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Climate, Vegetation, and Weathering across Space and Time in Lake Tanganyika (Tropical Eastern Africa)

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Climate, vegetation, and weathering across space and time in Lake Tanganyika (tropical eastern Africa)



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ABSTRACT

Climate and vegetation influence weathering rates and processes; however, evaluating the effects of each and feedbacks between systems, has yet to be accomplished for many types of landscapes. A detailed understanding of how these processes interact to shape landscapes is particularly crucial for reconciling future scenarios of changing climate, where profound alterations to both the biosphere and geosphere are anticipated. In the tropics, ecosystem services, such as soil and water quality, are linked to both vegetation and weathering processes that form a strong control on natural resources that are the foundation of many communities' daily subsistence. This understanding is further complicated by intensifying land-use within tropical watersheds, which decouples vegetation change from climate; it is yet unclear what the direct effects of vegetation change may be on erosion and weathering when operating independent of climate. Long term observational records tracking changes to the critical zone do not exist in tropical Africa, however, sedimentary paleo-records from lakes are often of sufficient length and resolution to record the impact of bioclimatic variability on surface processes. Here, we use a novel approach combining long (60ka) and intermediate-length (400yrs) lake sediment records along with historical repeat photography from Lake Tanganyika (Tanzania) to document changes and relationships among climate, vegetation, and weathering at multiple scales. These records illustrate that glacial-interglacial climate change did not significantly alter weathering intensity. Instead, we observe chemical and physical weathering responses only when the vegetation becomes more open beginning at the transition to the Holocene. Also, the largest change in chemical weathering intensity occurs only within the last ~3ka. This is consistent with a major reorganization of vegetation and is directly attributable to Iron Age human activity, rather than climate. Furthermore, anthropogenic landscape alteration as early as ~2.5ka, in addition to well-documented comparisons of historical land-use, suggest widespread responses of both chemical weathering intensity and enhanced soil erosion to human activity. This shows that changes in vegetation structure induced by anthropogenic activity, decoupled from climate change, generate a disproportionately large weathering response.

1. Introduction

In tropical eastern Africa, ecosystems services support rapidly growing populations living in isolated, low-income communities that have few resources to mitigate the impacts of environmental change (Field et al., 2014). Natural and anthropogenic changes that influence the landscape-molding processes of weathering and erosion can have profound effects on these ecosystem services (Pelletier et al., 2015). For

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example, complex environmental dynamics in sub-Saharan Africa threaten to undermine provisioning and regulating services such as the availability of clean water and access to food from local fisheries, animal husbandry, and rainfed agriculture (Cohen et al., 2016). The Intergovernmental Panel on Climate Change (IPCC) (Field et al., 2014) has highlighted this problem as a critical security and economic concern associated with global warming. Strategic management of these natural systems to preserve ecosystem services is thus very important, especially considering the projections for rapid population growth and the limited accessibility to resources across much of Africa (Linard et al., 2012). However, development of targeted management strategies requires predictions of geosphere alterations and a detailed understanding of the direct and indirect linkages to other systems, such as the biosphere and atmosphere. Climate and vegetation have both long been known to play important roles in determining weathering regimes on various time scales (Ivory et al., 2014, 2017). Although many studies focus on predicting changes to the atmosphere or biosphere in the future, feedbacks between these systems and their influence on the geosphere, such as altered chemical weathering and erosional intensity, have been largely unexplored (Brantley et al., 2011).

Weathering on the landscape encompasses interactions that link biotic (vegetation and other organisms) and abiotic (climate, regional geology) processes. Climate plays a fundamental role in physical and chemical weathering intensity through alterations of temperature, hydrology, and water availability, which regulate reaction rates and alter the transport of sediments and solutes (Jenny, 1994; White et al., 1999; Riebe et al., 2004; Rasmussen et al., 2011). The importance of biosphere-geosphere interactions has been highlighted in reviews (e.g. Brantley et al., 2011) as well as by modeling and observational studies in experimental watersheds (e.g. Egli et al., 2008; Goddéris et al., 2009; Acosta et al., 2015; Pelletier et al., 2016). These studies have pointed to the importance of vegetation, particularly vegetation structure, for modulating chemical weathering intensity and the magnitude of erosion through interactions with canopies and root networks, as well as through changes to soil chemistry (e.g. Goddéris et al., 2009; Bormann and Likens, 2012). Furthermore, although recent studies have highlighted the role of vegetation structure for directly driving the intensity of weathering and erosion over long time scales, vegetation change is also strongly related to climate change. This suggests that in addition to their individual roles in determining weathering regimes, strong feedbacks exist among vegetation, climate, and weathering (Ivory et al., 2014, 2017; Acosta et al., 2015; Garcin et al., 2017).

Although feedbacks between climate and vegetation are critical drivers of weathering intensity in Africa, anthropogenic activities such as land-use change decouples vegetation change from climate. In the case of Africa, intensive burning and wood harvesting have been noted as early as the Iron Age, resulting in a fundamental shift in lowland vegetation (Hall et al., 2008; Mumbi et al., 2009). More recently, dramatic population increases around the 1700s in areas isolated from devastation by the slave trade and disease, such as along the northern Tanzanian shore of Lake Tanganyika, have left documentation of large-scale deforestation due to the intensification of agriculture for staple crops like cassava (Koponen, 1988; Schoenbrum, 1998; Chrétien, 2003). Thus, being able to predict changes in weathering requires an understanding of the direct and indirect impacts of climate and vegetation both in the presence and absence of land cover conversion by people.

In this study, we use a strategy which couples both spatial and temporal approaches to investigate direct and indirect controls on weathering intensity in the watersheds of Lake Tanganyika, Tanzania. Our aim is to characterize the primary control or set of linked controls governing landscape evolution in the hinterland of a large tropical rift lake at different timescales using data from both source (repeat photography) and sink (long lake sediment cores). Lake Tanganyika is an excellent target for weathering studies, due to recent concerns about the effect of climate change and landscape degradation on aquatic habitats and fisheries in the area (Alin et al., 1999; Eggermont and Verschuren, 2003; McIntyre et al., 2005; Cohen et al., 2016). To do this, we used well-dated lake sediments to record a pre-Anthropogenic baseline of biosphere-atmosphere feedbacks on weathering, as well as shorter records from multiple sites within the same lake basin with different land-use histories to evaluate the effects of climate and vegetation. We use paired indicators of ecological change (fossil pollen, microcharcoal), erosion (grain size analysis, mass accumulation rates), and chemical weathering (elemental analysis) coupled with previously published records of climate from these same sediment cores. Lastly, we include several vintages of georeferenced repeat photographs, which provide a powerful visualization of the landscape changes implied by the sedimentological records from disturbed watersheds, which document degradation due to deforestation, agriculture, and fire.

