have shown seeds to successfully germinate after several decades, given suitability of light, diurnal fluctuation in temperature, and a period of desiccation (Arts & van der Heijden 1990). In Lake Beuven, Netherlands, *L. uniflora* recovered within a year of restoration as a result of a viable seed bank (Roelofs 1996). The longevity of *L. uniflora* seed banks over centennial timescales is not known, however, and remains of the species were sparse in the bulk samples from Barton so likelihood of *L. uniflora* being returned to Barton via dispersal through time seems low.

For Libo, presence of *E. hydropiper* remains in the sediments suggests that dispersal via the seed bank is possible and indeed seed abundance could be higher in other areas of the lake. Buried seeds of this species can remain dormant in sediment for at least 50 years, until stimulated by increased light intensity caused by low water levels in summer (Poschlod & Rosbakh 2018). Hence, there is potential for resurrection of this species where seeds are sufficiently abundant and where conditions are favorable. We conclude that, in the case of Libo, the response to the

question “Is there potential for dispersal through time?” is “Yes” but for Barton the likelihood is less easy to establish, logically leading to considerations of reintroduction and translocation to increase the chance of success.

Natural Recolonisation Versus Translocation

Broadly, there are two restoration approaches for establishing plant communities: natural recolonisation and active reintroduction (Choi et al. 2022). Of our three examples, natural recolonisation from nearby source populations may be an option for *E. hydropiper* at Libo, and natural colonization from the seed bank might be possible for *N. flexilis* at Esthwaite but for *L. uniflora* at Barton, reintroduction may be the only option available. In line with other studies, we view natural dispersal and recruitment from seed banks to be the preferred conservation options for restoring lost macrophyte populations where conditions allow, an approach that has been described as “passive” revegetation (De Steven et al. 2006). It not only offers a more cost-effective option than “active” approaches, such as reintroduction via planting and seeding, but is also more closely aligned with the good restoration practice of adopting nature-led approaches (Shuwen et al. 2001; Sayer et al. 2019). A major advantage of the passive approach is that it directs conservation effort at improving water quality and habitat conditions and, potentially, where appropriate, connectivity to other sites.

Passive approaches have met with some success, notably where sites being restored are in close proximity to source populations of target species (Shuwen et al. 2001; De Steven et al. 2006), where ecological conditions in the source and introduced populations are similar (Noël et al. 2011) or where seed banks are abundant and exhibit long-term persistence (Poschod & Rosbakh 2018). For example, restoration of ponds in eastern England by sediment removal has allowed many locally scarce plants to re-emerge including Slimy-fruited stonewort (*Nitella capillaris*) in Suffolk, thought to be extinct in Britain since the 1950s, and Grass-poly (*Lythrum hysopifolia*) in Norfolk, a very rare macrophyte in the United Kingdom which has not been officially recorded in Norfolk for a century (Sayer & Parmenter 2020). Reintroductions of rare species have become increasingly important and popular in conservation and, where none of the pre-conditions above exist, translocations might be needed to facilitate establishment of lost species and genotypes (Jeppesen et al. 2012). Movement of rare and at-risk species is difficult, and poor success has been attributed to ill-informed transplantation efforts (Fahsel 2007; Blindow et al. 2021; Fenu et al. 2023), hence careful decision-making involving feasibility and risk assessments is required (World Conservation Union 2013).

Our study demonstrates the importance of considering a combination of connectivity, historical baselines, and current conditions to guide freshwater macrophyte conservation, and specifically the role of palaeoecology in providing highly useful insights into what has been lost, while also affording a valuable tool for locating rare species or establishing their past presence. The examples presented here cover contrasting situations in terms of likelihood of species return. While improvements to

water quality may be necessary in all cases, potential for dispersal via space and time varies between the sites. It is hoped that the proposed decision-making framework, informed by a combination of contemporary and historical ecological information, will scientifically underpin conservation decisions and thus promote greater success in restoration programs. In light of the pace of biodiversity loss and climate change, a blend of passive and active restoration techniques may have to be considered in future and such decision-making frameworks will hence become more vital.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. ^{210}Pb concentrations in core LIBO-D1.

Table S2. Artificial fallout radionuclide concentrations in core LIBO-D1.

Table S3. ^{210}Pb chronology of core LIBO-D1.

Figure S1. Fallout radionuclide concentrations in core LIBO-D1, showing (a) total ^{210}Pb , (b) unsupported ^{210}Pb , and (c) ^{137}Cs and ^{241}Am concentrations versus depth.

Figure S2. Radiometric chronology of core LIBO-D1, showing the CRS model ^{210}Pb dates and sedimentation rates.

Figure S3. Summary diatom stratigraphy of LIBO-D1 (% relative abundance).

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