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Zoobenthos community turnover in a 1650-yr lake-sediment record of climate-driven hydrological change

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Abstract. In fluctuating lake ecosystems, the severity of anthropogenic disturbance is often difficult to assess because the magnitude of natural dynamics rivals or surpasses that of ecosystem alteration due to human impact. Consequently, it is also difficult to evaluate the resilience of these ecosystems' plant and animal communities to that impact. Unfortunately, lake ecosystem response to natural cycles of lake-level and salinity fluctuation at multi-annual time scales is poorly understood, due to complex relationships between hydrological dynamics and the local availability or distribution of ecological niches. We present a 1650-yr-long paleoecological record from Lake Naivasha in Kenya (East Africa) which traces community assembly and turnover in two prominent groups of benthic invertebrates (chironomids and ostracods) in response to a climate-driven sequence of 10 major lake-level fluctuations. Over this time period, lake depth (inferred from sedimentology) fluctuated between ~3 and >35 m, and salinity (inferred from fossil diatom assemblages) varied between ~100 and ~23,500 µS/cm. Prior to ~780 yr ago, the unique community response to salinity was stronger than to lake depth. Around that time the lake transitioned to a more open hydrology, relatively stable freshwater conditions and greater prevalence of macrophyte-associated benthic habitat, so that community response to variations in lake depth (and surface area) became stronger. Notably, major community restructuring in the course of this transition was not synchronous between the two groups, because it depended on the proliferation of key freshwater species in each group. Our results imply that (1) climate-sensitive lake ecosystems are more likely controlled by salinity change if both its amplitude and frequency are large enough to induce ecological species sorting; (2) community response to such salinity changes may be predictable, and likely to show coherence across different groups of aquatic biota; and (3) the timing of major community restructuring strongly depends on the ecology of key species, and whether the species sorting is driven by salinity change itself or indirectly by the salinity-dependent availability of ecological niches.

Key words: Africa; chironomids; community assembly; faunal turnover; lake ecosystem dynamics; lake-level fluctuation; ostracods; Ramsar; resilience; salinity; wetland.

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INTRODUCTION

Continental aquatic ecosystems contribute disproportionally to global biodiversity but also suffer record species extinction rates (Dudgeon et al. 2006), creating urgency to prioritize conservation measures (Silk and Ciruna 2013). However, effective allocation of conservation effort is to a large

extent system-specific, as it depends on the natural resilience of different types of continental aquatic ecosystem, which is often unknown and difficult to assess (here, resilience is defined as the ability of an ecosystem to return to its original state after disturbance; Müller et al. 2016). This need to understand the relative resilience of aquatic ecosystems to climate-related and other anthropogenic impacts on lake hydrology has reinvigorated interest in the ecological effects of lake-level and salinity changes (Jeppesen et al. 2015, Gownaris et al. 2018). Especially in tropical regions, the hydrology of many lakes is highly climate-sensitive, particularly when situated in an arid or semiarid climate regime. On time scales of decades to centuries, these aquatic systems may even fluctuate back and forth between being a deep lake with stratified water column and drying out completely, with shallow-lake and wetland phases in between. Yet, knowledge on the long-term ecological and biodiversity consequences of this fluctuating hydrology is exceedingly scarce (Zohary and Ostrovsky 2011, Kolding and van Zwieten 2012). A related and increasingly widespread problem requiring similar system-level understanding is the secondary salinization of inland waters due to water abstractions (Williams 1999, Kaushal et al. 2005).

One prominent obstacle to improved understanding of lake ecosystem response to hydrological change is the complex relationship between the environmental variables water depth, open-water surface area and salinity (Jeppesen et al. 2015), especially in the continental waters that are naturally climate-sensitive. Over very long time scales such lakes and ponds tend to be smaller, shallow and saline when water availability is low; and larger, deeper and more dilute when water availability is high. However, on intermediate time scales (years to decades) the relationship between these variables is most often non-linear (Langbein 1960, LaBaugh et al. 1996). This implies that in regional lake surveys, where those relationships are analyzed through space-for-time substitution, site-specific geology and hydrological trajectories (e.g., hysteresis effects during a cycle of transgression and regression) create noise which obscures a distinct ecological response to water depth, salinity, or both (Wigdahl et al. 2014). In this respect, long-term ecological time series linked directly to abiotic environmental data (Kalk 1979, McLachlan 1979, Vareschi and Vareschi 1984, Melack 1988) are much preferred, but also scarce because documenting the aquatic ecosystem response to climate-driven hydrological fluctuation requires multi-annual, often decades-long ecological monitoring. This makes paleoecological records particularly valuable for assessing the natural long-term dynamics and resilience of ecosystems (Seddon et al. 2014). As for the specific question raised above, long time series of paleoecological data may permit better discrimination between the aquatic community responses specific to changes in water depth and salinity. Unfortunately, high-quality paleoecological records from fluctuating lakes are also notably scarce, because such systems often fail to accumulate the undisturbed sediment sequences required to extract continuous time series of ecosystem response to hydrological change (Verschuren 2003).

This study investigates a 1650-yr-long fossil record of the zoobenthos community inhabiting the Crescent Island Crater (CIC) basin of Lake Naivasha (Kenya). Submerged within the main basin of Lake Naivasha (Fig. 1), CIC uniquely combines the climatic sensitivity of a shallow Rift Valley lake (a classic amplifier lake; Olaka et al. 2010) with the undisturbed sedimentation regime of a deep crater lake. Consequently, it has preserved a continuous record of decadal to century-scale fluctuations in water depth and salinity (Verschuren et al. 2000*a*, Verschuren 2001, Van der Meeren et al. 2019) as well as the ecological impacts of this dynamic abiotic environment on the local aquatic fauna (e.g., zooplankton: Mergeay et al. 2004, 2011). In this study, we focus on the history of its chironomid (larval non-biting midges) and ostracod (seed shrimp) communities, two important groups of zoobenthos in continental waters worldwide (Wetzel 2001). Crucially, diagnostic skeletal remains of both groups are well preserved in lake-sediment records (Walker 1987, De Deckker and Forester 1988). Specifically, we assess the timing and relative amplitude of their community-level response to past climate-driven changes in water depth and salinity to generate insight in the ecological resilience of this and other climate-sensitive tropical lake ecosystems to diverse and compounding natural and anthropogenic disturbance.

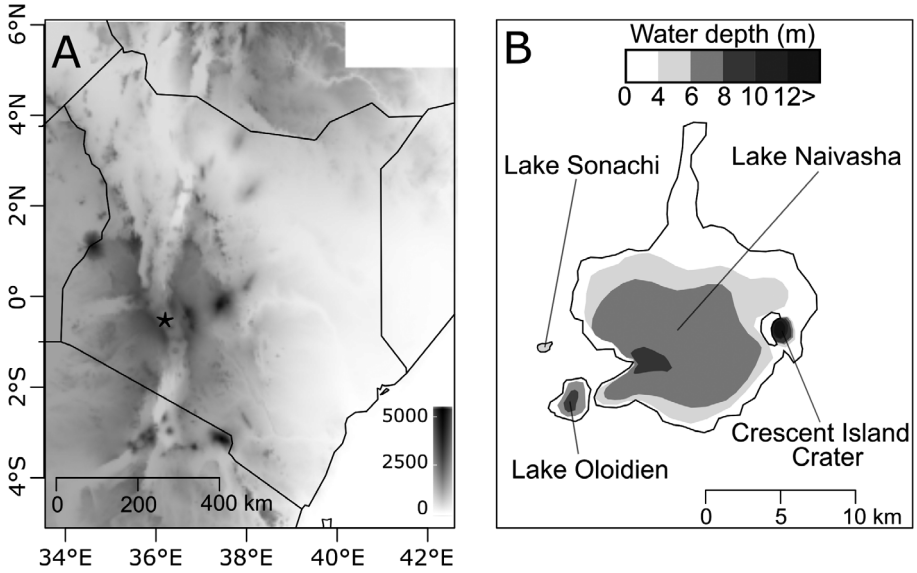

Fig. 1. (A) Location of the Lake Naivasha system (∗) in the central portion of the Eastern Rift Valley in Kenya (grayscale, with altitude in meter a.s.l.) and (B) Lake Naivasha, the submerged Crescent Island Crater and two satellite lakes Sonachi and Oloidien, all with simplified bathymetry relative to a surface level of 1886 m. a.s.l. (modified from Van der Meeren et al. 2019).