1.1. Modern setting

Lake Tanganyika (~5–9°S) is a rift lake located in the western branch of the East African Rift System (Fig. 1). It is the world's second deepest lake (1470 m), is permanently stratified below 150 m, and drains a watershed that includes much of central southeastern Africa (238,700 km²; Bootsma and Hecky, 2003). It has a single outlet, the Lukuga River, which drains into the Congo Basin; however, despite being hydrologically open, the shallow sill depth (<10 m) leads to basin closure with small lake-level fluctuations (Craig, 1974; Dettman et al., 2005). The bedrock geology of the watershed is dominated by Proterozoic gneiss, metasedimentary, and metavolcanic rocks, with minor Neogene-Quaternary volcanics only in the upstream Kivu basin, and Quaternary sedimentary deposits in the headwaters of the Malagarasi River watershed (Fig. 1; Craig, 1974). Although sediment delivered to shorelines may vary in composition related to local bedrock, at the basin-scale within the deep lake this localized effect is minimal (Soreghan, 2016). Therefore, relative bedrock homogeneity makes the Lake Tanganyika watershed an excellent natural laboratory for investigating spatial and temporal effects of climate and vegetation change on weathering.

Due to its large spatial extent, climate varies throughout the Lake Tanganyika basin. Rainfall shows a marked N–S gradient in timing and amount (Nicholson, 1996). Highest rainfall occurs in the northern highland watershed in two rainy seasons from March–May and September–December (1600 mm/yr), and lowest occurs in the south with single November–March rainy season (870 mm/yr). Temperature, however, varies little throughout the year (22.8–24.8 °C at 900m asl; 15.8–20.4 °C at 1500m asl; Ivory and Russell, 2016).

Vegetation in the noncultivated lowlands is dominated by miombo woodland. This low diversity, deciduous woodland grows in areas of highly seasonal rainfall and is dominated by trees such as Brachystegia, Berlinia, and Isoberlinia (White, 1983, Fig. 1). The composition and structure of these woodlands fall along a spectrum. Wetter assemblages with high canopy cover grow in areas with >1000 mm/yr rainfall. In areas with sandier soils or lower mean annual precipitation (MAP), drier miombo occurs, which is characterized by lower canopy cover and a higher proportion of understory grass and Combretaceae. In regions with heavy human disturbance, deciduous thickets and bushlands are common. In undisturbed highlands above 1500 m asl, afromontane forests dominate. These are commonly high stature, closed-canopy forests occurring in wetter or cooler areas with higher species richness. These forests are commonly composed of large, long-lived trees such as Olea capensis, Olea africana, Podocarpus spp., Juniperus procera, and Ericaceae. However, much of the Afromontane forest areas are relict in comparison to the extensive highland areas which has been cleared, largely for grazing.

2. Methods

2.1. Core locations

Cores for this study were taken in multiple locations throughout the lake. Cores KH3 and KH4 were collected from the Kalya Horst and

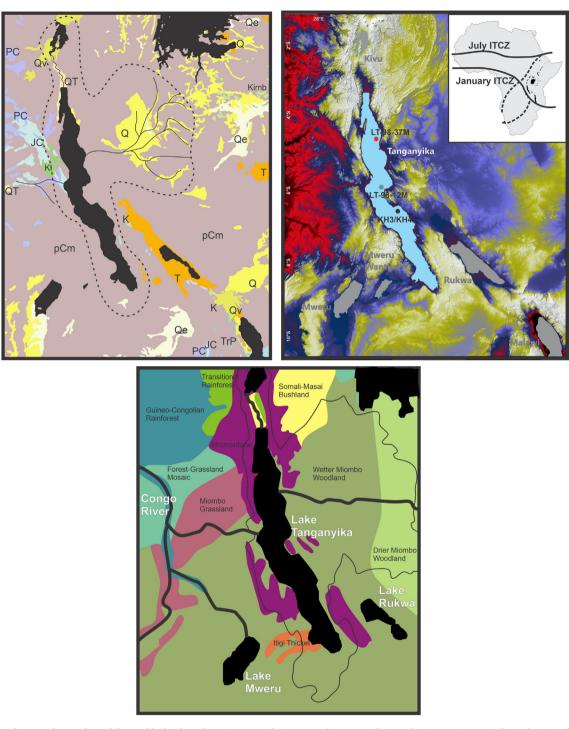


Fig. 1. (Upper Left) Map of East African lakes and bedrock geology. (Upper Right) Topographic map with inset showing major tropical circulation. Solid lines are the Intertropical Convergence Zone (ITCZ) and dashed lines are Congo Air Boundary, adapted from Ivory and Russell (2016). Core locations are shown in black (KH3/KH4), green (LT-98-12M), and red (LT-98-37M). (Lower Middle) Vegetation map of the Lake Tanganyika watershed.

Platform regions, south of Mahale Mountain National Park (Fig. 1; $6^{\circ}42'S$, $29^{\circ}50'E$ 600m and 330m water depth, respectively) in 2004. Further information about the cores and site can be found in Felton et al. (2007) and McGlue et al. (2008). KH3 comprises a ~60kyr record, and KH4 comprises a ~30kyr record. Age models for both cores are based on a mixed effect regression model presented in Tierney et al. (2008). The age model is based on 26 AMS ¹⁴C dates on KH3 and seven AMS ¹⁴C dates on KH4 between 450 and 640 cm core depth, as well as stratigraphic correlation between cores. A hiatus is observed in KH3 from 21 to 28ka that is not observed in KH4. Both cores have similar lithologies, consisting primarily of massive silty clays and clayey silts until the last deglacial transition, when laminated and massive diatomaceous silty clays predominate (Felton et al., 2007).

Other cores used in the study were collected in 1998 as part of the Lake Tanganyika Biodiversity Project (LTBP). Detailed information about the core locations, geochronology, and aquatic and terrestrial paleoecology can be found in Cohen et al. (2005a; 2005b), Msaky et al. (2005), Palacios-Fest et al. (2005), and McKee et al. (2005). However, we updated the chronologies by recalibrating the AMS ¹⁴C dates from these cores using SHCal20 (Reimer et al., 2020). We focus on three cores, LT-98-2M and LT-98-12M, which both come from off the Lubulungu River watershed, offshore of the Mahale Mountain National Park, and LT-98-37M from Mwamgongo River watershed along the northern Tanzanian border. LT-98-2M (6°10'S, 29°42'E; 110m water depth) is an ~4.5kyr record whose age model is based on a third order polynomial on four AMS ¹⁴C dates, as well the core top is assumed to be modern due to preservation of the sediment-water interface (McKee et al., 2005). LT-98-12M (6°10'S, 29°43'E; 126m water depth) is ~600yr record whose age model is based on a²¹⁰Pb chronology on the upper 4 cm and three AMS ¹⁴C dates. LT-98-37M (4°37'S, 29°38'E; 95m water depth) is also ~600 yr record whose age model is based on a²¹⁰Pb chronology on the upper 20 cm and three AMS ¹⁴C dates. LT-98-37M were chosen as they record similar time periods but contrasting land-use histories, and thus can be used to compare the influence of climate and human disturbance over a well recorded period in the basin.

Change point detection was conducted on sedimentological datasets produced on all cores. This analysis was conducted using the *changepoint* package in R using the "Segment Neighborhoods" method to identify multiple change points in a time series (Auger and Lawrence, 1989). This method allows for the statistical determination of shifts in mean or variability. All mentions in the text of changes to mean and variability of indicators described here were identified using this method.

