Eutrophication erodes inter-basin variation in macrophytes and co-occurring invertebrates in a shallow lake: Combining ecology and palaeoecology

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Abstract

Aquatic biodiversity is commonly linked with environmental variation in lake networks, but less is known about how local factors may influence within-lake biological heterogeneity. Using a combined ecological and multi-proxy palaeoecological approach we investigated long-term changes in the pathways and processes that underlie eutrophication and water depth effects on lake macrophyte and invertebrate communities across three basins in a shallow lake - Castle Lough, Northern Ireland, UK. Contemporary data allow us to assess how macrophyte assemblages vary in composition and heterogeneity according to basin-specific factors (e.g. variation in water depth), while palaeoecological data (macrophytes and co-occurring invertebrates) enable us to infer basin-specific impacts and susceptibilities to nutrient-enrichment. Results indicate that variability in water depth promotes assemblage variation amongst the lake basins, stimulating within-lake macrophyte assemblage heterogeneity and hence higher lake biodiversity. The palaeo-data indicate that eutrophication has acted as a strong homogenising agent of macrophyte and invertebrate diversities and abundances over time at the whole-lake scale. This novel finding strongly suggests that, as eutrophication advances, the influence of water depth on community heterogeneity is gradually eroded and that ultimately a limited set of eutrophication-tolerant species will become homogeneously distributed across the entire lake.

Introduction

Lakes have been regarded as ideal models for studying the influence of local environmental effects on species turnover in systems that are interconnected at the landscape level (Leibold and Norberg 2004). The structuring influence of environmental factors on within-lake spatial variation in community composition has, however, received less attention although such an idea is acknowledged theoretically by the "submetacommunity concept" of Leibold and Norberg (2004). This oversight may reflect the fact that research has largely focused on populations of mobile planktonic organisms assumed to be well-mixed within lakes. Lake environmental heterogeneity may, however, be important in influencing the distributions and abundances of taxa with limited mobility. Local distributions of aquatic macrophytes, for example, may depend on competition for space and tolerance to local environmental conditions (Barrat-Segretain 1996). Moreover, different areas within lakes may vary substantially, for example, in water depth, sediment type, wind exposure, proximity to inflows/outflows and the presence of shoreline vegetation. Such within-lake variation influences the spatial distribution of aquatic vegetation (Spence 1967; Carpenter and Titus 1984) and, in turn, associated invertebrates due to local variation in habitat, structural complexity and feeding opportunities (Lauridsen et al. 1996).

Studies of biological assembly dynamics in lake systems are generally limited to snapshots in time, focusing on short-term or contemporary patterns of species turnover or on biogeographical patterns. The interplay between spatial distributions and environmental drivers may, however, shift locally over time (Korhonen et al. 2010). Indeed, increasing evidence that colonisation histories, priority effects and temporal changes in environmental variables influence both local and regional species distributions highlights the importance of studying species turnover (beta-diversity) within lakes over time (Fukami and Morin 2003). For instance, contemporary and palaeolimnological studies of *Daphnia* colonisation patterns revealed that assembly history initially influenced species composition, but that changes in water temperature and lake stratification subsequently drove species turnover (Allen et al. 2011). Furthermore, species-specific differences in colonisation and adaptive capacity have

been shown to substantially influence temporal beta-diversity and to obscure direct relationships between *Daphnia* species distributions and environmental gradients (Urban and De Meester 2009). Palaeolimnological studies have also demonstrated that changes in the nature and intensity of local factors can influence distributions and abundances over time. For example, drivers of macrophyte assembly change were shown to shift from lake infilling during most of the Holocene to eutrophication around 120 years ago (Rasmussen and Anderson 2005).

By utilising a combined ecological and multi-proxy palaeoecological approach, this study aims to understand how key long-term environmental drivers (i.e. shallowing and nutrient-enrichment) influence temporal variation in the distribution of lake macrophytes and associated invertebrate assemblages across three basins of Castle Lough, a shallow lake in Northern Ireland, UK. Our study evaluates the hypothesis that variation in macrophyte and co-occurring invertebrate assemblages is reduced over time due to the homogenising influence of eutrophication.

Study system

Castle Lough is a small (surface area = 13 ha.), shallow (5 m maximum depth), lowland (45 m above sea level) lake located in the south of the Upper Lough Erne (ULE) system, a highly connected shallow lake network in Co. Fermanagh, Northern Ireland (54°12'N, 007°37'W). The lake has three distinct basins and moderate annual mean total phosphorus (29 μg TP L^{-1}) and total nitrogen (1.03 mg TN L^{-1}) concentrations. The River Finn connects the lake to the main ULE system (Fig. 1), which consists of a large "mother" lake and several linked satellite lakes.

Over the last 120 years hydrological change and eutrophication have profoundly influenced the ecology of the ULE system (Battarbee 1986; Gibson et al. 1995). Frequent flood events in the catchment caused by high rainfall led to the development of a major drainage scheme between 1880-1890 (Price 1890). Because of this scheme, water levels in the main lake dropped from around 46 to 44 m above

sea level (Price 1890). A second attempt to regulate water levels (dredging of 30 km of channel between the ULE and Lower Lough Erne systems) was undertaken in the early 1950s under the Erne Drainage and Development Act (Northern Ireland). Water levels have subsequently been maintained between 43-45 m, but the system (including Castle Lough) is still prone to major flood events (Mathers et al. 2002). Diatom-based palaeolimnological studies indicate a gradual acceleration of nutrient-enrichment in the ULE since the 1900s with a major phase of eutrophication after *c*. 1950 (Battarbee 1986; Gibson et al. 1995).

Materials and methods

Contemporary macrophyte surveys

To characterize present-day distributions and abundances of macrophytes in Castle Lough, we sampled three circular areas of 30 m radius in each of the lake's three main basins (Fig. 1) (Table 1). To ensure broad and equivalent sampling, each area was divided into three sub-areas delimited by 10 m radii (Fig. 1b). Six points were surveyed from the innermost area, and 18 and 36 points for the successively larger sub-areas, respectively (total = 60 points). We used the method of Canfield et al. (1984) to determine the percentage of lake volume filled by macrophytes (PVI) at each point. This entailed surveying macrophytes from a boat using a combination of grapnel sampling and visual observations made with a bathyscope. At each point water depth, average plant height and species percentage cover were recorded for an estimated area of 1 m^2. For each sampling point, PVI was calculated as: (macrophyte % cover x average height of macrophyte)/water depth.

Palaeolimnological analyses

124

125 We retrieved three sediment cores (NCAS1, NCAS2 and NCAS3) from the midpoint
126 of each of the sampling circular areas in each basin in June 2008 (Fig. 1b) using a
127 wide-bore (14 cm) "Big-Ben" piston corer (Patmore et al. 2014). Cores NCAS1,
128 NCAS2 and NCAS3 were collected from water depths of 117 cm, 180 cm and 160
129 cm, respectively, and were extruded in the field at 1-cm intervals. Lithostratigraphic
130 changes in the cores were recorded in the field. Core chronologies were determined
131 using ^{210}Pb gamma counting (Appleby et al. 1986) at the Bloomsbury Environmental
132 Isotope Facility (BEIF), University College London (UCL). Dates were ascribed
133 using the Constant Rate of Supply (CRS) model (Appleby and Oldfield, 1978).

134 Eleven 1-cm slices were analysed for macrofossils from each core at a
135 resolution of approximately 10-year intervals, spanning the last *c.* 110 years.
136 Exceptions were two 15-year intervals (1940-1955 and 1965-1980) due to differential
137 sedimentation rates between cores. Macrofossil analyses were performed using an
138 adaptation of standard methods (Birks 2001). We analysed approximately 70 cm^3 of
139 sediment and all samples were disaggregated in 10% potassium hydroxide (KOH)
140 before sieving. Three sieves of mesh sizes 355 μm, 125 μm and 90 μm were used to
141 separate plant, chironomid and other invertebrate remains. Given the high fossil retent
142 on the 125 μm and 90 μm sieves, we combined and mixed both samples after sieving,
143 and analysed a 20-mL subsample. Plant macrofossils included seeds and fruits, leaf-
144 spines, leaf fragments (including water lilies leaf tissue- sclereids), charophyte
145 oospores and *Isoetes* megaspores. Invertebrate macrofossils included bryozoan
146 statoblasts (counted as valves), daphnid ephippia, molluscs (counts of whole shells,
147 half shells, opercula, shell fragments and glochidia larvae), and chironomid head
148 capsules. Chironomids were prepared for analysis using standard methods (Brooks et
149 al. 2007). Plant and animal macrofossil data were standardised as the number of
150 fossils per 100 cm^3 and identified by comparison with reference material held at the
151 Environmental Change Research Centre (ECRC), UCL and the Natural History

Museum, London, and by using relevant taxonomic keys (Aldridge and Horne 1998; Birks 2001; Wood and Okamura 2005)

Given lower sedimentation rates for core NCAS2 (ESM1) and to establish decadal comparisons amongst the cores, we combined the macrofossil data for three time periods, 1941-1950, 1966-1980 and 1981-1990 for NCAS2. We used mean macrofossil abundances between adjacent sediment samples for each given time period. To avoid overestimating abundance values for the time intervals, we took a parsimonious approach and rounded values to the lowest adjacent number. For example, if adjacent sample values were 1 and 2 we gave a score of 1 for the sample average. If it was 1 and 0 we coded with 0 and so on.