Methods

Details about sediment-core collection, the processing of fossil samples, and previous work on the sediment record of CIC can be found in Appendix S1. Fossil chironomid remains were sampled at contiguous 4-cm intervals, and fossil ostracods at contiguous 2-cm intervals, throughout the 8.22-m sediment sequence. Two-by-two summation of the ostracod counts to 4-cm intervals produced matching chironomid and ostracod time-series data with 200 observations, each representing a time interval of on average eight years throughout the lake's 1650-yr history. Fossil assemblages with similar species composition (here defined as "ecological clusters") were identified on the basis of Hellinger-transformed percent species-abundance data, and grouped together using a Bray–Curtis distance matrix and Ward clustering algorithm. The optimal number of such groups (clusters) was assessed by means of k-means clustering (package *factoextra* in R, Kassambara and Mundt 2017). One sample with low ostracod count sum and monospecific assemblage (100% *Sclerocypris jenkinae*) at 648 cm (~800 CE) was omitted from this analysis because it produced outliers in the distance matrix. Stratigraphically constrained clustering (CONISS; Grimm 1987) was then used to determine the timing of the most prominent events of faunal turnover (i.e., shifts in community composition). Appendix S2 explains the classification of the recovered chironomid and ostracod species into the ecological salinity classes stenotopic freshwater, eurytopic freshwater to salt-tolerant, halophilic and halobiont.

Temporal dynamics in the zoobenthos community of CIC are assessed with reference to the history of its abiotic environment, as reflected in the independent reconstructions of (1) lake-level fluctuations based on sediment texture and bulk composition (Verschuren 2001, Van der Meeren et al. 2019) and (2) salinity variations based on changes in fossil diatom assemblages (Verschuren et al. 2000*a*, Van der Meeren et al. 2019). Constrained multivariate analysis was used to partition the observed temporal variation in fossil assemblages toward these two environmental forcings. Redundancy analysis (RDA; ter Braak 1994) and variance partitioning (VP; Borcard et al. 1992) were performed in R using package vegan version 2.3-3, on Hellinger-transformed

percent-abundance data of the fossil assemblages. Diatom-inferred conductivity values were log-transformed (base 10) to obtain a more even distribution. RDA and VP were performed for the complete 1650-yr record and separately for the older and younger parts of lake history, characterized respectively by alternating fresh and saline phases (pre-1240 CE) and predominant freshwater conditions (post-1240 CE). The timing of this division was determined by stratigraphically constrained cluster analysis (CONISS), using a Euclidean distance algorithm and with diatom-inferred conductivity as sole variable. Scores of the fossil assemblages along the first partial RDA axis allowed to extract time series of the unique community response to each variable.

Results

Variation in water depth and salinity over the past 1650 yr

Major variation in reconstructed water depth and salinity (Fig. 2) highlights the eventful environmental history of CIC over the past 1650 yr (Van der Meeren et al. 2019): Maximum water depth varied between ~3 m during the extreme low-stand which characterized the Medieval Climate Anomaly (MCA; c. 900–1200 CE) and >35 m during the pronounced high-stand which characterized the late Little Ice Age period (late LIA; c. 1600–1780 CE). Lake-water salinity fluctuated between minima of ~100 μS/cm (2.00 log units) and maxima up to 23,500 μS/cm (4.37 log units). Over the entire 1650-yr record of CIC, water depth and salinity are inversely correlated ($r = -0.38$; $P < 0.001$; $n = 275$): Low-stands were associated with evaporative concentration of dissolved salts and high-stands with more dilute conditions. Stratigraphically constrained cluster analysis of the reconstructed conductivity values reveals a major hydrological shift to have occurred around c. 1240 CE, linked to the major lake transgression which ended the MCA-period low-stand (Van der Meeren et al. 2019). Overall the pre-1240 CE period was characterized by a higher mean conductivity with higher variance (3099 ± 5290 μS/cm) compared with the post-1240 CE period (253 ± 152 μS/cm). Although the inverse correlation between lake depth and salinity is strong both before and after this transition (pre-1240 CE $r = -0.42$, $P < 0.001$, $n = 151$; post-1240 CE $r = -0.38$, $P < 0.001$, $n = 124$), at least five alternations between fresh high-stands and saline low-stands (>3000 μS/cm) occurred before 1240 CE, whereas post-1240 CE this important physiological threshold (Williams 1981, Hammer 1986) was never crossed.

Species-assemblage turnover and ecological clusters

The 200 pairs of fossil assemblages comprised 28 species of chironomids (Verschuren et al. 2000*a*) and 21 species of ostracods (Van der Meeren et al. 2019). Mean and maximum species richness of individual assemblages was 6.4 ± 1.7 (max. 11) for chironomids and 4.1 ± 1.9 (max. 13) for ostracods, based on a mean count sum of 62 ± 39 (max. 188) for chironomids and 184 ± 269 (max. 1626) for ostracods. Although the ostracod yield (carapax valves) was thus in general higher and more variable than that of chironomids (larval head capsules), temporal trends of fossil abundance in both groups are similar (Appendix S3: Fig. S1) and significantly correlated ($r = 0.34$, $P < 0.001$ based on log-transformed values). However, this should not be interpreted to reflect similar trends through time in the total live biomass or production of these two invertebrate groups. More likely it reflects congruence in the prevalence of post-mortem transport between shallow-water areas nearshore, where the densest populations of living zoobenthos occur, and their burial location at the offshore coring site (Verschuren et al. 2000*b*). More pertinently, both groups also display similar overall trends in species richness ($r = 0.27$, $P < 0.001$), especially a shared low diversity during the 17–18th century high-stand and a shared peak diversity around 1440 CE (Appendix S3: Fig. S1). No difference in mean species richness is found between the pre-1240 CE and post-1240 CE portions of the record in either chironomid or ostracod assemblages (P values are 0.56 and 0.32, respectively). In the chironomid record, the nine most common species together represent between 78% and 100% (mean 96%) of the fossil assemblage in any time interval (Appendix S4: Fig. S1). In the ostracod record, the five most common species together represent 50–100% (mean 98%) of any fossil assemblage (Appendix S4: Fig. S2).

