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Water-level fluctuations regulate the structure and functioning of natural lakes

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SUMMARY

1. Despite becoming one of the main pressures on aquatic ecosystems globally, understanding of the ecological impacts of altered water-level regimes in lakes lags far behind that of other human disturbances (e.g. eutrophication, acidification).
2. We employed a multifaceted approach to explore the potential importance of water-level fluctuations (WLF) for the structure and functioning of littoral zones and multiple trait responses of primary producers and benthic consumers across a range of natural lakes.
3. We found that lakes with high WLF had significantly more coarse littoral substrata with less coverage of macrophyte vegetation in the shallows than in lakes with low WLF. Lakes with high WLF also had greater proportions of motile diatom species and omnivorous benthic invertebrates in shallow waters, altered taxonomic and trophic structure of benthic consumers and more homogeneous algal and benthic invertebrate assemblages.
4. Variation along the littoral depth gradient needs to be examined when assessing the impacts of hydrological pressures in lakes. We found that depth interacted with WLF in its effects on habitat structure and mediated the response of both producer and consumer benthic assemblages to WLF.
5. Our results indicate that amplified WLF significantly affect both the structure and functioning of lake ecosystems. Given the growing importance of WLF as an increasingly pervasive pressure on lake ecosystems worldwide, our findings have important implications for the conservation and management of global aquatic biodiversity. Inclusion of both biological traits and sampling along a depth gradient in existing and in future monitoring programmes could improve significantly the ability to detect and predict effects of altered patterns of WLF on lake ecosystems.

Keywords: benthic, ecosystem functioning, habitat structure, hydrological disturbance, littoral

Introduction

Hydromorphological pressures are becoming one of the main threats to the ecological integrity of lake ecosystems globally (Bragg *et al*., 2003; Solimini *et al*., 2006; Wantzen *et al*., 2008b; Cardinale, 2011). Most lakes are subject to natural, mostly seasonal, fluctuations in water levels (Smith, Maitland & Pennock, 1987; Keough *et al*., 1999; White *et al*., 2008, Evtimova, 2013), and natural water-level variations may support the biodiversity and productivity of littoral zones (Gafny & Gasith, 1999; Coops & Hosper, 2002). However, alteration of natural patterns of WLF can compromise not only the ecological integrity of lakes (Wantzen *et al*., 2008b; Zohary & Ostrovsky, 2011; Deegan, White & Ganf, 2012; Yin & Yang, 2012), but also the provision of ecosystem goods and services and the sustainable use and management of standing water bodies in the face of a multitude of adverse human impacts (Johnson, Revenga & Echeverria, 2001; Coops, Beklioglu & Crisman, 2003; Schmieder *et al*., 2004; Beklioglu, 2007; Wantzen *et al*., 2008b; Palmer, 2010). This is because the ecological effects of WLF in lakes are likely to be greatest in littoral zones (Solimini *et al*., 2006; Wantzen *et al*., 2008b), where even

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small draw-downs can result in the conversion of large areas of standing water to air-exposed habitats and *vice versa* (Palomäki, 1994; Leira & Cantonati, 2008). Furthermore, littoral zones support the significant majority of biological diversity in lakes (Wetzel, 2001; O'Sullivan & Reynolds, 2004; Stendera & Johnson, 2008; Vadeboncoeur, Mcintyre & Zanden, 2011) and provide important feeding and breeding habitat (Sabo, Finlay & Post, 2009; Hampton *et al.*, 2011). Thus, impairing lake littoral zones could cause significant alterations to lake ecosystems, with consequences for associated terrestrial areas (Vander Zanden & Vadeboncoeur, 2002; Wesner, 2011; Yin & Yang, 2012).

Despite the growing significance of altered WLF as a global pressure on lakes, relatively little is known about the importance of different water-level regimes for the structure and ecological functioning of littoral zones. Many studies of water-level fluctuations comprise comparative studies of macrophytes (Rorslett, 1984; Furey, Nordin & Mazumder, 2004; Deegan *et al.*, 2012). This work has indicated that significant WLF may reduce the diversity and coverage of macrophytes (Rorslett, 1984, 1985; Valdovinos *et al.*, 2007), leading to reduced overall structural diversity of lake littorals (i.e. loss of habitats and food resources), increased erosion (Black, Barlow & Scholz, 2003; Valdovinos *et al.*, 2007), reduced organic matter availability and modified input of allochthonous matter from the riparian zone (Wantzen, Junk & Rothhaupt, 2008a). While previous studies have advanced understanding of the ecological role of water-level regimes of lakes, they are all limited in scope, as they are typically either single-lake studies or comparative studies of two water bodies with contrasting water-level regimes, or focus on single biotic groups and/or a particular assemblage trait.

