Effects of lake water level fluctuations on macrophytes and littoral macroinvertebrates.

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April 2020

Submitted to Biological and Environmental Sciences

School of Natural Sciences

University of Stirling

Scotland

For the degree of Doctor of Philosophy

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Statement of Originality

I hereby confirm that this PhD thesis is an original piece of work conducted independently by the undersigned and all work contained herein has not been submitted for any other degree.

All research material has been duly acknowledged and cited.

Signature of candidate:

Anwên Bill

Date:29.04.2020

“A lake is a landscape's most beautiful and expressive feature. It is Earth's eye; looking into which the beholder measures the depth of his own nature.

Henry David Thoreau, Walden

A select and privileged few have the opportunity to learn about and contribute to, the body of knowledge of a discipline that resonates within them. I am one of the fortunate, something I will be forever pleasantly surprised and immeasurably grateful for. (A. Bill)

Acknowledgments

My first and utmost thanks goes to Nigel Willby, my supervisor. Thank you for giving me this incredible opportunity and privilege, for taking a chance on someone who does not fit the typical mould, for your support and guidance throughout the years. You have given me your time, expertise, and encouragement. Your knowledge and endless enthusiasm in the field was a delight and truly inspirational. My thanks go also to Chris Bromley who also gave me this opportunity and provided training and encouragement. I extend this thanks to David Gilvear who provided advice for the first year.

I give enormous thanks to Alan Law who has been available to help, discuss, aid with statistics and anything needed – including field work! I also thank Charles Perfect who always made time for my queries and offered help readily.

I thank also, Bryan Spears (UK Centre for Ecology & Hydrology) and Ian Jones (University of Stirling), for their time and interest in my thesis. Their constructive comments have been enjoyable, thought provoking, and significantly improved the quality of the work herein.

A special thanks goes to Zarah Pattison, for your patience, support in every way over the years, and kicking my proverbial behind when needed. To Catherine Gibson-Poole, thank you for your natural enthusiasm, dedication, and knowledge, our survey trips were a joy that I will always treasure. To all mentioned above, thank you for always laughing at my mistakes in a kindly way and for your encouragement.

This thesis was funded by the University of Stirling and SEPAs IMPACT award which provided structure, training and data that were essential to the completion of this thesis, as was the insight, information or site access supplied by Alastair Stephen (Scottish Southern Electric), Amanda Hutcheson and Ian Morrison (Scottish Water), Peter Brown and Sarah-Louise Maclean (Scottish Forestry Commission), Phil Rider (Glen Finglas Woodland Trust).

The following people provided vital technical support in addition to knowledge, skills, and kindness, that keep the Biological and Environmental Science department running smoothly, so my sincere thanks to; Lynn Macgregor, Scott Jackson, Ronald Balfour, Sylvia Hodgson, James Weir, Pauline Monteith and Lorna English.

I thank these people who have helped me with my work, presentations, self-esteem, and sanity (in no order!): Zarah Pattison, Anna Doeser, Renée Kerkvliet-Hermans, Megan Layton, Jim Blaklie, Alex Seeney and Catherine Gibson-Poole.

My sincere thanks goes to the following, in no particular order, who helped me reach this stage, particularly through pregnancy, subsequent juggling of work, education, motherhood and a few other bumps along the way; Alistair Jump, Andre Gilburn, Andrew Tyler, David Gilvear, Clare Wilson, Colin Bull, Eileen Tisdall, Heather Price, Kirsty Park, Luc Bussiere, Mario Vallejo-Marin, Matthew Tinsley, Peter Hunter, Philip Wookey and Tim Whalley.

I could not have completed this work without the incredible support of my partner, Duncan Dowie. You have been my advocate. My heartfelt thanks for persuading me to apply for this PhD when I did not believe in myself. I will forever be grateful to you for seeing this through with me, supporting and believing in me. To our daughter, Tarian. You show me what true courage and determination are. You are the sunshine in my life. Thank you to you both, for joining me for surveys and listening to presentation practices despite glazed eyes! Special thanks to my siblings, Blythe, and Matthew, who have supported me in many ways throughout years of study and motherhood, in addition to life changing events. Lastly, thanks to my mother, Teresa Hart, for the love and strength you give that builds an inner resilience, helping me overcome the curve balls life threw at me while working at this thesis, (in addition to delivering healthy meals!) thank you.

General abstract

Freshwater systems are declining globally in both quality and extent and are currently losing biodiversity faster than other ecosystem types due to human impacts. Hydromorphological alterations are now the primary form of pressure on European freshwaters, occurring principally in the form of water level fluctuations (WLF) and altered flows. Modified, anthropogenic WLF remain a largely overlooked pressure on lake ecosystems, despite having a profound influence on the littoral zone, the part of a lake where biodiversity is usually concentrated. Anthropogenic alteration to lake water-level regime has been identified as a priority for investigation in order to increase understanding of ecological effects, assessment abilities and mitigation measures. There is a lack of research quantifying impacts of WLF on biota relative to other known pressures, despite the certainty that many lakes are exposed to these stressors. To address these knowledge gaps, this thesis focused on assessing the responses of littoral macrophytes and macroinvertebrates to WLFs in Scottish lakes, relative to other environmental drivers at lake and sub-lake levels.

The research presented in this thesis confirms that WLFs have a dominant and overall negative association with aquatic macrophyte species richness, altering community composition, and overriding effects of other established influences (i.e. elevation, lake surface area, and phosphorus). In addition, regulation of lake water levels *per se* was a negative environmental factor, relative to other predictors. WLF was also the dominant and negative factor related to macroinvertebrate family richness, relative to all other significant environmental predictors, including lake elevation, perimeter, and nutrient concentrations. The range of lake WLF was also established as a key factor in explaining variation in macroinvertebrate composition. Subdivision of lakes by the morpho-edaphic index (MEI), an index formulated from lake depth and alkalinity, revealed variation in the factors associated aquatic vegetation with lake type. Macrophyte richness in lower MEI lakes, being influenced by WLFs and regulation, and with clear distinctions between plant communities in higher vs lower MEI lake types.

Additional subdivision of lakes by stable or fluctuating water level regimes added further clarity. Macrophyte communities differed significantly with MEI and stability regime, with species indicative of each lake type showing contrasting life history and reproduction strategies, consistent with differences in their sensitivity to water level change. Invertebrate communities differed significantly with stability regime, with MEI having no importance. Indicator species varied by life-span, mobility and reliance on littoral vegetation. Stable regimes were characterised by Hydrachnidae, Asellidae, Haliplidae and several gastropod families, whilst Siphlonuridae were indicative of fluctuating regimes.

This thesis establishes water level mediated impacts, from sub-lake factors such as littoral substrate composition and shore slope, to the robust but declining isoetid plant, *Littorella uniflora*. Modification of water levels resulted in uncoupling of *L. uniflora* from the littoral zone by way of increasing shore slope, distance, and height. Morphological traits such as root-to-shoot ratios were influenced negatively by increased wave exposure, whilst leaf length-width ratios increased with distance from the water's edge. Biomass was negatively influenced by steeply sloping shores and sandy substrates versus coarser aggregates. This research suggests that an amplified WLF range, results in elongation of roots to access a deeper water table, may be at a cost to overall standing biomass.

This thesis demonstrates that WLF is the dominant stressor on littoral zone biota, and habitat parameters, relative to other environmental factors commonly considered in studies of lakes such as elevation, perimeter, and fertility. The influence of WLF pressure should be regarded as a priority for conservationist and managers of freshwaters. In light of the expected increase in impoundments globally and high-level pressure on European freshwaters from regulation activities, as well as future projections of climate change and population growth, it is imperative to include lake water level parameters to effectively manage freshwater resources and their associated biodiversity.

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Chapter 1

Introduction - Ecological responses of lakes to hydromorphological pressures

Freshwater ecosystems hold a rich diversity of habitats and species. If “Water is the driving force of nature” (Leonardo da Vinci, 1452-1519), then the factors that shape the flow of water and what lies within or beneath the surface of aquatic habitats are the vectors of that force, the influence of which extends well beyond our freshwater shores.

1.1 General pressures on freshwater ecosystems

Fresh water comprises just 0.01% of all water on this planet, yet this seemingly tiny resource offers far-reaching influence through the services that it delivers. Freshwater ecosystems support a disproportionate amount of life with almost 9.5% of globally described animal species (Balian et al., 2008). Lakes, rivers and reservoirs cover an estimated 2.3% of the Earth’s surface, with freshwater wetlands covering a further 5.4-6.8 % (Collen et al., 2014; Lehner & Döll, 2004)However, our freshwater ecosystems are now in crisis, and due to increasing threats from human impacts, are considered to be the most endangered of global ecosystems (WWF, LPI, 2018), with the damage often concealed below the water surface (Reid et al., 2019; Richter et al., 1997; Sala et al., 2000).

Over a decade ago Dudgeon et al. (2006), published a synthesis of the threats and challenges facing global freshwater biodiversity, including; over exploitation, water pollution, species invasion, habitat degradation and flow modification. Subsequently, these threats have all evolved or worsened as we progress into the now accepted epoch termed ‘The Anthropocene’ (Steffan et al., 2007). A recent synthesis of risks and challenges for freshwater biodiversity and conservation by Reid et al (2019), defines a deepening crisis with novel or intensifying risks to freshwater biodiversity with further emerging threats including; expanding hydropower, changing climate, and cumulative stressors, alongside the existing pressures of land use change, which is itself a major threat to freshwater ecosystem functioning and biodiversity (Sala et al., 2000).

The Water Framework Directive (WFD) (2000/60/EC) instigated a change in the perception of water quality and how it is assessed in Europe. The mind-set has shifted from one where water is considered solely as a resource to be monitored and safeguarded for human consumption to an overarching view that sees water as a heritage. There is now a legal requirement to assess more holistically the structure and functions of aquatic ecosystems based primarily on four groups of biota: phytoplankton, macrophytes, benthic macroinvertebrates and fish (Irvine et al, 2002; Solimini et al., 2006) which are designated as Biological Quality Elements (BQEs). In lakes, the majority of these BQEs inhabit the zone of highest biodiversity, the littoral zone (Wetzel, 2001).

1.2 Hydrological alteration

The latest European Waters Assessment (EEA, 2018), found that the most commonly occurring pressures affecting some 40% of European surface freshwaters were from hydromorphological alterations (Fig. 1), followed by diffuse source pollution mainly from atmospheric deposition and agriculture (38%). Recent work by Birk et al. (2020), finds the primary pressure to lakes to be nutrients, however this is based on 55 lake studies, 11 of which were assessing hydrological stressors, whilst the EEA, (2018) include 111 000 surface freshwaters from across Europe. Water bodies are subdivided further into hydromorphological categories of pressures with 26% affected by physical modifications in the channel, bed, shore or riparian zone, in addition 24% have a form of continuity interruption such as large dams for storage reservoirs or hydropower generation or barriers and locks, and a further 7% of other, unspecified hydrological alterations (EEA, 2018).

Hydrological alterations are those which alter the water levels or flow regime of surface (or ground) water. The most significant hydrological alteration pressures on water levels and flows in European fresh waters come from a form of abstraction or reservoir storage, predominantly used for public water supplies, irrigation, and hydropower production (EEA, 2018).

The 2012 European Environment Agency (EEA, 2012), assessment found water level regulation of lakes, to be one of the most common pressures overall and hydromorphological modifications, such as dam construction or shoreline modification are considered a major pressure on lakes (Solheim, 2008), second only to eutrophication.

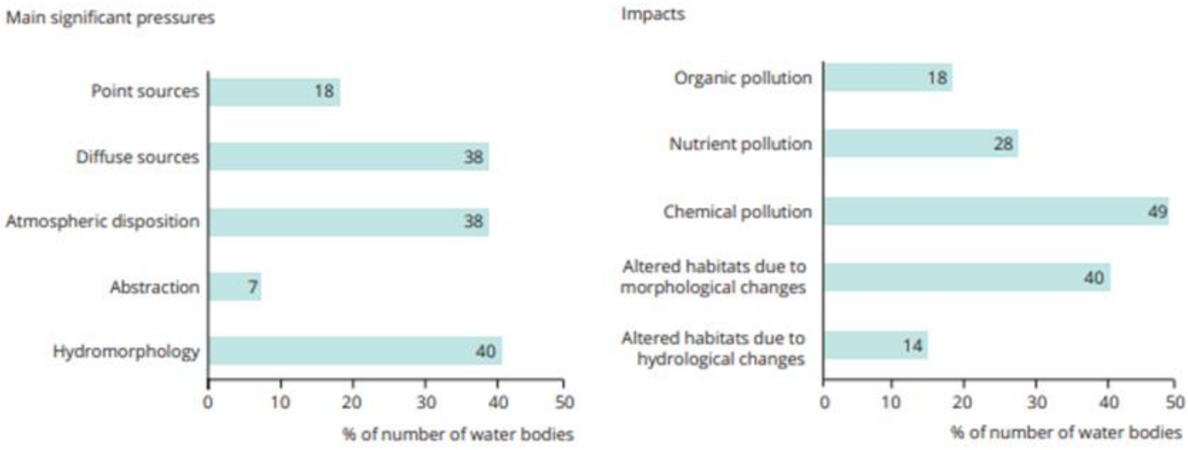

Fig. 1. Proportion of classified European surface water bodies main significant pressures and impacts as determined by the second River Basin Management Planning information (EEA, 2018), (atmospheric deposition was not included in the pressures from diffuse sources).

Water level fluctuation (WLF), through regulation activities has been an overlooked influence on lake ecology, but is of increasing relevance (Carmignani & Roy, 2017). Lake WLF are anticipated to be increase in variability with predicted impacts from climate change, population increases and land use change (Carmignani & Roy, 2017; Wantzen et al., 2008), all of which have the potential to alter nutrient availability, temporally and spatially (Hofmann, Lorke, & Peeters, 2008).. However, to date, our understanding of this pressure on aquatic life, relative to others such as eutrophication, remains poor and there is a vital need to better understand the links between biology, habitats and changes to hydromorphology (Reyjol et al., 2014).

1.3 Climate-based impacts

Climate change, is expected to alter lake water cycles directly through forecasted changes in precipitation patterns and amounts, wind speeds and lake temperatures (Fekete et al., 2010). In addition, climate change is anticipated to have indirect effects on lake water cycles through altered catchment processes, such as the effects of vegetational changes which can alter filtration rates before water enters lakes (Blenckner, 2005). The influence of climate change will vary depending on the location of the lake (geographic and elevation), the regional climate and individual lake features such as bathymetry, surface or perimeter area and fetch. The European and UK and North West European mean temperatures are expected to rise with warmer, wetter winters and dryer, hotter summers (IPCC, 2012), which will lead to changes in water availability (Haddeland et al., 2014). Such seasonal precipitation changes are expected to alter lake water levels by raising them in the winter but lowering in the summer, potentially increasing drying and evaporation from the littoral and shallowest areas.

Wind speed dynamics impact freshwater lakes. Climate change models predict an increase of wind energy over Northern Europe with a poleward shift of the North Atlantic jet stream (IPCC AR5, 2013), bringing a rise in winter mid-latitude cyclone intensity, which impact the North West of Europe, particularly Ireland (Nolan et al., 2012) and Scotland (Woollings, Hannachi, & Hoskins, 2010). However a decline in near-surface (~10 m) terrestrial wind speeds, termed “stilling” (Roderick et al., 2007) and surface roughness (due to land use change), have been observed globally, particularly in the Northern Hemisphere (Bichet et al, 2012; McVicar et al., 2012; Roderick et al., 2007; Vautard et al., 2010; Woolway et al., 2019;Torralba et al., 2017), with multiple implications for lake ecology. Wind predominantly effects the warmer epilimnion of stratified lakes, whilst having a minimal effect on lower layers (Woolway et al., 2019; Heaps & Ramsbottom, 1966). However, wind stilling can affect climate feedback processes such as evaporation (McVicar et al., 2012; Roderick et al., 2007), and therefore lake temperatures. Stilling can reduce vertical mixing through stronger and longer stratification, polarising temperatures further between upper and lower layers, and resulting in surface temperature increases, these effects are likely to have a cumulative influence with climatic warming (Magee & Wu, 2016; Woolway et al, 2017). Prolonged stratification can lead to oxygen depletion from respiration, due to decoupling of deep water from surface atmospheric oxygen, (Rippey & McSorley, 2009), leading to anoxic conditions and dead zones (Del Giudice et al., 2018). Conversely, shallow lakes are effected by wind induced turbulence, which adequately mixes waters of lakes with surface areas up to 10km², with resuspension of sediments from over 50% of the area not being unusual (Mooij et al., 2005) and reduction in primary production due to increased light attenuation as a result (Gons & Rijkeboer, 1990). In addition wind direction and energy effect on-shore, wind-wave exposure to lake littoral zones, this in turn impacts sediment transportation and re-distribution on shores (Pierce, 2004).

The relationship between climate induced changes and lakes are not one-way, with feedbacks caused by reservoir creation, drawdown and dewatering of the littoral zone leading to methane release. Carbon emissions from hydropower reservoirs are calculated for CO_2 and methane (CH_4) at 85g and 3g per KWh of hydroelectricity produced, respectively (Barros et al., 2011; Hertwisch, 2013). Therefore, the future addition of carbon to the atmosphere from hydropower installations is estimated for CO_2 and CH_4 to be, 280-1100Tg C and 10-40Tg C respectively, which corresponds to between 4% of the global carbon emissions by terrestrial waters (natural and human made)and 16% of those occurring from reservoirs (human made),(Raymond et al., 2013; Zarfl et al., 2015) . Future carbon emissions from hydropower dam creation will depend vary geographically with Amazonian areas representing higher levels of greenhouse gas emissions than other regions (Barros et al., 2011).

1.4 Human regulation of lakes

Human activities directly alter water level dynamics through damming for water storage or flood prevention, water abstraction for public consumption, and industrial and agricultural needs. These activities are escalating through the collective increased demand on water resources and the drive for greener energy sources, such as hydropower, with thousands of dams currently under construction or planned globally (Dorber, May, & Verones, 2018; Zarfl et al., 2014).

There are 57,985 large dams (height >15 m) operating globally, predominantly constructed for irrigation or hydropower purposes (ICOLD, 2019) and an estimated 2.8 million dams with reservoir areas over 0.001km^2 (0.1ha), (Lehner et al., 2011). River diversions or impoundments have resulted in 48% of the global river volume being moderately to severely impacted by either flow regulation, a form of continuity interruption (creating fragmentation), or both (Reid et al., 2019), with the creation of dams and reservoirs the dominant cause of fragmentation.

When hydropower is generated to provide energy in times of peak demand, the result is a specific type of hydrological alteration pressure called hydropeaking, which causes rapid artificial WLFs (EEA, 2018). Although lake water levels may remain within average ranges the duration and frequency of extreme events are likely to increase.

1.5 Hydropower

1.5.1 Global hydropower

Hydropower has been touted as green renewable energy. While this may be true in theory the global impacts are classed as severe due to species extinctions, driven by ecological changes resulting from fragmentation of river and island systems which inhibits dispersal of plants and animals along a river and laterally into riparian habitats (Jones et al., 2016; Reid et al., 2019). Fragmentation alters the natural flow regime and therefore, the nutrients, sediment, and organic matter, in addition to disrupting hydrological, geomorphic and ecological processes (Grill et al., 2019). While the understanding of these effects are generally well understood, the effects of interactive stressors are not (Reid et al., 2019) and WLFs are understudied.

Hydropower has undergone an unprecedented increase globally with a rise of global-installed hydropower capacity of 55% (omitting pumped storage) between 2000 and 2015. This is driven in part by economic and political incentives (Reid et al., 2019), such as the Renewables Obligation, which is an annually increasing the renewable quota for United Kingdom energy suppliers who are keen to increase hydropower production in an effort to meet European climate and energy goals (IHA, 2016).

There is no comprehensive data for worldwide dams, however reliable data for global hydroelectricity dams in operation number range from over 3700 to 6102 (Winemiller et al., 2016; Zarfl et al., 2015; ICOLD, 2019). Hydroelectricity generates 17% of global energy supplies (BHA, 2020), more than any other renewable energy type at over 4000 terawatt hours in 2018 with a 3.1% growth in 2018 alone, this is greater than global nuclear energy (2700TW with 2.4% increase) or wind and solar energy combined (1270TW, 12.6% and 584TW, 28.9% respectively. The six largest hydroelectric dams by installed capacity (> 10000 MW), globally are situated in China (3), Brazil/Paraguay, Brazil, and Venezuela (ICOLD, 2019). European dams do not make it in to the ICOLD (2019) top 20 largest hydroelectric dams however, the collective hydroelectricity generated equates to 642TW rising by 9.8% in 2018, with most of the installed capacity in Scandinavian and Alpine regions (IHA, 2016), the UK generated 5.5TW with an expansion from 2007-2017 of 1.6% (BPSTATS, 2019). Currently 30-40% of the UK's renewable energy is derived from hydropower (BHA, 2020 - British Hydropower Association), the vast majority of which is generated in Scotland (Renewables, 2019).

1.5.2 Scotland's Hydropower

In Scotland at least 312 water bodies, with an additional four protected areas (of international importance for wildlife), are susceptible to anthropogenic flow and water level pressures (depending on annual precipitation events). The majority of these pressures are from water abstractions servicing large scale hydropower reservoirs (Scottish Government, Natural Scotland, 2015). These pressures are forecast to increase with population and economic expansion in Scotland and globally, coupled with the expansion of energy demand, particularly hydropower, water storage requirements, flood defence, and climate change induced impacts (Erik Jeppesen et al., 2014; Natural Scotland, 2015; Reid et al., 2019; UN, 2019).The most recent report by the Scottish Government, Natural Scotland (2015) states the extent of these pressures are expected to increase based on the 105 approvals for significant modifications to water bodies for 2009- 2015, the vast proportion of which were for new hydroelectric schemes.

In addition, the Scottish Governments climate change target includes becoming a net-zero (carbon) nation by 2045 at the latest. To achieve this the 2017 Scottish Energy Strategy has set a target that 50% of Scotland's energy consumption to be met by renewable sources by 2030, in addition to developing a circular economy and "one planet living". This nation-wide effort involves private and public sectors and community partners, such as renewable energy action plans (REAPs), which assists development of local renewable energy projects, including hydro-electricity schemes, and secure the socio-economic benefits. In addition, the Scottish Government have created the Energy Investment Fund (EIF) which from 2019-2020 made £20 million available for community and commercial renewable and low-carbon energy solution projects. Based on the policies and targets set, Hydropower installations is expected to grow in number in the future in Scotland.

1.5.3 Small hydroelectric power (SHP) installations

Small hydroelectric power installations (SHP) are similarly expanding globally, up 10% from 2013 (WFD21d, 2012; Liu, etal., 2019). Globally installed SHP represents just 1.5% of global electricity installations, 7.5% of total hydropower capacity and 4.5% of total renewable energy (Liu et al., 2019), though accurate numbers are difficult to obtain due to a disparity in classification between countries (the majority define these as having maximum capacities of up to 10MW). However recent estimates place a conservative estimate at 82,891 SHP installations in over 150 countries (Couto & Olden, 2018). SHP are frequently cited as environmentally sustainable renewable energy source and in order to meet United Nations Sustainable Development Goal 7 (SDG7) targets of universal access "to affordable, reliable, sustainable and modern energy for all" by 2030 (IEA & World Bank, 2018) calls for expansion of SHP with projections for potential SHP are almost three times the current capacity (229GW versus current 78GW) (Liu et al., 2019).

However, the rapid expansion and investment of SHP has outpaced environmental scientific knowledge. Couto & Olden (2018), found just 5% of reviewed publications explicitly studied SHP despite there being at that time 11 SHP installations to every 1 large hydroelectricity (LHP) installation worldwide. In addition, many countries require little or no environmental impact assessments for SHP construction. Kilber and Tullos (2013) demonstrated that in China dams under 50MW capacity result in greater impacts, than LHP installations (>50MW) in regard to river channel length affected, modification potential to flow regimes, water quality and influence to protected or conservation areas.

1.5.4 Hydropower environmental impacts overview

There are environmental impacts from damming to create reservoirs including; altered flow regime, habitat fragmentation and sediment transport disruption and thermal alteration in tailwaters (Grill et al., 2019; I. L. Jones et al., 2016; Lehner & Döll, 2004; Olden & Naiman, 2010; Reid et al., 2019). Within a reservoir impacts to lake ecosystem functions through adaptation of water levels and lake volume include; modification of stratification patterns, water circulation, nutrient cycling and hydraulic residence times (Boon et al., 2019). In addition to these impacts are significant and irreversible losses of ecosystems and species, recorded by authors since the last published World Commission on Dams (2000), (Dai, Mei, & Chang, 2017; Dudgeon et al., 2006a; Fekete et al., 2010; Grooten et al., 2018; Reid et al., 2019; Winemiller et al., 2016).

Hydromorphological pressures (i.e. regulation of a lake or reservoir via damming or weir construction) alter the hydrologic regime and instigate functional changes, such as a reduction in heterogeneity and structural complexity of littoral habitats and altering natural water-level regimes thereby impacting, primarily, littoral zones physical structure, and vegetation cover (Brauns, Garcia, Walz, & Pusch, 2007a; Porst et al., 2019; Urbanič, Petkovska, & Pavlin, 2012; Zohary & Ostrovsky, 2011a). Clearly there is a delicate trade-off involved between socio-economic needs for water resources and the management and protection of freshwater habitats.

1.6 Alternative reservoir management

Reservoir creation or operation alters lake water level regimes (and connected rivers); however, they are a necessary aspect of modern human life required for the storage of water, which does not naturally fall where, or when, it is most in demand.

Natural lakes provide water storage, but are not always conveniently situated for human needs, and rivers are often too ephemeral in nature, with little capacity for storage or are adversely affected by human activities. Reservoirs serve to alleviate these challenges. Water storage is essential for consumption and agriculture, with even moderately dry regions requiring irrigation and as aforementioned for hydroelectricity production, as an alternative to the burning of fossil fuels (Moss, 2008), in addition to the growing need for flow regulation for flood prevention or habitat conservation and power generation.

Lake and reservoir water levels are altered for a myriad of reasons, balancing or ‘feeder’ ponds are used to stabilise canal waterways initially built for essential transport of goods. Today these are primarily for recreation and are of cultural and economic importance (IWAC, 2008). These waterways natural or otherwise, support a diverse range of aquatic plants, invertebrates, fish and mammals and serve as wildlife corridors, and require a balance between navigation functionality and biodiversity conservation (IWAC, 2008).

1.6.1 Ecosystem services

Lakes are used for recreation such as sailing, fishing and water skiing, with an aesthetic and societal value (Tallar & Suen, 2017). Management of reservoir water levels have been linked to visitor numbers and therefore have economic value (Neher, Duffield, & Patterson, 2013), however altering the regime of water levels i.e. raising them in vacation times to attract visitors can create a potential miss-match between the regime and seasonal requirements for lake biodiversity. Recreational use of lakes can introduce additional pressures such as, wave action from boating activities which impact lake shore characteristics increasing erosion and therefore sediment suspension and water turbidity (Anthony & Downing, 2003; Gabel et al., 2012). Increased turbidity reduces light availability and can clog invertebrate gills, thereby impacting negatively on macrophytes and invertebrates and contributing to nutrient fluxes. Where WLFs and enhanced wave action occurs it is likely to enhance erosional processes (Hellsten, 2000).

Lakes levels are also artificially managed for habitat or species conservation purposes in order to preserve a suite of species or habitat such as RAMSAR or Site of Special Scientific Interest (SSSI) sites. For example, Dunalastair Water in Scotland, a naturally shallow loch turned reservoir, is a SSSI selected for its reedswamp and fen habitats (Fig.10a), and breeding birds, with water levels managed by Scottish Southern Electric as part of a series of linked reservoirs that form the Tummel Valley hydroelectricity scheme. Water levels are restricted to preserve the extent of fen meadow, open water transition fen and open water habitats (Scottish Natural Heritage, 2010).

Water level management can be used as an inexpensive and effective weed management tool (Bentley et al., 2014). By using the known water level requirements of a given species to alter water levels to deleterious parameters such as, increasing draw down to expose or freeze a submerged species which reproduces vegetatively (Bellaud cited in Gettys, et al., 2014), for example *Elodea canadensis* (Bowmer et al, 1995; Zehnsdorf et al, 2015). However every management tool has its drawbacks and though inexpensive this method is not species specific, which would require due consideration before use (Barrat-Segretain & Cellot, 2007) in addition, it would not remove the existing seed bank.

1.7 Global lake water level regimes

Water level data is sparse globally for natural lakes, which often are not monitored. However, the natural WLF range lies between 1 – 3 m (Fig. 3a, Fig. 4a, Fig. 5 (Lake Constance) and Fig. 6, natural lake (Loch Lubnaig), depending on the size of the lake relative to the catchment area and topography. Differences in natural seasonal WLF trends are also affected by the regional climate. In Nordic countries (Mjelde et al, 2012), the natural hydrological cycle of lakes follows a pattern of refill from May onwards when water is released by ice-melt from upland catchments, this spring peak is mirrored in Lake Constance (Fig. 5), fed by the Rhine River originating in the South eastern Alpine region of Switzerland.

In contrast Scottish lakes refill over the wet winter months (Fig. 7), reducing from spring through to late summer when water levels are typically lowest.

Time series data for lakes or reservoirs water level is scarce, being described usually by area, volume or purpose, even for researching effects of imposed water level change (Jones et al., 2016; Scott Winton et al.,2019; Kennedy et al., 2016). Often the data is commercially sensitive and while remote sensing can be utilized to estimate annual ranges this is not suitable for research in terms of duration or frequency of WLF impacts to biota. Reservoirs typically experience greater WLFs than unregulated, natural lakes. Reservoirs created for hydropower frequently undergo annual changes of water level of tens of meters (Zohary & Ostrovsky, 2011a) as seen during extended drought, combined with abstraction in Australian lakes; Burragorang and Hume (Vilhena et al., 2010; Baldwin et al., 2008). In the USA, Lake Shasta fluctuates annually at approximately 18 m on average, though the range this can reach 47 m, whilst Lake Arancio in Italy has mean annual fluctuations of 3.3 m, its maximum range over the years reaches 20.5 m (Zohary & Ostrovsky, 2011). In China, the Three Gorges Reservoir water levels lowered by 27 m following winter flooding in 2008/2009 with a drawdown area of 350 km^2 (Chen et al., 2009).

1.7.1 Global case studies of natural lake and reservoir water regimes

The majority of globally registered dams are within China, U.S.A and India, with 23,841, 9263 and 4408 respectively (ICOLD, 2019). Brazil holds some of the largest dams in the world (ICOLD, 2019), but annual water level data is problematic to obtain at best.

Comparisons of natural lake and reservoir water regimes globally, illustrate the differences in range, seasonality, and oscillations of water levels. Examples to highlight similarities and differences between WLFs and impacts with geography are described below.

The Itaipu Reservoir is situated on the Brazil/Paraguay border and one of the largest hydroelectricity installations in operation globally, producing enough power in 2008 to meet global power consumption for 2 days (94.68 kWh) (Power Technology, 2020). Due in part to its size (1350 km^2) water levels usually fluctuate less than 1 metre annually. Conducting surveys over three years, Thomaz et al., (2006), captured severe and prolonged negative effects to macrophyte biomass after a brief (3 month) reduction of water levels reaching -5 meters with biomass reduced to zero at all survey sites for at least 14 months, illustrating the damage of a single drawdown event.

Work by Zohary et al., (2011) further illustrates differences in WLF regimes in temperate and subtropical lakes over 20 years with data from three natural lakes situated in Japan, Germany, and Israel, and three managed reservoirs situated in California, Sicily, and South Africa (Fig. 2). Research outcomes concluded that even moderate disturbance levels had adverse impacts to littoral habitats and biota, that symptoms of ecosystem destabilisation were detected such as reduction of key species, increased invasive species, lower biodiversity and increased internal nutrient loading, leading to more frequent and larger blooms of cyanobacteria. The work highlights the crucial need for a better understanding of the role of WLFs on aquatic ecosystems, particularly for water resource managers. Fig. 2 levels in natural lakes Biwa and Constance displays the relatively small range of water levels, typically less than 1m, (Fig 2) while Lake Kinnerat water levels which are dammed though no longer actively regulated, vary more due to a semi-arid climate and heavy use for water consumption, therefore its range to 6m.

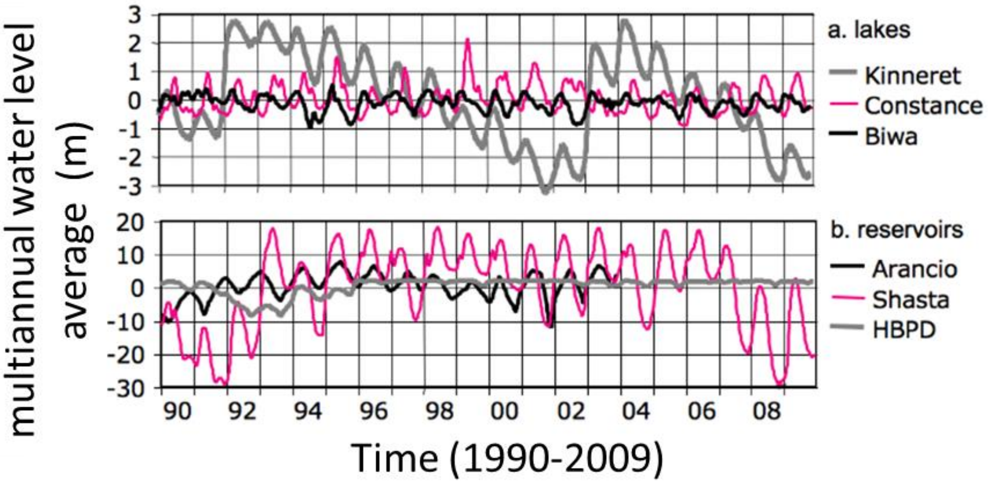

Fig. 2 Water level change over 20 years from global lakes that are; a) natural, Biwa (Japan), Constance (Germany), and Kinneret (Israel), and b) managed – Shasta (California), Arancio (Sicily), and Hartbeespoort Dam (HBPD, South Africa) (Zohary & Ostrovsky, 2011) (note the difference in scale).

Comparisons of two of the largest lakes in Europe, Lake Balaton and Lake Constance, with a ten years series of hydrographs (Varga, 2005, adapted by Wantzen, 2008) (Fig. 3.), highlight the difference in water level regime and magnitude between regulated (3m maximum range annually) and unregulated (0.5m annually), lakes which are similar in size and latitude. Though Lake Constance is fed by the Rhine and Alpine snowmelt, while Lake Balaton is fed from the Zala River, the main source of which is the hills of Austria and Slovenia, in addition Lake Balaton is regulated via the Sió River Sió-Channel.

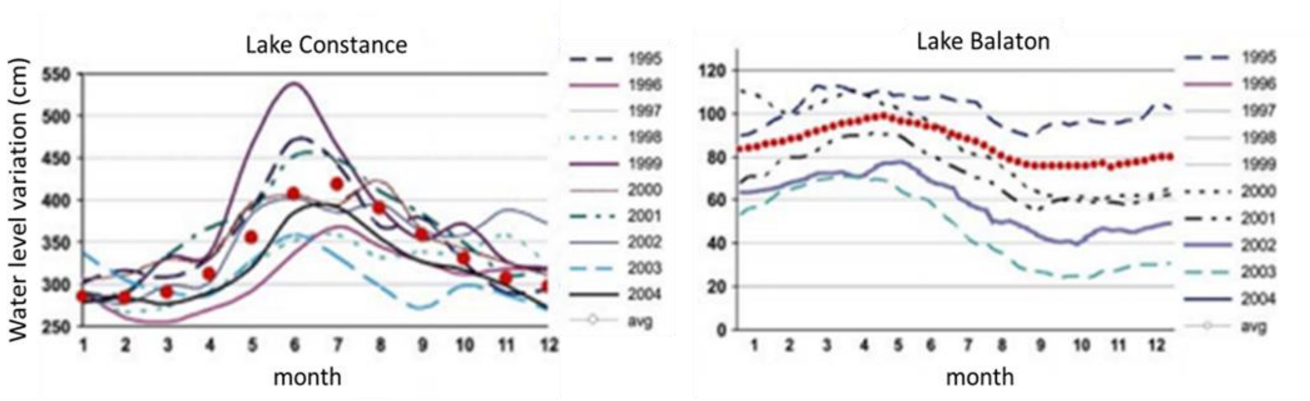

Fig. 3. Water level variation for a 12 month duration for lake Constance (regulated) and Lake Balaton (natural), (note the difference in scale),(Varga, 2005 cited and adapted by Wantzen et al., 2008).

In boreal regions, reservoirs commonly undergo drawdown over the winter months to match the peak needs from hydroelectricity. This reduction of water levels increases the occurrence of freezing of the exposed and shallow littoral zones. The variation in typical water level regime for naturally fluctuating lakes, or managed reservoirs for storage or consumption illustrate the clear difference of magnitude and seasonality between such systems (Fig. 4). This is apparent in the Finnish lake regimes presented by Aroviita & Hämäläinen, (2008) (Fig. 5), where natural systems are characterised by snow melt causing spring floods (though with a time lag or decreased signature in lakes). Whereas the inverse is mostly true for regulated lakes with water level draw down due to meet high energy demands, combined with reduced inflow from surrounding catchments.

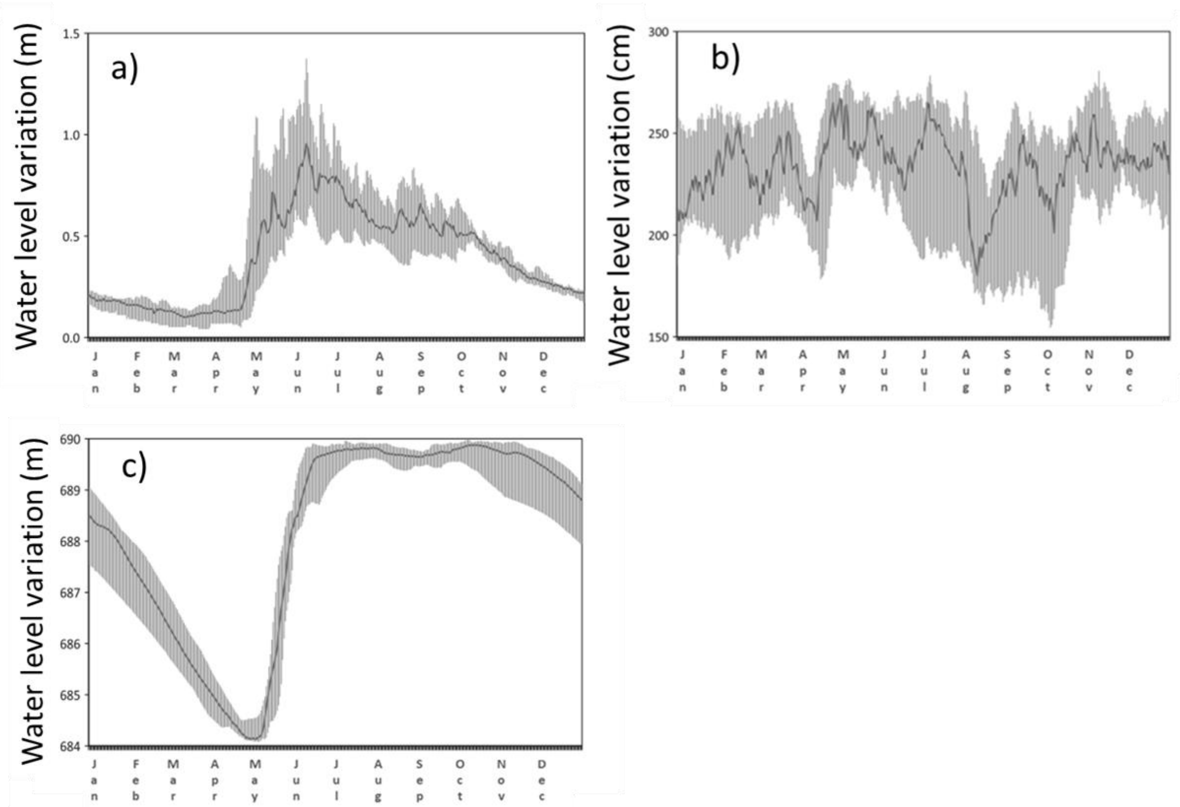

Fig. 4. Water level variation in three types of Nordic lakes for a) a natural lake, b) drinking water and c) reservoir and storage reservoir, the latter subject to winter drawdown (Mjelde et al., 2012).

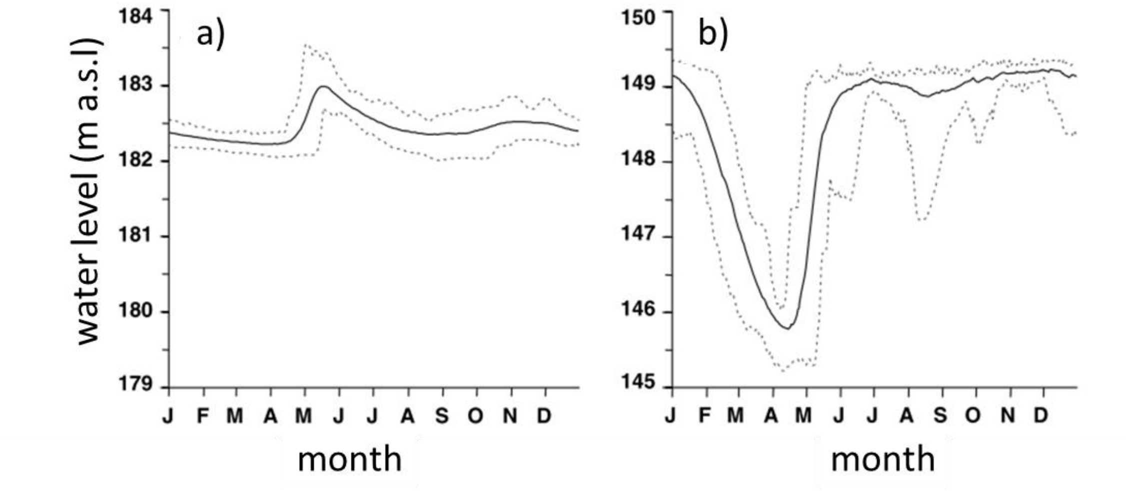

Fig. 5. Water level variation in two Finnish lakes, a) unregulated/natural (Lake Änättijärvi, b) regulated lake (Lake Phyäntä) (Aroviita & Hämäläinen, 2008).

1.8 Scottish natural lake and reservoir water level regimes

Scotland has diverse geology which has resulted in a variety of freshwater systems ranging from large productive lowland lakes to small infertile upland ones, sharing characteristics of those found in arctic and alpine regions. With a low population density of 5.44 million, (Scottish Government, National Statistics, 2019), many lakes and freshwater systems have been less impacted by human modification than in the rest of the UK (Maitland et al., 1994; Scottish Government, Natural Scotland, 2015) making this an ideal location in which to investigate the impacts to lake ecology from altered water level regimes.

Water level regimes of lakes and reservoirs differ in the frequency, duration, and timing of their fluctuations due to the variable balance of inflows, precipitation, outflows, and evaporation. Water levels of lakes in Scotland fluctuate naturally to known magnitudes of around 1-3 m, whilst regulated Scottish reservoirs fluctuate in range from 0.3 m to maximum of 30m (Smith et al., 1987). Annual hydrographs and river gauge flow data from 2012, show the differences in temporal variation of capacities of a few lakes in Scotland with different functions including, an unregulated “natural” lake (Fig. 6), and those used for storage of drinking water and storage reservoirs which serve to maintain water levels of other reservoirs (Fig. 7). Differences occur in annual water level regimes depending on reservoir purpose (Fig, 7). Flow data obtained from river gauges at the outlet of natural lakes is not ideal, but lacking time series lake water level data, it does display higher flows and variation through winter months, with reduced flow and variability during June (Fig. 7). Water levels of Loch Katrine a drinking water reservoir (Fig. 7a), and Glen Finglas a storage reservoir (Fig. 7b), also peak over the winter months and have lowest levels in early summer, though the latter ranges by 7m, while Loch Katrine WLF range in 1.5m. Storage reservoir, Loch Arklet (Fig. 7c), varies from the seasonal trend in 2012 by peaking in winter but reducing throughout the year and fluctuates in water level by 3.5m.

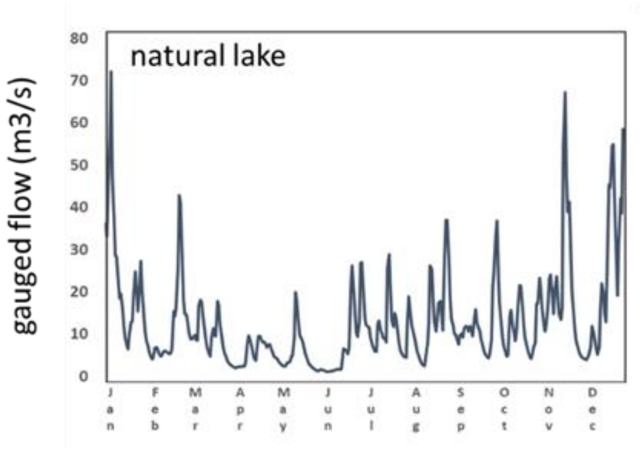

Fig. 6. Example of annual water level outflow from a) a natural lake (Loch Lubnaig), data spans 2012 from the Falls of Leny gauge (SEPA, 2020)

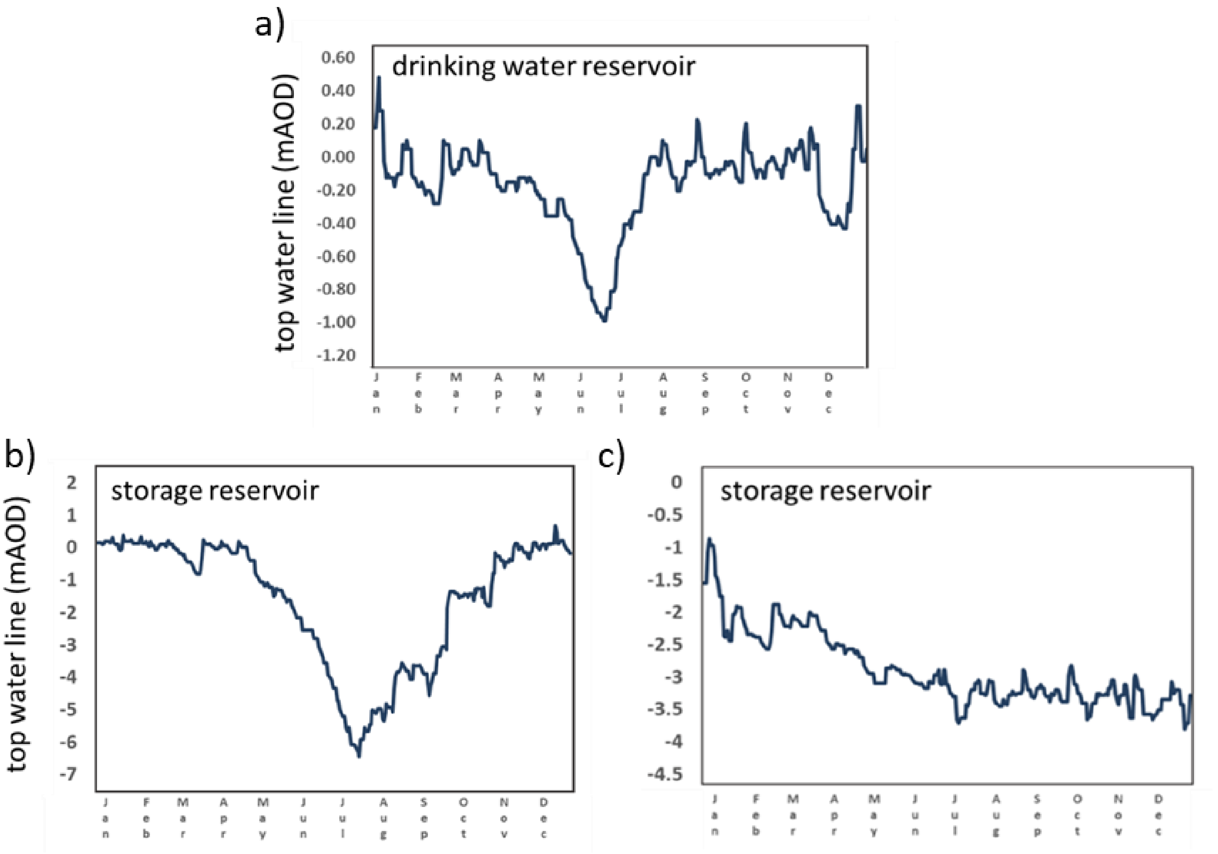

Fig. 7. Annual water level variation depending on the reservoir purpose for a) drinking water reservoir (Loch Katrine) and storage reservoirs b) Glen Finglas reservoir and c) a refill loch for Loch Lomond (Loch Arklet) data spans 2012 in all lakes. Loch Lubnaig data obtained from outflow river station (Leny at Anie data obtained UK National River Flow Archive), Loch Katrine, Glen Finglas and Loch Arklet data are measured relative to the top water level (data supplied by Scottish Water).

1.9 The littoral zone in natural, unregulated lakes

The littoral zone comprises areas of near-shore, shallow waters of a lake (Fig. 8), and extends to the depths of maximum light penetration in a lake (sufficient for vegetation growth), the lowest of the euphotic zone, typically extending to depths of 1-5 m in natural systems (Schmieder, 2004; Wetzel, 2001). The littoral zone is a naturally dynamic, transitional zone, undergoing disturbances due to WLFs and in temperate or cooler, northern regions, freeze/thaw events, particularly at the perimeter (Hellsten, 2000). These disturbances increase the structural complexity of littoral habitats, which provide resources and are ecotones for both aquatic and terrestrial organisms, as well as regulating interactions between different trophic levels, (Schmieder, 2004; Zohary & Gasith, 2014). The littoral zone structure of any lake will vary with an array of factors such as; shelf slope, extent of exposure to wind and wave energy, WLF regime, and dominant substrate type, examples of two unregulated lake littoral and shore zones are shown in Loch Chon and Loch Voil (Fig. 9 and Fig. 10).

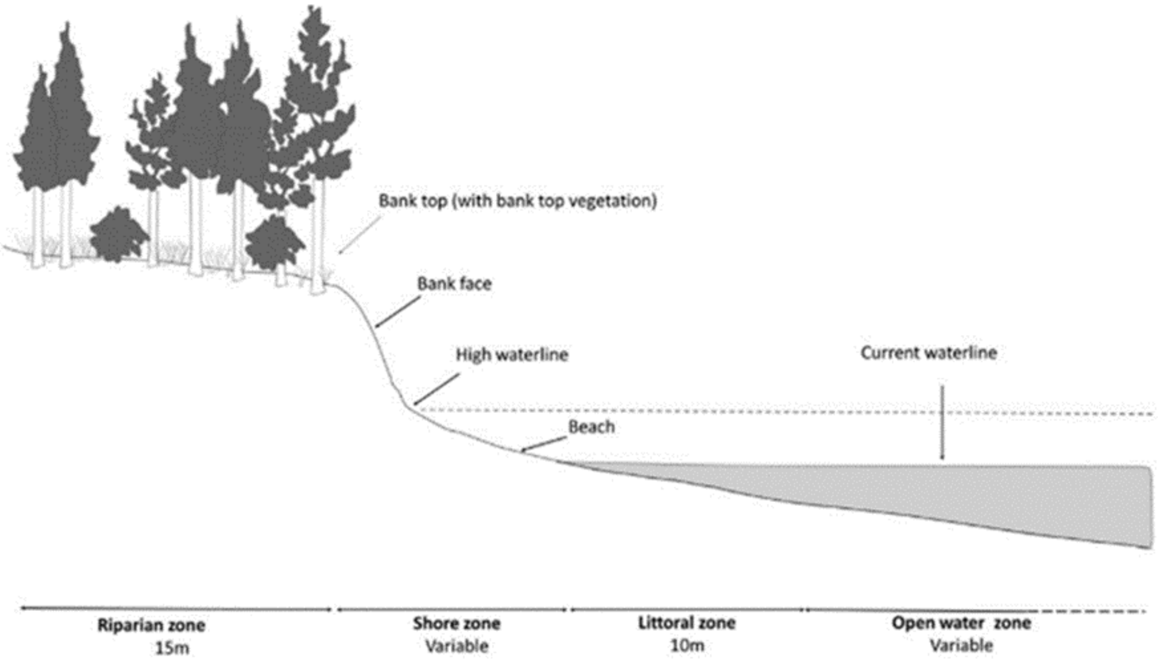

Fig. 8. The typically described four functional zones of a lake (Boon et al., 2019).

Natural lake WLFs boost productivity (Kolding & van Zwieten, 2012), and are important for ecosystem structure and functioning. Water level changes in deep lakes contribute to internal nutrient mixing (O’Reilly et al., 2003; Strayer & Findlay, 2010), whilst shallow lakes benefit from the seasonal pulses of nutrients via water ingress from rivers and riparian zones (Wantzen et al., 2008), and many littoral plants require both inundation and/or desiccation to stimulate propagation (Dinakar & Bartels, 2013).

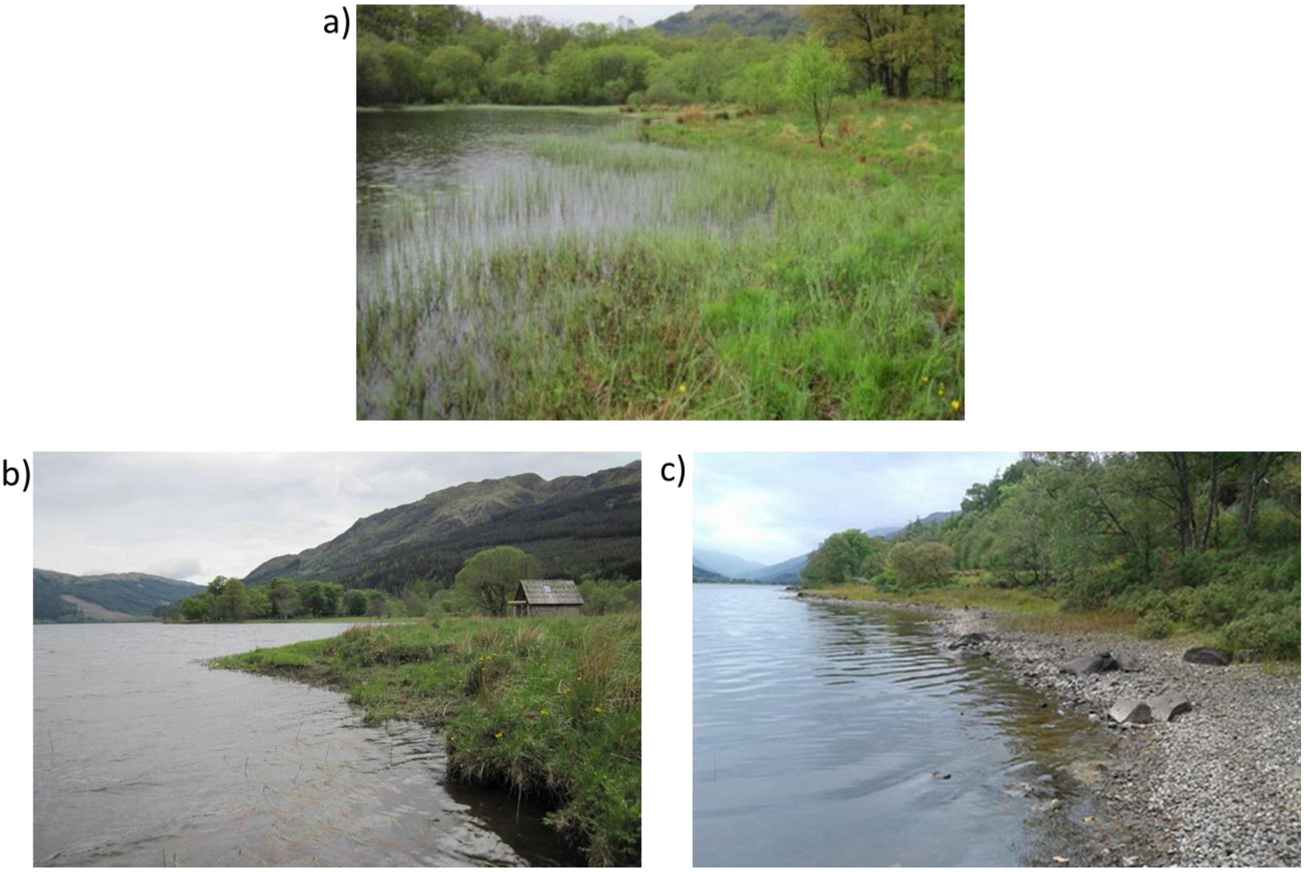

Fig.9. Unregulated research lakes differing in exposure, WLF and littoral to shore vegetation; a) Loch Chon, unregulated sheltered shore with lush submerged and emergent littoral vegetation and shore vegetation, (summer), water level range 0.9m, b) Loch Lubnaig, unregulated, moderately exposed shore, with submerged and some emergent littoral vegetation and shore vegetation and predominantly soil substrate (summer), water level range 1.2m, c) Loch Voil, unregulated, exposed shore with submerged littoral vegetation and predominantly stony shore (summer), water level range 1.6m

Lakes and freshwater basins undergo climatic and geological disturbances, and through time and natural selection, freshwater species have developed strategies to survive, grow and reproduce in this dynamic habitat, or to recolonize rapidly after flooding, freezing, desiccation and erosion, such as the plant *Littorella uniflora,* which actively requires desiccation to stimulate seed germination (Arts & van der Heijden, 1990; Murphy, Rørslett, & Springuel, 1990). Many freshwater species benefit from diapause or dormancy such as the mayfly *Siphlonurus lacustris*, this physiological mechanism enables it to respond to regular periods of environmental adverse conditions (Buffagni et al., 2009; Buffagni et al., 2020). Numerous macrophytes reproduce vegetatively from detached fragments, in addition to seed dispersal, the former contributing to the spread of some species fragmented in ice covered lakes, or through mismanagement of invasive species removal, like *Myriophyllum spicatum* (Li et al., 2015).

Though the littoral zone is inhabited by obligate aquatic organisms, including non-insect invertebrates and the majority of fish, many littoral zone organisms are fundamentally terrestrial in their physiology, but exploit freshwater resources to varying degrees, forming an integral link in redistributing energy and other resources to the wider environment, such as emergent vascular macrophytes, amphibians, mammals, birds and bats (Colvich et al., 1999; Horváth et al., 2012; Salvarina, Gravier, & Rothhaupt, 2018). Some aquatic insects and submerged plants have retained terrestrial features despite being unable to withstand desiccation, the latter often with aerial flowers which require pollination via terrestrial vectors or wind instead of water, such as *Lobelia dortmanna* (Philbrick & Les, 1996). Whilst many aquatic insects have juvenile aquatic stages, their adult phase is aerial, such as odonata, ephemeroptera, plecoptera and trichoptera. In addition, the littoral zone provides a crucial flow of energy in a lake ecosystem in the form of autochthonous and allochthonous organic matter (Boulion, 2019). In addition to catchment loads, sediment resuspension and phytoplankton, nutrient fluctuations in the littoral zone can vary spatially and rapidly due to the metabolic activity of plants (Barker, 2006). This diversity. and the structural and organismal complexity. make it difficult to generalise the outcomes of imposed pressures through environmental changes.

Littoral zone vegetation serves as a key habitat, food resource and refuge from predation for benthic invertebrates; it also provides a feeding ground for fish and is important as a spawning substrate for fish and nursery for fish fry (Heino, 2008; Hellsten, 2000). As such, alterations in littoral macrophyte composition and structure may severely impact on aquatic invertebrates (Law et al., 2019a; Smith, Maitland, & Pennock, 1987) resulting in decreased production and so abundance of zooplankton (Grimås, 1961, cited in Hellsten, 2000), and reduction in resources for fish (Sutela & Vehanen, 2008), water birds and the insectivorous bats (Vaughan, 1997).

Benthic invertebrates have an important role in lake ecosystems, as a link between the primary producers, detrital deposits of the littoral and the higher trophic levels (fish) of the pelagic habitat and riparian zone (Vaughan, 1997). As a result, aside from the direct effects of WLF on littoral invertebrates, such as desiccation, any changes in water level regime, nutrient levels, or types of degradation, should also be reflected in changes to the assemblage of the benthic invertebrate community. In addition, because many macroinvertebrates are ubiquitous, often long-lived and are relatively immobile in their aquatic stage, the community structure reveals a response from exposure to present or past stressors. Repeated disturbance due to water level alterations particularly impact on long-lived populations exposed to repeated events (Aroviita & Hämäläinen, 2008). Consequently, it is reasonable to direct sampling efforts towards littoral zone macrophyte and benthic macroinvertebrate assemblages of regulated and unregulated lakes (Sutela et al., 2013), as suitable indicators to use in assessing responses to hydromorphological pressures (JNCC, 2005).

1.10 The littoral zone in hydromorphologically altered lakes

Lake ecosystems are exposed to significant disturbances and pressures due to hydromorphological modifications (Coops et al., 2003), primarily impacting the littoral zone (Fig. 8), affecting the structure and composition of macrophytes and invertebrate communities (Aroviita & Hämäläinen, 2008; Brauns et al., 2011; Hellsten, 2000; Sutela, Aroviita, & Keto, 2013). Lake littoral biota form an integral component of lake ecosystem structure and function, with a major role in whole-lake food webs (Brauns et al., 2011).

Seasonal differences are often the most contrasting aspect of hydrologic regime between natural and regulated lakes (section 1.7), even if a lake fluctuates within a natural range the timing of peak and low water levels are not always synchronised with the seasonal interactions or requirements of species within or around a lake, creating potential for phenological mismatches. Phenological mismatches are a disruption in the synchronicity of timing between species, specifically interactions involving life cycles, such as plant and pollinator or predator and prey. The disruption coming from an altered environmental cue such as climate change or, in this instance temperature of water as a result of lowered water levels, which can be enhanced by climate change impacts. For instance, mayfly nymphs affected by temperature changes from climate change and reduced lake water volume, may interrupt lake water oxygen circulation and so also the mayfly life cycle (and emergence), which many insect-feeding organisms depend on in aquatic and terrestrial habitats (Stepanian et al., 2020) .

Littoral zone aquatic macrophytes are, logically, susceptible to alterations to enhanced water level regime (Mjelde et al., 2012). Where lakes are vulnerable to freezing, the effects of anthropogenically induced WLFs are enhanced (as in Scandinavian/Boreal regions), as this is particularly damaging to plants that are susceptible to freezing due to ice scouring. The decline of large sized isoetid plants impacted by altered water levels has been reported in studies in Scotland (Smith et al., 1987; Murphy et al., 1990) and northern Scandinavia (Rørslett, 1984; Rintanen, 1996; Hellsten, 2000).

Manipulated WLFs interact with the physical parameters of a lake system such as fetch, depth and shore slope and how these interplay with wave action and sediment, by extension the biota within a lake respond to changes to the habitat (Murphy, 2002). Depending on the scale and extent of WLF alteration, some alterations are often visually evident in reservoirs (Fig. 11).

Lake sediments are redistributed through the process of sediment focusing (Likens & Davis, 1975), which involves the erosion, transportation and subsequent deposition of materials by way of turbulence via wave energy, currents or slope, typically in the profundal zone of the lake (the zone of accumulation) (Hakanson, 1977). Wind energy drives sediment suspension and resuspension in lakes through wave action, predominantly in littoral zones or shallow lakes, the energy required (shear stress), is dependent on the sediment characteristics (size and texture) (Effler et al., 1998; Bloesch, 1995) and water depth (though even deep, stratified lakes have littoral zones).

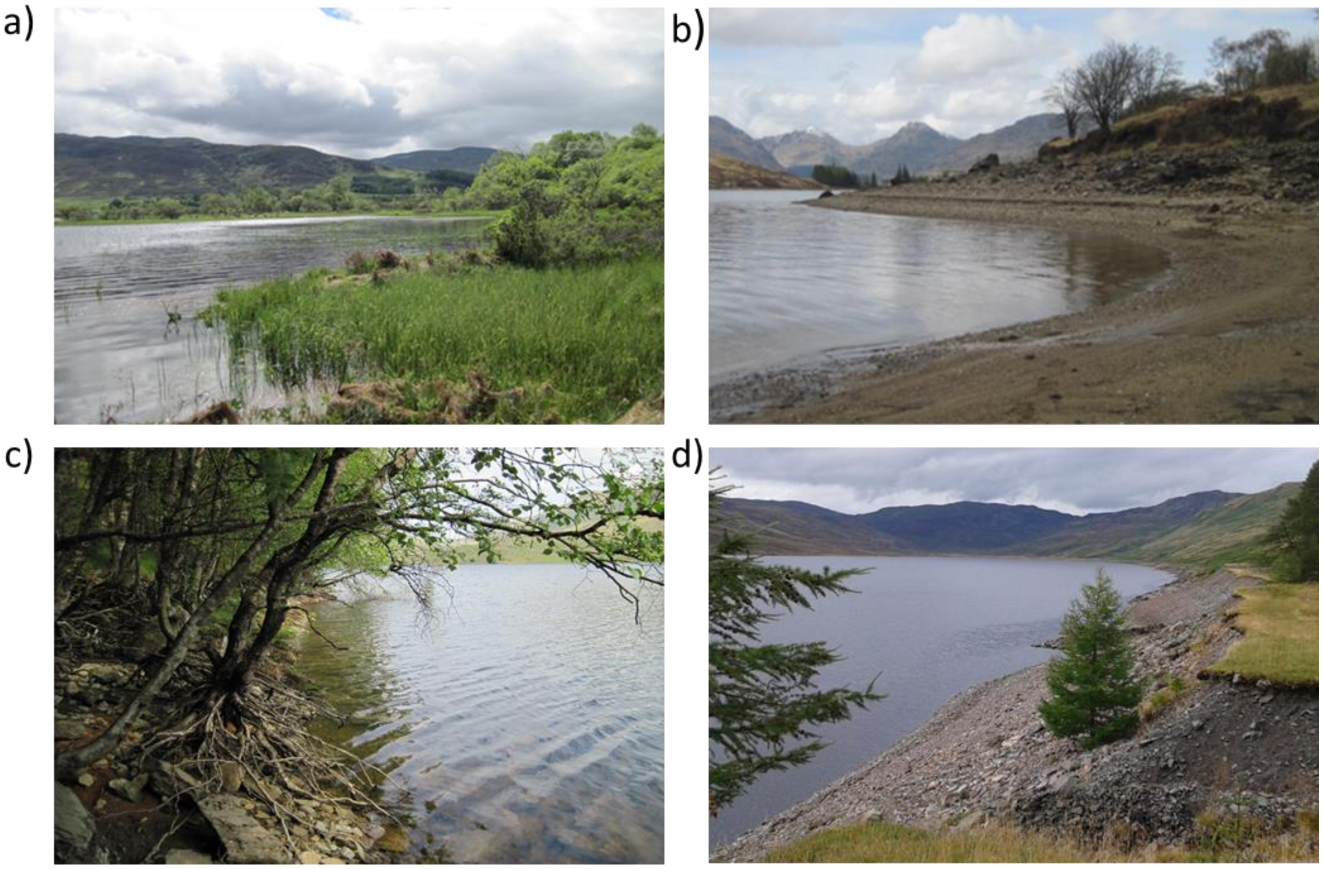

Fig.10. Littoral and shore zones of a selection of reservoirs included in this research including; a) Dunalastair Water, regulated, mean depth 7.1m, sheltered shore (summer), WLF 0.3m, b) Loch Arklet, regulated, mean depth, 7.4m moderately exposed shore (spring), WLF 3m, c) Glen Finglas Reservoir, regulated, mean depth 6.5m, moderately exposed shore (spring), WLF 7.8m, d) Loch Lednock, regulated, mean depth 7.5m, exposed shore, (summer), WLF 9m.