Data analysis

Contemporary environmental factors and macrophyte spatial distributions

As a measure of current lake environmental variation, we used the water depths derived from the PVI data for each macrophyte sampling point. Similarly, we used macrophyte percentage cover (for each sampling point) to characterise spatial distributions and abundances of plant species in the three basins. Relationships between macrophyte percentage frequencies and variation in water depth at the whole-lake and basin levels were analysed using generalized linear models (GLM), permutational analysis of multivariate dispersions (perMANOVA; Anderson 2001) and homogeneity multivariate dispersion analysis (HMD; Anderson 2006). Whole-lake scale analysis was assessed through a global GLM on all basin macrophyte frequencies and water depths. Adjusted goodness of fit (R^2) and Akaike Information Criteria (AIC) were used as GLM quality indicators. We evaluated the dispersion parameter phi (Residual deviance (full model)/ residual degrees of freedom) to assess any over-dispersion in the data and applied a negative binomial distribution if

178 necessary (i.e. phi >1). Lastly, logistic regression using presence/absence as a
179 response (with a binomial error distribution) was applied to evaluate the probability of
180 finding key environmentally sensitive macrophyte species that are commonly lost
181 following eutrophication across the observed depth profiles. Those macrophyte
182 species highly vulnerable to eutrophication-induced declines were selected according
183 to Madgwick et al. (2011). The explained percentage of macrophyte assemblage
184 variation was corrected following Peres-Neto et al. (2006) and expressed as R^2
185 adjusted.

186 HMD and perMANOVA were applied to assess independent variation in
187 macrophyte assemblages and water depth profiles amongst the three basins.
188 perMANOVA compares variability of dissimilarity distances within groups versus
189 variability between groups, while HMD comprises a distance-based test of the
190 homogeneity of multivariate dispersions between groups to their group centroid
191 (Anderson 2006). Macrophyte species dissimilarities were calculated using the Bray-
192 Curtis dissimilarity index and water depth dissimilarities using Euclidean distances.
193 Each basin was treated as independent (Anderson 2006). Using this approach, a basin
194 having high multivariate dispersion (high values of dissimilarities and/or mean
195 distance to group centroid) would be associated with large dissimilarities between
196 macrophyte species or water depth and thus high heterogeneity (Anderson et al.
197 2006). The significance of the analyses was assessed by ANOVA ($P< 0.05$). A
198 significant result indicates high variation between basins, while a lack of significance
199 denotes no variation in macrophyte assemblage or depth variation between basins
200 (Anderson et al. 2006).

201 To visualise how plant assemblage and depth variation were related across the
202 three basins, we used NMDS on Bray-Curtis dissimilarities for the PVI data (which
203 combines plant percentage cover and water depth into one measure). Of many
204 potential measures of dissimilarity, Bray-Curtis has been shown to have one of the
205 strongest relationships between site dissimilarity and ecological distance, hence
206 providing optimum ordination results for the NMDS technique (Faith et al. 1987).

207

208

209 To quantify change over time in the spatial distributions of plant and invertebrate
210 macrofossils (henceforth referred to as space-time interaction), we applied an
211 ANOVA space-time test analysis (Legendre et al. 2010). We used "Model 5" of
212 Legendre et al. (2010), which uses principal coordinates of neighbour matrices
213 (PCNM) variables to assess the interaction between space and time, and Helmert
214 contrasts, also called ''orthogonal dummy variables", to reconstruct a predictive
215 model assessing the independent effects of space and time.

216 To facilitate comparisons between cores, macrofossil data were expressed as
217 fluxes. As plant macro-remains include a variety of differentially produced plant
218 structures (e.g. spines, leaves and seeds), making realistic comparisons of taxon
219 abundances is notoriously challenging (Birks 2001). Consequently, similar to the
220 approach of Odgaard and Rasmussen (2001), we transformed each macrofossil flux
221 record into a 0-5 abundance scale, where 0 is absent and 5 is highly abundant, as
222 follows: (i) we merged macrofossil fluxes from all three cores into a single matrix and
223 ordered each taxon flux record from highest to lowest values; (ii) flux data were then
224 transformed into percentage frequencies by assuming 100% for the highest flux value
225 for each taxon; (iii) percentage frequencies were clustered using a DAFOR
226 (Dominant, Abundant, Frequent, Occasional, Rare) scale as follows: 5 (100%-80%); 4
227 (79%-60%); 3 (59%-40%); 2 (39%-20%); 1 (19%-1%). Macrophyte DAFOR data
228 were Hellinger transformed, while bryozoan, chironomid, mollusc and daphnid fluxes
229 were first log-transformed and then Hellinger-transformed prior to ANOVA space-
230 time analyses. Each taxon group was tested independently and we constructed a site-
231 by-taxon response data table with three-row blocks corresponding to a spatial and
232 temporal location (i.e. basin 1, basin 2 and basin 3 at time *i*). We divided the
233 macrofossil abundance data of each lake basin into 11 time-periods (a total of 33 data
234 points) as follow: *c.* pre-1900; 1901-1910; 1911-1920; 1921-1930; 1931-1940; 1941-
235 1950; 1955-1965; 1966-1980; 1981-1990; 1991-2000 and 2001-2008. To assess the
236 significance of each taxon group space-time interactions we used a significance of

0.05 and 999 permutations. Multidimensional scaling (NMDS) (Bray-Curtis metric) was used to visualize trends in assemblage variation in space and time and K-means partitioning analysis to detect significant changes in assemblage composition over time (‘‘cascadeKM’’ function of the ‘‘vegan’’ Package in R). The simple structure index (ssi) was used to identify the best partition. To summarise the main temporal changes in assemblage composition in relation to environmental driving factors, we identified characteristic species for each time-period using the IndVal method (‘‘indval’’ function of the ‘‘labdsv’’’ Package in R) of Dufrene and Legendre (1997). For simplification purposes, we divided the palaeo-record of each biological group into three synchronous time intervals of assemblage variation detected by K-means across the five groups (see ESM4). These three time intervals were: pre-1900-1940, 1941-1980, and 1981-present.

Results

Contemporary macrophyte spatial patterns

Fourteen macrophyte species were recorded among the three basins (Fig. 2a). *Elodea canadensis* Michx., *Nuphar lutea* (L.) Sm. *Sagittaria sagittifolia* L., and *Sparganium emersum* Rehmann were the most abundant species, occurring in all three basins. Filamentous algae (undifferentiated), *Lemna trisulca* L., *Nitella flexilis* L., and *Utricularia vulgaris* L., were also recorded in all basins but at lower percentage cover. *Chara globularis* J.L.Thuiller, *Potamogeton obtusifolius* Mert. & W.D.J. Koch, and *Stratiotes aloides* L. were present in basins 1 and 3 only, *Potamogeton praelongus* Wulfen. was absent in basin 1, *Callitriche* sp. and *Equisetum fluviatile* L. were absent in basins 1 and 3, and *Myriophyllum verticillatum* L. was absent in basins 2 and 3. Filamentous algae occurred in all three basins and were more abundant in basins 2 and 3.

263 Basin 1 was characterised by homogeneous shallow water depths (mean 116.7
264 ± 6.43 cm), basin 2 by more heterogeneous and deeper waters (mean 164.7 ±. 28.01
265 cm) and basin 3 by homogenous deeper waters (mean 152.1 ± 3.5 cm) (ESM2a).
266 Negative binomial GLM on macrophyte species percentage cover and water depth
267 values showed that water depth explained a highly significant (P<0.0001; R^2_{adj}=30%)
268 proportion of the variation in macrophyte assemblages at the whole-lake scale (Fig.
269 2b). A marked decline in macrophyte percentage cover was observed above a depth of
270 160 cm. Logistic regressions indicated that *M. verticillatum*, *C. globularis*, and *S.*
271 *aloides* were highly restricted (P<0.001 in all cases) by water depth (ESM3) with
272 probability of occurrences greatly declining above 115-120 cm. *P. praelongus* and *P.*
273 *obtusifolius* occurrences were similarly limited to depths between 115-160 cm but
274 with no statistically significant trend.

275 Multivariate analysis revealed substantial spatial variation in macrophyte
276 assemblages and water depths between the three basins (P=0.001 in all perMANOVA
277 and HMD cases) (ESM2b). HMD analysis revealed that macrophyte assemblage and
278 water depth profiles in basin 2 were significantly more heterogeneous than in the
279 other two basins (ESMS2c). The NMDS plot of PVI values showed a separation
280 between macrophyte Bray-Curtis dissimilarities of basin 1 (groups on the left-hand
281 side of the plot) and the other two basins (Fig. 3a). Bray-Curtis macrophyte
282 dissimilarities of basins 2 and 3 overlapped in some cases.

283

Historical spatial patterns

284

285 Plant and invertebrate macrofossils were detected throughout the cores from each
286 basin (Figs. 4-6). ^{210}Pb-based radiometric chronologies and sedimentation rates for
287 cores NCAS1, NCAS2 and NCAS3 are given in ESM1.

288 NMDS plots of all five taxonomic groups revealed a greater dissimilarity
289 between basin 1 assemblages and the other two sampling basins over time (Fig. 3 b-
290 e). The ANOVA space-time analysis of plant macrofossil abundances revealed a

291 highly significant space-time interaction (P=0.001) that explained 27% of assemblage
292 variation (Table 1). The analysis also revealed a significant (P=0.001) space-time
293 interaction for chironomids and molluscs, accounting for 32% and 29% of total
294 assemblage variation, respectively (Table 1).

295 Multivariate trajectory and K-means analyses revealed three significant time
296 intervals (ESM4a) in which plant macrofossil composition differed significantly
297 across the three basins (Fig. 4). These corresponded to *c.* pre-1900-1930, 1931-1980
298 and 1981-present. The initial changes are mostly attributed to early reductions in
299 bryophytes (including *Sphagnum* spp. leaf remains), *Najas flexilis* (Willd.) Rost and
300 Schmidt. seeds, *Isoetes lacustris* L. megaspores and *S. aloides* leaf-spines (Fig. 4,
301 Table 2). *Myriophyllum* spp. leaves and seeds were present at high abundances (in
302 particular in basin 1) along with *P. praelongus/lucens* (basins 2 and 3) during the
303 1930-1980s. After 1981 *Nitella* sp. oospores increased in basin 1 and remains of
304 floating-leaved taxa such as *L. trisulca*, Nymphaeaceae and *Sparganium* sp. increased
305 in all basins (Fig. 4, Table 2).