Results of a recent experiment on artificial lakeshores in large outdoor mesocosms (Evtimova & Donohue, 2014) demonstrated that amplified WLF reduce benthic algal biomass and both the density and taxonomic distinctness of littoral benthic invertebrate assemblages. Furthermore, both the taxonomic and trophic structure of benthic assemblages was altered significantly in mesocosms with extreme WLF. Results of observational studies in lakes are largely consistent with these findings, indicating that significant WLF can reduce both the density and diversity of littoral benthic invertebrate assemblages (Hunt & Jones, 1972; Smith *et al.*, 1987; Jurkiewicz-Karnkowska, 1989; Prus, Prus & Bijok, 1999; Scheifhacken, Fiek & Rothhaupt, 2007; Valdovinos *et al.*, 2007; Aroviita & Hämäläinen, 2008; Baumgärtner, Mörtl & Rothhaupt, 2008; Brauns, Garcia & Pusch, 2008; White *et al.*, 2008, 2010; McEwen & Butler, 2010). Evtimova & Donohue (2014) also found that WLF can modify biotic assemblages in distinct ways along the littoral depth gradient. These findings have important implications for the ecology and biological diversity of standing water ecosystems but have yet to be tested at larger spatial scales in natural lakes.

Elucidating the ecological impacts of disturbance on lake littoral zones is frequently hindered by highly heterogeneous distributions of organisms, a consequence of high local-scale variability in a range of factors, including water chemistry, shore morphology, habitat structure and biotic interactions (Karjalainen *et al.*, 1999; Nystrom *et al.*, 2001; Tolonen *et al.*, 2001, 2005; Schindler & Scheuerell, 2002; Leppä, Hämäläinen & Karjalainen, 2003; Brauns *et al.*, 2007; Donohue *et al.*, 2009a). In order to be able to capture key aspects of functional diversity, we used simultaneously taxonomy- and trait-based metrics of biotic response, as opposed to considering species mostly individually. Given the spatially heterogeneous nature of littoral zones within and among lakes, trait-based approaches (e.g. dietary preferences, motility) have particularly strong potential for detecting the impacts of amplified WLF on lakes (Evtimova & Donohue, 2014) and for the ability to generalise findings across ecosystems (Cavender-Bares *et al.*, 2009; Hillebrand & Matthiessen, 2009; Menezes, Baird & Soares, 2010). Accordingly, we followed a multi-trait approach to examine abiotic and biotic differences between sets of natural lakes that have experienced contrasting amplitudes of WLF over long timescales (at least three decades). Specifically, we examined whether (i) littoral habitat structure differed in lakes with contrasting WLF and, if so, how; (ii) a variety of taxonomy- and trait-based aspects of littoral benthic communities may reflect differences in the hydrological regimes of natural lakes and (iii) the compositional and/or functional heterogeneity of biotic assemblages in space is reduced significantly in lakes with high WLF.

Methods

Lake selection

We quantified habitat structure and the structure of algal and macroinvertebrate assemblages along the littoral depth gradient in eight lakes representative of both ends of the spectrum of WLF in natural lakes in Ireland (Table 1; Fig. S1) as annual and monthly ranges were identified as important descriptors of water-level regimes (Evtimova, 2013). Four of the lakes had high

Table 1 Characteristics of the lakes selected for field surveys, with mean (± SD) annual (AR) and monthly (MR) ranges, pH, alkalinity and total phosphorus concentrations and the year in which the water level recording commenced

WLF Group	Lake	Location (N, W)	Mean AR (m)	Mean MR (m)	Records began	Surface area (ha)	pH	Alkalinity (mg $CaCO_3$ L^{-1})	TP (μg P L^{-1})
High WLF	Anure	55°00′12″ 8°16′24″	1.06 ± 0.17	0.52 ± 0.21	1976	133	6.8	12	37
	Eske	54°41′37″ 8°03′32″	1.04 ± 0.07	0.44 ± 0.16	1977	385	7.5	11	6
	Muckno	54°06′48″ 6°40′57″	1.43 ± 0.32	0.46 ± 0.27	1976	354	8	47	38
	Oughter	54°00′32″ 7°28′16″	2.72 ± 0.38	0.78 ± 0.45	1977	658	7.9	70	72
Low WLF	Ennell	53°27′54″ 7°22′46″	0.65 ± 0.17	0.15 ± 0.10	1979	1151	8.1	154	17
	Moher	53°43′42″ 9°32′53″	0.59 ± 0.19	0.21 ± 0.12	1977	36	7.3	16	11
	Owel	53°34′09″ 7°21′50″	0.58 ± 0.22	0.10 ± 0.06	1975	1018	8.3	96	10
	Skeagh	53°57′07″ 7°00′22″	0.65 ± 0.13	0.16 ± 0.09	1975	61	7.3	30	40

mean annual (>1 m) and monthly (≥0.44 m) amplitudes of WLF (high WLF) and the remaining four had relatively minor variations in water level (low WLF; mean annual ranges ≤0.65 m; mean monthly ranges ≤0.21 m; Table 1, Fig. S1). The lakes were selected for sampling based on the following criteria: (i) presence of active water-level recorders, (ii) availability of at least 30 years of continuous water-level data, (iii) good data quality with minimal number of missing daily water-level readings and (iv) adequate availability of appropriate and accessible sampling habitat. Sampling was confined to stony substrata as they are easy and relatively economical to sample and their communities are known to respond to human-induced pressure, including water-level regulation (Brauns *et al.*, 2007; Aroviita & Hämäläinen, 2008; Donohue *et al.*, 2009a; Tolonen & Hämäläinen, 2010; White *et al.* 2010). In addition, lakes with total phosphorus concentrations in excess of 100 μg L^{-1} or with alkalinity less than 10 mg $CaCO_3$ L^{-1} were excluded from the study. Apart from the *a priori* determined differences in the amplitudes of WLF, the selected lakes in both WLF groups exhibited similar ranges of physical and chemical characteristics (Table 1). There was no difference in overall water chemistry between the two WLF groups (MANOVA; $F_{1,24} = 1.17$, $P = 0.32$).

