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CLIMATIC AND ANTHROPOGENIC IMPACTS ON AFRICAN ECOSYSTEMS

"CLANIMAE"

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Biodiversity

FINAL REPORT

CLIMATIC AND ANTHROPOGENIC IMPACTS ON AFRICAN ECOSYSTEMS

"CLANIMAE"

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SUMMARY

A. Context

The magnitude and geographic reach of human impact on Earth's biosphere has increased rapidly over the last century, in particular in East Africa where rates of population growth and the intensification of agriculture are among the highest in the world, and where developing economies strongly depend on water and other goods and services provided by natural ecosystems. Economic development with conservation of biodiversity and ecosystem functioning requires spatially and temporally explicit knowledge of the timing and relative magnitude of (pre-)historical and modern human impact on terrestrial and aquatic ecosystems to 1) evaluate the current health of these ecosystems and their resilience to anthropogenic disturbance, 2) model the range of their possible responses to future climatic, demographic and economic change, and from these 3) develop locally optimal strategies for land and water-resource management.

B. Objectives

CLANIMAE aimed to produce guidelines for sustainable management of land and water resources in tropical East Africa, partly through comparative study of pristine and disturbed ecosystems in the modern landscape, and partly by reconstructing the long-term historical perspective to climate-environment-human interactions affecting those ecosystems today. This '**the past is the key to the present (and future)**' approach was developed by coupling data of past vegetation and water-quality changes preserved in dated lake-sediment records to information on decadal to century-scale climate variability across the gradient from humid western Uganda to semi-arid eastern Kenya. With this methodology, CLANIMAE achieved to

1) separate the influences of past natural climate variability and past human activity on East African ecosystems, and determine the timing and relative magnitude of pre-20th century ecosystem disturbances by indigenous people compared to colonial-era and recent landscape alteration;

2) determine the severity of water-quality losses due to siltation and excess nutrient input directly caused by deforestation and agriculture, compared to temporal variability in water quality associated with natural long-term ecosystem dynamics; and

3) evaluate the resilience of African ecosystems, and the prospects for restoration of disturbed ecosystems if human pressure were to be reduced.

C. Major results and conclusions of the research

CLANIMAE activities were grouped in 5 work packages dealing with 1) the calibration and validation of paleoenvironmental indicators; 2) reconstruction of past climate variability; 3) reconstruction of (pre-)historical changes in terrestrial ecosystems; 4) reconstruction of (pre-)historical changes in water quality; and 5) data integration and causal attribution of past environmental change. Part of these activities were developed through comparative study of diverse crater lake ecosystems in western Uganda. We completed seven field campaigns, during which we surveyed a total of 66 lakes. For all lakes we collected data on basin morphometry, land use, water-column transparency and frequency of mixing, water chemistry, nutrients, aquatic biota (algae, zooplankton, zoobenthos) and aquatic productivity; and collected intact surface-sediment samples for calibration of diverse paleoecological proxies in relation to modern-day environmental gradients and the intensity of human activity within lakes' catchments. Analysis of the water-quality and environmental data revealed significant negative exponential relationships between transparency (measured as Secchi depth, SD) and total phosphorus concentration, and between transparency and algal biomass (measured as the concentration of chlorophyll *a*). This relationship allows rough estimation of the productivity of Uganda crater lakes using simple measurements of Secchi disk depth. There was no significant correlation between transparency and dissolved inorganic nitrogen. Our data indicate that the water column of most fresh Uganda crater lakes mixes completely at least occasionally, but only those less than about 30 m deep mix completely at least once per year. Meteorological conditions allowing the complete mixing of deeper lakes (cold air temperature coinciding with windy conditions) are relatively rare, on the order of once in several decades for some of the deepest lakes.

We then selected 30 principal study lakes to determine the influence of water-column depth and frequency of mixing on a lake's vulnerability to water quality loss when subjected to human exploitation of the surrounding landscape. We classified these lakes according to their aquatic productivity using the Trophic Lake index TLi = Chl *a*/SD. Among the 30 study lakes, 7 are oligotrophic (low productivity, $TLi < 0.02$), 9 are mesotrophic (moderate productivity, $0.02 < TLi < 0.12$), 11 are eutrophic (high productivity, $0.12 < TLi < 0.6$) and 3 are hypertrophic (very high productivity, $TLi \geq 0.6$). Uganda crater lakes not or little impacted by human activity tend to be oligotrophic when >90 m deep, and mesotrophic when <90 m deep. Lakes with significant human impact can be oligotrophic (depth >90 m), mesotrophic (depth range 35-90 m) or eutrophic/hypertrophic (depth <35 m). Thus, significant land use within a crater basin is likely to raise the productivity of shallow and moderately deep lakes, while very deep lakes remain relatively unaffected. The large volume of their rarely mixed lower water column allows more or less permanent nutrient storage, because the low frequency of deep mixing hampers nutrient recycling to the lake surface where production takes place.

CLANIMAE developed the first inference model to reconstruct past changes in the aquatic productivity of African lakes based on assemblages of fossil diatom algae preserved in lake sediments. Simultaneous investigation of the silicon-isotope composition of fossil diatoms as a possible geochemical tracer for past aquatic productivity resulted in improved understanding of the important silica cycle in African lakes. We also studied environmental controls on the distribution of aquatic plants in Ugandan crater lakes, similarly to explore their value as environmental indicators. This analysis revealed eight major ecological communities, each with particular indicator species and with distinct habitat requirements for local water depth, distance from shore, transparency (or its inverse, turbidity), temperature, dissolved ion content and dissolved oxygen. Use of fossil remains of aquatic plants to infer past changes in lake hydrology and water quality is compromised by poor preservation of several species, which introduces bias in paleo-environmental interpretation. This can be partly resolved by using well-preserved species as proxy indicator for particular aquatic plant communities. Parallel studies on the distribution of Cladocera (water fleas) and Ostracoda (mussel shrimps) in 62 Uganda crater lakes demonstrated their potential as biological indicators for water quality and ecosystem health in East African lakes. By playing an important role in the aquatic food web, both groups contribute to the ecological integrity of these lake ecosystems. The distribution of Cladocera among lakes was influenced mainly by nutrient availability (total phosphorus concentration), aquatic plant diversity, pH and the fraction of the lake basin under agriculture.

An important part of the work programme focused on reconstructing past vegetation dynamics based on analysis of fossil pollen in well-dated lake-sediment records. We also calibrated the magnitude of terrestrial ecosystem response to climate change as recorded in pollen data, by comparing the vegetation history of a pristinely natural and an anthropogenically disturbed landscape. We found that even a few decades of mildly wetter weather (5-

10% more rainfall), such as during the late 19th century and in the 1960s-1970s, caused significant migration of the grassland-woodland ecotone. This finding is important because this ecotone reflects the difference in ecological carrying capacity required for pastoralism vs. (irrigated) crop agriculture.

Some important African food staples such as banana can be traced in time using phytoliths, glass bodies present in plant tissue. Partly through a BelSPO-funded visiting postdoctoral fellowship, CLANIMAE validated fossil phytoliths as indicator of past banana cultivation by calibrating the relation between phytolith abundance in the sediments of 25 Ugandan lakes and the surrounding cover of banana plantations. This test classified land-cover in 6 types of natural vegetation, 16 types of cultivated crops, and 4 types of fallow agricultural land. We used the same sediment samples and land-cover data to calibrate the ecological indicator value of African non-pollen palynomorph microfossils recovered in fossil pollen preparations, also along a landscape gradient ranging from pristinely natural to severely impacted by human activity.

CLANIMAE produced new vegetation reconstructions for the Queen Elisabeth NP, Bunyaruguru and Kasenda areas of western Uganda, and for the eastern Lake Victoria and Mt. Kilimanjaro areas of southern Kenya. These and published records indicate that significant human impact on the East African landscape (deforestation, crop cultivation) dates back to (at least) ~1000 AD in sub-humid western Uganda, and to ~1700 AD in central Kenya. Semi-arid environments reveal tentative signatures of land use by pastoralists dating back up to 600 years, but the more intense vegetation and soil disturbance typical of crop cultivation, and the resulting water-quality loss, appears mostly limited to the last 70-80 years. Fossil-diatom data from Lake Chibwera showed no evidence of recently increasing productivity or water-quality loss, consistent with the undisturbed condition of savanna vegetation in Queen Elisabeth National Park. In contrast, data from the heavily impacted Lake Katinda (and Kanyamukali) indicate that anthropogenic water-quality loss started ~700 years ago. Earlier evidence for increased productivity can also be explained by temporary, climate-driven episodes of low lake level.

D. Contribution of the project to sustainable development policy

Referring to stated priorities of the 'Science for a Sustainable Development' (SSD) programme, CLANIMAE addressed important research questions with critical relevance to the environmental policy on 1) sustainable economic development, 2) natural resource management, 3) biodiversity conservation, 4) adaptation of vulnerable communities to global change, and 5) a more humane globalization. Project results particularly relevant to policy development on water and land resources in tropical Africa are:

1) The productivity of Uganda crater lakes can be monitored using simple, repeated measurements of water-column transparency with a Secchi disk.
2) The vulnerability of Uganda crater lakes to eutrophication and water-quality loss for a given intensity of land use is strongly related to lake depth and the associated frequency of water-column mixing. Lakes < 35 m deep are highly vulnerable, lakes > 90 m deep are relatively resistant to water-quality loss. In their pristine condition, shallow Uganda lakes are usually mesotrophic (with slightly elevated productivity), not oligotrophic (unproductive).
3) Clear-water crater lakes (now almost without exception >90 m deep) are a most valuable source of drinking-quality water, and should be managed for ecotourism and modest recreation only. More productive lakes of shallow or intermediate depth (35-90 m) already subject to intensive land use can be managed for fisheries development and agricultural water extraction, the latter within limits determined by lake volume and water renewal rate. In both shallow and intermediate-depth lakes, runaway algal production leading to noxious blooms and frequent fish kills can be avoided by creating buffer strips of vegetation preventing soil run-off from reaching the lake. Fish farming should be limited to productive shallow lakes, where added nutrients and food are continually recycled into the water column.
4) Variation in species of aquatic plants, diatom, zooplankton and zoobenthos along gradients of natural habitat and intensity of human impact confirm their applicability as biological water-quality indicators in African lakes.
5) Evidence for major natural vegetation response to modest historical rainfall variability shows that strategies for sustainable economic development must take into account large temporal variability in ecosystems, which affects their carrying capacity and realized service to society.
6) In semi-arid regions (e.g., the central Kenya Rift Valley), hydrological sensitivity of lakes to naturally large water-balance fluctuations requires creation of a water-resource buffer against intermittent severe drought. Studies of sedimentation help set appropriate limits to water extraction by identifying the lake-level threshold below which a clear-water, healthy ecosystem state switches to a turbid state with poor water quality.
7) The crater lakes of Uganda carry value well beyond their own economic significance as analogs of ecosystem functioning in the large lakes Victoria and Tanganyika, in their historical, present-day and possible future state.