2.2. Particle size

Terrigenous particle size (sand: > 62.5 μ m; silt: 3.9–62.5 μ m; clay: < 3.9 μ m) distributions were analyzed on core KH4 at the University of Kentucky. The interpretation of particle size within the framework of the lithostratigraphy is used as an indication of depositional processes and the hydrodynamic environment affecting sediment entrainment and movement. This indicator has been used for interpreting patterns of erosion and sediment transport in tropical watersheds in previous source-to-sink studies of African rift lakes (Ivory et al., 2014, 2017). Particle size analysis was conducted on the terrigenous fraction using a Malvern laser diffraction analyzer with a Hydro 2000S sample dispersion bench. Samples were chemically pre-treated to remove carbonate, biogenic silica, and organic matter using standard procedures, and dispersed using dilute sodium hexametaphosphate and a wrist-action shaker prior to analysis. Samples for the grain size analysis were collected from KH4 u-channels every ~10 cm.

2.3. Elemental analysis

Elemental analysis was conducted on core KH3 using ICP-MS measurements on quadruple distilled acid (HF, HNO₃, HClO₄, HCl) digested sediment samples; full methodological details are presented in Felton et al. (2007). Weight percentages of the oxides Al₂O₃, CaO, K₂O, and Na2O were calculated from elemental weights and from these values molar ratios were calculated to generate a Chemical Index of Alteration (CIA; Nesbitt and Young, 1982) chemostratigraphy. The CIA is one of the most widely used indices of chemical alteration of siliciclastic rocks, and numerous studies have shown that CIA can be used to infer past physical and chemical weathering conditions (e.g., Goldberg and Humayun, 2010; Bahlburg and Dobrzinski, 2011). The dimensionless CIA $(CIA = [Al_2O_3/(Al_2O_3+CaO^*+Na_2O + K_2O)] \times 100);$ where CaO* refers to silicate-bound Ca only) expresses the degree of chemical alteration of material from ~50 (unaltered feldspar) to 100 (bauxite; Nesbitt and Young, 1982). We applied a correction to the CaO* value to account for calcium carbonate content in the sediment using the approach of McLennan (1993). Kaolinite (CIA ~90) is commonly found in heavily leached soils in the tropics in areas marked by high rainfall and reflecting higher chemical weathering (Birkeland, 1984). Smectite (CIA ~80) is also typical in tropical soils, however, it is primarily found in semi-arid regions where climate is marked by high rainfall seasonality or in areas with extensive volcanic soils (Chamley, 1989; Weaver, 1989; Kalindekafe et al., 1996; Alizai et al., 2012). Soils with abundant feldspars and micas (illite and chlorite) exhibit lower CIA values and are generally interpreted to reflect environments influenced by physical weathering process rather than chemical leaching in soil profiles (Thiry, 2000).

2.4. Fossil pollen

Fossil pollen data from cores KH3 and KH4 were presented in Ivory and Russell (2016) and were processed following the standard methods of Faegri and Iverson (1989). Pollen data from LT-98-2M, LT-98-12M, and LT-98-37M were presented in Msaky et al. (2005). All pollen taxonomy was standardized following Vincens et al. (2007), and vegetation groupings presented in this study are based on biomes of White (1983) as well as prior pollen studies within the Lake Malawi and Tanganyika watersheds by DeBusk (1994), Vincens et al. (2007), and Ivory and Russell (2016).

2.5. Repeat photography

We present several series of repeat photographs (photographs taken in the same geographic position at different time points), which are powerful tools for conceptualizing the real effect of historical land-use impacts on the landscape (Schantz and Turner, 1958). Repeat photography around Lake Tanganvika allows us to investigate changes in vegetation type, individual plant species, their size and abundance, processes of urbanization, and geomorphic responses of landforms to these changes over a 97 year period (1920-2017) in the Kigoma region of western Tanzania. This work was based on photographs from sites taken by H. Shantz in 1920 and 1957 (Schantz and Turner, 1958). The Shantz photograph collection is presently housed in the herbarium of the University of Arizona. In 2005 as part of the Nyanza Project, many of the Shantz photograph sites were reoccupied based on his original field notes. A GPS unit was used to record coordinates and elevation for future reference. All 2005 photographs were taken July 21-30, with a tripod-mounted Nikon Coolpix 4500 digital camera. In May of 2017, the same sites were again reoccupied and digitally photographed with a pole-stabilized Nikon Coolpix A10 digital camera. A botanical interpretation of the photographs was conducted, and the resulting list of plants visible in the historical photographs from 1920, 1957, 2005 was compared with a current (2017) plant list for the area.

3. Results

3.1. KH3-KH4 (last 60kyr)

CIA values calculated using the major element data of Felton et al. (2007) have an average of 84.8 over the last 60ka (Fig. 2). In the early part of the record, these values remained near this long term average (85.6) and had very low variability (standard deviation = 1.6) prior to \sim 28ka. Following the hiatus, CIA showed a small decline (min = 81.5) until 16.8ka when an abrupt but small increase occurred. From 16-9ka, values remained once again near the long term average (86.2). However, during the early Holocene, although CIA mean values were stable (85.2) until \sim 4ka, the standard deviation increased to 3.01. In the upper portion of the record, mean CIA decreased gradually toward modern reaching minimum values of 66.6 at 3.3ka and 68.8 at 1.4ka, while variability remained very high (7.3).

The terrigenous grain size analysis and sedimentation rates of core KH4 showed relatively stable values, dominated by silty detritus until the Holocene (Fig. 2). Sedimentation rates remain quite low until the early Holocene when they rise to maximum values and remain high for the rest of the record. From the base of the core to \sim 20ka, silt:clay had a mean of 2.6. After \sim 20ka, there was brief rise to slightly higher values with a mean of 2.9 until \sim 14.9ka. At this point there was an abrupt return to pre-LGM mean values (2.6) followed by a very gradual increase until \sim 4.4ka. At \sim 4.4ka a decreasing trend begins, marked by higher standard deviation (0.76), which continued until the youngest sample in the

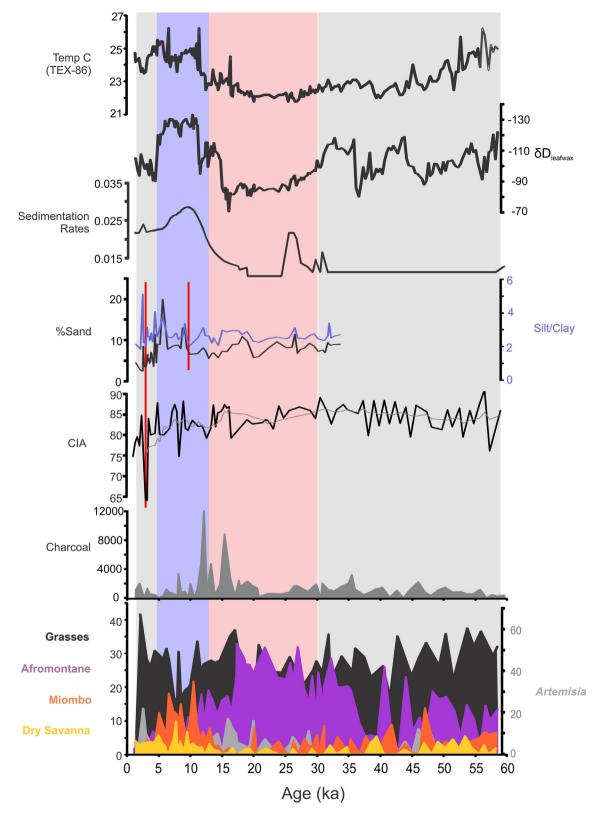


Fig. 2. Late Pleistocene-Holocene climate (TEX-86 and δD_{wax} , Tierney et al., 2008; 2010), sedimentological (chemical index of alteration [CIA], sedimentation rates, terrigenous grain size), and palynological (pollen and charcoal) indicators from cores KH3 and KH4 from Kalya Horst and Platform. For CIA, the light grey line is a 5 point running mean of the original dataset. All pollen data is reported in relative abundances (%). Charcoal influxes are in units of pieces/cm²/yr. Sedimentation rates are in m/yr. The red rectangle means drier than modern conditions, the blue rectangle means wetter than modern conditions, and grey means circa-modern conditions. Red line denotes the position of a significant change point with respect to mean and variability for grain size and CIA data, where the red line crosses a timeseries it represents a significant change in that series.