Field sampling and laboratory analyses

Lakes were sampled during an 8-week period between late May and July 2009, when WLF were relatively low (Evtimova, 2013), in order to avoid sampling flooded areas. Four straight-line transects were established in every lake, orientated perpendicular to the shoreline and extending to about 1 m water depth. Water samples were collected using a weighted 5 dm^3 polypropylene bottle thrown lakewards three times from the deepest end of each transect (Donohue & Irvine, 2008). Water column alkalinity (mg $CaCO_3$ L^{-1} after titration with sulphuric acid), pH, conductivity (using a microprocessor conductivity meter LF 196 WTW TetraCon® GmbH, Germany), total phosphorus [TP following Eisenreich, Bannerman & Armstrong (1975)], dissolved total organic carbon and total nitrogen [DTOC and TN, using a Vario TOC Cube, Elementar Analysensysteme GmbH (Hanau, Germany)] and chlorophyll *a* [quantified colorimetrically after methanol extraction (Standing Committee of Analysts, 1983)] were quantified from each site. All filtering was done immediately upon collection using 47-mm GF/C glass microfibre filter papers (Whatman®, Maidstone, UK).

Littoral habitat structure (inclusive of macrophyte cover), and benthic algae and invertebrate assemblages were quantified at three sampling sites (1 × 1 m) along each transect, with their mid-points being located at water depths of 0.1 m (shallow), 0.45 m (intermediate) and 0.8 m (deep site). We assessed habitat structure *in situ* by estimating the relative (%) coverage of each of sand/silt, gravel, pebbles, cobbles, boulders, bedrock, coarse woody debris (CWD), soil, flooded grass/roots, leaves/debris and macrophytes using a bathyscope and a 1 × 1 m Stafford Frame comprising 25 quadrats of equal size. The mid-point of the frame was located at the target water depth.

Epilithic algae were collected by washing a known area of the upper surface of stones from each sampling site (following Cameron, 1997). The samples were filtered for subsequent determination of algal biomass (as described previously) and organic matter (after loss on ignition at 550 °C for 3.5 h). Diatom assemblage structure was quantified from epilithic algal samples that were preserved with Lugol's iodine solution and kept in light-resistant glass bottles at <4 °C. Benthic invertebrate assemblages were sampled from each site by standard kick sampling (i.e. Ausden, 1997) using a 500-μm Freshwater Biological Association hand-held pond net. Faunal samples were standardised in area and time (1 m^2, 20 s) and were preserved in 75% ethanol. Diatoms and benthic invertebrates were identified to the highest taxonomic resolution practicable. Benthic invertebrates were assigned to functional feeding (trophic) groups and categories of locomotive capacity following Cummins & Klug (1979) and Schmidt-Kloiber *et al.* (2006). Owing to logistical constraints, the structure of benthic algae and invertebrate assemblages was quantified from a random subset of three of the four transects in each lake.

Data analyses

All statistical analyses comprised two fixed factors: amplitude of WLF (two levels: low and high) and water depth (three levels: shallow, intermediate and deep). Lake and transect number were incorporated as random factors and nested within, respectively, WLF and lake. Mixed-model analysis of variance (ANOVA) based on Type III sum of squares was used to test for differences in univariate response variables among lakes experiencing high and low WLF. Fisher's least significant difference *post hoc* tests provided pair-wise comparisons between levels of significant terms. When necessary, variables were transformed prior to analysis to meet assumptions of normality and homoscedasticity. Multivariate analyses were done with permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001; McArdle & Anderson, 2001) with the same model structure as the univariate analyses. These analyses were based on either Euclidian distance (habitat structure data) or Bray–Curtis similarity (biotic data; relative abundances were log [x + 1] transformed) matrices and were done with 9999 permutations of the residuals under a reduced model using PRIMER® 6.1.8 (PRIMER-E Ltd., Plymouth, U.K.). When the number of possible unique permutations was less than 100, *P*-values were estimated using Monte Carlo simulations (Anderson, 2005; Anderson, Gorley & Clarke, 2008). We used similarity percentage species contributions analysis (SIMPER; Clarke & Gorley 2006) to investigate the contribution of different habitat types, individual taxa, functional feeding groups and locomotive categories to the pair-wise dissimilarity between lakes with low and high WLF.

Taxon richness, Shannon's index of diversity and Pielou's evenness were used as metrics of diatom and benthic invertebrate assemblage diversity. Taxon richness was rarefied to the minimum number of individuals found in a sample (diatoms: 12; invertebrates: 27) to remove the confounding influence of abundance on estimates of richness (Hurlbert, 1971). The importance of WLF for phylogenetic and taxonomic richness of algal and invertebrate assemblages was examined by quantifying each of their total phylogenetic diversity (PD), taxonomic distinctness (TD) and total taxonomic distinctness (TTD) using PRIMER® 6.1.8. Phylogenetic diversity was calculated as the sum of the phylogenetic branch lengths among species (Faith, 1992), TD was calculated as the mean taxonomic distance between all pairs of taxa, while TTD is a modification of species richness that incorporates family inter-relatedness explicitly (Clarke & Warwick, 2001; Salas *et al.*, 2006). Hierarchical Linnaean classification served as a proxy for cladograms and a basis for measuring relatedness. The highest taxonomic resolution practicable across all taxa found was used (genus for benthic diatoms and family for the invertebrates). Equal weights were assigned to each of the principal taxonomic levels.