E. Keywords

Biodiversity, climate change, East Africa, ecosystem services, hydrology, natural resources, paleoecology, soil erosion, sustainable water-resource development, vegetation dynamics, water quality

1. INTRODUCTION

1.1 Context of the research

The magnitude and geographical reach of human impact on the Earth's biosphere has increased rapidly over the last 100-200 years, and rates attained in the last three decades are unprecedented (IGBP-LUCC, 2005). This has resulted in a critical situation of widespread biodiversity loss and ecological damage, which can only be countered by implementing targeted policies which successfully balance the needs of human populations with the space and resources available to them. To help marry the goal of sustainable development with meaningful conservation of natural ecosystems and biodiversity in a rapidly changing world, climate and natural-resource modelers urgently need both spatially and temporally explicit databases of historical land use at regional scales (Lambin & Geist 2001). Specifically, we critically need a long-term historical perspective to modern-day climate-environment-human interactions, in order to

1) properly evaluate the current health of regional ecosystems and their resilience to diverse anthropogenic disturbances,

2) model the range of potential ecosystem responses to future climate change and demographic pressures, and, based on this understanding,

3) develop sound local strategies for ecosystem management and biodiversity conservation.

In other words, we need to document the exact timing (onset), trajectory (evolution), and relative magnitude of ancient and modern human impact on the natural environment in specific world regions (HITE, 2002). This is particularly the case for tropical East Africa, where increases in population and natural resource use are among the highest in the world (**Fig. 1a**), and developing economies strongly depend on (often scarce) water resources and other goods and services provided by natural ecosystems (**Fig. 2**). Although most climate models predict East African rainfall to increase rather than decrease in a greenhouse world (IPCC 2007), its beneficial effect will most likely be lost because large-scale forest clearance has compromised the recharge of aquifers which used to provide a buffer against episodes of prolonged drought (Fischer & Heilig 1997). Large-scale stripping of natural vegetation in both sub-humid and semi-arid African landscapes (**Fig. 1b**) has also contributed to massive soil erosion, devastating floods, and excess nutrient inputs to lakes and

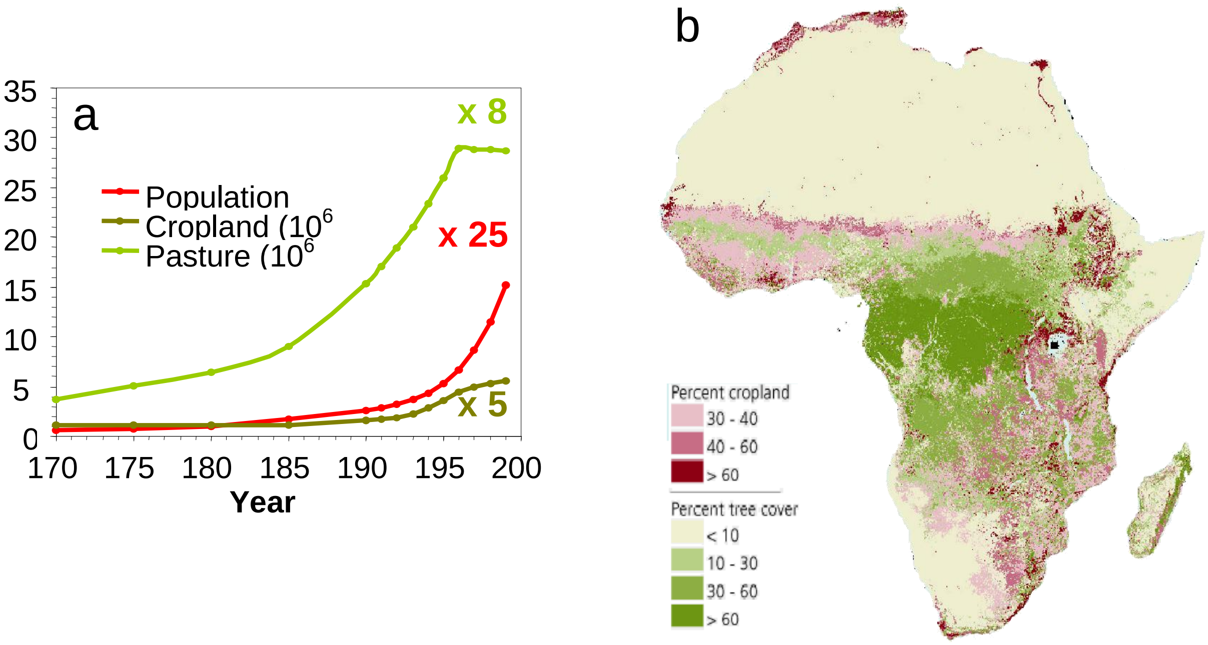
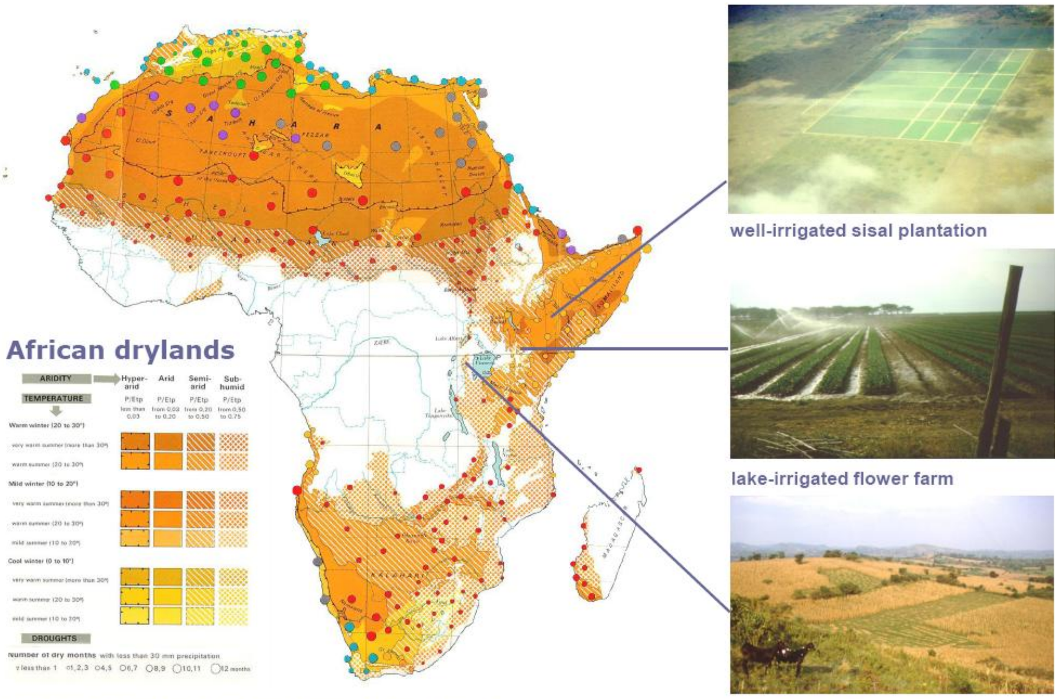


Fig. 1. a. The area of land under cropland and pasture in East Africa has multiplied over the past 200 years in proportion to population size, but in recent decades has reached a plateau, suggesting that unexploited land in suitable climate regimes and soils is becoming scarce. Based on data from Klein Goldewijk (2001). **b.** Human impact on the landscape in sub-Saharan Africa is most intensive in deciduous mosaic forest and grass or scrub savanna, located in sub-humid to semi-arid climate regimes.



well-irrigated sisal plantation

lake-irrigated flower farm

rain-fed maize cultivation

UNESCO Man and the Biosphere Technical Report 7 (1977).

Fig. 2. The west-to-east climate gradient from a humid climate regime in western Uganda to a semi-arid climate regime in eastern Kenya translates into a gradient of agricultural practices, from rain-fed cultivation to irrigated cultivation using surface waters (lakes, rivers) to irrigated cultivation using wells pumping fossil groundwater.

coastal marine habitat (**Fig. 3**). These impacts seriously threaten the natural functioning of terrestrial and aquatic ecosystems, and thus also the goods and services they provide to human society.

Fig. 3. Soil erosion and flooding due to the large-scale stripping of natural vegetation.

1.2 CLANIMAE research objectives and expected outcomes

The principal objective of the CLANIMAE project is to produce guidelines for sustainable management of land and water resources in tropical East Africa. Given the above-mentioned knowledge gaps, CLANIMAE specifically aimed to achieve the following outcomes:

1) separate the influences of past natural climate variability and past human activity on East African ecosystems;
2) determine the timing and relative magnitude of pre-20th century ecosystem disturbances by indigenous people compared to colonial-era and recent landscape alteration;
3) determine the severity of lake water-quality losses due to siltation and excess nutrient input directly linked to deforestation and agriculture, compared to temporal variability in water quality associated with natural long-term ecosystem dynamics;
4) determine the influence of water-column depth and frequency of mixing on a lake's vulnerability to water quality loss when subjected to human exploitation of the surrounding landscape; and
5) evaluate the resilience of African ecosystems, and the prospects for restoration of disturbed ecosystems if human pressure were to be reduced.