306 For chironomids, multivariate trajectory and K-means analyses revealed five
307 main time intervals (ESM4b) in which assemblages differed significantly
308 corresponding to *c.* pre-1900-1910, 1911-1940, 1941-1955, 1956-1980 and 1981-
309 2008 (Fig. 5). At *c.* pre-1900-1920 differences are mostly attributed to prevalence in
310 basin 3 of *Ablabesmyia* spp., *Cryptochironomus* spp*., Cladotanytarsus mancus,*
311 *Dicrotendipes nervosus, Pseudochironomus* spp., *Tanytarsus lugens, Tanytarsus*
312 *pallidicornis*, *Stempellina* spp., *Stilocladius* and the diamesine *Protanypus* sp. (Fig. 5,
313 Table 2). The second-time interval (1921-1940) was associated with a reduction or
314 disappearance of most of these taxa in basin 3, the appearance in subsequent time
315 interval (1941-1955) of *Glyptotendipes pallens* and, especially in basin 1, of *D.*
316 *nervosus, Endochironomus albipennis, Cricotopus intersectus, Cricotopus laricomalis*
317 and *Psectrocladius sordidellus.* After 1956 (the fourth-time interval), *Procladius* spp.
318 increased in abundance, especially in basin 2, together with a general increase in
319 numbers of *E. albipennis* (basins 1 and 2), and of both *G. pallens* and *Polypedilum*
320 *sordens*. From 1981 to present most of these taxa generally increased in abundance
321 and were similarly distributed across the three basins (Fig. 5, Table 2).

322 Multivariate trajectory and K-means analyses identified three time intervals in
323 which mollusc assemblages differed significantly (ESM4c) - *c.* pre-1900-1920, 1921-
324 1950 and 1951-present. In the two earlier time intervals, most of the current taxa were
325 absent and gastropods and the bivalves *Pisidium* spp. and *Anodonta cignea* L. (which
326 produces glochidia larvae) occurred in very low abundances. Mollusc abundances
327 showed a general increase in the 1950s (Fig. 6a, Table 2). The invasive bivalve,
328 *Dreissena polymorpha* Pallas, first appeared in the 1990s consistent with its known
329 recent arrival in the ULE system (Rosell et al. 1998).

330 No space-time interaction was revealed in the analyses of bryozoan statoblasts
331 and daphnid ephippia (Table 1). Independent tests on the spatial factor confirmed,
332 however, that both bryozoan and daphnid remains were strongly spatially structured
333 over time (P= 0.001 for both cases) (Table 1). Spatial patterns explained 64% of
334 assemblage variation for bryozoans and 41% for daphnids. For bryozoans, *Plumatella*
335 spp. were generally absent in basin 1 and *Plumatella fruticosa* Allman was abundant
336 in basin 3 (Fig. 6b, Table 2). Likewise*, Ceriodaphnia* spp. occurred abundantly
337 throughout basin 1, while *Daphnia* spp. dominated in basins 2 and 3 (Fig. 6c, Table
338 2). For bryozoans, K-means analysis detected four time intervals in which
339 assemblages differed significantly (ESM4d) at *c.* pre-1900-1940, 1941-1955, 1956-
340 1980 and 1981-present. These temporal changes occurred mostly in basins 2 and 3,
341 where the first-time interval was typified by dominance of *P. fruticosa* in basin 3. At
342 the second-time interval (1941-1955), *P. fruticosa* abundances declined while
343 *Plumatella* spp., increased. The third-time period (1956-1980) was characterised by
344 an increase in *C. mucedo* and *Plumatella* spp. as was the final post-1981 interval (Fig.
345 6b, Table 2). K-means analysis for daphnid ephippia resulted in three time intervals in
346 which assemblages differed significantly (ESM4e) at *c.* pre-1900-1955, 1956-1990
347 and 1991-present. The first early time interval was typified by dominance of
348 *Ceriodaphnia* spp. (basin 1), followed by a second-time period characterized by
349 increases in *Daphnia* spp. and minor reductions in *Ceriodaphnia* spp. (Fig. 6c, Table
350 2). The final time period was characterised by an increase in *Daphnia* spp. and
351 *Ceriodaphnia* spp. in basins 2 and 3.

The comparison of K-means analyses across the five biological groups revealed three relatively synchronous time intervals of assemblage variation across the five groups (ESM4) at pre-1900s-1940, 1941-1980, and 1981-1990. The first early time interval corresponded with synchronous changes in plant, chironomid and bryozoan remains, whereas synchronous changes characterised all five groups during the second and most recent time intervals.

Discussion

Contemporary distributions of macrophytes

Our analyses have revealed significant spatial heterogeneity in macrophyte assemblages across the three basins. Despite a general prevalence of the same three or four species, the results highlighted macrophyte heterogeneity across basins both in terms of species turnover and variation in species relative abundances. Furthermore, our data revealed associations between macrophyte assemblage variation and heterogeneity in water-depth (ESM1). This indicates that intra-basin variation may also create other complex, non-linear effects on macrophyte spatial patterns (e.g. greater niche availability with different depth profiles) (Anderson et al. 2006).

The detected strong relationship between water depth and spatial variation in macrophyte community structure likely reflects light limitation. This is supported by the peaty-brown colour of Castle Lough water and a general prevalence of macrophyte species with floating leaves (e.g. water lilies*, S. emersum* and *S. sagittifolia*) and high shade tolerance (e.g. *E. canadensis)* (Spence and Chrystal 1970; Fig. 2a). A widespread shading effect by water lilies (*N. lutea* and *N. alba*-both recently growing in the lake and greatly represented by sclereids in the paleo-data) likely also contributes to reducing the abundances of other submerged species such as *M. verticillatum*, *U. vulgaris* and *C. globularis* in the contemporary lake (Sculthorpe 1967). Other correlated abiotic factors may also influence macrophyte distributions. For example, basin 1 is relatively well protected by reedswamp and floating-leaved

379 species, while basins 2 and 3 are more exposed to wind and wave action (Fig. 1).
380 Exposure may reduce plant stands through fragmentation and uprooting (especially in
381 soft organic-rich sediments) and prevent the establishment of *M. verticillatum,* broad-
382 leaved species (e.g. *P. praelongus* and *P. lucens*; Barko and Smart 1986; Riis et al.
383 2001) and short and/or non-rooted species (e.g. *S. aloides;* Smolders et al. 2003),
384 which require sheltered habitats, a pattern consistent with our data (Fig. 2a). Increased
385 sediment transport with wave-movement can also influence propagule transport and
386 bury established plant stands (Keddy and Reznicek 1986). Differences in nutrient
387 concentrations between basins due to differential external loadings (e.g. proximity to
388 inflow (basin 1), pine woodland (basin 2), and the outflow (basin 3)) are also potential
389 co-associated factors influencing macrophyte spatial distributions (Carpenter and
390 Titus 1984).

391 In conjunction with water depth, plant seasonality and dispersal may also
392 contribute to macrophyte spatial distributions (Carpenter and Titus 1984, Sayer et al.
393 2010a). However, a strong concordance of our palaeo-data with observed macrophyte
394 spatial patterns suggests that the latter are informative, robust and not unduly
395 influenced by seasonality (Figs. 2a, 5). In contrast to the restricted and patchy
396 distributions of *C. globularis, M. verticillatum*, and *P. praelongus* in the present-day,
397 the palaeo-data indicate that these species were present across the whole lake in the
398 past. It can be inferred, therefore, that dispersal is probably sufficient to enable all
399 species to reach all lake basins, but species sorting has occurred over time linked to
400 between-basin variation in environmental forcing (Leibold et al. 2004).

401 The above considerations demonstrate that there may well be other drivers of
402 macrophyte assemblage structure in Castle Lough besides water depth that we did not
403 specifically measure. These drivers may act at similar or dissimilar spatial scales and
404 may also vary over time. In general, the detection of various drivers of assemblage
405 structure will be dependent on experimental design, the measurement of relevant
406 conditions at appropriate scales and times, the ability to conduct statistical analyses
407 focusing on measured drivers, and identifying or discounting other potential drivers
408 by evidence-based argument.

409

Drivers of temporal changes in community assembly

410

411 The palaeo-record suggests that the basins have retained similar depth profiles over
412 time. Temporal patterns in distributions of daphnid ephippia support this inference.
413 For example, *Ceriodaphnia* species are commonly reported to prefer macrophyte-
414 covered shallow waters (Lauridsen et al. 1996) and were mostly found in basin 1, the
415 shallowest basin (Fig. 6c, Table 2). On the other hand, some *Daphnia* species prefer
416 non-macrophyte dominated open water (Lauridsen and Lodge 1996; Davidson et al.
417 2010) and occurred throughout time in greater abundances in the less vegetated
418 deeper waters offered by basins 2 and 3 (Fig. 6c, Table 2). Similarly, the profundal-
419 associated chironomid taxa *Microchironomous* spp. and *C. anthracinus* exhibited
420 greatest abundances in basins 2 and 3 (Fig. 5, Table 2). These strong inter-basin
421 differences suggest that the current day, water depth variation has been an important
422 long-term driver of spatial ecology in Castle Lough.