We investigated the potential of established metrics of aquatic disturbance as indicators of WLF in lakes by focusing on two metrics that have been shown to respond to a range of different pressures in both rivers and lakes (Wallace, Grubaugh & Whiles, 1996; Sandin & Johnson, 2000; Schmidt-Kloiber *et al.*, 2006; O'Toole *et al.*, 2008); the average Biological Monitoring Working Party score per taxon (ASPT; Armitage *et al.*, 1983) and the richness and percentage of abundance classes of Ephemeroptera, Plecoptera and Trichoptera (EPT scores; Lenat, 1988).

To test hypotheses regarding the importance of contrasting regimes of WLF for compositional and functional heterogeneity of biotic assemblages at local spatial scales in natural lakes, we quantified spatial variability along the depth gradient as the coefficient of variation (CV; expressed as a percentage) calculated among samples within transects for univariate variables (benthic chlorophyll *a* and organic matter concentrations) and as the Euclidian distance among samples in Bray–Curtis similarity space [after log(x + 1)-transformation] for multivariate analyses of benthic community structure.

Statistical analyses were done using ANOVA following the statistical models described previously. We tested whether high WLF reduce the compositional and/or functional heterogeneity of benthic assemblages among lakes by comparing the Euclidian distances between samples taken at each depth in lakes with high and low WLF to their respective centroid in multivariate Bray–Curtis space (see Donohue *et al.*, 2009b). Significantly lower distances to centroids in lakes with high WLF would indicate that high WLF homogenise biotic assemblages among lakes.

Results

Habitat structure

Littoral habitat structure varied significantly with WLF along the depth gradient (PERMANOVA; interaction between WLF and water depth: pseudo $F_{2,60} = 3.09$, $P = 0.003$). *Post hoc* tests revealed that habitats differed significantly between lakes with high and low WLF at the shallow sampling depth (pseudo $t = 2.18$, $P = 0.003$), while differences at the intermediate depth were bordering on statistical significance (pseudo $t = 1.58$, $P = 0.073$). SIMPER analysis (Table 2a) revealed that lakes with high WLF had greater proportions of pebble, cobble, boulders and bedrock at the shallowest depth than lakes with low WLF. There was also a more than three-fold reduction in the percentage of gravel and macrophytes in lakes experiencing high WLF (Table 2a).

Benthic algae

A total of 222 benthic diatom taxa were recorded from the sampled lakes (Table S1). Of these, 54 taxa were found only in lakes with low and 28 in lakes with high WLF. No significant main or interactive effects of WLF were found on periphyton biomass or any measure of diatom diversity (taxonomic or phylogenetic). However, the interaction between WLF and water depth on benthic diatom assemblage structure was bordering on statistical significance (PERMANOVA; pseudo $F_{2,44} = 1.37$, $P = 0.064$). We found that the percentage abundance of motile diatom taxa varied significantly with WLF along the depth gradient (ANOVA; $F_{2,44} = 5.86$, $P = 0.006$; Fig. 1a). *Post hoc* tests revealed that the relative abundance of motile diatoms was significantly greater at the shallowest ($t = 3.47$, $P = 0.01$) and intermediate ($t = 6.80$, $P \leq 0.0001$) depths in lakes with high WLF (Fig. 1a, Table S1).

Table 2 Results of SIMPER analyses identifying the contribution (%) of different (a) fractions of littoral habitat structure, (b) trophic groups of benthic invertebrate consumers at the shallowest water depth sampled and (c) locomotive categories of benthic invertebrates at the deepest sampling depth to the dissimilarity between lakes with low and high water-level fluctuations. Untransformed data are shown for clarity

Response variable	Mean density (%) Low WLF	Mean density (%) High WLF	Contribution to dissimilarity (%)
(a) Habitat structure			
Gravel	46.3	17.8	32.5
Pebble	27.5	40.2	19.8
Cobble	5.2	17.7	17.6
Macrophytes	7.6	2.6	8.6
Soil	3.4	0.7	4.5
Bedrock	0	4.1	4.5
Boulder	0	6	4.1
Coarse woody debris	4.1	2.2	3.1
(b) Trophic structure			
Shredders	24.1	11.2	28.9
Gatherers/Collectors	46.5	46.5	26
Grazers and scrapers	15.1	17.1	16.7
Predators	7	10	11.2
Filter feeders	3.9	8.6	9.7
(c) Locomotive category			
Swimming	26.4	15.1	27.6
Burrowing/boring	11.1	21	27
(Semi) sessile	16.8	23.7	25.2
Sprawling/walking	45.7	40.2	20.3

Benthic invertebrates

One hundred and thirty taxa of littoral benthic invertebrates were recorded from the surveyed lakes (Table S2). Thirty-five invertebrate taxa were found only in lakes with low and 32 only in lakes with high WLF. Of these, six gastropod species were found only in lakes with low WLF. Non-operculate gastropod species were found in high densities at the shallowest depth of lakes with low WLF, while in lakes with high WLF these species together with the operculate gastropods *Bithynia tentaculata* and *Viviparus viviparus* were recorded mostly at the intermediate or deep sampling sites.