The types of sediment exposed to wave action and turbulence change as lake water levels are lowered (Gloor et al., 1994), with coarser littoral aggregates being exposed during drawdown (zone of exposure) and typically results in the lake margins being relocated to the lower littoral or deep-water zone (Fig. 8 and Fig 11b), more fitting the areas termed by Hakanson (1977), as the zones of transportation and accumulation. This results in the potential of resuspension of sediments, which has implications for nutrient and pollutant release, increased turbidity, and so light attenuation, in addition to the potential for desiccation of any organisms unable to move or at speeds sufficient to remain in the aquatic environment.

For mobile organisms the “new” littoral zone following moderate to high, or extended duration of drawdown is now increasingly homogenous (Evtimova & Donohue, 2016). This new littoral, lacks the variety of particle sizes that creates niche availability, which are provided on the upper shores of lakes, particularly in areas of exposure to wind and wave action (Cooley & Franzin, 2008). Finer particle sizes such as silt and sand will be suitable for fewer species, as has low structural complexity, whilst larger aggregates such as cobbles and pebbles (usually with fine materials around them in lakes), increase niche availability for a wider variety of species (Gasith & Gafney, 1998). Resuspended sediments may be relocated to margins of lakes with calmest waters, potentially covering biota in the sheltered areas, reducing the ability of photosynthesis for macrophytes and epiphytes or making these species less available as a resource for herbivores. The slope of a lake shore interplays with these factors as a steep slope can result in coarse grained aggregates at greater depths than could be translocated via wave action alone (Rowan, Kalff, & Rasmussen, 1992).

While macrophytes are shaped by the direct and indirect effects of the environment, they also modify their aquatic environment through metabolic activity and growth form (Madsen et al., 2001). Macrophytes, once established (and inundated) can increase the sedimentation rate and reduce turbidity levels through reducing localised current velocity (Petticrew & Kalff, 1992), they also add to the complexity of the littoral habitat zone.

Therefore heterogeneity of physical structures in the littoral zone via substrate type and abundance, vegetation and allochthonous inputs such as woody debris, affect lake biodiversity and all will be influenced by lake water levels and therefore, influence metabolic functions through organic matter availability and nutrient dynamics (Brauns, Garcia, & Pusch, 2008; Brauns et al., 2007; Gasith & Gafny, 1998). As a result, aquatic taxa are indicative of different lake types and reflect variations in chemical and physical attributes and consequently WLFs.

1.11 Approaches to analysing ecological responses in lakes

Impacts on lake ecosystems and responses of biota, are usually based on comparisons between regulated and reference lakes (spatial studies,) or prior and post morphological adaptation (temporal studies). Paired lake studies involving regulated and unregulated lakes (Valvodinos et al., 2007; Hellsten, 2000), or the study of a few or single lakes through time (Brauns et al., 2007; Mastrantuono et al., 2008; Hynes, 1961, cited in Hunt & Jones, 1972), allow for more intensive sampling, such as time series data or a wider suite of relevant factors and potentially manipulative approaches. Synoptic approaches investigating lake wide characteristics or impacts on flora and fauna have focused research over multiple lakes, within a catchment or distinct region (Aroviita & Hämäläinen, 2008; Smith et al., 1987; Brauns et al., 2007a; Heino, 2008; Donohue et al., 2009). This design approach is useful in determining responses to multiple hydromorphological and environmental pressures and relationships between taxonomic or functional diversity and habitat heterogeneity, without the problems created by larger scale biogeographical gradients. Hellsten (2000), separated environmental factors acting on lake macrophytes into lake specific, shore specific and site-specific factors. Adding to this conceptual design of often interrelated factors, research has since added knowledge to the partitioning of environmental, hydrological and landscape factors influencing aquatic biota which we present as; regional, lake wide and sub lake factors (Fig. 12). These factors, revealed by a review of the literature as influencing littoral biota, are necessary to consider and incorporate when determining the relative influence of lake WLFs on littoral biota.

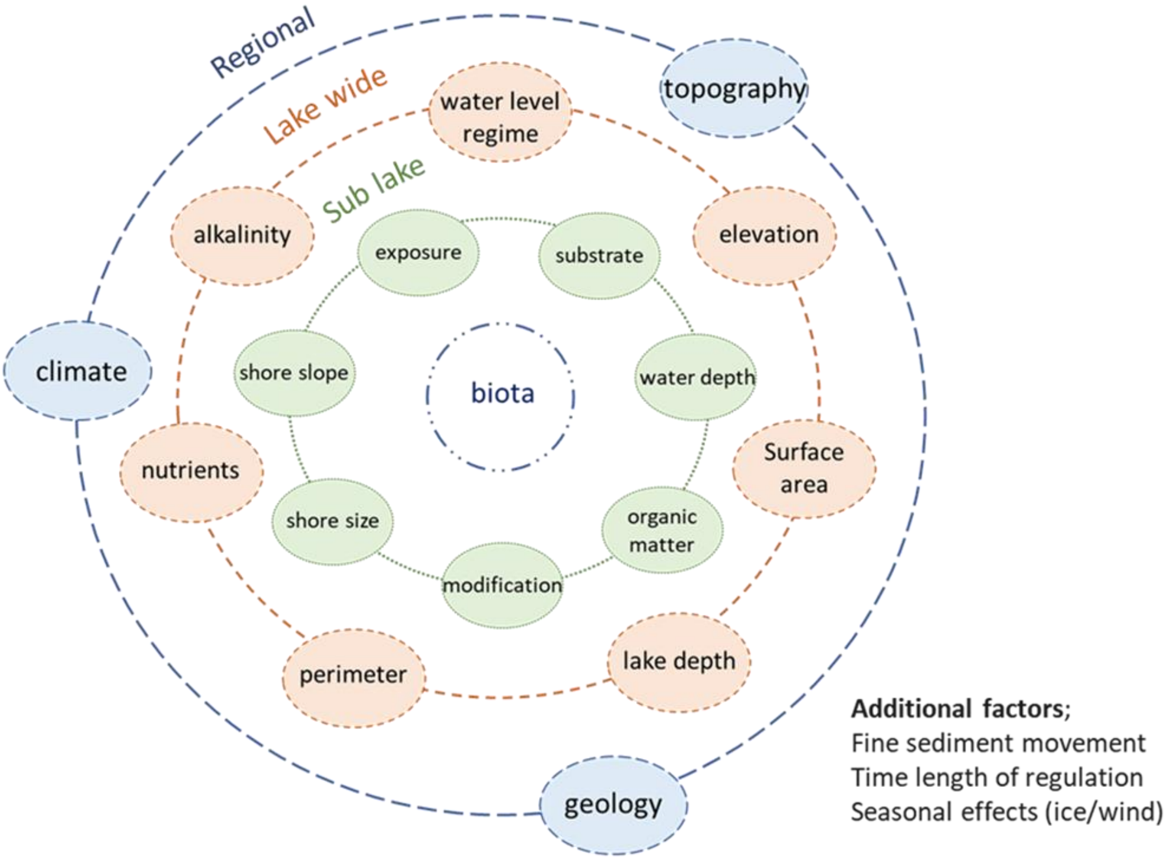

Fig. 11. Schematic view of environmental lake variables at regional, lake wide and sub lake scales, relevant to aquatic biota (macrophytes and macroinvertebrates).

1.11.1 Ecological responses in lakes to regional factors

A review of the literature highlighted the importance of using regionally specific data in freshwater lake studies. McGoff et al., (2013), demonstrates that macrophyte diversity may be regionally specific, that this is more likely driven by regional environmental gradients (particularly elevation/topography), rather than latitude *per se* (Alahuhta et al., 2017). Though effects from regional environmental gradients are linked to a regions latitude as are mediated by temperature; as seen with ice scour impacts and snow melt in Alpine regions; or high evaporation in Mediterranean areas (Mastrantuono et al., 2008). A regional approach is supported by Solheim et al. (2008), whose research revealed a higher similarity in macrophyte occurrence at varying levels of total phosphorus concentrations, between different lake types from within the same country, than was found between concurrent lake types from varying countries within Europe.

Specific regional gradients of climate, topography and geology were found to explain lake macrophyte community composition variation (O’Hare et al., 2012), highlighting the importance for future studies to take such variables into account in research design in agreement with other authors (Alahuhta et al., 2017; Elo et al., 2018; Vilmi et al., 2017). In addition, macroinvertebrate multimetrics in different geographical regions, vary in response to different hydromorphological pressures, indicating that assumptions should be tested regionally for validity (Solheim et al., (2008).

1.11.2 Ecological responses in lakes to lake-wide and sub lake factors

Macrophyte community composition and species richness have been determined to be mostly driven by the lake-wide environmental characteristics of; water quality (including pH, alkalinity and conductivity) and sub lake scale shoreline complexity (habitat heterogeneity measured as shoreline development), (see Table 1) (Elo et al., 2018). Rørslett (1991) gathered data from 641 Scandinavian lakes, including regionally scaled variables such as latitude, elevation and area and hydrological variables. Macrophyte species richness was explained mostly by lake area and attributed to larger sites having a greater diversity of habitat. Other factors identified as negatively influencing species richness and diversity included the lake wide factors of lake regulation, low pH, or eutrophication (Rørslett, 1991). However, local diversity in vegetation was attributed to sub lake factors of wind and wave exposure gradients, with fringe habitats of larger lakes such as sheltered bays, inlets/outlets, and polluted sites, holding 30-50% of all species present (Rørslett, 1991). The variation with exposure reinforces the importance of scaled sampling procedures, to identify significant pressures.

Sun et al., (2019) used regional (UK), and lake wide factors to investigate macrophyte composition (spatial turnover and nestedness between lake types), using a database of almost 1000 lakes. Subdivision of lakes by type, based on spatially structured factors, specifically alkalinity and elevation, revealed that hydrological connectivity differed within these lake types, with a greater role in macrophyte structuring in upland lakes. O'Hare et al, (2012), included 96 lakes of conservation importance within Scotland, to assess the relative impacts to macrophyte community structure from spatially structured environmental processes, including: regional (as mentioned previously), local (lake wide) and habitat (sub lake) factors. Of highlighted importance were the lake-wide predictors of alkalinity, total phosphorus, lake area and elevation, while the sub-lake factor of substrate rockiness was associated with submerged vegetation. The literature reviewed indicates the importance of lake-wide and sub-lake factors in regard to affecting littoral biota and therefore it would be advisable to account for such influences when determining the influence of another environmental variable such as WLF.

1.11.3 Ecological responses to sub-lake factors

Lake littoral zones are dynamic with naturally high habitat and biotic complexity. This inherent complexity creates a challenge to quantify how biotic communities respond to anthropogenic pressures, in particular indirect or multiple pressures (Mcgoff et al., 2013a; Strayer & Findlay, 2010c). In addition to directly affecting biota via inundation or dewatering, lake WLFs influence littoral biota indirectly through its influence on littoral habitats (sub lake features), (Hellsten, 1997, Elo et al., 2018) and therefore are necessary to account for in sampling and analysis when determining impacts from WLF.

The importance of including sub-lake (habitat), features in lake research design is further highlighted by McGoff et al. (2013), from studies of lakes in the UK and Ireland who discerned abundance of the more sensitive EPT taxa (Ephemeroptera, Plecoptera, Trichoptera), increased with increasing habitat quality. Conversely, Oligochaeta declined with increasing sub lake habitat quality. These results are fairly intuitive as Oligochaeta favour fine silt habitats (Bazzanti et al., 2010, cited in McGoff et al., 2013). Furthermore, where multiple pressures of hydromorphological disturbances and nutrient loading have been assessed, habitat type has repeatedly been found to be of greater importance than total phosphorus in affecting macroinvertebrate community composition in pan-European research (McGoff et al., 2013; Brauns et al., 2007a), though this has been suggested to be due to length of trophic gradient or lake size.

Our research highlights the need for the inclusion of regional, lake-wide, and sub lake factors, and the potential for sub-division of lakes by type to better determine ecological responses to such pressures.

1.12 Macrophyte and invertebrate responses to direct and indirect WLF pressures

Water level regulation predominantly affects life in the littoral zone through the rise or fall of water outside of natural variation in range or timing, via either desiccation or inundation. Lake regulation also leads to substantial geomorphic changes particularly in the littoral zone if levels are raised to expand storage capacity. Raising lake water levels can lead to changes such as erosion of minerogenic matter and breakdown of the organic surface layer, which can negatively impact on marginal and terrestrial vegetation (Nilsson, 1981). In turn, this affects the ability of vegetation to act as a buffer against erosion by wind, waves, and currents (Hellsten, 2000). In addition, enhanced WLFs affect light attenuation, and water depth, which coincide to restrict the growth of aquatic macrophytes at the lower parts of the littoral zone, where shade tolerant species such as *Isoetes lacustris* tend to dominate (Hellsten, 2000;

Rørslett, 1984). Such effects may be especially acute in humic lakes where vegetation is already light stressed.

Increased WLF ranges in lakes have directly resulted in species that are unable to follow receding water being stranded, and subject to desiccation, and indirectly influence species via alteration of shore factors (Avital Gasith & Gafny, 1990). Alteration of lake shores and littoral zones can result in the reduction of macrophyte stands that are used as food resources, and a decrease of refuge habitat availability, both of which threaten ecosystem integrity (Hellsten, 2002; Nishihiro et al., 2004; Schmieder, 2004; Strayer & Findlay, 2010b; Sutela et al., 2013). In addition, reduced aquatic macrophytes, impact on littoral macroinvertebrate communities illustrated by altered diversity, functioning and structure (Brauns e t al., 2007b, 2011; Hunt & Jones, 1972; Porst et al., 2019). The direct influence of hydromorphological pressures do not affect invertebrates in isolation, but are moderated by nutrients, specifically phosphorus, lake area and alkalinity (Jurca et al., 2012).

Consequentially species dependant on littoral macrophyte habitats have been found to decline where there is a reduction in macrophyte stands, such as, Ephemeroptera, Coleoptera, Hemiptera, Mollusca and Odonata (Hynes, 1961, cited in Hunt & Jones, 1972) (Declerck, Bakker, van Lith, Kersbergen, & van Donk, 2011). Potentially the association between these biotic components is determined more on the structural diversity of the aquatic macrophytes or on the cover of plants, than standard community measures such as richness (Law et al., 2019). Indirect effects of WLF have resulted in the losses of mobile species such as, Gammarus spp. Coleoptera, Corixidae and Hydracarina through changes to the littoral environment (Hynes, 1961, cited in Hunt & Jones, 1972; Mcgoff et al., 2013). Certain invertebrates have been observed as being able to move in line with (moderate) rates of water level variation, of up to 0.5 cm hr^{-1}, while some taxa recolonize habitats after rewetting over the course of three months, for others this takes only weeks (Winter, 1964, cited in Solimini et al., 2006; James et al. 2002, cited in Solimini et al., 2006).

1.12.1 Literature review of WLF effects of lake littoral biota

We present a sample of the literature summarizing known direct effects from lake regulation (WLF) on macrophytes (Table 1), macroinvertebrates (Table 2) and in Table 3, environmental factors that affect lake macrophytes, many of which will in turn be susceptible to changes in WLFs, and which may in turn, affect littoral invertebrate communities (Hellsten, 2000b; Mjelde et al., 2012).

Within regions it is shown that system connectivity is important, particularly when lakes are divided by alkalinity and elevation (Sun, et al., 2019). At a lake level, macrophyte richness and diversity are affected by lake elevation, surface area and alkalinity (Rørslett, 1991; O'Hare et al., 2012; Elo et al., 2018) in conjunction with nutrient enrichment and water clarity (Vestergaard & Sand-Jensen, 2000). Shore specific factors that are associated with macrophyte growth and abundance include shoreline complexity, exposure gradients (wave/wind), shore slopes and substrate type (Elo et al., 2018; Rørslett, 1991; Bailey-Watts & Duncan, 1981; Nilsson, 1981; Keddy, 1983). Many, if not all, of the environmental attributes included will be determined or altered by water level regimes in lakes, natural or otherwise, with cascade effects to wider lake and terrestrial ecology. Research regarding lake water level regimes impacts on lake macrophytes (Table 1), suggests a unimodal response to water level fluctuations in line with Grimes (1973) intermediate disturbance hypothesis (IDH). The overarching premise of the IDH is that species diversity peaks at the intermediate level of a given disturbance (Connell, 1978, cited in Townsend & Scarsbrook, 1997). The IDH may therefore relate to lake WLF effects on littoral biota as very low or static WLF promotes a species poor dominance of competitor species, whereas high levels of WLF, may result in dominance by few species tolerant to water stress. Therefore, intermediate levels of WLF, (potentially similar to the dynamic conditions of a lake without regulation) would be expected to encourage a higher diversity of species by preventing dominance of a few species, thereby allowing a suite of species with different water level and habitat requirements to persist and provide a diverse role of ecological benefits.

The literature below describes associations that appear to align with the IDH. Research reveals that artificially constrained water levels result in shore line macrophyte degradation, with encroachment by species which threaten wetland habitats (Shay et al., 1999; Coops & Hosper, 2002 Hosper, 1988), similarly invertebrate diversity reduces (Mastrantuono et al., 2000; McEwen & Butler, 2010) with changes to community structure (Table 2). Positive associations between moderate WLFs (comparable with natural ranges of 1 - 2.4 m) and macrophytes with increased diversity and an increased abundance stress-tolerant species (Rørslett, 1991; Rørslett, 1989), equally, invertebrate richness levels peaked in line with long term mean fluctuation rates but decreased if levels rose or fell beyond that threshold (White et al., 2008). Where water levels of lake regulation reduce by 5 m or more, the effects to macrophytes are reported as catastrophic to all but a few species if not all, Thomaz et al., 2006; Mjelde et al., 2012; Hellsten & Mjelde, 2009, while invertebrate communities alter in composition, cited as a shift away from semivoltine, larger bodies and less mobile species with higher dependency on macrophytes for habitat and food resources, all of which appear as indicative to reference lakes (Furey et al. Hynes, 1961 Aroviita & Hämäläinen, 2008).

Few studies have attempted to quantify the relationship between changes in lake biota with WLF, particularly in comparison with the body of work available on riverine ecosystems (Wantzen, 2008). Those that do are predominantly within Europe, particularly Nordic regions (Table 1), that predominantly focus on winter water draw down (Table 1). Comparisons can be inferred from winter water level drawdown (WWLD) and WLF research, such a decline in taxa sensitive to WLF e.g. Large isoetids (Hellsten & Mjelde, 2009), but inference should be made with caution. WWLD, like WLFs, are applied by reservoir managers for similar reasons, including hydropower, macrophyte and flood control. However they differ in dynamics to the majority of storage reservoirs in temperate regions, in terms of season, frequency and duration (Mjelde et al., 2012) (see Fig.4). Winter draw down is a regular annual event in the first months of the year. Reservoir water levels are reduced through the winter and subsequently raised, usually through decrease hydropower demand and melt water refill in the spring. Therefore changes in the littoral zone occur due to the dewatering, and heightened erosion of the exposed lake littoral bed from increased area of frozen zones, ice penetration and ice scour (Hellsten, 1997; Carmignani & Roy, 2017). Carmignani & Roy, (2017), synthesis established that despite some positive effects from WWLD on macrophyte diversity by some researchers (Rørslett, 1991,1989; Hellsten & Mjelde, 2009), overall richness of macrophytes and macroinvertebrates declined, with a compositional shift favouring taxa with traits that are stress tolerant to WWLD effects and with r-selected life history strategies. However, in much of North West Europe and especially the UK and Scotland, this extent of freezing does not occur and so the majority of lake littoral zones and biota are not affected by this pressure.

In addition, lake water level ranges are seldom provided, particularly in studies outside Europe and the USA. Brauns et al., (2007b) researched invertebrate composition in regard to anticipated water level changes driven by climate change in lowland lakes of East Germany. Using a method that calculated the change in eulittoral position with lowered waters to the current infralittoral. This work provided insights to the dependency of invertebrates on habitat features and resources, predominantly woody roots, and reed beds, in comparison, to other littoral characteristics and driven by taxonomic traits (Table 2). Mastrantuono (2008) also employed a single lake approach using varying water levels from previous years in a volcanic regulated lake in Italy. This work demonstrated the link between reduced water levels in addition to shore features such a slope with changes in littoral macrophytes and invertebrate communities (Table 2).

The last regional study of Scottish loch biota by Smith et al., (1987), some 33 years ago, investigated responses of biota to WLFs the previous year and encompassed 27 lakes with WLF designated as natural, minor (<5 m) and major (>5 m). For each survey, a single representative reach of stony shore was selected to record physical characteristics (littoral width, shore width and slope), aquatic macrophytes and benthic invertebrates. This work highlighted the importance of not just water level range but the rate and consistency of that change. 11 lochs absent of any macrophytes all had over 5 m of water level range with similar results found for invertebrates as communities were classed as “impoverished” where there was significantly lower diversity and abundance. Lochs with WLF ranges of up to 12-30m were recorded with no macrophytes and extremely low abundance or diversity of invertebrates (Smith et al., 1987). This work highlighted the impact of extreme WLF and indicated the importance of future work to extract a finer scale of WLF pressure-biota response associations, particularly in lakes with less than 12 m WLF range.

Table 1. Established relationships between lake water level regulation and aquatic macrophytes .

Environmental/abiotic factor	location	Relationship/effect	Macrophyte measure	Author / source
regulated/unregulated lakes	Finland	no significant dissimilarities	stability of vegetation	Hellsten, 2000
lake regulation	Nordic countries	negative association	species richness & diversity	Rørslett, 1991
lake regulation	Finland	negative association	large isoetids (*Isoetes lacustris, Lobelia dortmanna*) replaced by small isoetid (*Ranunculus repens, Eleocharis acicularis*) due to expansion of ice area	Hellsten, 2000 Also, re large isoetids - keto et al., 2006; Turner et al., 2005; Rørslett, 1984; Mjelde et al., 2012
Lake regulation	Temperate & sub-tropical	negative association	key species, biodiversity	Zohary et al., 2011
		positive association	invasive species, cyanobacteria blooms	
Lake regulation (water level and fluctuation decrease)	China	mixed response	biomass decrease, submerged plants persist	Yang et al., 2017
water level range (moderate) 1-3m yr^{-1}	Nordic countries	positive association	Diversity	Rørslett, 1991
water level range (moderate) 2.4m yr^{-1}	Nordic countries	positive association	abundance stress-tolerant species	Rørslett, 1989
water level drawdown index	Finland	clear association	tolerant and intolerant species	Hellsten & Mjelde, 2009
water level drawdown	Nordic lakes	negative (not significant)	Species number, tolerance	Mjelde et al., 2012
water level drawdown	Finland	negative (not significant)	Large isoetids (Finnish lakes)	Hellsten & Mjelde, 2009
		positive indication	Diversity (1-2m drawdown)	
water level drawdown		positive correlation	Heavily Modified Water Body index	
lowered water level (in small mesotrophic lakes)	Nordic countries	positive association	species richness	Rørslett, 1991
lowered water level “high” (>1m)	Ireland	negative correlation	macrophyte cover	Evtimova & Donohue, 2016
water level fluctuation & vertical littoral gradient	Sweden	related to	zonation	Quennerstedt, 1958 (cited in Hellsten, 2000)
lowering water levels in shallow lakes	Turkey	positive association	increased contribution of bacteria, ciliates, and Heterotrophic nano flagellates (due to reduced density of aquatic plants – less phytoplankton)	Özen et al., 2014
Reduced winter water level levels for 3 years (2-3m per year)	Canada	no response	phytoplankton biomass, species assemblages	Turner et al., 2005
		negative association	biomass and cover of floating-leaved and submerged plants (large initial decreases) inc. benthic algae	
		decrease	Isoetids i.e. *Eriocaulon septangulare*	
		increase	Pondweeds i.e. Potamogeton spirillus	
Reduced water levels for three months (-5m)	Brazil/Paraguay	negative association	Biomass reduced to zero. No recovery after 14 months	Thomaz et al., 2006
Water level increase (reduced drawdown by 1.7m)	U.S.A, Idaho	positive	Biomass – in drawdown zone of 1.4 -3.5m	Wagner & Falter, 2002
Water levels artificially restrained to 0.6m (prior to regulation range was >2.2m.	Canada	Distributional changes	Typha encroaching Phragmites, predicted to lead to infilling of marshland	Shay et al., 1999
Water level fixation (stabilisation)	Netherlands	Negative impacts	Reedbed degradation and shoreline vegetation	Coops & Hosper, 2002 Hosper, 1988; Coops & Van der Velde, 1996 cited in Coops and Hosper, 2002); Rea, 1996
Regulation structures (dam-based)	global overview	impact	hydrochory	Nilsson et al., 2005

Table 2. Established relationships between water level regulation and benthic macroinvertebrates.

Environmental/abiotic factor	location	Relationship/effect	Macroinvertebrate measure	Author / source
Lake regulation	Finland	Negative relationship	Taxon richness	Aroviita & Hämäläinen, 2008
		Negative, not significant	Abundance	
		Sensitive to regulation	Semivoltine (indicative of reference lakes); *Oulimnius Tuberculatus, Ephemera vulgata, Limnius volckmari, Sialis* sp.	
Lake regulation	Wales, UK	Observed as absent 5yrs post regulation (present previously)	Mayfly larvae; *Ephemera danica, Caenis luctuosa* and *Leptophlebia marginata*. Alderfly larvae: Sialis sp. Caddis larvae; *Polycentropus flavomaculatus*. Riffle beetles; *Oulimnius tuberculatus* and *Limnius volckmari*	Hynes, 1961
Lake regulation	Sweden	Absent (observed)	Larger bodies invertebrates including *Sialis lutaria*	Grimås, 1961
Lake regulation	Finland	Negative relationship	abundance	Hellsten, 2000
Water level amplitude – comparison regulated and unregulated (0.11-6.75m)	Finland	Strong association (ordination)	Community composition	Aroviita & Hämäläinen, 2008
		Negative association	Taxon richness	
		Negative association	Long-lived invertebrates (vulnerable)	
Water level range (>5m)	Scotland	Negative association	Taxon richness	Smith et al., 1989
Water level range regulated (Reg); 6-9m, compared with 0.5m natural lake (Nat)	Canada	No difference – exposure zone	Density and biomass	Furey et al., 2006
		Significant difference – exposure zone	Community composition. Reg: Ephemeroptera, Trichoptera & Pentaneurini/ Chironomidae (present in Reg, but absent in Nat) Nat: Gastropoda, Odondata, other Diptera, Chaoboridae, Hirudinea, Hydrachnida, and Diamesinae /Chironomidae (present in Nat, but absent in Reg)	
Reduced draw down (2.5m to 1.5m)	U.S.A	Significant decrease	Densities (at 1-2m depth); loss of amphipods and chironomids	McEwen & Butler, 2010
		Significant change	Community structure shift: from smaller to larger primary consumers, increase in mayfly larvae; *Hexagenia limbate,* alderfly larvae; *Sialis*	
		No change	Of density or community at depths 3-5m	
Water level reduction (0.6m)	Italy	Negative association	Diversity	Mastrantuono et al., 2008
		Decrease in individuals	Plant dependant species (scrapers & grazers): nematodes; Dorylaimina and *Ethmolaimus pratensis.* Water mites; *Unionicola, Limnesia, Arrenurus*, Halacaridae. Gastropods; *Bithynia tentaculate.* Naidid oligochaetes; *Nais variabilis*	
		Increase in individuals	Mobile species, (climbers & sprawlers) and omnivore/detritivore (shredders and collectors): Mayfly larvae; *Caenis*. Macrocrustacean; *Echinogammarus.* Midge larvae; *Psectrocladius* and *Cricotopus*	
Natural WLF (2m fluctuations annually)	Central Europe (Germany, Austria, and Switzerland)	Dissimilarities	Seasonal abundance and biomass, immobile large zebra mussels suffer in eulittoral due to predation and WLF. Recruitment comes from deeper zones. Depth zone abundance and biomass	Baumgärtner et al., 2008)
		Dissimilarities	Community composition, gradual transition with water depth	
		Dissimilarities	Community composition of drift line - season and prior WLF	
		Positive association	Richness decreased with increased or decrease long term mean	
Natural WLF	Canada–United States	Significant relationship (unimodal)	Highest richness within mean fluctuation levels (annual max 1.27, mean 0.26 ± 0.15m)	White et al., 2008
Anticipated water level reduction	East Germany	Significant difference	Community composition – eulittoral roots (vulnerable to WLF)	Brauns et al., 2008
		No difference	composition – between eulittoral roots and infralittoral reeds habitats	

Table 3. Effects of known abiotic factors on lake macrophytes.

Environmental/biotic factor	Relationship/effect	Macrophyte measure	author
geographical region	positive correlation	Diversity	McGoff et al., 2013
regional environmental heterogeneity (elevation)	driven by	Species turnover & nestedness	Alahuta et al., 2017
elevation / altitude (> or < 300m)	clear dissimilarities	species composition	Baláži et al., 2014
lake area	explained variation (most)	species richness	Rørslett, 1991
-in transparent lakes	positive association	species richness	Vestergaard & Sand-Jensen, 2000
- entire lakes or subset of eutrophic lakes	no association	species richness	Vestergaard & Sand-Jensen, 2000
shoreline complexity	positive association	species richness	Elo et al., 2018
shoreline development	significant dissimilarity	community composition (all species, shore plants & helophytes but not rhizophytes or free-floating species)	
human impact (WFD assessment criteria)	no dissimilarity	beta diversity (lakes grouped by impact)	
moderate status (relative to lakes of good or high status)	highest positive association	species richness	
exposure gradient (wave/wind)	related to	diversity	Rørslett, 1991
exposed shores (relative to sheltered)	reduced / lower scores	diversity and dissimilarities	Hellsten, 2000; Keddy, 1982, 1983; Nilsson, 1981
wave washed stony shores	negative association	abundance	Ratcliffe, 1977 (cited in Smith et al., 1987)
sheltered shores /silty shores	positive association	abundance	Bailey-Watts & Duncan, 1981
sheltered shores	positive association	species richness	Rørslett, 1991
		spices diversity	Nilsson, 1981; Keddy, 1983
predator / prey interaction effect with turbidity	positive effect	increased abundance	Nurminen et al., 2010
bottom substrate (exposure and depth)	related to	species diversity	Hellsten, 2001
bottom quality	no association	species diversity	Rørslett, 1985; Hellsten, 2000
erosion	no association	species diversity; stability of vegetation	Hellsten, 2000; Rørslett, 1987;Nilsson & Keddy, 1988
continuous slope (shore/littoral)	no correlation	species diversity	Hellsten, 2001
hypertrophication	negative association	species richness & diversity	Rørslett, 1991
mesotrophic lakes (relative to eutrophic or oligotrophic)	positive association	species richness	Rørslett, 1991
trophic index	no relationship	community structure	Penning et al., cited in (Lyche Solheim et al., 2008)
low acidity	negative association	species richness & diversity	Rørslett, 1991
alkalinity (medium-high) & low phosphorus	positive association (highest)	submerged species richness	O'Hare et al., 2012
alkalinity (medium-high) & high phosphorus	positive association	emergent species richness	O'Hare et al., 2012
alkalinity (correlated with pH & conductivity)	important driver	species richness	Elo et al., 2018
connectivity, alkalinity, and elevation (upland lakes)	important driver	composition (turnover and nestedness)	Sun et al., 2019

1.13 Key knowledge gaps

Past research on hydromorphological impacts on freshwaters, have predominantly focused on effects on river flow regime, sediment movement and migratory fish, with impacts on standing water systems being relatively neglected until the last few decades (Lyche Solheim et al., 2008; Solimini et al., 2006; White et al., 2008). Hydromorphological and hydrological pressures have been identified as requiring investigation and empirical information to increase understanding, assessment abilities and mitigation measures (Boon et al., 2019; EEA, 2018; Solimini et al., 2006; Heiskanen & Solimini, 2005).

However WLF effects on lentic systems have been largely overlooked (Wantzen et al., 2008). A review of the evidence demonstrates impacts to lake biota are influenced by often cofounding factors that operate across a hierarchy of scales from regional to lake and sub lake (shore) level changes. Lake-wide characteristics including; lake area and elevation, sediment and water quality, as well as the shore specific features of exposure and shoreline slope, in addition to biotic competition or predation (Heiskanen & Solimini, 2005; Hellsten, 2000).

Influencing factors are not isolated; lake ecosystems are simultaneously altered by nutrient enrichment and other pressures (e.g. biological invasions), due to natural or introduced anthropogenic influences, which may reinforce or mitigate the effects of hydromorphological alterations. Our review highlighted a lack of research quantifying WLFs impacts on biota in comparison to other known pressures. Also, impacts of combined pressures (e.g. WLF pressures and eutrophication or acidification), are virtually unknown, despite the reality that a combination of separate pressures occur in many lakes (Birk et al., 2020; Lyche Solheim et al., 2008). These pressures when combined in a system may interact to create affects to littoral biota which are antagonistic or synergistic in nature. Alternatively, it may be that one pressure dominates while another has negligible influence.

Recent work by Birk et al. (2020), found the premise of multiple stressors on freshwaters to be potentially overestimated with 39% of evaluated studies having a single significant stressor, with nutrient enrichment to be the dominant pressure in freshwater lakes, while rivers are influenced by multiple stressor interactions. Though in terms of hydrological stressors this should be taken with caution as only 11 studies were assessed. Prior to multiple stressors to freshwater lakes and reservoirs being investigated, there is a clear benefit in establishing the role of WLF in lakes relative to other pressures.

1.14 Design of thesis and aims

Based on a review of the literature, in order to research relationships between WLFs and littoral zone biota, specifically aquatic macrophytes and benthic macroinvertebrates, this thesis determined to include lakes across Scotland, being a region with numerous lakes and a wide range of environmental gradients, whilst limiting documented regional and latitudinal effects. This approach would ensure variability of characteristics at lake level (i.e. elevation, alkalinity, surface area) and sub-lake (shore) level factors (i.e. shore slope and wind/ wave exposure), (Fig. 11). We used a combination of archive and field data to establish an adequate sample size in order to detect such associations. We chose to use sampling and methodologies as used by environment agencies, specifically following Scottish Environment Protection Agency (SEPA) protocol, (O'Hare et al., 2007; WFD-UKTAG, 2014), and the Common Standards Monitoring Guidance (CSM) for Standing Waters (JNCC, 2005), as per Gunn et al., (2004) to ensure comparability with wide scale governmental and European research. The resulting 135 well monitored lakes covered a range of WLF regimes from 0.2m to 9.3m, and varied in exposure and shoreline characteristics, some examples of which can be seen in Fig.9, Fig, 10 and Fig. 12.

In view of the essential role that macrophytes and invertebrates play in lake ecosystem functioning it is vital to better understand how they respond to lake water level variation, in parallel to other environmental drivers. To this end, having already controlled for regional variation by restricting lakes to Scotland, our overarching aim was to determine the relative importance of WLF against a suite of factors at lake and sub-lake levels, guided by the importance past research has shown to have direct and indirect effects on lake biota. We hypothesised that;

i) Littoral macrophyte species responses (richness, community composition, indicator taxa), would be associated with WLF range water level ranges in lakes and other environmental factors such as lake area and altitude would be upheld. We further expected that responses would vary with lake types, with macrophytes in higher productivity waters, potentially benefiting from accelerated growth thereby offsetting moderate levels of WLF.

Approach; Conduct field research and combine with archived macrophyte data to form corresponding data for 135 well monitored Scottish lakes from 2007-2015, water nutrients, morphometry parameters and water level data. Ensure all methods are standardised following UK environmental body procedures for comparability. Use non-parametric techniques to reduce model complexity and generalised mixed models with random effects in analysis. Use non-parametric techniques to establish differences in species composition.

ii) Littoral invertebrates; sensitivity of different community elements, (richness, community composition and indicator taxa), would be correlated to water level ranges in lakes in addition to other established abiotic influences such as elevation, lake area and nutrient concentrations. We also hypothesised that invertebrate taxa absent from the higher ranges of WLF would be those with restricted mobility and long-life cycles.

Approach; acquire and harmonise archived data from 2007-2015, to form corresponding data for in 57 lakes Scottish lakes with 63 invertebrate surveys. Ensure all data are standardised following UK environmental body procedures for comparability. Use non-parametric techniques to reduce model complexity and generalised mixed models with random effects in analysis. Use non-parametric techniques composition analysis.

iii) We expected the stress tolerant isoetid, *Littorella uniflora,* would be directly associated with lake WLF given its ability for rapid morphological change to water stress. Further we hypothesised that environmental factors influenced by WLF in lakes such as wind and wave exposure would influence the biomass and morphology of *L. uniflora*, reducing both to diminutive levels.

Approach; design and conduct field research to capture differences in *L. uniflora* morphology and standing biomass in lakes with varied hydrological regimes based on WLF. Survey *L. uniflora* from two sites per lake contrasting exposure to wind and wave action. Use lake Habitat Survey techniques and standardised methods for sub-lake features including particle distribution and carbon content, in addition to shore slope, height and distance from water line. Use non-parametric techniques to reduce model complexity generalised mixed models with random effects in analysis.

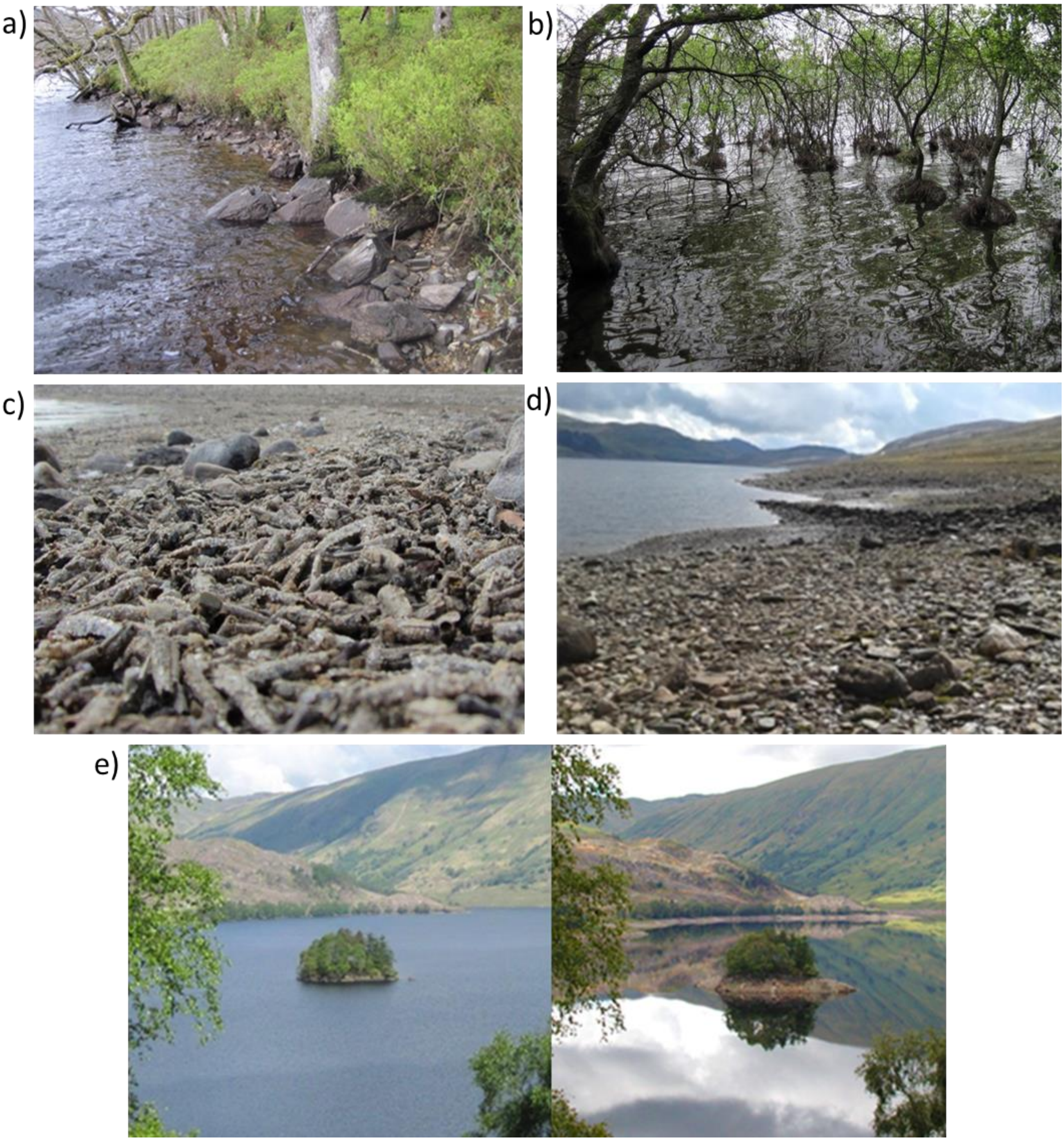

Fig.12 Examples of littoral and shore line variability with WLF and exposure to wind and wave energy, for a selection of Scottish lakes used for this research including, a) Loch Drunkie, regulated, semi sheltered shore, (spring) WLF 2.2m, b) Loch of Lintrathen, regulated sheltered shore, (spring) WLF 3m, c) Loch of Lintrathen, exposed shore, (summer) caddis fly larval cases, WLF 3m, d) Loch Lyon, regulated, exposed, (summer), WLF 9.3m, e) Glen Finglas reservoir, spring 2014 (left) and summer 2014 (right), WLF 7.8m

Chapter 2

Effects of water level fluctuations in freshwater lakes: Aquatic macrophyte responses relative to established pressures

2.0 Effects of water level fluctuations in freshwater lakes: Aquatic macrophyte responses relative to established pressures

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Planning submission to Freshwater Biology

Author comments: AB and NW jointly developed the project concept. Field data collection was carried out by AB and NW. The manuscript was prepared by AB with comments and statistical guidance from NW and AL.

Abstract: Water levels vary naturally in all standing waters and strongly influence littoral zones through the twin pressures of inundation and desiccation. Water level range is also commonly altered to meet societal needs such as hydropower generation, navigation, aesthetics, and recreation, drinking water provision or flood storage. Coupled with the increasing incidence of floods and drought associated with climate change water level variation represents a growing influence on lake ecology, that will potentially interact with other pressures such as eutrophication, yet its effects remain understudied**.** We assessed the importance of water level range (as a summary measure of water level regime) relative to other environmental factors in driving the composition and abundance of aquatic macrophyte species in 135 freshwater lakes in Scotland, ranging in status from oligotrophic to eutrophic. Stratifying lakes by their Morpho-Edaphic Index (MEI, the ratio of alkalinity to mean depth) and water level range was necessary to resolve relationships between environmental factors and ecological responses. Water level range proved the dominant determinant of vegetation composition in low productivity lakes, while regulation in any form was of secondary importance to chlorophyll and alkalinity-depth in high productivity lakes but remained a significant influence. Our findings emphasise the important influence of water level range on lake vegetation relative to other pressures and how baseline productivity regulates the importance of water level fluctuation. In addition, they highlight the need to better understand the mechanisms driving these relationships, and to explore specific aspects of water level regimes.

Keywords: Macrophyte, richness, composition, indicator species, water level range, lake, productivity.

2.1 Introduction

Water level fluctuation (WLF) has been an overlooked influence on lake ecology but is of increasing relevance. Anyone who has stood beside a regulated lake, where the water level has been lowered by 5-

10 m, cannot have doubted that water level variation must profoundly alter lake ecology. Yet, our understanding of that influence relative to other pressures is remarkably poor.

Hydromorphological modifications to lakes, are considered a major pressure on lakes (Solheim, 2008), second only to eutrophication. The 2012 European Environment Agency (EEA, 2012) assessment found water level regulation to be one of the most common pressures overall and *the* most important hydromorphological pressure affecting some 27% of European lakes. Pressures on lake biodiversity via water level regulation are increasing, driven by population increases coupled with climate change (Reid et al., 2019; UN, 2019a). Pressures include climate driven changes, in precipitation patterns and amounts, wind speed and lake temperature (Fekete et al., 2010), collective increased demand on water resources for irrigation and public consumption, and the drive for greener energy sources, such as hydropower, with thousands of dams under construction or planned globally (Zarfl et al., 2015; Dorber, May and Verones, 2018).

Water levels fluctuate naturally in all lakes, both seasonally and on an event basis, due to the variable balance in inputs (inflows and precipitation) and outputs (outflow and evaporation). These fluctuations enhance productivity (Kolding & van Zwieten, 2012) and are vital for ecosystem structure and functioning. Water level changes in deep lakes contribute to internal nutrient mixing (O'Reilly et al., 2003; Strayer & Findlay, 2010a), whilst shallow lakes benefit from the seasonal pulses of nutrients via water ingress from rivers and riparian zones (Wantzen et al., 2008), and many littoral plants require both inundation and/or desiccation to stimulate propagation (Dinakar & Bartels, 2013). However, imposed WLFs alter the natural water level regime in terms of range, frequency, duration, and seasonality. Relatively small alterations to a lake water levels can result in significant changes to the littoral habitat depending on the morphology of a freshwater system (Gownaris et al., 2018). Abiotic conditions such as organic matter content, temperature, nutrient levels and sediment characteristics are modified by amplified WLFs which indirectly drive changes in aquatic macrophyte assemblages (Bornette & Puijalon, 2011).

Water level range alterations primarily impact lake littoral zones (Solomini et al., 2006), where even small changes can negatively affect the extent, structure and composition of aquatic vegetation and thus lake-wide ecology (Smith, Maitland and Pennock, 1987; Brauns et al., 2011; Sutela, Aroviita and Keto, 2013). Given that the littoral zone holds most of a lake's biodiversity, and regulates exchanges between aquatic and terrestrial ecosystems, this area is critical as a habitat and food resource for aquatic and riparian organisms (Evtimova & Donohue, 2014). Littoral macrophyte communities (composed of bryophytes, large algae and vascular plants), are good indicators of hydromorphological changes, particularly water level change (Rørslett, Mjelde and Johansen, 1989; Hellsten, 2000; Gownaris et al., 2018), due to their stability and responsivity.

Desiccation caused by exposure, or inundation caused by water level rise, can have profound influences on plants. It is not surprising therefore that the composition of littoral vegetation is sensitive to WLF, varying according to the morphological and physiological adaptations of the species present. For instance, *Littorella uniflora,* rapidly adapts its morphology with emersion or exposure following water level changes (Robe & Griffiths, 2000), altering from vegetative reproduction to flowering and aquatic leaves to terrestrial form (W. E. Robe & Griffiths, 1998a). In contrast, desiccation-sensitive species such as *Nuphar lutea* require anoxic conditions to stimulate germination, whilst the seeds and submerged juvenile plants are susceptible to desiccation (Smits, Van Ruremonde and Van Der Velde, 1989; Van Geest et al., 2005).

In river ecology the effect of flow on vegetation has been widely studied (e.g. Chambers *et* al., 1991; Franklin, Dunbar and Whitehead, 2008) but, despite a recent trend for research of macrophyte responses to WLF pressures in lakes, key knowledge gaps remain (Carmignani & Roy, 2017b). In particular, the questions of how important WLF is relative to other factors, how it interacts with other known drivers of vegetation richness and composition, and the context-dependency of its importance, have not been addressed. Nordic studies have documented negative impacts on littoral macrophytes of winter drawdown in lakes, primarily for hydroelectricity (Rørslett, Mjelde and Johansen, 1989; Hellsten, 2002; Mjelde, Hellsten and Ecke, 2013; Sutela, Aroviita and Keto, 2013). However, in other parts of central and North West Europe lakes are characterised by different water level regimes or lack the additional influence of ice scour following break up. Consequently, the conclusions of Nordic studies may not be generally applicable, as Scottish lakes undergo less freezing in extent and duration.

Aquatic macrophytes play a crucial role in the structuring of aquatic environments functioning as ecosystem engineers (Asaeda, Rajapakse, & Kanoh, 2010; Baastrup-Spohr, Møller, & Sand-Jensen, 2016) affecting whole lake ecological resilience, influencing communities, providing physical structure, trapping sediment, and increasing habitat heterogeneity (Gurnell et al., 2006; O'Hare et al., 2017). Aquatic macrophytes also have a key role in preventing soil and organic matter desiccation, regulating trophic cascades and water quality (Liffen et al., 2011; Rocha et al., 2019; Sachse et al., 2014), which in turn influences fish, invertebrates and water birds.

Given the fundamental role that macrophytes play in lake ecosystem functioning it is critical to better understand how they respond to lake water level variation in comparison to other environmental variables, and to determine how responses may vary between lake types. To our knowledge no other study has established the association of lake WLF with littoral macrophytes relative to other pressures such as nutrient enrichment. In addition, the use of archived and field data collected using consistent survey techniques, adds power and novelty to this work. The aim of the current study was therefore two-fold; (i) to compare different types of vegetation responses (richness, community composition, rarity) to water level ranges in lakes relative to other environmental factors (e.g. elevation, lake area, nutrient concentrations), and (ii) to determine if these responses are context-dependent (i.e. do they vary between less productive and more productive lakes) or can they be generalised.

2.2 Materials and methods

In Scotland there are over 25,500 lakes and reservoirs (ranging from <0.01km^2 to >20km^2). Together these cover a combined area of ~2300km^2, including more than 670 registered reservoirs classified as having the capacity to hold 25,000m^3 or more of water above the natural level of the surrounding land (Scottish Natural Heritage, 2014). We selected 135 well monitored Scottish lakes, including 43 reservoirs and 92 unregulated lakes, to study the impacts of WLFs on macrophytes. These lakes were chosen to provide wide geographical spread (Fig.1) and coverage of the range of conditions known to influence the ecology of lakes across north west Europe, including water level ranges (natural and imposed), nutrient concentrations, lake size and elevation, but excluding areas with high levels of freezing and ice scour,. The only notable exception is ice scour which is not a regular feature of temperate lakes compared to boreal lakes (Mjelde at al., 2013).

Aquatic macrophyte data

Aquatic macrophyte data from 43 reservoirs and 92 unregulated lakes across Scotland, were used to assess vegetation responses to water level ranges relative to other environmental factors. Vegetation data were collected during June to September coinciding with the peak abundance of aquatic macrophytes. The 135 lake dataset comprised 112 lakes surveyed between 2007 – 2015 by the Scottish Environment Agency (SEPA), 9 lakes surveyed in 2013 as part of the Scottish Beaver Trial (Willby et al., 2014), as well as 14 additional lakes surveyed by the first author in 2013 and 2014. All macrophyte surveys were conducted using a belt transect method, following the Scottish Environment Protection Agency

(SEPA) protocol (WFD-UKTAG, 2014), based on the JNCC Common Standards Monitoring Guidance (CSM) for Standing Waters (JNCC, 2005), as per Gunn et al. (2004).

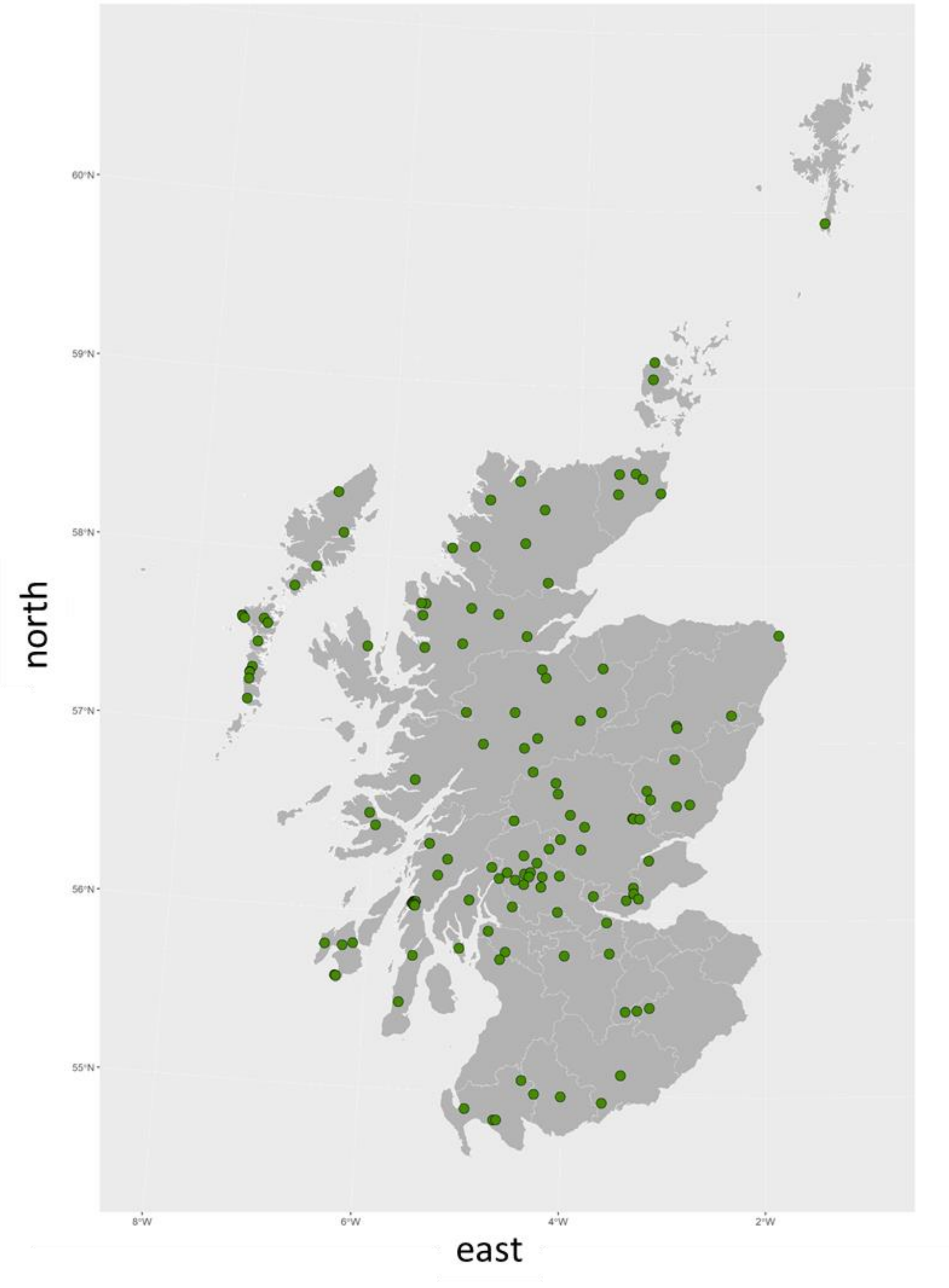

Fig. 1. Dispersal of lakes across Scotland used for macrophyte and environmental data

The JNCC / CSM method is based on discrete 100m sectors distributed around a lake, each sector containing five short transects running parallel to each other and perpendicular to the shore at 20m intervals. On each transect four quadrats, each of 0.5 x 0.5m are surveyed at water depths of 0.25, 0.5, 0.75m and >0.75m from the littoral to sublittoral zone, using a bathyscope or mask and grapnel rake, giving a total of 20 plots per sector. Shoreline perimeter surveys of the strand line are also conducted covering each 100m sector. In each lake four sectors are typically surveyed, with the number being adjusted to reflect the size of the lake.

Only full aquatic macrophytes (i.e. normally submerged or floating-leaved species) were included in further analysis. Macrophyte data for all lakes was transformed into water body cover percentage cover using the spreadsheet calculator developed for the Water Framework Directive classification tool LEAFPACS (WFD-UKTAG, 2014).

Predictors of macrophyte species

Water chemistry data were obtained for each lake, mostly for the period 2000 -2004, based on routine sampling undertaken by SEPA. Data were stratified by growing season (May–September) and averages calculated for all key determinants; Total Phosphorus (TP as mgL^{-1}), Chlorophyll a (CHl as ugL^{-1}), Total Organic Nitrogen (TON as mgL^{-1}), Alkalinity (Alk as $mEqL^{-1}$). Lake morphometry parameters, including area, perimeter, mean depth, elevation, and catchment area, were derived for each lake via the UK Lake Portal (Hughes et al., 2004). The morpho-edaphic index (MEI) originally used as a tool for estimating fish biomass in lakes (Ryder, 1965: Ryder et al., 1974) was used as an indicator of baseline productivity. MEI now has widespread application in limnology and lake ecological assessment. For the purposes of this research MEI was calculated as:

$$MEI = \log\left(\frac{mean\ alkalinity\ (mEq\ L)}{mean\ depth(m)}\right)$$

High values of MEI are thus associated with base-rich shallow lakes, where the geology is “soft” (phosphate rich, sedimentary rock) and therefore phosphorus is readily available through weathering, and where water depths are shallow implying limited stratification and potential for light to reach large areas of the lake bed baseline productivity is expected to be naturally high under these conditions. Low values of MEI are associated with base-poor deep lakes where the supply of P from rock weathering is expected to be low, and depth promotes stratification and so places much of the lake bed beyond the compensation depth for net production. Baseline productivity is expected to be naturally low in such cases. Shoreline Development Index (SDI) was calculated as the ratio of shore line length to the circumference of a circle of area equal to that of the lake (Wetzel, 2001) and serves as a proxy for complexity of shoreline, i.e., lakes with SDI close to 1 are near circular (uniform, simple shorelines), whereas lakes with SDI larger than 1 have increasingly complex shorelines, reflecting the potential for littoral communities to develop in sheltered bays. The complete list of explanatory variables, their definitions and units of measurement are provided in Table 1. Regulation *per se* (regulated or not), was included the data, for analysis this binary variable was altered to a continuous variable to fit the model by designating unregulated lakes as “-1” and lakes with water level regulation designated a “1”.

Lake water level range

How relationships between aquatic vegetation and lake abiotic and biotic factors change with imposed WLFs, are not known. One of the difficulties limiting this understanding, is the availability of water level data for freshwater lakes, particularly for reference lakes.

Data on water level fluctuation range (WLF), (i.e. the difference between effective mean annual maximum and minimum water levels) for regulated lakes were sourced from reservoir operators (Scottish Water, Scottish & Southern Electric). Where daily or weekly level data of water levels (measured as water level below spill level), were available the mean range was calculated based on the 10th and 90th percentiles to reduce the influence of rare extreme values (sometimes associated with reservoir management). Where direct lake level data were not available, data were taken from river monitoring stations in proximity of the outflow using the average level data range (SEPA Water Level Data). Disparities in water level data were resolved by online searches, direct communication with lake managers, and inspection of online aerial and other imagery available (e.g. Google Earth). In addition, field surveys recorded the lowest levels of water for 12 lake and the height to the uppermost visible strand line using a theodolite with height differences calculated using Pythagoras. Full time series (daily or weekly) water level data was only available for a small subset of lakes, whereas range data is commonly available, therefore we have used range as an indicator of regime. See appendix I, for method of water level data attainment and estimation for all lakes.

Exploratory and statistical analyses

Prior to statistical analyses all continuous explanatory variables (excluding pH) were log transformed, mean centred and scaled by 1 SD, to improve comparability between variables and to reduce the effect of outliers. To reduce model complexity principal components analysis (PCA) was applied to separate sets of water chemistry, physical and land use variables to identify those variables that maximised variation amongst sites (appendix II). Correlations between predictor variables were then assessed in a correlation matrix (appendix III) and checked for variance inflation (VIF). Where variables were highly correlated (VIF > 20) they were removed.

Table 1. Characteristics of the predictor data across 135 Scottish lakes. ID is the abbreviation used in the results.

ID	Variable	Unit	Description
Water Level / WLF	Water level fluctuation e	m	Lake water level range determined by the 10th to 90th percentile of full range or estimated range
Loch size	Lake surface area	km^2	Lake surface area
Elevation	Lake elevation	m	Lake elevation (AOD)
Depth	Lake depth	m	Lake depth (mean)
Alkalinity	Alkalinity	mEqL^{-1}	Alkalinity (mean)
TON	Total Organic Nitrogen	mgL^{-1}	Total organic nitrogen (mean)
TP	Total phosphorus	mgL^{-1}	Total phosphorus (mean)
Chlorophyll	Chlorophyll *a*	ugL^{-1}	Chlorophyll *a* (mean)
MEI	Morpho-edaphic index	unitless	Index of lake mean depth and alkalinity
SDI	Shoreline development index	unitless	Measure of shoreline complexity
CLR	Catchment to lake area ratio	unitless	Ratio of lake catchment area / lake area
Regulation	Regulated or unregulated lake water levels	unitless	Binary measure of regulation of lake water
all lake	All lakes	unitless	All lake = All 135 lakes
HM	High MEI lakes		High MEI lakes = subdivided by average
LM	Low MEI lakes		Low MEI
HMS	High MEI lake with stable water levels	unitless	High / Low MEI lakes subdivided by median water level range as approximation of stability versus fluctuating water levels (over median = fluctuating, below = stable)
HMF	High MEI lake with fluctuating water levels		
LMS	Low MEI lake with stable water levels		
LMF	Low MEI lake with fluctuating water levels		

Pearson's correlations and principal components analysis (PCA)**,** of physical predictors (lake size, elevation, depth etc), and nutrient predictors (TP, TON, chlorophyll etc) and expert knowledge was used for exploratory data analysis (EDA) of the All lake dataset (n = 135). Following initial analyses lakes were subdivided based on their MEI. Lacking any step changes (obvious partitioning within the data) in the MEI data lakes, were sub divided according to the median MEI (Table 2), resulting in 'high' MEI lakes (HM) (n=69), and 'low' MEI lakes (LM) (n=66), (Table 2). Lakes were further subdivided into 'stable' and 'fluctuating' lakes based on the median WLF within each MEI group. HM lakes with stable WLF (HMS), HM lakes with fluctuating WLF (HMF), LM lakes with stable WLF (LMS) and LM with fluctuating WLF (LMF). These simple typologies were exploratory but were supported by subsequent compositional analyses.

Count data on macrophyte species richness were analysed using generalised mixed effects models (glmer), with a Poisson family link function. Within these mixed models survey year was treated as a random factor. Pearson residuals were extracted and plotted against fitted values. For each glmer, following standard forward permutation testing, the optimal model was taken as that with the lowest AIC value. Unconstrained ordination was conducted using non-metric multidimensional scaling (NMDS) on a Bray-Curtis dissimilarity index (BCI) generated from a log-transformed species cover × sample matrix. Using the function 'adonis' within the vegan library (Oksanen et al., 2017) a permutational multivariate analysis of variance was used to test for differences in species composition between lake type based on MEI and water level stability.

Species indicative of lake type were derived using the Indval R function (Roberts, 2016) which identifies 'indicator' species from their fidelity for, and occupancy of, a group. Due to the differentiation between lake types observed in the NMDS analysis, the groups for the IndVal analysis comprised the four lake types based on MEI and water level stability. In this case significant indicator species were those indicative of either the high/low MEI and stable/fluctuating water level. The significance of indicator values was tested using random permutation tests. The threshold for interpreting indicator species scores was set at a minimum of 0.3, informed by ecological interpretation, as a measure the association between a species and a group, as lower values than this would equate to a weaker association than those with a higher score (Dufrêne and Legendre, 1997) and founded on ecological logic. Species-environment relationships in the All lake dataset and the subset of Low MEI and High MEI lakes were assessed using Canonical Correspondence Analysis (CCA), with final models being determined by forward selection tests.

All statistical analyses and graphics were produced using R Studio version 3.5.1 (http://www.rstudio.com/), with the additional packages; Corrplot (Wei et al., 2017), Factoextra (Kassambara et al., 2017), FactoMineR (Husson et al., 2018), ggplot2 (Wickham et al., 2019), labdsv (Roberts, 2016), lme4 (Bates et al., 2015), MuMin (Bartoń, K. 2019), plyr (Wickham, H. 2016), Psych (Revelle, W. 2018), sciplot (Morales et al., 2011) and vegan (Oksanen et al., 2013).

2.3 Results

A total of 105 aquatic macrophyte taxa were recorded in the All lake dataset (n = 135), including 80 taxa in LM lakes and 100 taxa in the HM lakes. Four lakes which had no species recorded were included in the richness analysis, though removed from CCA, NMDS and IndVal analyses.

Table 2. Environmental variables for All lakes and Low and high MEI subsets displaying the mean and difference from standard error (± SE) with the minimum and maximum below in brackets (min – max). CLR = Catchment to Lake Ratio, SDI= Shoreline Development Index, MEI= Morpho-edaphic Index, TON= Total Organic Nitrogen, CHl = Chlorophyll a.