423 Significant space-time interactions for macrophyte, chironomid and mollusc
424 assemblages and differing temporal trends in bryozoan and daphnid assemblages
425 between basins, suggest that the distributions of these groups have been modified
426 across basins over time in response to conditions unrelated to water depth. The
427 synchronous temporal changes in assemblages of all five groups (ESM4) and species
428 characteristic of each time-interval (detected by the IndVal analysis; Table 2), suggest
429 compositional changes reflecting a previously inferred acceleration of eutrophication
430 after around 1900 (Battarbee 1986). Before 1930, the lake was characterised by taxa
431 associated with low to intermediate nutrient conditions including the macrophytes *N.*
432 *flexilis*, *I. lacustris*, and bryophytes (Carpenter and Titus 1984; Sand-Jensen et al.
433 2008), the chironomids *Stempellina* spp., *Pseudochironomus* spp., *Orthocladius*
434 *consobrinus* and *Protanypus* spp. (Pinder and Reiss 1983; Brodersen and Lindegaard
435 1999) and the bryozoan *P. fruticosa* (Økland and Økland 2002) (Table 2). Post-1930
436 macrophytes converged spatially towards communities associated with mesotrophic-
437 eutrophic conditions, exemplified by increased abundances of *Myriophyllum* spp. and

438 *P. praelongus/lucens* (Sand-Jensen et al. 2008; Table 2). Subsequent dominance of
439 floating-leaved taxa (*L. trisulca,* water-lilies and *Sparganium* sp.), declines in the
440 macrophytes *I. lacustris* and *N. flexilis,* increases in *Plumatella* spp. (Hartikainen et
441 al. 2009) and concomitant reductions in chironomids intolerant of nutrient-rich
442 conditions (e.g. *Stempellina* spp., *Pseudochironomus* spp., *O. consobrinus* and
443 *Protanypus* spp.) in recent times (post 1981) collectively suggest further development
444 of eutrophication and its effects (Table 2).

445 Our data indicate that spatial and temporal dynamics of invertebrate
446 assemblages since 1931 are to a large extent linked to those of macrophytes (Table 2).
447 Indeed, many chironomids depend on macrophytes for food, with some (e.g.
448 *Microtendipes* and *Polypedilum* species) feeding on epiphytic algae (Moller Pillot
449 2009), and others relying on living (e.g. *Cricotopus* species) or decomposing (e.g.
450 *Stenochironomus* species) plants as a source of food or substratum (Vallenduuk and
451 Moller Pillot 2007; Moller Pillot 2013). Direct associations between macrophyte and
452 chironomid abundances have been demonstrated previously in both contemporary
453 (Langdon et al. 2010) and palaeolimnological studies (Brodersen et al. 2001). Our
454 analysis suggests a particularly close association between *Myriophyllum* spp. and the
455 majority of *Cricotopus* morphotypes in basin 1 (Figs. 4, 5), perhaps reflecting the
456 large surface area provided by finely dissected *Myriophyllum* leaves that can in turn
457 support dense epiphytic algal communities (Sculthorpe 1967). Similarly, post 1981
458 increases abundances of chironomids (*E. albipennis*, *G. barbipes* and *P.*
459 *nubeculosum*) and molluscs (*Pisidium* spp. and snails) coincident with the expansion
460 of floating-leaved plant taxa (e.g. water lilies) could reflect increased availability of
461 epiphytic food (Sculthorpe 1967) (Table 2).

462 It should be noted that K-means analysis did not detect the apparently close
463 links between macrophyte and invertebrate abundances after the early stages of
464 eutrophication in the 1930s as described above. Instead, K-means analysis indicated
465 that macrophyte assemblage variation remained stable until the 1980s, while
466 invertebrate assemblages varied in keeping with a proposed acceleration of nutrient-
467 enrichment in ULE after 1955 (Battarbee 1986). This apparent temporal disparity
468 between macrophyte and invertebrate dynamics could be attributed to a lack of

469 statistical power in the macrophyte data (Legendre et al. 2010). Between 1955-1980,
470 there were indeed strong increases in abundances of *Myriophyllum* spp. and of the
471 chironomid *Cricotopus* spp. but mainly in core NCAS1 (basin 1) (Figs. 4, 5). This
472 suggests that an important phase of change probably occurred earlier and was
473 undetected in the study.

474 Subsequent synchronous assemblage changes detected by K-means analysis
475 across all biological groups post-1981 suggest a distinctive phase in the ecology of the
476 ULE system. One possible explanation is the introduction of zebra mussels after the
477 mid-1990s (Fig. 6b). Zebra mussels are well known to alter lake environments and
478 food webs by reducing phytoplankton and hence grazer abundances and by
479 stimulating macrophyte growth due to increases in water transparency (Higgins and
480 Vander Zanden 2010). Our data provide little support for such zebra mussel effects,
481 however. For example, grazer abundances (e.g. *Daphnia* spp.) increased during the
482 same period, as did abundances of taxa tolerant of eutrophic conditions (e.g. the
483 macrophytes *L. trisulca, N. lutea, P. berchtoldii* and *P. pusillus*) (Table 2). Similarly,
484 ordination plots reveal convergence of macrophyte and chironomid assemblages to
485 associations of eutrophication-tolerant taxa (Fig. 3). Glochidia larvae of *Anodonta*
486 also increased during this time period. *Anodonta* competes directly with zebra mussels
487 for food, and populations commonly diminish after the establishment of zebra mussels
488 (Higgins and Vander Zanden 2010). Thus, all evidence points to negligible zebra
489 mussel impacts in Castle Lough so far.

490 As a caveat, we note that constraints in palaeo-data and radiometric analyses should
491 be considered when conducting plant macrofossil studies (Birks 2014). For example,
492 some species (e.g. *E. canadensis* and *U. vulgaris*) are poorly preserved in sediments
493 (Davis 1985; Davidson et al. 2005). However, surface sediment samples have also
494 been shown to faithfully record the main spatial patterns in plant assemblages (Zhao
495 et al. 2006; Clarke et al. 2014; Levi et al. 2014). Furthermore, the macrofossil record
496 can over- or under-represent certain macrophyte taxa (Birks 2001; Davidson et al.
497 2005). For example, *C. globularis, Nitella* spp*.,* and *N. flexilis,* produce large numbers
498 of oospores/seeds, while *Potamogeton* species produce low numbers of seeds. Such
499 disparity in propagule production can lead to misinterpretations of true plant

500 abundances (Zhao et al. 2006). Our use of a semi-quantitative abundance scale (as in
501 Odgaard and Rasmussen 2001) for the plant macrofossil data helps to reduce such
502 effects. Moreover, similar to previous plant macrofossil studies in lakes (Davidson et
503 al. 2005; Zhao et al. 2006; Salgado et al. 2010; Clarke et al. 2014; Levi et al. 2014),
504 our palaeo-data capture most of the contemporary macrophyte community and
505 faithfully reflect current spatial distributions and differences between basin 1 and
506 basins 2 and 3 (Figs. 2a, 3, Table 2). Finally, our study is based on characterising
507 relative abundances over space and time within the same localities. Constraints
508 therefore are not expected to substantially influence our inferences.

509

Implications for long-term changes in ecological processes

510 Our data suggest a trend of spatial convergence of macrophytes and co-occurring
511 invertebrate communities post-1981 (Fig. 3, Table 2). This suggests that, as
512 eutrophication advances, the influence of water depth variation on assemblage
513 heterogeneity is gradually eroded, and that ultimately a limited set of eutrophication-
514 tolerant species will become homogeneously distributed across the entire lake.
515 Previous evidence for eutrophication effects on macrophytes includes reductions in
516 diversity and changes in seasonality (Ayres et al. 2008; Sayer et al. 2010a), which
517 ultimately result in loss of resilience (Sayer et al. 2010a,b). However, prior to our
518 study little was known regarding changes in macrophyte spatial distributions in
519 response to long-term nutrient-enrichment processes, nor of associated invertebrate
520 taxa. Our data revealed minimal macrophyte species turnover over time, but
521 substantial changes in macrophyte relative abundances across sites. This suggests that
522 reduced spatial variation in macrophyte and invertebrate relative abundances may
523 reflect an ecological phase that precedes major changes in species richness and
524 turnover (Arts 2002; Anderson et al. 2006). Such spatial homogenisation of relative
525 abundances may contribute to the loss of resilience associated with eutrophication
526 (Donohue et al. 2009) and warrants examination in future studies.

527

Conclusions

Our study provides novel insights into how environmental influences have varied over time to structure within-lake assemblages. We have analysed contemporary ecological and palaeoecological data to collectively infer long-term changes in the pathways and processes that underlie eutrophication effects in shallow lakes. The contemporary data allow us to assess how macrophyte assemblages vary in composition and heterogeneity according to basin-specific factors (e.g. variation in water depth). In turn, the palaeoecological data enable us to infer basin-specific impacts of and susceptibilities to eutrophication exhibited by macrophytes and invertebrates.

Our results indicate that variability in water depth promotes contemporary assemblage variation amongst Castle Lough's basins, thus stimulating within-lake macrophyte and invertebrate assemblage heterogeneity and thus higher lake biodiversity (Anderson et al. 2006). These insights are in keeping with growing evidence for the importance of spatial heterogeneity in structuring local populations and assemblages and the concomitant implications of scaling up from small-scale studies (Ford et al. 2016). Our study also strongly suggests that eutrophication has acted as a homogenising agent of macrophyte and co-occurring invertebrate diversities and abundances over time at the whole-lake scale. Such homogenisation of communities may have profound implications for shallow lake ecosystem functioning including reductions in community resistance and resilience due to alterations in e.g. productivity and biomass production, variations in intra- and interspecific competition and increased vulnerability to species invasions (Hillebrand et al. 2008).

Currently, Castle Lough is in a mesotrophic-eutrophic condition, presenting high variation in assemblages between basins and relatively high species richness. Recently it has been inhabited by species regarded as sensitive to eutrophication and rare in Northern Ireland (e.g. *N. flexilis* and broad-leaved *Potamogeton* taxa). Unfortunately, hypertrophic states now characterise many water bodies of the ULE system because of nutrient loading deriving from increasing dairy farming and urban development (Gibson et al. 1995). If nutrient inputs continue, it is likely that Castle

557 Lough will soon be characterised by spatially homogenous assemblages comprising a
558 few tolerant taxa and the conservation value of the lake will be greatly diminished.

