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

--Manuscript Draft--

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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.
Suggested Reviewers:	Bent Vad Odgaard, PhD. Professor, Aarhus Universitet bvo@geo.au.dk Professor Odgaard is a leading scientist in macrofossils and environmental change
	Hillary H. Birks, PhD. Professor, Universitetet i Bergen Hilary.Birks@uib.no Professor Birks is a leading scientist in the application of plant macrofossils to investigate the effects of environmental change on temperate ecosystems
Response to Reviewers:	We are pleased to submit our revised manuscript entitled “Eutrophication erodes inter-basin variation in macrophytes and co-occurring invertebrates in a shallow lake: Combining ecology and paleoecology”. We have gone through both Reviewer’s and Guest Editor´s comments with care and have made nearly all the suggested revisions (detailed responses below). We are confident that these helpful reviews have enabled us to improve our manuscript without changing the conclusions of our work. We thank you, the Guest Editor (Dr. Thomas J. Whitmore) and our two Reviewers for taking the time to help us to improve our manuscript. If you have any questions please do not hesitate to contact me Sincerely, Jorge Salgado, PhD. General comment: We have edited our manuscript to address most of the Reviewers’ and the Editor’s concerns. One point that was raised by both Reviewers and the Editor was that it was hard to follow the temporal reconstruction of eutrophication and water depth effects between basins. Thus, we have included a new analysis (Indval) to identify characteristic species at each selected time interval and basin, and have created a new summary Table (Table 2), which includes the selected species ecology in relation to water depth, eutrophication and macrophyte cover. We hope this makes things clearer. Reviewer #1: Reviewer: This paper attempts to address the dynamics of changes in macrophyte assemblage from three distinct basins of Castle Lough, a shallow well-connected water body in 24 Northern Ireland, UK, by using the paleolimnological method to restore the historical changes of macrophyte assemblage and environmental factors such as water depth and nutrient loading. It is an interesting topic and the authors provide the potential to extend the ecological change record and dynamics analysis. I agree with the opinion of which the macrophyte distribution in space can help to explain the temporal change. But I have a concern that the three basins have so much similarity and the spatial heterogeneity is not large enough to explain the historical changes (as the first three or four dominant macrophyte species are same in three basins in Fig. 2), while the environmental conditions are not different significantly, which will result in the homogeneity in macrophyte spatial distribution and abundance. Response: The reviewer has not appreciated that our results and analyses have clearly identified a significant separation between basins in both macrophyte assemblages (variation in composition and relative abundance- PerManova analysis and HMD respectively) and water depth profiles (PerManova analysis, including differences in heterogeneity in water depths- HMD) (Figs. 2, ESM 2). Furthermore, our

study uniquely demonstrates that heterogeneity between basins is not only determined by differences in species composition but also by variation in relative abundances between basins.
On a temporal scale, the separation between basins was further supported by NMDS plots of the palaeo-data (Figure 3), which similarly showed that over the last two centuries, macrophyte communities at basin 1 have differed from the other two basins. Temporal patterns in distributions of daphnid ephippia and selected chironomid taxa support further the idea that the basins have retained similar depth profiles over time (Discussion section, Lines: 410-421).
This collective evidence demonstrates that environmental conditions linked to water depth variation between basins have been sufficiently large over time to explain the current spatial patterns in macrophyte communities. The parallel changes in macrophyte assemblages between basins and the observed convergence to similar associations over time in ordinational space (Fig. 3) suggest however that other environmental conditions have changed over time and all the multiproxy evidence points towards a strong effect of eutrophication (Discussion section, Lines: 422-443).

Reviewer: I believe the water level is an important factor regulating the macrophyte assemblage, composition and abundance, but there are other factors which would affect the macrophyte assemblage, such as the sediment, wind fetch and intensity, solid suspension, ammonia nitrogen, etc. How much degree of these factors influence on the macrophyte assemblage?
Response: In the discussion we address the potential co-influence of other factors besides water depth, like exposure and sediment characteristics (Lines: 368-389). We have also added a new paragraph at the end of this section (lines 400-407 that outlines more generally the issue of identifying drivers of assemblage change.

Reviewer: In addition, the macrophyte-reminds in the sediment, the flux or abundance index, how much accuracy it can explain the historical changes of macrophyte assemblage?
Response: There is a supportive literature showing a good accuracy of plant macrofossils explaining contemporary and historical changes including Zhao et al. 2006; Davidson et al. 2005; Salgado et al. 2010; Madgewick et al. 2012; Clarke et al. 2016; Lhevi et al. 2016. For clarification, we have included a new paragraph in the discussion section addressing this issues (Lines: 489-507).

Reviewer: Finally, the environmental driving factors, water depth and trophic level should be rebuilt since pre-1900 and clearly showed in the paper. The linkage between the macrophyte assemblage changes and environmental condition changes was not tightly and clearly demonstrated in the text.
Response: Lines 410-460 in discussion are dedicated to demonstrate these changes. To clarify the patterns we have produced a new summary Table (Table 2) derived from a new analysis (Indval) to identify characteristic species at each selected time interval and basin. The table includes the selected species ecology in relation to water depth, eutrophication and associations with macrophytes over three time periods.

Reviewer #2:

Reviewer: Comments on Salgado et al: Putting space into time: long-term shifts in the importance of water depth and eutrophication in structuring lake assemblages

This is an excellent paper taking forward the study of variation within a lake controlled largely by water depth and how the ecosystems within a lake have responded to eutrophication processes. Castle Lake is rather special in having three distinct basins. Perhaps a commentary on what happened over time in each basin would be useful, as the communities are different. These data are present in the paper, but are hard to isolate.
Response: Lines 423-502 in discussion are dedicated to demonstrate these changes and as outlined in our above response to Reviewer 1, we have now included our new summary Table 2 to clarify these changes.