2. METHODOLOGY AND RESULTS

2.1. Methodology of research

CLANIMAE has pursued these research objectives partly through comparative study of natural (pristine) and disturbed (impacted) ecosystems in modern-day western Uganda, and partly by reconstructing the long-term historical perspective to the climate-environment-human interactions affecting those ecosystems today. This '**the past is the key to the present and future**' approach was developed by coupling data of past vegetation and water-quality changes preserved in dated lake-sediment records to information on decadal to century-scale climate variability, across the climatic moisture-balance gradient from humid western Uganda to semi-arid eastern Kenya.

The essential characteristic of this project, therefore, is that it addressed questions of climate-environment-human interaction at the time scales at which the relevant processes actually occur. Our integrated paleoecological research method involved 1) calibration of new paleo-environmental proxies along modern-day regional gradients of environmental variables sensitive to human impact; 2) validation of those and more traditional proxies in the time domain; 3) production of a significant number of new, multi-proxy paleoenvironmental reconstructions from key sites in equatorial East Africa; and 4) regional integration of these site-specific reconstructions to obtain a coherent regional assessment of the timing, magnitude and principal causes of past landscape and water-quality changes.

Evidently, this project nor any research investment can ever achieve a fully complete reconstruction of historical climate-environment-human interactions throughout East Africa at the local scale (i.e., all individual lakes and terrestrial ecotones). Success in achieving our research objectives required 1) that the network of selected study sites adequately captured regional gradients in climate (humid to semi-arid) and human impact (historical versus recent, severe versus relatively benign), and 2) that all project sites produced data of comparable quality and information content. Project tasks were facilitated considerably by substantial previous work by UGent (partner 1) on the calibration and validation of climate proxies in African lakes, and availability of a substantial body of high-quality paleo-environmental reconstructions. By filling critical data and knowledge gaps, CLANIMAE optimally exploited these existing reconstruction methods and existing paleoenvironmental data sets. Activities funded by this project have largely focused on study lakes in the humid and sub-humid regions of western Uganda. All CLANIMAE fieldwork was conducted with research permission from the Uganda National Council for Science & Technology (UNCST permit NS21), the Uganda Wildlife Authority (UWA permit TBDP/RES/50), and the Permanent Secretary of the Ministry of Education, Science & Technology of Kenya (MOEST permit 13/001/11C).

2.2 Project results in relation to the work programme

CLANIMAE activities were grouped in 5 work packages dealing with 1) comparative analysis of modern-day lake ecosystems, and calibration of paleoenvironmental indicators; 2) reconstruction of past climate variability; 3-4) reconstruction of (pre-)historical changes in terrestrial ecosystems and water quality; and 5) data integration and causal attribution of past environmental change.

Work package 1 activities were developed through comparative study of the diverse crater lake ecosystems in western Uganda. We completed six field campaigns, during which we surveyed a total of 66 lakes, 38 lakes in the Kasenda-Fort Portal area; 28 lakes in the Kikorongo-Bunyaruguru area. For all lakes we collected data on basin morphometry, land use, water-column temperature, pH, oxygen content and transparency, water chemistry, nutrients, aquatic biota (phytoplankton, zooplankton, zoobenthos) and aquatic productivity (**Table 1**). In each lake we also collected intact surface-sediment samples from a mid-lake location to calibrate a range of paleoecological proxies in relation to modern-day ecological gradients and the intensity of human activity within the lakes' catchments. To record seasonal patterns of water-column stratification and mixing we installed chains of automatic water-temperature loggers in a total of eight study lakes, each consisting of four ONSET Tidbits v2 or VEMCO Minilog 12 thermistors. These loggers were downloaded in August 2008, yielding 18 contiguous months of data. The resulting collection of CLANIMAE field data were added to an accumulating long-term dataset of basin morphometry, temperature (e.g., **Fig. 4**), oxygen, transparency and algal productivity from a total of 83 Ugandan crater lakes (Verschuren et al., unpublished data). This includes all published data (Beadle, 1966; Melack 1978; Kizito et al., 1993; Chapman et al. 1998) and unpublished data previously collected by UGent (2000-2002), Dr. D. A. Livingstone (1994) and Dr. L. Chapman (late 1990s).

Pearson correlation coefficients between environmental characteristics of the Uganda crater lakes, based on pre-existing and new CLANIMAE data, are

Lake Name	Lake Depth (m)	Anthropic Impact index	Secchi Disk Depth (cm)	Depth to anoxia (m)	Turbidity (NTU)	Total Phosphorus (mg/l)	Total Nitrogen (mg/l)	Chlorophyll a (µg/l)	Trophic Lake index	Trophic Category
Kyasunduka	2	1	20	1,5	71,2	0,23	3,71	147,2	7,362	H
Nyungu	23	3	25	2,8	66,3	0,23		47,1	1,882	H
Nyamusingere	4	0	40	3,3	25,2	0,07	2,29	32,2	0,805	H
Katinda	16	3	58	3,0	34,0	0,10	1,66	31,7	0,552	E
Kitere	51	2	61	2,0	7,6	0,23	1,44	32,4	0,536	E
Saka	10	3	30	3,4	74,7	0,40		15,9	0,530	E
Mbajo	35	2	59	4,3	11,0	0,14	2,99	24,8	0,424	E
Mirambi	21	3	82	5,3	24,9			33,2	0,405	E
Kanyamansira	31	1	57	7,5	16,7	0,08	1,54	20,7	0,363	E
Lugembe	18	3	70	6,6	6,3	0,09	0,55	19,76	0,282	E
Kifuruka	5	3	75	4,0	11,7	0,02	0,66	15,6	0,208	E
Kasenda	14	2	95	6,4	6,2	0,04	0,62	17,28	0,182	E
Nyabikere	57	1	146	3,7	4,0	0,08	1,01	22,03	0,151	E
Kigezi	30	3	100	5,0	4,2	0,20	1,32	13,7	0,137	E
Nyahirya	98	3	125	7,3	6,2	0,08		13,6	0,109	M
Nkugute	59	3	139	12,8	3,1	0,05	0,96	11,5	0,083	M
Chiberwa	12	0	142	9,2	3,6	0,16	0,3	11,6	0,081	M
Nyanswiga	66	3	150	4,0	4,8	0,21		9,9	0,066	M
Kyanga	57	2	164	16,9	3,4	0,08	1,63	9,8	0,060	M
Kacuba*	15	0	210	9,0	2,0	0,07		11,5	0,055	M
Murabyo	16	0	283	8,5	2,3	0,05	1,13	12,1	0,043	M
Bugwagi	82	3	179	13,8	3,0	0,02		7,4	0,041	M
Kyerbwato	14	0	240	9,0	2,0	0,09	0,41	9,29	0,039	M
Katanda	149	2	342	21,4	1,5	0,02	0,45	5,24	0,015	O
Kyaninga	220	1	488	36,0	1,2	0,03	0,17	6,00	0,012	O
Mahuhura	269	2	593	36,0	0,8	0,23	0,234	6,2	0,011	O
Rukwanzi	172	1	526	19,0	1,4	0,05	0,56	5,24	0,010	O
Mwengenyi	138	3	370	13,9	1,4	0,20	0,79	3,61	0,010	O
Karolero	34	0	380	12,0	1,6	0,23	1,78	3,3	0,009	O
Kerere	77	0	406	12,0	1,4	0,02	0,88	3,47	0,009	O

Table 1. Productivity-related variables and mixed-layer (water column above the thermocline) nutrient concentrations of 30 CLANIMAE study lakes in western Uganda, and their trophic status (aquatic productivity) classification based on the TLi index. The Anthropic Impact index (AI) ranges from crater basins being pristine (0) to fully under agriculture (3); Lake trophic status: H = hypertrophic, E = eutrophic, M = mesotrophic, O = oligotrophic.