559

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560

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573

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Tables

819 **Table 1.** Effects of space, time and their interaction (S-T) on the abundances of
820 macrophytes, chironomids, molluscs, bryozoans and daphnid in three sediment cores
821 form Castle Lough. * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

	S-T			Space			Time		
	F	R^2	p	F	R^2	p	F	R^2	p
Macrophytes	2.8461	0.2722	0.001***	5.1164	0.1957	0.001***	1.2815	0.2451	0.173
Chironomids	2.6839	0.3153	0.001***	1.8326	0.0861	0.027*	1.0476	0.2461	0.599
Molluscs	2.2703	0.2863	0.02**	1.4394	0.0726	0,256	1.0414	0.2627	0.513
Bryozoans	1.6363	0.0994	0,18	2.6353	0.6402	0.001***	0.6435	0.0782	0.825
Daphnids	0.1188	0.0187	0,989	6.6253	0.4165	0.01**	0.2969	0.0933	0.987

822

823

824 **Table 2.** Summary of selected characteristic macrophyte, chironomid, mollusc, bryozoan and daphnid species identified by the greatest
825 abundance of each taxon from IndVal analysis during three time-periods: pre-1900-1930, 1931-1980, 1981-present. Information on their ecology
826 in relation to available information regarding nutrient-enrichment, water depth and habitat structure preferences provided by submerged
827 vegetation (+V = vegetation present; -V = vegetation absent.) in each study basin (1=basin 1; 2=basin 2; 3=basin 3) is given.

828

Species	Ecology	Pre-1900-1930			1931-1980			1981-present			References
		1	2	3	1	2	3	1	2	3	
Macrophytes											
Najas flexilis	**Oligo-mesotrophic**	**X**	**X**	**X**							**Carpenter and Titus 1984;**
Bryophytes	**Oligo-mesotrophic**	**X**		**X**					**X**		**Arts 2002; Sand-Jensen et al. 2008**
***Nitella* spp.**	**Oligo-mesotrophic**		**X**	**X**				**X**			**Arts 2002; Sand-Jensen et al. 2008**
Isoetes lacustris	**Oligo-mesotrophic**			**X**							**Arts 2002; Sand-Jensen et al. 2008**
Stratiotes aloides	**Meso-eutrophic**		**X**	**X**				**X**			**Smolders et al. 2003**
Potamogeton obtusifolius/friesii	**Meso-eutrophic**		**X**				**X**	**X**			**Sand-Jensen et al. 2008**
***Myriophyllum* spp.**	**Littoral; meso-eutrophic**				**X**	**X**	**X**				**Arts 2002; Sand-Jensen et al. 2008**
Potamogeton praelongus/lucens	**Profundal-mesotrophic**				**X**		**X**		**X**		**Riis et al. 2001; Arts 2002; Sand-Jensen et al. 2008**
Nymphaea alba	**Meso-eutrophic**						**X**		**X**		**Sand-Jensen et al. 2008; Madgwick et al. 2011**
Nymphaeaceae (*N. lutea/N. alba*)	**Meso-eutrophic**							**X**	**X**	**X**	**Sand-Jensen et al. 2008; Madgwick et al. 2011**
Lemna trisulca	**Meso-eutrophic**							**X**	**X**	**X**	**Sand-Jensen et al. 2008; Madgwick et al. 2011**
***Sparganium* sp.**	**Meso-eutrophic**							**X**	**X**	**X**	**Sand-Jensen et al. 2008; Madgwick et al. 2011**

Chara globularis	**Meso-eutrophic**					**X**	**X**	**X**		**Madgwick et al. 2011**
Chironomids										
Chironomus anthracinus	**Profundal; eutrophic**	**X**						**X**	**X**	**Pinder and Reiss 1983; Brodersen and Lindegaard 1999; Moller Pillot 2009**
Chironomus plumosus	**Profundal; eutrophic**	**X**				**X**		**X**		**Pinder and Reiss 1983; Brodersen and Lindegaard 1999; Moller Pillot 2009**
Orthocladius consobrinus	**Oligotrophic**	**X**							**X**	**Pinder and Reiss 1983; Brodersen and Lindegaard 1999; Moller Pillot 2013**
Protanypus	**Profundal; oligo-mesotrophic**	**X**		**X**						**Pinder and Reiss 1983; Brodersen and Lindegaard 1999**
Cladopelma lacophila	**Littoral; oligo-mesotrophic**	**X**	**X**	**X**					**X**	**Brooks et al. 2007; Moller Pillot 2009**
Stempellina	**Oligotrophic**		**X**	**X**						**Brooks et al. 2007; Vallenduuk and Moller Pillot 2007**
Pseudochironomus	**Littoral ;oligo-mesotrophic**		**X**	**X**						**Brooks et al. 2007; Vallenduuk and Moller Pillot 2007**
Microtendipes pedellus	**Littoral; mesotrophic**			**X**	**X**			**X**		**Moller Pillot 2009; Moller Pillot 2009**
Tanytarsus lugens	**Profundal; mesotrophic**				**X**			**X**	**X**	**Brooks et al. 2007; Vallenduuk and Moller Pillot 2007**
Tanytarsus pallidicornis	**Littoral; meso-eutrophic**			**X**			**X**	**X**		**Brooks et al. 2007; Vallenduuk and Moller Pillot 2007**
Cladotanytarsus mancus	**Littoral; meso-eutrophic**			**X**			**X**	**X**		**Brooks et al. 2007; Vallenduuk and Moller Pillot 2007**
Ablabesmyia	**+V**			**X**			**X**	**X**		**Brooks et al. 2007**
Tanytarsus mendax	**Littoral; meso-eutrophic**			**X**			**X**	**X**		**Brooks et al. 2007; Vallenduuk and Moller Pillot 2007**
Dicrotendipes nervosus	**Littoral; meso-eutrophic; +V**			**X**			**X**	**X**		**Brooks et al. 2007; Moller Pillot 2009**
Glyptotendipes pallens	**Littoral; meso-eutrophic; +V**				**X**		**X**		**X**	**Brooks et al. 2007; Moller Pillot 2009; Langdon et al. 2010**
***Psetroclaudius/Cricotopus* agg.**	**Littoral; meso-eutrophic; +V**				**X**	**X**	**X**			**Brodersen et al. 2001; Moller Pillot 2013**
Stenochironomus	**Littoral; meso-eutrophic; +V**					**X**			**X**	**Brodersen et al. 2001; Vallenduuk and Moller Pillot 2007**

Glyptotendipes barbibes	**Littoral; meso-eutrophic; +V**				**X**	**X**	**X**		**Brodersen et al. 2001; Langdon et al. 2010; Moller Pillot 2009**
Endochironomus albipennis	**Littoral; meso-eutrophic; +V**					**X**	**X**	**X**	**Brodersen et al. 2001; Moller Pillot 2009**
Polypedilum nubeculosum	**Littoral; meso-eutrophic; +V**					**X**	**X**	**X**	**Moller Pillot 2009; Langdon et al. 2010**
Procladius	**Profundal; meso-eutrophic**					**X**	**X**	**X**	**Brooks et al. 2007**
Microchironomus	**Profundal; meso-eutrophic**				**X**		**X**		**Brooks et al. 2007; Moller Pillot 2009**
Invertebrates									
Plumatella fruticosa	**Oligo-mesotrophic**	**X**	**X**	**X**					**Økland and Økland 2002**
***Daphnia* spp.**	**Profundal & shallow; -V/+V**	**X**					**X**	**X**	**Lauridsen and Lodge 1996; Lauridsen et al. 1996**
***Ceriodaphnia* spp.**	**Shallow; +V**	**X**		**X**				**X**	**Lauridsen and Lodge 1996; Lauridsen et al. 1996**
Cristatella mucedo	**Meso-eutrophic**				**X**	**X**	**X**		**Økland and Økland 2002**
***Plumatella* spp.**	**Eutrophic**						**X**	**X**	**Økland and Økland 2002; Hartikainen et al. 2009**
***Pisidium* spp.**	**+V**					**X**	**X**	**X**	**Jepessen et al. 2012**
Dreissena polymorpha	**Littoral & profundal; +V**					**X**	**X**	**X**	**Higgins and Vander Zanden 2010**
Gastropoda	**+V**					**X**	**X**	**X**	**Jepessen et al. 2012**
Glochidia larvae	**Fish parasites; +V**					**X**	**X**	**X**	**Cummins 1994**

829

Figure legends

830 **Figure 1.** (a) Castle Lough location; (b) Details of surrounding environment,
831 hydrological connectivity, bathymetry and sampling areas. Open circles represent
832 contemporary macrophyte sampling areas in each lake basin. Black circles indicate
833 locations of cores NCAS1, NCAS2 and NCAS3 within each basin.

834

835 **Figure 2**. (a) Box plots presenting the macrophyte percentage frequencies in each
836 basin; (b) Negative binomial generalized linear model (GLM) for total macrophyte
837 percentage frequency and water depth values at each sampling point across the three
838 study basins. AIC=1579; P=2e-16***; $_{adj}R^2$= 30.4%.

839

840 **Figure 3**. Plots of Non-Metric Multidimensional Scale (NMDS) analyses for: (a)
841 Contemporary macrophytes; (b) Plant-macrofossils; (c) chironomids; (s) Molluscs; (e)
842 Bryozoans; (f) Daphnids. 1 = basin 1; 2 = basin 2; 3 = basin 3. H = historical times *c.*
843 pre-1900; P = contemporary data (present-day)

844

845 **Figure 4.** Plant-macrofossil stratigraphy for cores NCAS1- basin 1 (black), NCAS2-
846 basin 2 (dark grey), and NCAS3- basin 3 (light grey). Dotted lines represent a *c*. 10-
847 year time-period. Solid black lines represent the zones determined by K-means
848 analysis, corresponding to *c.* pre-1900-1920, 1931-1980 and 1981-present.

849

850 **Figure 5.** Representative chironomid-macrofossil stratigraphy for cores NCAS1-
851 basin 1 (black), NCAS2- basin 2 (dark grey), and NCAS3- basin 3 (light grey). Dotted
852 lines represent a *c.* 10-year time-period. Solid black lines represent the zones
853 determined by K-means analysis, corresponding to *c.* pre-1900-1920, 1921-1940,
854 1941-1955, 1956-1980 and 1981-present.