dataset. This trend towards the modern was marked by the only substantial increase in fine-grained terrigenous material in the entire record, with clay percentages that transitioned from 16 to 34%. Finally, the sand fraction was relatively invariant and only comprised on average 8.1% of the terrigenous fraction until 6.3ka. At this transition, a peak marked the maximum sand content of 20% at 5.6ka. This was followed by a gradual decline until the modern, when minimum sand values reached 2.5% and fine-grained material dominated. at Lake Tanganyika from cores KH3–KH4 appears in Ivory and Russell (2016) and is summarized here in Fig. 2. From 60 to 40ka, afromontane forest pollen were at moderate values (~20%), suggestive of more extensive forests than today. A short-term decrease in all arboreal pollen occurred from 40 to 37ka, when grass pollen dominated (40%). After 37ka, afromontane tree pollen reached maximum abundances (40%) and remained high until 17ka. At 17ka, an increase in the disturbance indicator *Artemisia* occurred, coeval with decrease in afromontane forest pollen (20%) and increase in charcoal fluxes until the early Holocene

A detailed description of the vegetation dynamics over the last 60ka

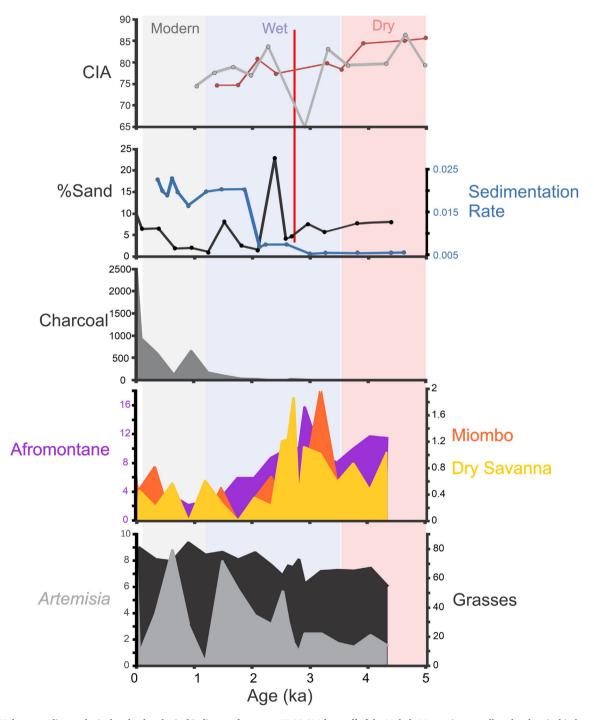


Fig. 3. Late Holocene sedimentological and palynological indicators from core LT-98-2M from off of the Mahale Mountains as well as the chemical index of alteration (CIA) calculated on KH3. For CIA, the red line is a 5 point running mean of the original dataset. All pollen data is reported in relative abundances (%). Charcoal influxes are in units of pieces/cm²/yr. Sedimentation rates are in m/yr. Red rectangle indicates dry climate, blue rectangle indicates wet climate, grey indicates near modern climate. Red line denotes the position of a significant change point with respect to mean and variability for grain size and CIA data, where the red line crosses a timeseries it represents a significant change in that series.

(Davies and Fall 2001; Munoz and Gajewski, 2010; Ivory and Russell, 2016). From 10-5ka, wet miombo tree pollen reached maximum abundances (10%), and grass pollen reached a minimum (30%) along with a decline in charcoal fluxes. Following 5ka, a decline in wet miombo tree pollen was coincident with increased dry savanna pollen (2%) and grass pollen (54%). The final transition occurred after 2.5ka. This included a final increase in *Artemisia* (max = 6.8%) as well as a small, but significant peak in charcoal fluxes (more than 1.5 times the standard deviation around the mean; Clifford and Booth, 2013).

3.2. LT-98 cores and repeat photography (4ka-present)

A detailed description of the palynological and sedimentological results of the shorter cores (Figs. 3 and 4; LT-98-2M, LT-98-12M, LT-98-37M) is found in Cohen et al. (2005a; 2005b), Msaky et al. (2005), and Palacios-Fest et al. (2005). Over the last ~4.2ka, terrigenous grain size from LT-98-2M showed values indicating a dominance of relatively fine-grained silty clays (<68 μ m fraction = average 94%) with a single peak of sand (20%) at 2.4ka. Charcoal influxes remained near zero until just after 2ka, when values rose steadily until modern. The vegetation was characterized by high abundances of dry savanna (1%), afromontane forest (10%), and miombo woodland (1.2%) until 2.6ka. After ~2.6ka, there was a sharp decline of all arboreal pollen as *Artemisia* (max = 9%), and grass pollen (max = 80%) abundances increased until modern.

LT-98-12M is located offshore from the Lubulungu River and its delta, in the Mahale Mountain National Park, a rugged and protected area that has undergone little historical anthropogenic alteration. This record shows a relatively low sedimentation rate of 0.05 gr/cm²/yr with a further decrease to 0.02 gr/cm²/yr around 1750 AD (Fig. 4). This record was also characterized by an increase in sand from ~5% to maximum values of 25% and a decrease in charcoal fluxes to near zero values by 1860 AD. The pollen record was marked by a minor increase in arboreal pollen (dry savanna, afromontane forest, and miombo woodlands) from 6% to 12%. LT-98-37M, in contrast, is from a watershed along the northern Tanzanian border that has likely undergone intense deforestation since the 1700s (Cohen et al., 2005a). This record shows decreasing sedimentation rates from 0.1 gr/cm²/yr to almost 0 gr/cm²/yr until 1900 AD, when average sedimentation rates abruptly increased to ~ 0.15 gr/cm²/yr until today. Sand abundances were very low, but decreased further from ~5 to 10%-2% by 1750 AD. Early charcoal values were similar to those in LT-98-12M (max = 4000 gr/cm²/yr and min = 1200 gr/cm²/yr); however, after 1700 AD, charcoal fluxes returned to high values of 4000 $gr/cm^2/yr$. The vegetation record was characterized by very high abundances of grass pollen that remain between 80 and 90% for the entirety of the record. The only major change was a large increase in Artemisia (from 1 to 5%) after 1600 AD.