There was no detectable difference between lakes experiencing low and high WLF in the total number of taxa, total density, taxonomic or phylogenetic diversity of benthic invertebrates or either of the two established metrics of disturbance (ASPT and EPT scores) that we quantified. However, the amplitude of WLF interacted significantly with water depth in their effects on both the evenness (ANOVA; $F_{2,44} = 2.91$, $P = 0.037$) and taxonomic structure (PERMANOVA; pseudo $F_{2,44} = 2.24$, $P < 0.001$) of benthic invertebrate assemblages, although the *post hoc* tests were inconclusive (at $P < 0.05$).

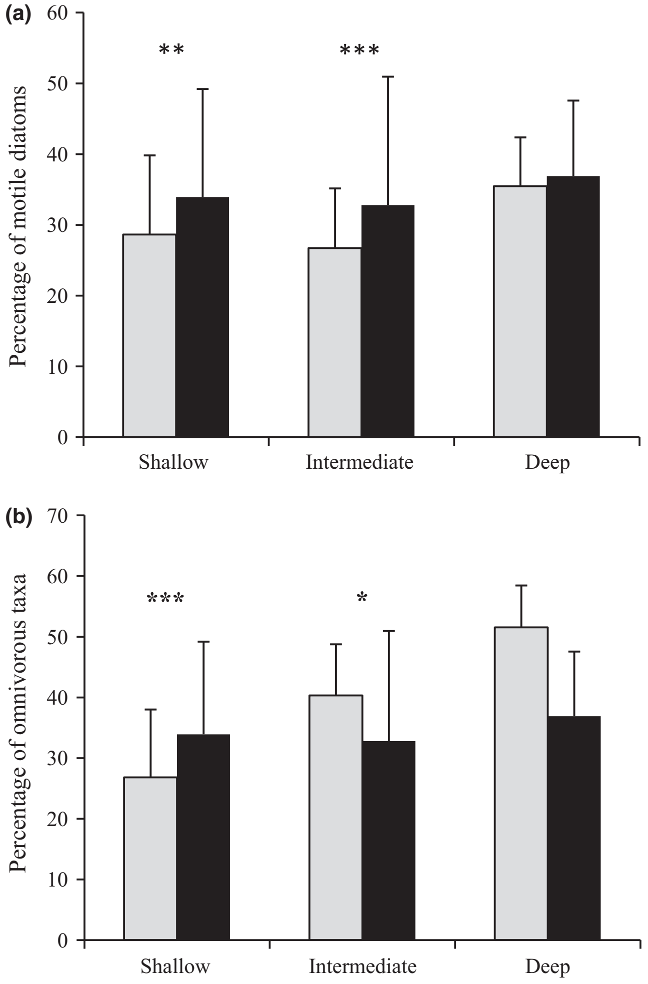

Fig. 1 Percentage of (a) motile diatoms and (b) omnivorous benthic invertebrate consumers (mean + SE, $n = 4$) at different water depths in lakes with low (grey bars) and high (black bars) water-level fluctuations. Untransformed data are shown here for clarity. Asterisks indicate the level of significance for the individual depths ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$).

SIMPER analysis (Table S3) revealed that lakes with higher WLF had higher densities of chironomids (at all sampling depths) and oligochaetes (at the deep sampling depth). Furthermore, we found notably lower densities of the native isopods and the amphipod *Gammarus duebeni* at all depths in lakes with high WLF. In contrast, densities of the non-native amphipods *Crangonyx pseudogracilis* and *G. pulex* were considerably higher at the shallow and intermediate depths in lakes with high WLF. Neither of the latter two species was found at the deep sampling sites in any of the lakes we surveyed.

The trophic structure of benthic invertebrate assemblages varied significantly between lakes with low and high WLF, regardless of littoral water depth (PERMANOVA; pseudo $F_{1,44} = 4.15$, $P = 0.043$). The relative abundance of shredders was lower and predators higher in lakes with high WLF (Table 2b). Moreover, the relative abundance of omnivorous species was significantly greater in lakes with high compared with low WLF (ANOVA; interaction between WLF and water depth: $F_{2,44} = 3.57$, $P = 0.037$) at the shallow water depth (*post hoc* test: $P = 0.0005$; Fig. 1b). However, the reverse occurred at intermediate water depths ($P = 0.022$). The locomotive structure of benthic invertebrate assemblages also varied significantly along the depth gradient in lakes with contrasting WLF (PERMANOVA; pseudo $F_{1,44} = 2.81$, $P = 0.045$). Pair-wise tests revealed significant differences between lake groups at the deepest sampling sites (pseudo $t = 2.10$, $P = 0.039$) with no difference detected at any of the other depths. This shift in locomotive structure was attributable to a decrease in the relative abundance of swimming and sprawling/walking species coupled with an increase in the relative abundance of burrowing, boring and semi-sessile taxa in lakes with high WLF (Table 2c).