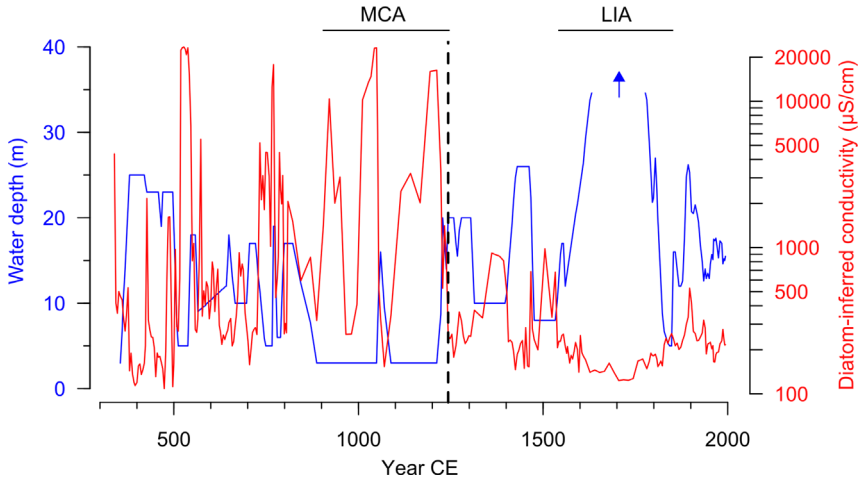

Fig. 2. Reconstructions of variation in the water depth (in m) and salinity (as diatom-inferred conductivity, in µS/cm) of Crescent Island Crater over the last 1650 yr, based, respectively, on sediment lithology and diatom-inferred lake-water conductivity (Verschuren et al. 2000*a*, Verschuren 2001; both updated by Van der Meeren et al. 2019); the dashed line marks the major hydrological transition around 1240 CE, separating the early and later phases of lake history; see text for details. The timing of the Medieval Climate Anomaly (MCA) and the main phase of the Little Ice Age (LIA) are indicated as general context of climate-driven hydrological change in Lake Naivasha during the period covered by this study; see Nash et al. (2016) and Van der Meeren et al. (2019) for additional information.

The 1650-yr CIC record reveals major turnover in the composition of its chironomid and ostracod communities (Fig. 3C, F) associated with temporal variation in water depth and salinity (Fig. 3D, E), with some similarities but also clear differences between the two zoobenthos groups. In the chironomid record, episodes with elevated salinity and (most often) shallow-water conditions were characterized by the presence of the halophilic species *Kiefferulus disparilis* and/or *Microchironomus deribae*. Often the dominant species during such low-stands was the salt-tolerant freshwater species *Cladotanytarsus pseudomancus*, which today is found together with these halophilic species in the soda lakes of the Ethiopian Rift Valley (Tudorancea and Harrison 1988), and is generally associated with sandy substrates in well-oxygenated but wind-sheltered habitats nearshore (Verschuren 1997, Eggermont et al. 2007). The ecological cluster defined by these three halophilic or salt-tolerant species (blue in Fig. 3B) prevailed in CIC during five lake episodes when conductivity rose to a maximum of 23,500 µS/cm, and which together amount to ~65% of the pre-1240 CE part of the record. After that time, it prevailed during two lake episodes with modest salinity (200–1000 µS/cm), the most recent of which ended c. 1540 CE.

At the other extreme of the salinity gradient, the stenotopic freshwater species *Psectrocladius viridescens* (Verschuren 1997 and references therein; Eggermont et al. 2006) has been a prominent member of the local zoobenthos community only after c. 1600 CE, when on average deeper water and more dilute conditions prevailed. High abundances of this species and of *Dicrotendipes septemmaculatus* characterize the freshwater ecological cluster (green in Fig. 3B). In relative abundance, the latter species often accounted for 30–50% (mean 37%) of the local chironomid community during freshwater lake episodes, whereas values <30% (mean 17%) are more typical for inferred saline lake episodes. In present-day Lake Naivasha, *D. septemmaculatus* is mostly associated with shallow mud bottoms (Clark et al. 1989) and with nearshore bottoms rich in organic debris, but it also occurs offshore in slightly greater water depths than *C. pseudomancus* and *P. viridescens* (Eggermont et al. 2007). Because of the common occurrence of *D. septemmaculatus* and *C. pseudomancus* in fossil assemblages representing either ecological cluster, the

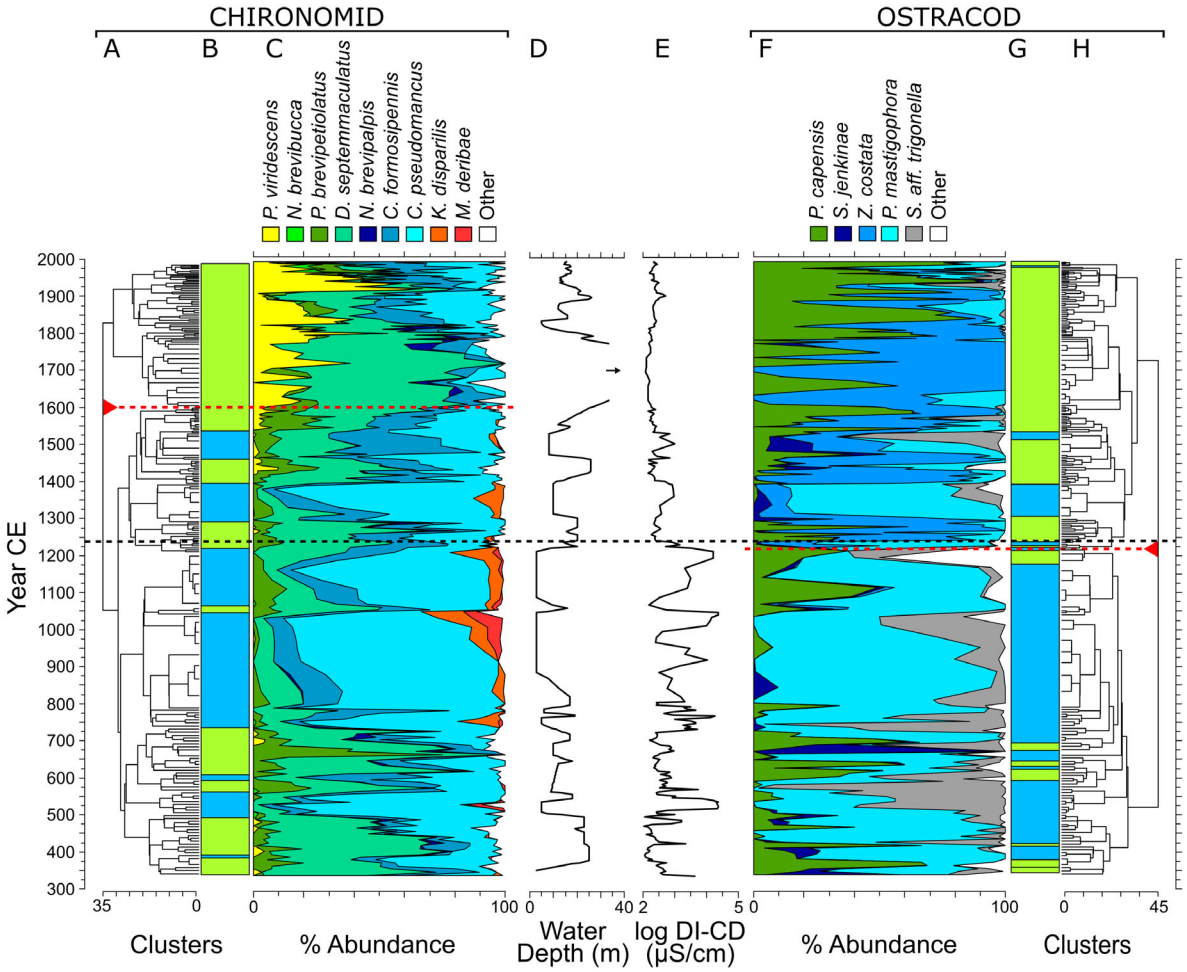

Fig. 3. Overview of changes in fossil chironomid and ostracod assemblages through time (A–C, F–H), in combination with the water-depth and salinity reconstructions (D, E). (A) and (H) show stratigraphically constrained clustering of 200 pairs of fossil assemblages, with the most prominent division in each indicated as a red dashed line. (B) and (G) show hierarchical clustering of the same assemblages without stratigraphic constraint, reflecting ecological clusters of species consistently occurring together. (C) and (F) show the percent abundances of the nine most common chironomid species, and five most common ostracod species, ordered from left to right according to increasing salinity optima; see text for details. Stenotopic freshwater species are indicated in yellow; eurytopic and salt-tolerant species with a gradient from green to blue; halophilic/halobiont species in orange and red. The ostracod *Sarscypridopsis* aff. *trigonella* (gray) could not be allocated to a specific ecological category due to lack of distribution data, and all less common species are together indicated in white. Water depth (D) is expressed in meter, salinity (E) as log-transformed diatom-inferred conductivity. The black dashed horizontal line indicates the hydrological shift around 1240 CE, as in Fig. 2; see text for details.

most notable shift in chironomid community composition as identified by CONISS is situated c. 1610 CE, when *P. viridescens* became co-dominant with *D. septemmaculatus*, often supplemented by *C. formosipennis* and *C. pseudomancus* (Fig. 3C).