Lake type	Water level (m)	Elevation (m)	Lake area (km^2)	Lake depth (m)	CLR	SDI	MEI
All (n=135)	1.5 ± 0.1 (0.2 - 9.3)	101.6 ± 8.6 (2 - 356)	3.47 ± 0.62 (0.001 - 55.33)	11.04 ± 1.39 (0.40 - 132.00)	34.87 ± 5.95 (2.50 - 580.71)	1.12 ± 0.04 (0.17 - 3.05)	-1.38 ± 0.13 (-3.31 - 0.05)
Low MEI (n=69)	2.0 ± 0.2 (0.3 - 9.3)	128.6 ± 13.6 (4 - 256)	5.72 ± 1.12 (0.02 - 55.33)	17.77 ± 2.46 (2.00 - 132.00)	41.59 ± 11.00 (2.63 - 580.71)	1.29 ± 0.07 (0.17 - 3.05)	-2.07 ± 0.05 (-3.31 - -1.39)
High MEI (n=66)	1.0 ± 0.1 (0.2 - 3.5)	73.3 ± 9.2 (2 - 297)	1.12 ± 0.26 (0.00 - 13.71)	4.01 ± 0.26 (0.40 - 12.10)	27.83 ± 3.91 (2.50 - 123.99)	0.94 ± 0.03 (0.41 - 1.88)	-0.67 ± 0.06 (-1.39 - 0.51)

Lake type	Alkalinity (mg/L)	Phosphorus (mg/L)	TON (mg/L)	CHl (µg/L)
All (n=135)	27.42 ± 3.95 (1.10 - 169.24)	0.03 ± 0.00 (0.00 - 0.51)	0.26 ± 0.04 (0.00 - 3.40)	8.83 ± 1.75 (0.08 - 197.25)
Low MEI (n=69)	6.52 ± 0.57 (1.10 - 23.30)	0.01 ± 0.00 (0.00 - 0.05)	0.11 ± 0.01 (0.04 - 0.29)	2.79 ± 0.26 (0.08 - 11.40)
High MEI (n=66)	49.27 ± 4.68 (1.40 - 169.84)	0.05 ± 0.01 (0.00 - 0.51)	0.43 ± 3.40 (0.00 - 3.40)	15.14 ± 3.41 (1.09 - 3.40)

Species richness

Several lake physicochemical variables were significantly associated with species richness in the All lake dataset (Appendix IV). Water Level range was the most dominant correlation, followed by elevation, both with a negative association (Table 3). Average species richness at WLF of 1.6 – 3.5m and 3.5 – 9m were lower than WLF of 0.2 to 1.5m, by 26% and 91% respectively.

TP concentration, MEI, lake area, Regulation and CLR, had significant roles explaining the variance of species richness in the All lake dataset, in descending order of effect size (Table 3). As MEI was shown to have a strong positive association in the global model (Fig. 2) the study lakes were divided into Low MEI (LM) and High MEI (HM) lake types to determine if the other variables had a generalised effect or if their importance differed with productivity (Table1).

Table 3. Species richness multivariate mixed model predictor effects for All lakes, Low MEI and High MEI lakes (all data transformed and scaled) glmers was used to test association significance p≤ 0.001***, p≤0.01**, p≤0.05* ('--' indicates that a variable was not included post standard forward permutation testing). CLR = Catchment to Lake Ratio, MEI= Morpho-edaphic Index, TON= Total Organic Nitrogen.

	All lakes	Low MEI lakes	High MEI Lakes
Water level	-1.81 ***	-2.54***	-0.05
Elevation	-1.51 **	-1.71**	-1.85**
Lake size	1.33 *	-0.29	2.36**
CLR	0.91 *	0.77	1.28*
Chlorophyll a	0.39	0.28	--
Phosphorus	-1.76 *	-0.42	-1.82**
TON	-0.66	0.81	-0.82
MEI	1.51 *	--	-0.72
Regulation	-1.33*	-1.21*	-0.84

Water level range and elevation were the most important predictors, being negatively associated with species richness followed by regulation in LM lakes (Fig. 2). Species richness was negatively correlated with TP and elevation, and positively correlated with lake area and CLR in HM lakes (Table 3, Fig. 3, Appendix V).

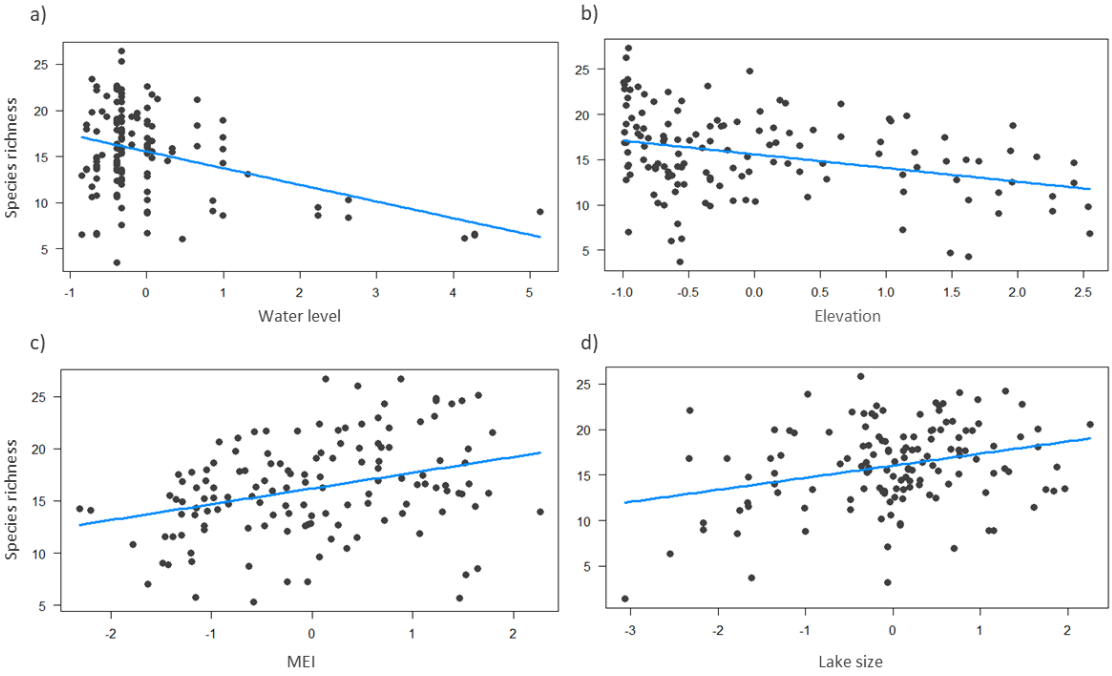

Fig. 2. Subset of modelled outputs of species richness for All lakes a) water level, b) elevation, c) MEI, d) lake size, (all predictor data transformed and scaled)

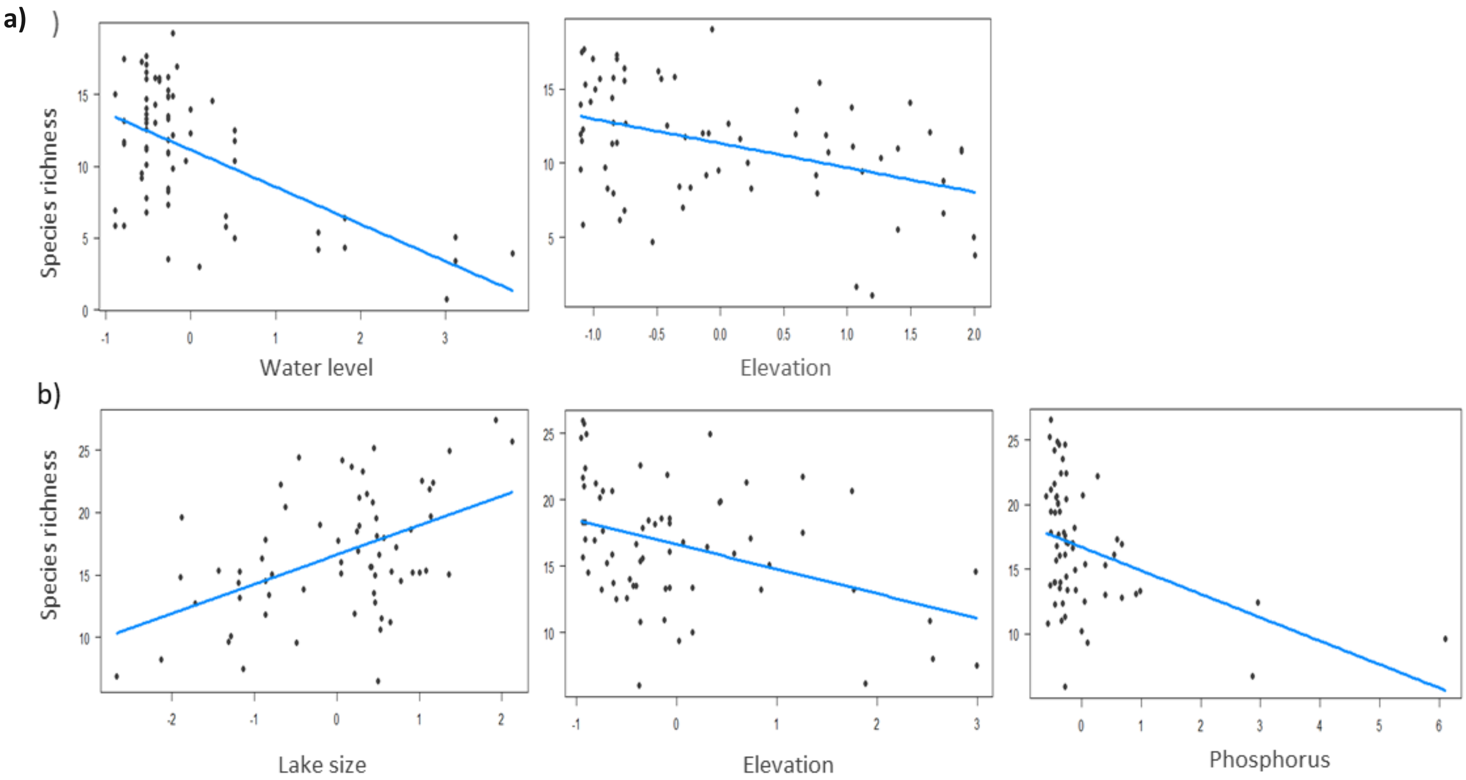

Fig. 3. Subset of modelled outputs of species richness for a) Low MEI lakes (Water Level (fluctuation), Elevation) and b) High MEI lakes Lake size (area), Elevation and total phosphorus, (all predictor data transformed and scaled)

To assess the possible influence of outlying values of phosphorus, HM lakes were reanalysed by excluding three sites with annual mean TP >0.25mg/L. A significant negative association (F=-2.160, 0.035) remained between TP and species richness (Fig. 4, appendix VI).

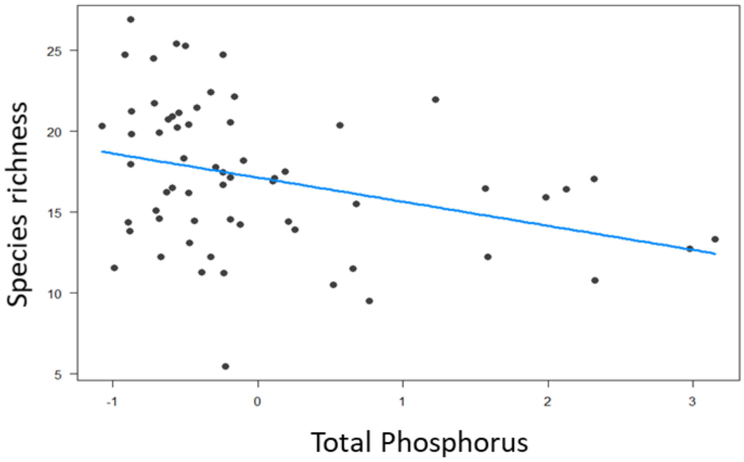

Fig. 4. Modelled output of species richness and total phosphorus, for High MEI lakes with TP <0.25 mgL^{-1} (all predictor data transformed and scaled)

Species composition

NMDS analysis confirmed that species composition differed significantly ($P < 0.001$) between the four sub-categories of lakes (of productivity and water level stability), (Fig.4). Clear species differences were apparent between lake types (LM or HM) and water level regime (stable and fluctuating), but these differences were more pronounced in relation to stable or fluctuating regime within the LM lakes (Fig.5).

Indicator species

Indicator species for All lakes (Table 4, Appendix VII), showed a clear distinction between lake types with indicator value threshold of 0.3 informed by ecological interpretation, resulting in *Isoetes lacustris*, *Lobelia dortmanna*, *Juncus bulbosus* and *Sparganium angustifolium* being indicative of LM stable lakes. LM fluctuating lakes were most typified by *Callitriche hamulata* though this did not meet the indicator value criteria (0.29, p=0.002). HM stable lakes had one species (*Elodea Canadensis)* indicative of this grouping whilst *Potamogeton perfoliatus*, *Potamogeton gramineus* and *Najas flexilis* were indicator species of HM fluctuating lakes.

Productivity lake types were analysed separately for indicator species (Low MEI with stable/fluctuating water levels and High MEI stable/fluctuating water levels), (Table 4), at an indicator value threshold of 0.3. Indicator species of LM stable lakes were; *Lobelia dortmanna, Isoetes lacustris, Myriophyllum alterniflorum* and *Sparganium angustifolium*. *Callitriche brutia var. hamulata* was an indicator of LM fluctuating lakes. High MEI fluctuating lakes indicator species were; *Littorella uniflora, Potamogeton perfoliatus, Juncus bulbosus* and *Potamogeton gramineus* and *Naja flexilis,* whilst no indicator species were produced for HM lakes with stable water level regimes.

Table 4. Indicator species and values for All lakes, cluster denotes; LMS = Low MEI lakes with stable water levels, LMF = Low MEI lakes with fluctuating water levels, HMS = High MEI lakes with stable water levels and HMF = High MEI lakes with fluctuating water levels. For separated analysis of Low MEI and High MEI lakes cluster denotes; S = stable water levels; cluster F = fluctuating water levels.

Lake group	Indicator species	cluster	indval	P value
All lakes	*Isoetes lacustris*	LMS	0.430	0.001
	Lobelia dortmanna	LMS	0.390	0.001
	Juncus bulbosus	LMS	0.368	0.002
	Sparganium angustifolium	LMS	0.306	0.001
	Callitriche brutia var. hamulata	LMF	0.293	0.002
	Elodea canadensis	HMS	0.323	0.002
	Potamogeton perfoliatus	HMF	0.456	0.001
	Potamogeton gramineus	HMF	0.369	0.001
	Najas flexilis	HMF	0.312	0.001
Low MEI lakes	*Lobelia dortmanna*	S	0.598	0.002
	Isoetes lacustris	S	0.576	0.023
	Myriophyllum alterniflorum	S	0.508	0.041
	Sparganium angustifolium	S	0.391	0.026
	Callitriche brutia var. hamulata	F	0.323	0.05
High MEI lakes	*Littorella uniflora*	F	0.632	0.001
	Potamogeton perfoliatus	F	0.541	0.027
	Juncus bulbosus	F	0.475	0.018
	Potamogeton gramineus	F	0.393	0.018
	Najas flexilis	F	0.341	0.010

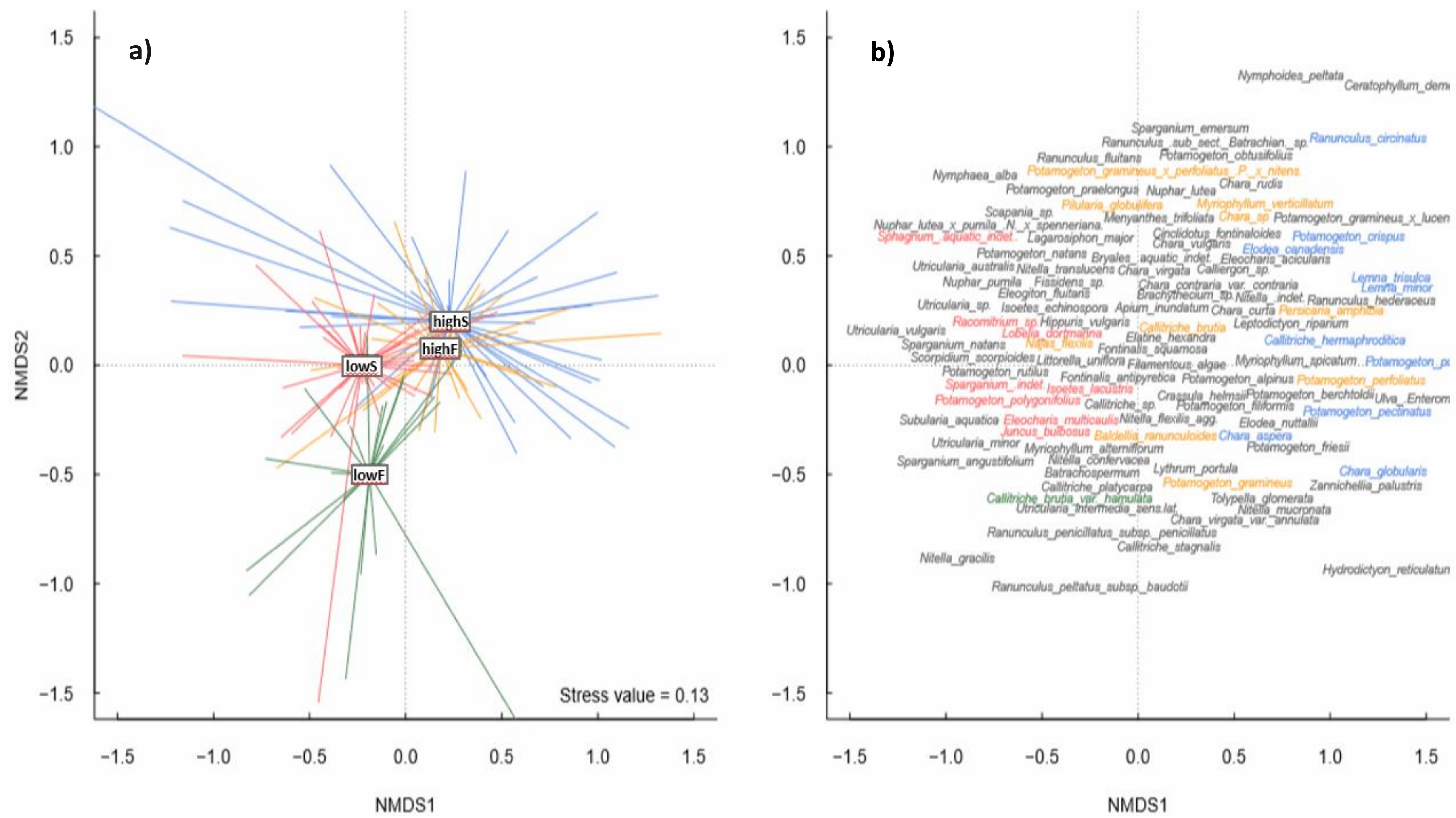

Fig. 5. Non-metric multidimensional scaling (NMDS) ordination for All lakes, with; a) showing a spider plot that represents each lake type (low MEI stable [lowS], low MEI fluctuating [lowF], high MEI stable [highS] and high MEI fluctuating [highF]), with sites connected by lines to the type centroid. b) NMDS species scores coloured for indicator species significantly associated ($P < 0.05$) with each lake type. All stress values were <0.15. Species most indicative of lake types coloured by corresponding colour in 5a)

Drivers of vegetation composition

When species assemblages were constrained by environmental variables using CCA the overall model was significant (P < 0.001) explaining 13% of variation, (table with all parameters appendix VIII). MEI, chlorophyll *a* concentration and water level range were most associated with the first axis which accounted for 35% of total explained variation. Lake area and elevation were most strongly associated with axis the second axis which accounted for 15% of total explained variance (Fig.6).

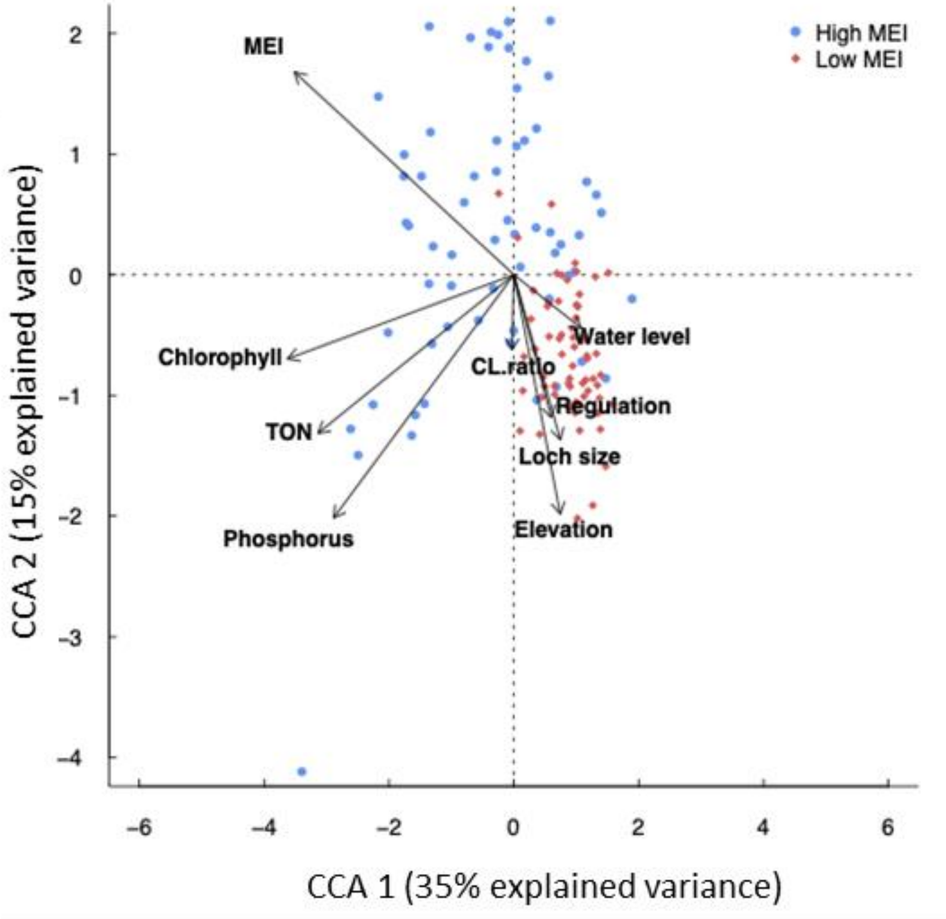

Fig. 6. Constrained ordination (CCA) of All lake dataset. Sites represented by dots.

Variation in species composition of LM lakes (Fig.7a) was most strongly explained by water level range (F=1.95, p=0.001), MEI (F=1.64, p=0.003), chlorophyll a (F= 2.02, p=0.012), followed by lake area (F=1.55, p=0.012), CLR (F=1.59, 0.014) and TON (F=1.47, p=0.025). Compositional variation in HM lakes was most strongly dependent on MEI (F=2.66, p=0.001), and chlorophyll a (F=2.047, p=0.001), followed by regulation (F=1.77, p=0.003), elevation (F=1.55, p=0.011) and lake area (F=1.64, p=0.017) (Fig.7b).

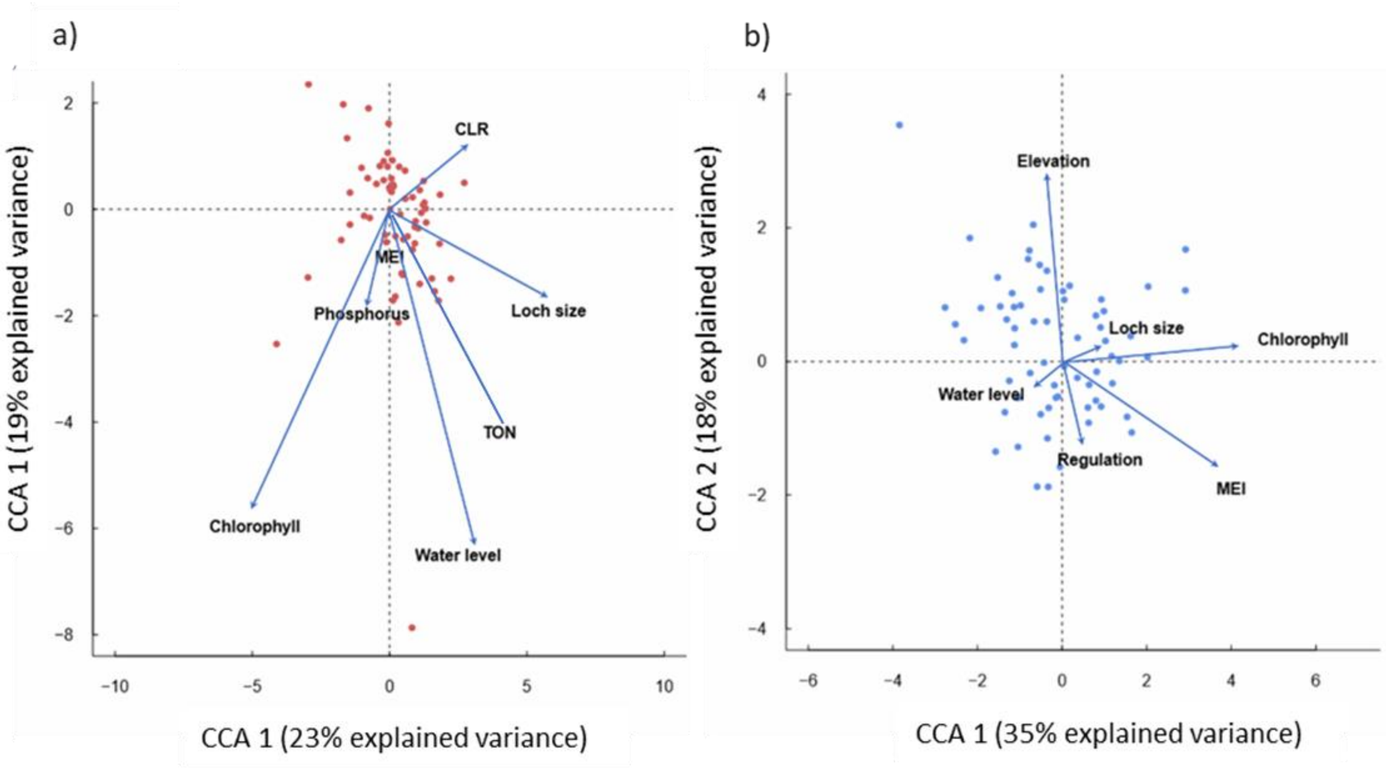

Fig. 7. Constrained ordination (CCA) of subsets of a) low MEI and b) high MEI lakes. Overall models significant (P < 0.001), explaining 17% and 20% of variation, respectively.

2.4 Discussion

Species richness

Water level fluctuation range (WLF) was the strongest driver of aquatic macrophyte richness in All lakes, and LM lakes, with increased water level ranges associated with decreased species richness.

Whilst moderate levels of WLF were expected to benefit some aquatic macrophytes, especially those with a ruderal life history, the overall effect was strongly negative. These findings are in keeping with previous research on Scottish and Nordic lakes (Smith, Maitland and Pennock, 1987; Mjelde, Hellsten and Ecke, 2013). Imposed stability of lake waters in general has been found to reduce species richness (Van Geest et al., 2005), while disturbances caused by decreased water levels can stimulate germination of charophytes (Bonis & Grillas, 2002), thereby increasing species richness (Hill, Keddy, & Wisheu, 1998), or may prevent competitive exclusion by desiccation-sensitive species such as *N. lutea* (Van Geest et al., 2005). However, the relationship between WLF and species richness is not linear as research shows that beyond species specific thresholds of WLF, both exposure-sensitive species, such as *L. dortmanna*, and exposure-tolerant species such as, *Juncus bulbosus,* will be lost entirely (Mjelde, Hellsten and Ecke, 2013). The importance of water level change as a predictor of plant species richness relative to other drivers of richness has however not been determined until now.

Species richness in HM lakes was not sensitive to WLF. Potentially due to the upper WLF limit of 3.5 m in these lakes being too constrained to impose significant desiccation or inundation stress on aquatic vegetation. HM lakes were also shallower and more fertile than LM lakes, potentially benefiting some aquatic species and buffering some negative effects of water level fluctuations, by removing the limiting growth factors of light attenuation and nutrients. Additionally, the overall species pool was 24% larger in the HM lakes, a similar result found by Vestergaard & Sand-Jensen (2000), increasing the likelihood of there being species present that are able to adapt to lower water levels (Mjelde, Hellsten and Ecke, 2013). Taken together the factors above may reduce the slope of any potential relationship between WLF and richness in HM lakes. However, it is clear that there is compensation within HM lakes, for the gains and losses of exposure tolerant/sensitive species across the WLF gradient, whereas in LM lakes there is an increasing deficit of species with increasing WLF, this is supported further by the indicator species analysis, when lakes where subdivided by MEI. Logically there will be a maximum threshold of WLF that macrophyte species can tolerate in HM lakes. We would expect this to be between 3.5 m and 5 m, based on the shallow depths of HM lakes, where increasing WLF would result an increased littoral area exposed to dewatering. It may be beneficial to examine such thresholds in mesocosm experiments, which would aid in understanding potential implications for droughts and increased WLF with future climate change impacts.

Whilst lake water levels fluctuate naturally, we found a negative relationship of any form of physical regulation of lake waters on species richness. This was apparent in LM lakes and likely due to the increased water level range of up to 9.3m in this subset of lakes. Increasing elevation was associated with decreased plant species richness in both low and HM lakes, though this relationship was stronger in the latter. The negative relationship observed between plant richness and elevation is recognised in the literature (Jones, Li, & Maberly, 2003a; Sun et al., 2019) and is typically explained with reference to temperature, nutrient limitation or duration of snow or ice cover (Suren & Ormerod, 1998), though elevation will also covary naturally with the fertility and base richness of the underlying geology (Vannote et al., 1980). For All lakes and LM lakes this well-established driver of species richness was secondarily important to water level range.

MEI as an indicator of baseline productivity, had a positive relationship with aquatic vegetation richness in the All lake dataset. Both aspects of MEI; alkalinity and depth, are well established predictors of lake macrophyte communities (Vestergaard & Sand-Jensen, 2000; Alahuhta et al., 2013; Alahuhta et al., 2014), due to their influence on stratification and the amount of light reaching the lake bed, and as these reflect inorganic carbon availability or the release of phosphorus by weathering of rocks.

Partitioning lakes by MEI type, revealed a decrease in species richness with rising phosphorus concentrations in HM lakes; counter to other studies, which have reported no effect on phosphorus on species richness (Jones et al., 2003), or a positive effect as seen in Finnish lakes (Wetzel, 2001), though the responses observed are perhaps partly dependent on the length of the available phosphorus gradient. Usually phosphorus would be a limiting factor in freshwater lakes, though the relationship with aquatic vegetation is not linear. Increased levels lead to algae (phytoplankton or epiphyte), growth and species richness decreases with increasing TP over <0.05mgL^{-1} (Jeppesen et al., 2000). The median concentration of total phosphorus (based on the growing season; May – September), in the HM lakes was 0.027 mgL^{-1} which is in line with average concentrations in all European lakes during the sampling years (2000-2004), (EEA, 2019) and in the lowest category in other research (Jeppesen et al., 2000). In comparison, in LM lakes, the median total phosphorus concentrations were 0.008 mgL^{-1} and no effect of phosphorus on species richness was observed, in line with Jones et al. (2003). A caveat to this work is that the Scottish lakes included offer only a limited gradient length (at the low end) for Phosphorus. However, the differences in species richness observed between lake types, highlights why subdivision of lakes by productivity is important when assessing impacts of WLF on aquatic vegetation.

Lake area was positively associated with species richness in All lakes and HM lakes, concurrent with other studies (Jones et al., 2003a; Rørslett, 1991). The positive relationship between area and species richness is well established, and founded in island biogeography (MacArthur & Wilson, 1967; Swinebroad, MacArthur, & Wilson, 2007). Lakes have often been used as inverse islands to test ecological theories (Dodson, 1992; Vestergaard and Sand-Jensen, 2000), since, despite their connectivity to other waterbodies and their catchment, basin area is easily estimated. The positive relationship between lake area and species richness is typically explained by the increasing area leading to higher habitat complexity, and therefore availability of suitable microhabitats for more species (Elo et al., 2018; Leira & Cantonati, 2008; River et al., 2004), although large water body size probably also increases the availability of avian or human dispersal vectors. There was no correlation with area in LM lakes, perhaps due to the combined influence of higher WLF, and median depths of 17.7m (in comparison to shallower HM lakes of 4m median depths). Typically, deeper lakes have steeper shore slopes, (first author observation), therefore a decrease in area of available to light penetration that can be colonised compared to shallow lakes, with shores that have low slope angles and therefore extend outwards in the photic zone. This effectively removes the presumption that increased total lake area will always equate to increased habitat availability and so complexity, therefore it may be that "colonisable area" (perimeter with a measure of littoral depth/slope) is a better predictor than lake area for macrophyte richness (Vestergaard and Sand-Jensen, 2000)

Regulation in the form of any type of flow modification was found to negatively impact All lakes, though this effect was not significant in HM lakes. That this relationship was illuminated in isolation of WLF suggests an untested relationship here, potentially due to the time lag following the physical modification of the system, or that the placing of a dam necessitates a full drawdown of the lake in order to clear silt from the dam sill. What is clear is that even this coarse measure adds a layer of clarity to our understanding of the impact of regulation relative to other drivers to macrophyte richness in lakes.

Species composition

Indicator species analysis revealed a clear distinction between lake types in All lake analysis, with species including; *I. lacustris* and *L. dortmanna* indicative of Low MEI stable water level lakes (LMS), *C. hamulata* the single indicator of Low MEI fluctuating water lakes (LMF) (though not meeting the threshold at 0.293, it was considered ecologically important to include in this instance). High MEI lakes with fluctuating water levels (HMF) were found to have species indicators such as *L. uniflora*, *P. perfoliatus and P, gramineus* with a single species; *E. canadensis*, indicative of High MEI lakes with stable water levels (HMS).

Differences in species composition between low and HM lakes were unsurprising and are covered in the literature. For example, Vestergaard and Sand-Jensen (2000), found high alkalinity lakes to be typified by fast growing, large elodeids, and floating-leaved species, while low alkalinity lakes are characterised by small amphibious plants, such as evergreen isoetids (Raun, Borum, & Sand-Jensen, 2010). However, differences in composition were more pronounced between stable and fluctuating regimes in the lower productivity lakes. Our work demonstrates species richness decreases in LM lakes with increasing WLF pressure, and further, that several common indicator species of LM lakes, such as *L. dortmanna*, are sensitive to increased water level fluctuations. However, in HM lakes the indicator species that persist and thrive with some WLF disturbance such as *L. uniflora* and *P. perfoliatus,* may counteract the loss of other WLF sensitive species. Our findings are compatible with previous work, that find lakes with fluctuating water levels may support hydrological stress-tolerant species, which typically require oxygenation for seed germination, from water draw down and low-competition habitats (Sand-Jensen & Frost-Christensen, 1999a), or are able to respond to water level variations via phenotypic plasticity (Andersson, 2001). Other common properties of HM lakes including, higher groundwater inputs, finer sediment, and a shallower littoral slope, may also be important in maintaining damp substrates during drawdown, which can mitigate the negative effects of water level range variation. By contrast, the differences in composition between water level regimes suggests that once vegetation is constrained by low fertility there is a much stronger filtering of sensitive taxa by water level range.

Identifying indicator species of the subdivided LM and HM lakes independently, by stable and fluctuating waters, enhanced our knowledge of water level range impacts to aquatic vegetation. Indicator species of LowS lakes were; *L. dortmanna, I. lacustris, M. alterniflorum* and *S. angustifolium*. The species indicative of LMS lakes are typical of nutrient-poor systems (Spence, 1967), require almost constant submergence, consistent with stable water level regimes, and each have a singular mode of reproduction. *L. dortmanna* and *I. lacustris* are small, slow growing, basal rosette hydrophytes, commonly confined to depths in the range 0.5-2.5m (Spence, 1967; Mjelde, Hellsten and Ecke, 2013) which makes them vulnerable to water level fluctuation or associated ice scour. Though low in competitive abilities this niche can be dominated by *L. dortmanna*, aided by seeds which can remain viable for 30 years (Arts & van der Heijden, 1990), its stalks raise up inflorescences from a basal rosette on the lake bed, to the surface for pollination and seed dispersal, and so require shallow stable water in order to reproduce. Our findings indicate these species appear to be filtered out at higher water level ranges, in agreement with previous work, emphasising the sensitivity of *L. dortmanna* and *I. lacustris* to lake drawdown (Mjelde, Hellsten and Ecke, 2013). Other indicator species of LMS lakes including; *M. alterniflorum* and *S. angustifolium,* commonly occupy deeper parts of the littoral zone. The former is highly competitive, investing in rapid biomass growth during the growing season and dispersing via fragmentation (Kautsky, 1988), the latter can dominate in large stands at depths of 0.3

to 1.5m, taking advantage of the light availability in clear oligotrophic lakes, and can grow terrestrially for periods over the summer on the exposed damp littoral margins (Preston and Croft, 1997), consistent with a naturally stable lake water level regime. These results are important in terms of habitat requirements for these species conservation, or for the restoration of lakes where these species are desired. Conversely *C. hamulata,* found to be the only species indicative of LMF lakes, can grow in a terrestrial form on damp ground, compatible with the more frequently exposed shores of these lakes (Preston and Croft, 1997). Where monitoring of a lake a reduction, or absence, of *L. dortmanna, I. lacustris, M. alterniflorum* and *S. angustifolium,* but *C. hamulata* is present this could indicate WLF stress, and highlight any changes required to the WLF regime for remedial action.

HMF lakes were characterised by species that tolerate or require this disturbance, specifically *L. uniflora, P. perfoliatus, J. bulbosus P. gramineus and Naja flexilis.* These species are reproductive generalists, with two or three strategies available, in contrast to the species indicative of LMS lakes which typically have a singular mode of reproduction (e.g. *L. dortmanna* which is limited to flowering). For example, *L. uniflora*, which often covers the exposed littoral substrate in reservoirs (authors observation), actively requires some water level fluctuation for seed drying and germination (Arts & van der Heijden, 1990) and can rapidly adjust its morphology in response to water stress, altering from reproduction via stolons to producing flowers within weeks (Robe & Griffiths, 2000). *P. perfoliatus* has a large flexible apical canopy which permits it to adjust to fluctuating water levels provided these are not too extreme, while *J. bulbosus* and *P. gramineus* are hydrological stress-tolerant species with terrestrial growth forms (Mjelde, Hellsten and Ecke, 2013). *P. gramineus* reproduces fragmentally, can re-grow from reserve buds and exhibits high phenotypic plasticity (Wiegleb, Brux, & Herr, 1991), these adaptations combined with lengths up to 3 metres, may aid dispersal by fragmentation in fluctuating water levels of HM lakes.

HMF lake vegetation in may be tolerant of the constrained range of water levels found in the research lakes (maximum of 3.5m), as these HMF lakes are naturally more fertile and commonly enriched further by anthropogenic activity. This may allow accelerated growth responses in plants thereby offsetting the potential impacts of moderate water level disturbance. HMF indicators *L. uniflora* and *P. gramineus* have declined significantly at the southern edge of their range in Britain due to eutrophication (Preston & Croft, 1997), and their persistence in such lakes may well depend on a certain degree of water level instability. *Najas flexilis* a rare species of European conservation importance, normally grows at depths of at least 1.5m,its presence in these fluctuating lakes is likely due to the seed dispersion of adult plants which either drop to the lake bed or are dispersed during high wind events in autumn when plants can be uprooted (Preston & Croft, 1997), given the maximum depth of 3.5m disturbance of the lake bottom would be feasible by such weather events.

Community composition drivers

MEI was found to drive macrophyte community composition in the All lake analysis. The relationship between MEI and lake macrophyte composition is well described and utilised in the WFD tool LEAFPACS to classify the ecological status of lakes and rivers in the UK (Willby, Pitt, & Phillips, 2009). Our results indicated that, macrophyte community composition was driven by Chlorophyll *a* for all of the lake types, as well as by TON in LM lakes.

The relationship between chlorophyll *a* and nitrogen, with aquatic macrophyte richness in lakes is well documented (Alahuhta et al., 2013; Lyche-Solheim et al., 2013; James et al., 2005). These factors follow a gradient of nutrient increase that leads eventually to an increase of phytoplankton and decreased light attenuation, tall, shade-tolerant plants replace sensitive ones and eventually submerged macrophytes are eliminated, typically being replaced by emergent plants (Kolada, 2010; Van Den Berg, Joosse, & Coops, 2003). Our work demonstrates how these associations may be impacted by WLF, particularly in lower productivity lakes as discussed below. The strongest driver of vegetation composition in LM lakes was WLF. It is widely known that aquatic plants in lakes are sensitive to water level alterations (Hellsten & Mjelde, 2009; Keto, Aroviita, & Hellsten, 2018; Rørslett et al., 1989; Sutela et al., 2013b) and other studies have revealed a strong gradient of compositional change with increasing water level drawdown (Lyche-Solheim et al., 2013). However, our results signpost that WLF is a key determinant of vegetation in lower productivity lakes, relative to all other known pressures within this work.

We found that regulation was the third strongest driver of aquatic vegetation composition in HM lakes. Because WLF in these lakes is confined to 3.5m, this relationship could be due to untested effects of other aspects of regime, such as the seasonality, frequency or duration of WLF, or it may simply reflect the presence for an outflow structure in any regulated lake, allowing water levels to be managed. Extreme events such as complete drainage of a lake, may not be considered part of the normal operating regime and therefore not included in WLF, but lake biota may take a decade or more to recover from this level of disturbance, though this is ecologically intuitive long term studies are lacking (Carmignani & Roy, 2017b)

2.5 Conclusion

Our analysis supports both lake elevation and area as established drivers of aquatic macrophyte richness and diversity in lakes, however water level range supersedes these as a driver of species richness and composition in LM lakes. Composition of aquatic plant species in lakes alters with increasing water level range, most likely depending on the regenerative strategies and phenotypic plasticity that characterise indicator species, and this in turn drives changes in species richness. The use of MEI to subdivide lakes helps resolve the relationships driving richness and composition of aquatic vegetation, as fertility may buffer impacts from water level fluctuations in HM lakes. Further division of lakes by water level stability and range lends clarity to the influence of previously accepted drivers of macrophyte composition. In addition, this sub-division informs potential WLF habitat requirements for species as revealed by indicator groups for LM and HM lakes with stable and fluctuating regimes.

Acknowledgments.

We thank Anna Doesser, Megan Layton, Catherine Gibson-Poole, Zarah Pattison and Duncan and Tarian Dowie for assistance with sampling. Water chemistry data and some of the lake macrophyte survey data used here were courtesy of the Scottish Environment Protection Agency (SEPA). Grateful thanks to Scottish Water, Scottish Southern Electric, Forestry Commission Scotland and The Woodland Trust for providing water level data and/or access to survey lakes. This research was financially supported by the University of Stirling and SEPA via an Impact Studentship

Chapter 3

Effects of water level fluctuations in freshwater lakes: responses of littoral macroinvertebrates relative to established pressures

3.0 Effects of water level fluctuations in freshwater lakes: responses of littoral macroinvertebrates relative to established pressures

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Planning submission to Freshwater Biology

Author comments: AB and NW jointly developed the project concept. Field data collection was carried out by AB and NW. The manuscript was prepared by AB with comments and statistical guidance from NW and AL. The initial results were presented at the British Ecological Society Annual meeting, London and HYTECH Interfaces within Aquatic Ecosystems Symposium, University of Aberdeen (2016).

Abstract: Water level regulation is the most important hydromorphological pressure on European lakes. Water levels vary naturally in all standing waters and greatly influence littoral zones through the pressures of desiccation and inundation. Lake water levels are frequently modified to meet societal needs such as, drinking water provision or flood storage, irrigation, and hydropower generation. Coupled with the increasing incidence of floods and drought associated with climate change, water level variation therefore represents a growing pressure on lake ecology, yet its effects remain under-studied.

We assessed the importance of water level range relative to other environmental factors in driving the composition and richness of littoral macroinvertebrates from 57 freshwater lakes in Scotland, covering wide gradients of productivity and size. Subdivision of lakes by water level regime, was used to clarify relationships between environmental factors and ecological responses. Water level range had a negative effect on macroinvertebrate family richness and outweighed the importance of all other significant predictors (lake elevation, dissolved oxygen, silicate, suspended solids concentrations and lake perimeter).

Water level range was also established as a key factor in explaining variation in community composition, in addition to lake perimeter and ammonia concentrations. Based on indicator species analysis stable lakes were most strongly characterised by a set of lentic taxa including Hydrachnidae, Asellidae, Haliplidae and several gastropod families, whilst Siphlonuridae were the only significant indicator of fluctuating lakes.

Our findings emphasise the major influence that water level range exerts on littoral invertebrates relative to other previously established pressures. As such water level regime should be given suitable attention in designing conservation and management goals for lakes. Mitigation of ecological impacts from water level regulation will also benefit from considering the wider environmental context in which this pressure has influence such as riparian insects, birds, and bats among other mammals.

Keywords: Invertebrate, richness, composition, indicator taxa, water level range, lake, productivity.

3.1 Introduction

Globally, freshwater species are declining more rapidly than those of marine or terrestrial ecosystems, with over double the loss of biodiversity since 1970 (WWF, 2018). Habitat degradation through flow modification poses a persistent and leading threat to freshwater biodiversity (Dudgeon et al., 2006; WWF, 2018). The recent Emergency Recovery Plan for Freshwaters (Tickner et al., 2020) highlights implementation of environmental flows and protecting or restoring of connectivity as two key strategies for reducing the rate of global freshwater biodiversity loss.

Of the pressures imposed on lakes by human activity, the most commonly occurring one, affecting some 40% of European surface freshwaters, is from hydromorphological alterations, (followed by diffuse source pollution affecting 38%, mainly from atmospheric deposition and agriculture (EEA, 2018). These pressures include physical modifications in the channel, bed, shore, or riparian zone (26%), of continuity interruption such as large dams for storage reservoirs or hydropower generation (24%), and a further 7% of other, unspecified hydrological alterations (EEA, 2018).

The most significant hydrological alteration pressures on water levels and flows in European fresh waters comes from some form of abstraction or reservoir storage, predominantly used for public water supplies, irrigation, and hydropower production (EEA, 2018). A collective increased demand on water resources for irrigation, public consumption, and the shift to invest in greener energy sources, such as hydropower (Dorber et al., 2018), is likely to magnify the pressure from water level variation. Pressures on lakes via water level fluctuations are also intensifying with climate change driven variations in precipitation patterns, wind speed and so lake temperature (Fekete et al., 2010) and changes in internal mixing (Anthony & Downing, 2003). Water level fluctuation caused by regulation activities and external drivers is therefore of increasing relevance to lake ecology. However, to date, our understanding of this influence, particularly on the biota of littoral habitats, relative to other pressures, such as eutrophication, is still largely lacking.

Natural water level fluctuations (WLF), occur in all lakes, enhancing their productivity (Kolding & van Zwieten, 2012), and are vital for ecosystem structure and functioning by way of internal nutrient mixing (O’Reilly et al., 2003; Strayer & Findlay, 2010a), and seasonal pulses of nutrients via water ingress from rivers and riparian zones (Wantzen et al., 2008). However, imposed WLFs through flow modifications, alter the natural water level regime in terms of range, rate of change, duration, and seasonality. Creation of flow modification structures, such as dams, and alterations to water level range primarily impact littoral zones (Solomini et al., 2006; Moss, 2008), with relatively small alterations having the potential to significantly impact littoral habitat (Gownaris *et al.*, 2018), including; changing sediment settling, nutrient retention, light attenuation and the depth profile, as well as residence times and heat budgets (Cyr, 1998; Palomaki, 1994; Finlay, Cyr & Shuter, 2001) [from McEwen, D. C., & Butler, M. G. (2010)].

Abiotic conditions such as organic matter content, temperature, nutrient levels, and sediment characteristics are modified by amplified water level range. These modifications can drive changes to aquatic vegetation (Bornette & Puijalon, 2011), for example, lowered water levels increase the impact of wave energy and can resuspend sediment, with implications for nutrient and pollutant release (Boon et al., 2019), turbidity and light attenuation. In addition, the desiccation or mechanical strain associated with water level fluctuation can impact heavily on aquatic plants, many of which naturally lack supportive tissues or cuticles (Bornette & Puijalon, 2011). Since macrophytes are an integral component of riparian and littoral habitat complexity and a recognised driver of macroinvertebrate diversity (Brauns et al., 2011; Jurca, 2012, Law et al., 2019) there are likely to be indirect effects on littoral macroinvertebrates.

Macroinvertebrates (>0.25 mm in length, Rosenberg & Resh, 1993), henceforth invertebrates, play an integral role in lake ecosystems, through substrate engineering, organic matter shredding, particulate filtering, predation, and grazing of macrophytes, epiphytes or biofilms (B. R. Malmqvist, 2002; Moore, 2006; Hölker et al., 2018). These activities form the basis of energy flow among producers, consumers or spatially within lake ecosystems (exchanges between water column and sediment or littoral and pelagic zones). The presence and actions of lake invertebrates support food resources for higher trophic levels, such as fish (Covich et al., 1999), through aerial emergence for birds (Horváth et al., 2012) and bats (Salvarina et al., 2018) and in contributing to wider flows of energy and matter at catchment scales. Altering invertebrate assemblages via water level regulation is therefore likely to have cascading effects on key lake ecosystem functions, including nutrient and carbon cycling, at different spatial scales.

Littoral invertebrates are directly affected by exposure and desiccation caused by reduced water levels. Further, given that habitat stability and structure, substrate particle size and thus availability of shelter changes for invertebrates with water depth (Brauns et al., 2008), organisms in the deeper littoral zone adapted to lower hydraulic stress, are exposed to this pressure when water levels are lowered (Baumgärtner et al., 2008). Slow moving animals or those with a burrowing life style, such as chironomids, that require fine substrates for feeding on fine detritus or biofilm, and predator avoidance (Malmqvist, 2002), may be especially susceptible to the instability of sediment induced by changes to wave action or water levels as a result of regulation, or indirectly through reduced organic matter or loss of fine sediments due to reduced primary production. In addition, suspension feeders and scrapers which live exposed on the sediment surface or in the water column, risk predation and dislodgment, or may be affected by changes to water depth and the extent of wave action. Physical barriers (natural or otherwise), can also impede the dispersal or migration of animals, further altering lake community composition, with impacts likely to be species-specific (e.g. barriers may prevent movement of some fish but not invertebrates (Pringle, 1977; Hamano and Hayashi, 1992)). Some lake biota are themselves ecosystem engineers, such as beavers, *Castor canadensis* who build natural dams, salmonids and other fish that construct nests, or chironomids which burrow in sediments (Moore, 2006). Where their loss is enforced by water level regulation this is likely to accentuate feedback effects.

Littoral invertebrate composition is reported to differ significantly between reservoirs and unregulated lakes, with taxon richness being negatively correlated with lake water level regulation amplitude (Aroviita & Hämäläinen, 2008). Since many invertebrates have comparatively long-life cycles (of a year or more) and are relatively immobile other than at small spatial scales, their sensitivity WLFs is likely to be high. Smith et al. (1987), found the invertebrate and vegetation of lakes with minor or natural fluctuations was reasonably abundant and diverse, while in lakes with high levels of fluctuations, invertebrates and vegetation were poorly represented, if not entirely absent. However, since then there have been few studies on the ecological effects of lake water level fluctuations on the ecology of UK lakes. Experiments and observational studies by Evtimova and Donohue, (2014; 2016), found that amplified WLF impacts were stronger in shallower and intermediate water depths, leading to reduced benthic invertebrate density, taxonomic distinctness and benthic algal biomass in mesocosm experiments. While observational studies of lakes (Evtimova & Donohue, 2016) established that WLF interacts with littoral depth along a gradient, influencing on habitat heterogeneity and the structure and functioning of invertebrate assemblages.

To our knowledge, there have been few attempts to elucidate the importance of water level range, relative to other drivers of lake invertebrate richness and composition, such as fertility, elevation, or catchment connectivity, across large scales. Establishing ecological impacts from water level fluctuations in lakes has also been impeded by a lack of water level monitoring in naturally fluctuating lakes, and by the complexity of covarying factors at catchment, lake, and shore scales that are likely to influence the littoral zone (Hellsten, 2000; Law et al., 2019). Among the relevant factors are catchment connectivity, wave action, lake productivity, littoral substrate and morphology, littoral vegetation and biotic interactions (Sun et al., 2019; Wilson, & Keddy, 1988; Brauns et al., 2008; Liffen et al., 2011; Law et al., 2019; Wesner, 2016), all of which require the relative importance to WLF to be established in terms of their impact on benthic assemblages. It is recognised that there are marked differences in invertebrate taxa prevalence, tolerances and interactions in different geographical regions (Marzin et al., 2012; McGoff et al., 2013), alongside important abiotic differences such as water colour and ice coverage, indicating the need for research in comparable areas of north west Europe.

Given the fundamental role that invertebrates play in lake ecosystem functioning it is critical to better understand how they respond to lake water level ranges relative to other environmental variables. The aim of this study was to compare the sensitivity of different community responses, including richness, composition, and indicator taxa, to water level ranges in lakes and other established abiotic influences such as elevation, lake area and fertility.

3.2 Methods

There are over 25,500 lakes (ranging from <0.01 km^2 to >20 km^2), across Scotland, which collectively cover a ~2300 km^2 area, and include over 670 registered reservoirs, classified as having a capacity to hold 25,000 m^3 or more of water above the natural level of the surrounding land (SNH, 2014). We collated comparable data for 57 Scottish lakes, some such as Loch Awe and Loch Lomond had multiple surveys included varying by exposure to wind and wave energy (due to the large size of the waterbody). These were chosen to provide wide geographical spread (Fig. 1) and coverage of the range of conditions known to influence the ecology of lakes in North West Europe, including water level ranges (natural and imposed), fertility, size, and elevation. The only notable exception is ice scour which is not a regular feature of lakes in temperate oceanic regions compared to those in boreal or temperate continental regions (Mjelde at al., 2013).

Invertebrate data

Comparable aquatic invertebrate data were extracted from lakes surveyed between 2007 – 2015 by the Scottish Environment Agency (SEPA). The final dataset comprised 63 invertebrate surveys, in 57 lakes (20 regulated and 43 unregulated lake surveys). Multiple surveys were carried out where lake size (over 40ha) or major differences in shoreline exposure (e.g. Loch Katrine), justified additional sampling in keeping with WFD-UKTAG (2014). Invertebrate data were mainly from quarter two (April to June), for the years 2007 or 2008. Those lakes sampled outside of these years were sampled from the same quarter with the effect of sample year being included in subsequent analyses. These survey data were used to assess richness and compositional responses to lake water level ranges and other environmental factors.

Invertebrate surveys (typically one per lake), were conducted using a standard 3-minute kick and sweep sampling procedure within the wadable part of the littoral zone, following Scottish Environment Protection Agency (SEPA) protocol (O'Hare et al., 2007). Samples were stored in 70% ethanol and identified in a laboratory. Identification was performed to variable levels across both taxa and sites; therefore, all invertebrate data was treated at the common family level.

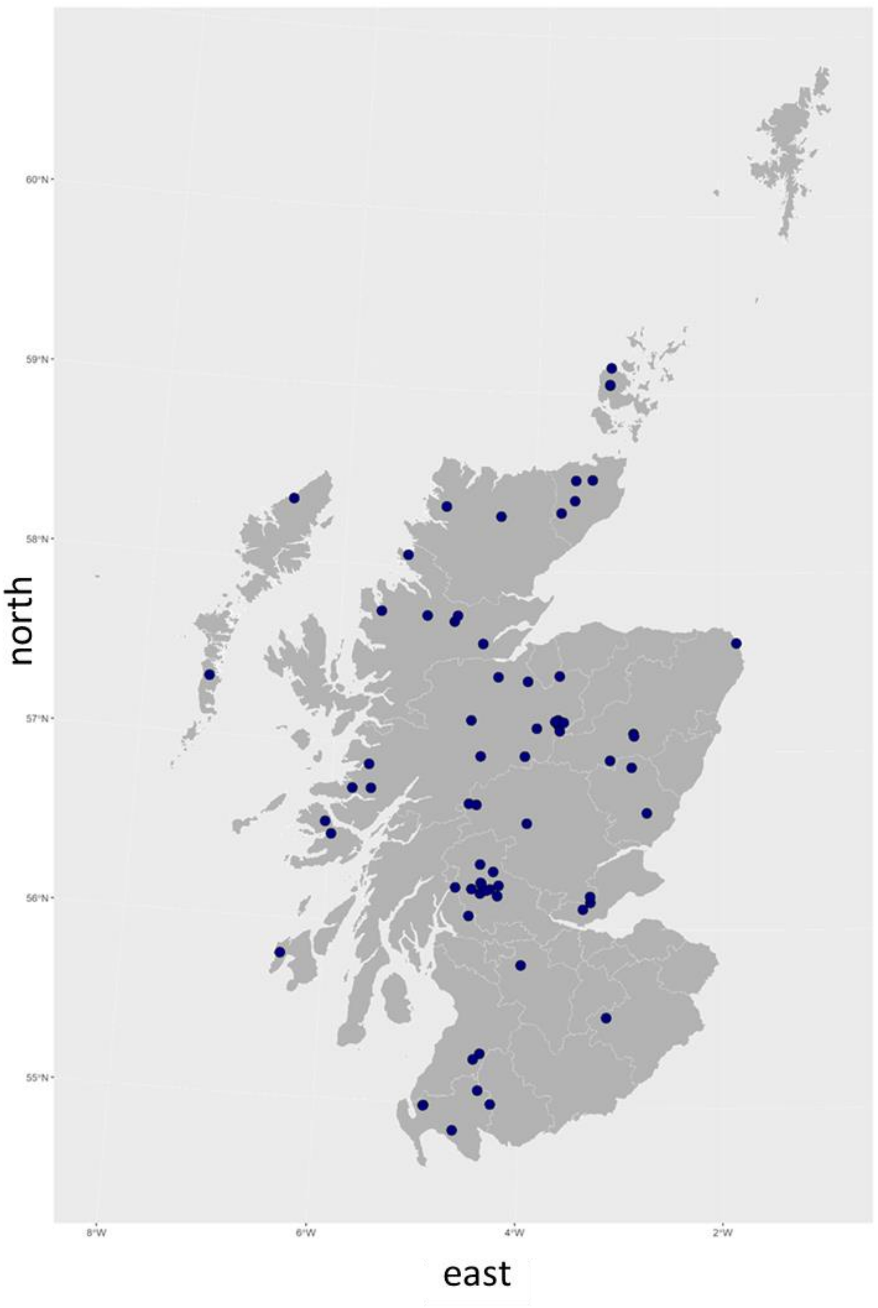

Fig. 1. Map of Scotland with indicating the wide geographical range of lakes sampled for benthic macroinvertebrates

Physicochemical measurements

Water chemistry data (usually monthly) were obtained for each lake, mostly for the period 2007 - 2009, based on routine sampling and analysis undertaken by SEPA. Data were averaged for years 2007 to 2009 for quarter two (April to June) to correspond with the time frame of invertebrate sampling for all key determinants including; Total Phosphorus (TP as mgL^{-1}), Chlorophyll a (Chl as ugL^{-1}), Total Organic

Nitrogen (TON as mgL^{-1}), and Alkalinity (Alk as $mEqL^{-1}$) (Table 1). Missing data were estimated using Beckers et al. (2003) and Taylor et al. (2013) methods of optimal interpolation (Appendix I).

Lake morphometry parameters, including area, perimeter, mean depth, elevation, and catchment area, were derived via the UK Lakes Portal (Hughes et al., 2004). Where data were absent for perimeter these were calculated by use of an online aerial mapping tool (e.g. Google Earth). The morpho-edaphic index (MEI) originally used as a tool for estimating fish biomass in lakes (Ryder et al., 1974), was used as an indicator of baseline productivity. MEI now has widespread application in limnology and lake ecological assessment. For the purposes of this research MEI was calculated as:

$$MEI = \log(\frac{mean\ alkalinity\ (mEq\ L)}{mean\ depth(m)})$$

High values of MEI are therefore associated with base-rich shallow lakes, where the geology is soft and phosphorus is thus likely to be more readily available through weathering, and where water depths are shallow inferring limited stratification and potential for light to reach large areas of the lake bed. Productivity is expected to be naturally high under these conditions. Low values of MEI are associated with base-poor deep lakes where the supply of phosphorus from rock weathering is expected to be low and depth promotes stratification and places much of the lake bed beyond the compensation depth for net production. Productivity is expected to be naturally low in such cases.

Shoreline Development Index (SDI) was calculated as the ratio of shore line length to the circumference of a circle of area equal to that of the lake (Wetzel, 2001) and serves as a proxy for complexity of shoreline, i.e., lakes with SDI close to 1 are increasingly circular (uniform, simple shorelines), whereas lakes with SDI larger than 1 have increasingly complex shorelines, reflecting the potential for within lake heterogeneity and for littoral communities to develop in sheltered bays. The complete list of explanatory variables and definitions are provided in Table 1. Where available, whole lake macrophyte species richness data from June to September 2007 -2015, was used in exploratory analysis. Macrophyte surveys of 43 lakes from employed the SEPA protocol based on the JNCC Common Standards Monitoring Guidance (CSM) for Standing Waters (JNCC, 2005), as per Gunn et al., (2004).

Table 1. Explanation of the environmental predictor data across 57 Scottish lakes. ID is the abbreviation used in the results

ID	Variable	Unit	Description
Water Level / WLF	Water level fluctuation range	m	Lake water level range determined by the 10th to 90th percentile of full range or estimated range obtained via aerial imagery and strandline indicators
Perimeter	Lake perimeter	km^2	Lake perimeter
Area	Lake area	km^2	Lake surface area
Elevation	Lake elevation	m	Lake elevation (AOD)
Depth	Lake depth	m	Lake depth (mean)
Alkalinity	Alkalinity	$mEqL^{-1}$	Alkalinity (mean)
Ammonia	Ammonia	mgL^{-1}	Ammonia as N (mean)
Nitrate	Nitrate	mgL^{-1}	Nitrate (mean)
O2_DO	Dissolved oxygen	mgL^{-1}	Dissolved oxygen (mean)
SuspSolids	Suspended solids	mgL^{-1}	Suspended solids (mean)
ElecCond	Electrical conductivity	uS/cm^{-1}	Electrical conductivity (mean)
Chlorophyll *a*	Chlorophyll *a*	uS/cm^{-1}	Chlorophyll *a* (mean)
Silicate	Silicon dioxide	mgL^{-1}	Silicon dioxide (mean)
MEI	Morphoedaphic index	unitless	Index of lake mean depth and alkalinity
SDI	Shoreline development index	unitless	Measure of shoreline complexity
CLR	Catchment to lake area ratio	unitless	Ratio of lake catchment area / lake area
Regulation	Regulated or unregulated lake water levels	unitless	Binary measure of regulation of lake water
Global (n=63)	All lakes	unitless	Global = 57 lakes with 63 stations (multiple stations on some lakes due to extensive size)
Lakes.S (n=35)	lakes with stable water levels	Unitless	Lakes with water level range of; <= 1m
Lakes.F (n=28)	lakes with fluctuating water levels	Unitless	Lakes with water level range of; >1 – 5.5m

Lake water level range

One of the key challenges in understanding relationships between freshwater biota and lake water level fluctuations has been the limited availability of water level data, in particular for unregulated lakes.

Data on water level fluctuation range (WLF), (i.e. difference between effective mean annual maximum and minimum water levels) for regulated lakes were sourced from reservoir operators (Scottish Water, Scottish Southern Electric). Where daily or weekly level data were available the mean range was calculated based on the 10th and 90th percentiles to reduce the influence of rare extreme values (sometimes associated with reservoir management). Where direct lake level data were not available, data were taken from river monitoring stations in close proximity to the lake outflow using the average level data range (SEPA Water Level Data). Remaining gaps in water level data were rectified by online searches, direct communication with lake managers, measurement of trash line elevations relative to summer water levels, and inspection of online aerial and other available imagery for different seasons (e.g. Google Earth). Time series water level data was only available for a small subset of lakes, whereas range data is commonly available, therefore we have used range as an indicator of regime, (See Appendix II, for method of water level data attainment for each lake).

Exploratory and statistical analyses

Invertebrate data were standardised from mixed taxon levels to family level for richness analysis (taxa, n =79) expect where the finest taxa level resolution available was consistently higher as with, Zygoptera, Oligochaeta, Ostracoda (Appendix III). For community level analysis the finest taxa resolution was typically family (taxa n=94), (Appendix IV). Count data were used in all analysis with counts of individuals being log transformed. Prior to statistical analyses all continuous explanatory variables were log transformed, mean centred and scaled by 1 SD, to improve comparability between variables and to reduce the effect of outliers.

To reduce model complexity principal components analysis (PCA), was applied to separate sets of water chemistry, and physical variables to identify those variables that maximised variation amongst sites (Factors included in Table 2). (Appendix V). Correlations between predictor variables were then assessed in a correlation matrix (Appendix VI) and checked for variance inflation (VIF). Where variables were highly correlated (VIF > 10) they were removed. Pearson's correlations and principal components analysis (PCA), of lake physical attributes (lake size, elevation, depth, etc.), and physicochemical variables (TP, Ammonia, chlorophyll, etc.) and expert knowledge was used for exploratory data analysis of the global lake dataset (n = 63 surveys). Lacking any step changes in the WLF data to reduce data into naturally divided water level range parameters, lakes were split according to the median WLF (Table 2), resulting in 'stable' (n = 35), and 'fluctuating' lake surveys (n = 28), (Table 1, Lakes.S and Lakes.F). These simple typologies were exploratory but supported by subsequent compositional analyses.