855 **Figure 6.** (a) Mollusc; (b) Bryozoan; and (c) Daphnid macrofossil stratigraphies for
856 cores NCAS1- basin 1 (black), NCAS2- basin 2 (dark grey), and NCAS3- basin 3
857 (light grey). Dotted lines represent a *c.* 10-year time-period. Solid black lines
858 represent zones determined by K-means analysis, corresponding to *c.* pre-1900-1930,
859 1931-1955, 1955-1980 and 1981-present.

860

Electronic supplemental material (ESM)

861 **Figure ESM1**. Radiometric chronologies and sedimentation rates for cores (a)
862 NCAS1; (b) NCAS2; and (c) NCAS3.

863

864 **Figure ESM2**. Boxplot of (a) depth variation between basins; (b) Macrophyte
865 average distance to centroid group and perMANOVA (F=13.414, P=0.001) and HMD
866 (F=7.87, P=0.001) results; (c) Depth distance to centroid group and perMANOVA
867 (F=137.84, P=0.001) and HMD (F=93.155, P<0.001) results.

868

869 **Figure ESM3.** Logistic regressions on presence/absence data of macrophyte species
870 sensitive to eutrophication across the observed depth profiles. (a) *Chara globularis*;
871 (b) *Myriophyllum verticillatum*; (c) *Stratiotes aloides*.

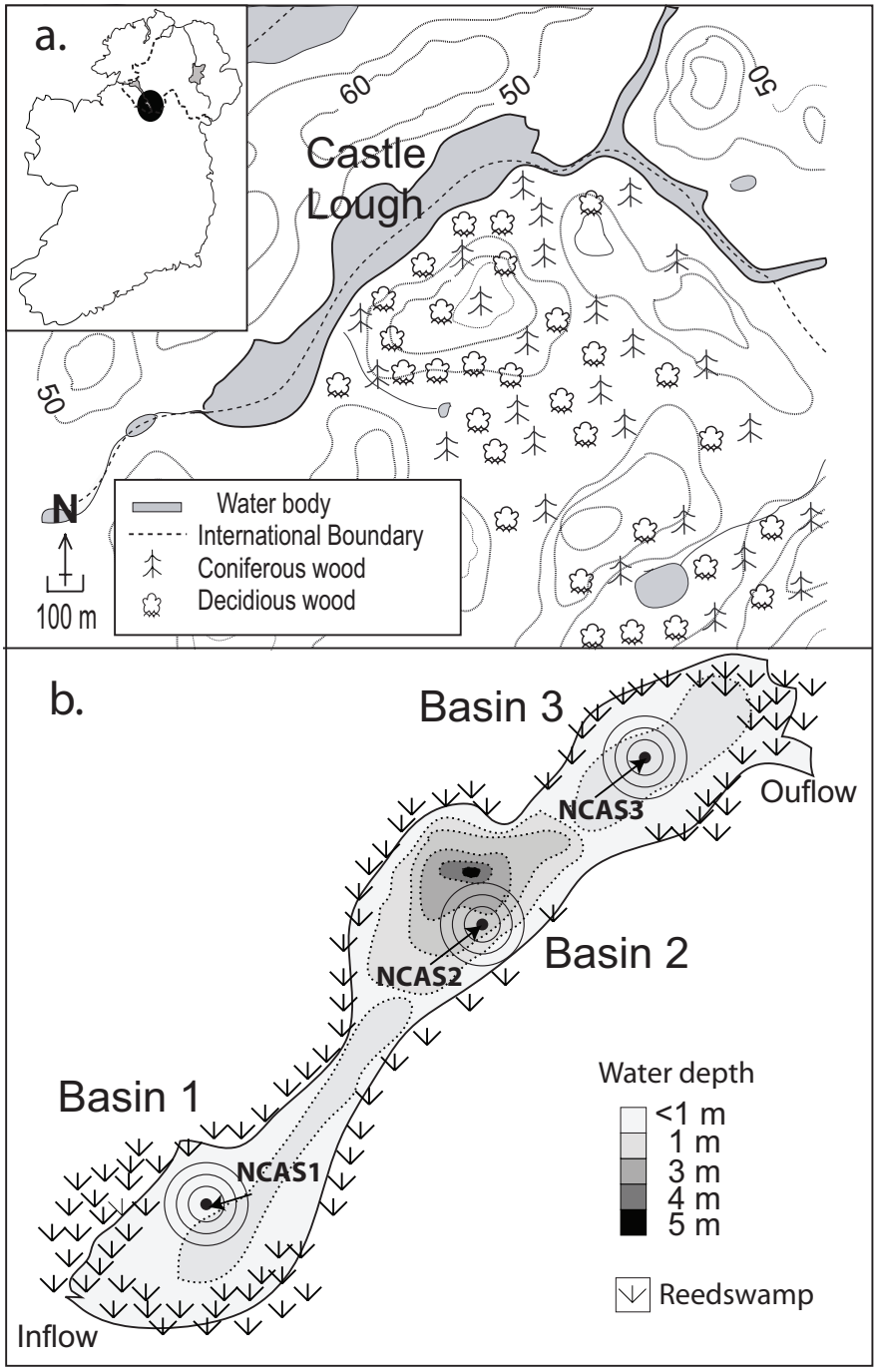
872

873 **Figure ESM4**. Spatiotemporal maps showing K-means partition of (a) Plant
874 macrofossils, (b) Chironomids; (c) Molluscs; (d) Bryozoans; and (e) Daphnid
875 assemblages in the cores NCAS1, NCAS2 and NCAS3. Simple structure index (ssi) is
876 indicated on the right-hand side of each map. Selected number of groups by ssi is
877 indicated with a bold black circle.

878

879

880 **Fig. 1**



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882

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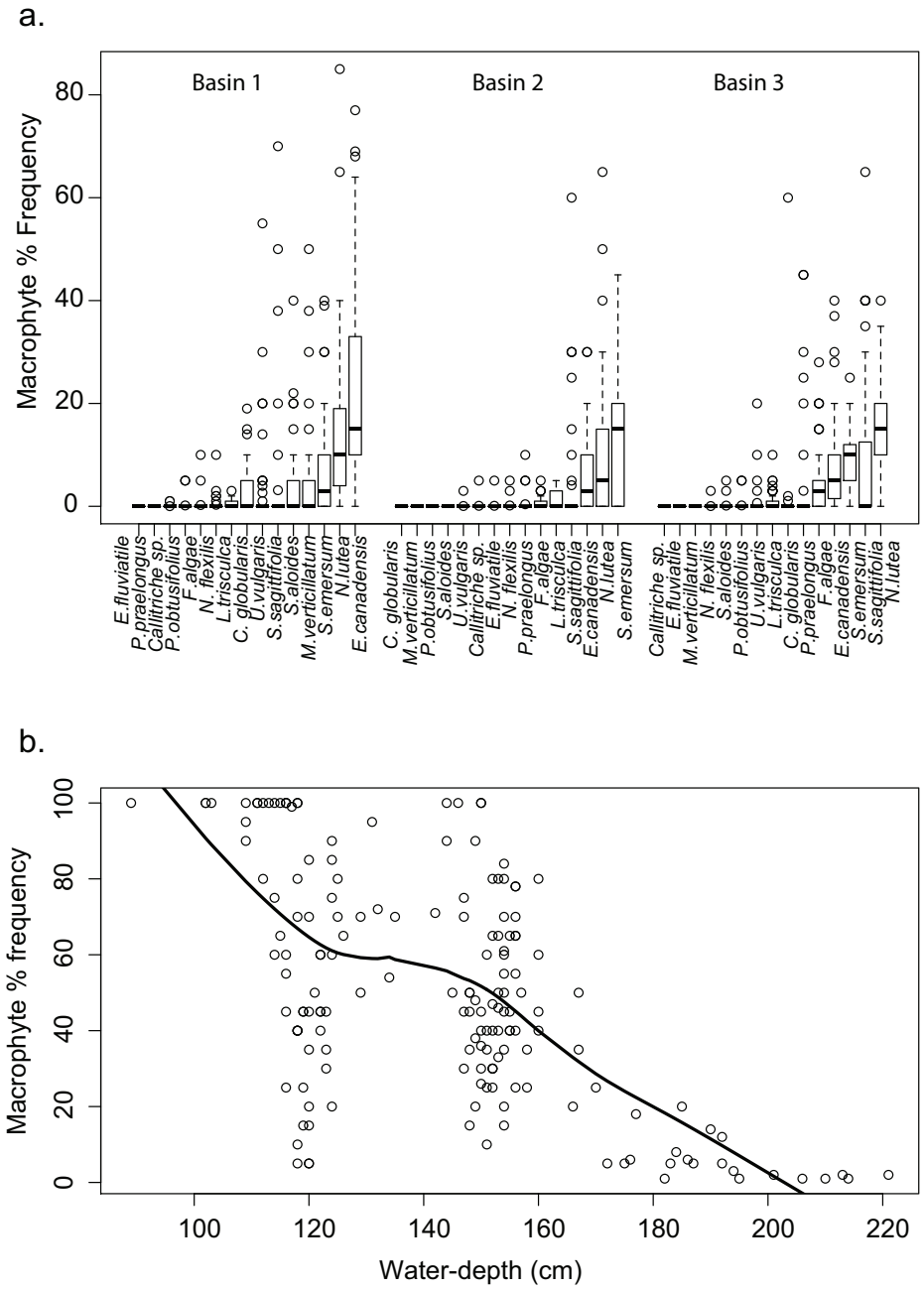
884