Reviewer: Studies on simple lakes have shown how macrophyte distributions vary with water depth and with position in a lake. Surface-mud samples have shown how

	macrofossil remains reflect these different communities. However, there is not much historical or palaeo-evidence to indicate how these separate communities originated within a lake and how they have responded to an overall driver such as nutrient enrichment. Here is the next challenge for these authors. Response: This is basically what we are addressing in this paper so we do not know how to address this comment. Perhaps the reviewer is simply stating that this is an important area for research. Reviewer: Title: I do not think 'Putting space into time' is very useful. It does not actually mean anything. Perhaps you could use something like - 'Tracking time in space' Response: We thank the reviewer for highlighting this issue. We have now changed the title to: “Eutrophication erodes inter-basin variation in macrophytes and co-occurring invertebrates in a shallow lake: Combining ecology and palaeoecology” We have made several changes in the document, which might have affected these specific changes and line numbers might not correspond anymore. We tried however to address most comments. Abstract Line 19: Aquatic biodiversity commonly increases with environmental variation ….. Done- Line 23 Line 20: replace 'influences' by 'factors' and 'impact' with 'influence' We changed most of the abstract structure so it does not apply anymore Line 24: We surveyed assemblages to provide contemporary data on macrophyte distributions and abundances and acquired palaeoecological data …… We changed most of the abstract structure so it does not apply anymore Line 32: after 'all groups' insert 'in recent decades' We changed most of the abstract structure so it does not apply anymore Line 34: replace 'positive effects' with 'driving influence' We changed most of the abstract structure so it does not pertain anymore Introduction Line 52: 'beavers' is not a good example; they have never occurred in Ireland in the Holocene. How about otters? We eliminated the sentences to avoid any problem with specific taxa (Lines: 51-55) Line 53: Such within-lake variation 'influences' spatial … Done-line 57 Line 79: after 'basins' add 'in a lake' We edit the whole paragraph so it does not apply anymore Palaeolimnological analyses Line 124: you actually retrieved cores from the mid-points of the areas sampled for macrophytes (Fig. 1) Amended- Lines 125-127 Line 140: delete ',' after 'included' Done Line 141: after 'seeds' add 'and fruits' Done-Line 143 Line 146: Move the sentence starting with 'Macrofossils ..' up to line 141, after Isoetes megaspores. Then all the methods relating to macrophytes are together. Response: Given that we selected macrofossils of different biological groups at the same time, we believed that it is better to have them all together as it is in the original manuscript.

Line 153: what about 1951-1965? Why is this decade missing? On the diagrams in Figures 4-6 and Suppl figure S5 this period is covered as 1941-1955 and 1956-1965. Please can you explain this?
Response: This has been clarified with a new sentence in the method section (lines: 134-137). “Exceptions were two 15-year intervals (1940-1955 and 1965-1980) due to differential sedimentation rates (see results) between cores.”

Line 158: you coded something with a presence of 1 as 0. But it was present! So this is a misrepresentation of the data. I think you should use 1 or perhaps better, '+'.
Response: This concern pertains to the way we average the missing time period data (due to slower sedimentation rates) in NCAS2 core to establish decadal comparisons amongst the cores (Lines 154-161). We took a parsimonious approach and in the particular case were adjacent samples were 1 and 0 prefer to coded them as 0. We believed that this is not a misinterpretation of the data as we really don´t know if it´s present, given that in the older sample is absent. Thus, we prefer to be cautious and not coding something present when there was not really evidence for that.

Reviewer: Historical spatial patterns: I like this! Often the H's are close and travel to P's which are also close. Basin 1 seems to be rather distinct from the other two, suggesting that water-depth is still the major environmental factor here, whereas the other shallower two are influenced more by nutrient enrichment.
Response: Basin 1 seems to be rather distinct from the other two as it is the shallowest of the three and the paleo-data suggest that his has been a common feature over the last two centuries. Thus, we believe that water depth is still a major environmental factor. Nonetheless, our paleo-data also shows that some biological changes attributed to eutrophication occurred early at basin 1 (e.g. the expansion of Myriophyllum) suggesting that all three basins have been influenced by nutrients over time (see Discussion section, Lines 469-480).

Line 335: replace Fig. 6a with 6b
Amended

Discussion
Line 368: Add 'Fig. 2a' after '1970)'. Next sentence was rather unclear to me. Perhaps you mean Widespread cover by the water lily Nuphar lutea provides dense shade which reduces the abundances of more light-sensitive ….. Although N. lutea is abundant in your plots, its seeds are very rare (characteristic of N. lutea). You should mention that it is represented more realistically by the trichosclereid record, although this also includes Nymphaea alba (whose seeds are not quite so rare). Curiously, although its seeds are more common than N. lutea, N. alba does not seem to be recorded from the present vegetation (Fig 2a). Did you include its leaves with N. lutea?
Response: We have amended the sentence and also have highlighted that was mostly represented by sclereids. Lines 373-377

Line 392: replace 'in' with 'at'
Done
Line 394: replace 'likely' with 'probably'
Done
Line 500: include Zhao et al. in the references
Done
Line 507: you should consider the essay by Birks HJB (2014), Vegetation History and Archaeobotany 23: 309-330
Response: This reference has been included in Line: 402

Conclusions
Line 525 onward: This conclusion is based on previous studies of eutrophic lakes
Response: We have amended the whole conclusion section so probably does not pertain any more but still pur conclusion is based on our own results

Line 529: What do you mean by 'good condition'? This is an anthropogenic value judgement! Please clarify (e.g. it is mesotrophic with a high diversity of taxa)
Amended- Line 550-551