Count data on invertebrate taxon richness were analysed using generalised mixed effects models (glmer), with a Poisson family link function. Within these mixed models invertebrate survey year and chemistry sample year were treated as random factors. For each glmer, following standard forward permutation testing, the optimal model was taken as that with the lowest AIC value. For a subset of sites where data was available on both macrophytes and invertebrates the relationship between invertebrate and macrophyte richness was analysed using a generalised mixed effects models (glmer), with a Poisson family link function due to the distribution and use of count data (Zuur et al., 2009).

Unconstrained ordination was conducted using non-metric multidimensional scaling (NMDS), on a Bray-Curtis dissimilarity index (BCI), generated from a log-transformed count × sample matrix. Using the function ‘adonis’ within the vegan library (Oksanen et al., 2017), a permutational multivariate analysis of variance was used to test for differences in invertebrate taxa composition between stable and fluctuating lake types. Taxa indicative of lake water stability were derived using the Indval R function (Roberts, 2016), which identifies ‘indicator’ taxon from their fidelity for, and occupancy of, a group, the groups in this case comprising lakes with stable or fluctuating water level. The significance of indicator values was tested using random permutation tests. The threshold for interpreting indicator taxa scores was set at a minimum of 0.3, informed by ecological interpretation. Invertebrate taxa-environment relationships were assessed using Canonical Correspondence Analysis (CCA), with final models being determined by forward selection tests. All predictors were assessed and transformed appropriately prior to centring and scaling.

All statistical analyses and graphics were produced using R Studio version 3.5.1 (http://www.rstudio.com/), with the additional packages; Corrplot (Wei et al., 2017), Factoextra (Kassambara et al., 2017), FactoMineR (Husson et al., 2018), ggplot2 (Wickham et al., 2016), labdsv (Roberts, 2016), lme4 (Bates et al., 2015), Psych (Revelle, W. 2018), sciplot (Morales et al., 2011), vegan (Oksanen et al., 2013) and Sinkr (Tayler et al., 2013).

3.3 Results

Taxon richness and drivers

A total of 94 invertebrate taxa (finest commonly available, predominantly family) were recorded in the global lake dataset (lakes = 57, surveys = 63) used for community analysis, with taxa degraded to 79 families for richness models. Once subdivided by water level regime this equated to 88 taxa in stable lakes (Lakes.S) and 71 taxa in fluctuating lakes (Lakes.F). Average family level richness of all lakes with WLF of 0.35 to 5.5m was 17 however, Lakes.S and Lakes.F were 20 and 16 respectively, equating to Lakes.F being 20% less rich (see appendix IX for full environmental variables by lake type). Several physicochemical variables significantly affected invertebrate taxon richness in the global dataset (Fig. 2, and Fig. 3).

Table 2. Environmental variables for all lakes (n=57) displaying; Median, Mean ± SE (min – max). CLR = Catchment to Lake Ratio, SDI= Shoreline Development Index, MEI= Morpho-edaphic Index.

Variable	median	mean	Min - max
Water Level / WLF (m)	1.00	1.45 ± 0.13	0.35 - 5.5
Lakes.S (WLF) (m)	0.9	0.81 ± 0.04	0.35 - 1
Lakes.F (WLF) (m)	1.75	2.25 ± 0.2	1.2 – 5.5
Perimeter (km^2)	9.96	17.02 ± 2.65	0.31 - 95.53
Lake area (km^2)	1954.92	5601.23 ± 1337.83	4.34 – 55333.60
Elevation (m)	113.00	144.54 ± 15.86	2.00 - 537
Depth (m)	7.73	16.16 ± 2.89	0.80 - 132
Fetch (m)	1775	2727 ± 436.25	18 - 23958
Alkalinity (mEqL^{-1})	7.95	23.98 ± 5058	1.11 – 197.00
Ammonia (mgL^{-1})	0.04	0.05 ± 0.01	0.003 – 0.24
Nitrate (mgL^{-1})	0.18	0.47 ± 0.09	0.004 – 4.26
TP (mgL^{-1})	0.028	0.042 ± 0.006	0.004 – 0.33
O2_DO (mgL^{-1})	13.20	13.25 ± 0.22	10.30 – 17.80
SuspSolids (mgL^{-1})	6.10	12.9 ± 2.29	0.50 – 86.00
ElecCond (uS/cm $^{-1}$)	75.80	185.61 ± 62.13	25.5 - 3730
Chlorophyll (uS/cm $^{-1}$)	6.75	17.70 ± 3.70	1.10 – 135.88
Silicate (mgL^{-1})	3.65	5.22 ± 0.64	0.44 – 31.40
MEI	-1.77	-1.66 ± 0.1084	-3.31 – 0.69
SDI	2.114	2.32 ± 0.11	1.25 – 5.10
CLR	17.20	35.95 ± 9.46	0.04 – 580.71

Water level range and lake elevation were the strongest and highly significant predictors, being negatively associated with family richness (Fig, 2, Table 3).

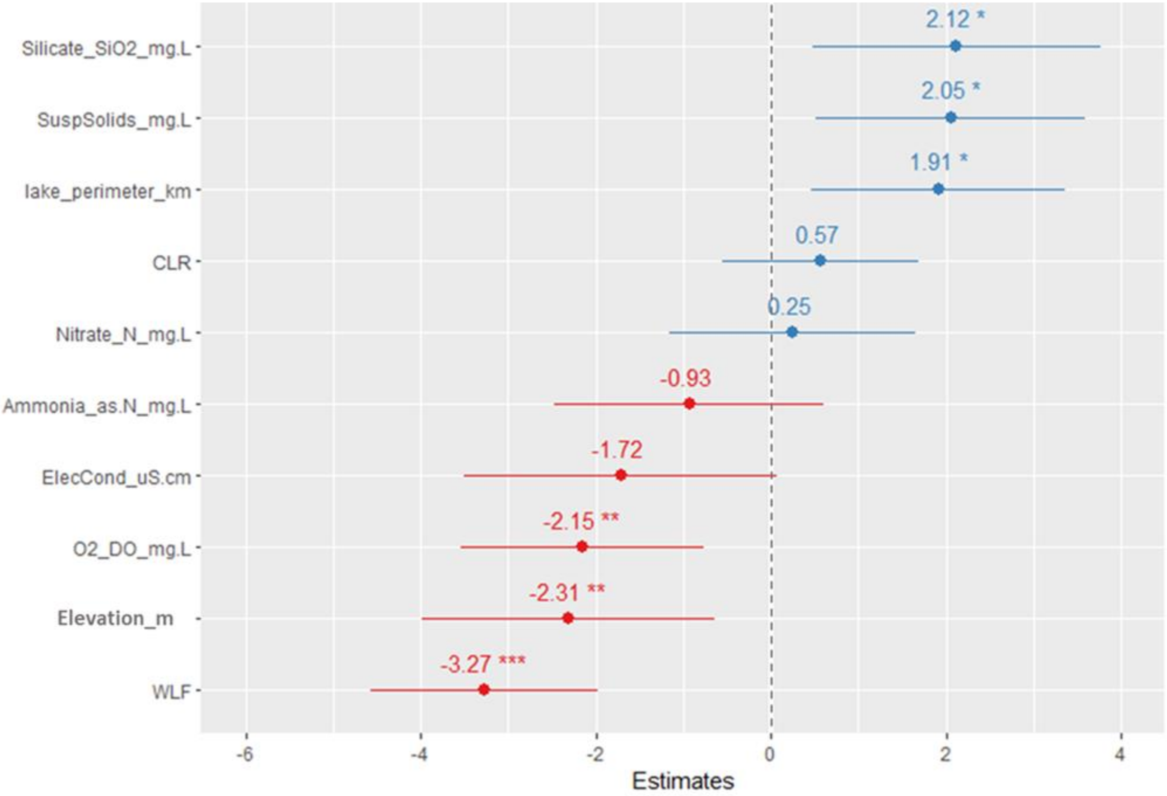

Fig. 2. Global family richness multivariate mixed model predictor effects (scaled and significance p= 0***, 0.001**, 0.005*, 0.1.), (all predictors transformed and data scaled), CLR= Catchment to Lake ratio, 02_DO = dissolved oxygen, WLF = Water level fluctuation)

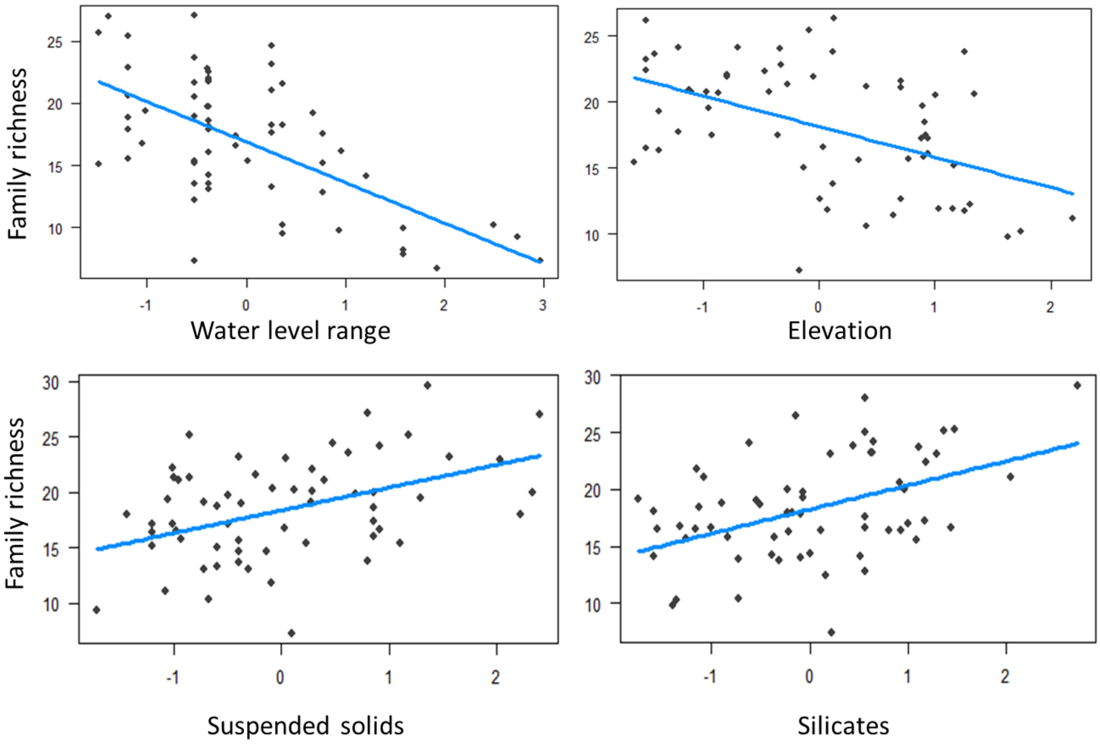

Fig. 3. Subset of modelled outputs of littoral invertebrate family richness vs. a) water level, b) elevation, c) Silicate, d) Suspended solids, (all predictors data scaled).

Average invertebrate family richness per lake was 59% lower at WLF of 3.5 – 5.5m than at WLF of 0.35 – 1 m. Dissolved oxygen had significant negative associations with family richness in the global dataset, while silicate, suspended solids and lake perimeter had significant positive roles in explaining the variance in family richness in the global dataset, in descending order of effect size (Fig 2).

In addition, multiple regression on a subset of 44 lakes from the invertebrate data, with concurrent macrophyte species richness data available, demonstrated a clear, significant, negative association between water level range and invertebrate richness, relative to other drivers, (Fig.4, Appendix VIII). Macrophyte species richness was not associated with invertebrate richness.

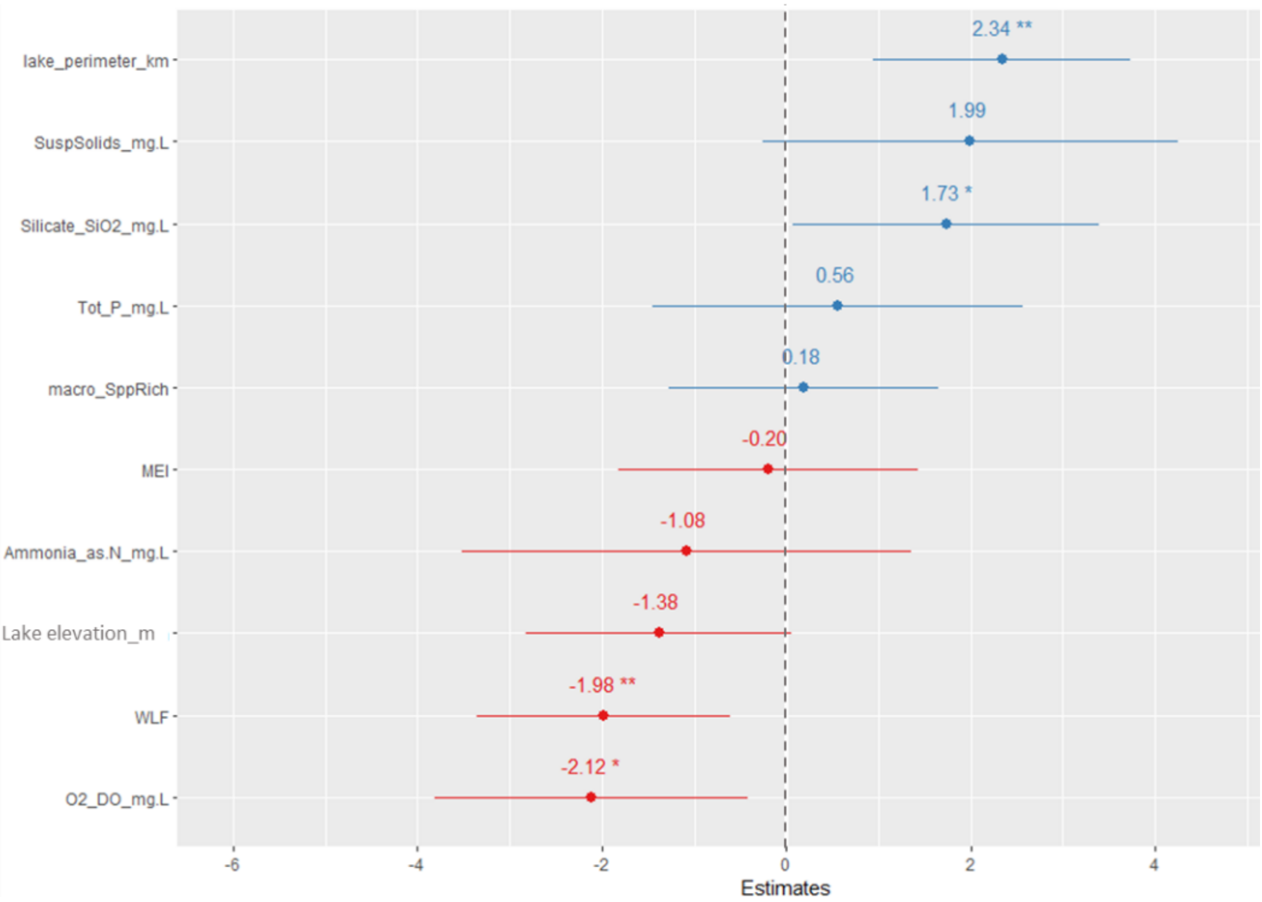

Fig 4. Family richness multivariate mixed model effect sizes for a subset of 43 lakes with both invertebrate and macrophyte species richness data (scaled and significance p= 0***, 0.001**, 0.005*, 0.1.)

Taxon composition

As WLF was shown to have a strong negative association with family richness (Fig. 1) the study lakes were divided into stable and fluctuating water level lake types to visualise the relationship with invertebrate community structure.

NMDS analysis confirmed that taxon composition differs significantly (P < 0.003) between the stable and fluctuating lakes (Fig. 5) despite clear areas of overlap between lake types.

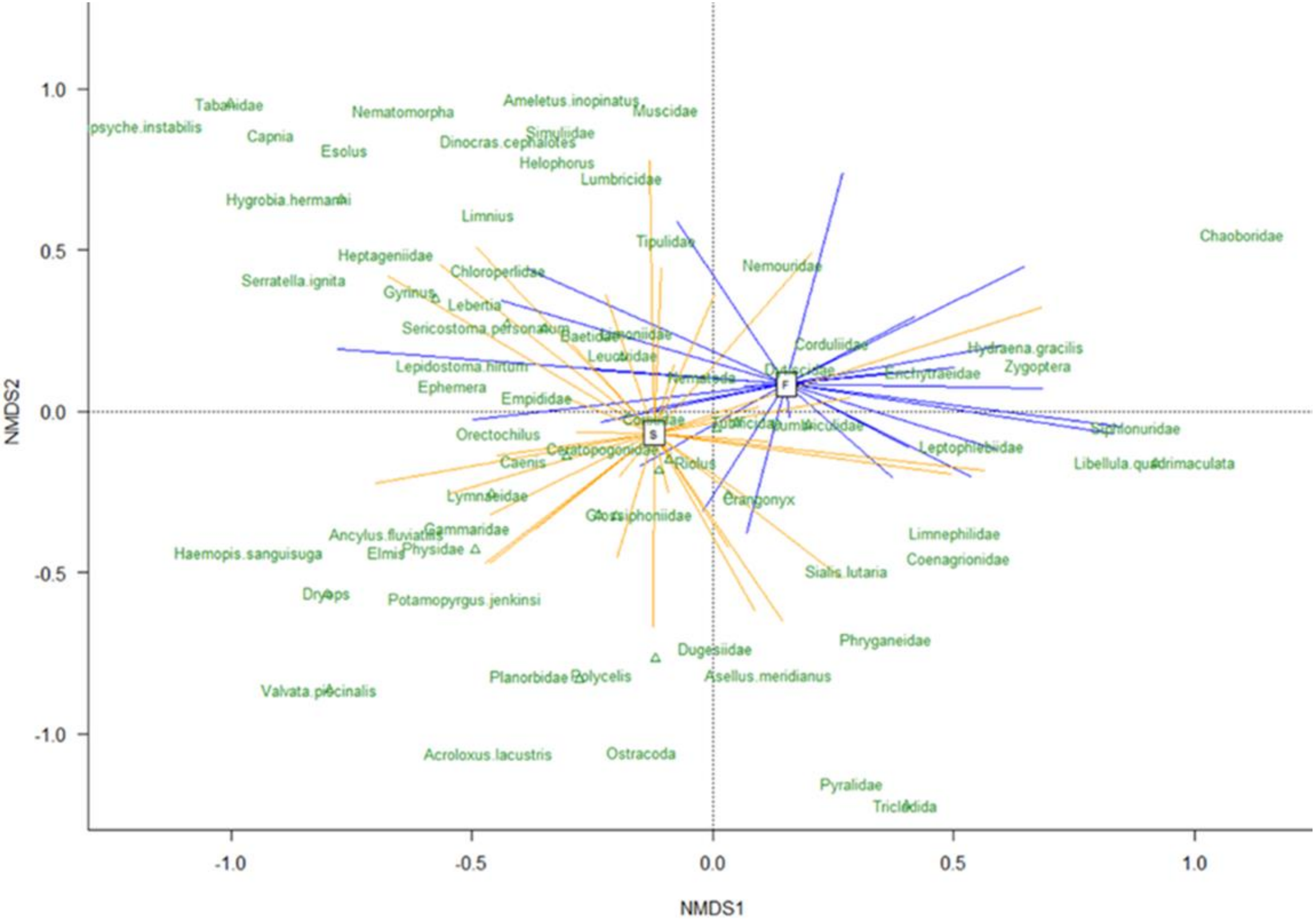

Fig 5. Non-metric multidimensional scaling (NMDS) ordination for all lakes, showing a spider plot that represents lake by water level regime type; (stable [S], fluctuating [F]. All stress values were <0.15.

Indicator taxa

Indicator taxa for (Table 3), show a clear distinction between lake types with indicator value threshold of 0.3 resulting in; Hydracarina, Lymnaeidae, Planariidae and Haliplidae strongly indicative of stable lakes, and Siphlonuridae indicative of fluctuating lakes.

Drivers of invertebrate composition

When invertebrate assemblages were constrained by environmental variables using CCA, the overall model was significant (P < 0.001) (Table 4) explaining 16% of variation in composition, a low but not unusual level of variation explained with the environmental variables measured, particularly as habitat specific variables were not included in analysis.

Table 3. Indicator taxa and values, where cluster 1 = stable water regime; cluster 2 = fluctuating water regime.

Indicator taxa	Cluster	Indicator value	Probability
Hydrachnidiae	1	0.6520	0.001
Lymnaeidae	1	0.3957	0.012
Planariidae	1	0.3671	0.004
Haliplidae	1	0.3475	0.042
Planorbidae	1	0.2571	0.012
Asellidae	1	0.1996	0.035
Siphlonuridae	2	0.4030	0.017

Table 4. Results of forward selection of environmental variables for CCA model, highlighting conditional effects in CCA model (scaled and significance p= 0***, 0.001**, 0.005*, 0.1 .)

Variable	ƒ	P value	significance
log lake perimeter	2.187	0.001	***
log ammonia	2.163	0.001	***
log WLF	1.606	0.003	**
log O^2_DO	1.578	0.009	**
log nitrate	1.724	0.016	*
Log SuspSolids	1.338	0.067	.

Ammonia and nitrate were most strongly associated with axis 1, with suspended solids also being important. The physical drivers, lake perimeter and water level range were most strongly associated with axis 2 (Fig. 6). Lake perimeter and ammonia concentrations were the dominant drivers of invertebrate composition, exceeding the importance of WLF, although this remained a highly significant explanatory variable.

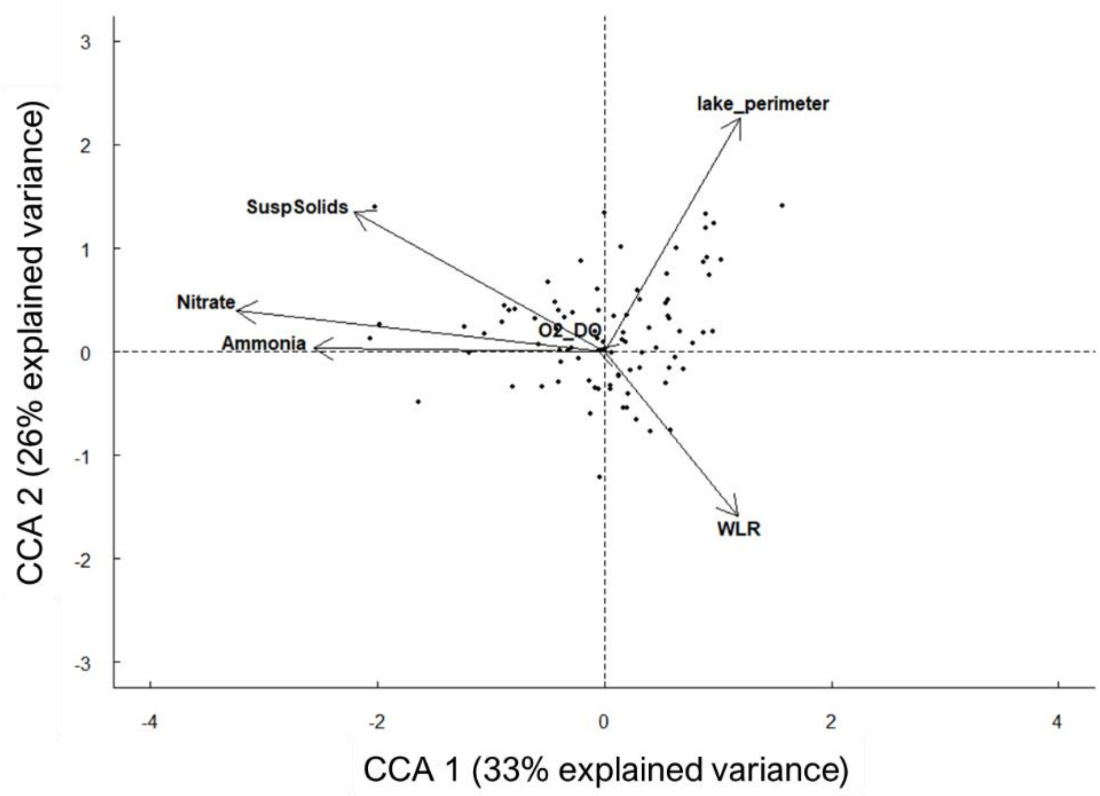

Fig. 6. Constrained ordination (CCA) of all lakes. Taxa represented by dots. Overall models significant (P < 0.001), explaining 33% and 26% of variation, respectively.

3.4 Discussion

Water level fluctuation range (WLF) was a prominent driver of littoral invertebrate family richness and composition in lakes. Additionally, invertebrate communities differed significantly with water level stability, with a clear distinction in indicator species between lakes with stable or fluctuating water levels. Our findings broadly support the outcome of other research on this topic, although, to our knowledge, the importance of WLF in lakes relative to other potential environmental determinants of invertebrate richness or composition has not previously been assessed.

Taxon richness

The relationship between water level range and invertebrate richness is consistent with previous research findings that indicate that amplified WLF leads to a reduction in richness and diversity of littoral invertebrate assemblages (Aroviita & Hämäläinen, 2008a; Brauns et al., 2008; Evtimova &

Donohue, 2014, 2016; Smith et al., 1987; Sutela et al., 2013a). The importance of WLF reflects the fact that it not only directly impacts benthic invertebrates via desiccation, but indirectly through impacts on factors that underpin lake ecology. For instance, as the majority of lake biodiversity is associated with the littoral zone (Evtimova & Donohue, 2014), it would be reasonable to expect the family richness-area relationship to alter if factors known to dictate the extent of viable habitat, such as perimeter and shore slope, are altered by changes in WLF (Evtimova & Donohue, 2016; O. Vestergaard & Sand-Jensen, 2000). On a gently sloping shore organisms stranded by a rapid drop in level face desiccation unless they have resistance adaptations, are highly mobile, or the water level decline is temporary (Vadher, Millett, Stubbington, & Wood, 2018).

Elevation and dissolved oxygen had a negative association with invertebrate family richness. It is typically accepted that these factors share a relationship; as temperatures decrease with increasing elevation so oxygen solubility increases (Crisp & Hynes, 1971) though no correlation was detected with elevation and dissolved oxygen in our study. Hence, the perception that warm lowland waters are less oxygen rich than cold mountainous waters being invoked to explain the distribution and adaptations of invertebrates found along altitudinal gradients in streams (Hynes, 1981; Jacobsen et al., 2003). Whilst dissolved oxygen has been found to be a limiting factor on aquatic invertebrates in streams and reservoirs (Connolly, Crossland, & Pearson, 2004; Dai et al., 2017; Kaller & Kelso, 2007), our work revealed increasing dissolved oxygen levels had a *negative* relationship on invertebrate richness. This could arise because higher elevation lakes, which tend to have a shorter growing season due to decreased temperatures (Dodds et al., 2019), are generally steeper sided than lowland lakes and also receive water directly from a high density of colder, well-oxygenated head water streams. This combination of features could potentially lead to increased flushing rates, lower productivity and reduced littoral zone development. DO may also increase in lakes with more turbulence and wave action which are likely to have negative effects on invertebrate richness, thereby offering another explanation for this effect.

Our research reveals lake productivity is an important factor relative to WLF, with a positive association with silicates and invertebrate family richness. Silicate (silicon dioxide (SiO_2)), is important in freshwater nutrient cycling and for invertebrates as it forms the cell walls of diatoms which are a primary food resource (Gordon, Neto-Cerejeira, Furey, & O'Gorman, 2018) of biofilm grazers, or is accessed via invertebrate shredders feeding on leaf litter (Schoelynck & Struyf, 2016). Silicates increase in concentration through weathering reactions (Dobrzyński, 2005), accumulating downstream as tributaries merge, before uptake by aquatic vegetation. Therefore, though elevation and silicates were not correlated, the positive relationship with silicates and invertebrate family richness may fit with the relationship found between increasing invertebrate richness with decreasing elevation. Though this may not be a linear relationship particularly given converging and diverging nature of catchment water flows or the uptake of silicates by aquatic vegetation. Alternative analysis using non-linear techniques may elucidate these associations further in the future (i.e. polynomial models or structural equation modelling (SEM)).

All streams and lakes have naturally occurring suspended solids (Ryan, 1991) but elevated concentrations caused by anthropogenic perturbations generally have negative associations with water quality and invertebrates in freshwaters systems, due to the impacts of high silt or fine sediment, leading to impacts such as decreased light penetration or the clogging of invertebrate gills or gut (Aldridge, Payne, & Miller, 1987; Bilotta & Brazier, 2008; Lloyd, 1987). The concentrations of suspended solids in our study (median 6.1 mgL^{-1}, range 0.50 – 86.00 mgL^{-1}) are at levels found to increase the rate of drift in streams, or reduce invertebrate density by 26% (Davies-Colley, Hickey, Quinn, & Ryan, 1992; Rosenberg & Wiens, 1978). However, in our work suspended solids were positively correlated with chlorophyll indicating that the main component of suspended solids is likely to be phytoplanktonic. As such, in our lakes suspended solids are likely to be an indicator of productivity, which would explain the positive effect on benthic invertebrate richness.

Lake wide habitat factors were also found to be important to invertebrate richness and composition. Taxon richness was positively associated with lake perimeter, which was correlated with lake area and maximum lake fetch. The relationship with family richness and perimeter area is analogous to the frequently confirmed species-area relationship (MacArthur & Wilson, 1967), and to the species-discharge concept applied to aquatic invertebrates and rivers, as river size is measured by discharge (Mccabe, 2010). Perimeter length is a better indicator of littoral zone extent than lake area and is therefore likely to be more relevant for invertebrate diversity in this zone. It is, however, notable that SDI was never a significant predictor of richness confirming that the significance of perimeter probably relates more to the areal extent of the habitat than heterogeneity of this habitat.

Based on a subset of 43 lakes where invertebrate and macrophyte richness were both available we found that littoral invertebrate richness is not directly driven by macrophyte richness. The direct and indirect relationships between littoral invertebrates and macrophytes needs to be elucidated further within the context of WLF and other drivers, such as nutrients, as each may respond differently over time (Declerck et al., 2011). It is also possible that the relationship between these biotic components is more dependent on the structural diversity of the vegetation than richness *per se* (Law et al., 2019) or on the abundance or cover of plants. Alternatively, the link may be more indirect and mediated via suspended solids, chlorophyll *a*, silicates, and dissolved oxygen, as our results suggest. It is, however, likely given the relatively limited level of vegetational development in our study lakes, (aside from a few productive lowland lakes), that invertebrates within our study, were potentially influenced by littoral zone complexity associated with substrate.

Drivers of invertebrate composition

WLF modified invertebrate composition in lakes, as did lake perimeter, suspended solids, dissolved oxygen, nitrate, and ammonia, although the relative effects of WLF in composition were weaker than for richness. Given that physical changes related to lake morphology, such as decreasing sediment size, are driven by WLF (Evtimova & Donohue, 2016), while benthic invertebrates have known specificities for sediment type and light penetration zones, these results are not unexpected. Lake perimeter was correlated with fetch, both of which are proxies for the combined effects of wave exposure and substrate composition which are known to influence littoral invertebrates (McEwen & Butler, 2010). Ammonia and nitrate occur naturally in low concentrations in freshwaters but can reach concentrations toxic to invertebrates if elevated by human activity. However, the average concentrations in our study lakes (Ammonia 0.05± 0.01 mgL^{-1} , Nitrate 0.47 ± 0.09 mgL^{-1}) are below those regarded to be background levels (EEA, 2019), and therefore potentially influence invertebrate assemblages via the role they play in macrophyte nutrition (Haynes & Goh, 1978) and leaf litter quality. The overall explained variance of the CCA remained low but not unusually so (Jurca et al., 2012)(Jurca, 2012), given that the data available was lake-wide in scale. Much greater variation can be explained when sub-lake (physical habitat) data are included such as, vegetation cover and water temperature (Dalu & Chauke, 2020; Jurca et al., 2012).

Community structure significantly differed between lakes with stable and fluctuating water level regimes, despite over lapping composition structure between the two groups. This was further clarified by distinct indicator taxa for each group. Hydracarina (water mites), Lymnaeidae (pond snails), Planariidae (flatworms) and Haliplidae (crawling water beetles) were found to be indicative of stable lakes, all being taxa typically associated with macrophyte rich waters, which is compatible with our previous findings that macrophyte species richness decreased with increasing WLF in lakes (Chapter 2). Siphlonuridae (primitive minnow mayfly), was the single family determined to be indicative of fluctuating lakes. The obvious distinguishing factor separating these taxa is life span in that all indicator taxa for stable lakes have lifespans of over 1 year (Sabatino, Gerecke and Martin, 2000; Pyron and Brown, 2015; Mangel, Bonsall and Aboobaker, 2016), with the exception of Haliplidae. These may be especially susceptible to WLF adaptations as they are perhaps the poorest of water beetle swimmers, preferring to crawl over vegetation, where they also lay their eggs, leaving them particularly vulnerable to dewatering (Ricciardi, 2015). Water mites are ubiquitous in freshwater environments and known to be indicative of "high" quality water, but there is no published work on the sensitivity of this group to water fluctuation impacts. These results suggest they are sensitive to WLF stress, therefore, Hydracarina may be a useful taxon for biomonitoring of water level regulation effects and in freshwater ecosystem assessments (Goldschmidt, 2016).

Finally, we address the single taxa found to be indicative of fluctuating waters, Siphlonuridae. Aside from larvae occurring in slower moving waters of streams, marshes and swamps there is limited literature relating to this taxa in lakes, particularly those with high water level ranges, however of the 63 surveys lakes in the study Siphlonuridae were recorded in 35%, showing this habitat may have been previously overlooked as important to this family, particularly lakes with increased WLF. Siphlonuridae are mobile and univoltine, as well as having a summer egg diapause (deWalt et al., 2010), which may reduce their sensitivity to larger WLF.

Attempts to establish unifying characteristics of taxa sensitive to regulation are scarce in the literature. Certain invertebrates can move in line with moderate rates of water level variation, of up to 0.5 cm hr^{-1}, while others recolonise after rewetting over the course of three months, but for others this takes only weeks (Winter, 1964, cited in Solimini et al., 2006; James et al., 2002). Others have inherent resistance strategies to drying events such as *Gammarus pulex,* which migrates vertically into subsurface gravel sediments as refuge in Intermittent rivers and ephemeral streams (Vadher, Leigh, Millett, Stubbington, & Wood, 2017; Vadher, Stubbington, & Wood, 2015). Aroviita & Hämäläinen (2008) recognised that four of the taxa they identified as sensitive to regulation amplitude were also semivoltine, including *Oulimnius tuberculatus, Ephemera vulgata, Limnius volckmari* and *Sialis* spp. Our data implies that invertebrates which may be particularly susceptible to anthropogenic water-level alterations, are those with a long-life cycle (two years or more), lower mobility and dependency on well vegetated habitats. Our results indicate a strong filtering of such taxa as WLF increases, with concomitant effects on invertebrate richness.

3.5 Management implications

Taxa found to be indicative of stable lake water regimes are important considerations for lake conservation and restoration and biomonitoring in ecosystem assessments.

In light of the expected global increase in impoundments and level of pressure on European freshwaters from regulation activities, as well as future projections of population and climate change it is imperative to effectively manage freshwater resources and their associated biodiversity effectively. We suggest scope for increasing perimeters of new and existing reservoirs be considered by increasing the complexity of shape and so provide additional potential habitat. In addition, creation of holding ponds adjacent to the main body of water may enable mobile organisms to persist there temporarily and re-colonize the reservoir once water levels rise. This may be particularly beneficial where water level ranges are not extreme but alter slowly such as in drinking water reservoirs.

3.6 Conclusions

Understanding the drivers of richness and invertebrate composition is important for habitat monitoring, conservation, and informing how management can promote the sustainability of fresh waters. We have demonstrated that water level fluctuation has pronounced associations with invertebrates, relative to other environmental factors commonly considered in studies of lakes such as elevation, perimeter, and fertility. It is also evident that ecological impacts are likely to be accentuated in low fertility water bodies. Further study may cast light on the effectiveness of mitigation strategies, or if there is scope to manipulate water level regimes in lakes to minimise ecological impacts, in the same way as is attempted on rivers. In addition, research into how the structure and cover of macrophytes in lakes is associated with invertebrate groups with WLF considered are required.

Acknowledgements

Data on water chemistry, invertebrates, and some of the lake macrophyte survey data used here were provided courtesy of the Scottish Environment Protection Agency (SEPA). We thank Anna Doeser, Megan Layton, Catherine Gibson-Poole, Zarah Pattison, Duncan and Tarian Dowie for assistance with sampling of additional lakes. Grateful thanks also to Scottish Water, Scottish Southern Electric, Forestry Commission Scotland and The Woodland Trust for providing water level data and/or access to survey lakes. This research was financially supported by the University of Stirling and SEPA via an Impact Studentship.

Chapter 4

Amphibious adaptations: effects of water level fluctuation and habitat on the morphology and biomass of the aquatic isoetid *Littorella uniflora* in Scottish lakes

4.0 Amphibious adaptations: effects of water level fluctuation and habitat on the morphology and biomass of the aquatic isoetid *Littorella uniflora* in Scottish lakes

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Planning submission to Freshwater Biology

Author comments: AB and NW jointly developed the project concept. Field data collection was designed by AB and carried out by AB, Megan Layton, and Anna Doesser. Laboratory work was planned by AB and carried out by AB and Megan Layton. The manuscript was prepared by AB with comments and statistical guidance from NW and AL. The results were presented at the Symposium for European Freshwater Sciences, Geneva (July, 205), and the 14th International Symposium on Aquatic Plants in Edinburgh (September 2015).

Abstract: In Europe, water level regulation is *the* most important hydromorphological pressure on lakes, often in the form of reservoirs and outflow dams. Water levels vary naturally in all standing waters and greatly influence lake littoral zones through changes to macrophyte growth, sediment stability and nutrient cycling. *Littorella uniflora* (L.) Ascherson (Shoreweed) is common and widely distributed in the highly changeable littoral margins of lakes and reservoirs in temperate-oceanic climates, often dominating where water-levels fluctuate. However, despite its resilience to water level fluctuations and capacity for rapid morphological change *L. uniflora* populations have declined dramatically in many areas of northern Europe, due to a combination of water level regulation, acidification, and eutrophication. Water level variation represents a growing pressure on lake ecology, particularly as impacts to the littoral zone are now being accentuated by increasing frequency of floods and drought, changes in precipitation events, temperature, and water abstraction rates. Nevertheless, its effects remain under-studied**.** This study investigated how *L. uniflora* morphology and biomass are affected by water level range and other associated abiotic factors in lakes. We harvested plants from 10 freshwater lakes in Scotland, covering a range of fertility, water level regimes and environmental variables at the lake, shore, and quadrat-scale. Water level range was not found to directly correlate with *L. uniflora* morphology or biomass. However, relationships were established with *L. uniflora* biomass or different aspects of morphology and environmental variables influenced by lake water level range including; distance, height, and slope of site from water surface, sediment aggregate size, organic matter content and potential wave exposure. A negative relationship was found between *L. uniflora* biomass and sandy substrates and increasing shore slopes. Morphological traits such as root-to-shoot ratios were influenced negatively with increased wave exposure, whilst leaf length-width-ratios increased with distance from the water's edge. Our findings add to the knowledge required to protect this amphibious species. Given its widespread status in lakes with artificial water level regimes and its key functional role in littoral habitats this should also help to mitigate the effects on wider lake ecology from the growing pressures of lake water regulation and climate change. Managers and conservationists should be aware that losses of this robust species or changes in its morphology may be indicative of wider ecosystem health impacts.

Keywords: *Littorella uniflora*, biomass, growth form, leaf morphology, water level range, sediment, organic matter, wave exposure, shore slope

4.1 Introduction

Water level fluctuation is a commonly overlooked pressure on lake ecosystems, despite being a major influence on natural habitat structure and vegetation zonation, particularly for amphibious species. Whilst water levels vary naturally in all lakes, regimes are being altered with changes to the volume and seasonality of precipitation, wind speeds and lake temperatures linked to climate change (Fekete et al., 2010). These changes are combined with increasing societal demands on water resources, and greener energy investment, such as hydropower (Dorber et al., 2018). Currently freshwater species are declining faster globally than those of marine or terrestrial ecosystems with over double the loss of biodiversity since 1970, with habitat degradation from flow modification highlighted as a persistent and prominent threat to freshwater biodiversity (Dudgeon et al., 2006; WWF, 2018). In Europe, the dominant pressures to surface freshwaters are from hydromorphological pressures, affecting 40% of these systems with diffuse source pollution mainly from atmospheric deposition and agriculture following second (38%) (EEA, 2018). Of these pressures water level regulation is one of the most frequent and important, affecting 27% of lakes (EEA, 2012). However, to date, our understanding of this pressure on aquatic organisms relative to others, such as eutrophication, is remarkably poor.

Lake water level fluctuations (WLF) engineer littoral zones, increasing temporal and spatial sediment and aggregate heterogeneity and the physicochemical habitat (Evtimova & Donohue, 2016; Hofmann et al., 2008). Therefore, the range of water level fluctuation influences the zonation of aquatic macrophytes, attributed in part, to substrate and sediment properties, which are directly linked to water levels, as sediments become finer with increased silt as the water deepens (Spence, 1967). In addition, distribution of vegetation is directly controlled by water turbulence, (altered by water depth and wind energy), or by the substrate itself and indirectly through its impacts on sediments (Spence 1964, cited in Spence, 1967).

Water level impacts on any individual lake shore, and therefore vegetation, depend on a suite of interrelated factors including; range, duration, seasonality and frequency of fluctuation events (Hirsch et al., 2017; Hofmann et al., 2008; Smith et al., 1987), fertility, (Jones, Obrecht, & Thorpe, 2011; Nürnberg, 2009; Nürnberg, 1996), and the inherent properties of the shore itself, such as dominant aggregate type and shore slope (Duarte & Kalff, 1986).

Slope is itself a controlling factor of shore sediment type and stability (Hakanson, 1977) and modulates the impact of wave action on littoral zone substratum (Duarte & Kalff, 1986). The relative instability of fine sediments in lake habitats and the inorganic and organic particles within the top sediment layers, are susceptible to water level or wave disturbance via sediment focusing (Fig. 1), (Hakanson, 1977; Hofmann et al., 2008; B. R. Malmqvist, 2002) which moves sediments from the shore to the deeper lake zones. Therefore, when water levels are reduced, finer particles and sediment are relocated further from the shore, disconnecting them from the exposed littoral zone, resulting in an exposed shore with reduced fine sediment, nutrients and organic matter with larger aggregate sized substrates and low nutrient or moisture storing ability (Carmignani & Roy, 2017; Cooley & Franzin, 2008; Furey, Nordin, & Mazumder, 2004; Madsen et al., 2001) (Fig. 2b). In addition, cohesion of sediments may alter following drainage, becoming more compact due to increased gravitational forces and loss of organic matter, potentially resulting in increased root anchorage for amphibious species upon re-submergence (James, Barko, & Eakin, 2004).

Fig. 1. Loch Lyon (illustrating clear particle sorting of sediments with water level).

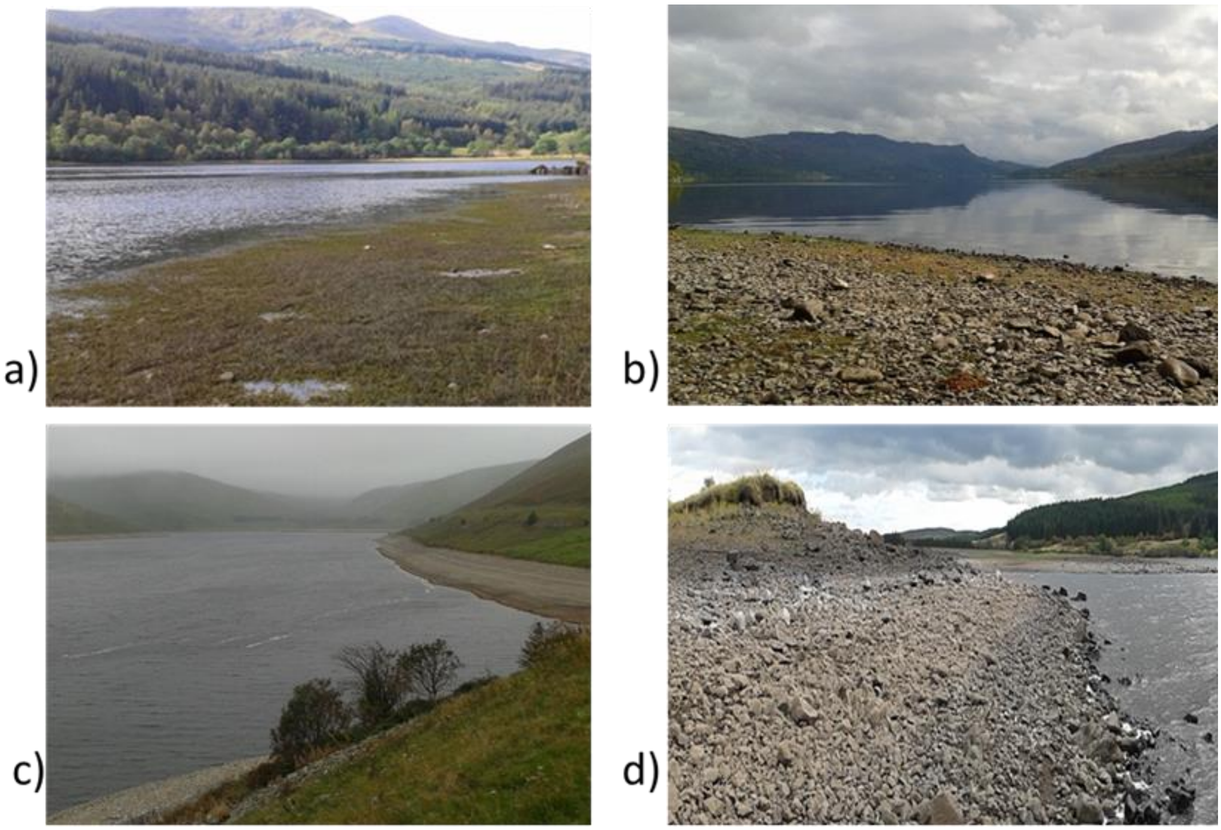


Fig. 2. Sample of research sites: a) natural site at Loch Lubnaig (mostly *Littorella uniflora*) with moderate potential wave exposure; b) regulated Loch Katrine (sparse *Littorella uniflora*) with high potential wave exposure; c) Megget Reservoir (mostly unvegetated) with high potential wave exposure, and d) Carron Valley reservoir (mostly unvegetated) with moderate potential wave exposure.

Aquatic plants are ecosystem engineers, reducing or altering velocity of water flow (Madsen et al., 2001), stabilising substrate, trapping particulates and influencing biogeochemical cycles through sequestering carbon and oxygen within the rhizosphere (Jeppesen et al., 1998; Madsen, Olesen, & Bagger, 2002; Sand-Jensen & Frost-Christensen, 1999; Willby, Pitt, & Phillips, 2009). Amphibious plants are a significant component of lake and wetland ecosystems, with isoetids being among the most widespread group of macrophytes in Scottish lakes (Farmer & Spence, 1986). The eponymous species of the lake littoral zones is the amphibious isoetid, *Littorella uniflora* (Shoreweed). This small, evergreen plant is almost ubiquitous on the shores of Scotland's lakes and has been found to be indicative of soft water, shallow lakes with fluctuating water levels (authors work, *unpublished*). It frequently dominates the littoral and shore zone, forming monospecific stands or lawns on coarse sand and gravel/pebble dominated shores (Fig. 2) (Murphy, 2002; Nielsen & Sand-Jensen, 1997), extending from to 3-4 metres below the water level to one metre or more above it on exposed shores in late summer (West, 1910 cited in Preston & Croft. 1997; Baastrup-Spohr, Møller, & Sand-Jensen, 2016; authors observation).

Littorella uniflora is a key lake macrophyte, playing a crucial role in wider lake ecology as a primary producer, providing habitat for bacteria and epiphytic algae and as a resource for filtering and grazing invertebrates (Willby et al., 2009). The considerable phenotypic plasticity of *L. uniflora* makes it a resilient littoral species persisting where other species are displaced by water level range (authors work, *unpublished*) or low nutrients (Madsen et al., 2002). In addition, *L. uniflora* is better equipped to resist competition than other isoetids, such as *Lobelia dortmanna*, as it is faster growing and able to tolerate limited eutrophication. Consequently, it is broadly distributed in lakes of varying productivity compared to other isoetid species (Farmer & Spence, 1986; Preston & Croft, 1997).

L. uniflora alters its morphology in response to internal and environmental conditions, including plant age, season, light availability, inundation and water depth, CO_2 and O_2 sediment concentrations (Baastrup-Spohr et al., 2016; Robe & Griffiths, 2000). Physical adaptions favouring low nutrient and fluctuating water environments include a comparatively small size, the stiff shoots arranged in a rosette life form, with well-developed and continuous gas lacunae between shoots and roots (Raven et al., 1988; Robe & Griffiths, 1990). Roots form the bulk of the biomass of *L. uniflora,* with a high root to shoot ratio, contributing towards an ability to meet over 80% of carbon requirements from sediment (Boston, H & Adams, M, 1987; Nielsen & Sand-Jensen, 1991; Raven et al., 1988) where pore-water hold higher CO_2 concentrations than the overlying water (Gruca-Rokosz & Tomaszek, 2015). In addition, *L. uniflora* is able to fix CO_2 via the Crassulacean Acid Metabolism (CAM), which not only facilitates dark uptake and recycling of 75-80% CO_2 from the lacunae, but is a well-known adaptation for drought tolerant plants, enabling night time gas-exchange, when water vapor pressure deficits are lower (Nielsen & Sand-Jensen, 1991; Tranvik et al., 2009). The carbon conserving mechanism of CAM is advantageous in standard isoetid habitats (Madsen et al., 2002).

L. uniflora reproduces vegetatively via stoloniferous growth when submerged, but exposure stimulates germination of seeds and mature plants shift to produce flowers within 3-4 weeks (Arts & van der Heijden, 1990; Farmer & Spence, 1986; Hostrup & Wiegleb, 1990; Robe & Griffiths, 1998). *L. uniflora* leaves form a basal rosette mostly of cylindrical leaves (Bagger & Madsen, 2004), which upon emersion form aerial leaves within a 2 - 5 days, (submerged leaves die within 24 hrs) (Hostrup & Wiegleb, 1991), that develop stomata, reduce the size of lacunae and develop a thicker cuticle (Hostrup & Wiegleb, 1991; Nielsen & Sand-Jensen, 1997). Leaf size, usually 4–12 cm long, depends on the presence and type of stress factors, such as changing water levels (Hostrup & Wiegleb, 1991), and exposure and age (Robe & Griffiths, 1998). In these ways *L. uniflora* exhibits remarkable phenotypic plasticity in response to water level changes (Robe & Griffiths, 1998).

Despite its stress tolerant attributes *L. uniflora* has declined widely in Britain, especially at the southern edge of its range, attributed to reservoir construction, acidification and eutrophication (Farmer & Spence, 1986; Preston & Croft, 1997). Elsewhere in Europe, *L. uniflora* has forgone a dramatic population decline since the 1950s and its persistence in certain lakes may well depend on a certain degree of water level instability, especially in the face of eutrophication. The remarkable capacity of *L. uniflora* for rapid morphological change in response to various stress factors, including water stress, and its importance to lake ecosystem processes, makes this a model species for research into direct and indirect impacts of water level fluctuation, particularly as a CAM plant, due to predictions of increasing precipitation, lake water level ranges and drought, with climate change. As a highly adaptable, robust species, losses or reduction in abundance may be indicative of wider, negative impacts to lake ecosystems. In addition, there is a need for better understanding of its responses to lake wide water level fluctuation (WLF) and sub lake habitat factors in order to mitigate further losses. Our aim was to establish an empirical basis for how *L. uniflora* morphology and biomass are related to water level range and associated abiotic factors in lakes such as wind and wave exposure, shore slope and substrate type. We hypothesised the stress tolerant isoetid, *Littorella uniflora,* would be directly and associated with lake WLF given its ability for rapid morphological change to water stress. We anticipated that moderate levels of WLF may be beneficial to *L. uniflora* biomass and morphology but that there would be an upper threshold to this relationship after which WLF would have a negative association. Further we hypothesised that environmental factors influenced by WLF in lakes such as wind and wave exposure would influence the biomass and morphology of *L. uniflora*, reducing both to diminutive levels.

4.2 Methods

Littorella uniflora plants were sampled from ten lakes in central Scotland. The lakes were selected to be constrained by geographical situation, predominantly in the Trossachs (Fig. 3) but within a 160 km radius of NS813980 (Central Scotland/Stirling), under 400 m A.O.D elevation and lake areas over 0.15 km^2. In addition, lakes were selected to encompass a range of fertility and water level regimes, including six reservoirs and four unregulated lakes identified in earlier work (Chapter 2) as having *L. uniflora* present. Water nutrient data were obtained for each lake predominantly between 2007 and 2009, based on routine sampling and analysis undertaken by the Scottish Environmental Protection Agency (SEPA). Data for each key determinants were averaged, for years 2007 to 2009, including Total Phosphorus (TP as mgL^{-1}), Ammonia as N (TON as mgL^{-1}), Alkalinity (Alk as mgL^{-1}) (Table 1).

Lake area (km^2) and elevation (m A.O.D) were derived for each lake via the UK Lakes Portal (Hughes et al., 2004). Data on water level fluctuation range (WLF), (i.e. difference between effective mean annual maximum and minimum water levels) for regulated lakes were sourced from reservoir operators (Scottish Water and Scottish Southern Electric).

Where direct lake level data were not available, data were taken from river monitoring stations situated in close proximity to the outflow using the average level data range (SEPA Water Level Data). Disparities in water level data were supplemented by direct measurement of trash line elevations, and inspection of online aerial and other imagery available (e.g. Google Earth). Full time series (daily or weekly) water level data were only available for a small subset of lakes, whereas range data was commonly available, therefore we have used range as an indicator of regime. Field measurements and estimates obtained via online imagery were compared with time series data for a number of lakes and reservoirs and found to be comparable.

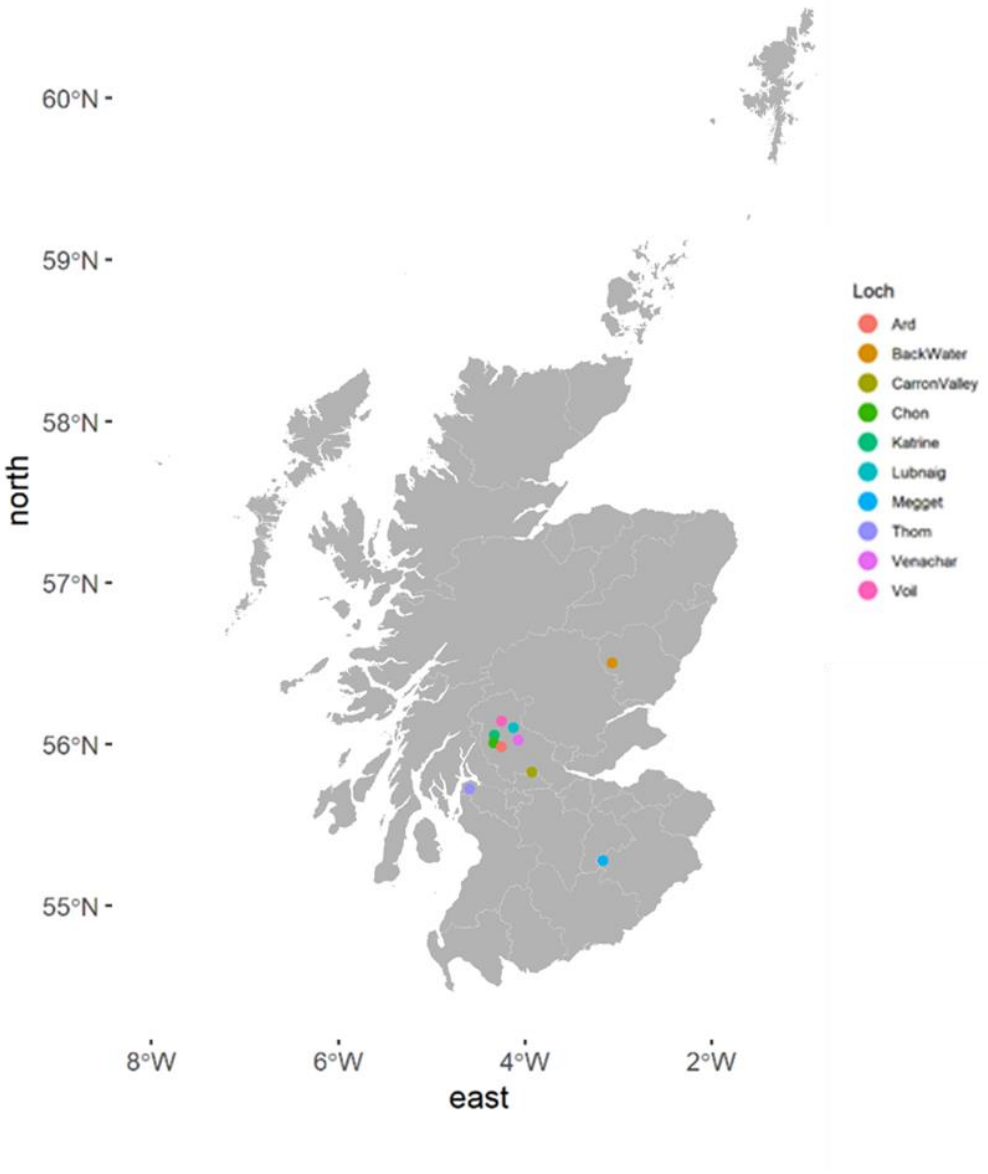


Fig. 3. Locations of survey lakes for *Littorella uniflora* and sediment samples.

(Scottish Water, Scottish & Southern Electric). Where daily or weekly level data were available the mean range was calculated based on the 10th and 90th percentiles to reduce the impact of atypical extreme values (sometimes associated with reservoir management).

Field Sampling

All field sampling and surveys were conducted within a two-week period at the end of September 2014, when water levels are at their lowest in the majority of Scottish lakes and reservoirs. 2014 was the hottest year recorded in Scotland for over 100 years, and for September 2014 the lowest rainfall recorded since 1972 (and 2nd lowest in our 100 years) (Met Office National Climate Information Centre, 2020), reservoir levels were at the lowest expected levels (except for full drainage activities) as were unregulated lakes.

All samples were collected between 10.00 and 18:00 to mitigate for natural variability in morphology during the year and day versus night (Robe & Griffiths, 2000; Robe & Griffiths, 1992). Each of the ten lakes were sampled at two stations with contrasting potential wave exposure. Maximum fetch to survey station was obtained using grid coordinates and on-line mapping (Digimap and GoogleMaps), then adjusted for predominant wind duration and direction (average for 10 years prior) using wind rose data obtained from the closest available Met Office station (Appendix I).

Fig. 4 Transect and quadrats from the water line to the uppermost growth site of *L. uniflora* at Loch Lubnaig

At each of the 10 lakes, there were two stations per lake, varying by sheltered or exposed sites, with the exception of Megget Reservoir where *L. uniflora* was recorded in only one station (quadrats, n=3) and Loch Katrine where 3 transects were collected from one station and, a single transect from the other station (quadrats, n=12); total samples, n=63. Each transect was placed on a representative section of the shore, perpendicular to the water's edge. Transect lengths were determined by the highest and lowest positioned plants on the exposed shore relative to the water's edge. On each transect three quadrats, (area = 0.0625 m²), were situated at the area of. *L. uniflora* growth, (Fig. 2) which was the highest, mid distance and lowest to the water line. All plants harvested from within each quadrat were extracted to maximum root depth, where possible. A manual theodolite was used to measure the height and distance of each quadrat relative to the lake water level line and to establish the slope to each sample and slope of the surveyed shore overall (Table 1). Substrate samples were obtained immediately adjacent to each quadrat to quantify organic matter and particle size distribution. *L. uniflora* samples were wet-sieved gently on site to separate and remove attached soil and substrate, then stored for a maximum of two weeks in the dark at 5^{o}C. Shore-wide particle size and abundance were assessed using the Lake habitat survey (LHS) (100 m wide section of shore) method of visual assessment of percentage cover of five particle size classes (using the Krumbein phi scale, based on a modified Wentworth scale); (i) sand (diameter 0.25– 2 mm), (ii) gravel (2–16 mm), (iii) pebble (16–64 mm), (iv) cobble (64–256 mm), and (v) boulder (256– 1024 mm), (Rowan et al., 2006).

Table 1. Characteristics of predictor data across 10 Scottish lakes. ID is the abbreviation used in the results.

Variable scale	ID	Variable	Unit	Description
Lake	Water Level	Water level range	m	Lake water level range determined by the 10th to 90th percentile of full range or estimated range obtained via aerial imagery and strand-line indicators
	Area.km2	Lake surface area	km²	Lake surface area
	Elevation	Lake Elevation	m	Lake elevation (AOD)
	Alkalinity	Alkalinity	mgL^{-1}	Alkalinity as CaCO3
	Ammonia	Ammonia	mgL^{-1}	Ammonia as N (mean)
	TP	Phosphorus	mgL^{-1}	Total phosphorus (mean)
Shore	Potential.Wave.Exp	potential wave exposure	m	Maximum potential wave exposure at survey shore
	Av.LHS.phi	weighted average of shore substrate phi grade	ϕ scale	Weighted average sediment / aggregate size for shore from LHS survey using Krumbein *phi* (ϕ) scale
	Shore slope	shore slope/angle	degree (°)	Slope of shore at transect from lake water line at survey time to farthest sampled site
Quadrat	Q.Height	height difference to quadrat	m	True height of quadrat relative to water line
	Q.Dist	distance difference to quadrat	m	Horizontal distance of quadrat from water line
	Q.Slope	shore slope to quadrat	degree (°)	Slope from water line to quadrat
	Q.OMCont	Organic matter	g	Organic matter derived by LOI from quadrat sediment (mean)
	Av.Sed.Phi	Average sediment size	(ϕ) scale	Weighted average sediment / aggregate size per quadrat, using Krumbein *phi* (ϕ) scale
	WghtPctH20	Percentage of pore water in sediment	%	pore water moisture content of sediment per quadrat

Laboratory methods

Organic content of the substrate was quantified via loss on ignition (6 h at 450 °C). Sediment was separated to aggregate size using wet/dry sieving, with each fraction being dried until constant weight at 105°. The corresponding amounts for each quadrat were recorded and used to calculate pore water and weighted average particle size based on the Wentworth scale and adapted by the Krumbein *phi* (ϕ) scale (a logarithmic scale useful for statistical analysis) (Krumbein, 1938; Wentworth, 1922). LHS shore particle sizes were adapted to obtain the weighted average of aggregate size for shore using the Wentworth-Krumbein scale.

Fresh to dry weight ratios and water content of shoots, stems and roots were determined for each plant (Table 2), with plants dried to a constant weight at 60°C as per Robe & Griffiths, (2000). Root to shoot ratio (RSR) was calculated (Table 2), as it is likely related to uprooting potential of *L. uniflora* and sediment organic matter concentrations (Spierenburg et al., 2013). In addition, we calculated leaf shape as leaf length (L) to leaf width (W) ratio for live shoots and dead shoots (Table 2). These ratios were made to enable comparison of morphology between environmental predictors and with other research (Robe & Griffiths, 1992). The total number of *Littorella* rosettes per quadrat were counted, with 10 rosettes then randomly selected, washed gently and blotted dry. These individuals were then weighed, dissected, and measured. Shoots (leaves) stems and roots were separated for individual measurements and weights. Stolons were removed and disregarded. All widths and lengths were measured using vernier calipers with a binocular loupe (x20 magnification) for accuracy.

Exploratory and statistical analyses

To reduce model complexity principal components analysis (PCA) was used to separate sets of water chemistry data and the environmental predictors to identify those variables that maximised variation amongst sites (Appendix II). Correlations between predictor variables were assessed in a correlation matrix (Appendix III) and checked for variance inflation (VIF). Where variables were highly correlated (VIF > 10) they were removed. Pearson's correlations and PCA of lake physical attributes (lake size, elevation, depth, etc.), physicochemical variables (TP, Ammonia, chlorophyll, etc.) and expert knowledge was used for exploratory data analysis of the global lake dataset (n = 63 samples).

Table 2. Morphological attributes of *Littorella uniflora* calculations. Each calculation is based on the mean of 10 randomly sampled individual rosettes from each sampled quadrat.

ID	Variable	Unit	Description
Tot.St_Biom_Q	Total standing biomass per quadrat (roots, shoot and stem)	g/m²	Total standing biomass = mean combined dry weight of all tissues (shoot, stem & root) per rosette / plot area (0.0625m²) * number of rosettes per quadrat
ABG.Biomass_Q	Above ground standing biomass (shoots and stem)	g/m²	Standing biomass = mean combined dry weight of above ground tissues (shoot & stem) / plot area (0.0625m²) * number of rosettes per quadrat
TotalWaterCont.avg	Water content of whole plant	g	Fresh weight-dry weight of whole plant (stem, shoot and root) (mean)
Shoot_Mass	Combined dry weight of ?? green leaves	g	Weight of dried shoots per rosette (mean)
LeafLength_Green	Length of longest fresh shoot per rosette	mm	Length of longest fresh shoot per rosette (mean)
LeafLength_Decay	Length of dead shoot (attached to rosette)	mm	Length of dead shoot (attached to rosette) (mean)
LeafWidth_Green	Width of fresh shoot per rosette	mm	Width of fresh shoot (mean)
LeafWidth_Decay	Width of dead shoot (attached to rosette)	mm	Adjusted shoot width; average proportional change from round to flat shoot width (mean)
NShoots_Gr	Number of fresh shoots per rosette	count	Number of fresh shoots per rosette (mean)
NShoots_Dec	Number of dead shoots per rosette	count	Number of dead shoots per rosette (mean)
RootLength	Root length	mm	Length of longest root (mean)
Root_Mass	Dry weight of roots per rosette	g	Dry weight of roots per rosette (mean)
RSR	Root to Shoot ratio	na	ratio of dry weight root weight (mean) /shoot weight (mean)
L:W.Live	Shoot length to width ratio (fresh shoot)	na	Shoot length (mean) to width (mean) ratio (fresh shoot)
L:W.Dead	Shoot length to width ratio (dead shoot)	na	Shoot length (mean) to width (mean) ratio (dead shoot)

To further reduce model complexity, a PCA was applied to *L. uniflora* morphological attributes after correlations between response variables were assessed in a correlation matrix (Appendix III) and checked for variance inflation (VIF). Where variables were highly correlated (VIF > 10) they were removed. Subsequently all models were analysed using generalised mixed effects models (glmer) with Poisson family link function and lake included as a random factor, the dispersion of each model was checked and did not violate model assumptions. For each glmer, following standard forward permutation testing, the optimal model was taken as that with the lowest AIC value (see Appendix IV for model outcomes of best model of each response variable).