Repeat photography at multiple locations around the Kigoma region of the lake's watershed illustrates that many plant taxa that were present in the 1920 and 1957 photographs were no longer present in the area by 2005 and 2017 (Fig. 5). In particular, this change is characterized by an increase in croplands and grasslands at the expense of native tree cover. The four photosets from the Nondwa Hill area (1: $4^{\circ}52'S$, $29^{\circ}37'E$, 802masl; 2: $4^{\circ}52'S$, $36^{\circ}54'E$, 796masl; 3: $4^{\circ}52'S$, $29^{\circ}37'E$, 792m asl) show trees of various species (e.g., *Vitex fischeri* and *Randia* spp.) are dominant

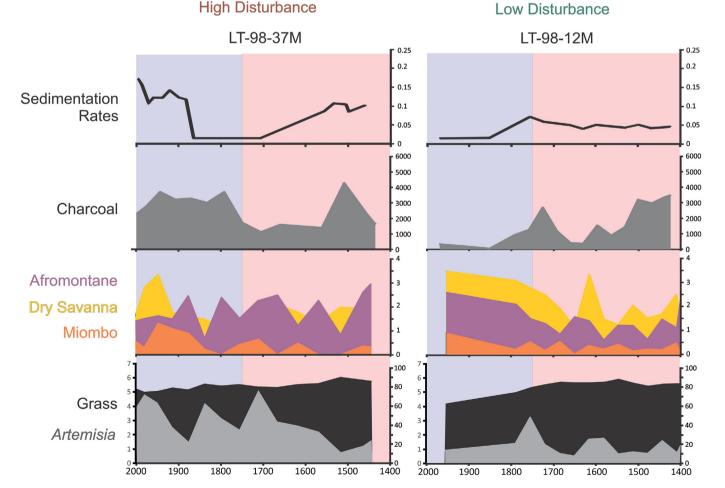


Fig. 4. Historical period sedimentological and palynological indicators from cores LT-98-12M (low disturbance) and LT-98-37M (high disturbance). All pollen data is reported in relative abundances (%). Charcoal influxes are in units of pieces/cm²/yr. Sedimentation rates are in cm/yr. Red rectangle indicates dry climate, blue rectangle indicates wet climate.

in 1920. Photoset 1 shows a replacement by grasses and herbs, particularly introduced crops such as okra, tomatoes, maize, eggplant, oil palm, and mango trees. Photoset 2 shows a high diversity of grasses and forbs, and the trees present are predominantly fire tolerant species, suggesting increased disturbance by fire. Photoset 3 also suggests increased fire frequency due to a decrease in trees and increase in grasses and dwarf shrubs and trees, which include *Brachystegia bussei*, *Isoberlinia*, and *Pterocarpus*. Photoset 4 shows active cultivation of cassava in thin, rocky soils denuded of native vegetation on the steep hillside itself, in addition to the presence of grasses, dwarf shrubs and trees.

4. Discussion

4.1. Late Pleistocene-Holocene transition

Over the last 60kyr, climate and vegetation in southeast Africa varied dramatically (Fig. 2). Reconstructions of rainfall based on hydrogen isotope ratios from plant leaf waxes (δD_{wax}) on core KH3 have shown that, over the last 60ka, Lake Tanganyika has undergone large-scale wetdry cycles associated with glacial-interglacial cycles and Heinrich events (Tierney et al., 2008). Aridity during the last glacial maximum (LGM) culminated in a >260 m lake level drop at \sim 21ka, which was the result of a ~42% decrease in effective moisture (P-E) (McGlue et al., 2008). In contrast, during the African Humid Period (AHP; ~10-5ka) Lake Tanganyika had an outlet during a period of enhanced monsoons and high summer rainfall, suggesting modern lake levels (Tierney et al., 2008). Temperature change generally followed global temperatures particularly within the last 40ka, with gradually decreasing values until the LGM $(-4 \,^{\circ}C)$, followed by a stepwise increase to the early Holocene, when mean temperatures were slightly higher than today (Tierney et al., 2008, 2010). In sum, the last 60ka at Lake Tanganyika shows extremely high temporal variability in both moisture and temperature such that the LGM to early Holocene climate range essentially equates to a transition from cool semi-arid to wet tropical environments.

However, despite the high amplitude climate variability at Lake

Tanganyika, vegetation structure changed very little over the last 60ka, until the mid to late Holocene (Fig. 2; Ivory and Russell, 2016). From 60ka through the end of the LGM, the watershed was dominated by afromontane forests, which gradually become more extensive regionally despite decreased precipitation (Ivory and Russell, 2016). Following the LGM, stepwise increases in monsoon intensity and rising temperatures resulted in a collapse of the montane forest around 17ka and increased wildfire activity until ~15ka; however, humid lowland forest and woodland established shortly after at 15ka and dominated the record until 4ka. This was coincident with the end of the AHP and resulted in a gradual reduction in moist miombo woodland in favor of thickets and scrubland. This transition to thickets and scrubland dominated by Combretaceae and herbaceous taxa represents the largest alteration in vegetation structure of record. Although wetter conditions prevailed after \sim 3ka as indicated by δD_{wax} , thicket and dry woodland dominated until the end of the record at ~1ka (Fig. 2). Some studies in East Africa have noted a similar lack of moister woodland recovery attributed to human activity during the Iron Age, due to a peak in the disturbance indicators (e.g. Ricinus communis, Artemisia) and charcoal (Taylor and Marchant, 1994; Vincens et al., 2005; Heckmann et al., 2014; Ivory and Russell, 2018).

Terrigenous particle size data show little change throughout the LGM and deglaciation, despite the large climate fluctuations (Fig. 2). In fact, no change point in variability or mean is detected until the Holocene. During the AHP, change point analysis of percent sand shows an increase in variability beginning at 9.3ka and continually increasing until ~5ka. This enhanced variability is coincident with the gradual decline of wet miombo woodland after a peak at 6.5ka. The largest change in the terrigenous particle size record comes at the end of the AHP, when a change is recorded towards finer grained material, marked by declines in both percent sand at 4.1ka and silt:clay at 2.4ka. The decrease in sand is coincident with enriched values of δD_{wax} , suggesting a decrease in monsoon intensity, which previously drove transport of riverine-derived coarse-grained sediment by nephaloid plumes deeper into the basin. The overall fining of sediments on the Kayla Platform from lithologies

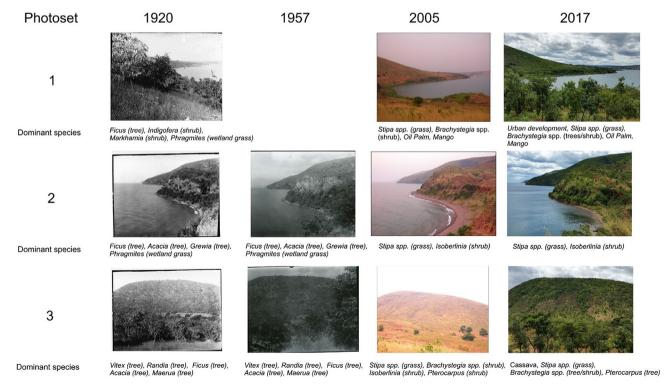


Fig. 5. Repeat photography from three sites along the Tanzanian shoreline from 1920 to 1957 (Shanz and Turner, 1958), 2005 and 2017 photographs were taken in the same locations. Note that the 2017 photographs were taken just after the wet season in comparison to the 2005 photographs which were taken in the dry season.

dominated by clayey silts to silty clays occurred 1.7kyr after the decrease in sand and increase in aridity, suggesting the fining may result from another mechanism.