	Line 531: rewrite: … that the lake ecosystem is responding to increasing eutrophication and a homogenous assemblage … Amended What is causing eutrophication of Castle Lake at present? Are and how are these factors predicted to increase in intensity in the future? How long do you think it will take for the ecosystems to become homogenous, given the known stressors and rates of change? Is there a conservation priority here? Some taxa are already extinct in parts of the lake (e.g. Najas flexilis) - others may follow? Response: We have included a new paragraph in lines: 550-558 Line 534: replace 'illustrates' with 'adds to'. There are several other studies of eutrophication processes already. Amended Line 539: after 'impacts that' add 'affect the ecosystems in the individual basins at first, depending on their susceptibility to nutrient input. If the nutrient inputs continue, it is likely that the assemblages will become homogenous over the whole lake (see Donohue et al. 2009).' Response: We have included a new paragraph in lines: 550-558 Figure 1 a. Distances are usually given in km. The text is too small to read even with a magnifying glass! c. - a distance scale is needed. The key should be labelled as 'water depth' Amended Editor comments: 1.Line 105: the possessive apostrophe can be removed from “1950’s” Amended 2. Line 115: Percent volume “infestation” is a term that has been used in some contexts, and although I studied and worked for a time with Canfield, I have much trouble with that term and would like to suggest an alternative. Infestation is an older management term that implies that all aquatic plants are problematic (Canfield formerly worked at the “Center for Aquatic Weeds” at University of Florida) and indeed many of the people associated with Canfield are plant-management chemical applicators. For an ecological perspective, as in the present study, perhaps it might be preferable to paraphrase your statement, such as “using the method of Canfield et al. (1984) to determine the percent of lake volume filled by macrophytes,” and to avoid “infestation” or the usual acronym. (Sometimes I’ve described it as percent volume infilled.) In most instances, the space saved by an acronym is minimal in a publication, and writing things out makes it clearer for all readers. In this case, "infestation" and the acronym have unfortunate connotations that are not very ecologically oriented. Amended in lines: 117-123 3. For appendices presented as Electronic Supplementary Material, please use an ESM numbering sequence, such as ESM1, ESM2, etc. rather than indicating the type of material and an S designation Amended 4. Table 1 and in the text: if the intention is to demonstrate strength of relationships, wouldn’t correlation coefficients [r] be more appropriate than coefficients of determination [r2]? R values demonstrate the strength of a relationship between variables, but r2 values are used when the intention is to construct a predictive model and show the proportion of variation in the dependent variable explained by an independent variable, as you know and state elsewhere in the text. Perhaps I am missing a point here. Response: We agree with the editor´s concern but the original aim of the tests on space-time interactions developed by Legenedre et al. (2010) was indeed to construct a predictive model to show how much of the variation was explained by these two

	independent variables. Thus results are presented on R2 values. We similarly wanted to go further than just a demonstration of the strength of relationship between variables. 5. Figure 1 legend: please remove “see Methods for details”, as the journal tends to discourage internal pointers Amended 6. Line 149: please remove “e.g.” from all citations for journal format needs Amended 7. Line 267-268: in this wording, you are explaining the proportion of variation based on GLM: should this read R2adj rather than Radj? Amended 8. Reviewer 1 makes a good point about similarity of the basins, homogeneity, and the potential to minimize “other factors which would affect the macrophyte assemblage, such as the sediment, wind fetch and intensity, solid suspension, ammonia nitrogen, etc.”. One useful thing that I did learn from Canfield pertained to “scale of analysis”, which relates to the fact that a wide range of studies about relationships between macrophytes and environmental variables will demonstrate a wide range of conclusions about what the important factors are that most influence macrophyte communities. It might be helpful to address the reviewer’s concern by mentioning that conclusions about important factors that influence macrophyte communities are often determined by the experimental design and local conditions, that is, when all other factors tend to be homogeneous, the factors that vary will assume apparent importance in explaining community differences. Readers might otherwise generalize to conclude that the important factors in one situation will prove most important in all other contexts. Response: In the discussion we address the potential co-influence of other factors besides water depth, like exposure and sediment characteristics (Lines: 368-389). We have also added a new paragraph at the end of this section (lines 400-407 that outlines more generally the issue of identifying drivers of assemblage change. Perhaps Reviewer 2 expresses similar concerns with this statement, but I must admit that the meaning is not entirely clear to me: “Studies on simple lakes have shown how macrophyte distributions vary with water depth and with position in a lake. Surface-mud samples have shown how macrofossil remains reflect these different communities. However, there is not much historical or palaeo-evidence to indicate how these separate communities originated within a lake and how they have responded to an overall driver such as nutrient enrichment. Here is the next challenge for these authors.” Response: As we have indicated, we are also not entirely sure with this concern as it basically what we are trying to show. 9. Regarding Reviewer 1’s second principal concern about “In addition, the macrophyte-reminds [sic] in the sediment, the flux or abundance index, how much accuracy it can explain the historical changes of macrophyte assemblage?” I think that can be addressed by describing findings from other studies by the authors. I note, for example, that Reviewer 2 recommends “include Zhao et al. in the references”. Amended 10. Reviewer 1’s concern “Finally, the environmental driving factors, water depth and trophic level should be rebuilt since pre-1900 and clearly showed in the paper” appears to be a helpful suggestion for a summary figure. Reviewer 2, as well, notes “Perhaps a commentary on what happened over time in each basin would be useful, as the communities are different. These data are present in the paper, but are hard to isolate.” Response: Lines 411-461 in discussion are dedicated to demonstrate these changes. And, as pointed out above, we have provided a new summary table (Table 2) deriving from a new analysis (Indval) to identify characteristic species at each selected time interval and basin. The Table includes the selected species’ ecologies in relation to water depth, eutrophication and associations with macrophytes over three time periods.

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

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Keywords: Anthropogenic impact; Community heterogeneity; Historical dynamics; Light limitation; Lough Erne System; Multi-proxy study;

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 in-filling 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

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

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

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

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

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

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

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

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

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

Historical spatial patterns

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

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

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

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

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

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

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

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

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

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

Drivers of temporal changes in community assembly

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

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

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

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

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

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

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

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

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

Implications for long-term changes in ecological processes

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

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

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

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Tables

Table 1. Effects of space, time and their interaction (S-T) on the abundances of macrophytes, chironomids, molluscs, bryozoans and daphnid in three sediment cores 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

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

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 1996; 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**

Figure legends

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

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

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

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

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

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

Electronic supplemental material (ESM)