In contrast with the chironomid record, no true stenotopic freshwater or halophilic/halobiont species can be identified among the most common ostracods inhabiting CIC over the past 1650 yr (Van der Meeren et al. 2019). The stratigraphic distribution of *Sarscypridopsis* aff.

trigonella is however clearly associated with low-stands and elevated salinity, suggesting high salinity tolerance. *Potamocypris mastigophora*, although reported only from freshwater sites in a survey of Kenyan and Ugandan lakes and ponds (Rumes et al. 2016, Van der Meeren et al. 2019), likely also has high salinity tolerance, as indicated by its presence during episodes of hydrological closure in Lake Oloidien (Verschuren et al. 2000*b*) and its occurrence in Lake Abijata, a soda lake in Ethiopia (Van der Meeren et al. 2019 and references therein). This species is further linked to sandy or silty substrates (Verschuren et al. 2000*b*), which tend to expand relative to muddy substrates during low-stands. Thus, co-dominance by *S*. aff. *trigonella* and *P. mastigophora* in the fossil ostracod community characterizes a saline low-stand ecological cluster (blue in Fig. 3G).

The ostracod *Zonocypris costata* is known for its strong association with aquatic littoral vegetation, both in living or recently dead material from Lake Naivasha (Verschuren et al. 2000*b*) and in live ostracod collections from across Kenya and western Uganda (Van der Meeren et al. 2019 and references therein). Nevertheless, this species must be considered eurytopic/salt-tolerant (not stenotopic freshwater as in Cohen et al. 1983), because living populations have been reported from lakes with conductivity values exceeding 3000 μS/cm (Van der Meeren et al. 2019). Consequently, its predominant occurrence in freshwater habitats can be inferred to result from the limited salinity tolerance of most aquatic macrophytes in African lakes (Kipkemboi 2016). The species *Physocypria capensis* is only loosely associated with the presence of aquatic vegetation, but more strictly tied to freshwater conditions (Van der Meeren et al. 2019). Dominance by either *Z. costata* or *P. capensis* characterizes the freshwater ecological cluster (green in Fig. 3F). According to CONISS, the onset of *Z. costata* prominence c. 1220 CE represents the most important shift in the ostracod community of CIC (Fig. 3H).

Community response to fluctuating water depth vs. salinity

Redundancy analysis variance partitioning indicates that for both groups of zoobenthos, salinity fluctuation explains a larger unique fraction of the variation in fossil assemblages than water depth (Fig. 4; Appendix S5: Table S1). The total amount of variance explained is comparable (22% in chironomids, 25% in ostracods), and also the fraction of variation that cannot be attributed to a single variable (the shared partition, due to collinearity) is of the same order of magnitude. When considering the pre- and post-1240 CE periods separately, salinity and water depth together explain a larger fraction of compositional variation in pre-1240 CE chironomid assemblages than post-1240 CE; the opposite is the case for the ostracod assemblages. However, in both groups the unique influence of salinity variation is largest pre-1240 CE, while that of water-depth variation is largest post-1240 CE (Fig. 4).

The pRDA scores of fossil assemblages allow to quantify the unique responses to water depth and salinity over time (Appendix S6). For water depth, the two groups show substantial divergence in pRDA1 scores, especially in the pre-720 CE part of the record and during the period 1400–1600 CE (Fig. 4; $r = 0.28$ between ostracod and chironomid pRDA1 scores; $P < 0.001$). For salinity, the pulsed-response long-term trend is more similar in both groups of zoobenthos (Fig. 5; overall $r = 0.54$; $P < 0.001$) except during a few brief episodes (e.g., 420–460 CE).

Discussion

Disentangling the ecological responses to variation in water depth and salinity

Sound application of paleolimnological data to infer past changes in ecological communities critically depends on the integrity of the studied lake-sediment record as representing a long-term ecological time series (Leavitt and Findlay 1994, Cohen 2003). For reasons of conciseness, this evaluation is here presented in Appendix S7.

Variance partitioning of our fossil-abundance data, each representing one of 200 time windows in the 1650-yr history of Lake Naivasha, revealed a clear response of its zoobenthos community to fluctuation in water depth and salinity (Fig. 4). Yet, between 22% and 44% of the constrained portion of this response could not be attributed uniquely to one variable. The principal reason for this outcome is the strong hydrological link between lake depth and salinity at multi-decadal

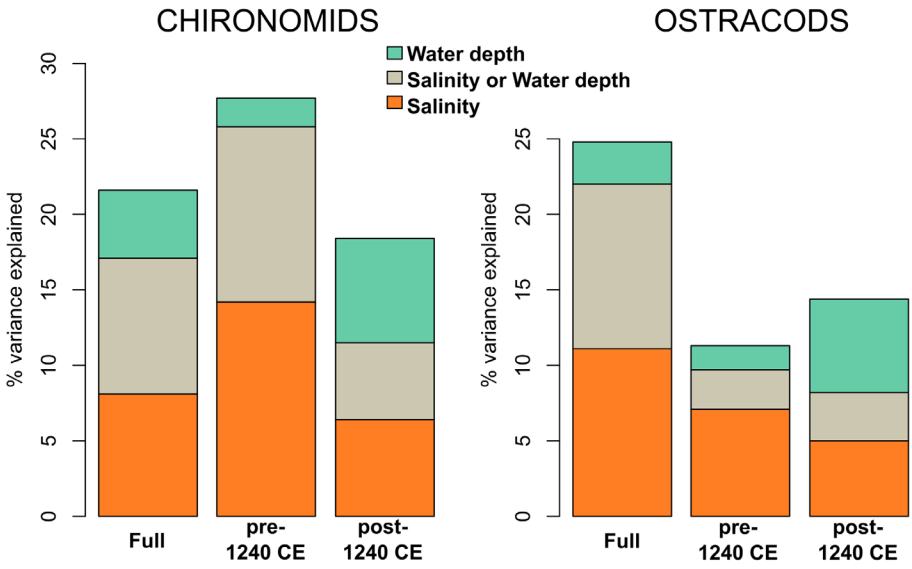

Fig. 4. Overview of variance partitioning (pRDA) results for the chironomid and ostracod assemblages. For each group, the percentage of variance in assemblage composition that can be uniquely attributed to variation in water depth and salinity is shown, as well as the shared partition of variance that cannot be attributed to either one of these factors. Explained fractions are shown for the entire 1650-yr record (Full, 200 time slices), and for the older (pre-1240 CE, 123 time slices) and younger (post-1240 CE, 77 time slices) parts separately.

and longer time scales, creating collinearity and complicating the extraction of unique ecological responses (Jeppesen et al. 2015). In the pre-1240 CE period, both this un-partitioned constrained variance and the total explained variance are greater in chironomids than in ostracods (Appendix S1: Table S1). This tighter link of the chironomid communities with the studied environmental drivers, especially in the pre-1240 CE period, is also visible in the alternation of ecological clusters (Fig. 3). Apparently the joint response of multiple chironomid species outweighs that of a more limited number of common ostracod species. In the post-1240 CE part of the record, the un-partitioned constrained variance is relatively modest compared to the unique effects of water depth and salinity in both chironomids and ostracods, in line with the now diminished correlation between water depth and salinity. This is mostly because prolonged phases of open hydrology after 1240 CE, and especially during the 17–18th century high-stand, flushed the CIC basin of remnant salts (Verschuren et al. 2000*a*).