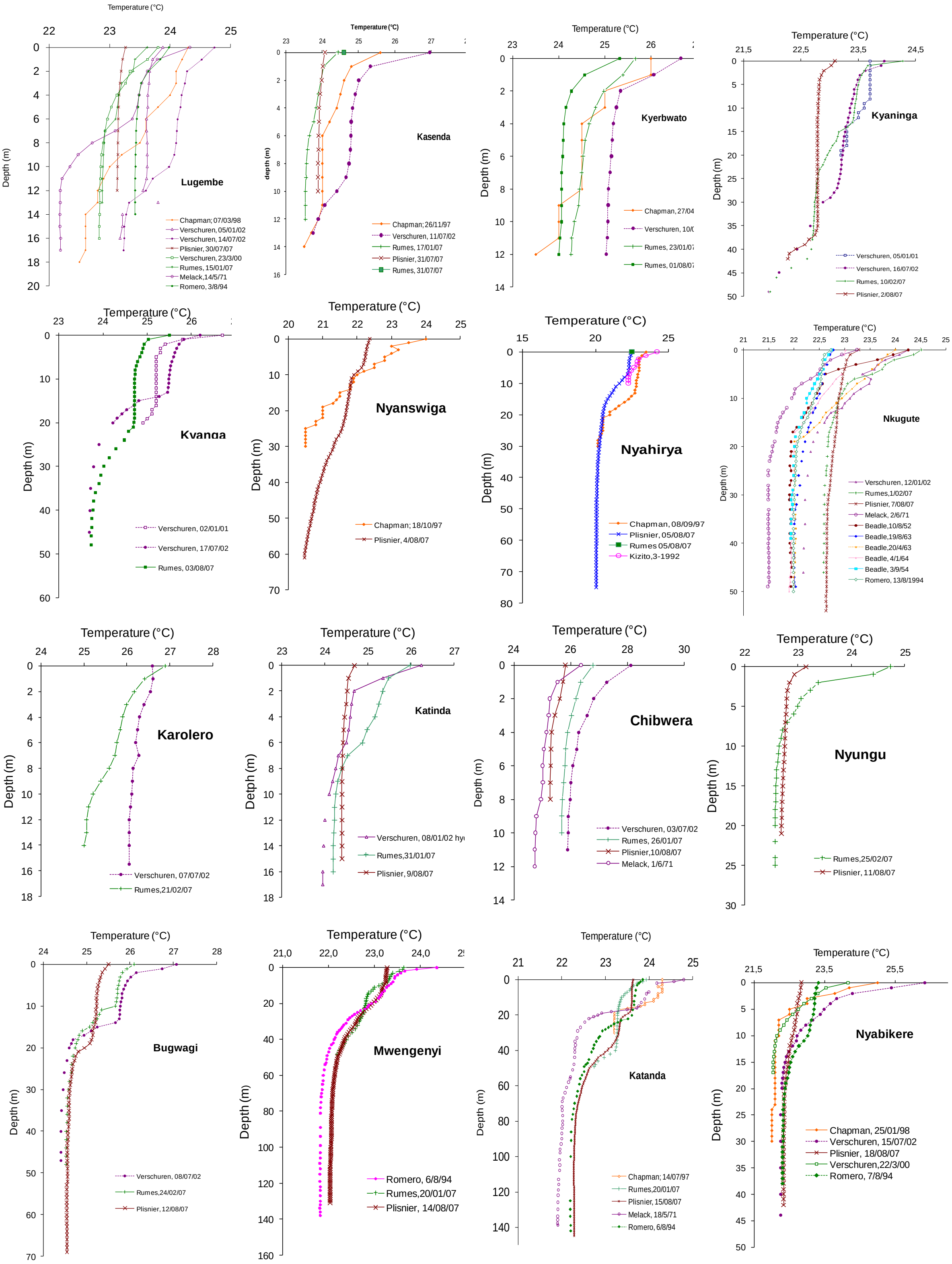


Fig 4. New (CLANIMAE) and previously collected continuous temperature profiles through the water column of 16 Uganda crater lakes, at various times of the year.

presented in **Table 2**. Analysis of the water-quality and environmental data revealed significant negative exponential relationships between transparency (measured as Secchi disk depth, SD) and total phosphorus concentration (**Fig. 5**), and between transparency and algal biomass (measured as the concentration of the ubiquitous algal pigment chlorophyll *a*, Chl *a*; **Fig. 6**). These relationships allow rough estimation of the aquatic productivity of Uganda crater lakes using simple measurements of Secchi disk depth. We also found a strong, linear and positive relationship between transparency and the depth of anoxic water (defined as the level where dissolved oxygen falls below 0.5 mg/l; **Fig. 7**). This is because in more productive (less transparent) lakes, decomposition of dead algae settling during the stratified season more rapidly depletes the deep-water oxygen supply, causing the oxycline to move up towards the thermocline. There was no significant correlation between transparency and dissolved inorganic nitrogen.

We selected 30 principal CLANIMAE study lakes to determine the influence of water-column depth and frequency of mixing on a lake's vulnerability to water quality loss when subjected to human exploitation of the surrounding landscape. These lakes cover a large gradient of relative depth and have drainage basins with contrasting levels of human impact, expressed by Anthropic Impact index values between 0 (pristine, no human impact), 1 (cultivated surface < 33%), 2 (33-66%) and 3 (>66%). Most of these lakes, including the 'shallow' lakes mentioned above, develop pronounced temperature and oxygen stratification during part of the year; our study included only three truly shallow lakes (<5-6 meter) of which the water column is mixed on a daily basis. In these 30 lakes we combined water-column measurements of temperature, dissolved oxygen, dissolved ion content (measured as specific ion conductance, or conductivity), and pH with measurements of surface- and deep-water concentrations of algal biomass (Chl a) and the essential nutrients silicon, phosphorus and nitrogen. We classified lakes according to their aquatic productivity using the Trophic Lake index TLi = Chl a/SD. Among these 30 study lakes, 6 are oligotrophic (low productivity, TLi < 0.02), 10 are mesotrophic (moderate productivity, 0.02 < TLi < 0.12), 11 are eutrophic (high productivity, 0.12 < TLi < 0.6) and 3 are hypertrophic (very high productivity, TLi ≥ 0.6).

Marked differences between the nutrient content of surface and deep water in deep (> 30 m) lakes suggested a strong influence of mixing frequency on the contribution of recycled deep-water nutrients to lake productivity. In our

N obs		66	22	59	55	77	67	78	77	78	78	78	77	78	77	76	71	76	51	83
		SD (cm)	*Chla (µg/l)*	*PEA*	*AnoxD-Moy*	*Surf. Area A0 (ha)*	*Max depth Zm (m)*	*Mean Diam (m)*	*Max L (m)*	*ShorelineL (km)*	*L theor*	*Shor dev (L/Ltheor)*	*crater area A (Ha)*	*rim height max (m)*	*rim height min (m)*	*A/A0*	*Diam/Rim height*	*Max L/rim min*	*(Depth/(A/A0)*	*Alt (m)*
66	SD (cm)	1,00																		
22	Chla (µg/l)	**-0,54**	1,00																	
59	PEA	**0,43**	-0,30	1,00																
55	AnoxD-Moy	**0,90**	-0,44	**0,36**	1,00															
77	Surf. Area A0 (ha)	-0,24	0,13	-0,07	-0,12	1,00														
67	Max depth Zm (m)	**0,64**	-0,42	0,71	**0,61**	-0,18	1,00													
78	Mean Diam (m)	-0,25	0,17	-0,04	-0,08	**0,92**	-0,15	1,00												
77	Max L (m)	-0,20	0,15	-0,06	-0,02	**0,94**	-0,14	**0,95**	1,00											
78	ShorelineL (km)	-0,23	0,17	-0,07	-0,06	**0,95**	-0,14	**0,96**	**0,98**	1,00										
78	L theor	-0,22	0,16	-0,04	-0,04	**0,93**	-0,13	**1,00**	**0,95**	0,97	1,00									
78	Shor dev (L/Ltheor)	-0,13	0,11	-0,12	-0,03	**0,37**	-0,12	**0,35**	**0,50**	0,53	**0,35**	1,00								
77	crater area A (Ha)	-0,30	0,23	-0,06	-0,12	**0,91**	-0,23	**0,84**	**0,86**	0,85	**0,84**	**0,35**	1,00							
78	rim height max (m)	0,05	0,28	0,14	0,22	0,01	0,15	0,10	0,05	0,06	0,11	0,01	0,08	1,00						
77	rim height min (m)	0,04	-0,27	**0,39**	0,18	-0,09	0,14	-0,06	-0,08	-0,09	-0,05	-0,10	0,04	**0,64**	1,00					
76	A/A0	-0,18	0,03	0,00	-0,10	-0,14	-0,17	-0,27	-0,21	-0,22	-0,27	0,08	0,01	0,10	0,15	1,00				
71	Diam/Rim height	-0,16	-0,05	-0,08	-0,15	0,71	-0,15	**0,53**	**0,65**	0,59	**0,54**	0,24	**0,54**	-0,23	-0,14	-0,07	1,00			
76	Max L/rim min	-0,23	0,24	-0,18	-0,09	**0,57**	-0,26	**0,58**	**0,60**	0,63	**0,58**	**0,36**	**0,41**	-0,23	**-0,52**	-0,11	**0,33**	1,00		
51	(Depth/(A/A0)	**0,54**	-0,42	**0,62**	**0,59**	-0,07	**0,93**	0,03	0,03	0,02	0,06	-0,02	-0,07	0,18	0,23	-0,30	-0,13	-0,07	1,00	
83	Alt (m)	**0,49**	**-0,39**	0,21	0,32	-0,37	0,43	**-0,43**	**-0,32**	**-0,35**	**-0,43**	-0,03	**-0,47**	-0,12	-0,24	-0,16	-0,17	-0,07	**0,23**	1,00

Table 2. Pearson correlation coefficients for linear regressions between various limnological and topographic characteristics of Uganda crater lakes, based on CLANIMAE and other available data. The number of observations are listed on top; topographic data derived from maps are available on 78 lakes in total; CLANIMAE surveyed 66 lakes in the field.

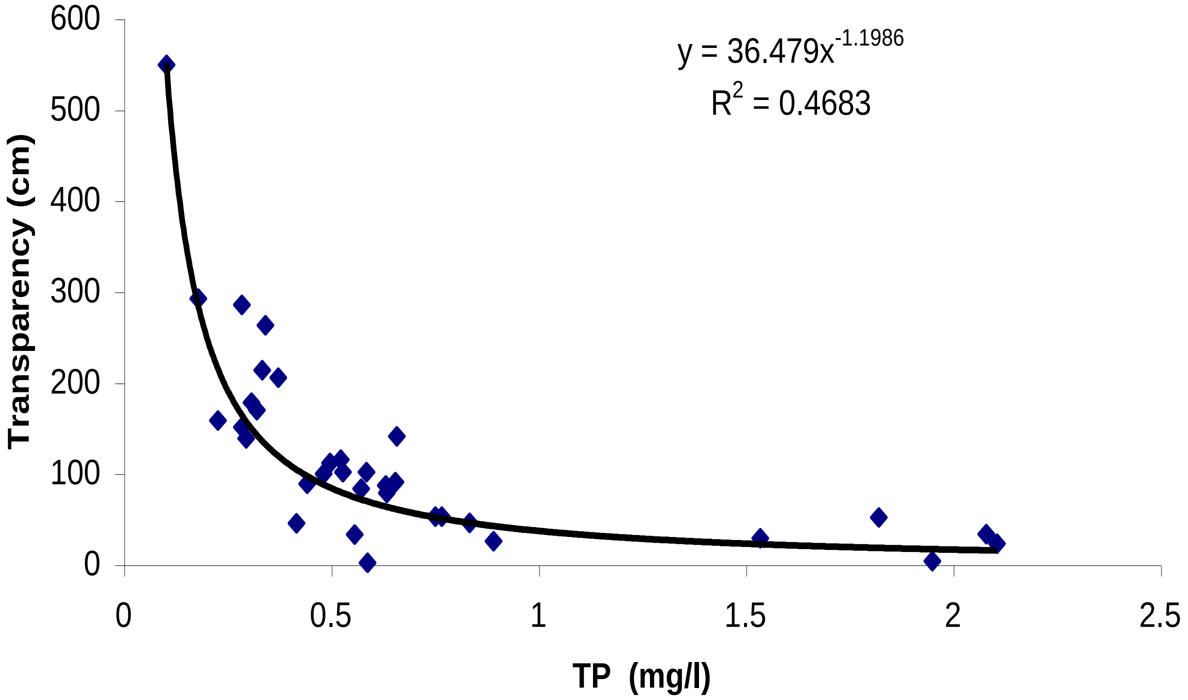


Fig. 5. Relationship between Secchi disk transparency (SD) and total phosphorus (TP) concentration in 55 Uganda crater lakes.