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

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

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

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

Figure 1

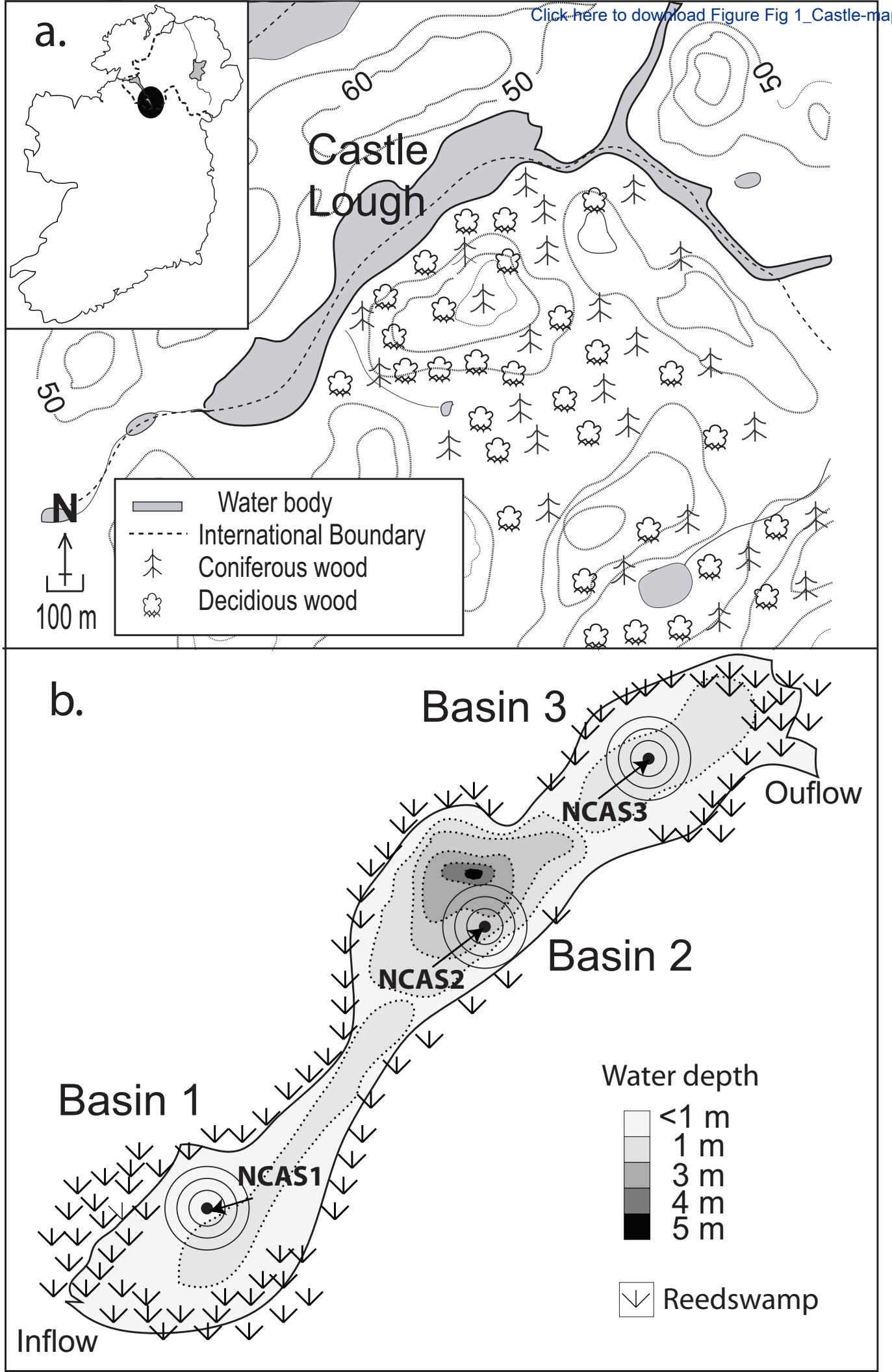

Figure 2

Click here to download Figure Fig.2_FA_vs-Depth.eps

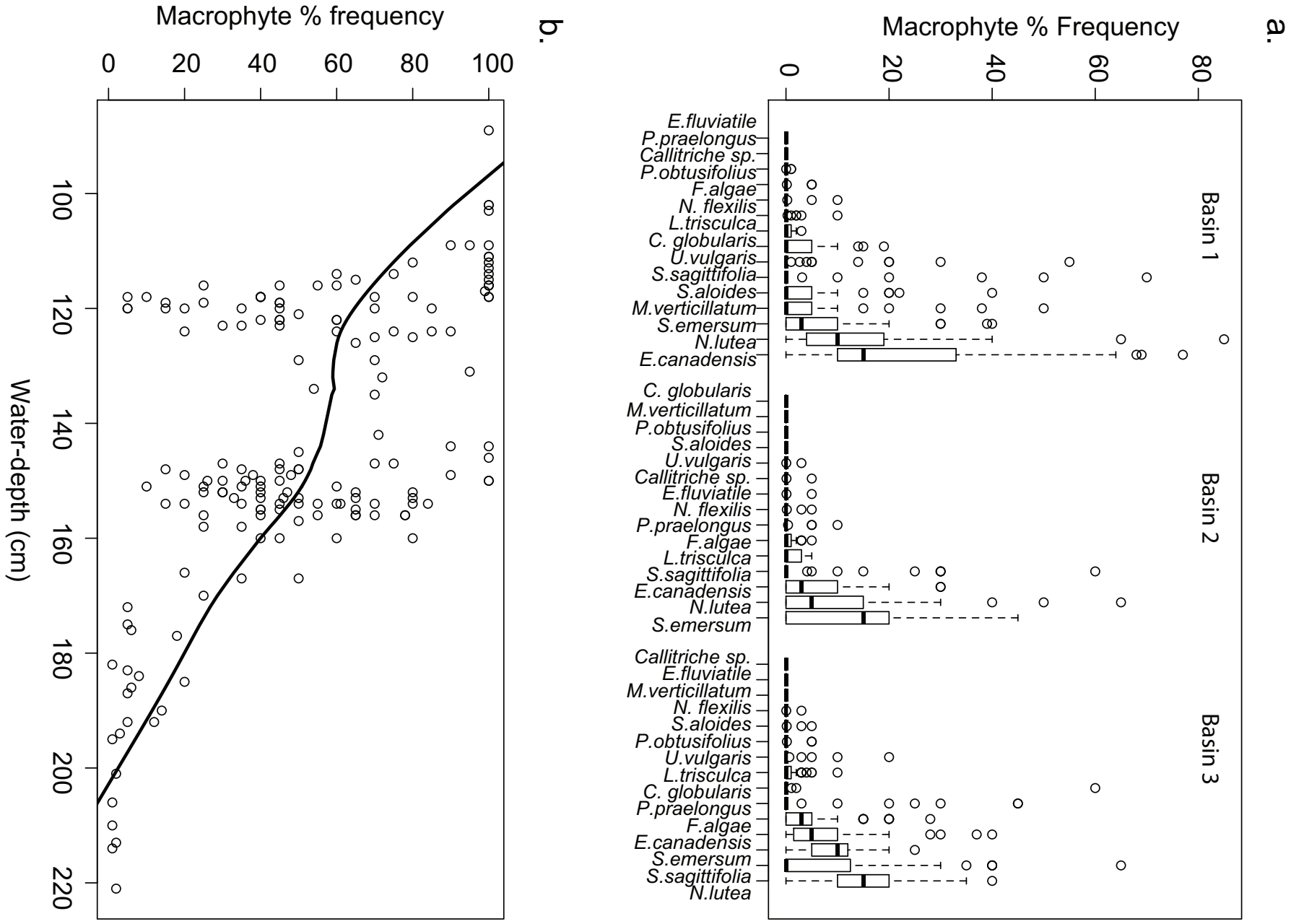

Figure 3

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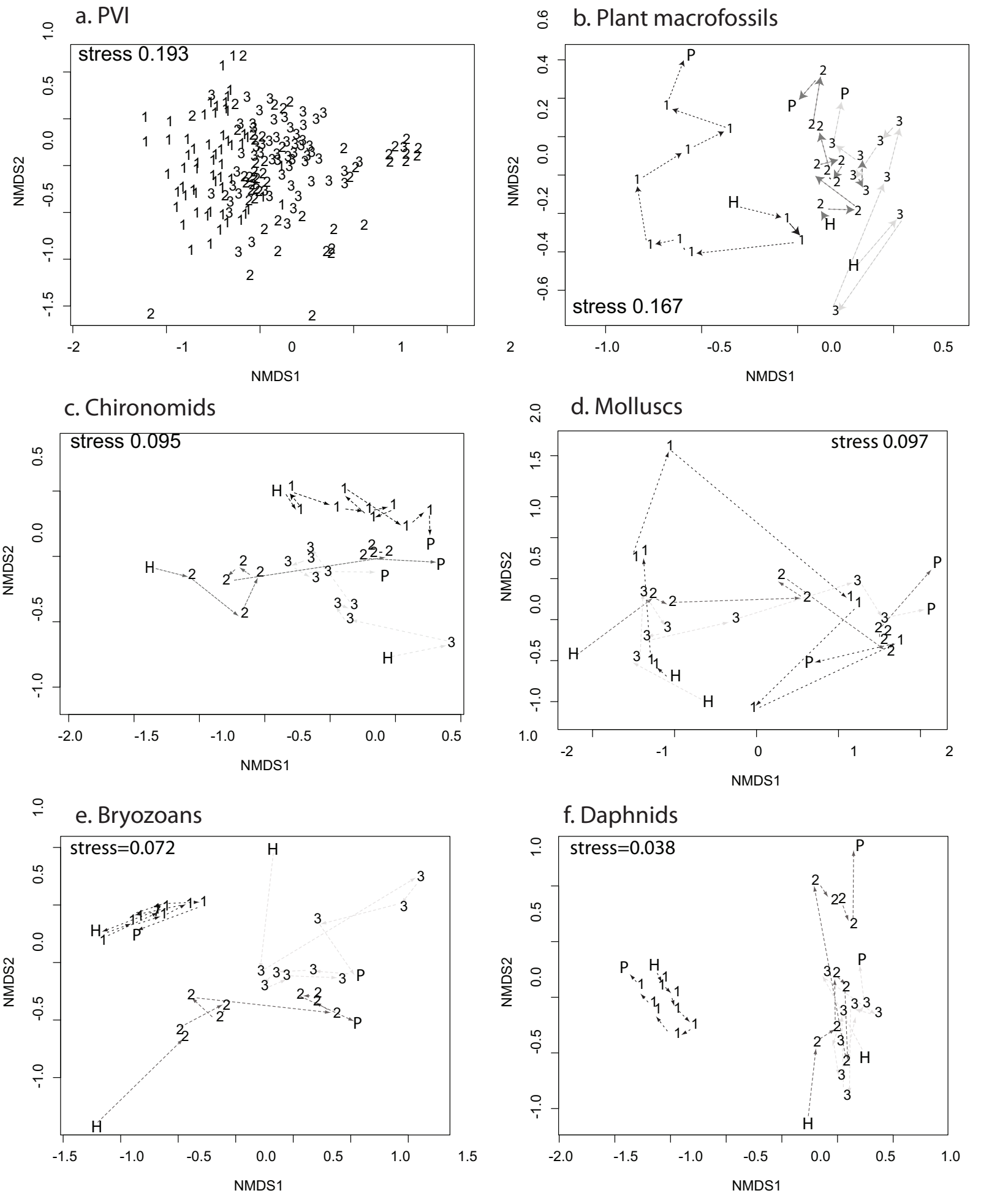