All statistical analyses and graphics were produced using R Studio version 3.5.1 (http://www.rstudio.com/), with the additional packages; Corrplot (Wei et al., 2017), Factoextra (Kassambara et al., 2017), FactoMineR (Husson et al., 2018), ggplot2 (Wickham et al., 2019), lme4 (Bates et al., 2015), sciplot (Morales et al., 2011) and vegan (Oksanen et al., 2013).

4.3 Results

A total of 10 lakes were included in the analysis with measurements of environmental variables on lake, shore, and quadrat scales. The most variable characteristic (relative to the lake water) was quadrat height, with the least variable characteristic being the average shore *phi* grade (Table 3).

Table 3. A summary of environmental characteristics per lake, (lakes, n=10; stations n=19; samples n=63), displaying; Median, Mean ± SE, min – max. (TP=total phosphorus, Av.LHS.phi = average LHS phi grade across shore, Q= quadrat, Av.Q.Sed.Phi (Q)= average sediment phi grade at quadrat level, WghtPctH20 = weight percentage of water in quadrat sediment)

Variable	Median	Mean	Min – Max
Water Level / WLF (m) n=10	1.6	1.91 ± 0.12	0.91 – 4.3
Lake area (km²) n=10	2.59	4.42 ± 0.56	0.67 – 13.26
Elevation (m) (A.O.D) n=10	121	149 ± 10.39	36 – 328
TP (mgL^{-1}) n=10	0.007	0.010 ± 0.001	0.005 – 0.025
Alkalinity (mgL^{-1}) n=10	6.66	7.34 ± 0.81	1.44 – 23.94
Ammonia mgL^{-1} n=10	0.027	0.027 ± 0.001	0.01 – 0.036
Shore slope (°) n=19	4.210	4.64 ± 0.36	1.61 – 14
Potential wave exposure (m) n=19	1947	2378 ± 181	978 – 5908
Av.LHS.phi (ϕ) scale n=19	-3.06	-3.02 ± 0.15	-5 - -0.44
Q.Height (m) n=63	0.16	0.64 ± 0.15	0 – 5.58
Q.Dist (m) n=63	2.8	8.15 ± 1.62	-0.2 – 55.2
Q.Slope (°)n=63	3.31	3.72 ± 0.36	0 – 15.9
Q.OMCont (g) n=63	3.46	5.43 ± 0.68	0.34 – 20.61
Av.Q.Sed.Phi(Q)(ϕ) n=63	-0.231	-0.225 ± 0.08	-0.3 - -0.189
WghtPctH20 (%)n=63	26.1	29.5 ± 2.48	0.93 -72.5

L. uniflora measures of morphological attributes were recorded and RSR and L:W ratios for live and dead shoots calculated (Table 4).

Positive correlations were identified between above ground standing biomass and total standing biomass, potential wave exposure with lake area and fetch, sediment organic matter content with percentage of pore water, as well as quadrat height and quadrat distance. *L. uniflora* morphological attributes were significantly associated with several physicochemical variables measured (Fig. 5 Table 5, Appendix X) including shoot mass, length of live leaves, plant water content and root length all of which were positively related to shore slope. Leaf length:width ratio of dead leaves had a positive relationship with quadrat distance from the water line. Negative relationships were established between above ground biomass, root:shoot ratio, root length and length:width ratio of dead leaves with the average sediment *phi* grade of the shore. Root:shoot ratios and dead leaf length to width ratios were negatively associated with ammonia concentrations.

Water level range was not significantly associated with any measured attributes of *L. uniflora*. Potential wave exposure had negative relationships with the length:width ratios of live leaves, root:shoot ratios, root lengths and the dead leaf length:width ratios (Fig. 5, Table 5, Appendix X).

Table 4. Morphological variables measured per quadrat (n = 63) displaying; Median, Mean ± SE (min – max). All values are based on means calculated from 10 rosettes randomly sampled from each quadrat (0.0625 m^2).

Variable	median	mean	min - max
Total standing dry biomass (g/m^2)	113.67	129.49 ± 12.94	0.58 - 414.27
Above ground standing dry biomass (g/m^2)	36.47	53.15 ± 6.01	0.36 - 230.03
Water content (plant)(g)	0.15	0.17 ± 0.01	0.02 - 0.61
Shoot mass (g)	0.02	0.02 ± 0.00	0.01 - 0.04
Leaf length (live) (mm)	33.26	34.24 ± 1.25	14 - 63.72
Leaf length (dead) (mm)	35.6	36.54 ± 1.6	0.0 - 70.09
Leaf width (live) (mm)	1.24	1.34 ± 0.06	0.64 - 3.34
Leaf width (dead) (mm)	1.3	1.31 ± 0.06	0. - 2.87
Number of fresh shoots per plant	3.2	3.31 ± 0.11	0.5 - 6.70
Number of dead shoots per plant	5.1	5.15 ± 0.25	0.0 - 10
Root Length (mm)	60.76	60.62 ± 1.8	34.66 - 106.9
Root Mass (g)	0.03	0.03 ± 0	0.01 - 0.1
Root mass : shoot mass ratio (RSR)	1.67	1.78 ± 0.12	0.2 - 5.35
Live leaf length : width ratio (L:W.Live)	26.59	26.71 ± 0.89	11.08 - 42.86
Dead leaf length : width ratio (L:W.Dead)	28.71	29.94 ± 1.52	0.00 - 132.05

The strongest relationships derived for measures of *L. uniflora* morphology were the positive effect on dead shoot length:width ratio and environmental predictors (Fig.5 Table 5), primarily increasing with distance from the water's edge (a coarse measure of time exposed). Above ground biomass (correlated with total biomass), was significantly negatively associated with shore aggregate size as was root:shoot ratio, root length and the length:width ratio of dead leaves (Fig. 5, Table 5). Above ground biomass was also negatively associated with shore slope from the water line.

Table 5. Multivariate mixed model predictor effects for subset of morphological response variables (scaled and significance P = 0***, 0.001**, 0.005*, 0.1.), (all predictors transformed where required and data scaled) (full results Appendix X) (ABG.Biomass_Q = above ground biomass at quadrat level, L:W.Live = leaf:width ratio live leaves, L:W.Dead = leaf:width ratio for dead leaves, RSR= root:shoot ratio. Av.LHS.phi = average LHS phi grade across shore, Q= quadrat, WghtPctH20 = weight percentage of water in quadrat sediment, Potential.Wave.Exp = maximum potential wave exposure)

Morphological response	Environmental predictor	Effect Size (t)	P value	Significance
ABG.Biomass_Q	Av.LHS.phi	-3.011	0.0377	**
ABG.Biomass_Q	Q.slope	-1.786	0.0795	.
Shoot_Mass	Shore slope	1.671	0.0999	.
L:W.Live	Potential.Wave.Exp	-1.7	0.096	.
LeafLength_Green	Q.OMCont	2.514	0.0145	*
TotalWaterCont.avg	Shore slope	2.253	0.0279	*
TotalWaterCont.avg - w/o outlier fr0m backwater	Shore slope	1.744	0.00801	**
RSR	Ammonia_mg.L	-2.813	0.00636	**
RSR	Q.OMCont	-2.529	0.01394	*
RSR	Potential.Wave.Exp	-2.316	0.0238	*
RSR	Av.LHS.phi	-2.188	0.03237	*
RootLength	Av.LHS.phi	-2.541	0.0135	*
RootLength	Potential.Wave.Exp	-2.403	0.0192	*
RootLength	Shore slope	1.852	0.0687	.
L:W.Dead	Q.dist	4.171	0.00011	***
L:W.Dead	Av.LHS.phi	-3.262	0.001793	**
L:W.Dead	Potential.Wave.Exp	-2.754	0.007854	**
L:W.Dead	Ammonia_mg.L	-1.916	0.07985	.

Leaf length (live) was significantly and positively correlated with substrate organic matter content while the Root:Shoot ratio was negatively correlated with organic matter content. Root:Shoot ratio and Length:Width ratios of dead leaves were significantly negatively associated ammonia concentrations.

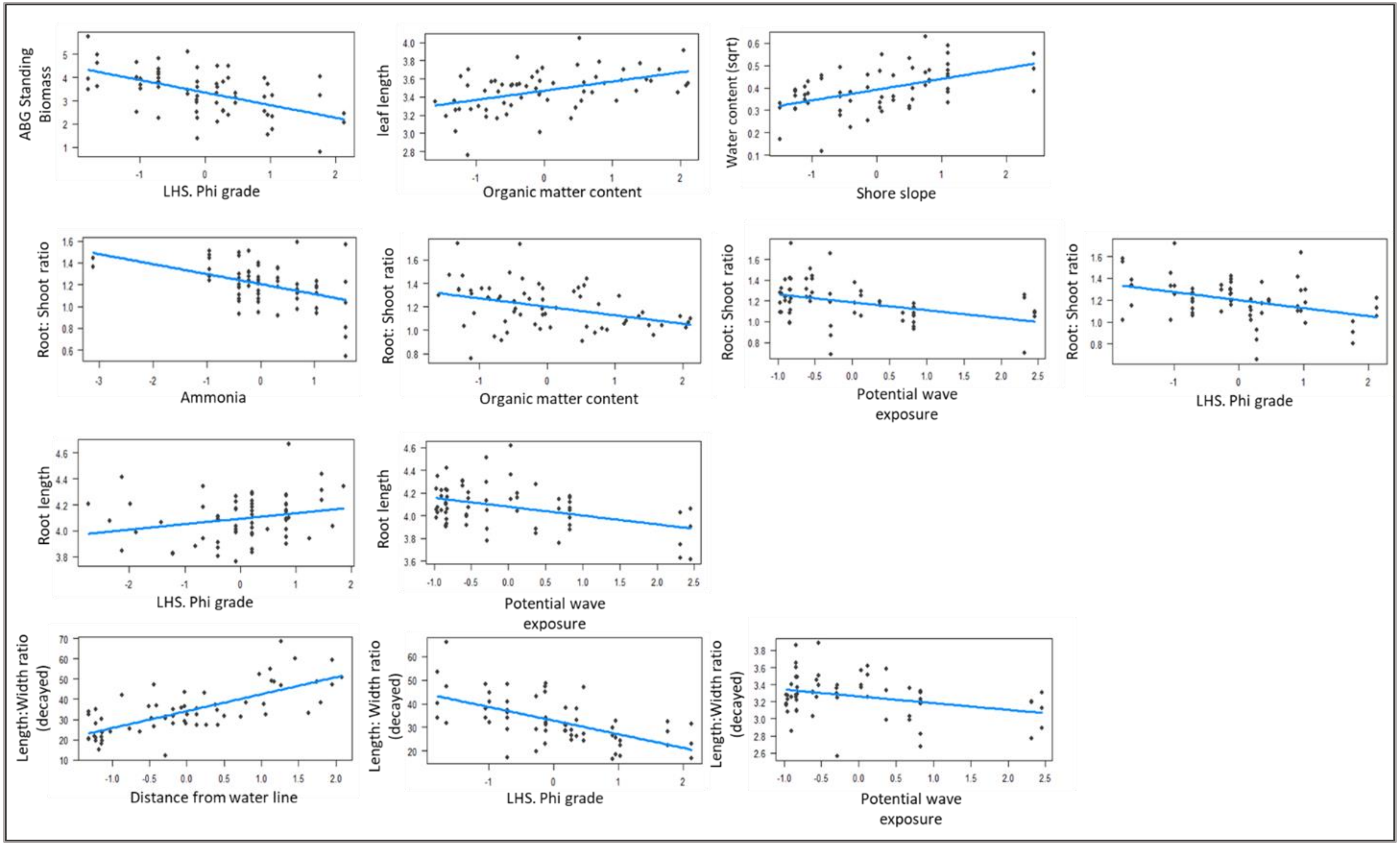


Fig. 5. Subset of multivariate mixed model predictor effects for subset of morphological response variables including; ABG.Biomass_Q, Leaf Length (live), TotalWaterCont.avg, RSR, RootLength (all predictors data scaled), subset= significant to; p>=0.005) (Table 5, full results Appendix VI).

4.4 Discussion

Our study reveals that the morphology and biomass of *Littorella uniflora*, a key component of lake vegetation, were directly associated with a combination of environmental factors, in particular sediment type and quadrat location (position on shore), relative to lake water levels.

Environmental influences on morphology

Increased shore slope was associated with increased plant water content (here essentially a reflection of plant size), root length and shoot mass, whilst also associated negatively with above ground and total biomass (Fig. 6). This implies that there was a lower density longer, slender rosettes sparsely situated and therefore lower biomass on steep slopes, while on gentle slopes plants tend to be a dense lawn of small plants (with higher biomass).

Increased plant water content suggests increased plant size and so water retention increased with higher shore slopes, relative to lake water levels. Added to this, root length and shore slope had a strong positive, but not significant, relationship.

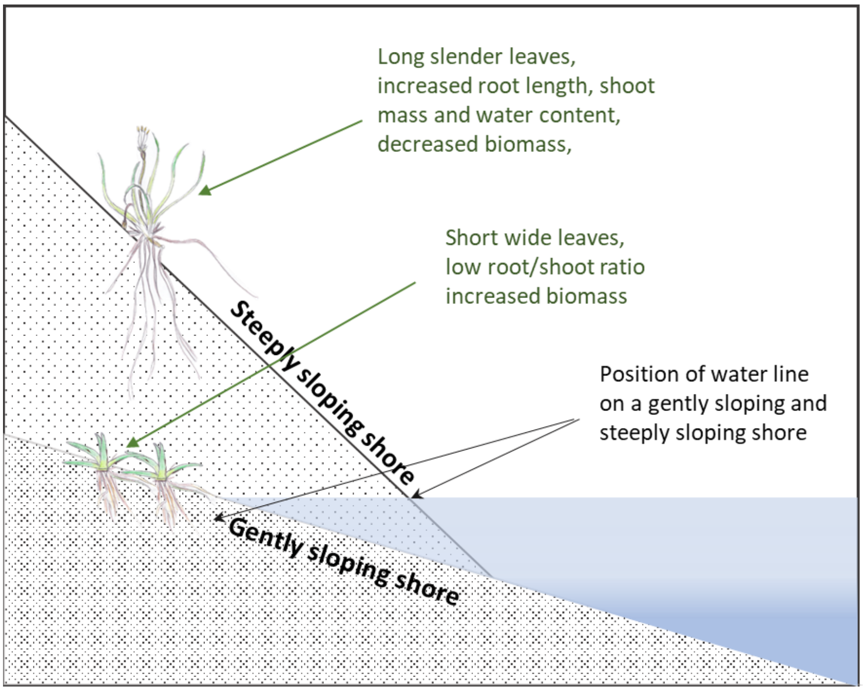


Fig. 6. Idealised shore slope profile showing water line positions dependant on slope with measured morphological differences of *L. uniflora* (adapted from Pierce, 2004), gently sloping shore = 1 to 5 degrees, steeply sloping shores = > 5 degrees.

These findings could be attributed in part to the method of photorespiration used by *L. uniflora's* - Crassulacean Acid Metabolism (CAM) - which is more commonly recognised as an adaptation of drought-resistant plants (Nobel, 1976; Ting, Dean-Thompson, & Dugger, 1967). However, while development of CAM in aquatic plants is attributed to low ambient CO_2 availability in the aquatic environment (Keeley, 2014), it is also likely that this adaptation conserves water in emergent *L. uniflora* leaves, as does the reported thickening of the cuticule upon emergence (Hostrup & Wiegleb, 1991).

With increased shore slope from water's edge, above ground biomass of *L. uniflora* reduced (correlated with total biomass), while root length increased, indicating an increased investment in this attribute over above-ground shoot investment, in line with an effectively lower water table (Fig. 6). These results concur with previous studies of *L. uniflora* which concluded that terrestrial forms which had been separated from the lake water were found to have the longest roots (Szmeja, 1994), consistent with a widely observed root elongation response in plants to maintain access to soil water. Additionally, we found negative, though non-significant relationship between above ground biomass and root:shoot ratio, (Appendix V), indicating that investment in roots may be at the cost of the shoots and vice versa. In addition, shoot mass increased on steeper shore slopes (Fig. 6), which may be related to the aforementioned thickening of the cuticula, or an increase in number or size of leaves.

Conversely, stand biomass was higher on gently sloped shores. Given that these shores will be terrestrial for weeks due to seasonal exposure, this may correspond with Arts and van der Heijden (1990), who showed that desiccation was the most stimulatory factor in seed germination with a 76% germination rate following 2-4 weeks of drying. Seedling germination may enhance biomass by increasing the densities of small plants that tend to be associated with high biomass stands. Despite seasonal desiccation, plants growing on a shore with a gentle slope (1-5 degrees), would access the water table more readily, than those growing on higher slopes (Fig. 6), therefore lacking the cost of increased root investment potentially leading to increased resources for reproduction. During years when water levels remain high and the zone of germination remains submerged, seeds will remain viable for decades, waiting for the environmental que of desiccation, after which, once seeds are rewetted this results in rapid and almost synchronous germination (Preston & Croft, 1997). In addition, the reduced shoot mass on these slopes could explain the increasing standing biomass at this lower zone of shore (relative to the water level regime), as a set area will hold a higher number of small plants, than is possible with larger plants. Length:width ratio of dead leaves increased with shoots becoming longer and slimmer with greater distance of the individual plant away from the water's edge, this change in morphology is similar to that observed on terrestrial shoots in late September by Robe & Griffith (1998).

While plants further from the water (correlated with height of the quadrat relative to the water's edge) would logically be exposed for longer both time emersed and distance/height on the shore will be determined by lake water level fluctuations (distance and height on the shore was correlated with WLF, Appendix V). In addition, dead leaves may reduce by width whilst losing moisture, whilst length remains constant leading to an enhanced length:width ratio. Our research reveals that L. uniflora morphology is influenced by potential wave action. Wave and wind energy influence littoral sediment properties (i.e. bulk density, pore water content and grain size) and thereby slope, through the influence of lake morphometric attributes including water depth, shoreline fetch, substrate and exposure (Blais & Kalff, 1995; Hellsten, 1997; Rowan et al., 2006).

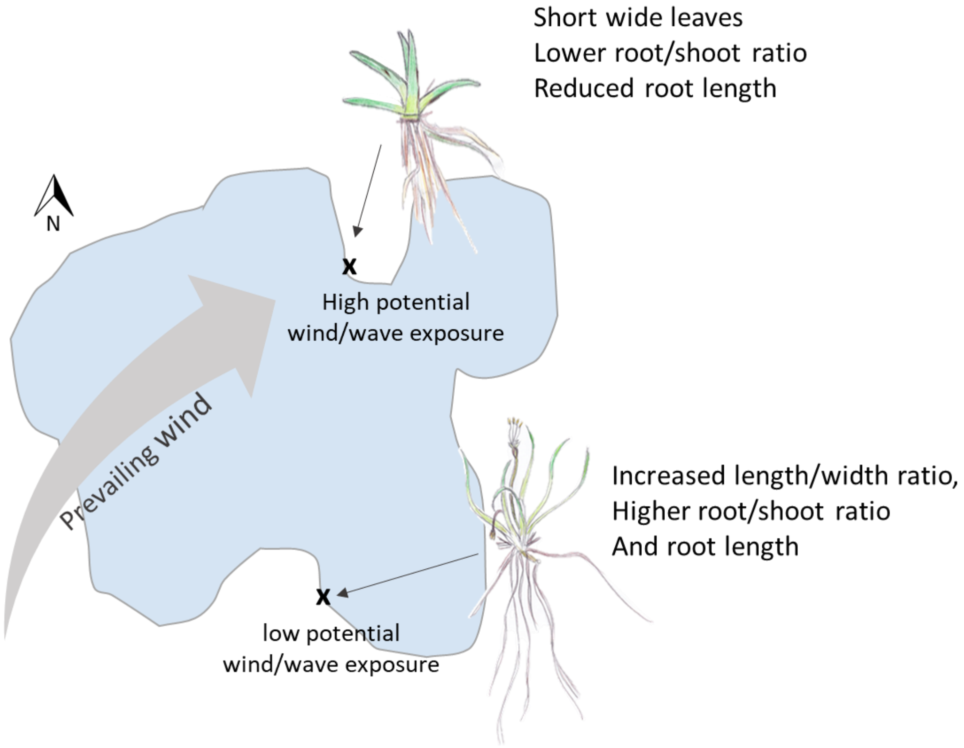


Fig. 7. Idealised lake depicting sampling sites with contrasting potential wave exposure and the measured differences in *L. uniflora* morphological attributes at each (sheltered/exposed sites).

Length:width ratios of dead and live leaves, root length and root:shoot ratios were found to be negatively associated with increasing potential wave exposure (Fig. 7). This infers that *L. uniflora* inhabiting shores with increased exposure to wave action, have shorter, wider leaves, in addition to shorter roots and less investment in roots than shoots, than those in sheltered areas. This is in contrast to the inferred investment in root biomass as an adaptation to resist uprooting (Raven et al., 1988). Risk of uprooting may increase with areas exposed to wave action due in part to the extensive air-filled lacunae of *L. uniflora*, which would increase buoyancy potential. Uprooting potential of aquatic plants is a function of pulling hydraulic forces relative to the strength of the anchorage (Spierenburg et al., 2013), and therefore cohesive structure of the substrate. Plausibly with increased potential wave action the shore will retain more moisture in the splash zone in comparison to a sheltered shore. Therefore, root investment is not required if this adaptation is primarily for water conservation and reducing risk of desiccation, rather than anchorage. In addition substrates exposed to intermittent wave action, particularly on lake littoral fringes which are subjected to increased water level fluctuations, may become more compacted due to a loss of organic matter following drainage, combined with compaction from gravitational forces, in this event sediment density may act to prevent uprooting once sediments are re-submerged (Baastrup-Spohr et al., 2016).

L. uniflora are small plants so may gain protection through avoidance of wave action, through their diminutive size, furthermore they grow in a dense, cohesive matt like structure, which may provide additional protection from uprooting for each individual. Therefore, despite each individual having reduced investment in roots, collectively this may be a beneficial strategy. In addition, Spence (1964), describes how distribution of macrophytes within individual lakes are influenced directly by water turbulence and through the influence of this on the substrate, as well as directly by the substrate (Spence, 1967). Our study suggests this is equally true of morphology. These findings imply that human pressures from water level regulation which result in, increasing water level fluctuations and decreasing water depths, along with natural pressures, from wind energy and wave action, may have additive negative impacts on *L. uniflora* morphology. As such the littoral lake bed, will have a reduced height of water above it, or will be dewatered due to reduced water levels, and therefore will be more exposed to any turbulence due caused by wind and wave energy.

Substrate influence

The relationship between *L. uniflora* morphology and moisture availability is mediated by the sediment aggregate properties which determine variability in moisture retention. A fine-textured soil high in organic matter retains moisture (as shown by the positive correlation in our data with organic matter and interstitial pore water, Appendix V), whilst sediments with increasing proportions of sand are more effective at water filtration. Therefore, a plant that exhibits morphological adaptations to water content should be intrinsically influenced by the type of substrate it grows upon when emersed, in conjunction with the water available from a lake and precipitation.

Our study locations were constrained in sediment type from predominantly coarse sand to gravel/pebble shores (Fig. 2a and b), based on where *L. uniflora* is capable of growing. By implementing *phi* (ɸ) scale from LHS data, to create a continuous scale from gravel-pebble dominated shores to coarse sandy shores, our study reveals that morphological attributes of *L. uniflora* are mediated by the sediment and aggregate size where it grows. Predominantly coarse sand shores were associated with reduced *L. uniflora* above ground biomass (correlated positively with total biomass), reduced leaf length:width ratio and a larger investment in root mass relative to shoot mass (R:S ratio), despite reduced root lengths (Fig. 8).

Increased investment in root mass versus shoot mass may be due to the high filtration capacity of granular sand, if, once water levels drop, roots investment increases to track moisture resources from a lower water table. It is worth noting that coarse, sandy shores are typically the sheltered shores of lakes which were also associated with increased root to shoot ratios (Fig. 7); therefore, this investment may be at a cost of total and above ground biomass.

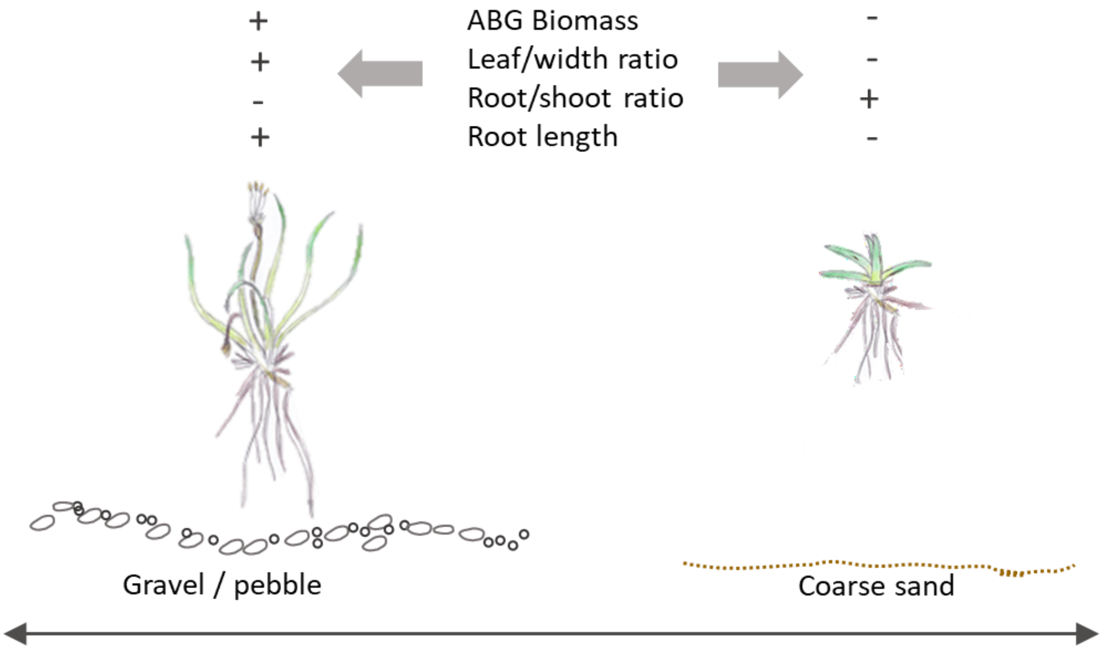


Fig. 8. Differences in *L. uniflora* morphology measured with predominant shore aggregate.

Gravel-pebble shores were associated with increased *L. uniflora* root length (Fig. 8). Sandy shores are typical of areas in lakes with less wind and wave exposure, whereas predominantly gravel-pebble aggregates are found in high wind and wave exposed areas of lakes (Fig. 2a and b), (Pierce, 2004). However, with regulation this can change when lake water levels are at their lowest, as the water's edge then occurs where finer particles have been withdrawn and deposited from further up shore. Therefore, root length may be explained by the frequency of water being supplied to more exposed sites via breaking waves. Gravel-pebble rich sediments with large pore spaces should increase the rate of drainage away from the sediment surface, therefore increased investment by *L. uniflora* in root length in these sites may be expected. However, the consistent wave exposure may resupply moisture more frequently to these environments. Additionally, the armouring effect of coarser aggregates may increase stability of rooted plants during high wind/wave exposure such as storm events. On mostly sandy shores, where roots extend to find moisture, this same strategy may reduce uprooting in what is a more mobile substrate, as described by Baastrup-Sphor et al. (2016). The increased leaf length:width ratio of *L. uniflora* on gravel/pebble shores may further reduce uprooting with wave exposure as a result of reduced buoyancy potential (Farmer & Spence, 1986; Szmeja, 1994), which may be more likely on sandy shores but is perhaps altered if these shores are steeply sloped (Fig. 6) (though no such correlation was found).

Investment in moisture conservation by *L. uniflora* is suggested by the physical adaptations found associated with organic matter content; we found leaf length increased with organic matter (OM), (positively correlated with the percentage of pore-water), as well as a negative relationship with root-shoot ratio. Therefore, in a high OM, high pore-water habitat, *L. uniflora* invests proportionally more in shoot mass and length than in root enhancement, potentially, as there is no requirement to extend roots due to a sufficient level of moisture. Increasing organic matter with increased shoot investment is not a unidirectional relationship however, as the leaves of *L. uniflora* are continually renewed and recycled (Nielsen & Sand-Jensen, 1991). In this way *L. uniflora* is dependent on the substrate but also engineers the substrate surrounding it and will contribute directly to the organic matter content.

Dense stands of *L. uniflora* covering a shore should mediate the cohesive structure of the underlying substrate, retaining fine particles of silt and nutrients which are otherwise reduced on shore zones with the impacts of lake drawdown via drying and enhanced erosional processes (Cooley & Franzin, 2008; Effler et al., 1998; Effler & Matthews, 2004), as are nutrients and organic matter, particularly in areas of exposure (Cooley & Franzin, 2008). Non-cohesive sediments, such as primarily sand and gravel-sized material (≥0.063mm to 64mm), that would be friable without OM become increasingly cohesive

(Ekwue, 1990; Shrestha & Bloomberg, 2005). In this regard *L. uniflora* is also a chemical engineer (Pulido et al., 2011), releasing oxygen into the rhizosphere through radial oxygen loss (ROL) from photosynthesis, (Pedersen et al., 1995; Sand-Jensen, Prahl, & Stokholm, 1982), thereby promoting mineralisation of sediments (Wium-Andersen & Andersen, 1972), and increasing available nitrate via nitrification which ROL promotes (Roelofs, Schuurkes, & Smits, 1984; Sand-Jensen et al., 1982). Recent studies reveal a high diversity of aquatic arbuscular mycorrhizal fungi (AMF), colonization of *L. uniflora* roots further influencing sediment chemistry (Sudová et al., 2020; Sudová, et al., 2015), and highlighting the importance of this isoetid as a host plant.

It is worth highlighting that this AMF association may further account for some of the ability of *L. uniflora* to thrive in fluctuating waters when waters levels are reduced, as it has been shown to help prevent any drop in turgor by maintaining leaf water potential under water-stress conditions (Bahadur et al., 2019). This also may be implicated in the positive association between shore slope and plant water content.

Water productivity

Increasing ammonia concentrations (in lake water), were associated with a decrease in root to shoot investment, which may be a reflection of the plants time within the aquatic environment, as the requirement to invest in roots through a moisture deficit is removed, and investment in light capturing above-ground structures take precedent. Water column fertility may also be reflected by sediment fertility, so there may be less requirement for active foraging of nutrients by *L. uniflora roots* in lakes with moderate to high nutrient concentrations. Alternatively, or in combination, more fertile conditions may promote growth of other species in the littoral with which *L. uniflora* competes for light, causing a shoot elongation response at the expense of root biomass. While we found no literature to explain such an association it is worth noting that Roelofs et al. (1984), found that that nitrate was the main source of N in waters where *L. uniflora* dominated.

4.5 Conclusion

Separating the environmental factors linked to the morphology and biomass of *L. uniflora* is intrinsically complex as many factors covary and not all were feasible to include in this study (such as shore shape and sediment nutrients). In addition, our study was constrained by necessity to sample lakes with populations of *L. uniflora* which very rarely occur where water level range exceeds 4.3 m; this range is modest relative to strongly regulated lakes in Scotland where levels may vary by >10m to a maximum of 30m.

However, this study points to the importance of environmental factors which directly influence the morphology of *L. uniflora*, in particular the separation of coarse or variable shore aggregates from lake water levels (associated with amplified lake water drawdown, where finer sediments dominate the littoral zone) as this was negatively associated with biomass. We highlight the effect of disconnecting *L. uniflora* from lake water levels by way of increased shore slope, distance, and height, as these too are associated with reductions of biomass and dead long slender shoots, and yet positively associated with moisture conservation and root length. Upper shore plants of *L. uniflora* are typified by a high root:shoot ratio, but our results indicate this may be at a cost to overall standing biomass, and probably therefore, the contribution of *L. uniflora* to the functioning of the littoral zone.

Our results also indicate that shore variables will be mediated by water level changes in lakes. Predicted changes to our climate and lake shore environment through increased variability in precipitation and drought events, higher water levels, increased wave activity and shore erosion, coupled with growing demands on water resources, will increase stress to aquatic communities. Our work adds to the body of knowledge on this highly versatile amphibious plant which is critical to lake ecology. However, as *L. uniflora* is a species shown to be unusually resilient to changes in habitat caused by water level variability, evidence of declining biomass or prevalence should serve as a warning that wider level impacts are imminent or have already occurred.

Acknowledgements

We thank Anna Doeser, Duncan Dowie and Megan Layton for assistance with sampling and laboratory work. Water chemistry and nutrient data was provided for some lakes by the Scottish Environment Protection Agency (SEPA). Grateful thanks to Scottish Water, Scottish Southern Electric, Forestry Commission Scotland and The Woodland Trust for providing water level data and/or access to survey lakes. This research was financially supported by the University of Stirling and SEPA via an Impact Studentship

Chapter 5

General summary, implications, and recommendations

5.0 General summary, implications, and recommendations

Rising pressure due to human impacts means freshwater ecosystems are now one of the most globally threatened habitats (Reid et al., 2019; WWF, 2018), with flow modification a form of habitat degradation that poses a leading and persistent threat to freshwater biodiversity globally (Dudgeon et al., 2006; Reid et al., 2019; WWF, 2018).

Hydromorphological alteration pressures occur predominantly in the form of water level fluctuations and flows from abstraction or reservoir storage, primarily due to a collective increase in demand on water resources for used for public water supplies, irrigation, and the shift to invest in greener energy sources, such as hydropower (Dorber et al., 2018; EEA, 2018). Currently pressures from hydromorphological alterations on European freshwaters have overtaken those of diffuse source pollution (affecting 40 % and 38% respectively) (EEA, 2018).

Across Europe pressures of phosphorus and nitrate enrichment have been identified and mitigated with varied success. Nitrate concentrations in groundwater bodies across Europe have remained constant, however phosphorus concentrations have reduced markedly by approximately 1.6% per year due to control measures (Fig. 1). This suggests that hydromorphological pressures may be becoming proportionally more significant.

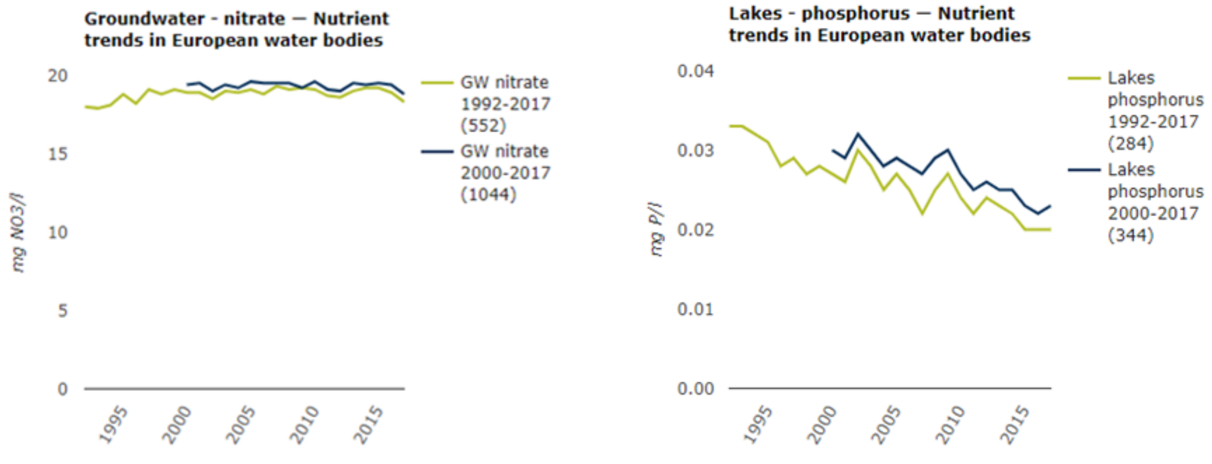


Fig.1. Annual mean concentrations for groundwater bodies of Nitrate and phosphorus in Lakes in Europe, 1992 to 2017 (Nitrate lake trends not available) (EEA, 2019)

However, pressures arising from regulation activities have been a neglected influence on lake ecology (Wantzen et al., 2008), despite an increase of water level alteration driven by population increases, resource demand and climate change (Fekete et al., 2010). To date, our understanding of this influence on lake ecology, particularly the biota of littoral habitats, relative to other pressures, such as eutrophication, is lacking.

Lakes contain approximately 90% of all global surface fresh water (Shiklomonov & Rodda, 2003) and support a high share of freshwater biota, within, below and surrounding them (Balian et al., 2008). The vast majority of lake biodiversity is held in the littoral zones, but this same habitat is most dependant on natural water level changes and most vulnerable to adapted water level fluctuations. The verdant littoral and shore zone of Dunalastair Water displays this wonderfully (Fig. 2.), a RAMSAR and SSSI site with water levels maintained within parameters for habitat conservation.

Fig. 2. Dunalastair Water, Scotland.

Water level fluctuations occur naturally in all lakes, enhancing productivity (Kolding & van Zwieten, 2012) and are crucial for ecosystem structure and functioning, by way of seasonal nutrient pulses through water ingress from riparian zones and rivers (Wantzen et al., 2008) and internal nutrient mixing (O'Reilly et al., 2003; Strayer & Findlay, 2010a). Conversely, imposed water level fluctuations (WLF), through creation of flow modification structures such as dams, modify the natural water level regime in terms of range, duration, frequency, and seasonality, which in turn primarily impact littoral zones (Solomini et al., 2006; Moss, 2008). Moderate variations of WLF can substantially impact littoral habitats (Gownaris et al., 2018), through alterations in residence times, nutrient retention, sediment redistribution, light attenuation, and temperature (Cyr, 1998; Finlay et al., 2001; Furey et al., 2004; McEwen & Butler, 2010).

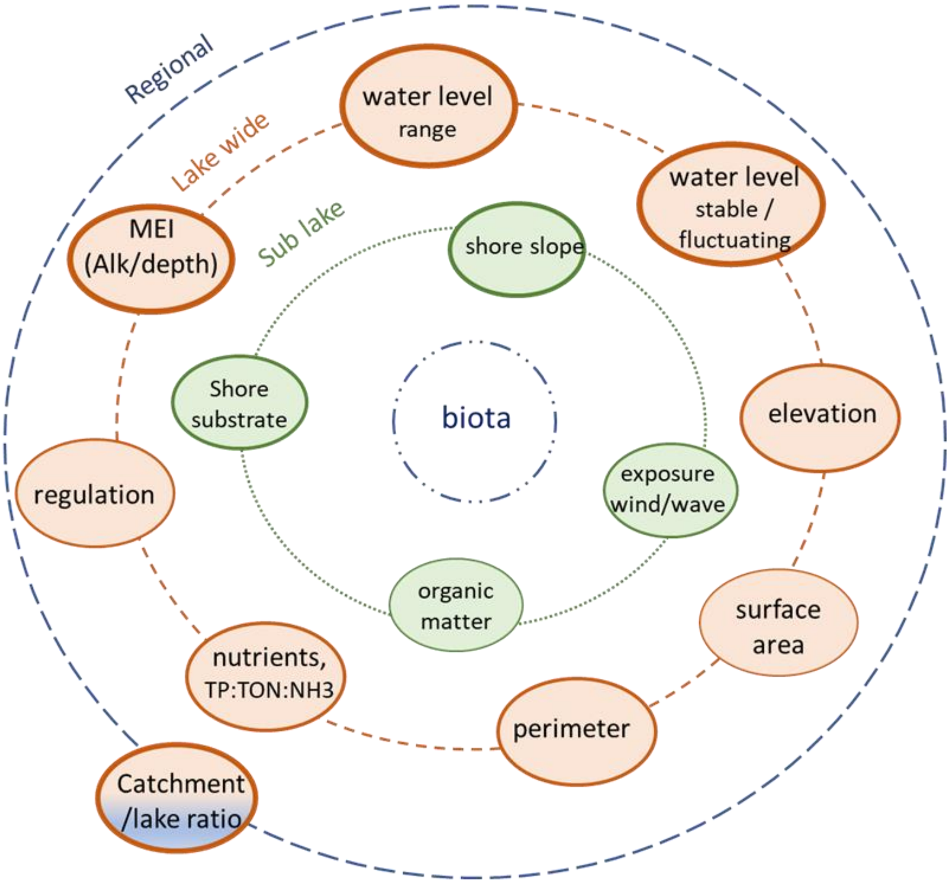
Modified abiotic conditions in the littoral zone drive changes to biota. Aquatic vegetation are directly affected through desiccation, through mechanical strain on support tissues caused by dewatering (Bornette & Puijalon, 2011) and submersion where WLF are increased. Indirect influences to aquatic vegetation from WLF occur through changes in wave energy, sediment resuspension, light attenuation, organic matter and temperature (Boon et al., 2019; Bornette & Puijalon, 2011). In turn macroinvertebrates are impacted directly by WLF by desiccation of sessile animals or those with sufficiently restricted mobility to remain in the aquatic environment, and indirectly influenced due to invertebrate dependency on littoral macrophytes as components of littoral habitat complexity, for food and habitat resources.

Macrophytes are an integral component of riparian and littoral habitat complexity, and recognised driver of macroinvertebrate diversity (Brauns et al., 2011; Jurca, 2012, Law et al., 2019). Macroinvertebrates, (termed invertebrates from this point), have a vital role in lake ecosystems through substrate engineering (Malmqvist, 2002; Moore, 2006; Hölker et al., 2018), consumption of fine particulate organic matter, algae and detritus, which impact carbon and nutrient cycling. Impacts to life in the littoral zone, predominantly macrophytes and littoral macroinvertebrates, are still be comprehensively quantified. While anyone standing on a lake shore, can see the results of water level fluctuation where levels have been reduced by 5m or more, there is a critical need improve empirical understanding of ecological effects in order to refine assessment abilities and mitigation strategies (Boon et al., 2019; EEA, 2018; Heiskanen & Solimini, 2005; Solimini et al., 2006b), and reduce biodiversity loss through effective management of freshwater resources.

To this end, the study lakes used in this project varied in regulation and magnitude of WLF, encompassing a range of regional, lake-wide and sub lake factors. We selected littoral aquatic macrophytes and invertebrates to investigate changes to the littoral communities in lakes from WLF, as they are responsive, ubiquitous and represent the majority of life in the littoral zone. From a review of the literature it was apparent that changes to water levels strongly impact the biota of the littoral zone. What was missing however, was an appreciation of how WLF impact biodiversity relative to other known drivers such as elevation, lake area, nutrient levels, and substrate characteristics.

5.1 Thesis summary

Results from the literature meta-analysis (Chapter 1) indicated that water level fluctuation impacts on macrophytes and invertebrates had not been analysed on a regional basis in North West Europe, with numerous lakes and relative to regional, lake-wide, and sub-lake factors. This analysis also highlighted the importance of studying ecological responses to water level fluctuations in the context of lake wide factors such as elevation, alkalinity (Rørslett, 1991; O'Hare et al., 2012; Elo et al., 2018; Sun et al., 2019) water depth (McEwen & Butler, 2010; Brauns et al., 2008; Evtimova & Donohue, 2014) and sub lake factors such as substrate and exposure (Fig. 3.)



Additional factors;
Latitude
Topography
Geology
Connectivity
Fine sediment movement
Time length of regulation
Seasonal effects (ice/wind)
Shoreline modification
Littoral depth

Fig. 3 Thesis findings; environmental factors found to impact littoral biota. Thickness of line denotes overall association with littoral macrophytes and invertebrates (updated from Chapter 1, Fig. 8).

The first two data chapters of the thesis determined that relative to other known pressures on lakes, WLF is a key determinant of macrophytes richness (particularly in LM lakes) and composition, whilst for invertebrates this is true for both richness and composition (Chapter 2 and Chapter 3). Average macrophyte species richness at WLF of 1.6 – 3.5m and 3.5 – 9m were lower than WLF of 0.2 to 1.5m, by 26% and 91% respectively. Average invertebrate family richness at WLF of 1.6 to 3.5m and 3.6 to 5.5m were lower than WLF of 0.35 to 1.5m, by 28% and 56% respectively.

Relationships between environmental variables and macrophyte responses were found to be mediated by the Morpho-Edaphic Index (MEI, the ratio of alkalinity to mean depth), with lake types separated into; low MEI (low alkalinity, deep lakes with WLF up to 9.3m), and high MEI (high alkalinity, shallow lakes with WLF up to 3.5m), (Table 1), the overall macrophyte species pool was 24% larger in the HM lakes. Elevation was a consistent negative influence on macrophyte (low MEI only) and invertebrate richness. Both biotic richness measures were positively associated with measures of habitat availability, macrophyte species richness with lake area (with high MEI lakes only) and invertebrate family richness with lake perimeter (Table 1 & Table 2). In addition, macrophyte richness was negatively associated in low MEI lakes by WLF, elevation and regulation, whilst high MEI lake macrophyte richness was positively associated with lake area, and catchment to lake ratio, but negatively by elevation and phosphorus.

Aside from the predominant influence of WLF and elevation, on invertebrate richness, this was associated with measures of lake productivity, negatively with dissolved oxygen and positively with silicates likely linked to regional topography and geography, in addition to suspended solids (correlated with chlorophyll as a measure of productivity rather than turbidity through suspended mineral particles). This work is unique within the literature as other studies typically examine either regulation or drawdown with the influence of ice scour or without inclusion of regional, lake-wide and sub lake scaled factors, and none have employed the use of a MEI with water level range to examine ecological responses (Fig. 3). MEI was not found to be associated with invertebrate richness or composition but was clearly important when considered in conjunction with macrophyte biodiversity and the role of MEI with WLF.

Further, we tested the relationship between macrophyte species richness and invertebrate family richness, including consistent environmental factors, from 44 lakes. Despite both ecological responses being strongly associated with WLF, no direct association between macrophyte and invertebrate richness was determined when all variables were considered. Given established associations between these two biota by Braun. (2008) and Law et al. (2019), it is likely that alteration of macrophyte richness and therefore morphological diversity may be detectable by a change in invertebrate composition. The use of macrophyte form as a surrogate would be valuable in saving time and resources to identifying and mitigation of impacts from WLF pressures, though in this instance perhaps such relationships would be better clarified with within low MEI lake types (where water level fluctuations were determined to have the clearest influence on richness), but there were insufficient data to investigate this.

WLF strongly drove macrophyte composition in all lake types, in agreement with previous literature (Rørslett, 1991; Hellsten & Mjelde, 2009; Evtimova & Donohue, 2016), though my research uniquely establishes WLF as the dominant pressure relative to all other environmental factors in these lakes. However, the subdivision of lakes by MEI highlighted disparate environmental drivers within each broad lake type which are paramount to consider in assessment and conservation of lake biodiversity (Table 1), with lower MEI lakes clearly being more sensitive to the additional disturbance imposed by WLF. In addition, the study is unique within the literature by further stratifying each lake type into stable or fluctuating regime, as this approach added another layer of clarity to the knowledge of water level range impacts by identifying macrophyte species and invertebrate families indicative of each lake type (Table 1 and Table 2).

The subdivision of lake types revealed that macrophyte indicator species of low MEI lakes with stable regimes, (such as Loch Chon, Fig. 4.) were slow growing species, typical of nutrient-poor systems (Spence, 1967), with singular reproduction methods including, *L. dortmanna, I. lacustris, M. alterniflorum* and *S. angustifolium*, which require almost constant submergence with consistent stable water level regimes. The single indicator species of low MEI fluctuating regimes *Callitriche hamulata* tolerates exposure through a terrestrial growth form (Preston and Croft, 1997). This division of species was suggestive of a strong filtering effect of water level regime. No species were found to be indicative of stable regimes in high MEI lakes, while those of fluctuating waters (such as Loch of Lintrathen, Fig. 5.), were species that either tolerated or even required some enhanced variation in water level to persist. These were reproductive generalists that exhibit higher phenotypic plasticity, such as *Littorella uniflora*, *P. perfoliatus, J. bulbosus P. gramineus,* but also included the scarce pioneer species *Najas flexilis* which has an obligate annual life history.

This knowledge is important for biodiversity assessments or in efforts to conserve or enhance water bodies or populations of priority species. These findings as well as field observations formed the basis of research into *L. uniflora* responses to WLF relative to other drivers (Chapter 4).

Table 1. Associations between lake water level regulation and aquatic macrophytes (MEI = Morpho-edaphic Index, CLR = Catchment to lake ratio, TON = total organic nitrogen, WLF = water level fluctuation), where low or high MEI lakes are indicated the association is with this lake type only.

Environmental factor	Relationship/effect	Metric , species abiotic / biotic factor
Water level range	negative	Macrophyte richness (low MEI lakes)
Water level range	No association	*L. uniflora* morphology or biomass
Lake regulation	negative	Macrophyte richness (low MEI lakes)
Lake area	positive	Macrophyte richness (high MEI lakes)
Lake elevation	negative	Macrophyte richness
Phosphorus	negative	Macrophyte richness (high MEI lakes)
MEI	positive	Positive for All lakes, but by MEI type, (negative but non- significant in high MEI lakes).
CLR	positive	Macrophyte richness (high MEI lakes)
CLR	driver	Macrophyte composition (low MEI lakes)
Phosphorus	driver	Macrophyte composition (low MEI lakes)
Chlorophyll *a*	driver	Macrophyte composition
TON	driver	Macrophyte composition (low MEI lakes)
MEI	driver	Macrophyte composition
Lake area	driver	Macrophyte composition
Water level range	driver	macrophyte composition (high MEI lakes)
Lake elevation	driver	Macrophyte composition (high MEI lakes)
Lake regulation	driver	Macrophyte composition (high MEI lakes)
MEI and WLF regime	driver	Significant difference in composition with low and high, stable, and fluctuating
WLF regime (stable/fluctuating)	driver	Macrophyte indicator species (mediated by MEI)
Low MEI stable regime	Indicator species	*Lobelia dortmanna*
Low MEI stable regime	Indicator species	*Isoetes lacustris*
Low MEI stable regime	Indicator species	*Myriophyllum alterniflorum*
Low MEI stable regime	Indicator species	*Sparganium angustifolium*
Low MEI fluctuating regime	Indicator species	*Callitriche brutia var. hamulata*
High MEI fluctuating regime	Indicator species	*Littorella uniflora*
High MEI fluctuating regime	Indicator species	*Potamogeton perfoliatus*
High MEI fluctuating regime	Indicator species	*Juncus bulbosus*
High MEI fluctuating regime	Indicator species	*Potamogeton gramineus*
High MEI fluctuating regime	Indicator species	*Najas flexilis*
Shore slope	positive	*L. uniflora* water content*,* shoot mass and root length
Distance / height from water line	positive	*L. uniflora* leaf (discarded) length:width ratio
Maximum potential wave exposure	negative	*L. uniflora* leaf length:width ratio and root length
Sediment properties; *phi grade, (water %, aggregate type) coarse sand shores*	negative	*L. uniflora* total biomass, root:shoot ratio and leaf length:width ratio
Lake nutrients (ammonia)	negative	*L. uniflora* root:shoot ratio
Organic matter	positive	*L. uniflora* leaf length
Organic matter	negative	*L. uniflora* root:shoot ratio

Fig.4. Loch Chon, a low MEI lake type with stable water levels (unregulated, WLF 0.9m)

Fig.5. Loch of Lintrathen, a high MEI lake type with fluctuating water levels (regulated, WLF 3m)

MEI was not associated with invertebrate richness, however, the use of water level stability or fluctuation, revealed that taxon composition differed significantly with these variables. This approach identified Siphlonuridae as indicative of fluctuating regimes, which has not been recognised for its presence in lakes in previous literature but was documented in 35% of the study lakes. In addition, the approach used finds agreement with previous research, that taxa with semivoltine, or largely sessile traits are less tolerant of imposed WLF (Hynes, 1961; Aroviita & Hämäläinen, 2008; Mastrantuono et al., 2008).

Table 2. Associations between water level regulation and benthic macroinvertebrates (O2 dissolved = dissolved oxygen, WLF = water level fluctuation)

Environmental factor	Relationship/effect	Metric , species abiotic / biotic factor
Water level range	negative	Invertebrate richness
Water level range	driver	Invertebrate composition - (mediated by stable/fluctuating regime)
WLF regime (stable/fluctuating)	driver	Invertebrate indicator species
Lake perimeter	positive	Invertebrate richness
Lake perimeter	driver	Invertebrate composition
Lake elevation	negative	Invertebrate richness
O_2 dissolved	negative	Invertebrate richness
O_2 dissolved	driver	Invertebrate composition
Silicate	positive	Invertebrate richness
Suspended solids	positive	Invertebrate richness
Ammonia	driver	Invertebrate composition
Nitrate	driver	Invertebrate composition
WLF regime (stable/fluctuating)	driver	Invertebrate composition (stable/fluctuating)
Stable water regime	Indicator taxa	Hydrachnidiae
Stable water regime	Indicator taxa	Lymnaeidae
Stable water regime	Indicator taxa	Planariidae
Stable water regime	Indicator taxa	Haliplidae
Fluctuating water regime	Indicator taxa	Siphlonuridae

This research found a clear distinction between invertebrate richness and composition with physical and nutrient drivers. A similar separation was found with richness and composition, particularly in the associations with phosphorus and nitrates. This suggests that nutrients play a role in modifying WLF impacts on biota or vice versa; in high MEI lakes phosphorus is an additional negative influence on macrophyte richness and nitrate was a driver of composition in low MEI lakes, whilst dissolved oxygen, nitrate, and ammonia all modified invertebrate composition (Table 2). Nutrient enrichment remains a significant pressure for aquatic biota in UK lakes, despite trends indicating Europe-wide reductions in lake phosphorus levels, (EEA, 2019). However, nitrate concentrations in European water bodies have not reduced in line with phosphorus or nitrate in water bodies (EEA, 2019), (Fig. 1). In addition to WLF, regulation was found to be negatively associated with macrophyte richness in low MEI lakes and a driver of composition in high MEI lakes, indicating that any form of hydromorphological alteration can have negative impacts in addition to any alteration to water level regime.

Our study of *Littorella uniflora* (Chapter 4), highlighted the importance of sub-lake shoreline factors which influence *L. uniflora* biomass and morphology (Table 1), and which can be modified with amplified water level fluctuations in lakes. In particular, the known effect of WLF on separation of *L. uniflora* swards (by moving and reducing the scale of viable shoreline habitat) (Rørslett, 1984), and coarse-grained, or variable, shore aggregates from the littoral zone , altering this habitat to one increasingly dominated by homogenous, fine sediments (Carmignani & Roy, 2017; Cooley & Franzin, 2008; Furey et al., 2004b).

Fig. 6. Loch Arklet, lacking in *L. uniflora* , displaying the separation of coarser aggregates on high slopes with increasingly fine, homogenous sediments towards the water line. In Chapter 2, this lake is classed as low MEI with fluctuating waters.

Water level fluctuations or range did not directly drive changes in *L. uniflora* morphology, however as a species that requires and even thrives with some WLF, this perhaps is unsurprising. Additionally, our study lakes were constrained by WLF ranges of 0.91 to 4.3m, since lakes with WLF > 5m were found to lack *L. uniflora*, as did the shallow, artificially stable Dunalastair Water (*authors survey work*). However, this study did highlight the influence of uncoupling *L. uniflora* from lake water levels by way of increasing shore slope, distance, and height, (Fig. 6, regulated Loch Arklet, with WLF of 3m contained no *L. uniflora*), as these factors were associated with reductions of biomass and dead long slender shoots, and yet positively associated with moisture conservation (associated with the size of shoots), and root length. The relevance of shore slope to WLF is often overlooked but, as Mastrantuono et al. (2008) found, a relatively minor reduction in water level can result in a recession of shoreline creating a vast area of dewatered lake perimeter, on gently sloped shores and littoral zones. The littoral zone of Loch Venachar East undergoes this annually with no shore being recorded in Spring 2013 but 420m of near horizontal (0-5 degrees) beach formed of exposed littoral habitat emerging 3 months later (*authors data*). Loch Lubnaig undergoes natural fluctuations of 1.2m, with a gently sloping shore (5-30 degrees), the *L. uniflora* pictured (Fig. 7), would be isolated with a minor amplification of WLF. Finally, although *L. uniflora* are characterised by a high root to shoot ratio, our results suggest that with amplified WLF conditions, this may be at a cost to overall standing biomass. Further, that rather than elongation of roots occurring to prevent uprooting, as suggested in previous literature, *L. uniflora* reduces its above-ground size with increased exposure or non-cohesive substrate (coarse sand) and this, in addition to the collective sward structure, results secondarily in protection from uprooting by wave action, while the investment in morphological attributes is primarily for resource acquisition.

Fig.7. Loch Lubnaig, a low MEI lake with naturally fluctuating water levels, the exposed late summer shore is gently sloped and dominated by a *L. uniflora*, the only gaps in the dense growth are a result of removal for sampling.

Our results emphasise that water level fluctuations in the form of range, and artificially stable or fluctuating regimes, have important associations with littoral macrophytes and invertebrates relative to other previously established lake-wide and sub-lake scale pressures. In addition, it emphasizes the additional influence that environmental factors including MEI, nutrients, availability of habitat, shore slope and shore/littoral aggregate size, and wave/wind exposure, have on littoral communities. Macrophyte species and invertebrate families, indicative of specific lake types and water level regimes have been identified, for assessment, conservation, and management interests, to assist in the mitigation of impacts from water level regulation. Our research regarding *Littorella uniflora* goes further; determining impacts from sub-lake factors, mediated by lake water level changes, on the habitat and performance of this species is of high importance to lake ecology.

Our study demonstrates that habitat variables known to be altered by water level changes in lakes, such as aggregate type, shore slope and organic matter, impact *L. uniflora*, a species recognised as both important to lake ecology and adaptable to water level fluctuations. Due to its inherent tolerance, where *Littorella*-dominated communities are reduced this should alert water managers and conservationists that other, less robust species are likely to be negatively affected. Unless we can measure and identify impacts from hydromorphological activity such as water level fluctuation, the prospect of reducing loss of biodiversity in these littoral freshwater communities is small. Macrophytes and benthic macroinvertebrates are almost ubiquitous and clearly respond to anthropogenic impacts in addition to natural variability imposed by region and latitude. By elucidating the relative importance of such pressures, this work adds significantly to the body of knowledge available to those responsible for assessing, conserving, and enhancing our aquatic biodiversity.

5.2 Research Limitations

The single most limiting factor for research into the effects on lake biota from water level fluctuations is a lack of suitable paired biology-environment datasets for regulated and unregulated lakes, or lakes where vegetation and invertebrates are simultaneously surveyed. Out of 160 lakes with data for one or the other (including authors research), only 44 lakes had data for both biological elements. Scotland has a low population density (Scottish Government, National Statistics, 2019), and is rich in water bodies which have undergone less human modification than other areas of the UK (Maitland et al., 1994), with over 63% of lochs surface areas at good to high overall status (Scottish Government, 2014), compared with a UK figure of 35% (JNCC, 2019). Therefore, there is a good opportunity to establish lake water level data for unregulated reference lakes to identify differences in aquatic biodiversity, within systems of natural hydrologic variability, and to contrast this with lakes and reservoirs with altered water level regimes. This work benefited from the quality of data available, all data were gathered with consistent methodology as set out by the WFD and Scottish Environment Protection Agency, allowing for comparability. However, with daily or weekly water level data it would be possible to identify pressures, not just from the range of water levels as we were restricted too, but also the frequency, timing and duration of events, which would logically be presumed to impact aquatic macrophytes and invertebrates depending on individual traits. Wider availability of higher resolution water level time series data would undoubtedly improve our understanding of underlying mechanisms by which water levels affect lake biota, which would help in managing both these lakes and the freshwater systems connected to them.

On reflection, omitted from this work has been some measure of the time since implementation of any flow modification structure (although in practice this would not always be straightforward to establish). In addition, years with extreme droughts, should be researched, which would lower both lakes and reservoirs to varying degrees depending on the use and catchment. It is well established that time is an important component in how habitats and organisms respond to disturbance and that biota require time to recover a new equilibrium, particularly after extreme drawdown events. With an understanding of this in terms of regulated lakes and reservoirs we may better placed to predict and mitigate future pressures, particularly from drought due to anticipated climate change impacts or operational drawdown events.

5.3 Management and future research

It is clear that modern society requires water to be stored and abstracted, for a multitude of purposes, not least to meet energy and food demands of a growing population and in remote or developing societies, without reliance on fossil fuels. Until recently the placement of such engineered structures was reasonably determined by the most physically practical and cost-effective reasons. As the pressures from hydromorphological alterations grow, and overlap with other anthropogenic pressures, such as nutrient inputs or shoreline modification, it is clear that the initial predicted costs have increased by way of cyanobacterial blooms, impacts to fish stocks, aesthetically and especially the integral value of biodiversity. Fragmentation imposed by discontinuities between water bodies may serve to accentuate these impacts (Sutela et al., 2013; Liu et al., 2015; Alahuta et al., 2017).

This thesis shows that whilst reservoirs are necessary, the impacts from WLF can override those from other measured factors which have tended to be prioritised. How then are the needs of humans and lake conservation to be balanced?

As both are necessary, we put forward that conservation triage should be employed to reduce impacts and enhance conservation in other waterbodies. Already terrestrial conservation has focused on habitat protection, over specific species, and highlighted that aggregating areas of protection to reduce impacts from fragmentation and enhance conservation efforts is effective (Bottrill et al., 2008; Rybicki & Hanski, 2013). Further triage requires prioritisation of where conservation efforts are invested and clearly, which areas they are not invested in, to the benefit of overall biodiversity. Alahuta et al. (2017) determined regions globally where efforts should be prioritised to conserve diversity of aquatic macrophytes. They concluded that these regions should cover wide environmental gradients with a large number of lakes, in agreement with Socolar et al. (2016), and that within a specific region protection should be focussed on multiple lakes which cover a range of environmental gradients. We suggest that aggregating the lakes chosen for conservation efforts, will further enhance any measures taken. Many lake-rich regions in north-west Europe fit the parameters discerned by Alahuta et al. (2017), and may benefit from this approach, Scotland being among them.

Where triage is employed it stands to reason that to meet societal needs a limited number of 'sacrificial' waterbodies are required to become major heavily modified water bodies (HMWB), but particularly with multiple uses, these would undoubtedly incur an absolute loss of biodiversity, but out of necessity to best protect and enhance other water bodies. On what parameters then should these sacrificial waterbodies be selected? First, we suggest placement needs to consider the areas known to have naturally lower biodiversity, to reduce losses, our research confirms that increasing elevation has a negative association with macrophyte and invertebrate biodiversity, so sacrificial water bodies would best be in uplands regions. In addition, we found low alkalinity, deep lakes to be lower in macrophyte richness than high alkalinity shallow lakes, therefore low MEI waterbodies would incur fewer absolute losses and their physical parameters of depth suit the needs for extreme drawdown. It may not be a palatable solution, or in line with WFD, however if we do not have adequate resources to protect or improve *all* of our surface waters, on what basis then are waterbodies selected for preservation or improvement, or rather is this sufficient, and what are the alternatives for long term freshwater connectivity, health and biodiversity?

One of the predominant impacts from hydromorphological alteration comes from the loss of connectivity among water bodies. If a few sacrificial lakes were used for a greater number of water requirements, it should relieve the need to acquire these needs from other waterbodies, lessening their WLF, thereby enhancing conditions in many lakes and reservoirs and reducing overall fragmentation. This is particularly true of lakes with WLF >3.5m. If these can be lakes can be reduced in number and range, moderated below 3.5m, this should lessen WLF as a stressor, and increase ecosystem functionality, as observed in Scandinavian water bodies with moderate WLF (Rørslett, 1991; Rørslett, 1989; Hellsten & Mjelde, 2009)

We propose that where sacrificial lakes are situated, remedial measures are taken to reduce impacts to tail waters. Sun et al. (2019) found the structuring role of hydrological connectivity to be higher for macrophytes in upland environments. Other waterbodies with natural or moderate WLF, with environmental flows (Tickner et al., 2020), can feed into the tail waters, replacing loss of sediment and nutrient flows and enhancing connectivity. In lowland lakes enhancement can learn from nature. For example, beaver dams have positive habitat heterogeneity outcomes via the creation of caches of woody debris, a system of linked ponds and high aquatic plant biomass interlinked by areas of free-flowing water (Law et al., 2016). In addition, lakes with current or predicted rises to WLF due to climate change, would potentially benefit from installed reedbed habitats in the current eulittoral as a proactive measure to account for a vertical reduction of the littoral with low water levels (Brauns et al., 2007a). Pressures from nutrient enrichment remain ongoing, with tools for reducing internal nutrient loads such as Phoslock® demonstrated as being highly effective (Spears et al., 2016). Lessening or reducing the number of simultaneous pressures (e.g. enhanced WLF and nutrient load), would likely benefit lake biodiversity and surrounding habitats.

The study on *Littorella uniflora* shows that where one species is particularly resilient to pressures, conservationists and managers should be alerted when populations diminish or morphology changes, as this species could be an effective canary of lake biodiversity and ecosystem functioning.

We suggest scope for increasing perimeters of new and existing reservoirs be considered to increase the complexity of shape and provide potential habitat. In addition, creation of holding ponds adjacent to the main body of water may enable mobile organisms to persist there temporarily and re-colonize the reservoir once water levels rise. This may be particularly beneficial where water level ranges are not extreme but alter slowly such as in drinking water reservoirs.