Despite high amplitude fluctuations in both moisture and temperature, CIA also remains stable for much of the last 60ka (Fig. 2). Many studies suggest that increased reaction rates that drive the chemical alteration of siliciclastic rocks should increase during warmer, wetter times (e.g. Singer, 1984; Jenny, 1994); thus, it might be expected that CIA should be very high during the warm, moist early Holocene and lowest during cool, dry LGM. However, this does not appear to be the case. Instead, average CIA values are within 1 standard deviation of the long-term mean, indicating no significant changes. The CIA has a long term mean of 85, reflecting a strong contribution of highly weathered clay minerals into the basin during both cool/arid and warm/humid periods.

Marked changes in CIA occur at 2.4ka, when a decrease in mean and increase in variability occurred (Fig. 2). Although lower CIA values could be explained by a cooling or drying, this change point actually occurs during a relatively moist period between arid intervals centered at 4ka and 2ka in the region (Russell et al., 2005; Tierney et al., 2008). Furthermore, even these late Holocene arid episodes are relatively small in magnitude in comparison to Heinrich 1 and the LGM, which resulted in no significant change in CIA, suggesting that climate is not driving this decrease in chemical weathering intensity.

Instead, we note that the change points detected in CIA and silt:clay occur contemporaneously (Fig. 2). This indicates that the change in clay content to less weathered material, such as illite or smectite, is accompanied by an increase in overall clay abundance. At this same time, the pollen record suggests increased disturbance, inferred from the presence of *Artemisia*, as well as moderately increased charcoal influxes. This implies that vegetation structural alterations, particularly reduced vegetation density and increased disturbance, may be driving the decrease in particle size and chemical weathering intensity rather than climate. However, although the Kalya core records suggest that vegetation alteration may be driving the largest changes in weathering intensity over the last 60ka, the low sampling resolution in the last 4ka makes this conclusion challenging.

4.2. Late Holocene

In order to better tease apart these signals during the late Holocene, we refer to higher resolution palynological and sedimentological analyses from the 4.2kyr LT-98-2M core record collected to the north of the Kalya core site (Fig. 3). Over the course of this record, which corresponds to the gradual decline and increased variability in CIA observed in the KH3 core, we observe a similar vegetation transition characterized by an abrupt decrease in trees, particularly afromontane forest and miombo woodland, followed by a decrease in dry savanna taxa. This final decline in drier trees abruptly followed an increase in grass and indicators of disturbance (Artemisia). Furthermore, the expansion of more open disturbed vegetation, detected at 2.3ka, is immediately followed by a peak in terrigenous sand input (25%), an increase in sedimentation rates, and finally gradually increasing charcoal. The timing of the sedimentological changes, directly following the vegetation opening, suggests that there is a strong linkage between reduced tree cover on the landscape and flushing events accompanied by higher basinal sedimentation until the end of the record.

The higher resolution record of the late Holocene is in agreement with the longer record, suggesting that the weathering response detected in the basin was partially decoupled from climate in the late Holocene. We find that although δD_{wax} records in cores from both Lakes Malawi and Tanganyika indicate severe wet-dry transitions over this interval, neither the vegetation opening, nor the sedimentological response correspond to large-scale regional climate fluctuations (Fig. 3). In fact, following the AHP, widespread drier conditions lasted until modern with highest aridity from ~5.5–3.4ka (Konecky et al., 2011; Tierney et al., 2011). At

~3.2ka, however, rainfall increased based on a small depletion of δD_{wax} (Tierney et al., 2011). Although another drought occurred from ~2.1–1.8ka, recorded further north at Lake Edward, this drought post-dated the changes observed along the Mahale Mountains at Lake Tanganyika (Russell et al., 2005; Konecky et al., 2011). Furthermore, given the lower resolution of the CIA from the Kalya core, it is difficult to precisely resolve the timing of the decline and increase in variability in comparison to the high-resolution record from LT-98-2M; however, as change point analysis suggests that this occurred between 3.4–2.4ka, it is plausible that both the physical and chemical weathering responses occurred in response to the vegetation change.

Although the late Holocene episodes of aridity do not easily explain the observed vegetation and sedimentological changes, there are indications throughout East Africa of human mediated land-cover changes (e.g. Taylor and Marchant, 1994; Vincens et al., 2005; Hall et al., 2008; Mumbi et al., 2009; Colombaroli et al., 2014; Battistel et al., 2017; Ivory and Russell, 2018). This timing is coincident with a few important events. For example, it has been demonstrated that this period corresponds to the expansion of Bantu-speaking people in the region, increases in human populations, and, importantly, the development of metal-working such as iron smelting throughout the region resulting in the beginning of the Iron Age (Huffman, 1989; Ashley, 2010). The increase in slash-and-burn agriculture coupled with iron smelting, which required massive amounts of wood for fuel, may have resulted in large-scale loss of biomass, as well as increased wildfire risk from smelting fires. Because of this, many paleoecological records observe increases in disturbance taxa, like Artemisia and charcoal (Davies and Fall 2001; Munoz and Gajewski, 2010; Ivory and Russell, 2016). In fact, at Lake Tanganyika, Ivory and Russell (2016) suggest that human disturbance at the onset of the Iron Age is the most likely explanation for the lack of moist woodland recovery during the late Holocene. This is supported by evidence of early Bantu sites in Burundi and Tanzania near the lake which date to 3-2kyrs BP (Russell et al., 2014; Isern and Fort, 2019). If this is the case, it suggests that human disturbance resulted in changes to vegetation structure, promoting more open disturbed woodlands. This change of structure, particularly the lack of extensive root networks that control apparent soil cohesion and wet under-canopy microclimates, led directly to a tipping point throughout the basin that resulted in initial delivery of coarser sediment followed by a longer-term fining associated with higher sedimentation rates and a change in the dominant clay types flushed from the landscape.

4.3. Historical period

Although there are indications both at Lake Tanganyika and throughout East Africa that Iron Age people were responsible for the vegetation cover modifications that our interpretation links to changes weathering patterns, no specific demographic information exists within the Tanganyika basin to directly tie these events (e.g. Taylor and Marchant, 1994; Vincens et al., 2005; Hall et al., 2008; Mumbi et al., 2009; Bayon et al., 2012; Colombaroli et al., 2014; Battistel et al., 2017; Ivory and Russell, 2018). However, to illustrate the effects of direct anthropogenic land-use pressure, we can use short cores and repeat photographs taken over the historical period when records exist to document human population demography in the region and examine these linkages on a smaller scale. This allows us to holistically compare responses in highly disturbed versus undisturbed watersheds. Although disturbance type may change, for example forest clearance for iron smelting transitions to forest clearance from a mixture of charcoal production and agriculture. However, we would expect the reduction of trees from deforestation to be a common and dominant control. Fig. 4 shows sedimentation rates and palynological data from two sites within the Lake Tanganyika watershed. Core LT-98-12M was taken in central Tanzania just offshore from the Lubulungu River delta in the Mahale Mountain National Park protected area (Cohen et al., 2005a). This location samples a watershed that underwent very little historical

disturbance by Holoholo people, even before the park was established in 1985. In contrast, core LT-98-37M was taken in northern Tanzania outside of the borders of Gombe Stream National Park (Cohen et al., 2005a). In this region, records suggest dense human populations have existed since at least the 1700s, with intensive deforestation beginning around the mid-1700s. Furthermore, the period recorded by these cores includes the wet-dry transition associated with the Little Ice Age (LIA) and the transition to modern conditions. Thus, the watersheds linked to these two core sites have very contrasting land-use histories but were subject to similar climatic conditions allowing us to fingerprint of the influence of human presence alone.