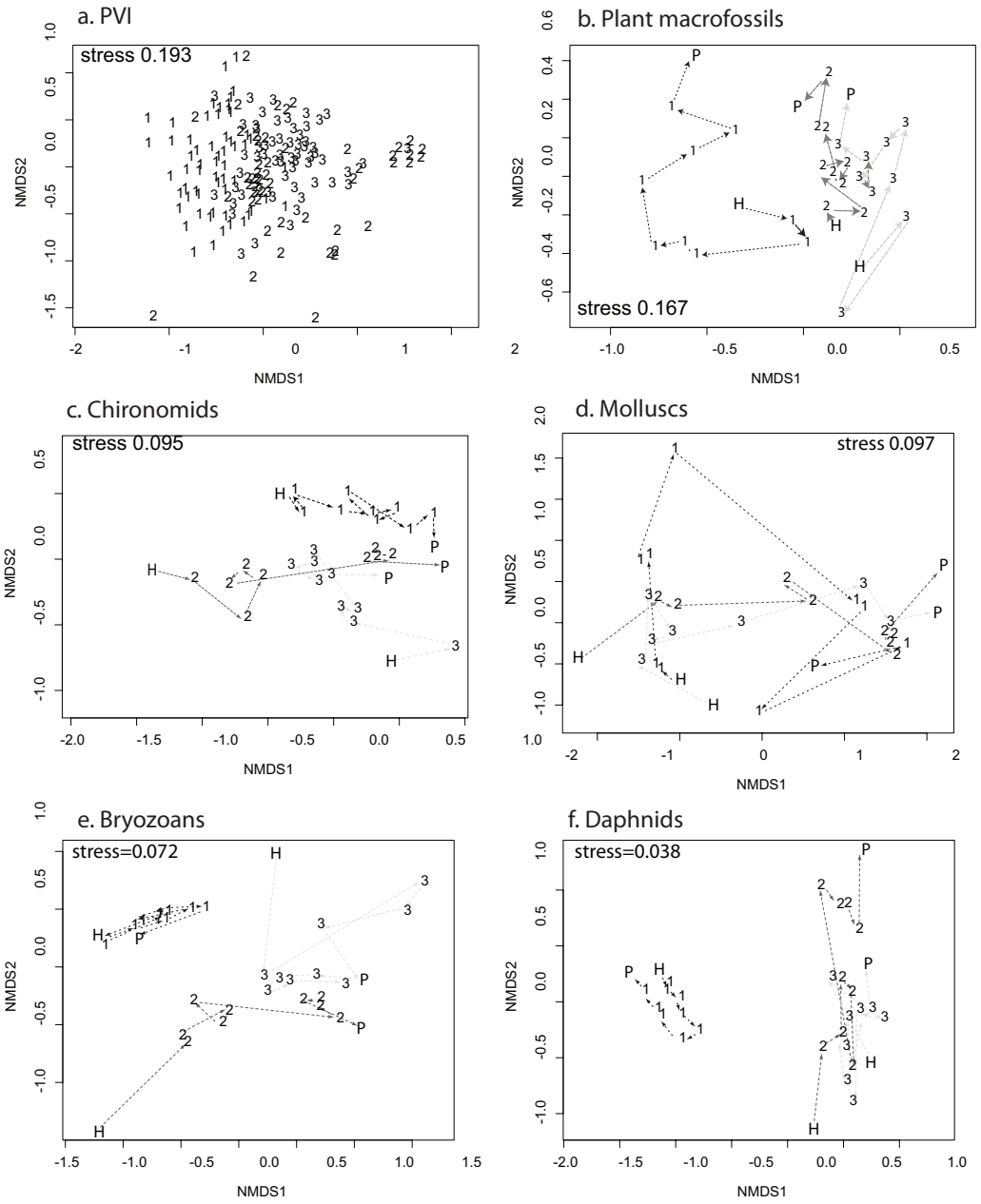
885 **Fig. 2**



886

887

888 **Fig. 3**



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891

892

Fig. 4

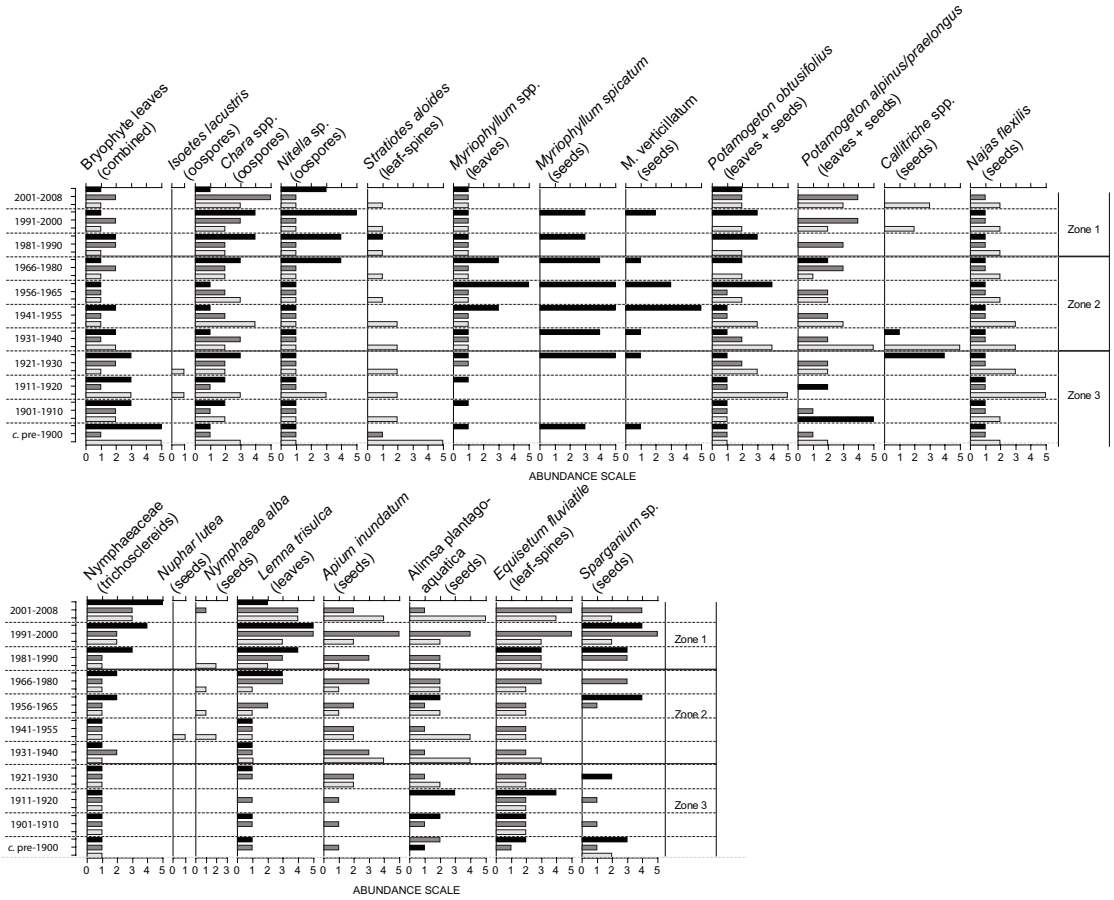

Bryophyte leaves (combined)
Isoetes lacustris (oospores)
Chara spp. (oospores)
Nitella sp. (oospores)
Stratiotes aloides (leaf-spines)
Myriophyllum spp. (leaves)
Myriophyllum spicatum (seeds)
M. verticillatum (seeds)
Potamogeton obtusifolius (leaves + seeds)
Potamogeton alpinus/praelongus (leaves + seeds)
Callitriche spp. (seeds)
Najas flexilis (seeds)
2001-2008
1991-2000
1981-1990
1966-1980
1956-1965
1941-1955
1931-1940
1921-1930
1911-1920
1901-1910
c. pre-1900
Zone 1
Zone 2
Zone 3
ABUNDANCE SCALE
Nymphaeaceae (trichosclereids)
Nuphar lutea (seeds)
Nymphaeae alba (seeds)
Lemna trisulca (leaves)
Apium inundatum (seeds)
Alimsa plantago-aquatica (seeds)
Equisetum fluviatile (leaf-spines)
Spargarium sp. (seeds)
ABUNDANCE SCALE