In the near-continuous freshwater conditions prevailing after 1240 CE, community response to water depth is stronger than that to salinity in both chironomids and ostracods (Fig. 4). In both groups, this response is mostly driven by the temporal dynamics of just one species, respectively *P. viridiscens* and *Z. costata*. The rise to prominence of these two freshwater species (from c. 1610 CE and 1230 CE, respectively; Fig. 3) is reflected in the more positive pRDA scores on water depth in both groups (Appendix S6: Fig. S1). For chironomids, this is noteworthy because *D. septemmaculatus*, which occurs throughout the CIC record (Fig. 3) and has been found to respond positively to water depth in spatial contexts (Verschuren et al. 2000*a*, Eggermont et al. 2007), apparently did not do so in this long-term temporal context, as long as salinity fluctuated significantly. Part of the reason for this stronger response to water depth may be that zoobenthos communities thrived after each lake transgression due to the high-quality food source provided by flooded littoral vegetation, as has been documented by McLachlan (1979) at Lake Chilwa (Malawi). Zoobenthos response to changes in aquatic macrophyte abundance (linked to water depth and open-water surface area) may also be stronger during freshwater

phases than during saline episodes, due to lagged vegetation response in the latter. This is exemplified by Lake Oloidien post-1970 CE (Verschuren et al. 2000*b*), where salinity-intolerant aquatic vegetation failed to recolonize the lake margin for decades after the end of a saline lowstand. This lag was likely due to remnant salts in sediment pore waters. In the case of CIC, such lagged vegetation response would have been enough to bridge most (short-lived) freshwater episodes before 1240 CE. In this conceptual model, zoobenthic community response to variation in water depth is mediated by (or even depends on) the local occurrence of (abundant) littoral vegetation. The few occurrences of the stenotopic freshwater chironomid *P. viridescens* in the pre-1240 CE period (Fig. 3C), all without *Z. costata* (Fig. 3F), may reflect the occurrence of vegetation-poor benthic habitat during transient freshwater conditions associated with brief episodes of wetter climatic conditions.

Based on the 200 time-slice observations in this study, we find that, respectively, 22% and 25% of the observed variance in fossil chironomid and ostracod assemblages can be explained by the independently reconstructed (not measured) variation in water depth and salinity. These fractions are comparable to those typically found in regional hydro-ecological surveys, organized to cover the widest-possible regional gradient in water depth and salinity (and also measuring a multitude of other environmental variables). For example, 27% in an ostracod survey across 26 Kenyan lakes (Rumes et al. 2016) and 33% in a chironomid survey across 60 Canadian lakes (Larocque et al. 2006). Analyses of community response across modern-day environmental gradients potentially involve a greater amount of noise from secondary gradients and site-specific conditions than is the case with long-term monitoring or paleoenvironmental reconstruction at a single site (Jeppesen et al. 2014). This is because a

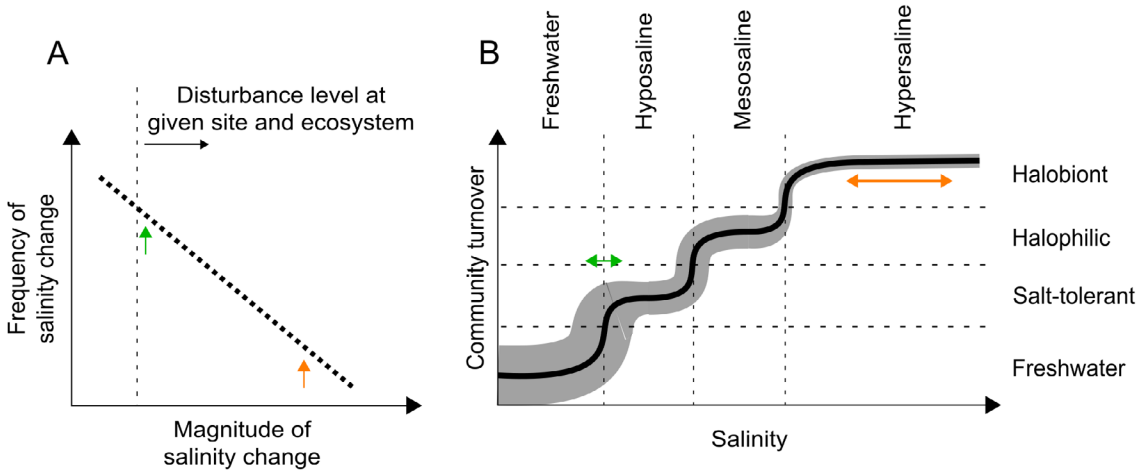

Fig. 5. Schematic representation of aquatic ecosystem response to salinity. (A) Community-scale response to salinity change is generated above a threshold magnitude and associated frequency (modified from White and Jentsch 2001). The exact shape of the negative correlation between magnitude and frequency (here conceptually indicated by a linear slope) depends on the local system. (B) Turnover in aquatic invertebrate communities along the complete inland salinity gradient as commonly encountered in hydro-ecological surveys, with major salinity classes separated by commonly occurring thresholds for aquatic biota (Hammer 1986, and references therein). In the freshwater range, multiple communities exist depending on, for example, pH, trophic state, depth, food-web interaction, etc. The hypersaline range typically supports a single and species-poor halobiont community. Hydroclimate-sensitive aquatic ecosystems are likely regulated by salinity only when its communities are frequently pushed across a common and shared salinity tolerance limit (vertical stippled lines), irrespective of the magnitude of salinity change (green vs. orange arrows). See section *Ecological functioning of hydroclimate-sensitive lakes* for further information.

number of processes (hydrology, hydrochemistry, nutrient dynamics) are generally more variable among a set of regional lakes than within a single lake over time. Thus, even though the environmental gradient covered by temporal sampling at a single site is most often shorter than that accomplished in a spatial survey, this disadvantage is compensated by a more limited impact of confounding factors. This benefit may become particularly important for ecosystem management when collinearity between stressors obscures ecosystem response to each of them (De Laender et al. 2012).

Hydrology-driven shifts in the zoobenthos community

Faunal turnover between salt-tolerant/halophilic and more typical freshwater zoobenthos in the CIC record is generally consistent between the two analyzed groups (Fig. 3). Pre-1240 CE, there is an overall dominance of salt-tolerant species, mostly associated with pronounced low-stands which resulted in hydrological closure of the crater basin (Verschuren 2001, Van der Meeren et al. 2019); post-1240 CE (from c. 780 yr ago), this shifts to a dominance of more strictly freshwater species. Even during rapid environmental fluctuation (e.g., the low-stand centered on 750 CE, which lasted less than 50 yr), both groups often displayed equivalent shifts in the abundance of salt-tolerant/halophilic species, albeit not always with the same amplitude. The high explanatory power of salinity before 1240 CE suggests similarity with the process of invertebrate species sorting in temporary wetlands (Waterkeyn et al. 2008). Analogous to the drought-induced compositional similarity of aquatic communities tolerant to desiccation (Chase 2007), the freshwater ostracod and chironomid assemblages which inhabited CIC before 1240 CE (green clusters in Fig. 3) show remarkably little compositional drift over almost 1000 yr of repeated salinity crises. This is consistent with the notion that high frequencies of disturbance reduce the importance of competition and priority effects (Grime 1979). Yet, long-term persistence of aquatic habitat in CIC may to a large degree dampen environmental (and thus habitat) unpredictability in comparison with true ephemeral lakes (Comín et al. 1991).