First, both records follow a similar trajectory in vegetation and sedimentation rate before the 1700s, prior to increased human impacts (Fig. 4; Cohen et al., 2005b). East African climate during the Little Ice Age (LIA) was generally drier than today (Russell et al., 2007; Stager et al., 2009). Both records reflect this climatic state, with very high grass percentages in addition to higher charcoal influxes until the mid-1500s, suggesting open vegetation and enhanced wildfire activity. Additionally, both cores show relatively low sedimentation rates over this period. However, after 1700 AD, the landscape histories of each watershed diverge. Wetter conditions were established around 1750 AD in this region, and this is reflected in the low disturbance record by an increase in trees and decrease in grasses toward the modern (Fig. 4). Furthermore, this natural afforestation following climate is accompanied by a decline in charcoal, suggesting reduced wildfire activity, and the slowest sedimentation rates of the record. In contrast, the high disturbance record shows a decoupling of vegetation from the regional wetting, such that grass remains dominant and trees do not increase in abundance. Furthermore, high values of Artemisia beginning at 1700 AD are a testament to disturbance despite wetting, and charcoal influxes also increase in the mid-1700s. Finally, a large increase in sedimentation rates begins in the mid-1800s, likely as a result of enhanced erosion from deforestation. Higher sedimentation rates are accompanied by a change at this time within the cores from lithologies characterized by green silty clays to red clays. Cohen et al. (2005b) suggested that this resulted from enhanced soil erosion of the red lateritic clay soils that dominate this area. Soreghan (2016) used trace element geochemistry and mineralogy to confirm this hypothesis; chemical fingerprinting of offshore mud in the Kigoma region (~20 km south of core LT-98-37M) showed that surficial red mud within the nearshore region are strongly associated with eroding hillslopes in developed areas, rather than nearby deltaic sources.

Although the low disturbance site records changes in vegetation and wildfire that can be explained by climate, the high disturbance watershed record appears to be decoupled from climate with no forest regrowth during wetting after 1750 AD. The first appearance of Artemisia about 50 years before indications of increased wildfire, and ~125 years prior to increased sedimentation rates, suggests that initial deforestation was localized and therefore did not immediately result in a sedimentary signal recorded in the lake. However, as human populations grew and needs became greater for fuel and agricultural space, the opening of the landscape passed a tipping point. Also, as deforestation intensified with the population increase, more active wildfires prevailed. These fires appear to have created a positive feedback that augmented vegetation opening from deforestation, such that wildfires prevented even fallow land from reforesting. A further tipping point occurs once deforestation and wildfires have cleared sufficiently dense vegetation such that soils are much less stable due to a loss of apparent cohesion. The absence of root networks and a canopy to intercept moisture effectively conditioned hillslopes for soil erosion through mass wasting and diffusive processes (e.g., creep, rainsplash, sheetwash) as pore pressures rise with increasing rainfall. This led to a rapid increase in sedimentation of red clays derived from terrigenous red lateric soils in the watershed due to enhanced soil erosion.

Repeat photography performed at sites along the Tanzanian shore of Lake Tanganyika in the vicinity of Kigoma provides a visualization of these disturbances and their effects (Fig. 5). Around these known disturbed watersheds, we note changes between the modern vegetation observed at the sites and that observed in the 1957 and 1920 images. Many of the plant species observed earlier in the 20th century were no longer present by 2005, due in large part to decreases in native tree cover in favor of agricultural species and fire tolerant grasslands. Furthermore, geomorphological changes on the landscape accompany the vegetation alteration. Most striking is the receding headland cliff in photoset 2. In humid regions with dense vegetation and thick soils, slope evolution is commonly controlled by diffusive processes for soil mantled hills (slope decline), and mass wasting for bedrock via slope retreat. On this headland, we observe an overall reduction in the diversity and abundance of tree species, in favor of higher abundances of grasses and forbs, most likely linked to enhanced fire disturbance and human modifications of this area, which is within walking distance to the large population center at Kigoma. The repeat photo set shows evidence for parallel slope retreat, which suggests mass wasting processes affected this landform over the past century. The thin soils and shallow root networks associated with grasses may have allowed rainfall to infiltrate pre-existing planes of weakness with the bedrock, helping to promote mass wasting by increasing pore pressure and therefore reducing shear strength (Bierman and Montgomery, 2013). Further, weathering lowers rock strength over time, by increasing porosity and reducing cohesion, since both factors alter slope hydrology. Human clearing of native vegetation with fire is one likely mechanism reducing rock strength in this setting, thus helping to promote slope retreat by rock falls and topples. Alternative mechanisms exist that could promote the same response, for example earthquakes; however, earthquakes are infrequent and would not explain the vegetation clearance observed.

This visual evidence from the repeat photographs is consistent with observations in the sedimentological records collected offshore (Fig. 4). Together, these pieces of evidence strongly point to vegetation removal by people resulting in a decoupling from climate. This decoupling was enhanced by changes to wildfire regimes which prevented any recovery following deforestation. Finally, the long term lack of vegetation appears to have affected the landscape though enhanced hillslope erosion resulting in a landscape transformation, a mechanism that has been observed elsewhere in the watershed (Soreghan, 2016).

These records also illustrate the effect of human-mediated disturbance of terrestrial processes on the aquatic habitats and lacustrine ecosystem services (Cohen et al., 2005a,b; Palaicios-Fest et al., 2005). In most of the disturbed watersheds examined as part of the LTBP, a transition to disturbance-tolerant aquatic benthos occurred following indicators of deforestation (Palacios-Fest et al., 2005). This suggests that changes to terrestrial environments can have long term downstream effects on species composition within aquatic habitats through changes to deposition. This also suggests that the long term changes currently underway due to further landscape modification may be driving large-scale alteration to aquatic communities which are the foundation of important food webs.

4.4. Vegetation-climate-weathering feedbacks

We observe strong feedbacks among climate, vegetation, and weathering over numerous temporal and spatial scales at Lake Tanganyika. However, in terms of linking the scale of weathering changes to climate change, on the longest time scales representing the largest temperature and rainfall shifts in both directions, alterations to chemical and physical weathering regimes are relatively small. Instead, the largest changes in particle size and CIA over the 60ka more closely mirror vegetation structure. This suggests that weathering intensity may be indirectly or only partially coupled with climate. In other words, it appears that the strongest role of climate in determining weathering intensity is linked to the influence of complex interactions of climatic (P:E, seasonality) and ecological dynamics (disturbance) on the landscape for engineering vegetation structure.