Spatial heterogeneity

Benthic chlorophyll *a* concentrations varied significantly less along the depth gradient (i.e. within transects) in lakes with high than in lakes with low WLF (ANOVA; $F_{1,24} = 6.53$, $P = 0.043$; dependent variable log-transformed; Fig. 2a), while similar results for organic matter were bordering on statistical significance (ANOVA; $F_{1,24} = 5.09$, $P = 0.065$; dependent variable log-transformed). The interactive effect of high WLF and depth in reducing the compositional heterogeneity of benthic diatom assemblages along the depth gradient was also bordering on statistical significance (ANOVA; $F_{1,22} = 3.67$, $P = 0.068$). We found no difference between the WLF groups in the heterogeneity of any of the taxonomic, functional or locomotive structure of benthic invertebrate assemblages along the depth gradient.

At among-lake scales, the taxonomic structure of benthic invertebrate assemblages in lakes with high WLF was significantly more homogeneous than in lakes that experienced relatively low WLF, irrespective of water depth (ANOVA; $F_{1,66} = 4.87$, $P = 0.031$; Fig. 2b), with the similar effect on trophic structure bordering on statistical significance (ANOVA; $F_{1,66} = 3.54$, $P = 0.064$). Somewhat in contrast to these results, benthic invertebrate assemblages in lakes with high WLF had more variable locomotive structure at the intermediate sampling depth compared to lakes with low WLF (ANOVA; $F_{2,66} = 3.85$, $P = 0.026$; *post hoc* test for differences at the intermediate depth: $P = 0.024$). There was no difference between WLF

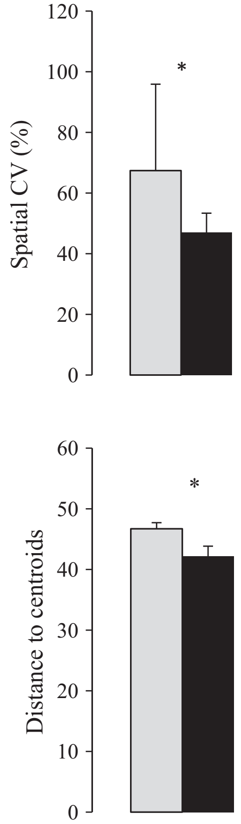

Fig. 2 Spatial heterogeneity of benthic (a) chlorophyll *a* concentration (measured as spatial CV) among sampling depths within transects and (b) regional scale (i.e. among lake) spatial heterogeneity in taxonomic structure in lakes experiencing low (grey bars) and high (black bars) amplitudes of water-level fluctuations.

groups in the compositional heterogeneity of benthic diatom assemblages at among-lake scales.

Discussion

Our results indicate clearly that contrasting water-level regimes drive significant differences in the ecology of lake littoral zones, affecting not only the structure and functioning of benthic assemblages, but also littoral habitat structure. Most, though not all, of the differences between lakes with high and low amplitudes of WLF were mediated by the depth gradient, being generally strongest in the zone of water fluctuation (i.e. at the shallowest and to a lesser extent the intermediate water depths). Our findings suggest that contrasting WLF generated a suite of community responses, altering the taxonomic and trophic structure of benthic consumers and homogenising algal and benthic invertebrate assemblages. These findings are consistent with those of the experimental mesocosm study by Evtimova & Donohue (2014) and demonstrate clearly the strong potential to link multivariate (community) and trait-based (e.g. dietary preferences or motility) biological responses to changes in patterns of WLF. Given this, our findings should facilitate the development of robust tools for assessment of impacts of WLF across a broad range of lake types and locations.

Littoral habitat structure in lakes experiencing high WLF differed from that in lakes with low fluctuations at the shallowest sampling depth. Higher monthly and annual amplitudes of WLF were associated with decreased contributions of smaller sized substratum fractions, consistent with the observations of Furey *et al.* (2004). Furthermore, the largest sized fractions at the shallow depths were found only in lakes with high WLF. This probably reflects the altered position of the more turbulent upper littoral zone as a result of a rise (conversion of terrestrial into aquatic habitat) or drop (shift of the littoral zone lakewards) in water levels winnowing the fine particles from the shore zone. Therefore, extreme WLF appear to modify directly the particle size distribution of benthic substrata in lake littoral zones and are responsible for increased physical stress and related habitat displacement and loss. These findings are consistent with the speculations of Hofmann, Lorke & Peeters (2008) that long-term WLF could induce a slow shoreline displacement, with continuous interplay between short-term (weekly/monthly) and long-term (annual/decadal) fluctuations being responsible for shaping shore morphology and sediment grain size distribution. Both Black *et al.* (2003) and Valdovinos *et al.* (2007) suggested that significant WLF might also increase erosion through impairing macrophyte assemblages. Lakes are much less dynamic physical environments than rivers, with residence times that are orders of magnitude longer. Thus, multi-annual patterns presumably have a much stronger influence on habitat structure in lakes than in rivers (Wantzen *et al.*, 2008a; García Molinos & Donohue, 2014).

A myriad of environmental factors shape habitat structure (Dodds, 2002; Hofmann *et al.*, 2008). Aquatic and near-shore faunal distribution depends largely on the environment, with high diversity of habitats and food resources generating correspondingly diverse littoral communities (Wallace, 1996; Weatherhead & James, 2001; Schindler & Scheuerell, 2002; Stendera & Johnson, 2008; Tolonen & Hämäläinen, 2010). Alteration of substrata may trigger changes in lake geomorphology or wave dynamics, thus affecting vegetation zonation indirectly (Schmieder, 2004). Extreme WLF have been shown to have an adverse effect on macrophytes, decreasing their diversity and cover, with associated decreases in the structural diversity and productivity of littoral habitats (Rorslett, 1984, 1985; Hellsten, 2002; Acreman *et al.*, 2005; Valdovinos *et al.*, 2007). Our findings of reduced macrophyte cover at shallow depths in lakes experiencing high WLF are consistent with this. Associated reductions in the structural diversity, and hence niche availability, of littoral habitats probably affect further lake biodiversity and impoverish ecosystems, reducing the resistance and resilience of lakes to the ecological impacts of anthropogenic disturbances (Cardinale, 2011; Donohue *et al.*, 2013).