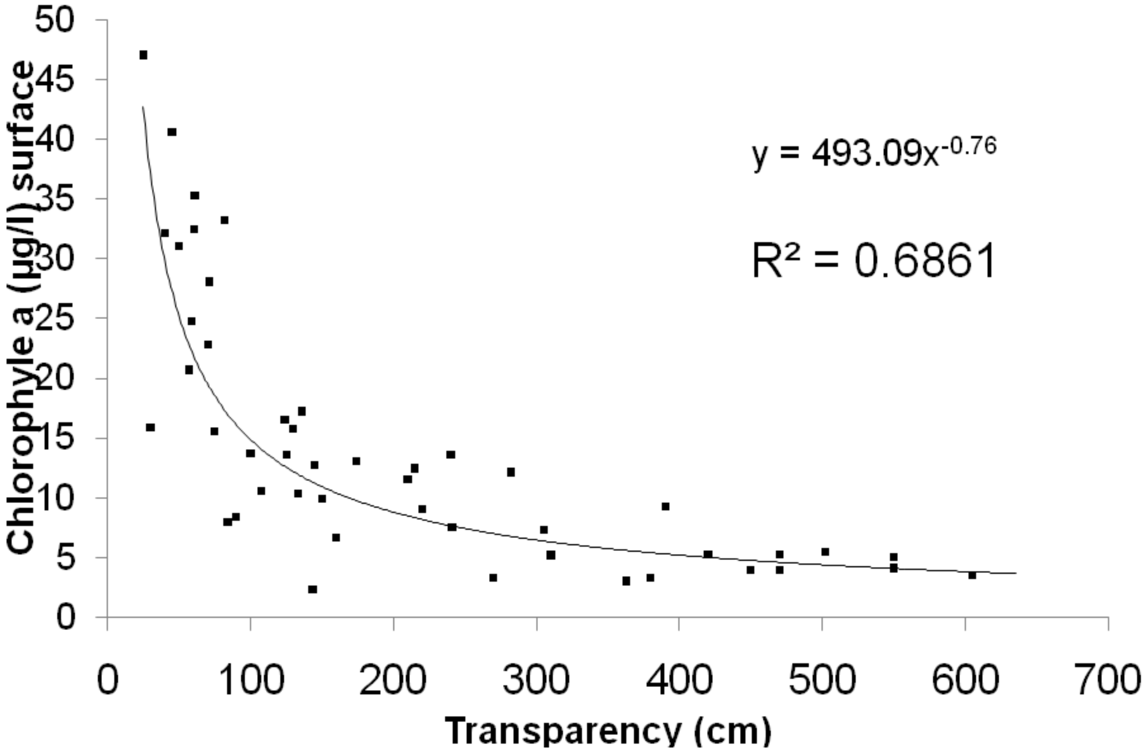


Fig. 6. Relationship between Secchi disk transparency (SD) and surface-water Chlorophyll a concentration in 55 Uganda crater lakes.

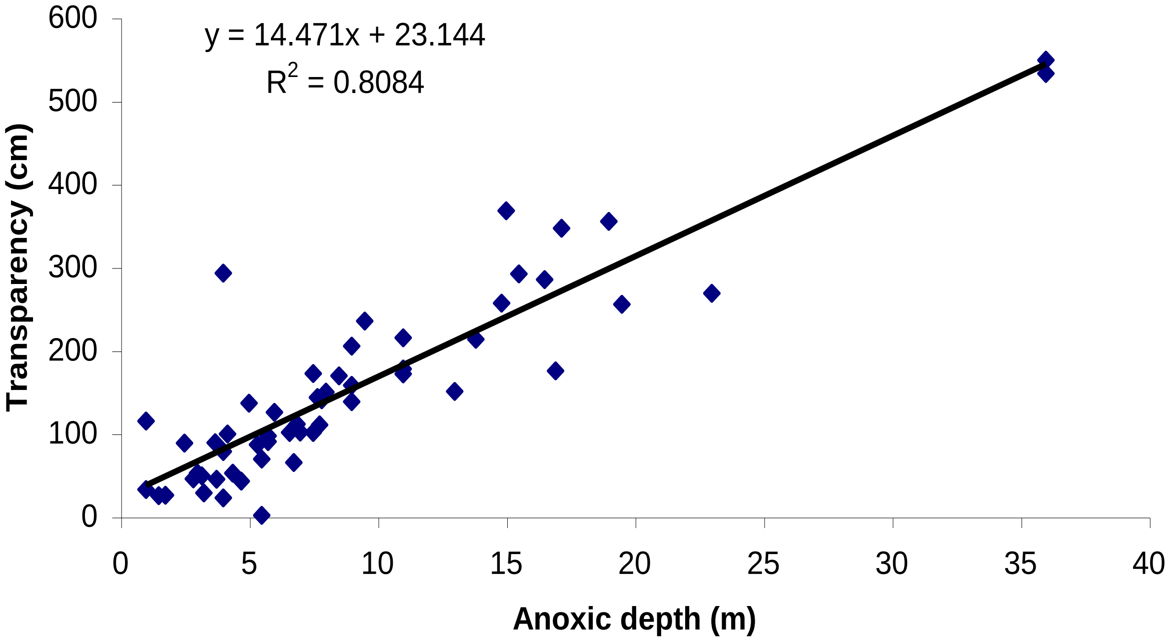


Fig. 7. Relationship between Secchi disk transparency (SD) and the uppermost depth occurrence of anoxic water in 55 Uganda crater lakes.

wet- and dry-season surveys the nitrogen to phosphorus molar ratio in surface waters usually exceeded the Redfield ratio of 16, indicating that lake productivity is more often limited by phosphorus than by nitrogen. Yet, several lakes (e.g., Katanda, Mahuhura, Mwengenyi) may be nitrogen-limited during the dry-season period of water-column mixing. Uganda crater lakes not or little impacted by human activity tend to be unproductive (oligotrophic) when >90 m deep, and moderately productive (mesotrophic) when < 90 m deep (**Fig. 8**). Lakes with significant human impact can be oligotrophic (when > 90 m), mesotrophic (in the depth range 35-90 m) or eutrophic/hypertrophic (< 35 m). Thus, significant land use within a crater basin is likely to raise the productivity of shallow and moderately deep lakes, whereas the water quality of very deep lakes remains relatively unaffected.

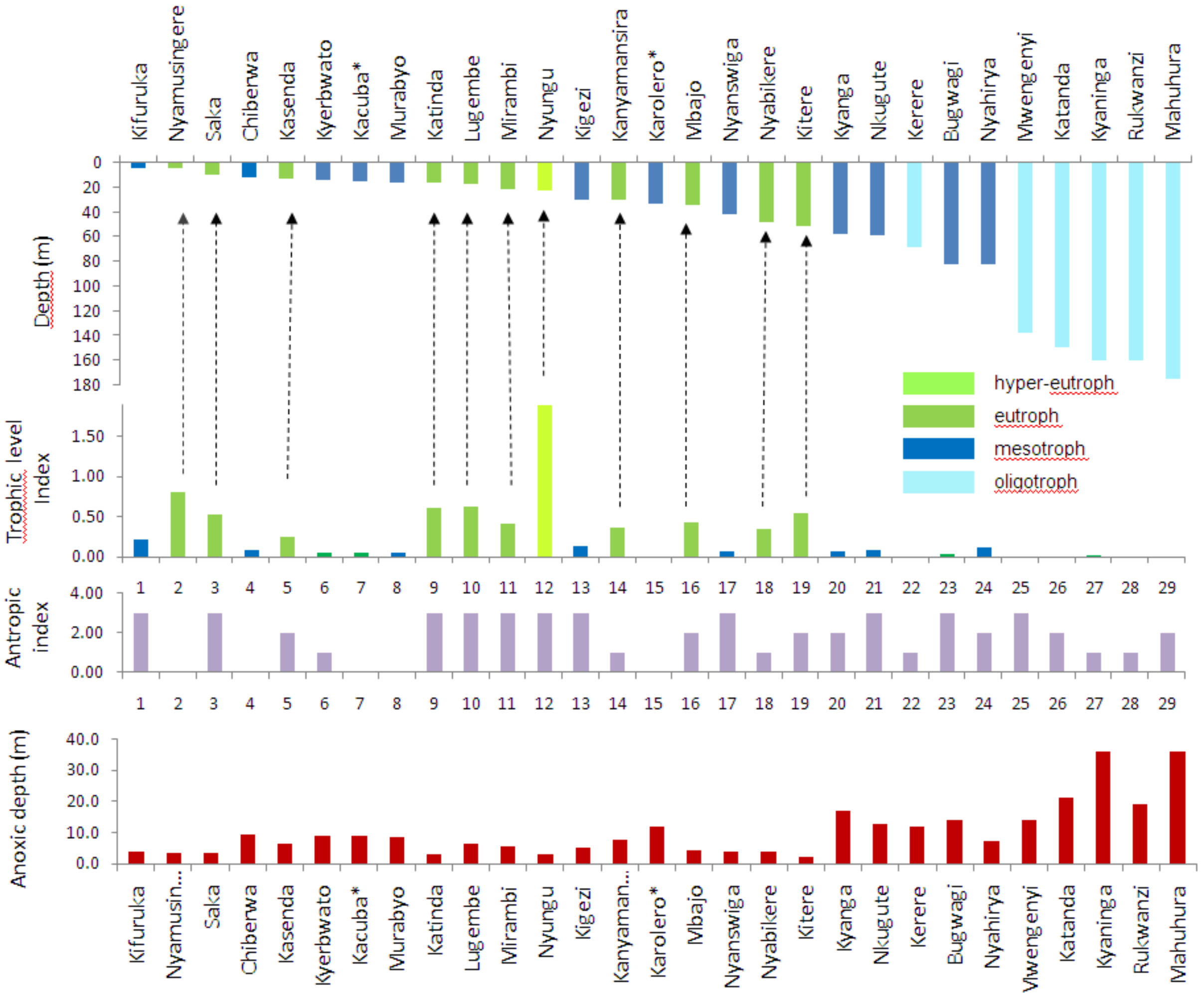


Fig. 8. Selection of 29 CLANIMAE study lakes arranged in order of increasing lake depth (top), colour-coded according to their aquatic productivity. In lakes shallower than ~35 m, human impact has increased productivity; deep lakes (> 90 m) remain relatively unaffected. Note that shallow lakes are naturally mesotrophic (e.g., the pristine forest lake Karolero and the pristine savanna lake Chibwera).