Figure 4

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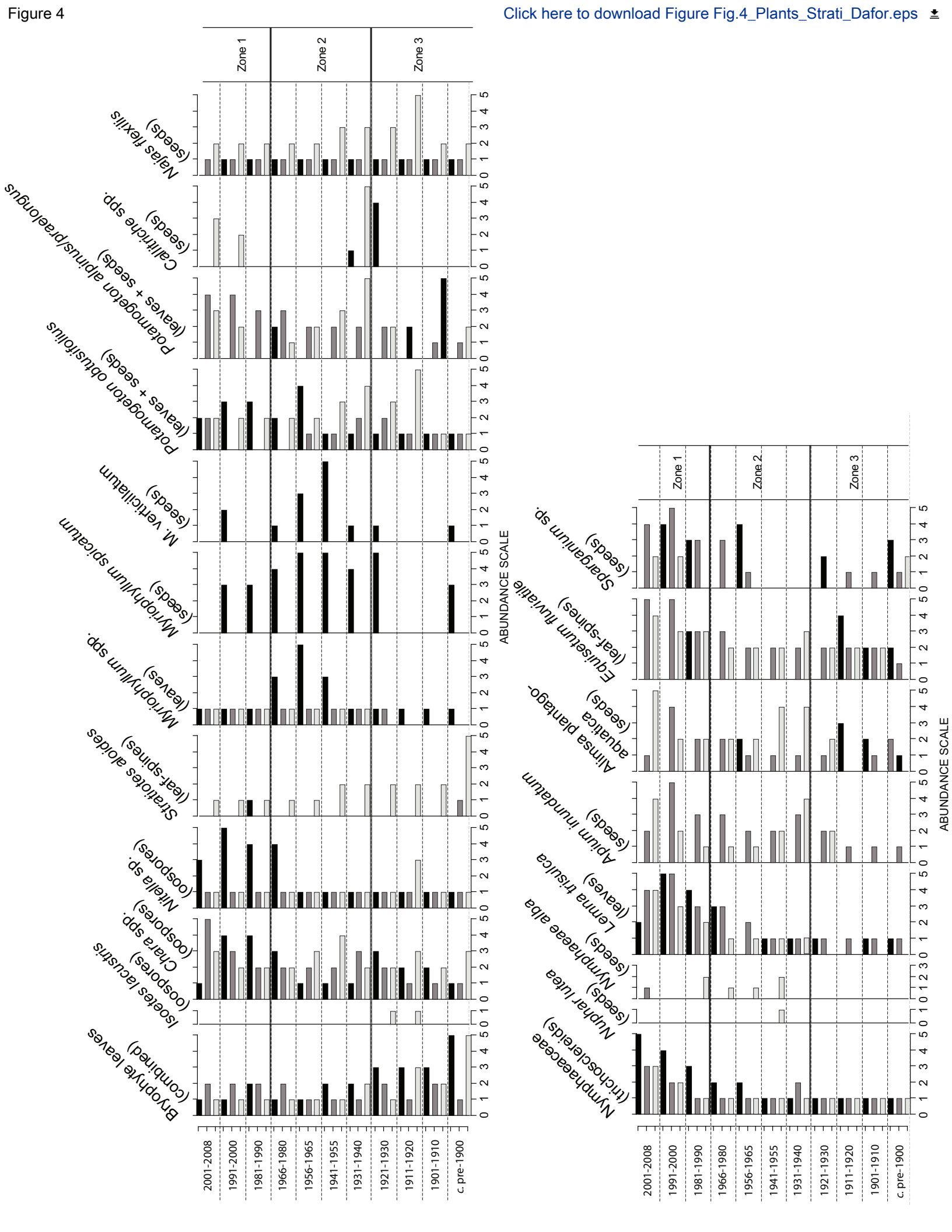

Figure 5

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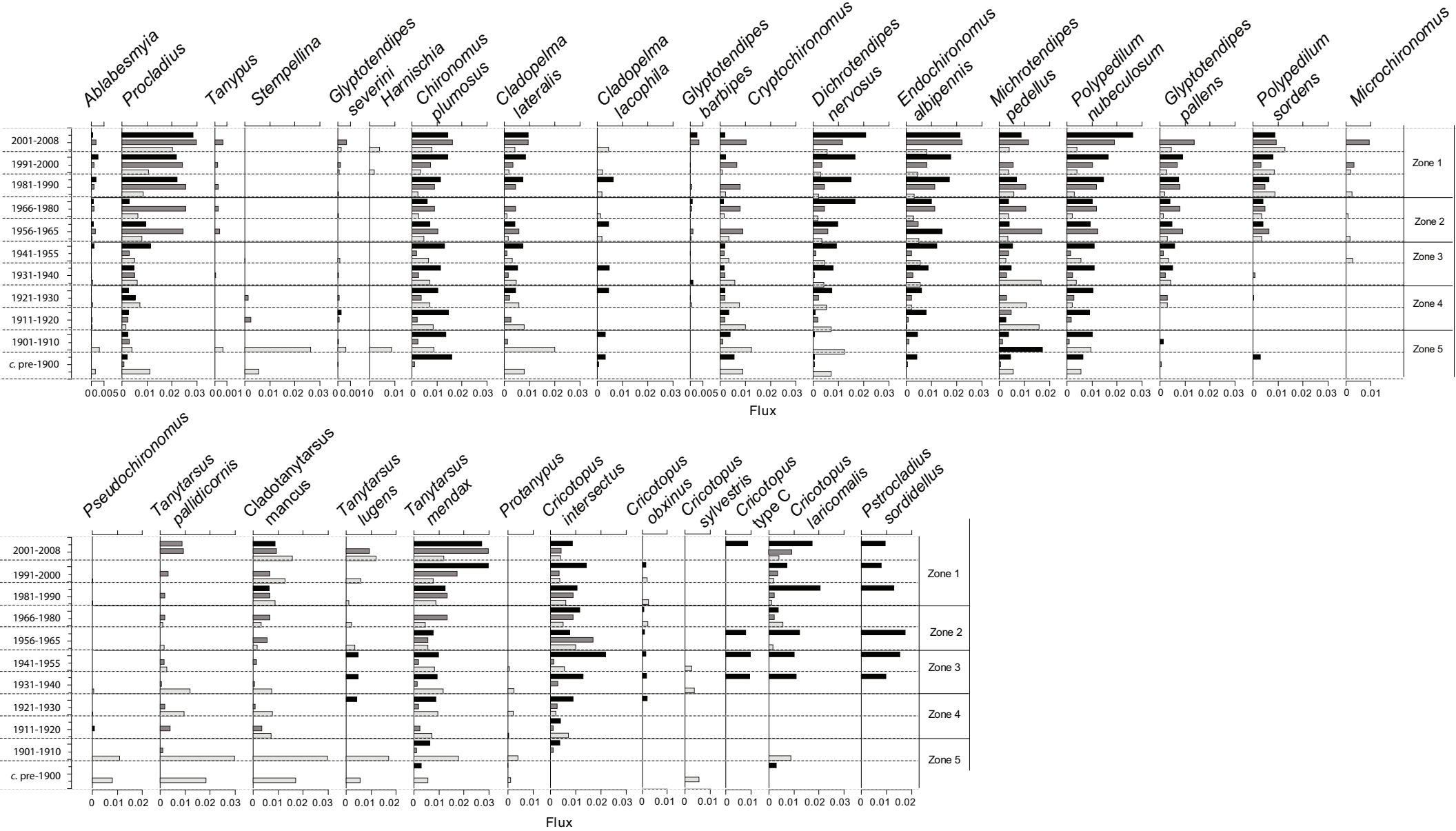