The defining hydrological shift c. 780 yr ago, from a fluctuating lake alternating between fresh and saline conditions to one maintaining fresh conditions, reduced the synchrony between the two zoobenthos groups in faunal turnover. Whereas in ostracods the prominent rise of *Z. costata* around 1230 CE practically coincides with this transition, among chironomids the key species *P. viridescens* only established sizeable (>10%) and stable abundances some 400 yr later (c. 1610 CE). Whereas *P. viridescens* is a stenotopic freshwater species (never recorded in African lakes above 700 µS/cm; Eggermont et al. 2006), *Z. costata* is clearly tolerant of higher salinities (up to 5800 µS/cm; Van der Meeren et al. 2019). This means that the low-stands centered on 1360 and 1510 CE (with reconstructed conductivities peaking at a modest 900 and 800 µS/cm; Fig. 3E) would still have negatively affected *P. viridescens* but not *Z. costata*. Eradication of the former species during these two low-stands, despite being associated with shallow-water habitats (Eggermont et al. 2007), is clearly consistent with a direct salinity response. In contrast, the near-continuous prominence since 1230 CE of *Z. costata*, of which the distribution among East African lakes is strongly associated with aquatic vegetation (Van der Meeren et al. 2019), points to permanent establishment of vegetated shallow-water areas around that time. Thus, whereas in chironomids the most prominent community shift of the past 1650 yr was controlled by one key species' physiological limit of salinity tolerance, in ostracods it was controlled by an indirect effect of salinity change, namely the proliferation of benthic habitats associated with freshwater macrophytes (Verschuren et al. 2000*b*).

Ecological functioning of hydroclimate-sensitive lakes

A large body of literature is available on faunal turnover along salinity gradients in lakes (Hammer 1986, Hart et al. 1991, Green 1993, Schagerl and Burian 2016), most of it based on surveys of aquatic invertebrate communities in (a suitably large number of) lakes with varying salinity. These studies also spawned several paradigms on the ecological functioning of hydroclimate-sensitive lakes. One of these, the intermediate salinity hypothesis of Herbst (1988), states that at high salinities the abundance of (salt-tolerant)

organisms is primarily limited by physiological stress, whereas in the more diverse communities prevailing at low salinities it is controlled by ecological factors such as predation and competition. Based on the distribution of halobiont Ephydridae in North-American salt lakes, this hypothesis concerns environmental sorting at the species level. In contrast, Williams et al. (1990) and Williams (1998), who mainly referred to the distribution of invertebrate communities in Australian lakes, advocated an important role for factors other than salinity at elevated salinities, and greater importance of salinity also at the lower end of the salinity range. More recent work added an explicit temporal dimension by coupling salinity response of aquatic communities to specific hydrological regimes, but mainly for wetlands (Waterkeyn et al. 2008, Nielsen and Brock 2009) where the ecological response to seasonal hydrological and salinity changes are more easily monitored than in lakes. The unique effects of salinity vs. lake-level fluctuations on aquatic community composition and persistence thus remained largely unresolved (Jeppesen et al. 2015).

Based on our data documenting long-term temporal dynamics in the zoobenthos community of Lake Naivasha, we propose that the ideas formulated thus far can be reconciled at the ecosystem level, and that a broader framework emerges when generalizing these ideas to explain aquatic community turnover along the full salinity gradient. In the temporal framework that we consider, salinity is the dominant environmental stressor or regulator (relative to other abiotic factors such as water depth, and biotic factors such as food-web interactions) when one or more salinity threshold values common to many biota, either physiological or indirect, are crossed with a certain frequency, and this irrespective of the magnitude of salinity change (Fig. 5). Thus, even large and/or relatively frequent salinity changes will fail to elicit strong ecosystem response when the disturbance regime does not cross the salinity tolerance limit of key phytoplankton, zooplankton, aquatic macrophyte, benthic invertebrate, or fish species. Two examples of lakes with considerable salinity fluctuation not inducing ecological turnover are the hypersaline Mono Lake and Dead Sea (Williams 1998). This is because halobiont communities thriving in the hypersaline range tend to consist of relatively few species with extreme tolerance toward salinity fluctuation (Hammer 1986). Conversely, even modest salinity change can elicit major ecosystem response when it involves the crossing of a salinity threshold common to one or more key species in the local ecosystem. The latter is exemplified by the phytoplankton dynamics of saline Lake Elementeita, immediately north of Lake Naivasha in the Kenya Rift Valley, where population crashes of dominant species were found to cause cascading ecosystem shifts (Melack 1988). In the present study, the ecological importance of salinity fluctuations is exemplified by the pre-1240 CE portion of the CIC record. Firstly, although not stretching over a huge salinity range, the disturbance imposed by an on average rather dry hydroclimate regime before and during the MCA (Verschuren et al. 2000*a*, Nash et al. 2016) prevented establishment of the aquatic macrophyte beds known to provide diverse microhabitats for typical freshwater species. Secondly, frequent crossings of the conductivity values 1000 and 3000 μS/cm, representing salinity thresholds common to multiple groups of aquatic organisms (Hammer 1986, Green 1993, Eggermont et al. 2006), created clear and deterministic community shifts in both groups of zoobenthos (Fig. 3). Onset of a similarly variable but on average wetter hydroclimate regime about 800 yr ago induced a long-term transition toward more continuous freshwater conditions and establishment of a wide spectrum of macrophyte-associated benthic habitats (Verschuren et al. 2000*a*, Van der Meeren et al. 2019). Consequently, it caused a shift from salinity to water depth as dominant driver of the lake's zoobenthos community dynamics.

Besides the direct and indirect effects of abiotic thresholds being crossed, the trajectory and eventual outcome of community assembly is also affected by the varied dispersal strategies of different groups of aquatic biota (De Bie et al. 2012) as well as by ecological succession or priority effects (Mergeay et al. 2011), which all create additional variation in the presence and relative abundance of individual species in an aquatic community at any one time. The notion that historical (i.e., preceding) disturbances and ecosystem trajectories play a fundamental role in community assembly, and co-determine the

ecological drivers of a system (Ricklefs 1987), is well established in river ecology (Boulton et al. 1992, Haghkerdar et al. 2019) but appears underappreciated in research on dynamic lake systems. High-quality paleoecological archives can play an important role to fill this gap. The regulatory role of salinity in the history of Lake Naivasha presents a case of how the long-term dynamics of an aquatic community can be driven by the frequency and magnitude of past disturbances, which are thus part and parcel of the invisible preset (Magnuson 1990).

Relative magnitude of anthropogenic and natural disturbance

Anthropogenic climate change and water extraction cause increasing stress on hydrologically dynamic aquatic ecosystems worldwide, necessitating a robust framework to understand the longer-term vulnerability of such systems and to develop prognoses for their future (Jeppesen et al. 2015). However, this is complicated by the often diverse hydrochemical response of lakes to hydrological change, even within relatively small regions (Tweed et al. 2011). Moreover, ecosystems are to some degree stochastic due to ecological drift (Chase 2007), limiting hope to predict the direction and magnitude of community shifts in naturally dynamic environments. Without long-term reference frame, it may be impossible to conclude if a lake at any given moment is experiencing a relatively predictable and reversible shift in ecological state (cf. the pre-1240 CE alternation between saline and freshwater communities in CIC), or a more fundamental and permanent regime shift (such as occurred there c. 800 yr ago). Given that human alteration of lake hydrology often extends over multiple decades or even centuries, only paleoecological data can provide the system-level long-term perspective required to properly assess the relative magnitude of anthropogenic impacts and natural dynamics (Anderson et al. 2006, Willis and Birks 2006, Bennion et al. 2011, Gell et al. 2013).