Very probably the large volume of their rarely mixed lower water column represents more or less permanent nutrient storage space, because the low frequency of deep mixing hampers nutrient recycling to the surface water where primary production takes place. As a result, a significant positive relationship exists between lake depth and transparency (as measure for algal biomass: **Fig. 6**) for each of the four lake disturbance categories (AI index 0 to 3; **Fig. 9**). The Trophic Lake index (TLi) is also generally inversely related to lake depth. This implies that when the depth of a lake is significantly reduced, either because of climatic drying (a long period of low rainfall) or through excessive water abstraction, aquatic productivity and lake trophic status are likely to increase, and water transparency is likely to decrease.

Meteorological information has been compiled from various sources obtained from the Meteorological Department in Kampala. The annual average cycle in air temperature at Kabale (1.25°N, 29.9 °E) and Kasese (0.18 N, 30.1 E; **Fig. 10**) indicate the seasonal difference with a warmer rain season from March to April and a cooler dry season in October-November. The high radiation budget during the rain season leads to stronger temperature stratification and reduced internal nutrient recycling, leading to lower algal productivity and higher transparency.

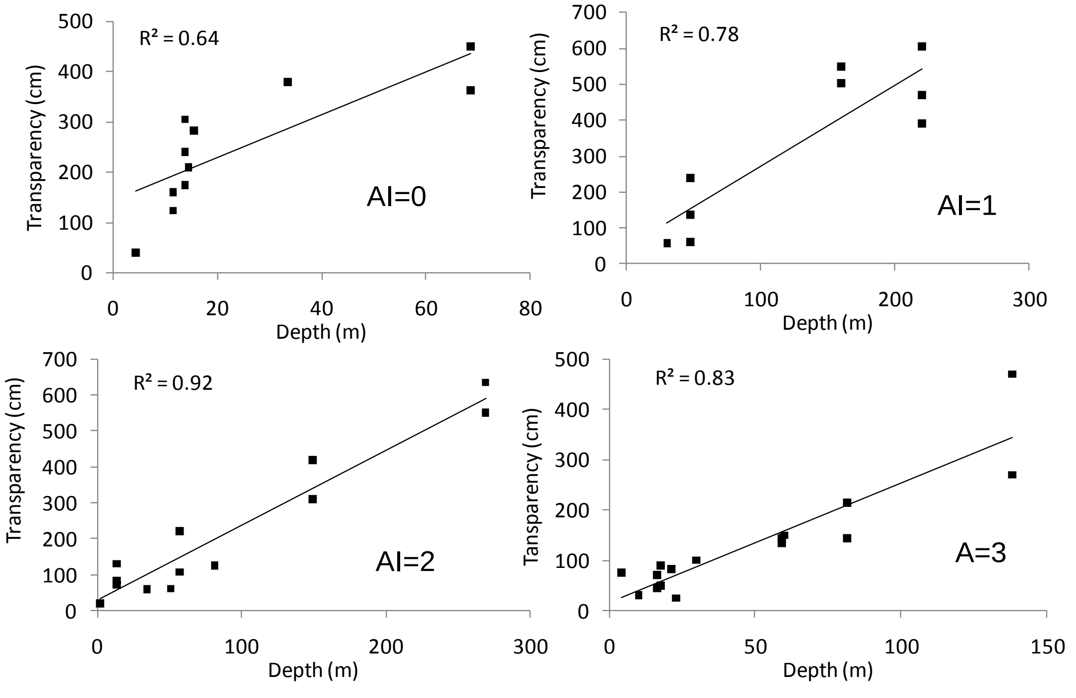


Fig. 9. Relationship between the depth and transparency of Uganda crater lakes for four categories of increasing human impact (Anthropic Impact index 0 to 3).

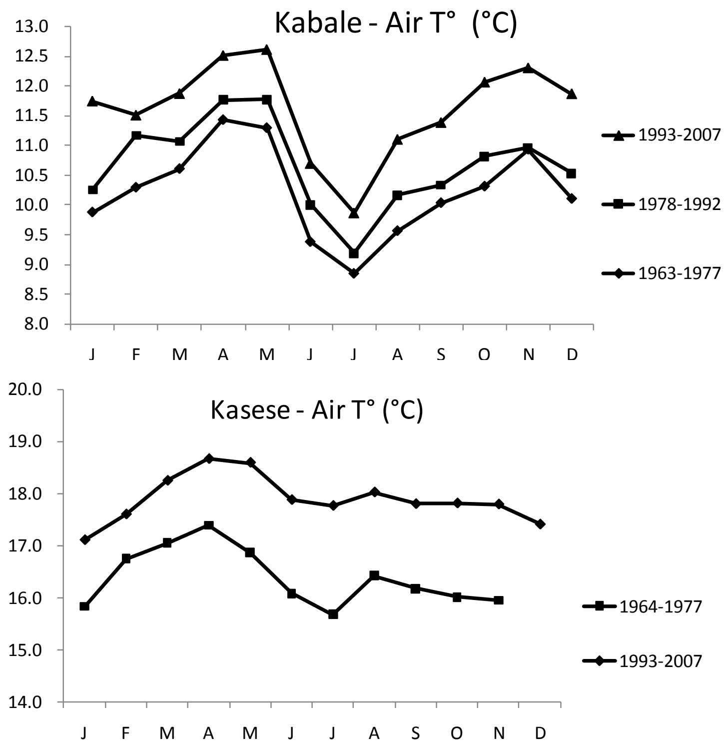


Fig. 10. Annual cycle of mean monthly air temperature at Kabale and Kasese meteorological stations during the periods 1963-1977, 1978-1992 and 1993-2007 (Kasese data 1978-1992 are incomplete).

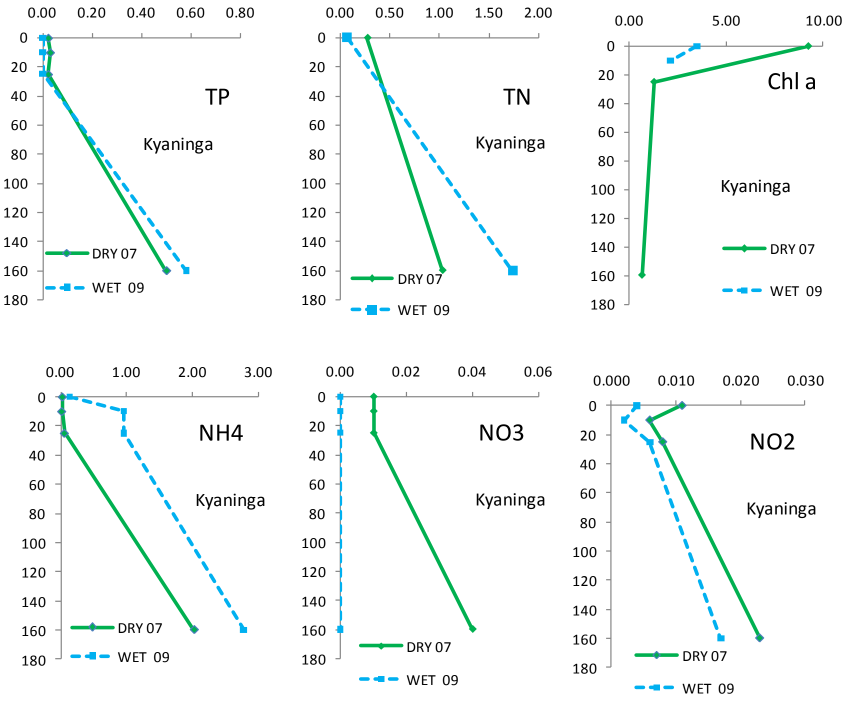


Fig. 11. Vertical profiles of total phosphorus (mg/l P), total nitrogen (mg/l N), Chlorophyll a (µg/l), ammonia (mg/l N), nitrates (mg/l N) and nitrites (mg/l N) during the dry (July) and wet (April) season at Lake Kyaninga.

This process overwhelms the effect of rainfall on the input of new nutrients. Water-column mixing during the dry season affects surface-water chemistry (e.g., Lake Kyaninga: **Fig. 11**) by increasing concentrations of phosphorus and nitrogen compounds, except the concentration of ammonia which is oxidized to nitrate.