Many studies (Townsend, Scarsbrook & Doledec, 1997; Statzner, Dolédec & Hugueny, 2004; Bjelke, Bohman & Herrmann, 2005; Hillebrand & Matthiessen, 2009; Menezes *et al.*, 2010; Céréghino *et al.*, 2012; Lange, Townsend & Matthaei, 2014) have suggested that using biological traits might provide greater insight into revealing the impacts of environmental conditions and habitat changes in lake biota. We found that lakes with high WLF had greater proportions of motile diatom species (Table S1) and omnivorous benthic invertebrates in the shallows (i.e. *Bithynia tentaculata*, *Galba truncatula*, *Potamopyrgus antipodarum*, *Gammarus pulx*, *Asellus aquaticus*). This is most likely a consequence of species with these traits being more adaptable to dynamic water levels and better able to cope with moderate drawdowns or rising of water levels. Omnivory (i.e. benefiting from resources from more than one trophic level) is characteristic of animals that display functional plasticity and possess physiological, morphological and behavioural adaptations necessary to forage and process resources that differ in chemical composition, morphology and nutritional value (Lancaster *et al.*, 2005). However, increased prevalence of omnivory in lakes with high WLF may reduce the stability of these systems and increase their susceptibility to other disturbances with strong and (occasionally) intermediate omnivory destabilising the system (Gellner & McCann, 2012).

We found highly significant differences in the taxonomic structure of benthic invertebrate assemblages between lakes with low and high WLF. There was an overall lower density of crustacean species at all sampling depths in lakes with high WLF, consistent with the findings of Evtimova & Donohue (2014). Loss of littoral species may be followed by re-colonisation provided water levels are stable (Hunt & Jones, 1972; Hynes & Yadav, 1985), thus giving the opportunity for new (including alien) species to establish in the ecosystem as a result of freeing-up habitat niches. Altered water-level regimes have been associated not only with reductions in species richness but also with frequent dominance by invasive plant species (Van Geest *et al.*, 2005). We found lower densities of both native amphipods and isopods in lakes with high WLF, coincident with greater densities of the invasive amphipod *Crangonyx pseudogracilis*. *Gammarus pulex*, another alien amphipod (Dick, Elwood & Irvine, 1990; Costello, 1993; Dick, Macneil & Anderson, 1999; Dick, 2008), and the invasive alien bivalve *Dreissena polymorpha* were recorded only from lakes experiencing high WLF. High amplitudes of WLF are likely to disturb oxygen regimes (Acreman *et al.*, 2005; Hofmann *et al.*, 2008) and modify food sources for macroinvertebrates (Wantzen *et al.*, 2008a). These, in tandem with intraguild predation, the more aggressive nature of *G. pulex* and its greater rate of population growth, probably facilitate the replacement of the native *G. duebenii* by *G. pulex* (Dick *et al.*, 1990; Costello, 1993; Macneil, Dick & Elwood, 1997; Dick, 2008). These results suggest that the amplification of WLF increases the susceptibility of lakes to successful colonisation by invasive species.

We found more gastropod taxa in lakes with low WLF, and non-operculate snails were found exclusively in this group. On the rare occasions when recorded in lakes with high WLF, gastropods were found at the intermediate or deep sites. In addition to the direct physical disturbance through shifting of the littoral zone, gastropods in lakes with high WLF may also be subjected to trophic stress. They rely partially on macrophytes as a food source (Cummins & Klug, 1979) and, as demonstrated here and elsewhere (Hill, Keddy & Wisheu, 1998; Mastrantuono *et al.*, 2008; Wantzen *et al.*, 2008b), WLF are associated with reductions in macrophyte biomass and diversity. Moreover, both gastropod species found only in lakes with high WLF had an operculum, enabling them to resist desiccation (Gibson, 1970), survive periods of drought and thus a probable displacement of the littoral zone. These results are consistent with those of Evtimova & Donohue (2014), and suggest that gastropods could be useful biological indicators of the magnitude and timing of WLF (Mastrantuono *et al.*, 2008).

The trophic structure of invertebrate assemblages differed significantly among WLF groups, owing mostly to a more than two-fold decrease of shredders in lakes with high WLF. This is attributable to reduction in food availability (i.e. benthic algae, macrophytes, riparian vegetation and leaf litter). These specialised feeders are typically sensitive to perturbations owing to their more restricted range of available food sources (Rawer-Jost *et al.*, 2000). Shredders feed on coarse particulate matter with preferences for the most microbially colonised material (Cummins & Klug, 1979). They depend on the input of allochthonous matter from the riparian zone, which could be impeded by shifting of the littoral zone in lakes with high WLF (Weatherhead & James, 2001; Wantzen *et al.*, 2008b). On the other hand, higher densities of generalist feeders (i.e. gatherers, collectors and filter feeders) in lakes with high WLF could be attributed to their ability to employ various feeding strategies and to tolerate changes in food availability owing to their broad range of potential food sources (Cummins & Klug, 1979; Barbour *et al.*, 1996). The significantly higher percentage of predators in lakes with high WLF was likely to be driven by the potentially high availability of prey organisms, both aquatic and terrestrial, that were unable to track the more rapid fluctuations of water levels. These results are consistent with the experimental findings of Evtimova & Donohue (2014) and with results for rivers (Marks, Power & Parker, 2000).