A final measure for the mediation of WLF in lakes, particularly in Scotland would be the investment in monitoring of lake water levels, in both regulated and unregulated waterbodies. Understanding impacts of WLF on lakes was regarded as “urgent” in 2008 (Wantzen et al., 2008a), and has not lessened in the past decade. The UK has a wealth of accessible, nation-wide data on river flows, but in contrast, lakes, and reservoirs, which are threatened in terms of biodiversity loss (Boon et al., 2019; Nilsson et al., 2005; Reid et al., 2019), are relatively data-poor.

5.4 Future work

With the data now available future aims would be to determine a water level drawdown index for Macrophytes in British Lakes/ Scottish lochs as done for Nordic regions by Mjelde et al. (2012), as Scotland is exempt from the impacts of ice scour and our reservoirs follow dissimilar seasonal regimes. Thresholds for species may be best established with mesocosm experiments whereby other related factors such as nutrient concentrations, may be more readily controlled

In addition, it would be feasible to investigate both macrophyte and benthic invertebrate responses to littoral habitat quality in lakes with a range of nutrients, as well as the interactions between them. Sampling both biota, at specific depth gradients, using synchronised survey stations across lakes, would allow for comparison both between lakes and within lakes, thereby improving our ability to assess threats to the ecological status of lakes and how these might best be reduced. For this a habitat-specific site approach (e.g. contrasting sheltered, exposed, intermediate and modified shorelines) would be used with lake shore habitat variables recorded using the habplot design adopted in Lake Habitat Survey (Rowan, 2006: McGoff & Irvine 2009), alongside government standards used in this research for macrophyte sampling i.e. JNCC Common Standards Monitoring Guidance (CSM) for Standing Waters (JNCC, 2005), as per Gunn et al., (2004), and invertebrates following Scottish Environment Protection Agency (SEPA) protocol, (O'Hare et al., 2007).

In addition, an experimental approach could investigate the benefits of installing various stands of vegetation and/or physical structures within reservoir littoral zones, such as wooden matting or similar resource that can be used as a food and/or habitat resource in addition to capturing fine, materials. A variety of substrates could be placed in the eulittoral of lakes with annual moderate drawdown. Sampling the benthic assemblages, trapped fine sediment and organic matter, would reveal potential benefits or improvements to placing. If effective, this may be a simple and relatively low-cost mitigation measure to reduce negative effects on lake ecology from artificial and climate change related changes in lake water level regimes.

5.5 Conclusions

Average macrophyte richness is higher in lakes with high alkalinity and shallow depths (higher MEI), than in deep lakes with low alkalinity (lower MEI). There was no discernible effect from WLF in higher MEI lakes, whilst in the lower MEI lakes both WLF and regulation were found to reduce richness. Macrophyte composition in both lake types was associated with the water level regime. While WLF was also negatively associated with invertebrate richness, it was found that invertebrate composition was partly rather than predominantly related to WLF. However, there was a clear difference in indicator taxa for stable and fluctuating regimes.

Macrophyte and invertebrate richness was highest at WLF of 0.2m to 1.5m, with 28% and 20% reduction at WLF 1.6m to 3.5m and 75% and 50% reduction respectively in WLF of over 3.5m. This research finds that invertebrate composition and macrophyte richness (higher MEI lakes), and composition (lower MEI lakes), are influenced by additional anthropogenic impacts through phosphorus and nitrate concentrations, and to a lesser degree by WLF.

Naturally occurring associations with aquatic biota were determined, primarily with elevation as a negative factor for invertebrate and macrophyte richness, and for macrophyte composition in higher MEI lakes. While the number of macrophyte species in all lakes reduced with increasing elevation, only macrophyte composition in shallow lakes with high alkalinity were associated this way. Other effects from geography and topography occurred through catchment to lake ratios (positively associated with macrophytes in higher MEI lakes), silicates and dissolved oxygen concentrations. For the lakes included in this research, suspended solids were correlated with chlorophyll *a* and so were regarded as a reflection of productivity.

WLF was associated with changes in shore habitat and altering the placement of the littoral zone (vertically). The research into how *L. uniflora* responds to shore characteristics, mediated by WLF, provides additional information on how a species robust in terms of WLF adapts such changes, and highlights potential risks for species with lower phenotypic plasticity. This is especially pertinent as predicted changes to climate and lake shore habitat will increase stress to aquatic communities through increased variability in precipitation and drought events, higher water level fluctuations and increased wave activity and therefore shore erosion (Pierce, 2000, 2004).

This thesis demonstrates that imposed water level fluctuations in lakes have clear, and mostly dominant associations with littoral zone macrophytes, benthic macroinvertebrates, and sub lake habitat parameters, relative to the other environmental factors commonly considered in studies of lakes such as elevation, perimeter, and fertility. The influence of this pressure should be regarded as a priority for freshwater conservationists and managers. Understanding the stressors to macrophyte and invertebrate richness and composition is important for habitat monitoring, conservation, and informing how management can promote the sustainability of freshwaters. It is imperative to include water level fluctuation parameters to effectively manage, preserve and restore freshwater resources and their associated biodiversity.

“*In the end, we will conserve only what we love; we will love only what we understand, and we will understand only what we are taught*”

Baba Dioum, 1968

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Appendices

Chapter 2

Appendix I

Method of water level data attainment for each research lake.

WBID	Loch	Regulated Y/N	WLF (m)	WLF main source
14293	A_BHRAOIN	N	1	GoogleEarth, OS & web search
24744	ACHRAY	y	1.2	Scottish Water
24892	ARD	N	0.9	first author field data and outflow gauge data
24668	ARKLET	Y	3	Scottish Water
24025	AWE_NORTH	Y	1.5	GoogleEarth, OS & web search
24025	AWE_SOUTH	Y	1.5	GoogleEarth, OS & web search
23684	BA_(MULL)	N	1	GoogleEarth, OS & web search
22610	BACKWATER_RESEVOIR	y	3.53	Scottish Water
14585	BAD_AN_SCALAIG	Y	1	SEPA, GoogleEarth, OS & web search
25144	BARNLUASGAN	N	0.5	The Scottish Beaver Trial: Knapdale lochs 2008-2013
25242	BUIC	N	0.4	The Scottish Beaver Trial: Knapdale lochs 2008-2013
2358	CALDER	Y	1.5	GoogleEarth, OS & web search
25400	CARRON_VALLEY	Y	3	first author field data
27899	CASTLE_LOCH_(LOCHMABEN)	N	0.9	GoogleEarth, OS & web search. JNCC
28493	CASTLE_LOCH_(MACHARS)	N	0.9	GoogleEarth, OS & web search. BNHS
26392	CASTLE_SEMPLE	N	0.9	email to clydemuirshiel. SEPA. GoogleEarth, OS.
24754	CHON	N	0.9	first author field data
20573	CLUANIE	Y	5.5	GoogleEarth, OS & web search.SSE
26416	COBBINSHAW	Y	2.5	GoogleEarth, OS & web search. Scottish canals
25179	COLLIE_BHAR	N	0.5	The Scottish Beaver Trial: Knapdale lochs 2008-2013
25160	CREAG_MHOR	N	0.3	The Scottish Beaver Trial: Knapdale lochs 2008-2013
27523	DAER_RESERVOIR	Y	3	Scottish Water
16902	DAMH	N	1.25	GoogleEarth, OS & web search
21123	DAVAN	N	0.35	SEPA based on kinord
27948	DEE	N	1.2	loch Dee outlet
22308	DOILET	N	1	GoogleEarth, OS & web search
18607	DRUIDIBEG	N	1	GoogleEarth, OS & web search
25202	DUBH	N	0.2	The Scottish Beaver Trial: Knapdale lochs 2008-2013
20196	DÙN_NA_CILLE	N	1	GoogleEarth, OS & web search
22787	DUNALASTAIR	y	0.7	Scottish Southern Electric
19214	DUNTELCHAIG	Y	1.66	Scottish Water
24132	EARN	y	0.54	Scottish Southern Electric
24996	ECK	Y	2	Scottish Water
21795	ERICHT	y	2.8	Scottish Southern Electric
22419	ERROCHTY	y	1	Scottish Southern Electric
26275	FAD	N	0.9	GoogleEarth, OS & web search
23601	FINGASK	N	0.7	GoogleEarth, OS & web search
25128	FITTY	N	0.9	GoogleEarth, OS & web search
23254	FORFAR	N	1	GoogleEarth, OS & web search

23711	FREUCHIE	N	1	GoogleEarth, OS & web search
23216	FRISA	N	1	GoogleEarth, OS & web search
25038	GARTMORN	Y	1.5	GoogleEarth, OS & web search
25077	GELLY	N	0.9	GoogleEarth, OS & web search
14677	GHEARRAIDH_MHIC_18972	N	1	GoogleEarth, OS & web search
14315	GLASCARNOCH	Y	5.5	Scottish Southern Electric
24623	GLEN_FINGLAS	Y	7.8	Scottish Water
26893	GLENASTLE	N	1	GoogleEarth, OS & web search
26168	GORM	N	0.9	GoogleEarth, OS & web search
28130	GRANNOCH	N	1.5	GoogleEarth, OS & web search
14677	GROGARY_(CROGHEARRAIDH)	N	1	GoogleEarth, OS & web search
14677	GROGARY_UPPER	N	1	GoogleEarth, OS & web search
1753	HARRAY	N	0.9	GoogleEarth, OS & web search
4444	HEMPRIGGS	N	0.9	GoogleEarth, OS & web search
2490	HOPE	N	1.5	GoogleEarth, OS & web search
20860	INSH	N	1.9	SEPA Gauge map. Kincraig outflow
24531	KATRINE	Y	1.6	Scottish Water
28003	KEN	Y	1	Scottish Power
26566	KILBIRNIE	N	1	GoogleEarth, OS & web search
28288	KINDAR	N	0.9	GoogleEarth, OS & web search
21189	KINORD	N	0.35	SEPA gauge map
12055	LACASDAIL	Y	1.5	GoogleEarth, OS & web search
21576	LAGGAN	N	2.2	GoogleEarth, OS & web search
12978	LANGABHAT	N	1	GoogleEarth, OS & web search
16986	LEATHAN	Y	1.5	GoogleEarth, OS & web search
23938	LEDNOCK	Y	4.9	Scottish Southern Electric
21945	LEE	Y	0.03	Scottish Water
24843	LEVEN	Y	1	GoogleEarth, OS & web search. SEPA/cranmore sluice
24422	LINDORES	N	0.5	GoogleEarth, OS & web search
25687	LINLITHGOW	N	0.5	GoogleEarth, OS & web search
25145	LINNE	N	0.3	GoogleEarth, OS & web search
22942	LINTRATHEN	Y	3	Scottish Water
18825	LOCHINDORB	N	0.58	GoogleEarth, OS & web search. SEPA gauge map
21328	LOCHY	Y	1	Scottish Water
24447	LOMOND_(SOUTH_BASIN)	Y	0.99	Scottish Water
24447	LOMOND_(TARBET_ISLE)	Y	0.99	Scottish Water
25209	LOSGUNN	N	0.3	GoogleEarth, OS & web search
26217	LOSSIT	N	1	GoogleEarth, OS & web search
26883	LOWER_GLENASTLE	N	1	GoogleEarth, OS & web search
24459	LUBNAIG	N	1.6	first author field data and SEPA gauge data
23624	LYON	Y	9.3	Scottish Southern Electric
24742	MAHAICK	N	0.5	GoogleEarth, OS & web search
14057	MAREE	N	1.5	GoogleEarth, OS & web search
25264	MCKAY	N	0.2	The Scottish Beaver Trial: Knapdale lochs 2008-2013
27315	MEGGET	Y	8	Scottish Water
24919	MENTEITH	N	1	GoogleEarth, OS & web search
19038	MHADAIDH	N	1	GoogleEarth, OS & web search

12995	MIGDALE	N	1	GoogleEarth, OS & web search
28506	MOCHRUM_(MACHARS)	N	0.9	GoogleEarth, OS & web search
23610	MONK_MYRE	N	0.5	GoogleEarth, OS & web search
24171	MONZIEVARD	N	0.5	GoogleEarth, OS & web search
6140	MORE_(CAITHNESS)	Y	2	GoogleEarth, OS & web search. Thurso estate
20657	MORLICH	N	0.9	GoogleEarth, OS & web search
19013	NAN_CNAMH_19013	N	1	GoogleEarth, OS & web search
26482	NAN_GAD	N	0.7	GoogleEarth, OS & web search
9401	NAN_RITHEANAN	N	1.5	GoogleEarth, OS & web search
6405	NAVER	N	1.3	SEPA gauge map, GoogleEarth & OS
24016	NELL	N	1	GoogleEarth, OS & web search
18767	NESS	Y	1.2	GoogleEarth, OS & web search. SSE
14749	NORTH_SCADABHAGH	N	0.5	GoogleEarth, OS & web search. SEPA Gauge map
16624	OLABHAT (Eilean Dhomhnaill)	N	0.9	GoogleEarth, OS & web search
19261	OLAIDH	N	2.5	GoogleEarth, OS & web search
25006	ORE	N	0.9	GoogleEarth, OS & web search
11189	OSGAIG	N	0.9	GoogleEarth, OS & web search
23192	RESCOBIE	N	0.9	GoogleEarth, OS & web search
14899	RUNABHAT	N	1.5	GoogleEarth, OS & web search
14739	SCARAIDH	N	0.9	GoogleEarth, OS & web search
2499	SCARMCLATE	N	0.9	GoogleEarth, OS & web search
16906	SGAMHAINN	N	1.5	GoogleEarth, OS & web search
9048	SHIN	Y	3	GoogleEarth, OS & web search
20757	SKENE	Y	0.9	GoogleEarth, OS & web search
26257	SKERROLS	N	0.9	GoogleEarth, OS & web search
24522	SLOY	Y	8	Scottish Southern Electric
15265	SOUTH_SCADABHAGH	N	0.5	GoogleEarth, OS & web search. SEPA Gauge map
21437	SPEY_RES	Y	1.5	GoogleEarth, OS & web search. Hydro-Electric Power
1570	SPIGGIE	N	0.9	GoogleEarth, OS & web search
27309	ST_MARYS	Y	2.5	GoogleEarth, OS & web search. Scottish Water
5350	STACK	N	0.5	GoogleEarth, OS & web search
16275	STRATHBEG	N	1	GoogleEarth, OS & web search
26447	STRATHCLYDE	Y	0.5	GoogleEarth, OS & web search
1678	SWANNAY	N	1	SEPA gauge map & GoogleEarth, OS
27322	TALLA	Y	2.81	Scottish Water
27234	TANGY	N	0.6	GoogleEarth, OS & web search
20633	TARFF	N	1	GoogleEarth, OS & web search
23515	TAY	N	1.5	GoogleEarth, OS & SEPA gauge map
25889	THOM	Y	1.6	Scottish Water
14098	TOLLAIDH	N	1	GoogleEarth, OS & web search
25168	UNNAMED NORTH	N	0.4	The Scottish Beaver Trial: Knapdale lochs 2008-2013
4284	URRAHAG (Urghag/Bruthadel)	N	1.5	GoogleEarth, OS & web search
16456	USSIE	N	0.9	GoogleEarth, OS & web search
24758	VENACHAR	Y	1.6	Scottish Water
10719	VEYATIE/Loch Mheathadaidh	N	1.5	GoogleEarth, OS & web search
24295	VOIL	N	1.6	first author field data
2712	WATTEN	N	0.9	GoogleEarth, OS & web search

28344	WHITE_(STRANRAER)	N	1	GoogleEarth, OS & web search
23607	WHITE_PERTH	N	0.5	GoogleEarth, OS & web search

Additional methods of estimation and measures for lakes with no water level data

Our data set consisted of 92 lakes with no time series water level data. We conducted strand line surveys and used online information to provide estimates of WLF range for these waterbodies.

It was not feasible to conduct the strand line surveys on all 92 unregulated lakes within our data set. Therefore we used a combination of aerial photographs, internet searches for images or drone footage from geography and fishing websites, and forums or google images of the lochs in different seasons, along with google earth imagery and measuring tools to estimate the range in water level fluctuation occurring to each lake. We also used river gauge data from SEPA websites when these were proximal to the lakes outflow, and compared the measures gained from this approach with field surveys of strand lines as outlined below.

10 lakes and reservoirs were surveyed in late September 2014. The wettest winter in over 100 years was followed by the driest Septembers on record in Scotland since 1972, with the warmest spring and the 15th highest summer mean temperatures recorded since 1884, see: (https://www.metoffice.gov.uk/pub/data/weather/uk/climate/datasets/Tmean/ranked/Scotland.txt)

We reasoned that at late September that year, the preceding weather should result in lakes with no WLF regulation being close to their minimum water levels, with the strand lines on the shores reflecting the highest water levels from winter months.

The range of water level drawdown was measured as the height difference between the highest strand line evident on the lake bank and the waterline of the lake or reservoir at that time. A manual theodolite was used for the surveys.

Included in the surveys were reservoirs that we held WLF data for. This enabled some measure of comparison - though the regimes of these reservoirs are altered so that late summer does not necessarily mean the time for lowest water levels, particularly those which are re-filled by other “holding” reservoirs (as per the data below for, Backwater reservoir, Loch of Lintrathen and Loch Katrine). However, this method did allow us to compare the calculated range in water level from the surveys, with river gauge outflow data obtained from CEH and SEPA on line resources (see below for, Loch Katrine, Loch Lubnaig and Loch Ard).

Water levels range from strandline measures, compared with time series of gauge data

waterbody	height difference strandline to water line (m)	time series data WLF (80%) (m)	outflow data CEH (m)
Backwater reservoir	0.58	3.5	
Loch of Lintrathen	1.99	3.11	
Loch Lubnaig	1.37	n/a	1.8
Loch Venachar	1.95	1.62	
Loch Drunkie	1.89	2.18	
Loch Katrine	1.25	1.6	1.2
Loch Arklet	3.52	2.74	
Loch Chon	0.91	n/a	
Loch Ard	0.91	n/a	0.8
Glen Finglas reservoir	6.65	7.8	

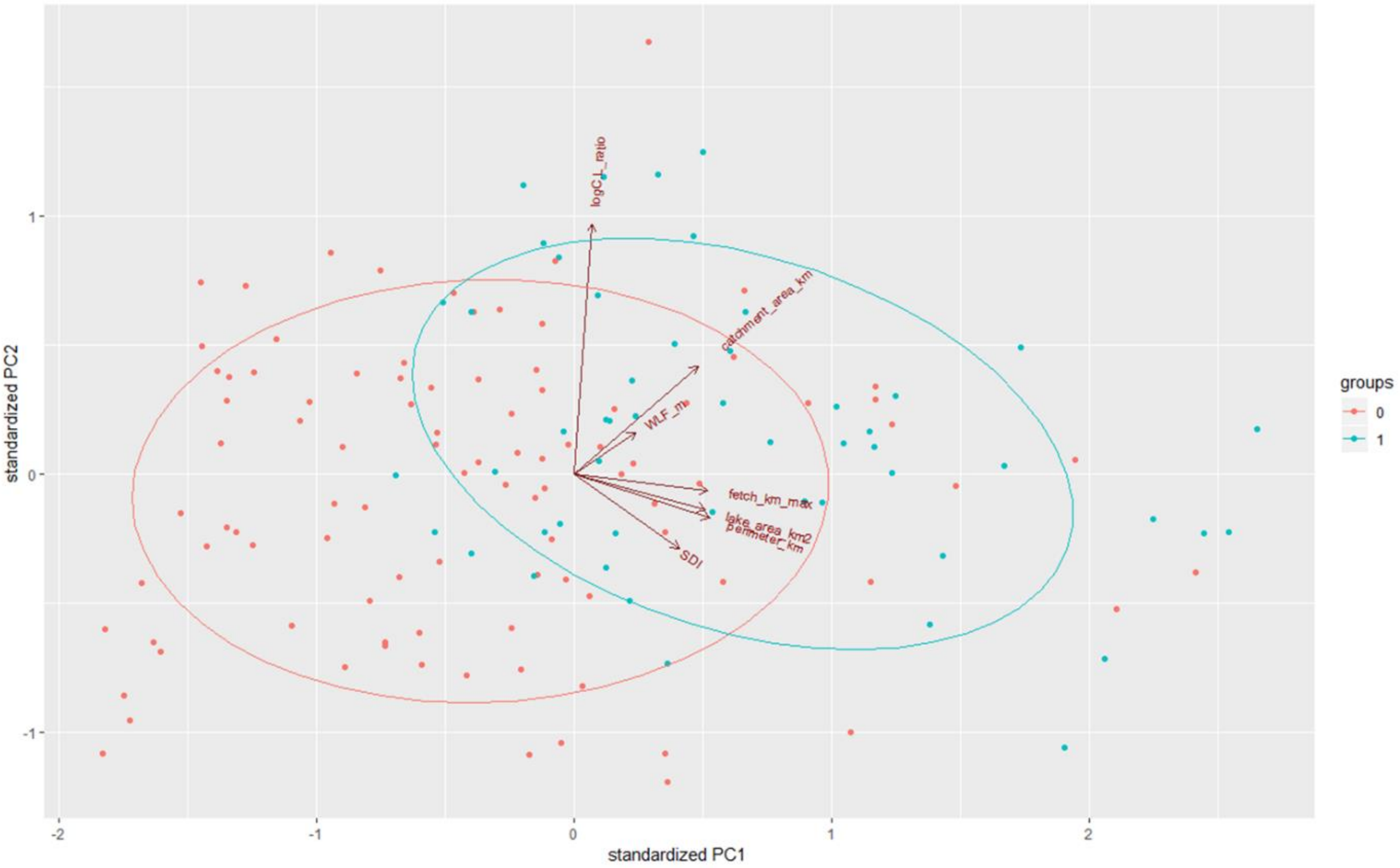
There are minor differences between the measures, for instance, the measured range at Loch Arklet is greater than the time series data by 0.78 m. The discrepancies were likely due to variation between a) the time series data being based on calculations (and excluding the minimum and maximum 10th percentiles) from previous years and b) the year of the survey (2014) was unusually dryer and hotter for spring and summer. Loch Lubnaig was measured as 1.4 m the gauge was 1.8 m therefore, we estimated this as mid-way between the two at 1.6 m, this was because the disturbance and substrate around Lubnaig banks from cattle and camping or rip rap make strandline detection problematic. For Loch Ard and Loch Chon there is less shore line disturbance, and we were confident on our measures so used 0.9 in the analysis. As river outflow data looked approximate to the measured data, we used this as a guide in conjunction with aerial images, reports, forums as well as contact with fishing groups or land managers, to estimate the other unregulated lakes across Scotland. Each waterbody was assessed individually in this way.

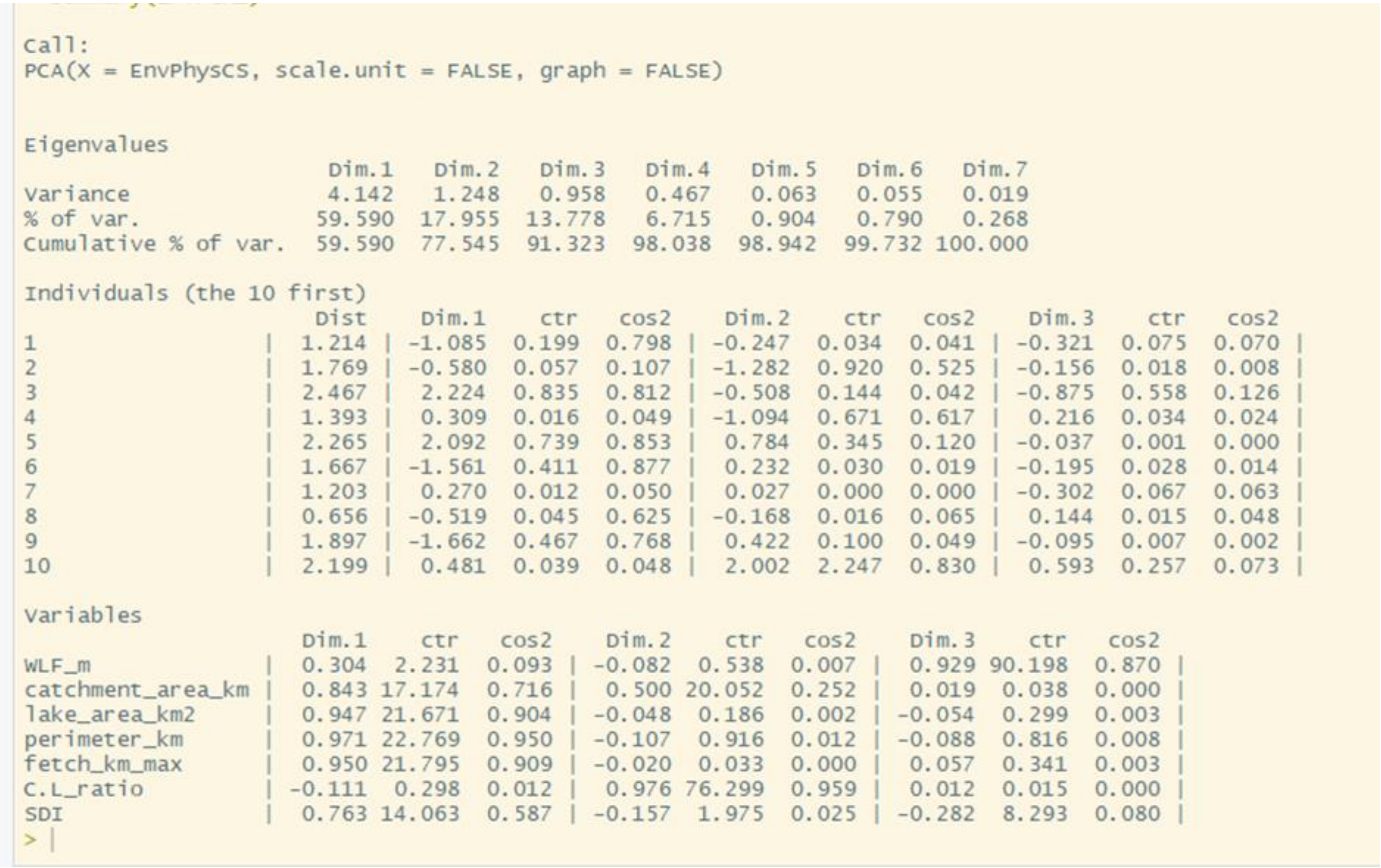
We further compared our ability to estimate the WLF regime of lakes, by estimating for reservoirs using the same methods. I researched and estimated the WLF range and then compared these in a blind test with Prof. N Willby, who held the WLF time series data at that time. We were satisfied with my estimations. In addition, Prof. Willby used his expert knowledge of individual lochs across Scotland to assess all estimations for any uncertain results. This approach obviously lends uncertainty to the data. However, with limited data, time, and finances this was decided to be the best practicable method and is likely to result in estimated water level ranges that are within 0.5m of the true value for typical years.

Appendix II;

Principal components analysis (PCA) used to separate sets of water chemistry, physical and land use variables to identify those variables that maximised variation amongst sites.

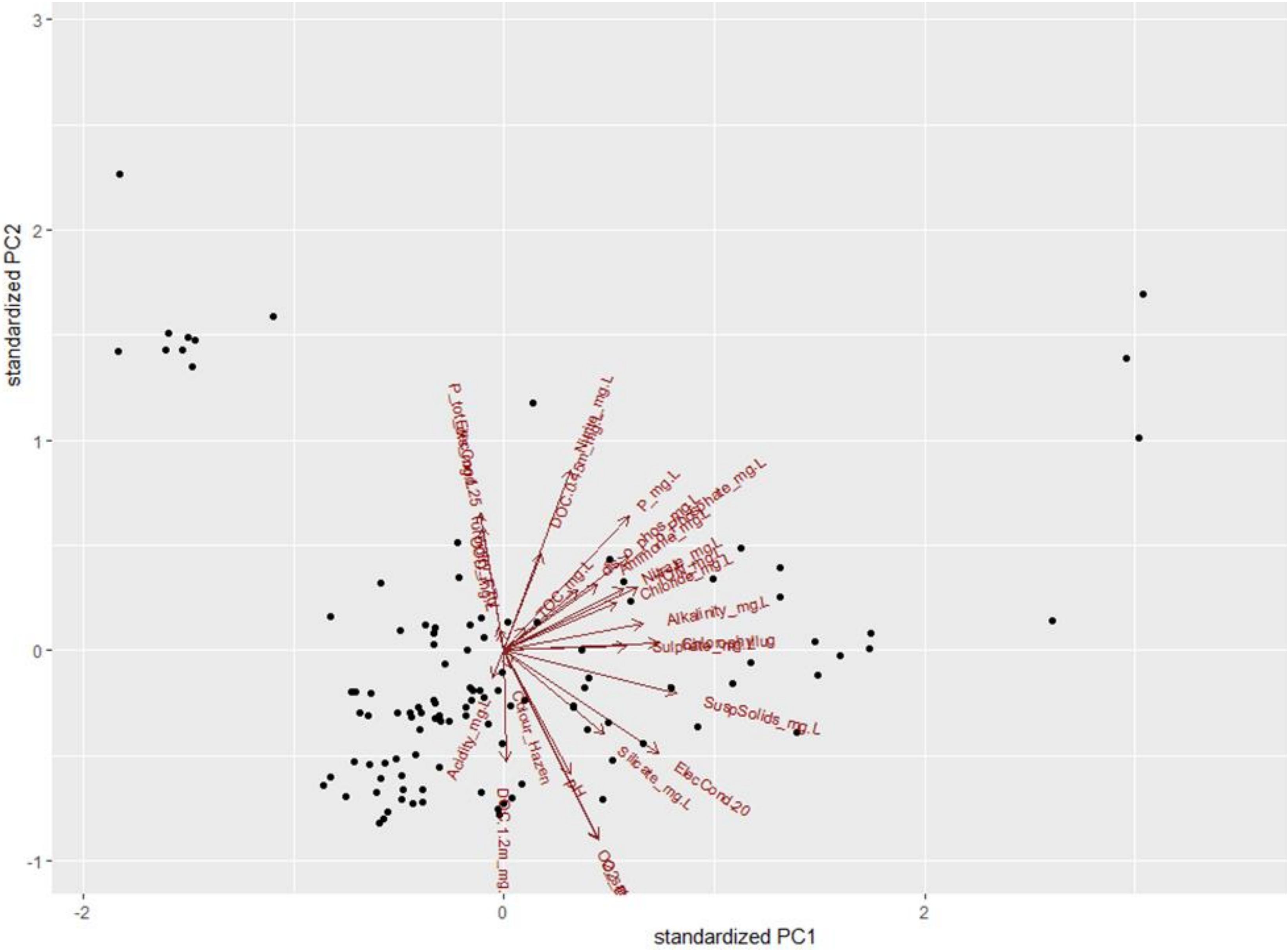
Physical variables

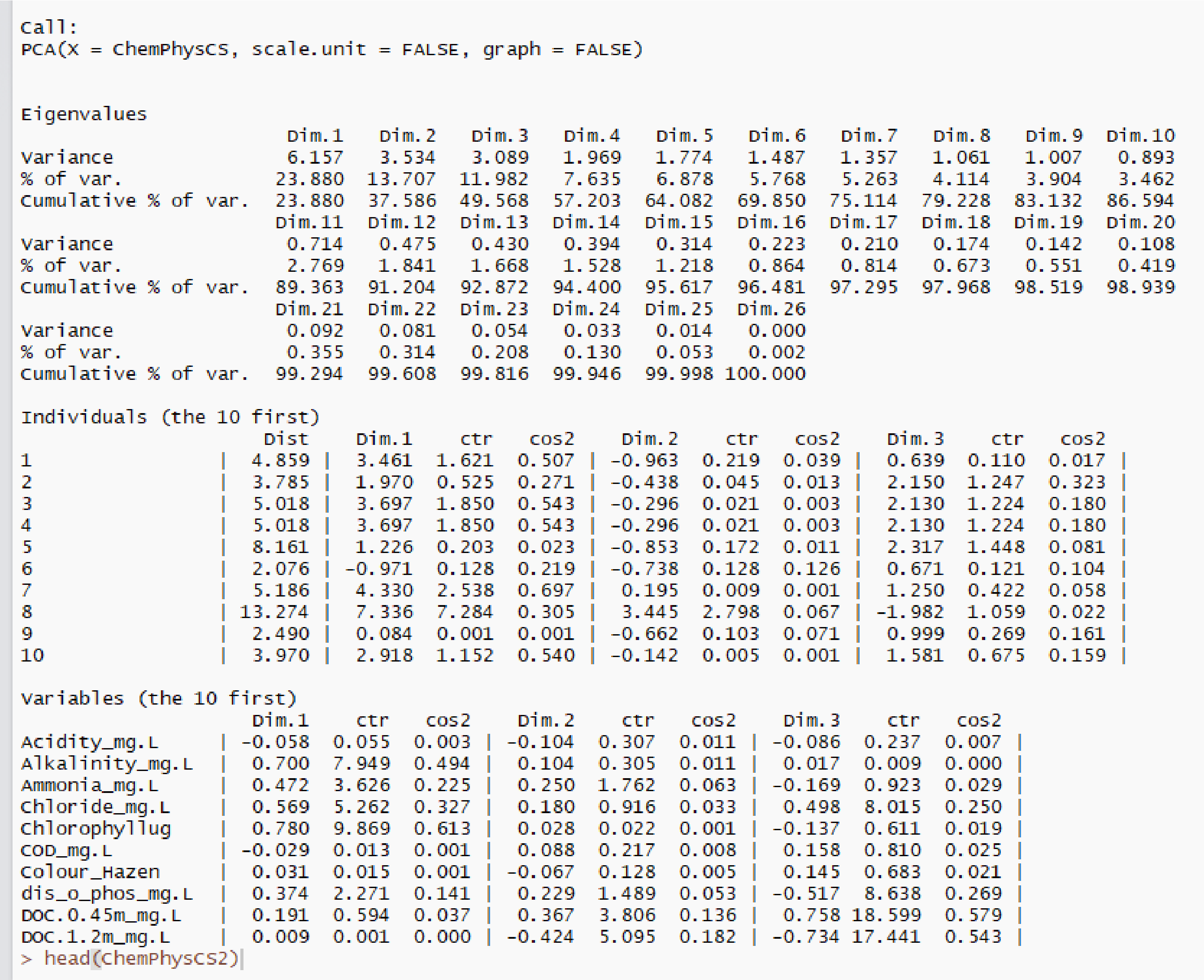




```
Call:
PCA(X = EnvPhysCS, scale.unit = FALSE, graph = FALSE)


Eigenvalues
                       Dim.1   Dim.2   Dim.3   Dim.4   Dim.5   Dim.6   Dim.7
Variance               4.142   1.248   0.958   0.467   0.063   0.055   0.019
% of var.             59.590  17.955  13.778   6.715   0.904   0.790   0.268
Cumulative % of var.  59.590  77.545  91.323  98.038  98.942  99.732 100.000

Individuals (the 10 first)
                     Dist    Dim.1    ctr   cos2    Dim.2    ctr   cos2    Dim.3    ctr   cos2  
1                 |  1.214 | -1.085  0.199  0.798 | -0.247  0.034  0.041 | -0.321  0.075  0.070 |
2                 |  1.769 | -0.580  0.057  0.107 | -1.282  0.920  0.525 | -0.156  0.018  0.008 |
3                 |  2.467 |  2.224  0.835  0.812 | -0.508  0.144  0.042 | -0.875  0.558  0.126 |
4                 |  1.393 |  0.309  0.016  0.049 | -1.094  0.671  0.617 |  0.216  0.034  0.024 |
5                 |  2.265 |  2.092  0.739  0.853 |  0.784  0.345  0.120 | -0.037  0.001  0.000 |
6                 |  1.667 | -1.561  0.411  0.877 |  0.232  0.030  0.019 | -0.195  0.028  0.014 |
7                 |  1.203 |  0.270  0.012  0.050 |  0.027  0.000  0.000 | -0.302  0.067  0.063 |
8                 |  0.656 | -0.519  0.045  0.625 | -0.168  0.016  0.065 |  0.144  0.015  0.048 |
9                 |  1.897 | -1.662  0.467  0.768 |  0.422  0.100  0.049 | -0.095  0.007  0.002 |
10                |  2.199 |  0.481  0.039  0.048 |  2.002  2.247  0.830 |  0.593  0.257  0.073 |

Variables
                     Dim.1    ctr   cos2    Dim.2    ctr   cos2    Dim.3    ctr   cos2  
WLF_m             |  0.304  2.231  0.093 | -0.082  0.538  0.007 |  0.929 90.198  0.870 |
catchment_area_km |  0.843 17.174  0.716 |  0.500 20.052  0.252 |  0.019  0.038  0.000 |
lake_area_km2     |  0.947 21.671  0.904 | -0.048  0.186  0.002 | -0.054  0.299  0.003 |
perimeter_km      |  0.971 22.769  0.950 | -0.107  0.916  0.012 | -0.088  0.816  0.008 |
fetch_km_max      |  0.950 21.795  0.909 | -0.020  0.033  0.000 |  0.057  0.341  0.003 |
C.L_ratio         | -0.111  0.298  0.012 |  0.976 76.299  0.959 |  0.012  0.015  0.000 |
SDI               |  0.763 14.063  0.587 | -0.157  1.975  0.025 | -0.282  8.293  0.080 |
> |
```

Nutrient & Chemistry



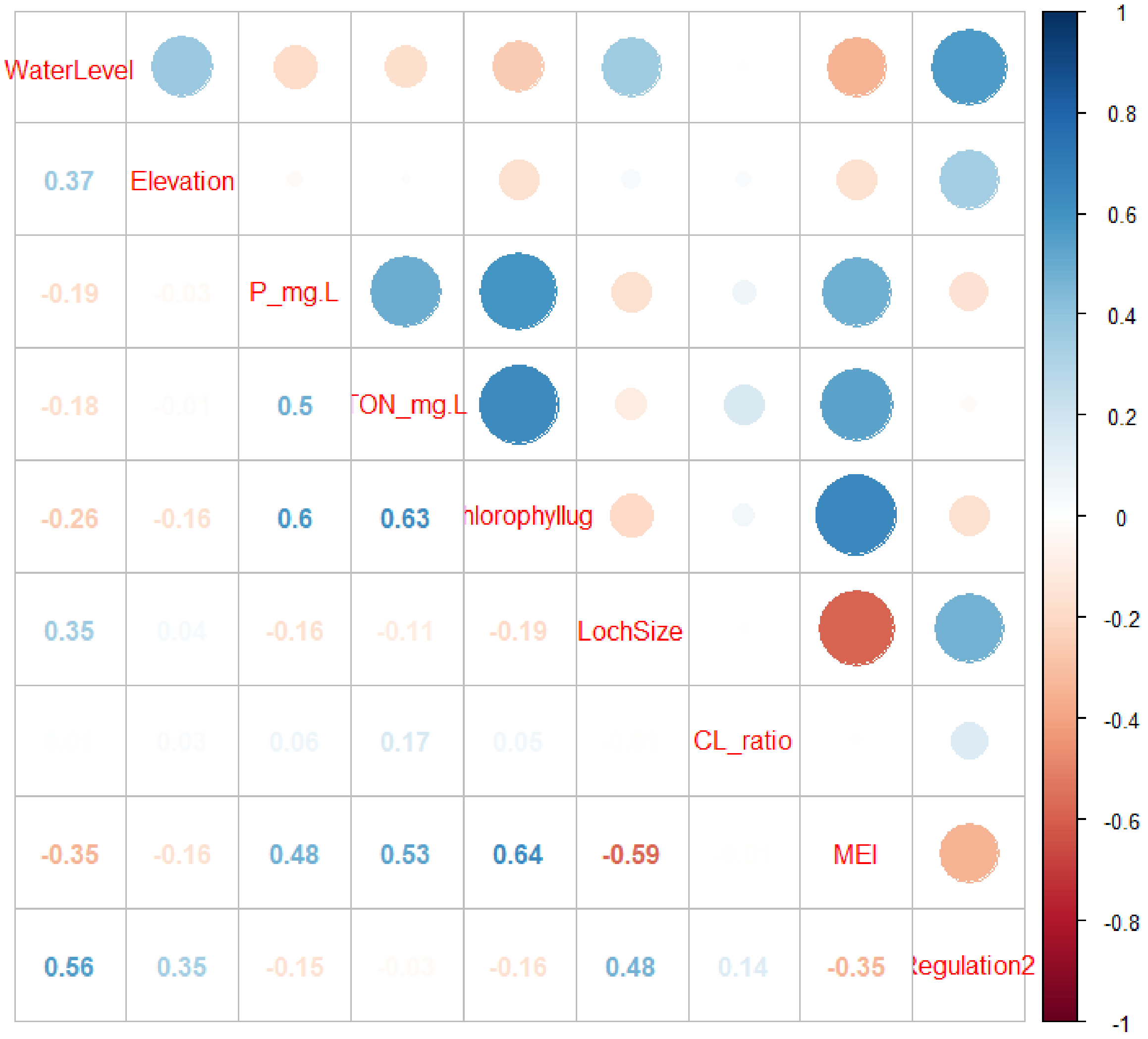


```
Call:
PCA(X = ChemPhysCS, scale.unit = FALSE, graph = FALSE)


Eigenvalues
                       Dim.1   Dim.2   Dim.3   Dim.4   Dim.5   Dim.6   Dim.7   Dim.8   Dim.9  Dim.10
Variance               6.157   3.534   3.089   1.969   1.774   1.487   1.357   1.061   1.007   0.893
% of var.             23.880  13.707  11.982   7.635   6.878   5.768   5.263   4.114   3.904   3.462
Cumulative % of var.  23.880  37.586  49.568  57.203  64.082  69.850  75.114  79.228  83.132  86.594
                      Dim.11  Dim.12  Dim.13  Dim.14  Dim.15  Dim.16  Dim.17  Dim.18  Dim.19  Dim.20
Variance               0.714   0.475   0.430   0.394   0.314   0.223   0.210   0.174   0.142   0.108
% of var.              2.769   1.841   1.668   1.528   1.218   0.864   0.814   0.673   0.551   0.419
Cumulative % of var.  89.363  91.204  92.872  94.400  95.617  96.481  97.295  97.968  98.519  98.939
                      Dim.21  Dim.22  Dim.23  Dim.24  Dim.25  Dim.26
Variance               0.092   0.081   0.054   0.033   0.014   0.000
% of var.              0.355   0.314   0.208   0.130   0.053   0.002
Cumulative % of var.  99.294  99.608  99.816  99.946  99.998 100.000

Individuals (the 10 first)
                      Dist    Dim.1    ctr   cos2    Dim.2    ctr   cos2    Dim.3    ctr   cos2  
1                 |  4.859 |  3.461  1.621  0.507 | -0.963  0.219  0.039 |  0.639  0.110  0.017 |
2                 |  3.785 |  1.970  0.525  0.271 | -0.438  0.045  0.013 |  2.150  1.247  0.323 |
3                 |  5.018 |  3.697  1.850  0.543 | -0.296  0.021  0.003 |  2.130  1.224  0.180 |
4                 |  5.018 |  3.697  1.850  0.543 | -0.296  0.021  0.003 |  2.130  1.224  0.180 |
5                 |  8.161 |  1.226  0.203  0.023 | -0.853  0.172  0.011 |  2.317  1.448  0.081 |
6                 |  2.076 | -0.971  0.128  0.219 | -0.738  0.128  0.126 |  0.671  0.121  0.104 |
7                 |  5.186 |  4.330  2.538  0.697 |  0.195  0.009  0.001 |  1.250  0.422  0.058 |
8                 | 13.274 |  7.336  7.284  0.305 |  3.445  2.798  0.067 | -1.982  1.059  0.022 |
9                 |  2.490 |  0.084  0.001  0.001 | -0.662  0.103  0.071 |  0.999  0.269  0.161 |
10                |  3.970 |  2.918  1.152  0.540 | -0.142  0.005  0.001 |  1.581  0.675  0.159 |

Variables (the 10 first)
                     Dim.1    ctr   cos2    Dim.2    ctr   cos2    Dim.3    ctr   cos2  
Acidity_mg.L      | -0.058  0.055  0.003 | -0.104  0.307  0.011 | -0.086  0.237  0.007 |
Alkalinity_mg.L   |  0.700  7.949  0.494 |  0.104  0.305  0.011 |  0.017  0.009  0.000 |
Ammonia_mg.L      |  0.472  3.626  0.225 |  0.250  1.762  0.063 | -0.169  0.923  0.029 |
Chloride_mg.L     |  0.569  5.262  0.327 |  0.180  0.916  0.033 |  0.498  8.015  0.250 |
Chlorophyllug     |  0.780  9.869  0.613 |  0.028  0.022  0.001 | -0.137  0.611  0.019 |
COD_mg.L          | -0.029  0.013  0.001 |  0.088  0.217  0.008 |  0.158  0.810  0.025 |
Colour_Hazen      |  0.031  0.015  0.001 | -0.067  0.128  0.005 |  0.145  0.683  0.021 |
dis_o_phos_mg.L   |  0.374  2.271  0.141 |  0.229  1.489  0.053 | -0.517  8.638  0.269 |
DOC.0.45m_mg.L    |  0.191  0.594  0.037 |  0.367  3.806  0.136 |  0.758 18.599  0.579 |
DOC.1.2m_mg.L     |  0.009  0.001  0.000 | -0.424  5.095  0.182 | -0.734 17.441  0.543 |
> head(ChemPhysCS2)
```

Appendix III:

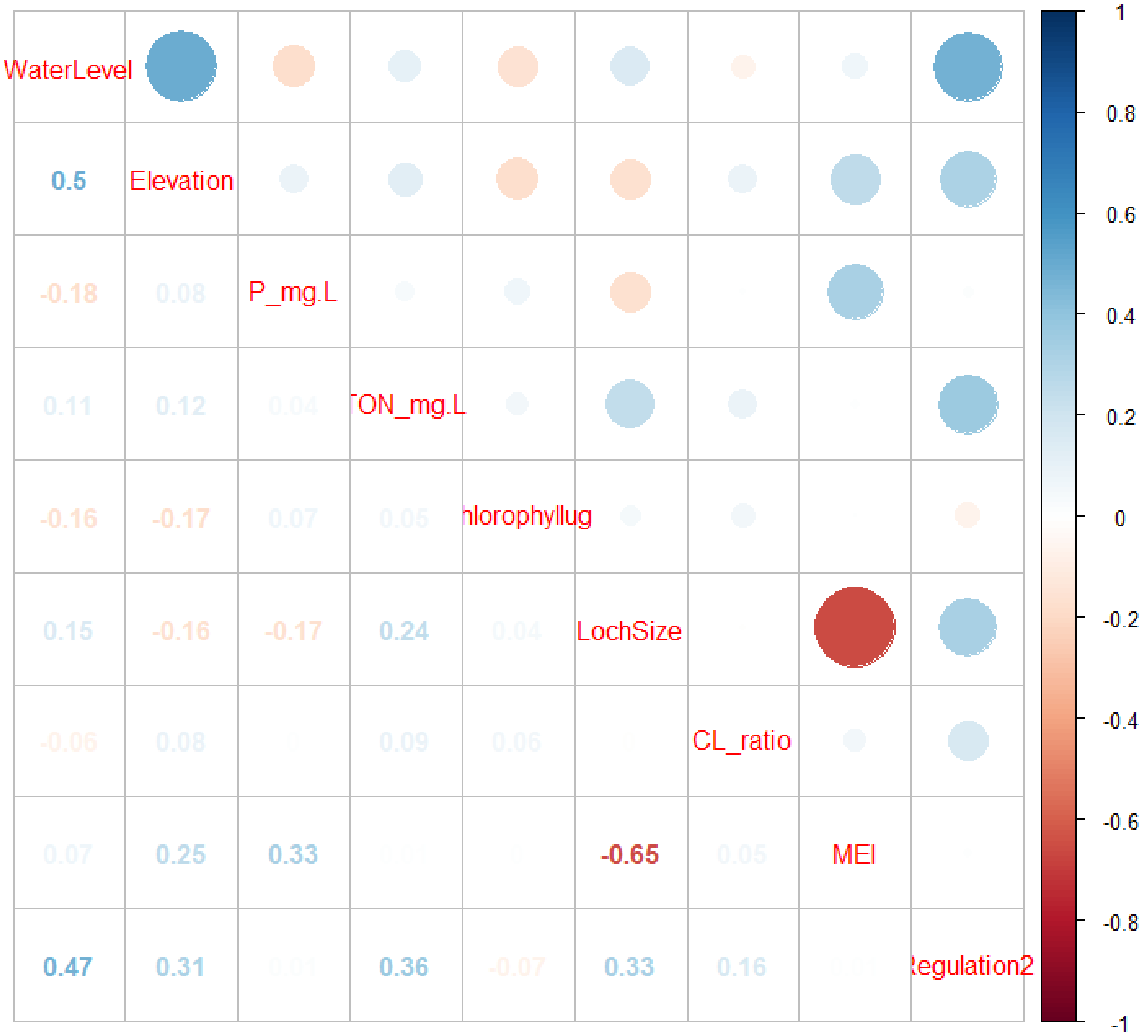
Correlations between predictor variables and VIFs

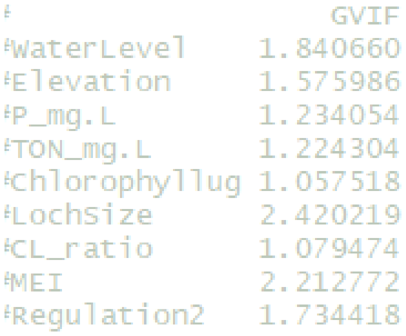
All lake predictors



```
GVIF
WaterLevel     1.652620
Elevation      1.303386
P_mg.L         1.673863
TON_mg.L       1.997590
Chlorophyllug  2.543332
LochSize       2.091172
CL_ratio       1.079987
MEI            3.108366
Regulation2    1.876783
```

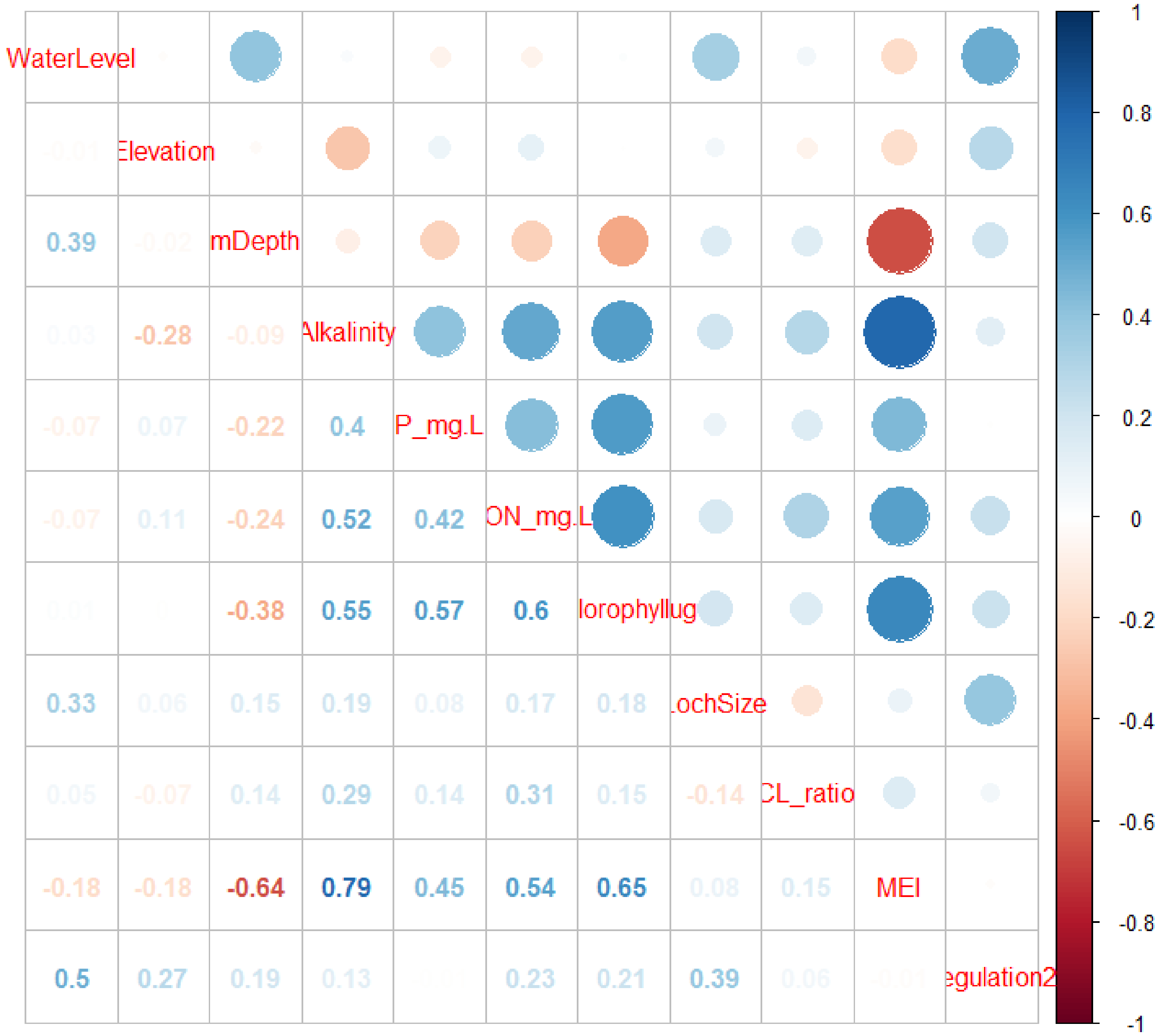
Low MEI lake predictors

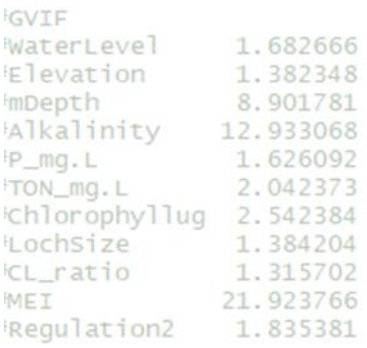




```
#                       GVIF
#WaterLevel     1.840660
#Elevation      1.575986
#P_mg.L         1.234054
#TON_mg.L       1.224304
#Chlorophyllug  1.057518
#LochSize       2.420219
#CL_ratio       1.079474
#MEI            2.212772
#Regulation2    1.734418
```

High MEI lake predictors

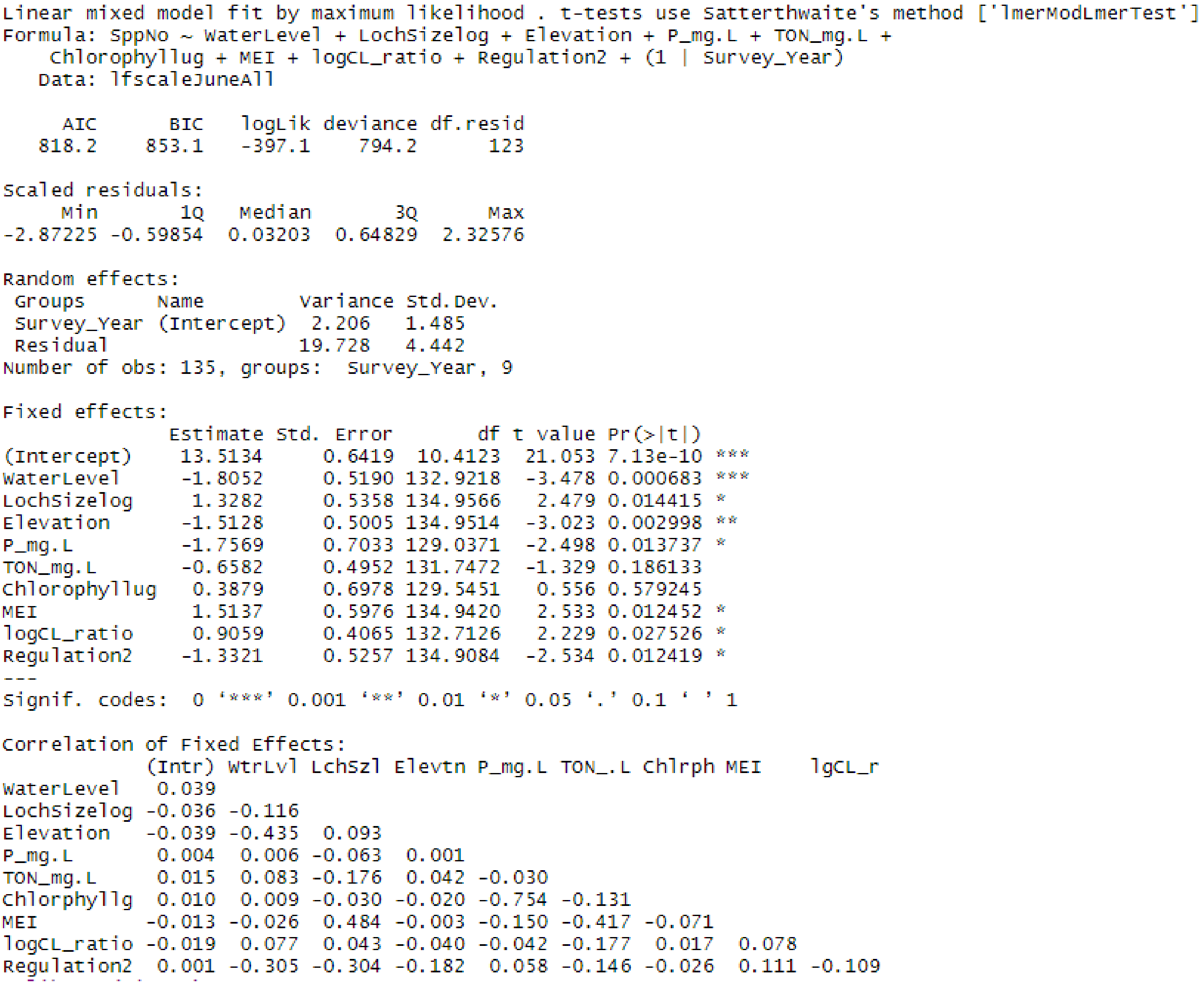



```
GVIF
WaterLevel      1.682666
Elevation       1.382348
mDepth          8.901781
Alkalinity     12.933068
P_mg.L          1.626092
TON_mg.L        2.042373
Chlorophyllug   2.542384
LochSize        1.384204
CL_ratio        1.315702
MEI            21.923766
Regulation2     1.835381
```

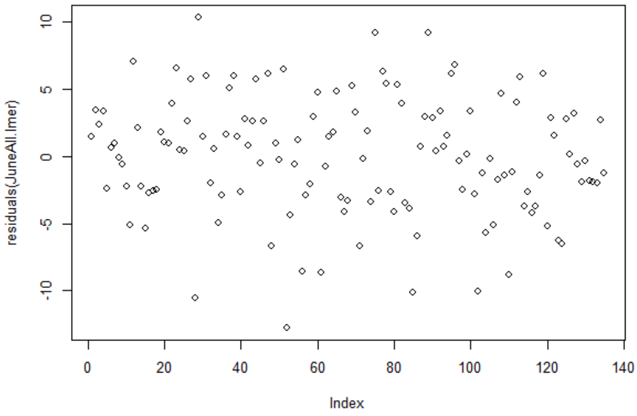
Appendix IV;

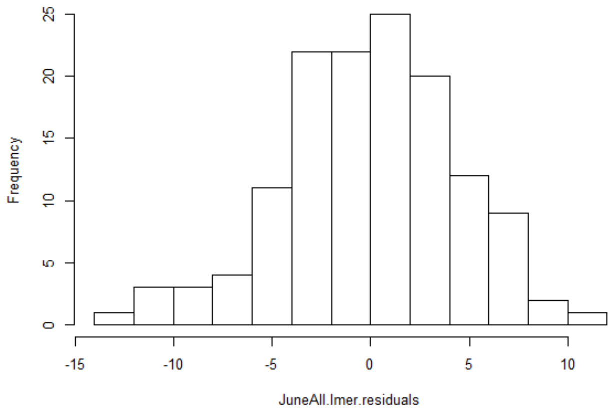
All lake model for species richness (lmer)

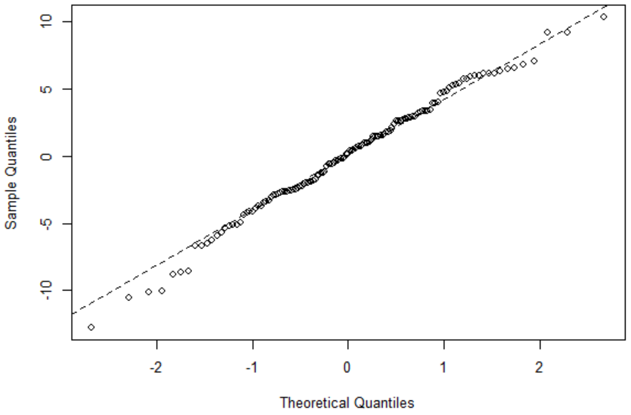
All lake model:



```
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: SppNo ~ WaterLevel + LochSizelog + Elevation + P_mg.L + TON_mg.L +
    Chlorophyllug + MEI + logCL_ratio + Regulation2 + (1 | Survey_Year)
   Data: lfscaleJuneAll

     AIC      BIC   logLik deviance df.resid
   818.2    853.1   -397.1    794.2      123

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.87225 -0.59854  0.03203  0.64829  2.32576

Random effects:
 Groups      Name        Variance Std.Dev.
 Survey_Year (Intercept)  2.206   1.485
 Residual                19.728   4.442
Number of obs: 135, groups:  Survey_Year, 9

Fixed effects:
              Estimate Std. Error       df t value Pr(>|t|)
(Intercept)    13.5134     0.6419  10.4123  21.053 7.13e-10 ***
WaterLevel     -1.8052     0.5190 132.9218  -3.478 0.000683 ***
LochSizelog     1.3282     0.5358 134.9566   2.479 0.014415 *
Elevation      -1.5128     0.5005 134.9514  -3.023 0.002998 **
P_mg.L         -1.7569     0.7033 129.0371  -2.498 0.013737 *
TON_mg.L       -0.6582     0.4952 131.7472  -1.329 0.186133
Chlorophyllug   0.3879     0.6978 129.5451   0.556 0.579245
MEI             1.5137     0.5976 134.9420   2.533 0.012452 *
logCL_ratio     0.9059     0.4065 132.7126   2.229 0.027526 *
Regulation2    -1.3321     0.5257 134.9084  -2.534 0.012419 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) WtrLvl LchSzl Elevtn P_mg.L TON_.L Chlrph MEI    lgCL_r
WaterLevel   0.039
LochSizelog -0.036 -0.116
Elevation   -0.039 -0.435  0.093
P_mg.L       0.004  0.006 -0.063  0.001
TON_mg.L     0.015  0.083 -0.176  0.042 -0.030
Chlorphyllg  0.010  0.009 -0.030 -0.020 -0.754 -0.131
MEI         -0.013 -0.026  0.484 -0.003 -0.150 -0.417 -0.071
logCL_ratio -0.019  0.077  0.043 -0.040 -0.042 -0.177  0.017  0.078
Regulation2  0.001 -0.305 -0.304 -0.182  0.058 -0.146 -0.026  0.111 -0.109
```




Histogram of JuneAll.lmer.residuals

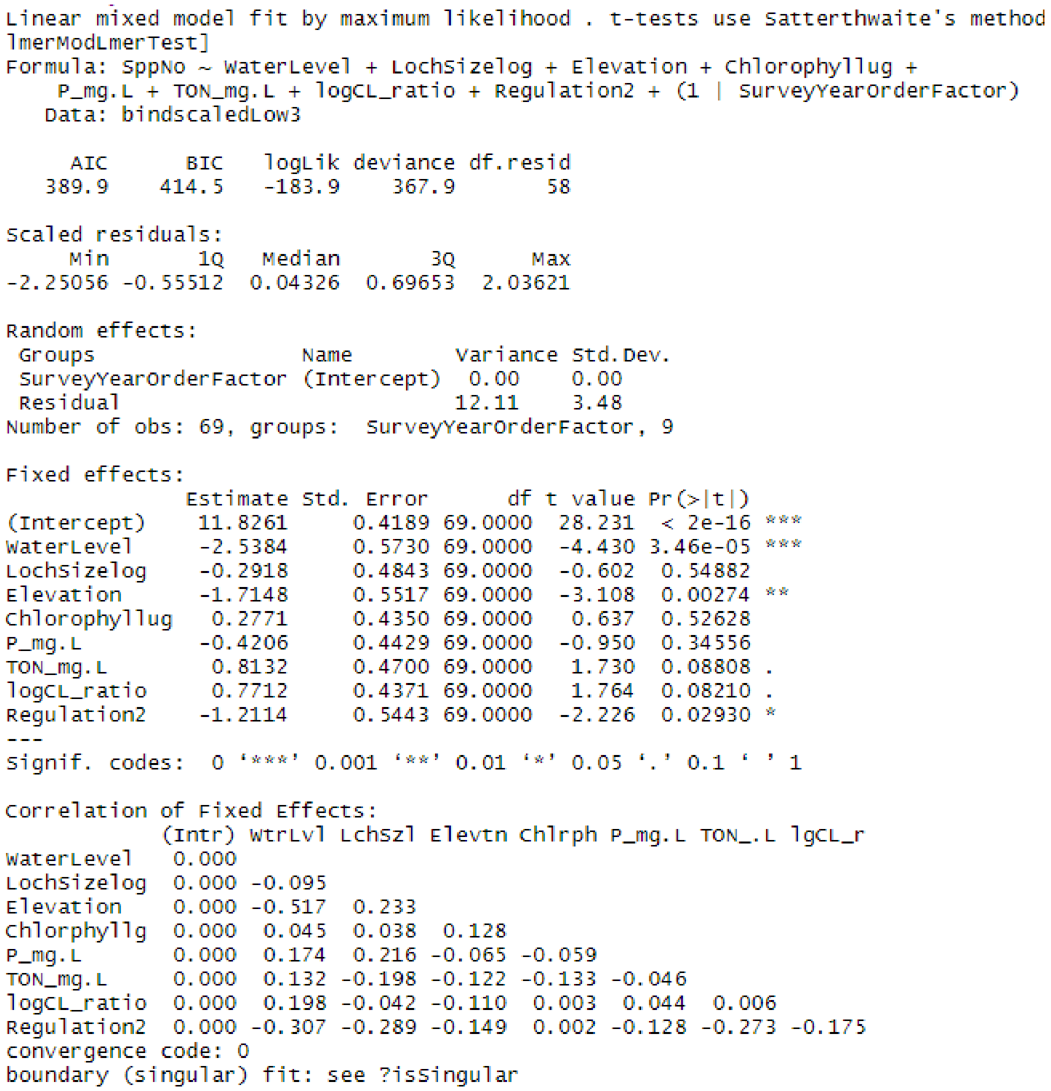

Normal Q-Q Plot

Shapiro-Wilk normality test data:
JuneAll.lmer.residuals W =
0.99049, p-value = 0.4895