Fig. 5

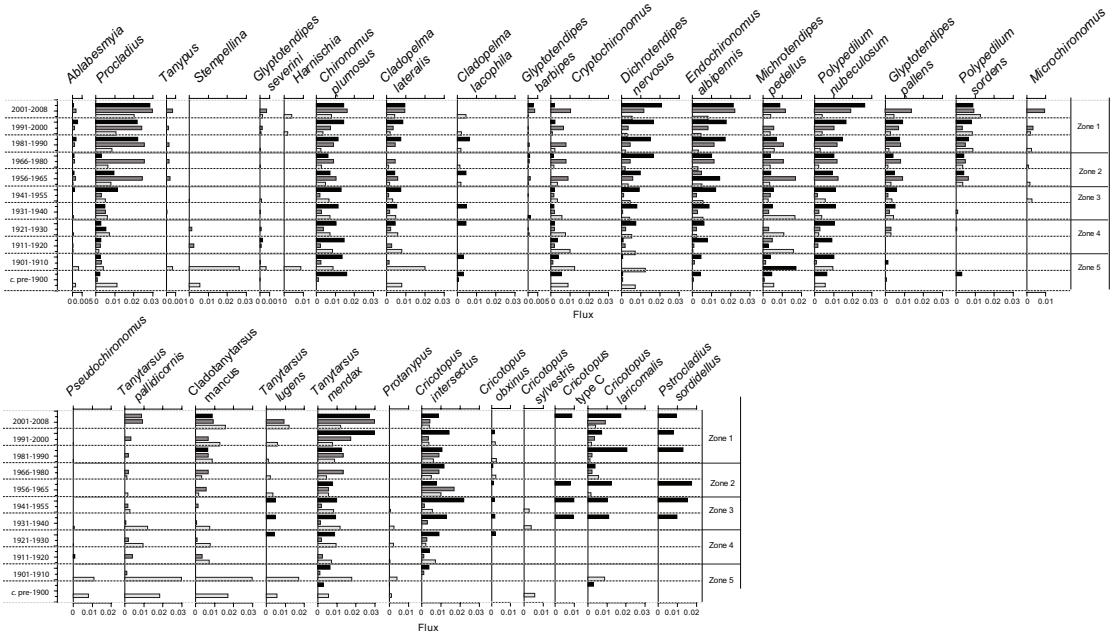
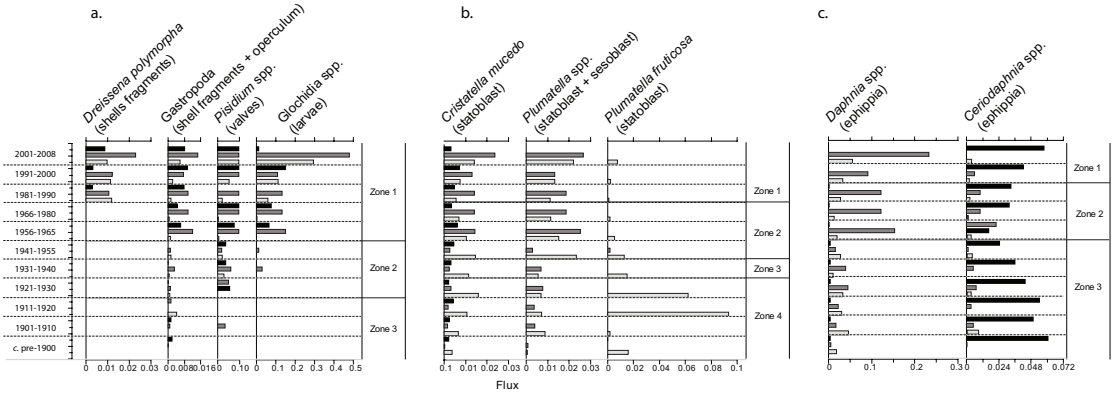
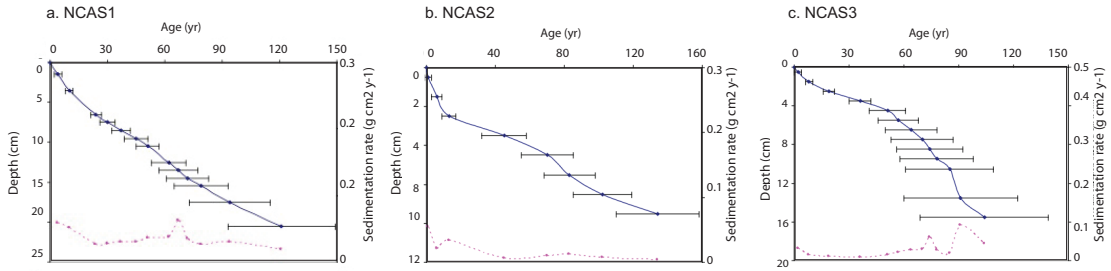

Ablabesmyia
Procladius
Tanypus
Stempellina
Glyptotendipes severini
Harnischia
Chironomus plumosus
Cladopelma lateralis
Cladopelma lacophila
Glyptotendipes barbipes
Cryptochironomus
Dichrotendipes nervosus
Endochironomus albipennis
Michrotendipes pedellus
Polypedilum nubeculosum
Glyptotendipes pallens
Polypedilum scrdens
Microchironomus
Pseudochironomus
Tanytarsus pallidicornis
Cladotanytarsus mancus
Tanytarsus lugens
Tanytarsus mendax
Protanypus
Cricotopus intersectus
Cricotopus obximus
Cricotopus sylvestris
Cricotopus type C
Cricotopus laricomalis
Pstrocladius sordidellus
2001-2008
1991-2000
1981-1990
1966-1980
1956-1965
1941-1955
1931-1940
1921-1930
1911-1920
1901-1910
c. pre-1900
Zone 1
Zone 2
Zone 3
Zone 4
Zone 5
Flux

Fig. 6

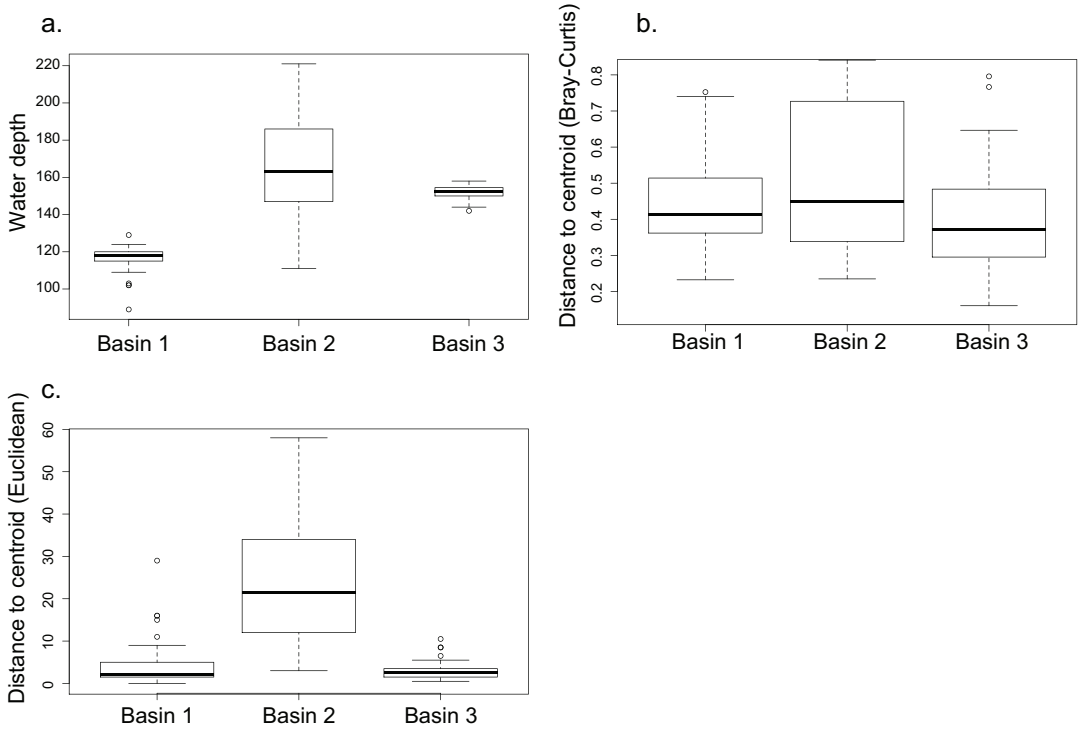

a.
b.
c.
Dreissena polymorpha (shells fragments)
Gastropoda (shell fragments + operculum)
Pisidium spp. (valves)
Glochidia spp. (larvae)
Cristatella mucedo (statoblast)
Plumatella spp. (statoblast + sessoblast)
Plumatella fruticosa (statoblast)
Daphnia spp. (ephippia)
Ceriodaphnia spp. (ephippia)
2001-2008
1991-2000
1981-1990
1966-1980
1956-1965
1941-1955
1931-1940
1921-1930
1911-1920
1901-1910
c. pre-1900
Zone 1
Zone 2
Zone 3
Zone 4
Flux

911 **ESM1**



912

913 **ESM2**



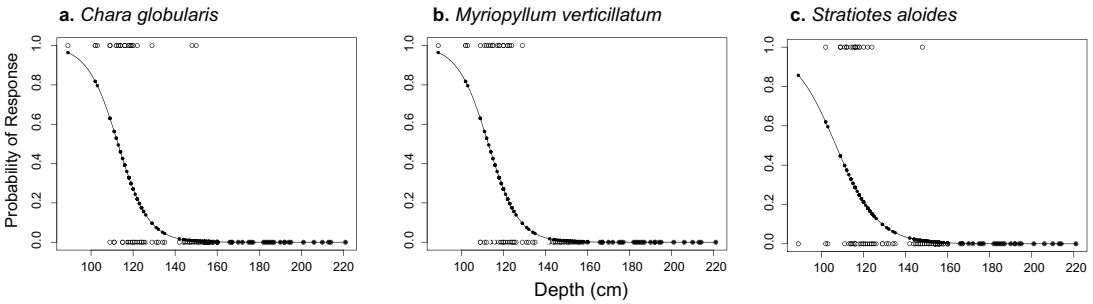
914

915

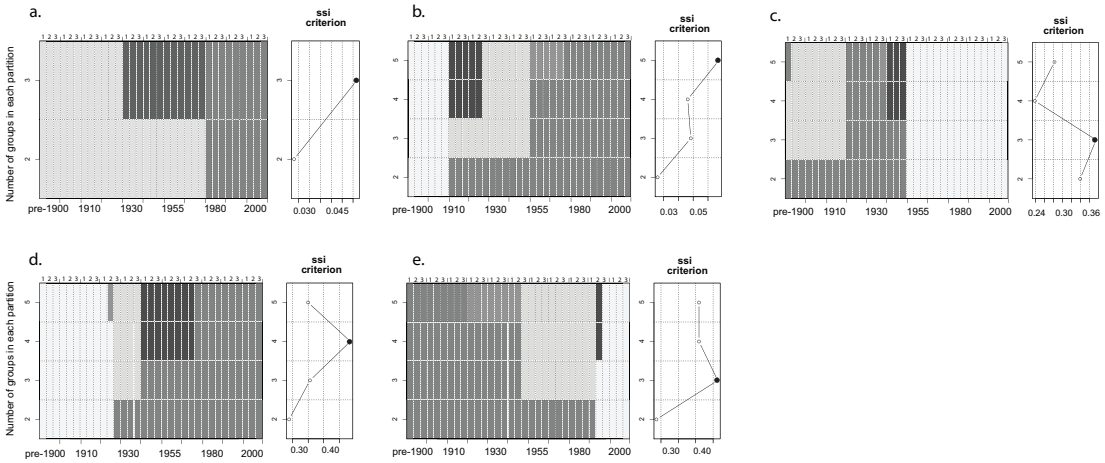
916

917

ESM3


a. Chara globularis
b. Myriopyllum verticillatum
c. Stratiotes aloides
Probability of Response
Depth (cm)

ESM4


a.
b.
c.
d.
e.
ssi criterion
Number of groups in each partition
pre-1900
1910
1930
1955
1980
2000