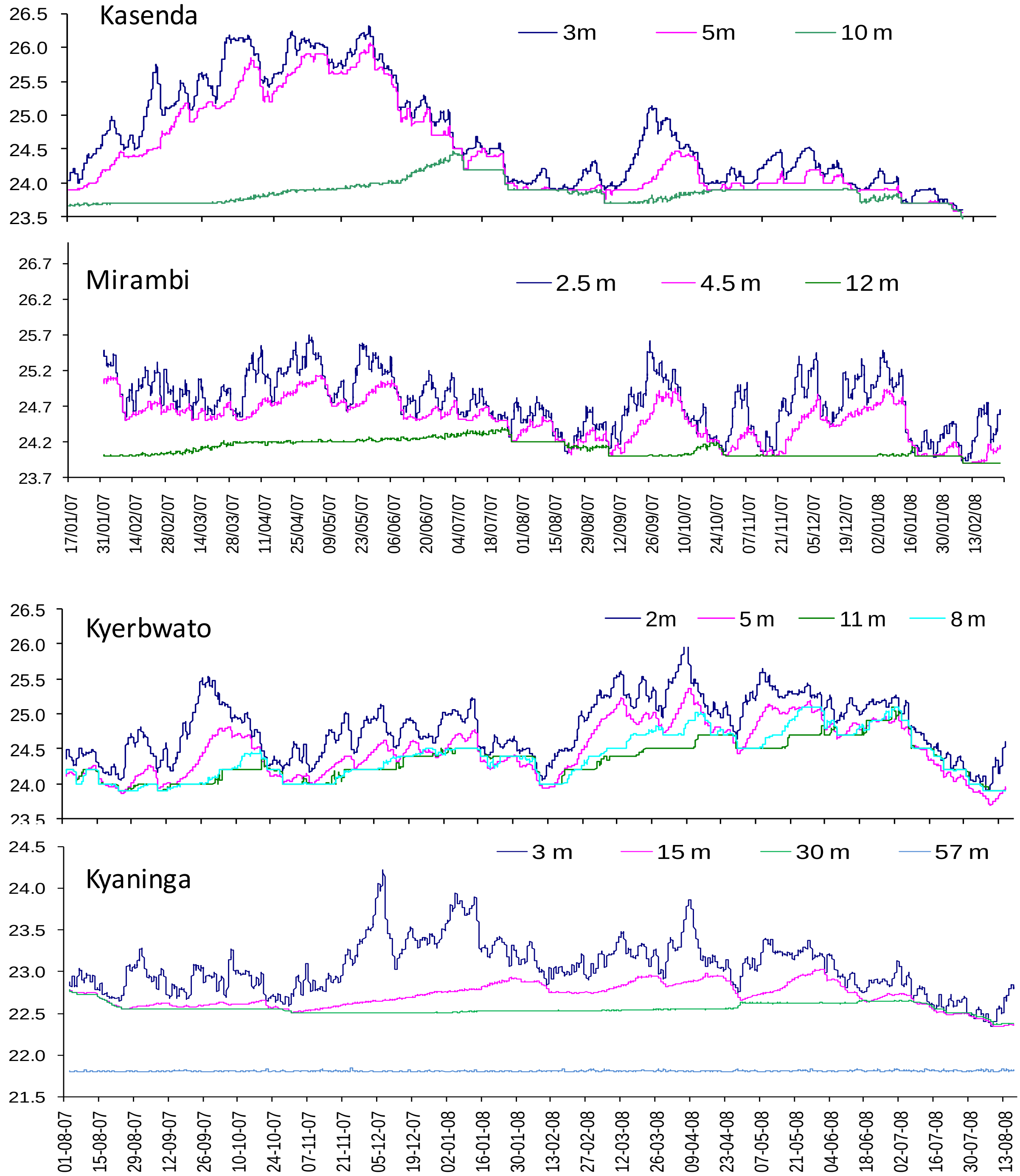


Fig. 12. Continuous temperature measurements at 3 or 4 depth levels in the water column of four Uganda crater lakes: January 2007 to February 2008 at Kasenda and Mirambi, and from August 2007 to August 2008 at Kyerbwato and Kyaninga.

Continuous (2h-interval) temperature measurements using thermistors suspended at discrete depths in the water column (**Fig. 12**) illustrate the inverse relationship between depth and frequency of mixing, with conditions for deep wind-induced mixing improving when surface-water temperature is at a minimum. Shallow lakes such as pristine Kyerbwato (14 m) and impacted Kasenda (14 m) and Mirambi (21 m) are monomictic (mixing completely at least once per year) to polymictic (mixing completely several times each year) independent of their productivity. Lake Kyaninga (>220 m) mixes at least once per year down to 30 m depth, but not down to 57 m (**Fig. 12**).

Water temperature versus air temperature, and a possible global-warming signature in Uganda crater lakes. The relationship between lake temperature, local annual mean air temperature and lake altitude (**Fig. 13**) is important to relate meteorological information available from only a few dispersed meteorological stations with observations of lakes situated at altitudes ranging between 900 and 1600 m above sea level (a.s.l). Lake surface temperature at any one time reflects weather-related variability in day-time solar insolation and night-time or wind-driven cooling. The bottom temperature of deep stratified lakes approximates the lowest annual surface-water temperature, and is therefore a guide to long-term trends. The bottom temperature of 55 Ugandan crater lakes surveyed in this study ranges between 20.0 and 26.6 °C, which is greater than the regional, altitude-related variation in mean annual air temperature (21-25 °C). The higher variability in bottom temperature mainly reflects variation in lake depth (shallower lakes have higher bottom temperatures) and differences in exposure to solar radiation and wind.

Preliminary evaluation of all available historical and recent temperature profiles indicates an apparent deep-water warming trend in the Uganda crater lakes, such as Lake Katanda (**Fig. 14**), superimposed on inter-annual variability reflecting notable warmer (e.g., 2002) and colder (e.g., 2007-2008) years. The temperature increase is around 0.2 to 0.7 °C in the last decades, comparable to that observed in Lake Victoria (Hecky et al., 1994), Lake Tanganyika (Plisnier, 2000) and Lake Malawi (Vollmer et al., 2005). This warming trend in the western Uganda crater lakes mirrors the regional increase in air temperature observed between 1963 and 2007 (**Fig. 10**).

Finally, information on recent or historical fish kills collected during this project or from the published literature reveals a broad inverse relationship between the frequency of fish kills and lake depth (**Table 3**). Since fish kills occur when a large volume of anoxic water suddenly mixes with surface water, fish kills

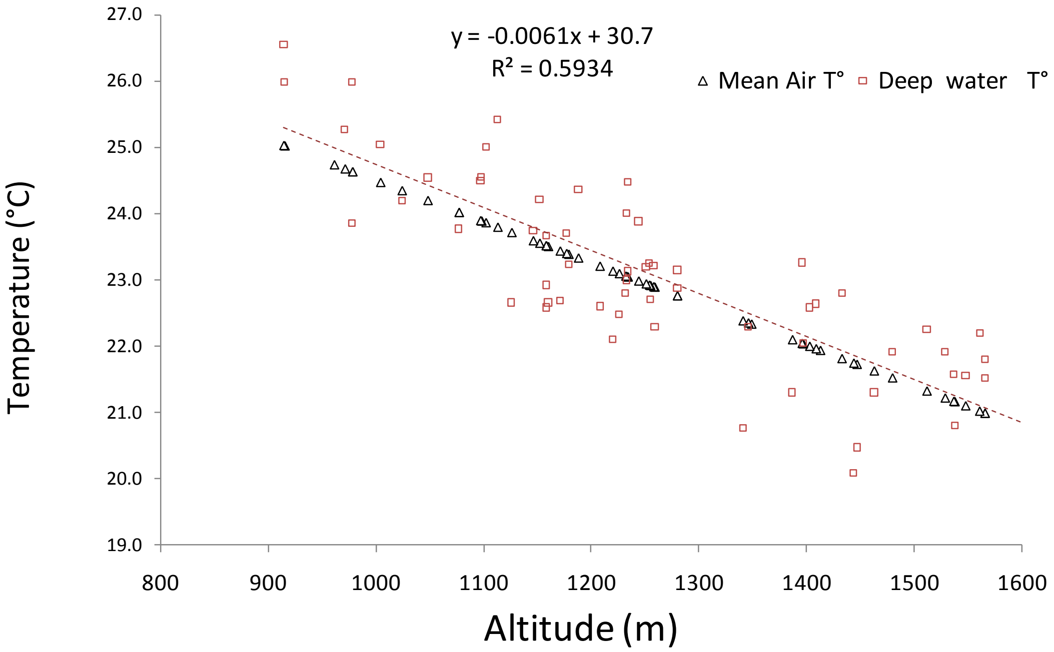


Fig. 13. FAO mean annual air temperature data from 63 meteorological stations, between 1.4° S and 1.0° N and 29.5° to 31° E, corrected with recent data from the Meteorological Department of Uganda, compared with near-bottom water temperature in 55 Ugandan crater lakes. Lake data from the last 30 years: Kizito et al. (1993); Chapman et al., (1998); Verschuren & Rumes (unpublished data); this study.

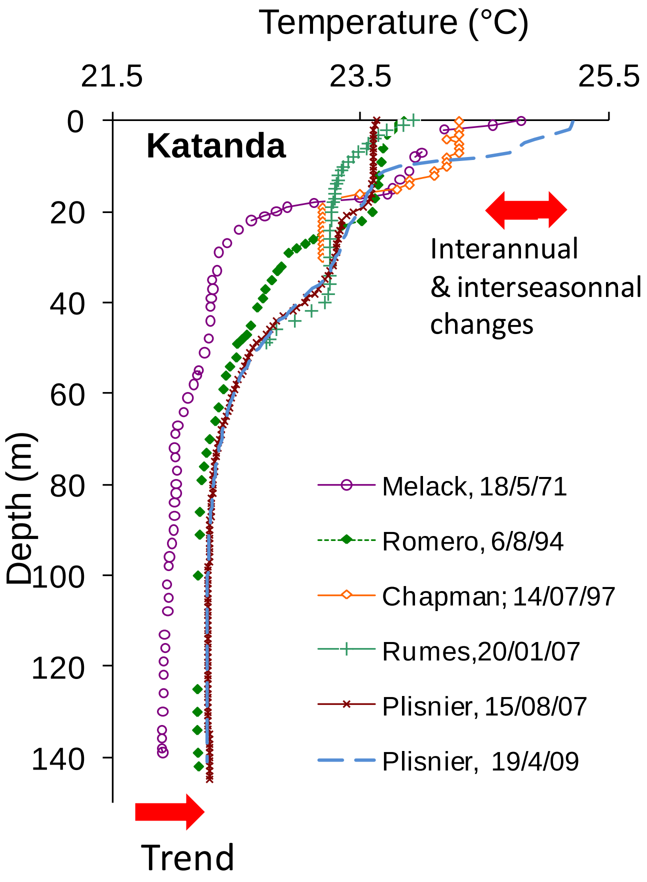


Fig. 14. Variability in surface and deep-water temperature at Lake Katanda between 1971 and 2009, suggesting a deep-water warming trend.