In this context, also Lake Naivasha (including CIC) has been profoundly altered by human impacts since the early 20th century; this includes increased sediment and nutrient loadings from agriculture, stocking of fish and crayfish, water abstraction, and the introduction of exotic plants (Harper et al. 1995, Becht and Harper 2002, Mergeay et al. 2004, Stoof-Leichsenring et al. 2011). Even within this historical period, multi-faceted anthropogenic ecosystem alteration is superimposed on the ecosystem effects of major natural fluctuation in lake depth (Fig. 3D) and surface area (between ~100 and >200 km^2), in recent decades supplemented by changes in the lake's water balance associated with anthropogenic climate change. Given this multitude of simultaneous stressors, it is altogether striking that the zoobenthos community of Lake Naivasha, as represented by the chironomids and ostracods, has remained largely similar during the 20th century as during the three centuries prior. Having been confronted with a highly dynamic environment through the ages, high resilience in this zoobenthos community is perhaps to be expected (Holling 1973). On the other hand, highly dynamic aquatic ecosystems such as Lake Naivasha complicate the setting of ecological baseline conditions (Kotiaho et al. 2016) and/or a limit of acceptable change (Finlayson et al. 2015), in the context of environmental restoration: Although the varied anthropogenic stressors may seriously affect ecosystem functioning, this may not be uniquely discernible at the level of its biological communities, nor may it be possible to formulate adequate restoration targets with regard to these communities. Lake Naivasha is protected as a wetland of international importance under the Ramsar Convention since 1995, and managed in a basin-integrated and research-guided manner by the Lake Naivasha Riparian Association, with representation of all domestic and industrial stakeholders (Evrard and Harper 2002, Harper and Mavuti 2004, Geheb and Kelly 2005). In this context, paleoecological research can contribute meaningful data to define the boundary conditions within which the ecological character of this and other important tropical wetlands can be maintained under the Ramsar Convention (Finlayson et al. 2015). Rather than concrete restoration targets, the long-term paleoecological data presented here provide the necessary framework to truly understand habitat dynamics and ecosystem functioning in fluctuating aquatic ecosystems under natural conditions, as all-important benchmark in relation to anthropogenic disturbance.

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Literature Cited

Anderson, N. J., H. Bugmann, J. A. Dearing, and M.-J. Gaillard. 2006. Linking palaeoenvironmental data and models to understand the past and to predict the future. Trends in Ecology & Evolution 21:696–704.

Becht, R., and D. M. Harper. 2002. Towards an understanding of human impact upon the hydrology of Lake Naivasha, Kenya. Hydrobiologia 488:1–11.

Bennion, H., R. W. Battarbee, C. D. Sayer, G. L. Simpson, and T. A. Davidson. 2011. Defining reference conditions and restoration targets for lake ecosystems using palaeolimnology: a synthesis. Journal of Paleolimnology 45:533–544.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73:1045–1055.

Boulton, A. J., C. G. Peterson, N. B. Grimm, and S. G. Fisher. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. Ecology 73:2192–2207.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences USA 104:17430–17434.

Clark, F., A. Beeby, and P. Kirby. 1989. A study of the macro-invertebrates of Lakes Naivasha, Oloidien and Sonachi, Kenya. Revue D'hydrobiologie Tropicale 22:21–33.

Cohen, A. S. 2003. Paleolimnology: the history and evolution of lake systems. Oxford University Press, Oxford, UK.

Cohen, A. S., R. Dussinger, and J. Richardson. 1983. Lacustrine paleochemical interpretations based on eastern and southern African ostracodes. Palaeogeography Palaeoclimatology Palaeoecology 43:129–151.

Comín, F. A., R. Julià, and P. Comín. 1991. Fluctuations, the key aspect for the ecological interpretation of saline lake ecosystems. Oecologia Aquatica 10:127–135.

De Bie, T., et al. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15:740–747.

De Deckker, P., and R. M. Forester. 1988. The use of ostracods to reconstruct continental palaeoenvironmental records. Pages 175–199 *in* P. De Deckker, J.-P. Colin, and J.-P. Peypouquet, editors. Ostracoda in the Earth sciences. Elsevier, Amsterdam, The Netherlands.

De Laender, F., D. Verschuren, R. Bindler, O. Thas, and C. R. Janssen. 2012. Biodiversity of freshwater diatom communities during 1000 years of metal mining, land use, and climate change in central Sweden. Environmental Science & Technology 46:9097–9105.

Dudgeon, D., et al. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163–182.

Eggermont, H., P. De Deyne, and D. Verschuren. 2007. Spatial variability of chironomid death assemblages in the surface sediments of a fluctuating tropical lake (Lake Naivasha, Kenya). Journal of Paleolimnology 38:309–328.

Eggermont, H., O. Heiri, and D. Verschuren. 2006. Fossil Chironomidae (Insecta: Diptera) as quantitative indicators of past salinity in African lakes. Quaternary Science Reviews 25:1966–1994.

Evrard, M., and D. M. Harper. 2002. Towards the sustainability of the Lake Naivasha Ramsar site and its catchment. Hydrobiologia 488:191–203.

Finlayson, C. M., S. J. Clarke, N. C. Davidson, and P. Gell. 2015. Role of palaeoecology in describing the ecological character of wetlands. Marine and Freshwater Research 67:687–694.

Geheb, K., and K. Kelly. 2005. Lake Naivasha: local management of a Kenyan Ramsar site. Eastern Africa Regional Programme of the International Union for the Conservation of Nature (Nairobi) and Lake Naivasha Riparian Association (Naivasha). Lake Naivasha Riparian Association, Karagita, Kenya.

Gell, P., K. Mills, and R. Grundell. 2013. A legacy of climate and catchment change: the real challenge for wetland management. Hydrobiologia 708:133–144.

Gownaris, N. J., K. J. Rountos, L. Kaufman, J. Kolding, K. M. M. Lwiza, and E. K. Pikitch. 2018. Water

level fluctuations and the ecosystem functioning of lakes. Journal of Great Lakes Research 44:1154–1163.

Green, J. 1993. Zooplankton associations in East African lakes spanning a wide salinity range. Hydrobiologia 267:249–256.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, UK.

Grimm, E. C. 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Computers & Geosciences 13:13–35.

Haghkerdar, J. M., J. R. McLachlan, A. Ireland, and H. S. Greig. 2019. Repeat disturbances have cumulative impacts on stream communities. Ecology and Evolution 9:2898–2906.

Hammer, U. T. 1986. Saline lake ecosystems of the World. Springer, Dordrecht, The Netherlands.

Harper, D. M., C. Adams, and K. Mavuti. 1995. The aquatic plant communities of the Lake Naivasha wetland, Kenya: pattern, dynamics and conservation. Wetlands Ecology and Management 3:111–123.

Harper, D. M., and K. Mavuti. 2004. Lake Naivasha, Kenya: ecohydrology to guide the management of a tropical protected area. Ecohydrology and Hydrobiology 4:287–305.

Hart, B. T., P. Bailey, R. Edwards, K. Hortle, K. James, A. McMahon, C. Meredith, and K. Swadling. 1991. A review of the salt sensitivity of the Australian fresh-water biota. Hydrobiologia 210:105–144.

Herbst, D. B. 1988. Comparative population ecology of *Ephydrahians* Say (Diptera: Ephydridae) at Mono Lake (California) and Abert Lake (Oregon). Hydrobiologia 158:145–166.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Jeppesen, E., et al. 2014. Climate change impacts on lakes: an integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes. Journal of Limnology 73:88–111.

Jeppesen, E., et al. 2015. Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. Hydrobiologia 750:201–227.

Kalk, M. 1979. Zooplankton in Lake Chilwa: adaptations to changes. Monographiae Biologicae 35:123–141.

Kassambara, A., and F. Mundt. 2017. factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.5. https://CRAN.R-project.org/package=factoextra

Kaushal, S. S., P. M. Groffman, G. E. Likens, K. T. Belt, W. P. Stack, V. R. Kelly, L. E. Band, and G. T. Fisher. 2005. Increased salinization of fresh water in the northeastern United States. Proceedings of the National Academy of Sciences USA 102:13517–13520.