Figure 6

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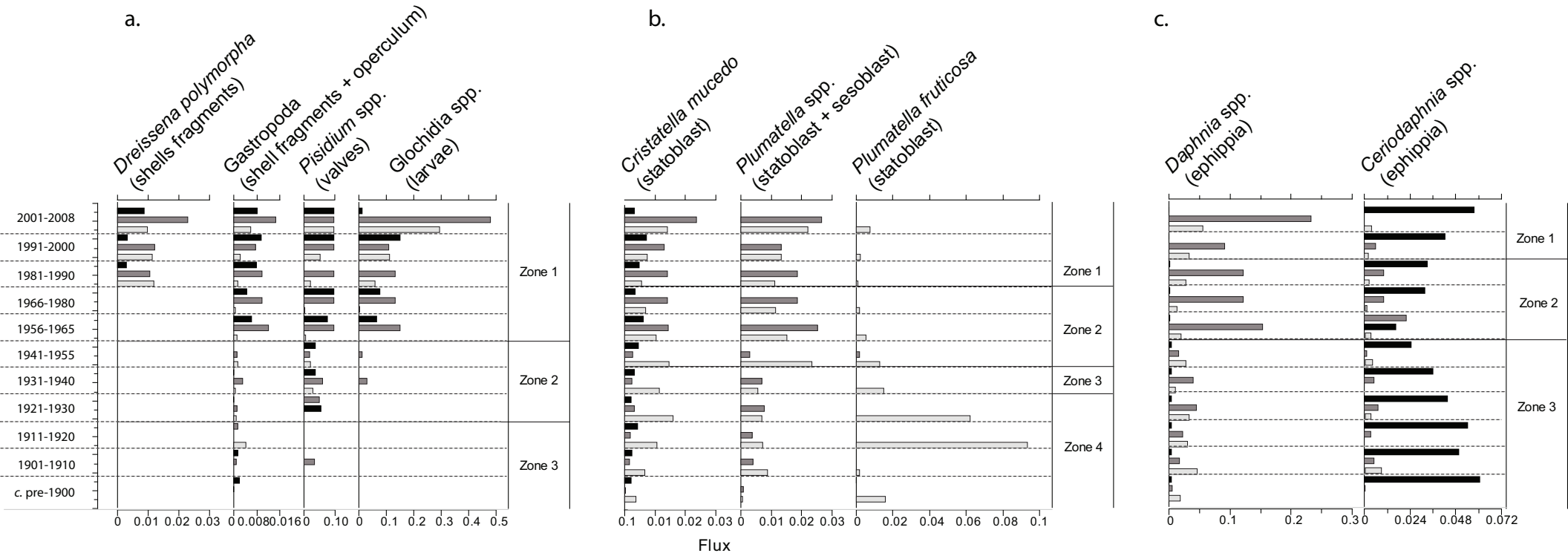

Figure ESM1

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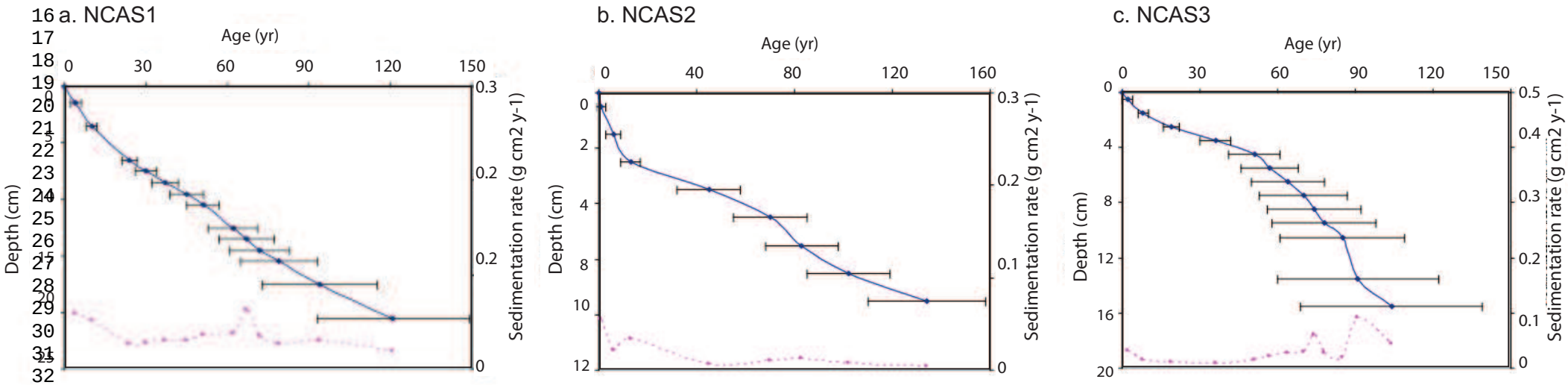