However, in the case of anthropogenic deforestation, part of the

feedback loop linking climate to vegetation is broken. Although wet-dry cycles occur over the late Holocene and historical period, they were relatively minor in comparison to the large-scale climate changes over the last 60ka. Instead, vegetation structure fundamentally shifts to a more open, disturbed mosaic of woodland and thicket beginning regionally at 2.5ka and intensifying in the last two hundred years due to anthropogenic activity. Thus the increase in sandy detritus and less altered, terrigenous material toward the modern is related to a change in the structural component of the vegetation, regardless of the background climate.

Finally, the capacity for fisheries is one of the most critical ecosystem services provided by large lakes, and enhanced sediment erosion associated with the removal of native vegetation has already been shown to negatively impact several different trophic levels of the food web in Lake Tanganyika. At the top of the food web, fish represent crucial dietary protein and one of the only sources of cash income for lakeshore human populations (Coulter, 1991; Hecky et al., 1991). Although Lake Tanganyika is not highly productive, its pelagic food web has historically vielded up to 200,000T of fish per year, most of which is exploited locally (Edmond et al., 1993; Mölsä et al., 2002). Previous studies have demonstrated connections between productivity and reduced upwelling from higher temperatures as well as reduced winds (Cohen et al., 2016; McGlue et al., 2020). As the threats from changing climate and diminished water availability materialize, the regional demand for fish in sub-Saharan Africa is rising, and factors such as geographic isolation, political volatility, refugee crises, and limited infrastructure renders the security of this key food resource an issue of mounting importance to the growing riparian populace (Brown et al., 2007; Kimirei et al., 2008; McIntyre et al., 2016). As a result, fish catch in the last few decades rarely exceeds 80,000T annually (Kimirei et al., 2008). A transition towards unsustainable agricultural practices along steep lake shorelines, motivated by declines in fish stocks, is one consequence of a changing climate that could be made more severe by vegetation changes shaped by anthropogenic global warming.

Further, the linkage between reduced fish catch and reliance on agriculture creates a positive feedback that could result in further reduction of pelagic productivity (Fig. 6). In this system, decreased fish catch related to an initial change in climate results in forest clearance for agriculture which in turn results in increased sediment pollution and lowered fish catch. In this model, the exacerbating impacts of climate and land-use create a destabilizing feedback which reduces resilience and could lead to ecological collapse both in the watershed and within the lake itself.

5. Conclusions and implications

Here we demonstrate that despite large-scale change in regional temperature and rainfall over the last 60ka, chemical and physical weathering processes are most sensitive to changes in vegetation structure at Lake Tanganyika. Furthermore, we suggest that change over the late Holocene and historical period are unprecedented in the last 60ka and best explained by land-use change (deforestation) by people. Although many long-term weathering studies have focused on the role of climate, many have not comprised independent records of vegetation in order to disentangle effects. These results are consistent with a few studies in both the tropics as well as temperate regions which pair sedimentological and palynological data (Egli et al., 2008; Goddéris et al., 2009; Dosseto et al., 2010; Ivory et al., 2014, 2017). In particular, we show that in tropical Africa, there is a consistent sedimentological response associated with decreasing canopy cover along a spectrum of dense woodland to wooded grassland/semi-arid bushland.

We suggest that the decoupling of vegetation cover from climate change could have disastrous consequences to pelagic fisheries as a result of the relationship between fish catch and increased forest clearance for agriculture. It has been shown that deforestation for road building and agriculture has also led to sediment pollution of Lake Tanganyika's

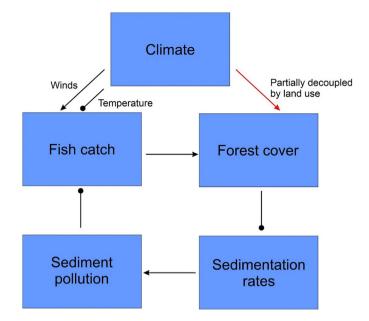


Fig. 6. Systems diagram showing the linkage between climate, fish catch, and deforestation. Arrows represent positive couplings and lines with circles represent negative coupling. The red arrow linking climate and forest cover denotes that this natural coupling is partially decoupled by land use based on sediment core data.

littoral zone, with a pronounced effect on fish, mollusk and ostracod diversity, as well as benthic primary productivity from loss of light penetration and water clarity, and changes in benthic substrate type associated with siltation (Cohen et al., 1993; Alin et al., 1999; Lucas et al., 2020). Such changes have implications for Lake Tanganyika's littoral food web, which over short timescales is strongly influenced by top-down processes (McIntyre et al., 2006), as well as nearshore-offshore biotic interactions. Laboratory simulations of snail response to sand inundation upon rocky habitat also suggested the potential for declines in abundance (Donohue and Irvine, 2003). Other studies (McIntyre et al., 2005) have demonstrated that sediment inundation into nearshore habitats impacts predator-prey interactions and body size of individual mollusk species more directly than assemblage level declines in abundance and diversity. Snail predation (by crabs) and parasitism (by trematode flatworms) appears to be reduced in littoral areas blanketed by extra-basinal sediment, though the precise connection between these processes and excess sediment is not fully clear. Food quality for benthic herbivores declines in areas impacted by sediment pollution, which is positively correlated with lower body sizes and reproduction rates, suggesting that life history for macrobenthos may likewise be negatively influenced by areas impacted by land-use change driven sediment pollution (Soreghan, 2016).

Further, Soreghan (2016) examined the impact of recent sedimentation on mollusk shell beds which serve as habitat for at least 16 endemic species of shell-dwelling cichlid fish, numerous gastropods, sponges, crabs, and bryozoans (Cohen, 1989; Marijnissen et al., 2009; McGlue et al., 2010; Ryan et al., 2020). Heavy blankets of fine-grained sediment were observed accumulating and, in some instances, burying shelly substrates (Busch et al., 2018). These mud blankets reduce viable benthic habitat on the shell beds and may result in mortality for obligate shell-bed dwellers. Furthermore, by fingerprinting the material, Soreghan (2016) determined that spatially distinct blankets of sediment originated from lateritic hillslopes that had been stripped of native vegetation for local urbanization, and from progradation of the Luiche River delta, which had been altered in order to cultivate banana, cassava, and corn. It is probable that the red muds encountered near the tops of the LTBP cores from impacted watersheds is derived from the easily eroded hill slopes conditioned by land cover change.

Studies that link landscape processes and downstream effects are particularly important in southeast Africa, as this region is dominated by such woodlands that today are one of the most densely populated natural systems in the world (Campbell, 1996). Our data suggests that anthropogenic pressures within these systems can lead to feedbacks which could significantly alter ecosystem services. Over the last several thousand years, deforestation for intensification of agricultural as well as disturbance for fuel harvesting during the Iron Age both substantially altered the composition and structure of vegetation. As both of these activities are still common in the region today, it is crucial to put management systems in place at the community level that may prevent further landscape degradation. For example, recommendations to limit woodland clearance on steep lakeshore slopes for cultivation would greatly reduce sediment inputs to the littoral zone.

Data availability statement

All sedimentological/mineralogical data presented in this paper will be submitted to the Pangeae Database at time of publication. All pollen data will be submitted to the Neotoma Paleoecological Database and African Pollen Database at the time of publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Quaternary Science Advances 3 (2021) 100023

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