Kipkemboi, J. 2016. Vascular plants in Eastern Africa Rift Valley saline wetlands. Pages 285–293 *in* M. Schagerl, editor. Soda lakes of East Africa. Springer International Publishing, Chamonix, Switzerland.

Kolding, J., and P. A. M. van Zwieten. 2012. Relative lake level fluctuations and their influence on productivity and resilience in tropical lakes and reservoirs. Fisheries Research 115:99–109.

Kotiaho, J. S., B. Ten Brink, and J. Harris. 2016. A global baseline for ecosystem recovery. Nature 532:37.

LaBaugh, J. W., T. C. Winter, G. A. Swanson, D. O. Rosenberry, R. D. Nelson, and N. H. Euliss. 1996. Changes in atmospheric circulation patterns affect midcontinent wetlands sensitive to climate. Limnology and Oceanography 41:864–870.

Langbein, W. B. 1960. The salinity and hydrology of closed lakes. Journal of Geophysical Research 65:1635.

Larocque, I., R. Pienitz, and N. Rolland. 2006. Factors influencing the distribution of chironomids in lakes distributed along a latitudinal gradient in northwestern Quebec, Canada. Canadian Journal of Fisheries and Aquatic Sciences 63:1286–1297.

Leavitt, P. R., and D. L. Findlay. 1994. Comparison of fossil pigments with 20 years of phytoplankton data from eutrophic lake 227, experimental lakes area, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 51:2286–2299.

Magnuson, J. J. 1990. Long-term ecological research and the invisible present – Uncovering the processes hidden because they occur slowly or because effects lag years behind causes. BioScience 40:495–501.

McLachlan, A. J. 1979. Decline and recovery of the benthic invertebrate communities. Monographiae Biologicae 35:143–160.

Melack, J. M. 1988. Primary producer dynamics associated with evaporative concentration in a shallow, equatorial soda lake (Lake Elmenteita, Kenya). Hydrobiologia 158:1–14.

Mergeay, J., L. De Meester, H. Eggermont, and D. Verschuren. 2011. Priority effects and species sorting in a long paleoecological record of repeated community assembly through time. Ecology 92:2267–2275.

Mergeay, J., D. Verschuren, L. Van Kerckhoven, and L. De Meester. 2004. Two hundred years of a diverse Daphnia community in Lake Naivasha (Kenya): effects of natural and human-induced environmental changes. Freshwater Biology 49:998–1013.

Müller, F., et al. 2016. Assessing resilience in long-term ecological data sets. Ecological Indicators 65:10–43.

Nash, D. J., G. De Cort, B. M. Chase, D. Verschuren, S. E. Nicholson, T. M. Shanahan, A. Asrat, A.-M. Lezine, and S. W. Grab. 2016. African hydroclimatic variability during the last 2000 years. Quaternary Science Reviews 154:1–22.

Nielsen, D. L., and M. A. Brock. 2009. Modified water regime and salinity as a consequence of climate change: prospects for wetlands of Southern Australia. Climatic Change 95:523–533.

Olaka, L. A., E. O. Odada, M. H. Trauth, and D. O. Olago. 2010. The sensitivity of East African rift lakes to climate fluctuations. Journal of Paleolimnology 44:629–644.

Ricklefs, R. E. 1987. Community diversity – Relative roles of local and regional processes. Science 235:167–171.

Rumes, B., T. Van der Meeren, K. Martens, and D. Verschuren. 2016. Distribution and community structure of Ostracoda (Crustacea) in shallow waterbodies of southern Kenya. African Journal of Aquatic Science 41:377–387.

Schagerl, M., and A. Burian. 2016. The ecology of African soda lakes: driven by variable and extreme conditions. Pages 295–320 *in* M. Schagerl, editor. Soda lakes of East Africa. Springer International Publishing, Chamonix, Switzerland.

Seddon, A. W. R., et al. 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. Journal of Ecology 102:256–267.

Silk, N., and K. Ciruna. 2013. A practitioner's guide to freshwater biodiversity conservation. The Nature Conservancy, Boulder, Colorado, USA.

Stoof-Leichsenring, K. R., A. Junginger, L. A. Olaka, R. Tiedemann, and M. H. Trauth. 2011. Environmental variability in Lake Naivasha, Kenya, over the last two centuries. Journal of Paleolimnology 45:353–367.

ter Braak, C. J. F. 1994. Canonical community ordination. Part I: basic theory and linear methods. Ecoscience 1:127–140.

Tudorancea, C., and A. D. Harrison. 1988. The benthic communities of the saline lakes Abijata and Shala (Ethiopia). Hydrobiologia 158:117–123.

Tweed, S., M. Grace, M. Leblanc, I. Cartwright, and D. Smithyman. 2011. The individual response of saline lakes to a severe drought. Science of the Total Environment 409:3919–3933.

Van der Meeren, T., E. Ito, K. Laird, B. Cumming, and D. Verschuren. 2019. Ecohydrological evolution of Lake Naivasha (central Rift Valley, Kenya) during the past 1650 years, as recorded by ostracod assemblages and stable-isotope geochemistry. Quaternary Science Reviews 223:105906. https://doi.org/10.1016/j.quascirev.2019.105906

Vareschi, E., and A. Vareschi. 1984. The ecology of Lake Nakuru (Kenya): IV. Biomass and distribution of consumer organisms. Oecologia 61:70–82.

Verschuren, D. 1997. Taxonomy and ecology of subfossil Chironomidae (Insecta, Diptera) from Rift Valley lakes in central Kenya. Archiv für Hydrobiologie 107:467–512.

Verschuren, D. 2001. Reconstructing fluctuations of a shallow East African lake during the past 1800 yrs from sediment stratigraphy in a submerged crater basin. Journal of Paleolimnology 25:297–311.

Verschuren, D. 2003. Lake-based climate reconstruction in Africa: progress and challenges. Hydrobiologia 500:315–330.

Verschuren, D., K. R. Laird, and B. F. Cumming. 2000*a*. Rainfall and drought in equatorial east Africa during the past 1,100 years. Nature 403:410–414.

Verschuren, D., J. Tibby, K. Sabbe, and N. Roberts. 2000*b*. Effects of depth, salinity, and substrate on the invertebrate community of a fluctuating tropical lake. Ecology 81:164–182.

Walker, I. R. 1987. Chironomidae (diptera) in paleoecology. Quaternary Science Reviews 6:29–40.

Waterkeyn, A., P. Grillas, B. Vanschoenwinkel, and L. Brendonck. 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. Freshwater Biology 53:1808–1822.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems. Academic Press, San Diego, California, USA.

White, P. S., and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62:399–450.

Wigdahl, C. R., J. E. Saros, S. C. Fritz, J. R. Stone, and D. R. Engstrom. 2014. The influence of basin morphometry on the regional coherence of patterns of diatom-inferred salinity in lakes of the northern Great Plains (USA). Holocene 24:603–613.

Williams, W. D. 1981. Inland salt lakes – an introduction. Hydrobiologia 81:1–14.

Williams, W. D. 1998. Salinity as a determinant of the structure of biological communities in salt lakes. Hydrobiologia 381:191–201.

Williams, W. D. 1999. Salinisation: a major threat to water resources in the arid and semi-arid regions of the world. Lakes & Reservoirs: Research and Management 4:85–91.

Williams, W. D., A. J. Boulton, and R. G. Taaffe. 1990. Salinity as a determinant of salt lake fauna – A question of scale. Hydrobiologia 197:257–266.

Willis, K., and H. J. B. Birks. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314:1261–1265.

Zohary, T., and I. Ostrovsky. 2011. Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. Inland Waters 1:47–59.

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