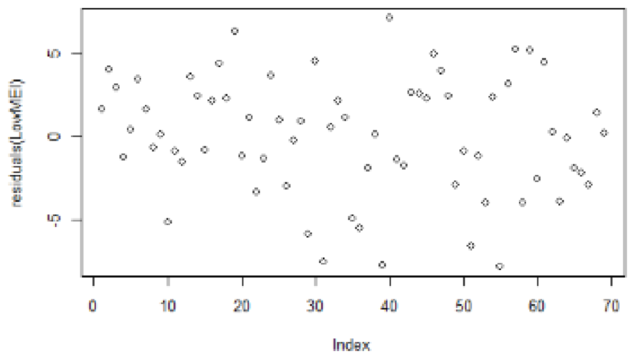
Appendix V:

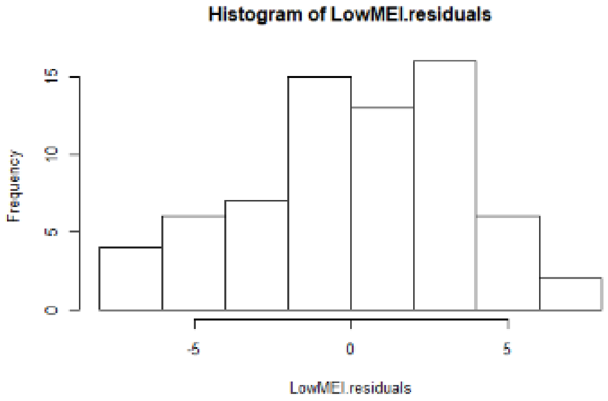
Low and High MEI lake models for species richness

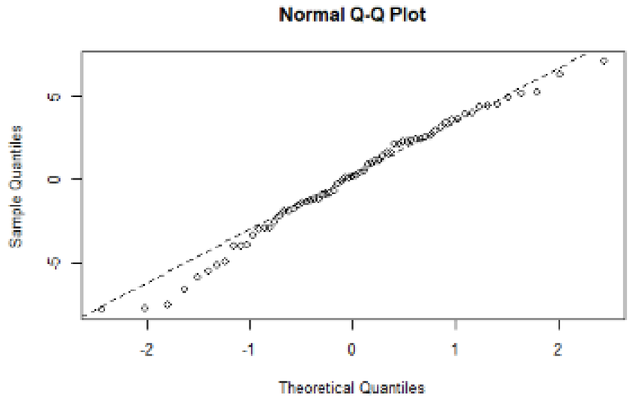
Low MEI lake model:



```
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method
lmerModLmerTest]
Formula: SppNo ~ WaterLevel + LochSizelog + Elevation + Chlorophyllug +
    P_mg.L + TON_mg.L + logCL_ratio + Regulation2 + (1 | SurveyYearOrderFactor)
   Data: bindscaledLow3

     AIC      BIC   logLik deviance df.resid
   389.9    414.5   -183.9    367.9       58

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.25056 -0.55512  0.04326  0.69653  2.03621

Random effects:
 Groups                Name        Variance Std.Dev.
 SurveyYearOrderFactor (Intercept)  0.00    0.00
 Residual                          12.11    3.48
Number of obs: 69, groups:  SurveyYearOrderFactor, 9

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)    11.8261     0.4189 69.0000  28.231  < 2e-16 ***
WaterLevel     -2.5384     0.5730 69.0000  -4.430 3.46e-05 ***
LochSizelog    -0.2918     0.4843 69.0000  -0.602  0.54882
Elevation      -1.7148     0.5517 69.0000  -3.108  0.00274 **
Chlorophyllug   0.2771     0.4350 69.0000   0.637  0.52628
P_mg.L         -0.4206     0.4429 69.0000  -0.950  0.34556
TON_mg.L        0.8132     0.4700 69.0000   1.730  0.08808 .
logCL_ratio     0.7712     0.4371 69.0000   1.764  0.08210 .
Regulation2    -1.2114     0.5443 69.0000  -2.226  0.02930 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) WtrLvl LchSzl Elevtn Chlrph P_mg.L TON_.L lgCL_r
WaterLevel   0.000
LochSizelog  0.000 -0.095
Elevation    0.000 -0.517  0.233
Chlorphyllg  0.000  0.045  0.038  0.128
P_mg.L       0.000  0.174  0.216 -0.065 -0.059
TON_mg.L     0.000  0.132 -0.198 -0.122 -0.133 -0.046
logCL_ratio  0.000  0.198 -0.042 -0.110  0.003  0.044  0.006
Regulation2  0.000 -0.307 -0.289 -0.149  0.002 -0.128 -0.273 -0.175
convergence code: 0
boundary (singular) fit: see ?isSingular
```

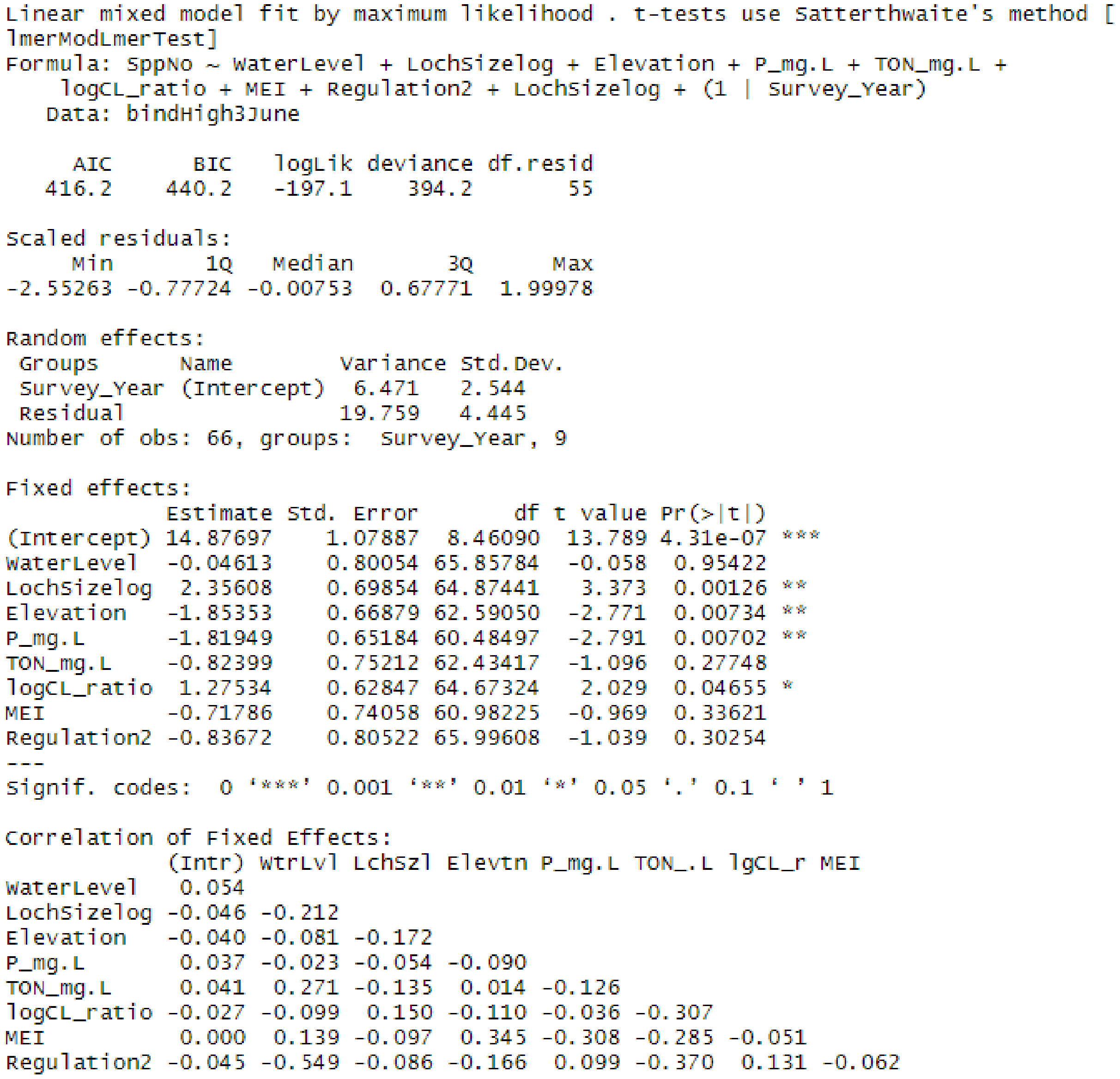




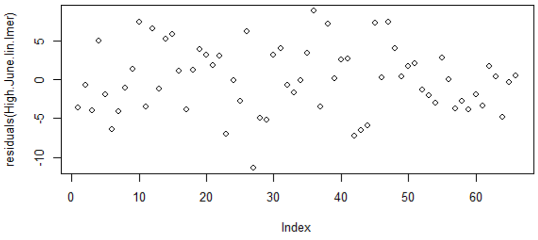


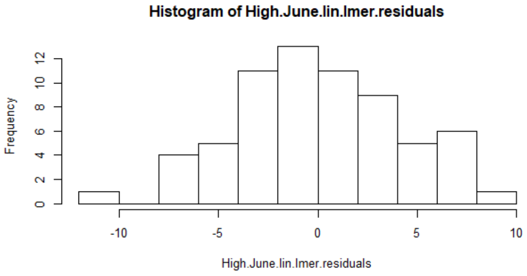
```
Shapiro-Wilk normality test

data:  LowMEI.residuals

W = 0.98125, p-value = 0.3876
```

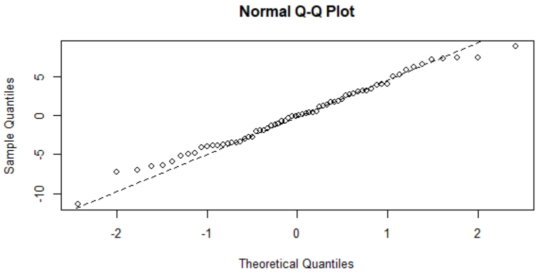
High MEI lake model lmer:



```
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method [
lmerModLmerTest]
Formula: SppNo ~ WaterLevel + LochSizelog + Elevation + P_mg.L + TON_mg.L +
    logCL_ratio + MEI + Regulation2 + LochSizelog + (1 | Survey_Year)
   Data: bindHigh3June

     AIC      BIC   logLik deviance df.resid
   416.2    440.2   -197.1    394.2       55

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.55263 -0.77724 -0.00753  0.67771  1.99978

Random effects:
 Groups      Name        Variance Std.Dev.
 Survey_Year (Intercept)  6.471   2.544
 Residual                19.759   4.445
Number of obs: 66, groups:  Survey_Year, 9

Fixed effects:
            Estimate Std. Error       df t value Pr(>|t|)
(Intercept) 14.87697    1.07887  8.46090  13.789 4.31e-07 ***
WaterLevel  -0.04613    0.80054 65.85784  -0.058  0.95422
LochSizelog  2.35608    0.69854 64.87441   3.373  0.00126 **
Elevation   -1.85353    0.66879 62.59050  -2.771  0.00734 **
P_mg.L      -1.81949    0.65184 60.48497  -2.791  0.00702 **
TON_mg.L    -0.82399    0.75212 62.43417  -1.096  0.27748
logCL_ratio  1.27534    0.62847 64.67324   2.029  0.04655 *
MEI         -0.71786    0.74058 60.98225  -0.969  0.33621
Regulation2 -0.83672    0.80522 65.99608  -1.039  0.30254
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) WtrLvl LchSzl Elevtn P_mg.L TON_.L lgCL_r MEI
WaterLevel   0.054
LochSizelog -0.046 -0.212
Elevation   -0.040 -0.081 -0.172
P_mg.L       0.037 -0.023 -0.054 -0.090
TON_mg.L     0.041  0.271 -0.135  0.014 -0.126
logCL_ratio -0.027 -0.099  0.150 -0.110 -0.036 -0.307
MEI          0.000  0.139 -0.097  0.345 -0.308 -0.285 -0.051
Regulation2 -0.045 -0.549 -0.086 -0.166  0.099 -0.370  0.131 -0.062
```



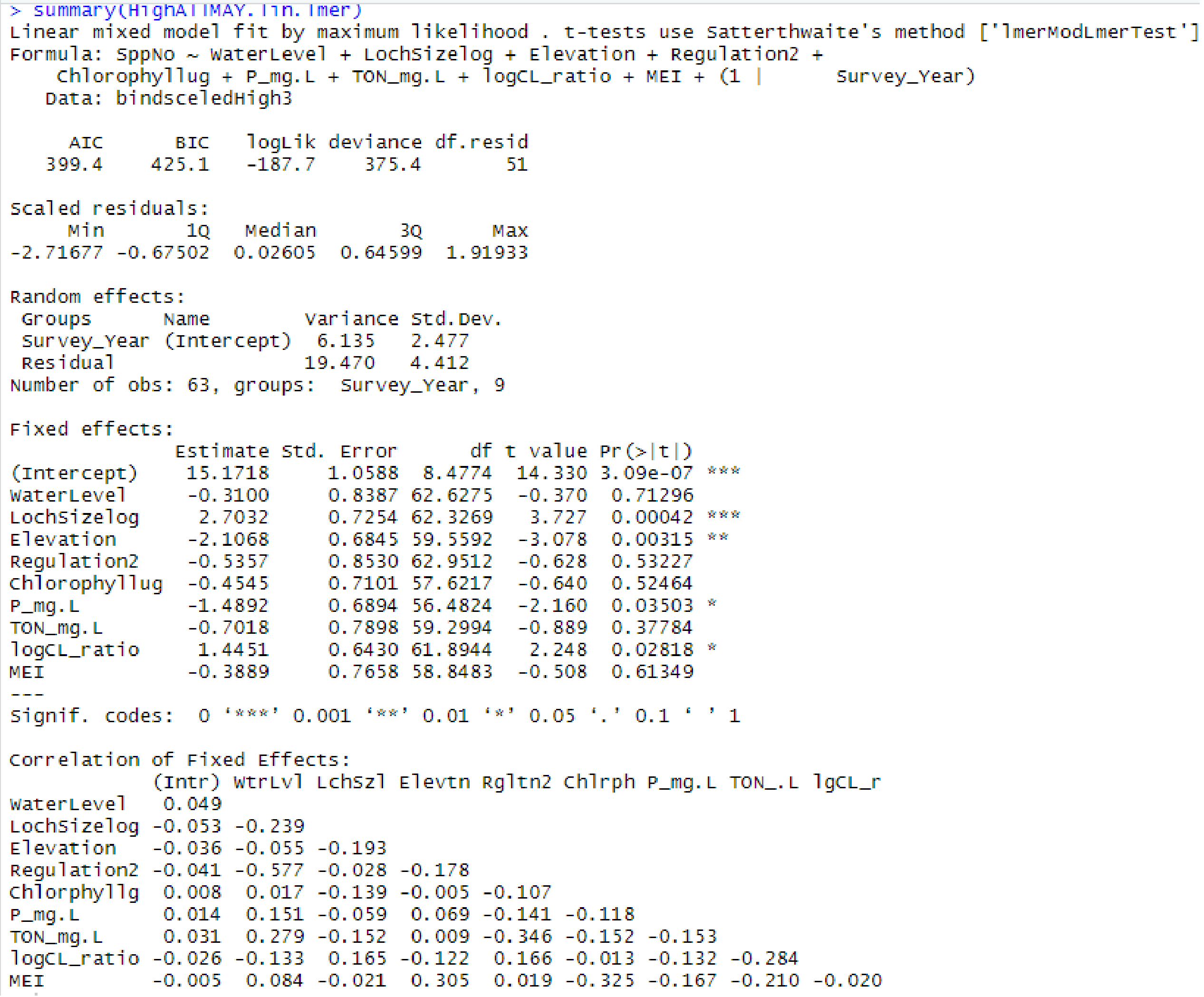




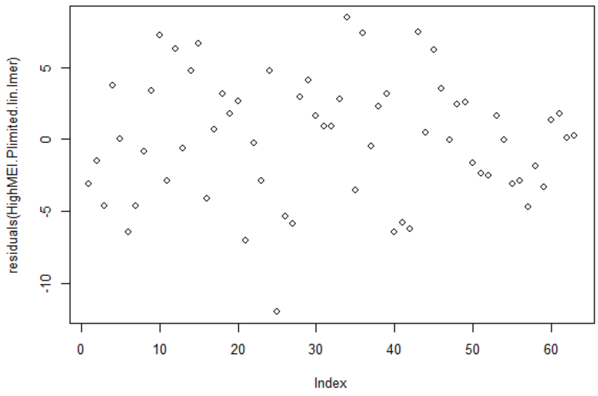
```
        Shapiro-Wilk normality test

data:  High.June.lin.lmer.residuals

W = 0.98789, p-value = 0.7706
```

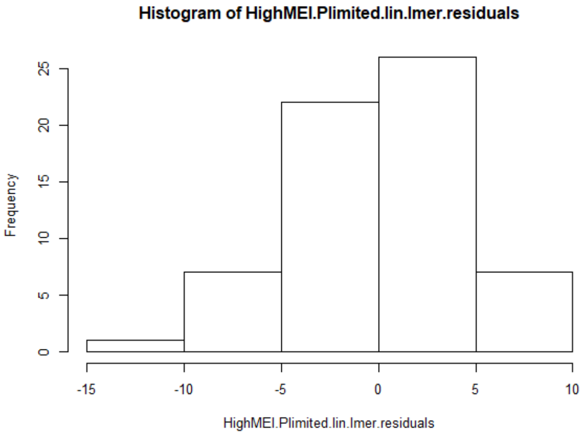
Appendix VI:

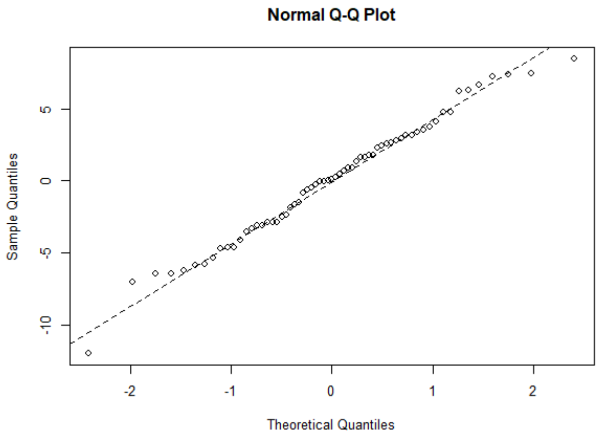
High MEI lake mixed model effects with P limited to 0.25mg/L (to examine the influence of three lakes with outliers of high P)



```
> summary(HighAllMAY.lin.lmer)
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: SppNo ~ WaterLevel + LochSizelog + Elevation + Regulation2 +
    Chlorophyllug + P_mg.L + TON_mg.L + logCL_ratio + MEI + (1 |      Survey_Year)
   Data: bindsceledHigh3

     AIC      BIC   logLik deviance df.resid
   399.4    425.1   -187.7    375.4       51

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.71677 -0.67502  0.02605  0.64599  1.91933

Random effects:
 Groups      Name        Variance Std.Dev.
 Survey_Year (Intercept)  6.135   2.477
 Residual                19.470   4.412
Number of obs: 63, groups:  Survey_Year, 9

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)    15.1718     1.0588  8.4774  14.330 3.09e-07 ***
WaterLevel     -0.3100     0.8387 62.6275  -0.370  0.71296
LochSizelog     2.7032     0.7254 62.3269   3.727  0.00042 ***
Elevation      -2.1068     0.6845 59.5592  -3.078  0.00315 **
Regulation2    -0.5357     0.8530 62.9512  -0.628  0.53227
Chlorophyllug  -0.4545     0.7101 57.6217  -0.640  0.52464
P_mg.L         -1.4892     0.6894 56.4824  -2.160  0.03503 *
TON_mg.L       -0.7018     0.7898 59.2994  -0.889  0.37784
logCL_ratio     1.4451     0.6430 61.8944   2.248  0.02818 *
MEI            -0.3889     0.7658 58.8483  -0.508  0.61349
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) WtrLvl LchSzl Elevtn Rgltn2 Chlrph P_mg.L TON_.L lgCL_r
WaterLevel   0.049
LochSizelog -0.053 -0.239
Elevation   -0.036 -0.055 -0.193
Regulation2 -0.041 -0.577 -0.028 -0.178
Chlorphyllg  0.008  0.017 -0.139 -0.005 -0.107
P_mg.L       0.014  0.151 -0.059  0.069 -0.141 -0.118
TON_mg.L     0.031  0.279 -0.152  0.009 -0.346 -0.152 -0.153
logCL_ratio -0.026 -0.133  0.165 -0.122  0.166 -0.013 -0.132 -0.284
MEI         -0.005  0.084 -0.021  0.305  0.019 -0.325 -0.167 -0.210 -0.020
```







Shapiro-Wilk normality test

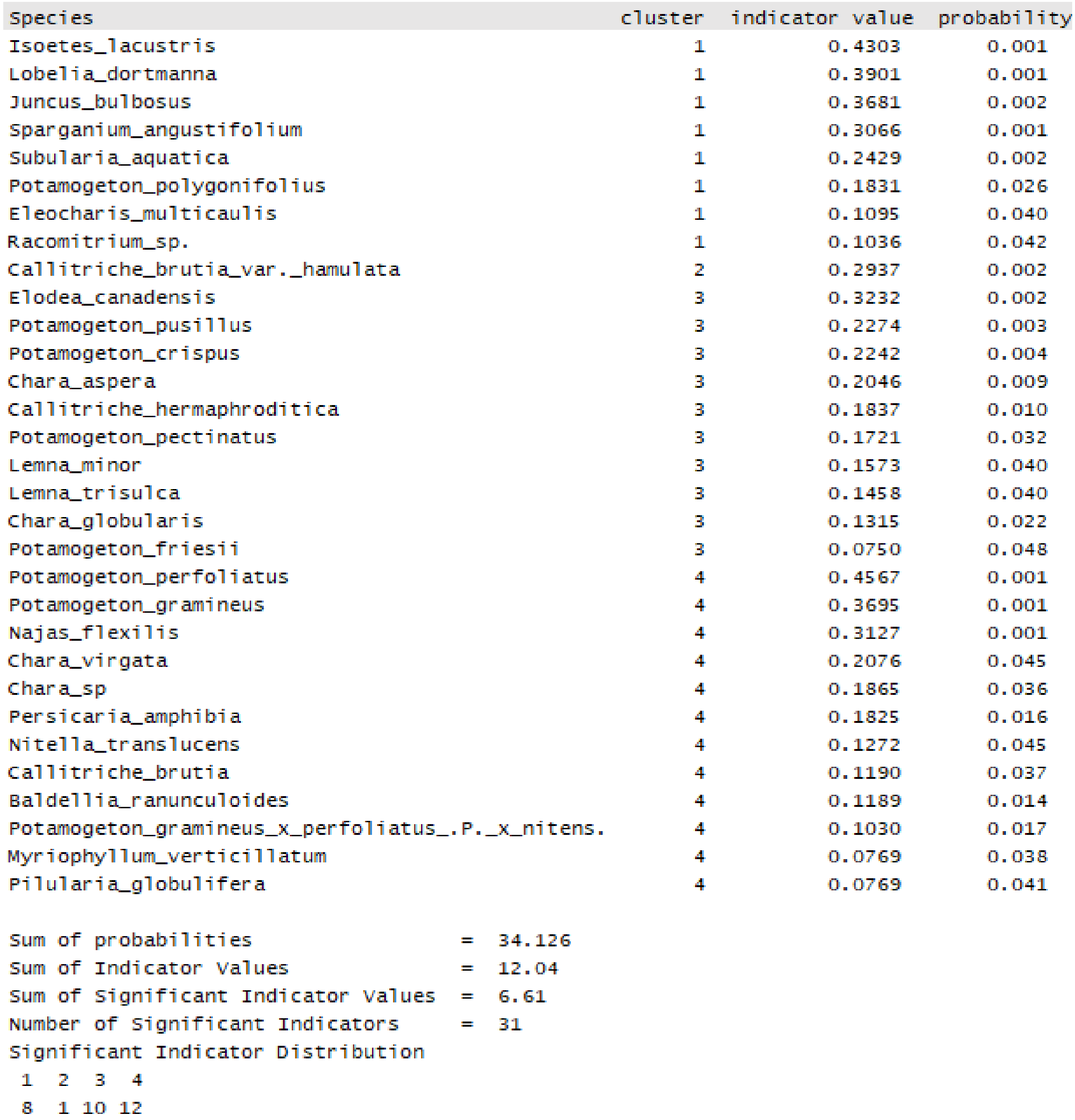
data: HighMEI.Plimited.lin.lmer.residuals

W = 0.98569, p-value = 0.6766

Appendix VII:

Indicator species clusters for All lakes.

Cluster 1	Low MEI lakes with stable water levels
Cluster 2	Low MEI fluctuating water levels
Cluster 3	High MEI stable water levels
Cluster 4	High MEI fluctuating water levels

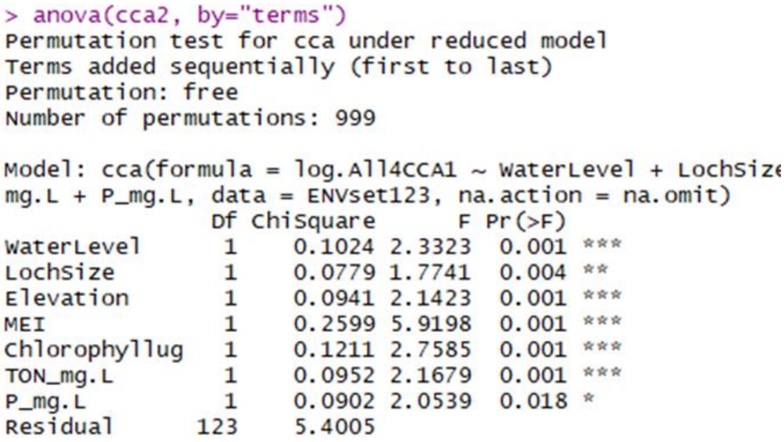


```
Species                                              cluster  indicator value  probability
Isoetes_lacustris                                          1           0.4303        0.001
Lobelia_dortmanna                                          1           0.3901        0.001
Juncus_bulbosus                                            1           0.3681        0.002
Sparganium_angustifolium                                   1           0.3066        0.001
Subularia_aquatica                                         1           0.2429        0.002
Potamogeton_polygonifolius                                 1           0.1831        0.026
Eleocharis_multicaulis                                     1           0.1095        0.040
Racomitrium_sp.                                            1           0.1036        0.042
Callitriche_brutia_var._hamulata                           2           0.2937        0.002
Elodea_canadensis                                          3           0.3232        0.002
Potamogeton_pusillus                                       3           0.2274        0.003
Potamogeton_crispus                                        3           0.2242        0.004
Chara_aspera                                               3           0.2046        0.009
Callitriche_hermaphroditica                                3           0.1837        0.010
Potamogeton_pectinatus                                     3           0.1721        0.032
Lemna_minor                                                3           0.1573        0.040
Lemna_trisulca                                             3           0.1458        0.040
Chara_globularis                                           3           0.1315        0.022
Potamogeton_friesii                                        3           0.0750        0.048
Potamogeton_perfoliatus                                    4           0.4567        0.001
Potamogeton_gramineus                                      4           0.3695        0.001
Najas_flexilis                                             4           0.3127        0.001
Chara_virgata                                              4           0.2076        0.045
Chara_sp                                                   4           0.1865        0.036
Persicaria_amphibia                                        4           0.1825        0.016
Nitella_translucens                                        4           0.1272        0.045
Callitriche_brutia                                         4           0.1190        0.037
Baldellia_ranunculoides                                    4           0.1189        0.014
Potamogeton_gramineus_x_perfoliatus_.P._x_nitens.          4           0.1030        0.017
Myriophyllum_verticillatum                                 4           0.0769        0.038
Pilularia_globulifera                                      4           0.0769        0.041

Sum of probabilities                 =  34.126
Sum of Indicator Values              =  12.04
Sum of Significant Indicator Values  =  6.61
Number of Significant Indicators     =  31
Significant Indicator Distribution
 1  2  3  4
 8  1 10 12
```

Appendix VIII:

Drivers of vegetation composition CCA ALL lakes

When species assemblages were constrained by environmental variables using CCA the overall model was significant (P < 0.001) explaining 13% of variation.

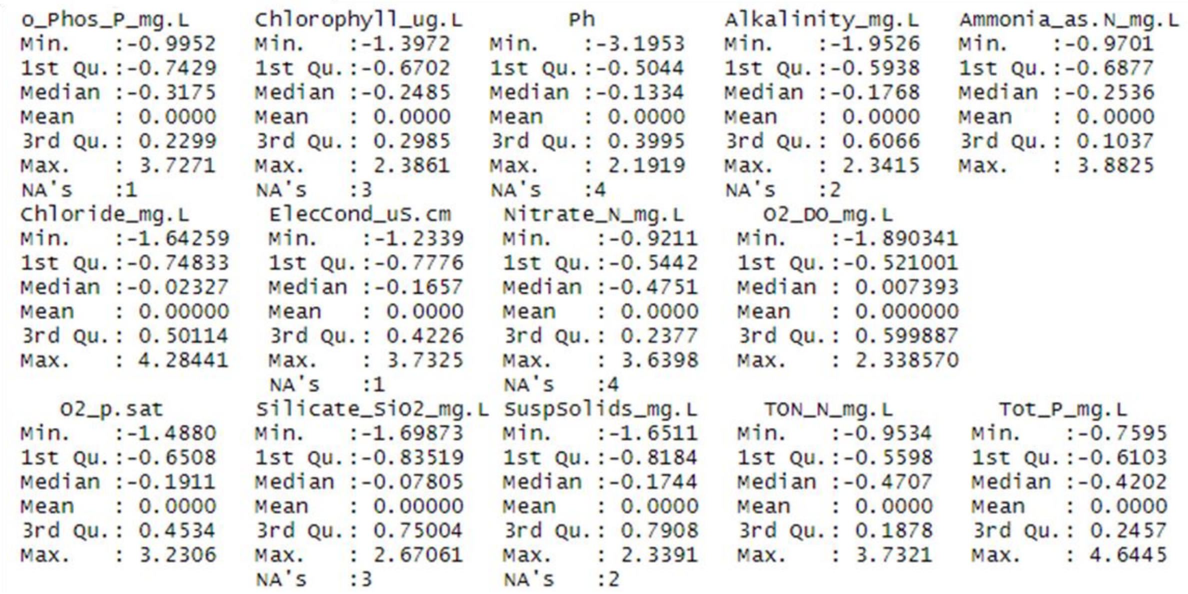


```
> anova(cca2, by="terms")
Permutation test for cca under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

Model: cca(formula = log.All4CCA1 ~ WaterLevel + LochSize
mg.L + P_mg.L, data = ENVset123, na.action = na.omit)
               Df ChiSquare      F Pr(>F)    
WaterLevel      1    0.1024 2.3323  0.001 ***
LochSize        1    0.0779 1.7741  0.004 ** 
Elevation       1    0.0941 2.1423  0.001 ***
MEI             1    0.2599 5.9198  0.001 ***
Chlorophyllug   1    0.1211 2.7585  0.001 ***
TON_mg.L        1    0.0952 2.1679  0.001 ***
P_mg.L          1    0.0902 2.0539  0.018 *  
Residual      123    5.4005                  
```

Chapter 3

Appendix I:

Missing data, (n=19) calculated for using Beckers et al. (2003) and Taylor et al. (2013) methods of optimal interpolation



```
 o_Phos_P_mg.L      Chlorophyll_ug.L          Ph           Alkalinity_mg.L    Ammonia_as.N_mg.L
 Min.   :-0.9952    Min.   :-1.3972    Min.   :-3.1953    Min.   :-1.9526    Min.   :-0.9701
 1st Qu.:-0.7429    1st Qu.:-0.6702    1st Qu.:-0.5044    1st Qu.:-0.5938    1st Qu.:-0.6877
 Median :-0.3175    Median :-0.2485    Median :-0.1334    Median :-0.1768    Median :-0.2536
 Mean   : 0.0000    Mean   : 0.0000    Mean   : 0.0000    Mean   : 0.0000    Mean   : 0.0000
 3rd Qu.: 0.2299    3rd Qu.: 0.2985    3rd Qu.: 0.3995    3rd Qu.: 0.6066    3rd Qu.: 0.1037
 Max.   : 3.7271    Max.   : 2.3861    Max.   : 2.1919    Max.   : 2.3415    Max.   : 3.8825
 NA's   :1          NA's   :3          NA's   :4          NA's   :2
 Chloride_mg.L        ElecCond_uS.cm     Nitrate_N_mg.L      O2_DO_mg.L
 Min.   :-1.64259    Min.   :-1.2339    Min.   :-0.9211    Min.   :-1.890341
 1st Qu.:-0.74833    1st Qu.:-0.7776    1st Qu.:-0.5442    1st Qu.:-0.521001
 Median :-0.02327    Median :-0.1657    Median :-0.4751    Median : 0.007393
 Mean   : 0.00000    Mean   : 0.0000    Mean   : 0.0000    Mean   : 0.000000
 3rd Qu.: 0.50114    3rd Qu.: 0.4226    3rd Qu.: 0.2377    3rd Qu.: 0.599887
 Max.   : 4.28441    Max.   : 3.7325    Max.   : 3.6398    Max.   : 2.338570
                     NA's   :1          NA's   :4
    O2_p.sat        Silicate_SiO2_mg.L SuspSolids_mg.L      TON_N_mg.L         Tot_P_mg.L
 Min.   :-1.4880    Min.   :-1.69873   Min.   :-1.6511    Min.   :-0.9534    Min.   :-0.7595
 1st Qu.:-0.6508    1st Qu.:-0.83519   1st Qu.:-0.8184    1st Qu.:-0.5598    1st Qu.:-0.6103
 Median :-0.1911    Median :-0.07805   Median :-0.1744    Median :-0.4707    Median :-0.4202
 Mean   : 0.0000    Mean   : 0.00000   Mean   : 0.0000    Mean   : 0.0000    Mean   : 0.0000
 3rd Qu.: 0.4534    3rd Qu.: 0.75004   3rd Qu.: 0.7908    3rd Qu.: 0.1878    3rd Qu.: 0.2457
 Max.   : 3.2306    Max.   : 2.67061   Max.   : 2.3391    Max.   : 3.7321    Max.   : 4.6445
                    NA's   :3          NA's   :2
```

Appendix II:
Method of water level data attainment for each lake

WBID	Loch	Regulated Y/N	WLF (m)	WLF main source
14293	a_Bhraoin	N	1	GoogleEarth, OS & web search
6236	Airigh_Leathaidh	N	0.5	GoogleEarth, OS & web search
21649	an_t_Seilich	Y	3.5	Scottish Southern Electric: Cruaich hydro: OS & web
24892	Ard	N	0.9	first author field data
23684	Ba_Mull	N	1	GoogleEarth, OS & web search
27638	Bradan	y	3	GoogleEarth, OS & web search
2358	Calder	Y	1.5	GoogleEarth, OS & web search
24754	Chon	N	0.9	first author field data
20725	Craobh_Loisgte	N	0.4	GoogleEarth, OS & web search.SSE
21123	Davan_5	N	0.35	SEPA based on kinord
27948	Dee	N	1.2	loch Dee outlet
22308	Doilet	N	1	GoogleEarth, OS & web search
27604	Doon	Y	3	Scottish Power
18607	Druidibeag	N	1	GoogleEarth, OS & web search
24798	Drunkie	Y	2.18	Scottish Water
22840	Eigheach	Y	4.5	Scottish Southern Electric
21848	Eilt	N	1	GoogleEarth, OS & web search
23216	Frisa	N	1	GoogleEarth, OS & web search
14315	Glascarnoch	Y	5.5	Scottish Southern Electric
26168	Gorm	N	0.9	GoogleEarth, OS & web search
28130	Grannoch	N	1.5	GoogleEarth, OS & web search
1753	Harray	N	0.9	GoogleEarth, OS & web search
20860	Insh	N	1.9	SEPA Gauge map. Kincraig outflow
24531	Katrine_Stone_Bay	Y	1.6	Scottish Water
24531	Katrine_W_ELL	Y	1.6	Scottish Water
21189	KINORD	N	0.35	SEPA gauge map
21576	LAGGAN	N	2.2	GoogleEarth, OS & web search
22839	Laidon	N	2	GoogleEarth, OS & web search
21945	Lee	Y	0.03	Scottish Water
24843	Leven	Y	1	GoogleEarth, OS & web search. SEPA/cranmore sluice
18825	Lochindorb	N	0.58	GoogleEarth, OS & web search. SEPA gauge map
24447	Lomond_Sth	Y	0.99	Scottish Water
24447	Lomond_Tarbet_N	Y	0.99	Scottish Water
24459	Lubnaig	N	1.6	first author field data
14057	Maree	N	1.5	GoogleEarth, OS & web search
24919	Menteith	N	1	GoogleEarth, OS & web search
28506	Mochrum	N	0.9	GoogleEarth, OS & web search
6140	More_Caith	Y	2	GoogleEarth, OS & web search. Thurso estate
20657	Morlich	N	0.9	GoogleEarth, OS & web search
19079	Moy	N	0.5	GoogleEarth, OS & web search
21790	Muick	N	1	GoogleEarth, OS & web search
20739	na_Beinne_	N	0.5	GoogleEarth, OS & web search
20712	nan_Geadas	N	0.5	GoogleEarth, OS & web search
6405	Naver	N	1.3	SEPA gauge map, GoogleEarth & OS
18767	Ness	Y	1.2	GoogleEarth, OS & web search. SSE
25006	Ore	N	0.9	GoogleEarth, OS & web search
11189	Osgaig	N	0.9	GoogleEarth, OS & web search
28158	Penwhirn_Dam	Y	3	Scottish Water
24863	Reoidhte	N	0.5	GoogleEarth, OS & web search
23192	Rescobie	N	0.9	GoogleEarth, OS & web search
2499	Scarmclate	N	0.9	GoogleEarth, OS & web search
21925	Shiel	N	0.9	GoogleEarth, OS & web search
27309	St_Marys	Y	2.5	GoogleEarth, OS & web search. Scottish Water
5350	Stack	N	0.5	GoogleEarth, OS & web search
16275	Strathbeg	N	1	GoogleEarth, OS & web search
1678	Swannay	N	1	SEPA gauge map & GoogleEarth, OS
20633	Tarff	N	1	GoogleEarth, OS & web search
23515	Tay	N	1.5	GoogleEarth, OS & SEPA gauge map
4284	Urrahag	N	1.5	GoogleEarth, OS & web search
16456	Ussie	N	0.9	GoogleEarth, OS & web search
24758	Venachar	Y	1.6	Scottish Water
14032	Vaich	Y	5	Scottish Southern Electric;GoogleEarth, OS & web search
24295	Voil	N	1.6	first author field data

Additional methods of estimation and measures for lakes with no water level data

Our full original data set consisted of 92 lakes with no time series water level data. The 57 lakes used in this study were extracted from the original data set. We conducted strand line surveys and used online information to provide estimates of WLF range for these waterbodies.

It was not feasible to conduct the strand line surveys on all 92 unregulated lakes within our data set. Therefore we used a combination of aerial photographs, internet searches for images or drone footage from geography and fishing websites, and forums or google images of the lochs in different seasons, along with google earth imagery and measuring tools to estimate the range in water level fluctuation occurring to each lake. We also used river gauge data from SEPA websites when these were proximal to the lakes outflow, and compared the measures gained from this approach with field surveys of strand lines as outlined below.

10 lakes and reservoirs were surveyed in late September 2014. The wettest winter in over 100 years was followed by the driest Septembers on record in Scotland since 1972, with the warmest spring and the 15th highest summer mean temperatures recorded since 1884, see: (https://www.metoffice.gov.uk/pub/data/weather/uk/climate/datasets/Tmean/ranked/Scotland.txt)

We reasoned that at late September that year, the preceding weather should result in lakes with no WLF regulation being close to their minimum water levels, with the strand lines on the shores reflecting the highest water levels from winter months.

The range of water level drawdown was measured as the height difference between the highest strand line evident on the lake bank and the waterline of the lake or reservoir at that time. A manual theodolite was used for the surveys.

Included in the surveys were reservoirs that we held WLF data for. This enabled some measure of comparison - though the regimes of these reservoirs are altered so that late summer does not necessarily mean the time for lowest water levels, particularly those which are re-filled by other “holding” reservoirs (as per the data below for, Backwater reservoir, Loch of Lintrathen and Loch Katrine). However, this method did allow us to compare the calculated range in water level from the surveys, with river gauge outflow data obtained from CEH and SEPA on line resources (see below for, Loch Katrine, Loch Lubnaig and Loch Ard).

Water levels range from strandline measures, compared with time series of gauge data

waterbody	height difference strandline to water line (m)	time series data WLF (80%) (m)	outflow data CEH (m)
Backwater reservoir	0.58	3.5	
Loch of Lintrathen	1.99	3.11	
Loch Lubnaig	1.37	n/a	1.8
Loch Venachar	1.95	1.62	
Loch Drunkie	1.89	2.18	
Loch Katrine	1.25	1.6	1.2
Loch Arklet	3.52	2.74	
Loch Chon	0.91	n/a	
Loch Ard	0.91	n/a	0.8
Glen Finglas reservoir	6.65	7.8	

There are minor differences between the measures, for instance, the measured range at Loch Arklet is greater than the time series data by 0.78 m. The discrepancies were likely due to variation between a) the time series data being based on calculations (and excluding the minimum and maximum 10th percentiles) from previous years and b) the year of the survey (2014) was unusually dryer and hotter for spring and summer. Loch Lubnaig was measured as 1.4 m the gauge was 1.8 m therefore, we estimated this as mid-way between the two at 1.6 m, this was because the disturbance and substrate around Lubnaig banks from cattle and camping or rip rap make strandline detection problematic. For Loch Ard and Loch Chon there is less shore line disturbance, and we were confident on our measures so used 0.9 in the analysis. As river outflow data looked approximate to the measured data, we used this as a guide in conjunction with aerial images, reports, forums as well as contact with fishing groups or land managers, to estimate the other unregulated lakes across Scotland. Each waterbody was assessed individually in this way.

We further compared our ability to estimate the WLF regime of lakes, by estimating for reservoirs using the same methods. I researched and estimated the WLF range and then compared these in a blind test with Prof. N Willby, who held the WLF time series data at that time. We were satisfied with my estimations. In addition, Prof. Willby used his expert knowledge of individual lochs across Scotland to assess all estimations for any uncertain results. This approach obviously lends uncertainty to the data. However, with limited data, time, and finances this was decided to be the best practicable method and is likely to result in estimated water level ranges that are within 0.5m of the true value for typical years.

Appendix III:

Macroinvertebrate taxa list for “family richness” models

Acroloxidae
Ameletidae
Apataniidae
Asellidae
Baetidae
Caenidae
Capniidae
Ceratopogonidae
Chaoboridae
Chironomidae
Chloroperlidae
Coenagrionidae
Cordulegastridae
Corduliidae
Corixidae
Corxidae
Crangonyctidae
Curculionidae
Dendrocoelidae
Dryopidae
Dugesiidae
Dytiscidae
Elmidae
Empididae
Enchytraeidae
Ephemerellidae
Ephemeridae
Erpobdelliadae
Gammaridae
Glossiphoniidae
Glossosomatidae
Goeridae
Gyrinidae
Haemopidae
Haliplidae
Heptageniidae
Hydraenidae
Hydrobiidae
Hydrophilidae
Hydropsychidae
Hydroptilidae
Hygrobiidae
Lebertiidae
Lepidostomatidae
Leptoceridae
Leptophlebiidae
Leuctridae
Libellulidae
Limnephilidae
Limoniidae
Lumbriculidae
Lymnaeidae
Lymnephilidae
Muscidae
Naididae
Nemouridae
Oligochaeta
Pediciidae
Perlidae
Perlodidae
Phryganeidae
Physidae
Planariidae
Planorbidae
Planorboidea
Polycentropodidae
Psychomyiidae
Pyralidae
Sericostomatidae
Sialidae
Simuliidae
Siphlonuridae
Sphaeriidae
Tabanidae
Tateidae
Tipulidae
Tubificidae
Valvatidae
Zygoptera

Appendix IV:

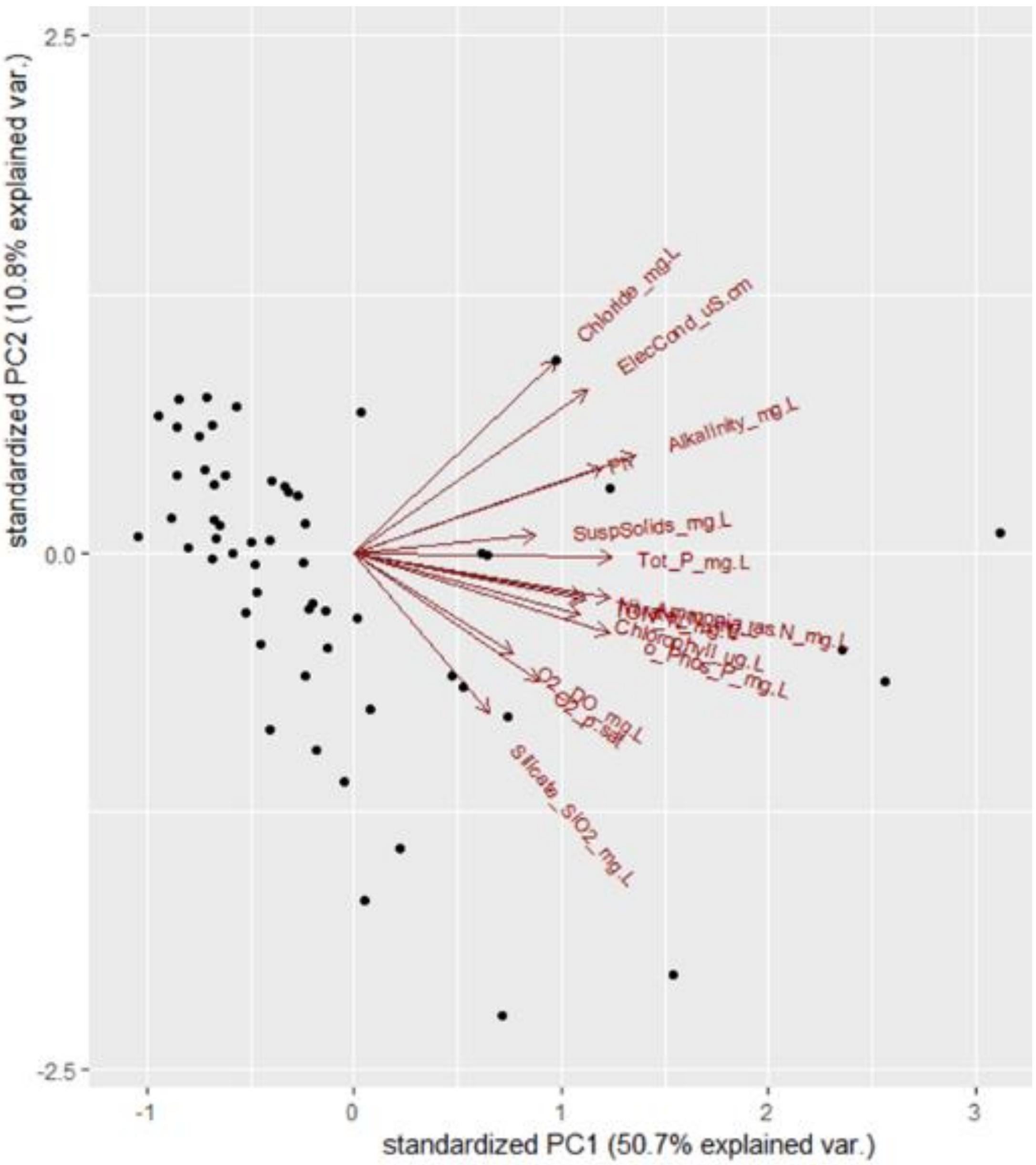
Finest macroinvertebrate taxa list for CCA, NMDS and Indicator taxa analysis

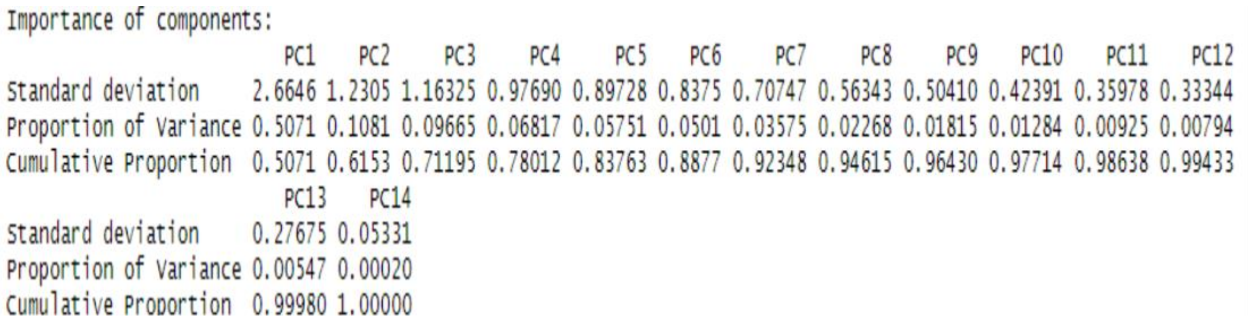
Species	**Genus**	**Family**	**Other - specify**
Acroloxus lacustris	*Caenis*	Baetidae	Nematomorpha - phylum
Agapetus fuscipes	*Capnia*	Ceratopogonidae	Nematoda - class
Ameletus inopinatus	*Crangonyx*	Chaoboridae	Ostracoda - class
Ancylus fluviatilis	*Dicranota*	Chironomidae	Collembola - sub class
Apatania wallengreni	*Dryops*	Chloroperlidae	Nemouridae - sub class
Asellus aquaticus	*Elmis*	Coenagrionidae	Tricladida - order
Asellus meridianus	*Ephemera*	Corduliidae	Hydracarina – super family
Cordulegaster boltonii	*Esolus*	Corixidae	
Cyrnus trimaculatus	*Gyrinus*	Curculionidae	
Dendrocoelum lacteum	*Helophorus*	Dugesiidae	
Dinocras cephalotes	*Lebertia*	Dytiscidae	
Goera pilosa	*Limnius*	Empididae	
Haemopis sanguisuga	*Orectochilus*	Enchytraeidae	
Hydraena gracilis	*Oulimnius*	Erpobdelliadae	
Hydraena palustris	*Planaria*	Gammaridae	
Hydropsyche instabilis	*Polycelis*	Glossiphoniidae	
Hydropsyche siltalai	*Riolus*	Haliplidae	
Hygrobia hermanni		Heptageniidae	
Lepidostoma hirtum		Hydrobiidae	
Libellula quadrimaculata		Hydroptilidae	
Potamophylax latipennis		Leptoceridae	
Potamopyrgus jenkinsi		Leptophlebiidae	
Sericostoma personatum		Leuctridae	
Serratella ignita		Limnephilidae	
Sialis lutaria		Limoniidae	
Valvata piscinalis		Lumbricidae	
		Lumbriculidae	
		Lymnaeidae	
		Muscidae	
		Naididae	
		Nemouridae	
		Perlodidae	
		Phryganeidae	
		Physidae	
		Planorbidae	
		Polycentropodidae	
		Psychomyiidae	
		Pyralidae	
		Simuliidae	
		Siphlonuridae	
		Sphaeriidae	
		Tabanidae	
		Tipulidae	
		Tubificidae	

Appendix V:

Principal components analysis (PCA) used to separate sets of water chemistry variables to identify those variables that maximised variation amongst sites.

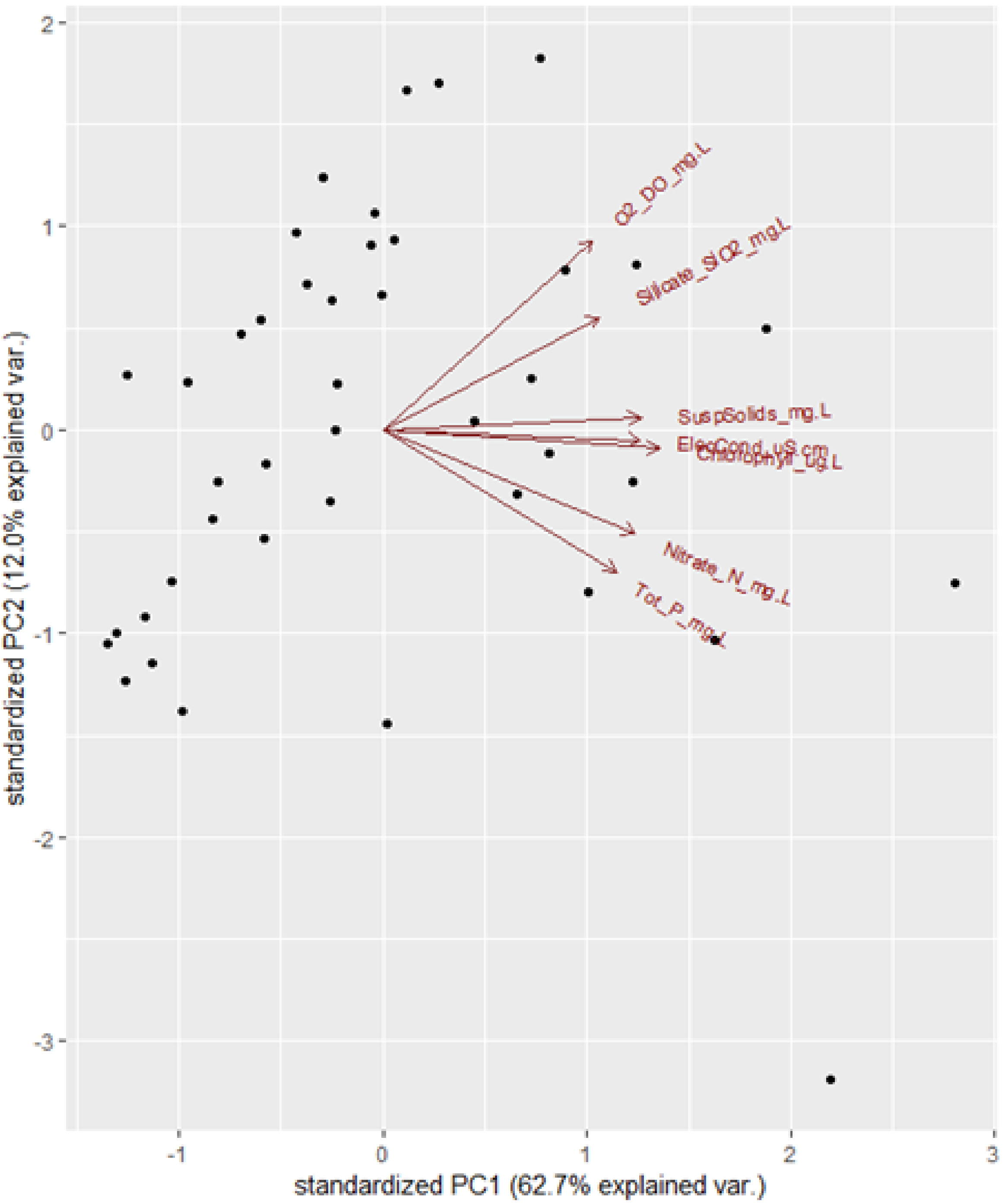
Global data

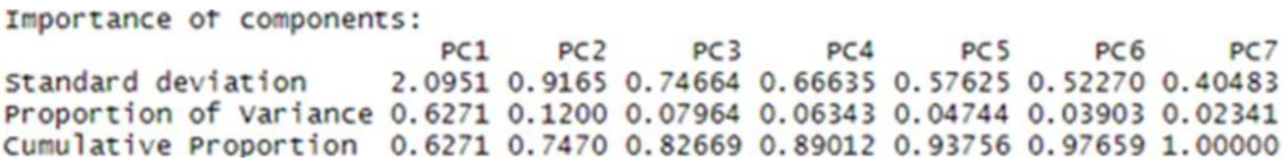




```
Importance of components:
                          PC1    PC2     PC3     PC4     PC5    PC6     PC7     PC8     PC9    PC10    PC11    PC12
Standard deviation     2.6646 1.2305 1.16325 0.97690 0.89728 0.8375 0.70747 0.56343 0.50410 0.42391 0.35978 0.33344
Proportion of Variance 0.5071 0.1081 0.09665 0.06817 0.05751 0.0501 0.03575 0.02268 0.01815 0.01284 0.00925 0.00794
Cumulative Proportion  0.5071 0.6153 0.71195 0.78012 0.83763 0.8877 0.92348 0.94615 0.96430 0.97714 0.98638 0.99433
                          PC13    PC14
Standard deviation     0.27675 0.05331
Proportion of Variance 0.00547 0.00020
Cumulative Proportion  0.99980 1.00000
```

Subset data for invertebrate/macrophyte models

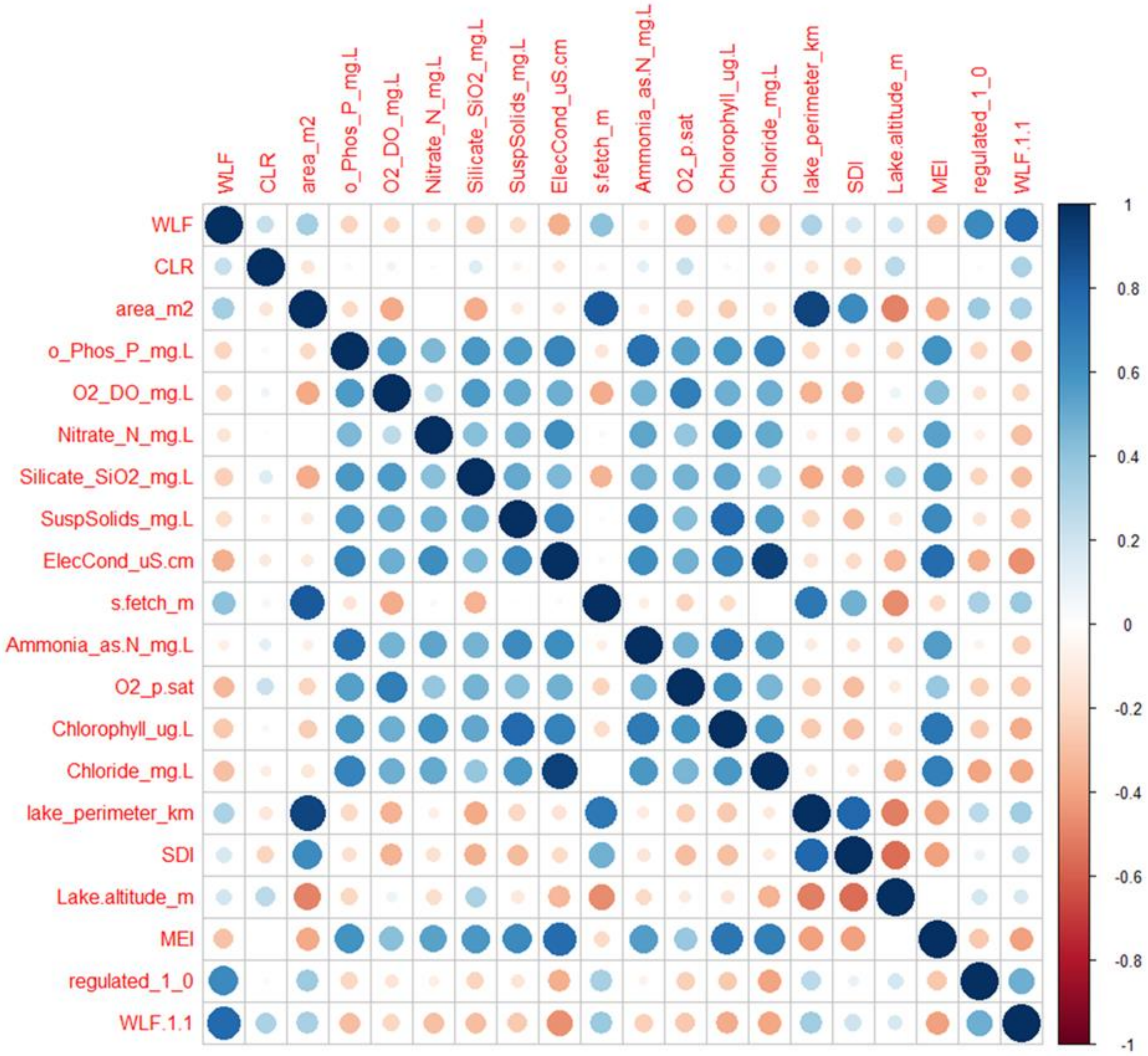




```
Importance of components:
                          PC1    PC2     PC3     PC4     PC5     PC6     PC7
Standard deviation     2.0951 0.9165 0.74664 0.66635 0.57625 0.52270 0.40483
Proportion of Variance 0.6271 0.1200 0.07964 0.06343 0.04744 0.03903 0.02341
Cumulative Proportion  0.6271 0.7470 0.82669 0.89012 0.93756 0.97659 1.00000
```

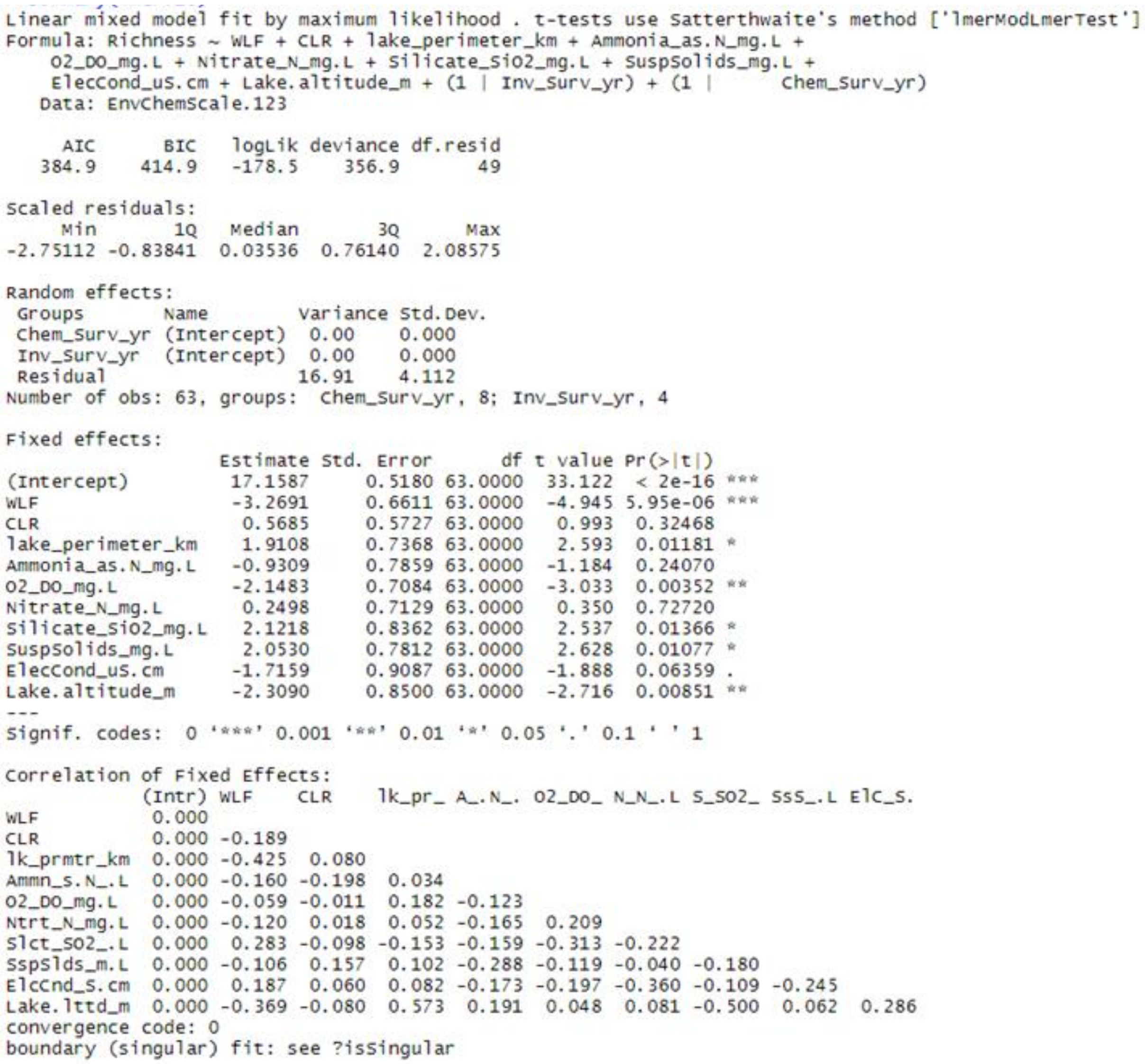
Appendix VI:

Correlation matrix for global data variables

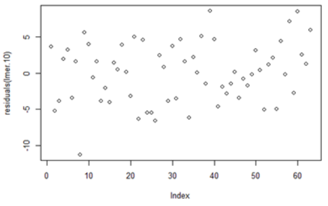


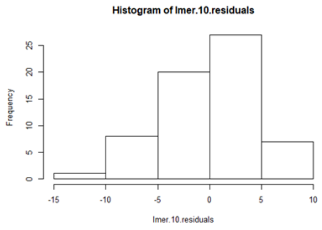
Appendix VII:

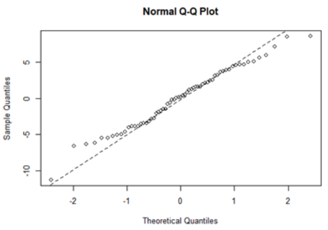
Global family richness model output and normality tests



```
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: Richness ~ WLF + CLR + lake_perimeter_km + Ammonia_as.N_mg.L +
    O2_DO_mg.L + Nitrate_N_mg.L + Silicate_SiO2_mg.L + SuspSolids_mg.L +
    ElecCond_uS.cm + Lake.altitude_m + (1 | Inv_Surv_yr) + (1 |      Chem_Surv_yr)
   Data: EnvChemScale.123

     AIC      BIC   logLik deviance df.resid
   384.9    414.9   -178.5    356.9       49

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.75112 -0.83841  0.03536  0.76140  2.08575

Random effects:
 Groups       Name        Variance Std.Dev.
 Chem_Surv_yr (Intercept)  0.00    0.000
 Inv_Surv_yr  (Intercept)  0.00    0.000
 Residual                 16.91    4.112
Number of obs: 63, groups:  Chem_Surv_yr, 8; Inv_Surv_yr, 4

Fixed effects:
                   Estimate Std. Error      df t value Pr(>|t|)
(Intercept)         17.1587     0.5180 63.0000  33.122  < 2e-16 ***
WLF                 -3.2691     0.6611 63.0000  -4.945 5.95e-06 ***
CLR                  0.5685     0.5727 63.0000   0.993  0.32468
lake_perimeter_km    1.9108     0.7368 63.0000   2.593  0.01181 *
Ammonia_as.N_mg.L   -0.9309     0.7859 63.0000  -1.184  0.24070
O2_DO_mg.L          -2.1483     0.7084 63.0000  -3.033  0.00352 **
Nitrate_N_mg.L       0.2498     0.7129 63.0000   0.350  0.72720
Silicate_SiO2_mg.L   2.1218     0.8362 63.0000   2.537  0.01366 *
SuspSolids_mg.L      2.0530     0.7812 63.0000   2.628  0.01077 *
ElecCond_uS.cm      -1.7159     0.9087 63.0000  -1.888  0.06359 .
Lake.altitude_m     -2.3090     0.8500 63.0000  -2.716  0.00851 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) WLF    CLR    lk_pr_ A_.N_. O2_DO_ N_N_.L S_SO2_ SsS_.L Elc_S.
WLF          0.000
CLR          0.000 -0.189
lk_prmtr_km  0.000 -0.425  0.080
Ammn_s.N_.L  0.000 -0.160 -0.198  0.034
O2_DO_mg.L   0.000 -0.059 -0.011  0.182 -0.123
Ntrt_N_mg.L  0.000 -0.120  0.018  0.052 -0.165  0.209
Slct_SO2_.L  0.000  0.283 -0.098 -0.153 -0.159 -0.313 -0.222
SspSlds_m.L  0.000 -0.106  0.157  0.102 -0.288 -0.119 -0.040 -0.180
ElcCnd_S.cm  0.000  0.187  0.060  0.082 -0.173 -0.197 -0.360 -0.109 -0.245
Lake.lttd_m  0.000 -0.369 -0.080  0.573  0.191  0.048  0.081 -0.500  0.062  0.286
convergence code: 0
boundary (singular) fit: see ?isSingular
```



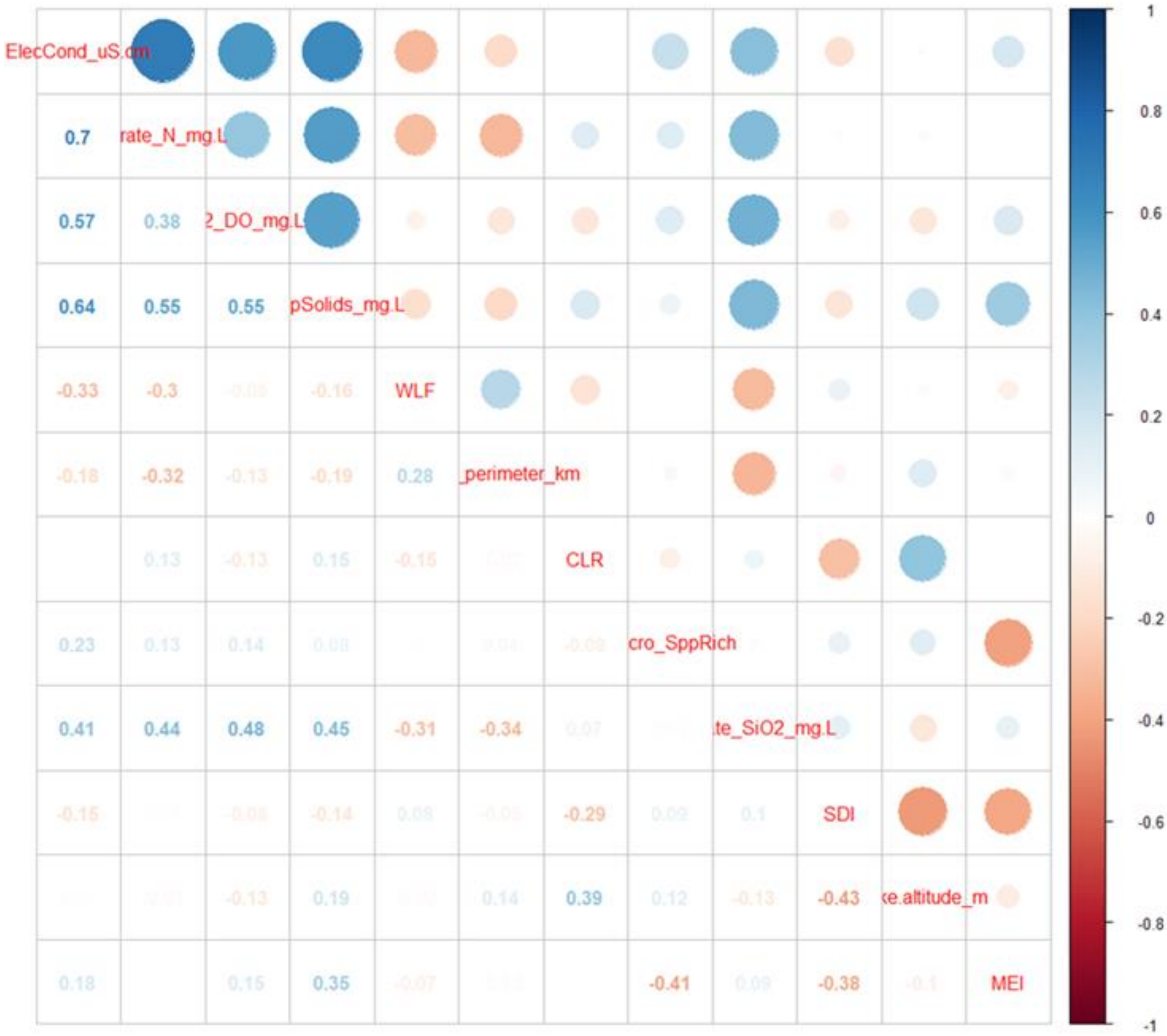


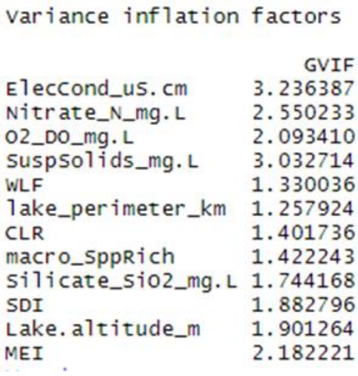


Shapiro-Wilk normality test ; W = 0.98489, p-value = 0.6335

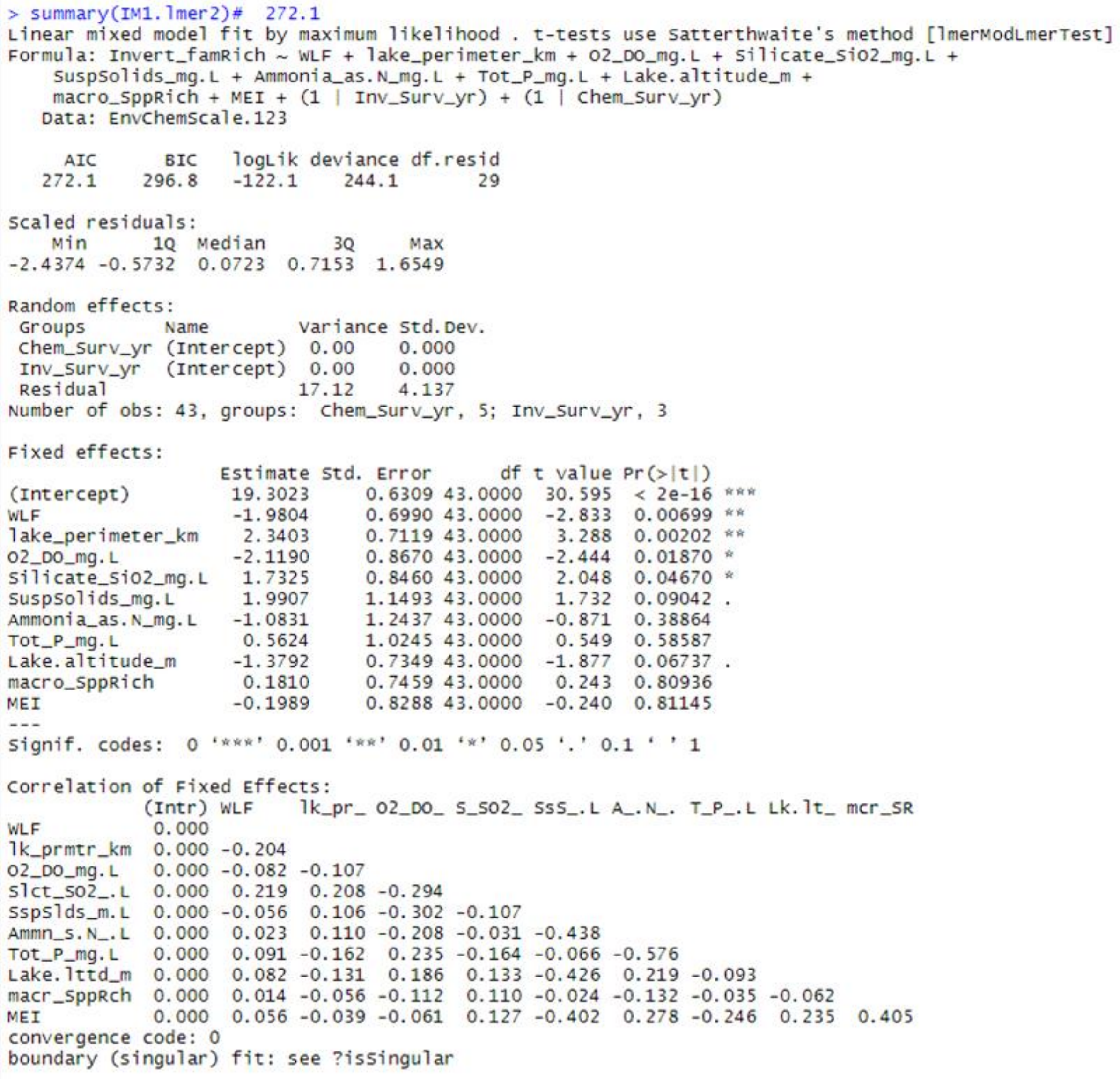
Appendix VIII:

Subset family invertebrate richness with macrophyte richness correlations and model output with normality tests

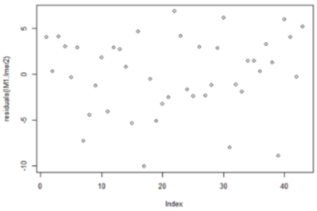


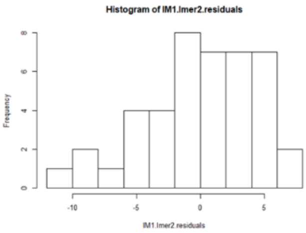


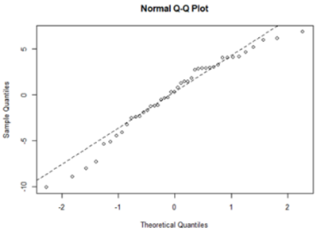
```
Variance inflation factors

                        GVIF
ElecCond_uS.cm      3.236387
Nitrate_N_mg.L      2.550233
O2_DO_mg.L          2.093410
SuspSolids_mg.L     3.032714
WLF                 1.330036
lake_perimeter_km   1.257924
CLR                 1.401736
macro_SppRich       1.422243
Silicate_SiO2_mg.L  1.744168
SDI                 1.882796
Lake.altitude_m     1.901264
MEI                 2.182221
```



```
> summary(IM1.lmer2)#  272.1
Linear mixed model fit by maximum likelihood . t-tests use Satterthwaite's method [lmerModLmerTest]
Formula: Invert_famRich ~ WLF + lake_perimeter_km + O2_DO_mg.L + Silicate_SiO2_mg.L +
    SuspSolids_mg.L + Ammonia_as.N_mg.L + Tot_P_mg.L + Lake.altitude_m +
    macro_SppRich + MEI + (1 | Inv_Surv_yr) + (1 | Chem_Surv_yr)
   Data: EnvChemScale.123

     AIC      BIC   logLik deviance df.resid
   272.1    296.8   -122.1    244.1       29

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4374 -0.5732  0.0723  0.7153  1.6549

Random effects:
 Groups       Name        Variance Std.Dev.
 Chem_Surv_yr (Intercept)  0.00    0.000
 Inv_Surv_yr  (Intercept)  0.00    0.000
 Residual                 17.12    4.137
Number of obs: 43, groups:  Chem_Surv_yr, 5; Inv_Surv_yr, 3

Fixed effects:
                   Estimate Std. Error      df t value Pr(>|t|)
(Intercept)         19.3023     0.6309 43.0000  30.595  < 2e-16 ***
WLF                 -1.9804     0.6990 43.0000  -2.833  0.00699 **
lake_perimeter_km    2.3403     0.7119 43.0000   3.288  0.00202 **
O2_DO_mg.L          -2.1190     0.8670 43.0000  -2.444  0.01870 *
Silicate_SiO2_mg.L   1.7325     0.8460 43.0000   2.048  0.04670 *
SuspSolids_mg.L      1.9907     1.1493 43.0000   1.732  0.09042 .
Ammonia_as.N_mg.L   -1.0831     1.2437 43.0000  -0.871  0.38864
Tot_P_mg.L           0.5624     1.0245 43.0000   0.549  0.58587
Lake.altitude_m     -1.3792     0.7349 43.0000  -1.877  0.06737 .
macro_SppRich        0.1810     0.7459 43.0000   0.243  0.80936
MEI                 -0.1989     0.8288 43.0000  -0.240  0.81145
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) WLF    lk_pr_ O2_DO_ S_SO2_ SsS_.L A_.N_. T_P_.L Lk.lt_ mcr_SR
WLF          0.000
lk_prmtr_km  0.000 -0.204
O2_DO_mg.L   0.000 -0.082 -0.107
Slct_SO2_.L  0.000  0.219  0.208 -0.294
SspSlds_m.L  0.000 -0.056  0.106 -0.302 -0.107
Ammn_s.N_.L  0.000  0.023  0.110 -0.208 -0.031 -0.438
Tot_P_mg.L   0.000  0.091 -0.162  0.235 -0.164 -0.066 -0.576
Lake.lttd_m  0.000  0.082 -0.131  0.186  0.133 -0.426  0.219 -0.093
macr_SppRch  0.000  0.014 -0.056 -0.112  0.110 -0.024 -0.132 -0.035 -0.062
MEI          0.000  0.056 -0.039 -0.061  0.127 -0.402  0.278 -0.246  0.235  0.405
convergence code: 0
boundary (singular) fit: see ?isSingular
```







Shapiro-Wilk normality test
#W = 0.96161, p-value = 0.1587

Appendix IX:

Environmental variables split by stable lakes (Lakes.S) and fluctuating Lakes (Lakes.F)

Lake type	Variable	median	mean ± SE	min - max
Lakes.S	(WLF) (m)	0.9	0.81 ± 0.04	0.35 - 1
Lakes.F	(WLF) (m)	1.75	2.25 ± 0.2	1.2 – 5.5
Lakes.S	Perimeter (km)	7.5	13 ± 3.22	0.3 - 92
Lakes.F	Perimeter (km)	13.16	22.09 ± 3.8	4.86 – 95.5
Lakes.S	Lake area (km^2)	1057.1	4341.6 ± 1621.4	4.34 - 51587
Lakes.F	Lake area (km^2)	2602	7176 ± 1989	516.37 - 55334
Lakes.S	Elevation (m)	76	133.1 ± 23.5	2 - 537
Lakes.F	Elevation (m)	127	159 ± 18	4 -424
Lakes.S	Depth (m)	5.9	12.4 ± 3	0.8 – 73.8
Lakes.F	Depth (m)	12	21 ± 4.7	1.3 - 132
Lakes.S	Max Fetch (m)	2460	3245 ± 572	110 - 17330
Lakes.F	Max Fetch (m)	4155	6359 ± 1178	1440 - 36320
Lakes.S	Alkalinity (mgL^{-1})	11.1	37.92 ± 9.4	1.79 - 197
Lakes.F	Alkalinity (mgL^{-11})	4.73	9.38 ± 2.03	1.11 – 59
Lakes.S	Ammonia (mgL^{-1})	0.047	0.063 ± 0.009	0.003 – 0.24
Lakes.F	Ammonia (mgL^{-1})	0.023	0.04 ± 0.01	0.003 – 0.223
Lakes.S	Nitrate (mgL^{-1})	0.218	0.636 ± 0.15	0.004 – 4.26
Lakes.F	Nitrate (mgL^{-1})	0.173	0.26 ± 0.07	0.015 – 2.33
Lakes.S	TP (mgL^{-1})	0.02	0.025 ± 0.003	0.002 – 0.083
Lakes.F	TP (mgL^{-1})	0.012	0.014 ± 0.002	0.001 – 0.069
Lakes.S	O2_DO (mgL^{-1})	13.6	13.57 ± 0.29	10.4 – 16.9
Lakes.F	O2_DO (mgL^{-1})	13.1	12.9 ± 0.28	10.3 – 17.8
Lakes.S	SuspSolids (mgL^{-1})	7.9	16.63 ± 3.80	1.5 - 86
Lakes.F	SuspSolids (mgL^{-1})	4.25	8.24 ± 1.54	0.5 - 37
Lakes.S	ElecCond (uS/cm $^{-1}$)	81.4	283.55 ± 110	27.9 - 3730
Lakes.F	ElecCond (uS/cm $^{-1}$)	44.13	63.2 ± 7.58	25.5 - 224
Lakes.S 26.45 ± 6.27	Chlorophyll (uS/cm $^{-1}$)	7.9	26.45 ± 6.27	1.3 -135.88
Lakes.F	Chlorophyll (uS/cm $^{-1}$)	5.17	6.76 ± 0.92	1.1 – 22.04
Lakes.S	Silicate (mgL^{-1})	5.99	3.34 ± 0.94	0.44 – 31.4
Lakes.F	Silicate (mgL^{-1})	2.62	3.83 ± 0.68	0.61 – 19.2
Lakes.S	MEI	-1.47	-1.35 ± 0.15	-3.05 – 0.69
Lakes.F	MEI	-2.12	-2.05 ± 0.11	-3.31 - -0.31
Lakes.S	SDI	2	2.19 ± 0.14	1.28 – 4.81
Lakes.F	SDI	2.30	2.5 ± 0.15	1.25 – 5.1
Lakes.S	CLR	13.47	22.59 ± 4.39	0.04 – 119.43
Lakes.F	CLR	25.83	52.67 ± 18.2	5.98 – 580.71

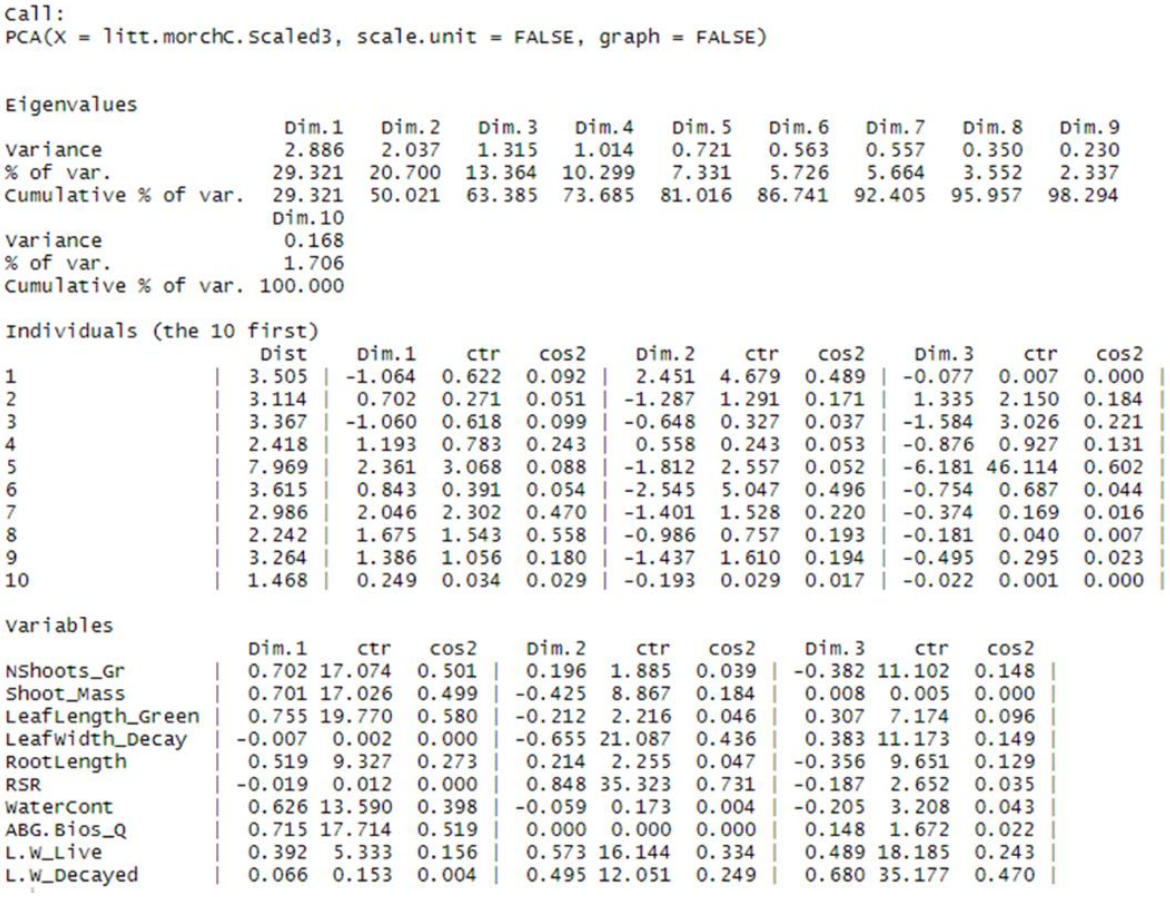
Appendix I:

Maximum potential wave action /exposure with fetch and wind-rose data

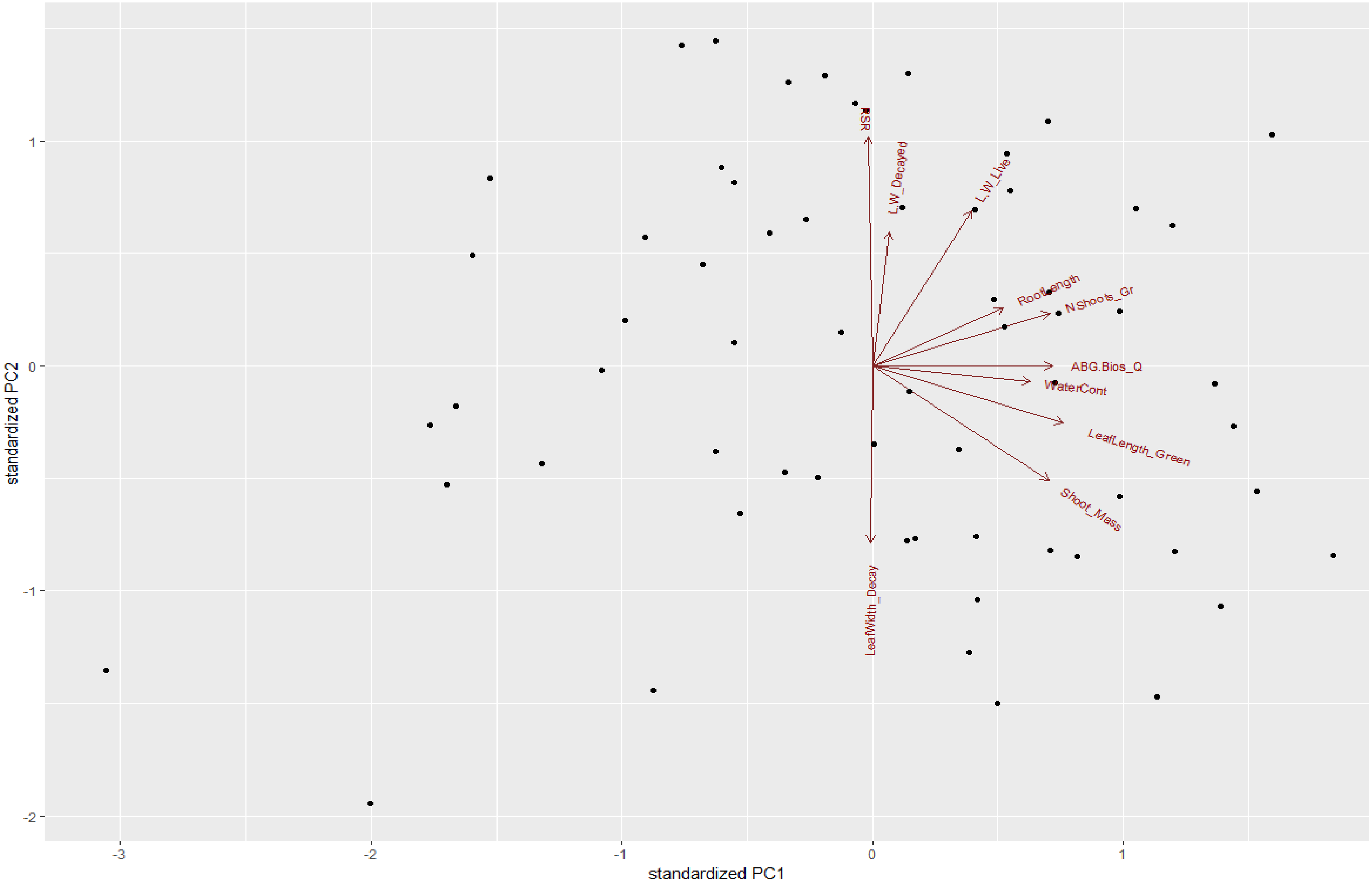
Loch/reservoir	BNG	FETCH DISTANCE (m)	Angle (°)of predominant fetch	equates to	closest wind rose used	time % of wind at that angle (from windrose)(10yr data)	weighted fetch	potential wave action
BACKWATER shelt	NO2552761492	1078	350	N	Dundee	0.73	7.8694	1086
BACKWATER expsd	NO25650 60385	1580	182	S	Dundee	1.61	25.438	1605
CARRON_VALLEYshelt	NS67374 85543	983	100	E	Glasgow	2.35	23.1005	1006
CARRON_VALLEY expsd	NS71062 83860	2197	250	WSW	Glasgow	15.78	346.6866	2544
ARD shelt	NN45397 01284	1173	80	NNE	Glasgow	0.92	10.7916	1184
ARD expsd	NN45957 02121	2894	110	ESE	Glasgow	0.73	21.1262	2915
CHON shelt	NN41966 06155	1070	190	S	Glasgow	9.26	99.082	1169
CHON exp	NN42111 05556	1476	160	SSE	Glasgow	1.43	21.1068	1497
KATRINE shelt	NN40403 12149	3523	150	SSE	Glasgow	1.43	50.3789	3573
KATRINE expsd	NN4376 710205	5660	112	ESE	Glasgow	0.73	41.318	5701
LUBNAIG shelt	NN5639515085	1150	150	SSE	Glasgow	1.43	16.445	1166
LUBNAIG exp	NN57079 14393	2410	138	SE	Glasgow	0.72	17.352	2427
THOM shelt	NS2532271549	1138	55	NE	Glasgow	4.86	55.3068	1193
THOM expsd	NS2532271549	1801	182	S	Glasgow	9.26	166.7726	1968
VENACHAR shelt	NN57835 05954	1320	230	SW	Glasgow	18.92	249.744	1570
VENACHAR exp	NN59592 05856	5321	270	W	Glasgow	11.03	586.9063	5908
VOIL shelt	NN52493 20293	901	61	ENE	Glasgow	8.59	77.3959	978
VOIL exp	NN49460 19853	1682	250	WSW	Glasgow	15.78	265.4196	1947
MEGGET one only	NT17958 21862	3209	78	ENE	Edinburgh	4.71	151.1439	3360

Appendix II:

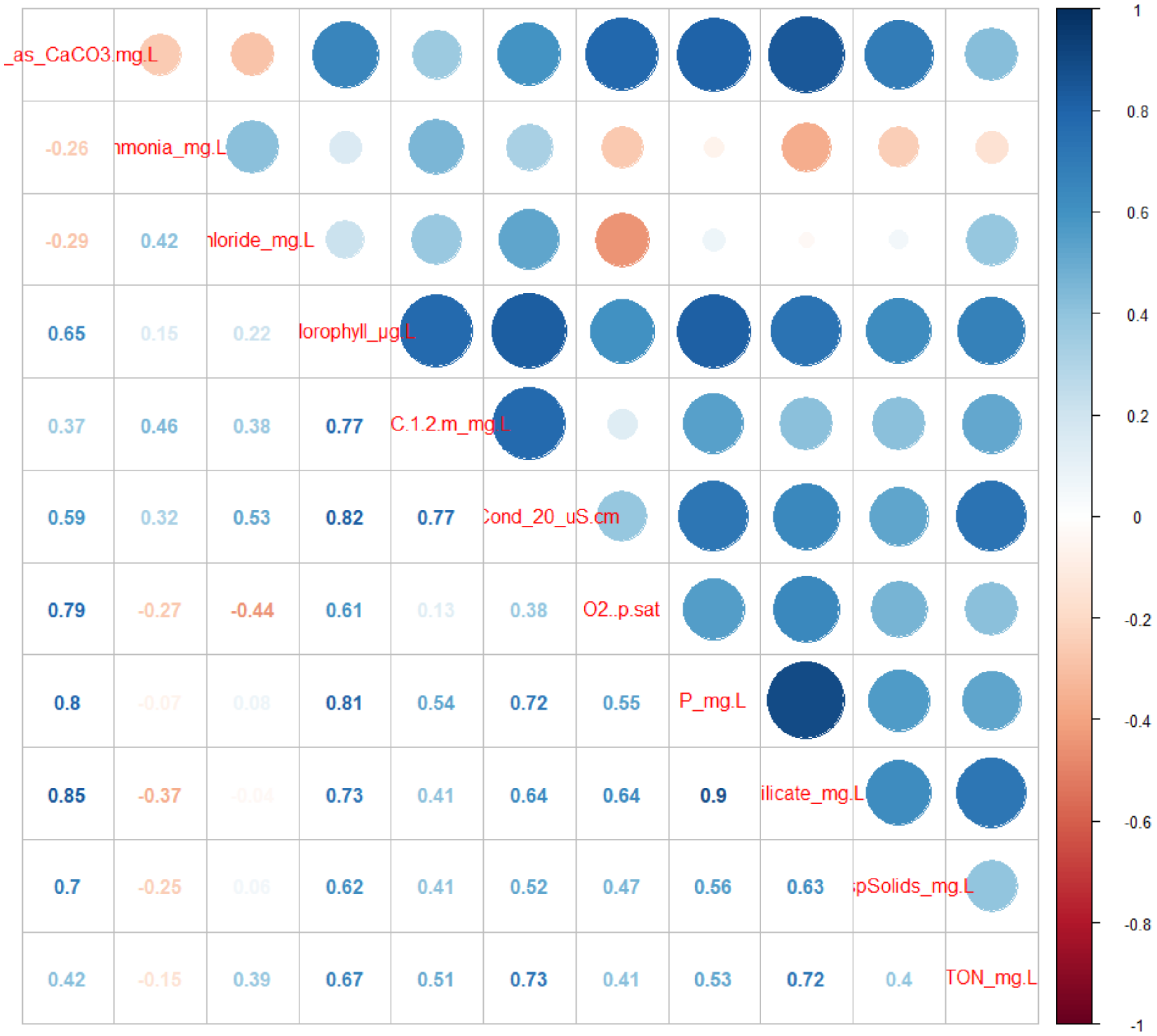
Principal Components Analysis (PCA) of *Littorella uniflora* morphological attributes



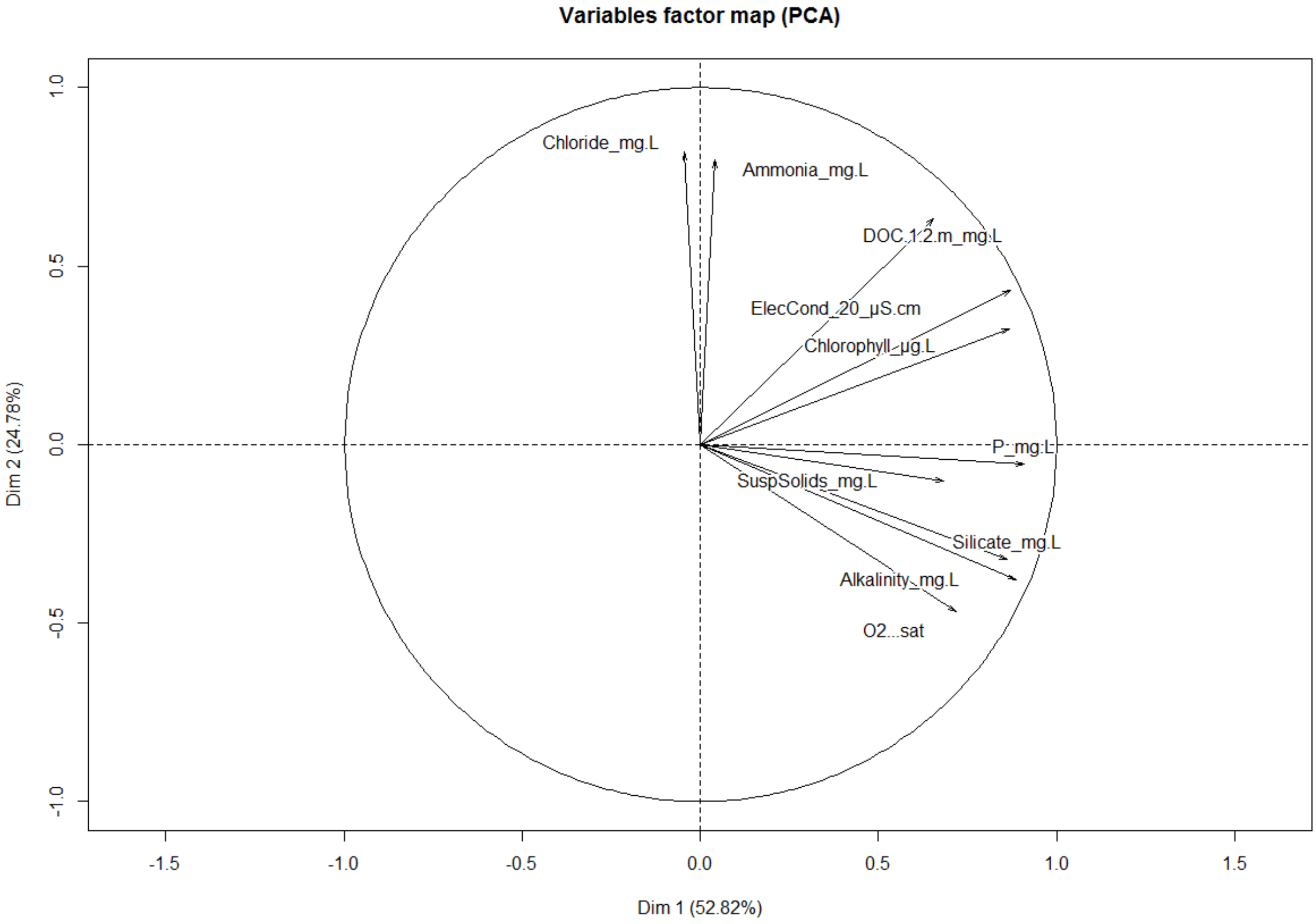
```
Call:
PCA(X = litt.morchC.Scaled3, scale.unit = FALSE, graph = FALSE)


Eigenvalues
                       Dim.1   Dim.2   Dim.3   Dim.4   Dim.5   Dim.6   Dim.7   Dim.8   Dim.9
Variance               2.886   2.037   1.315   1.014   0.721   0.563   0.557   0.350   0.230
% of var.             29.321  20.700  13.364  10.299   7.331   5.726   5.664   3.552   2.337
Cumulative % of var.  29.321  50.021  63.385  73.685  81.016  86.741  92.405  95.957  98.294
                      Dim.10
Variance               0.168
% of var.              1.706
Cumulative % of var. 100.000

Individuals (the 10 first)
                      Dist    Dim.1    ctr   cos2    Dim.2    ctr   cos2    Dim.3    ctr   cos2  
1                 |  3.505 | -1.064  0.622  0.092 |  2.451  4.679  0.489 | -0.077  0.007  0.000 |
2                 |  3.114 |  0.702  0.271  0.051 | -1.287  1.291  0.171 |  1.335  2.150  0.184 |
3                 |  3.367 | -1.060  0.618  0.099 | -0.648  0.327  0.037 | -1.584  3.026  0.221 |
4                 |  2.418 |  1.193  0.783  0.243 |  0.558  0.243  0.053 | -0.876  0.927  0.131 |
5                 |  7.969 |  2.361  3.068  0.088 | -1.812  2.557  0.052 | -6.181 46.114  0.602 |
6                 |  3.615 |  0.843  0.391  0.054 | -2.545  5.047  0.496 | -0.754  0.687  0.044 |
7                 |  2.986 |  2.046  2.302  0.470 | -1.401  1.528  0.220 | -0.374  0.169  0.016 |
8                 |  2.242 |  1.675  1.543  0.558 | -0.986  0.757  0.193 | -0.181  0.040  0.007 |
9                 |  3.264 |  1.386  1.056  0.180 | -1.437  1.610  0.194 | -0.495  0.295  0.023 |
10                |  1.468 |  0.249  0.034  0.029 | -0.193  0.029  0.017 | -0.022  0.001  0.000 |

Variables
                     Dim.1    ctr   cos2    Dim.2    ctr   cos2    Dim.3    ctr   cos2  
NShoots_Gr        |  0.702 17.074  0.501 |  0.196  1.885  0.039 | -0.382 11.102  0.148 |
Shoot_Mass        |  0.701 17.026  0.499 | -0.425  8.867  0.184 |  0.008  0.005  0.000 |
LeafLength_Green  |  0.755 19.770  0.580 | -0.212  2.216  0.046 |  0.307  7.174  0.096 |
LeafWidth_Decay   | -0.007  0.002  0.000 | -0.655 21.087  0.436 |  0.383 11.173  0.149 |
RootLength        |  0.519  9.327  0.273 |  0.214  2.255  0.047 | -0.356  9.651  0.129 |
RSR               | -0.019  0.012  0.000 |  0.848 35.323  0.731 | -0.187  2.652  0.035 |
WaterCont         |  0.626 13.590  0.398 | -0.059  0.173  0.004 | -0.205  3.208  0.043 |
ABG.Bios_Q        |  0.715 17.714  0.519 |  0.000  0.000  0.000 |  0.148  1.672  0.022 |
L.W_Live          |  0.392  5.333  0.156 |  0.573 16.144  0.334 |  0.489 18.185  0.243 |
L.W_Decayed       |  0.066  0.153  0.004 |  0.495 12.051  0.249 |  0.680 35.177  0.470 |
```


RSR
L.W_Decayed
L.W_Live
RootLength
N.Shoots_Gr
ABG.Bios_Q
WaterCont
LeafLength_Green
Shoot_Mass
LeafWidth_Decay
standardized PC2
1
0
-1
-2
-3
-2
-1
0
1
standardized PC1

Principal Components Analysis (PCA) and correlations of lake nutrients



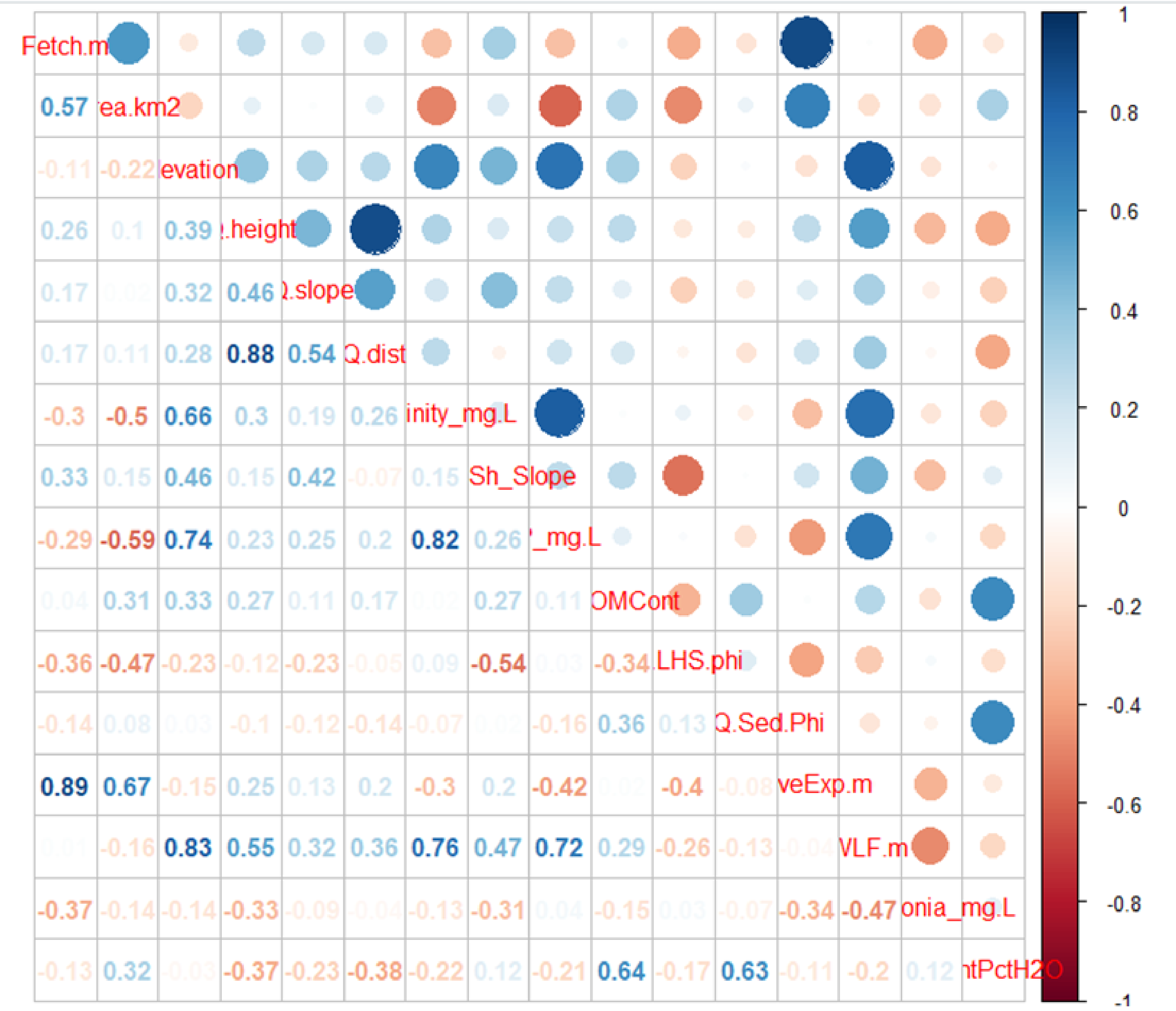
_as_CaCO3.mg.L										
-0.26	monia_mg.L									
-0.29	0.42	loride_mg.L								
0.65	0.15	0.22	lorophyll_µg.L							
0.37	0.46	0.38	0.77	C.1.2.m_mg.L						
0.59	0.32	0.53	0.82	0.77	ond_20_uS.cm					
0.79	-0.27	-0.44	0.61	0.13	0.38	O2..p.sat				
0.8	-0.07	0.08	0.81	0.54	0.72	0.55	P_mg.L			
0.85	-0.37	-0.04	0.73	0.41	0.64	0.64	0.9	ilicate_mg.L		
0.7	-0.25	0.06	0.62	0.41	0.52	0.47	0.56	0.63	pSolids_mg.L	
0.42	-0.15	0.39	0.67	0.51	0.73	0.41	0.53	0.72	0.4	TON_mg.L



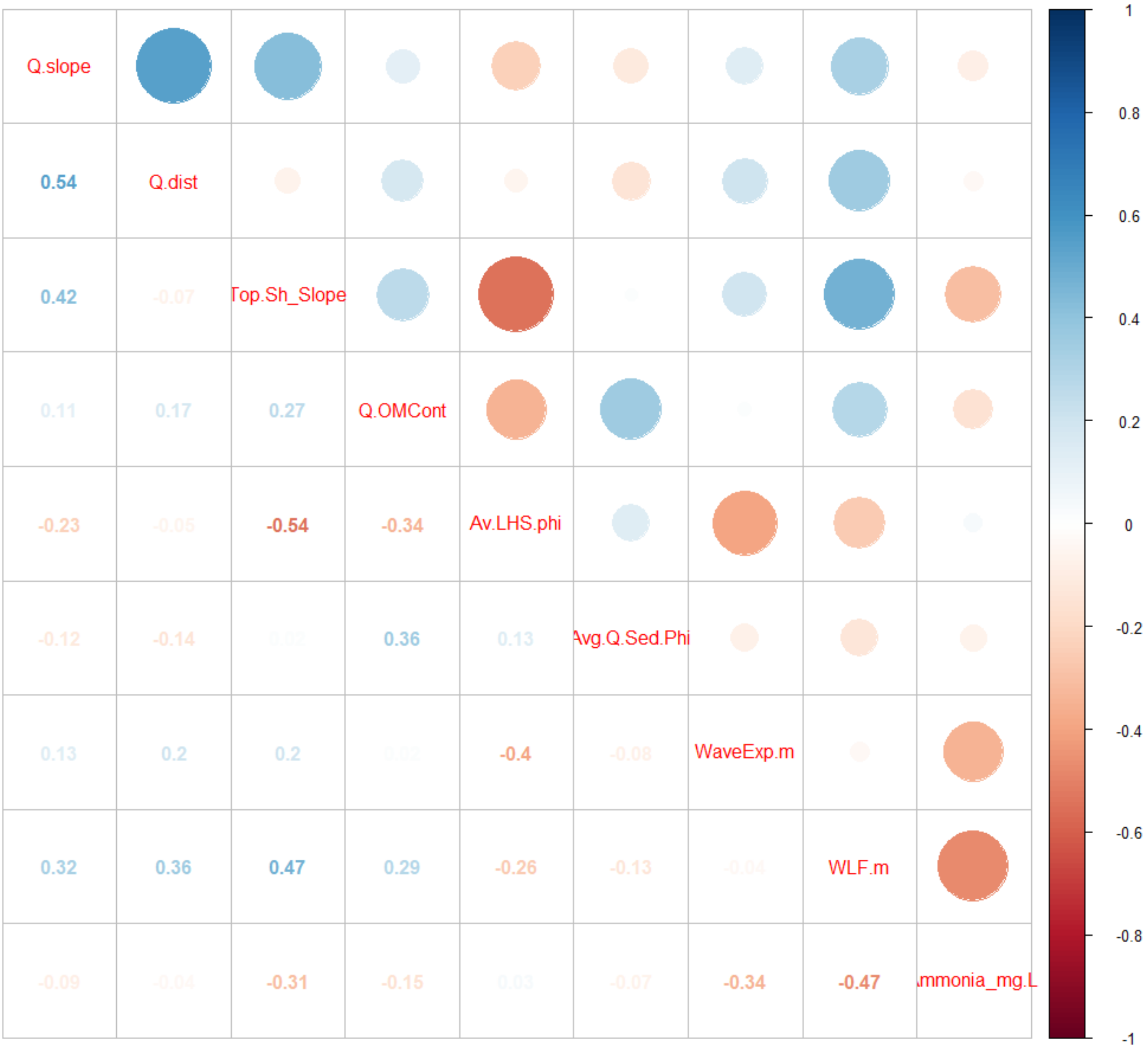
```
$Dim.1 - $Dim.1$quanti
                              correlation      p.value
ElecCond_20_µS.cm            0.8923008        0.0005159003
P_mg.L                        0.8881677       0.0005966795
Chlorophyll_mg.L             0.8765492        0.0008732151
Alkalinity_mg.L              0.8683225        0.0011186539
Silicate_mg.L                0.8641922        0.0012591735
TON_mg.L                     0.7921370        0.0063014134
O2...sat                     0.6925454         0.0264365267
DOC.1.2.m_mg.L               0.6682246         0.0346841047
SuspSolids_mg.L              0.6625473         0.0368333505
$Dim.2 - $Dim.2$quanti
                             correlation       p.value
Chloride_mg.L                0.8118613        0.004338277
Ammonia_mg.L                  0.8008290       0.005371858
```

Appendix III:

Correlations and VIF; Environmental Variables



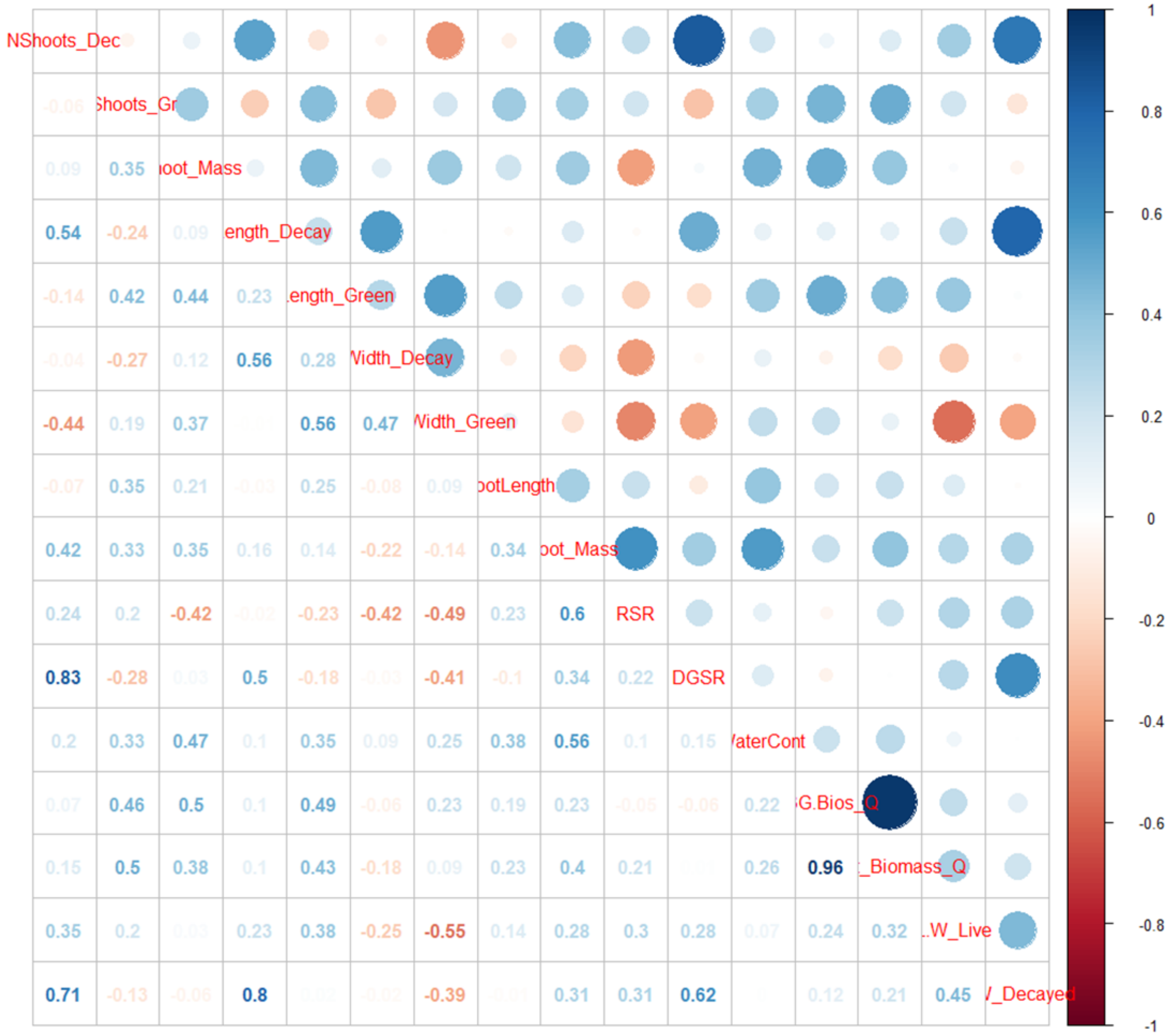
```
Variance inflation factors

                      GVIF
Fetch.m           8.280088
Area.km2          5.346992
Elevation         6.160761
Q.height         14.948208
Q.slope           2.851487
Q.dist           15.563058
Alkalinity_mg.L   7.159450
Top.Sh_Slope      4.214471
P_mg.L           10.815371
Q.OMCont          5.173659
Av.LHS.phi        3.041175
Avg.Q.Sed.Phi     2.628919
WaveExp.m         9.855472
WLF.m            24.782052
Ammonia_mg.L      5.686214
WghtPctH2O        8.315401
```



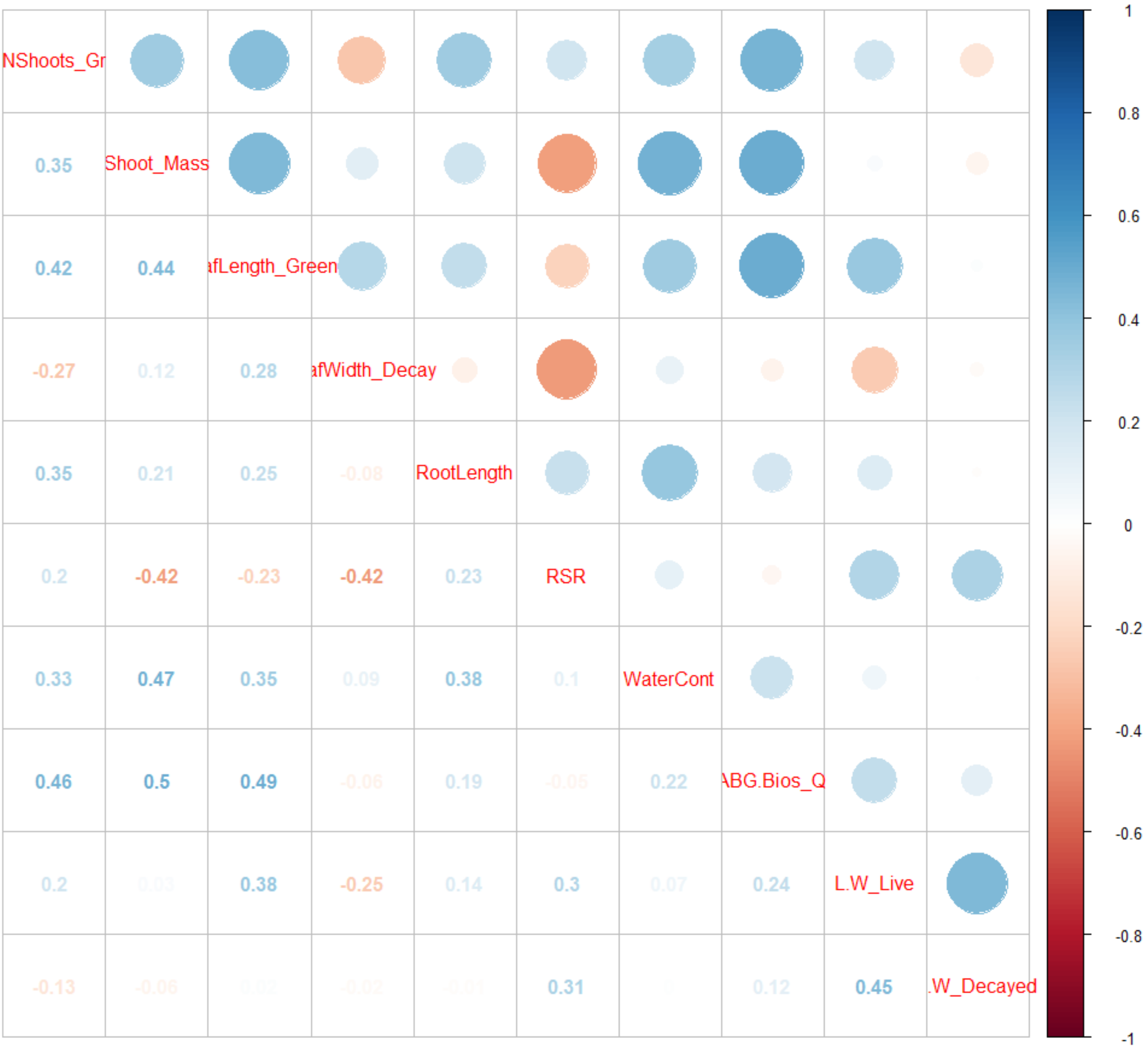
Variance inflation factors

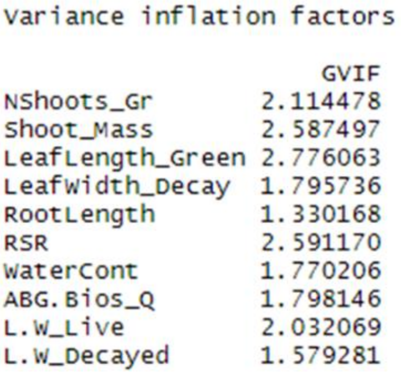
	GVIF
Q.slope	2.211854
Q.dist	2.762376
Top.Sh_Slope	2.797356
Q.OMCont	1.648939
Av.LHS.phi	2.270070
Avg.Q.Sed.Phi	1.399320
WaveExp.m	2.165498
WLF.m	2.902398
Ammonia_mg.L	2.119755

Correlations and VIF; Morphological Variables



```
Variance inflation factors

                        GVIF
NShoots_Dec         7.969911
NShoots_Gr          3.199313
Shoot_Mass          8.787226
LeafLength_Decay   60.030306
LeafLength_Green  115.928944
LeafWidth_Decay    21.334791
LeafWidth_Green   139.037329
RootLength          1.513442
Root_Mass          11.032977
RSR                18.041050
DGSR                5.145529
WaterCont           2.463881
ABG.Bios_Q        319.024581
Tot.St_Biomass_Q  328.033337
L.W_Live          111.382777
L.W_Decayed        46.110814
```





```
Variance inflation factors

                      GVIF
NShoots_Gr        2.114478
Shoot_Mass        2.587497
LeafLength_Green  2.776063
LeafWidth_Decay   1.795736
RootLength        1.330168
RSR               2.591170
WaterCont         1.770206
ABG.Bios_Q        1.798146
L.W_Live          2.032069
L.W_Decayed       1.579281
```

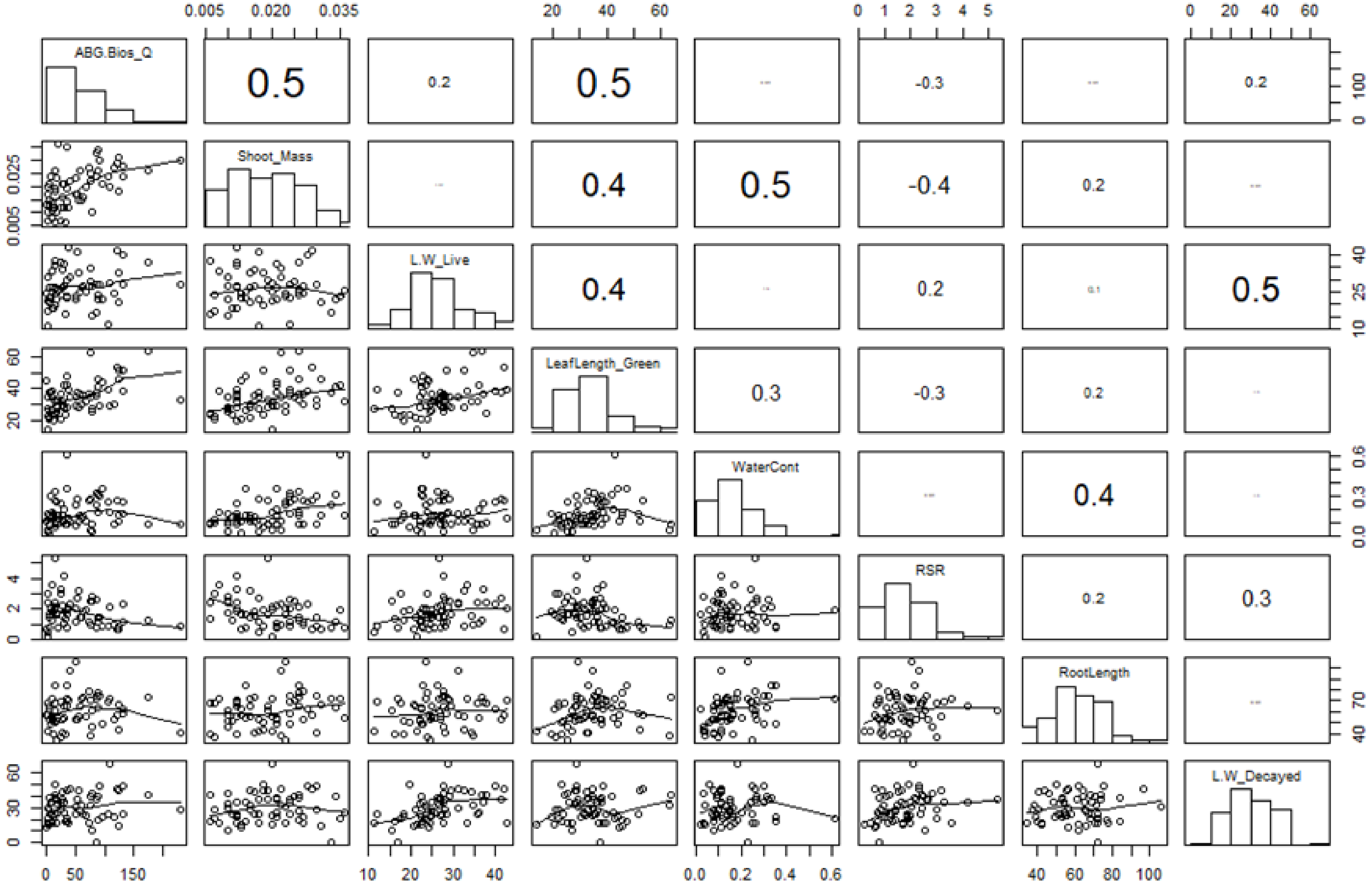
Appendix IV:

Multivariate mixed model predictor effects for subset of morphological response variables (scaled and significance p= 0***, 0.001**, 0.005*, 0.1.), (all predictors data scaled)

Morphology response	Best model/ Transformation	AIC	Shapiro_Wilk normality test	Environmental predictor	Effect Size (t)	P value	Significance
Tot.St_Biom_Q	cubed	191.2	0.9475	Av.LHS.phi	-3.712	0.00056	***
				Ammonia_mg.L	-2.83	0.02095	*
				Q.dist	2.006	0.05177	.
				Q.slope	-1.816	0.07534	.
ABG.Biomass_Q	cubed	189.4	0.9505	Av.LHS.phi	-3.011	0.03770	**
				Q.slope	-1.786	0.07950	.
TotalWaterCont.avg	sqrt	-88.5	0.9920	Shore slope	2.253	0.02790	*
TotalWaterCont.avg	sqrt w/o outlier	-83.5	0.8054	Shore slope	1.744	0.00801	**
Shoot_Mass	sqrt	-266.1	0.7811	Shore slope	1.671	0.09990	.
LeafLength_Green	log	20.8	0.8587	Q.OMCont	2.514	0.01450	*
LeafLength_Decay	untransformed	492.4	0.0593	Potential.Wave.Exp	-1.968	0.05350	.
LeafWidth_Decay	untransformed	92.1	0.0788	Ammonia_mg.L	2.561	0.02170	*
				Q.dist	-2.326	0.02420	*
				Potential.Wave.Exp	1.889	0.06470	.
				Q.OMCont	1.855	0.06890	.
				Av.LHS.phi	1.759	0.08400	.
NShoots_Dec	untransformed	91.1	0.0788	Q.dist	4.233	0.00018	**
				Q.slope	-1.836	0.07140	.
L:W.Dead	untransformed	477.8	0.1791	Q.dist	4.171	0.00011	***
				Av.LHS.phi	-3.262	0.00179	**
				Potential.Wave.Exp	-2.754	0.00785	**
				Ammonia_mg.L	-1.916	0.07985	.
L:W.Live	log	23.6	0.2815	Potential.Wave.Exp	-1.7	0.09600	.
RSR	cubed	-16.8	0.3960	Ammonia_mg.L	-2.813	0.00636	**
				Q.OMCont	-2.529	0.01394	*
				Potential.Wave.Exp	-2.316	0.02380	*
				Av.LHS.phi	-2.188	0.03237	*
RootLength	log	-18.2	0.2373	Av.LHS.phi	-2.541	0.01350	*
				Potential.Wave.Exp	-2.403	0.01920	*
				Shore slope	1.852	0.06870	.
N shoots gr	model na		0.0001				
Root_Mass	correlated with water content		n/a				
Leaf Width Green	model na		0.0179				

Appendix V:

Relationships between morphological variables (untransformed)



Relationships between environmental variables (untransformed data)