Figure ESM2

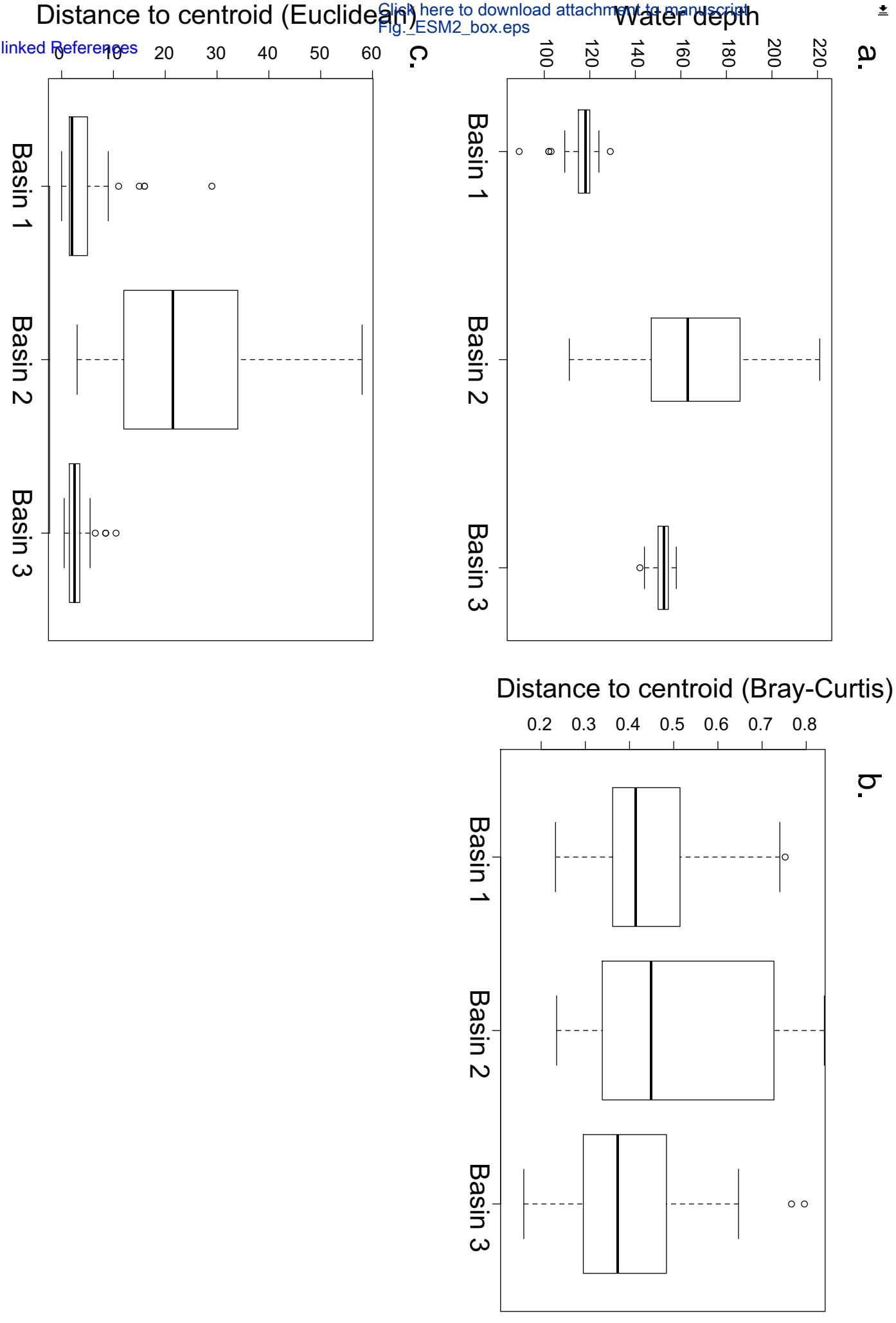

Figure ESM3

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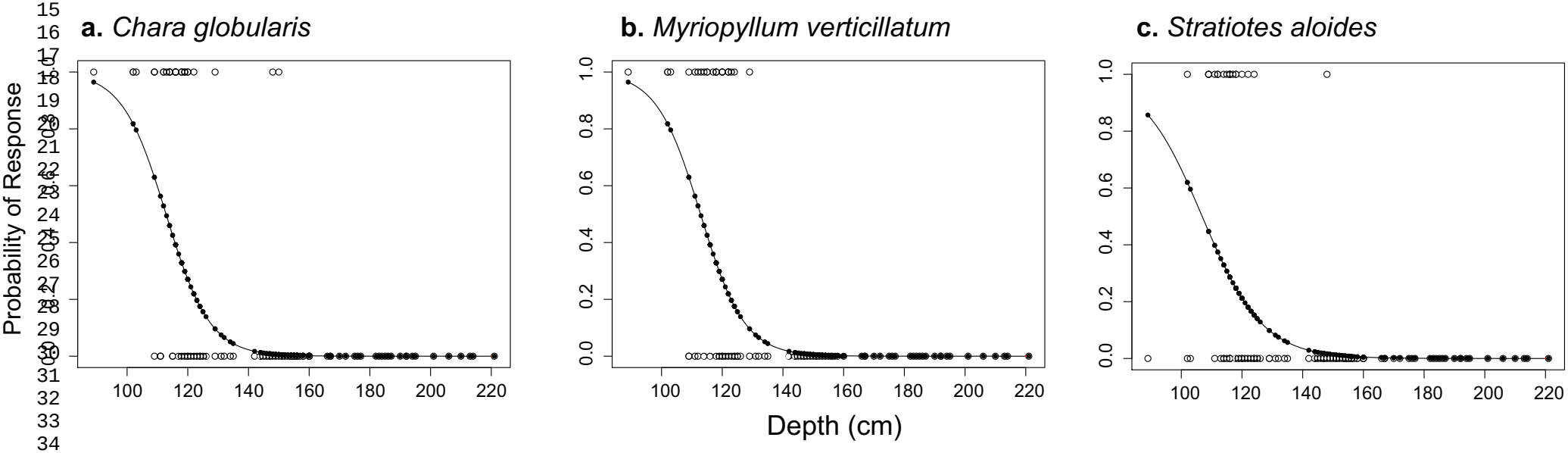

Figure ESM4

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