We found a decrease in the relative abundance of motile invertebrate species at the deepest sites. This shift in locomotive structure could be an indirect effect of high WLF, associated with the reduction of aquatic macrophytes and decreased contributions of smaller sized substratum fractions that resulted from high fluctuations in water level. Alteration of key aspects of functional diversity (e.g. trophic or locomotive structure) of benthic consumers could not only affect essential ecosystem services that support human well-being, such as fisheries (Menezes *et al.*, 2010), but could also trigger changes throughout entire lake ecosystems. Littoral invertebrates occupy an intermediate position in energy and matter flow in lakes and lake littoral zones provide important food subsidies both to adjacent terrestrial habitats and to associated aquatic ecosystems (Vander Zanden & Vadeboncoeur, 2002; Sabo *et al.*, 2009; Wesner, 2010, 2011; Kaufmann *et al.*, 2014).

Benthic chlorophyll *a* concentrations were significantly less variable along the littoral depth gradient in lakes experiencing high WLF. This is consistent with results from mesocosms (Evtimova & Donohue, 2014) and indicates potential for inclusion as an indicator of high WLF in lakes. Our results also indicate that high monthly and annual WLF homogenise benthic consumer assemblages among lakes. These results have important implications for the conservation and management of global aquatic biodiversity, owing to the growing importance of WLF as an increasingly pervasive pressure on lake ecosystems worldwide. This, together with associated reductions in diversity at among-lake scales, may have unpredictable effects on whole aquatic ecosystems, with potentially considerable ecological and evolutionary consequences (Olden *et al.*, 2004; Donohue *et al.*, 2009b).

Although the experimental mesocosm study of Evtimova & Donohue (2014) found highly significant effects of amplified WLF on many univariate taxonomic and phylogenetic diversity metrics, our field surveys found no such differences between lakes with high and low WLF. The scaling-up of this study to incorporate the complexity of whole-lake ecosystems, and the consequent inclusion of significant abiotic and biotic heterogeneity both within and among lakes, undoubtedly reduced the ability of our study to detect many of the perhaps more subtle effects of amplified WLF. A key strength of our study is that the variability both within and among lakes was accounted for explicitly in our statistical models and any effect of WLF was over and above these differences among lakes. Thus, we have identified key effects of contrasting patterns of WLF that were consistent and significant across a range of lakes with a variety of biotic and abiotic characteristics. This suggests that our findings are likely to be broadly relevant and applicable to a wide range of lakes.

Our results demonstrate the potential of linking both trait- and multivariate community-based responses to hydrological disturbance to expand biomonitoring approaches beyond traditional taxonomically based assessments that identify ecological effects. Another key finding of our study is that the littoral depth gradient needs to be taken into account when studying the impacts of hydrological pressures. Depth mediated the response of both primary producer and consumer benthic assemblages to fluctuations in water level and interacted with WLF in moderating habitat structure. The importance of depth pertains to the physical shifting of the littoral zone, resulting either in the conversion of terrestrial habitats into aquatic ones, or converting the sub-littoral into eulittoral. In addition, incorporating the timing of extreme events and amplitude of fluctuations at various temporal scales (Evtimova, 2013; García Molinos & Donohue, 2014; García Molinos *et al.*, 2015) into field sampling programmes, coupled with sampling on more than one occasion, could enhance significantly our knowledge and assist in developing robust metrics for quantifying impacts of hydrological disturbances. Potential alterations to the amplitude or seasonality of WLF impact not only on ecosystem health and stability, but also have important implications for flood risk assessment, water management (Fitzpatrick & Bree, 2001; Jackson *et al.*, 2001; Johnson *et al.*, 2001; Baron *et al.*, 2002; Brown *et al.*, 2010) and the delivery of ecosystem goods and services, including water supply, fisheries and agricultural and recreational activities (Kosarev & Yablonskaya, 1994; Graynoth, 1999; Brunberg & Blomqvist, 2003; Okun, Lewin & Mehner, 2005; Okun & Mehner, 2005).

In conclusion, our study indicates clearly that including both biological traits and sampling along a depth gradient in existing and in future monitoring programmes could improve significantly the ability to detect and predict effects of altered patterns of WLF on lake ecosystems. Furthermore, it comprises an important step towards improved understanding of the ecological effects of modified WLF and, therefore, towards improved ability to assess and predict the ecological impacts of this globally important pressure on standing water ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Long-term time-series plots of (a) annual (AR) and (b) monthly (MR) ranges for the sampled lakes.

Table S1. Benthic diatom taxa found in the surveyed lakes.

Table S2. Benthic macroinvertebrate taxa found in the surveyed lakes.

Table S3. Results of SIMPER analysis identifying the five benthic invertebrate taxa that contributed most strongly to the dissimilarity between lakes with low and high amplitudes of water-level fluctuations along the depth gradient.

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