Lakes	*Depth (m)*	*Prob. mix. type*	*Observations*	*Source*
Katinda	17	dimictic	Fish kill every July and December (3 days)	Pers. com.
Mirambi	21	dimictic	Fish kill every June and November (3 days)	Pers. com.
Nyungu	25	dimictic	Fish kill every July and December (3 days)	Pers. com.
Mbajo.	35	dimictic?	Some dead fish in February 2008	Gelorini & Lebrun, pers.com.
Njarayabana	38	dimictic?	Fish breathing near the surface in Feb 2008	Gelorini & Lebrun, pers.com.
Bunyoni	45	oligomictic	Serious fish kill in 1964	Beadle, 1981
Nyabikere	48	oligomictic	Fish kill +/- 2 years ago (2005?); not every year	Pers. com.
Nkugute	58	oligomictic	Fish Kill 8-7-1956 and some years before	Beadle, 1966
Nyanswiga	61	oligomictic	Fish kill observed (in March or June)	Kizito, 1993
Bugwagi	85	oligomictic	Last fish kill in 1989 (before: every 10 y+/-)	Pers. com.
Kyaninga	58/135	oligomictic	Fish kills every 5 years - Fish kill in 2006	Beadle, 1966 & pers. Com.
Mwengenyi	140	oligomictic	Fish kill in 1998 (2 weeks in July) & every lakes in the region	Pers. com.
Katanda	152	oligomictic	Fish kill in 1998 (2 weeks in July) & every lakes in the region	Pers. com.
Mahuhura	154	oligomictic	Fish kill observed but date not remembered	Pers. com.

Table 3. Frequency of fish kills in 14 Uganda crater lakes (in sequence of increasing depth) in relation to their probable seasonal mixing regime.

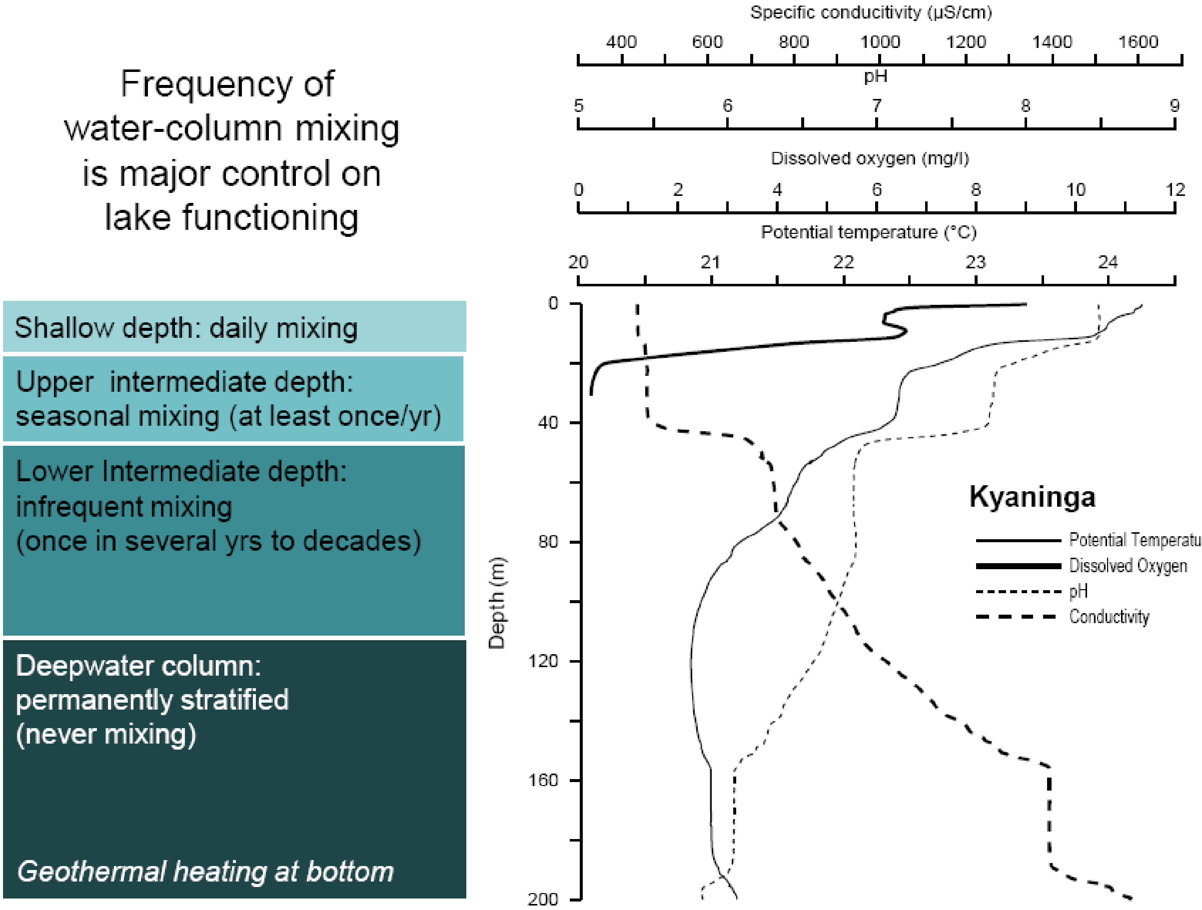


Fig. 15. Relationship between depth and frequency of mixing, with Lake Kyaninga as example. The approximate transition depths can be derived from changes in the physical parameters temperature, dissolved oxygen, pH and specific conductance.

are associated mostly with deep lakes, and the frequency of fish kills is an indicator of the frequency of deep water-column mixing. The upwelling of ammonia in surface water must also play a role in fish kill events, particularly when pH increases during algal blooms, because these conditions promote higher surface-water concentration of toxic ammonia.

Bottom anoxia also occurs in relatively shallow Ugandan crater lakes: it was observed in all lakes sufficiently deep to develop seasonal temperature stratification (i.e., their temperature profile contains a marked thermocline; Fig. 3), with the exception of the pristine Lake Kyerbwato in Kibale National Park, where 0.8 mg/l of oxygen was measured near the bottom at 12 m depth. Overall our physical data indicate that the water column of most fresh Ugandan crater lakes mixes completely at least occasionally, but only the more shallow lakes (<30 m) tend to mix completely at least once per year. Meteorological conditions allowing the complete mixing of deep lakes (cold air temperature coinciding with windy conditions) are relatively rare, on the order of once in several decades for some of the deepest lakes. Lake Kyaninga (>220 m deep) is one of a handful Uganda crater lakes with a deep-water zone that never mixes; this permanently stratified deep-water zone is characterized by slightly elevated dissolved ion concentrations (measured as specific conductance; **Fig. 15**). We use the terms oligomictic and meromictic as defined by Hutchinson (1957): oligomictic are lakes mixing completely at frequencies of less than once a year, and meromictic are lakes with a part of the lower water column that is permanently stratified. The term dimictic could be used to refer to lakes which mix completely during each of the two dry, colder and windy seasons. However, true dimictic lakes are restricted to high-latitude regions where cold surface stratification (<4°C) can develop during winter. The Uganda lakes mixing twice each year remain in a warm temperature range, therefore could be defined as 'warm dimictic'.

Diatom-based inference model for aquatic productivity in East African lakes. CLANIMAE aimed to develop the first diatom-based inference model for past changes in the aquatic productivity of African lakes, as already exist for lakes in Europe (Bennion et al. 1996) and North America (Hall & Smol 1999). We calibrated diatom species distribution along a wide productivity gradient involving 48 Uganda crater lakes, through analysis of fossil diatom assemblages in recently deposited surface sediments. This produced a reference dataset on the modern distribution of African diatom species in relation to nutrients (total phosphorous, total nitrogen, dissolved silica; **Fig. 16**) and other measures of aquatic productivity (Secchi disk depth, Chl a; **Fig. 17**). Analyses of algal pigments by the HPLC technique (courtesy of the UGent research group Protistology & Aquatic Ecology) on water-filtration residues produced data on total phytoplankton community composition. This allowed to analyse associations between diatom species recorded in surface sediments and important communities of African phytoplankton (which are often dominated by other groups of algae or cyanobacteria). For 27 lakes these data were calibrated with semi-quantitative data on phytoplankton species composition based on microscopic cell counting of preserved dry-season samples. For example, the characteristic phytoplankton community of Lake Kyogo with several common desmid species (e.g., *Staurastrum*, *Closterium*, *Cosmarium*) can be detected only by direct microscopic analysis, because their pigments are identical to those of other green algae. **Table 4** shows species abundance data in 11 of these lakes, in five abundance classes from sporadic (X) to abundant (XXXXX). Finally, wet-season (April 2009) phytoplankton collections allowed assessment of seasonal dynamics in the lakes' diatom communities.

In all studied lakes, the phytoplankton was dominated by Cyanobacteria (blue-green algae) and Chlorophyta (green algae). Oligotrophic lakes were characterized by *Aphanocapsa* and *Aphanizomenon* (Cyanobacteria), *Chlorobium* (Chlorophyta) and *Urosolenia* and *Cyclotella* (diatoms). Mesotrophic lakes were characterized by *Lemmermaniella* (Cyanobacteria) and *Kirchneriella* (Chlorophyta). Eutrophic lakes were characterized by *Cyanobium*, *Oscillatoria* and *Synechococcus* (Cyanobacteria), *Chlorella*, *Pseudoquadrigula*, *Crucigenia* and *Pediastrum* (Chlorophyta), *Lepocyclis* (Euglenophyta) and *Ulnaria* and *Aulacoseira* (diatoms). Principal Components Analysis (PCA) of the distribution of 49 genera of phytoplankton in 25 crater lakes showed oligotrophic lakes separated from eutrophic lakes along PCA axis 1 (**Fig. 18**), confirming the dominant influence of lake productivity on phytoplankton community composition in the Uganda lakes. Our preliminary diatom-based inference model for aquatic productivity uses the relationship between diatom species composition in surface sediments and the surface-water concentration of total phosphorus (TP, i.e. phosphorus in particulate and dissolved form) in our 48-lake reference data set (**Fig. 16**).

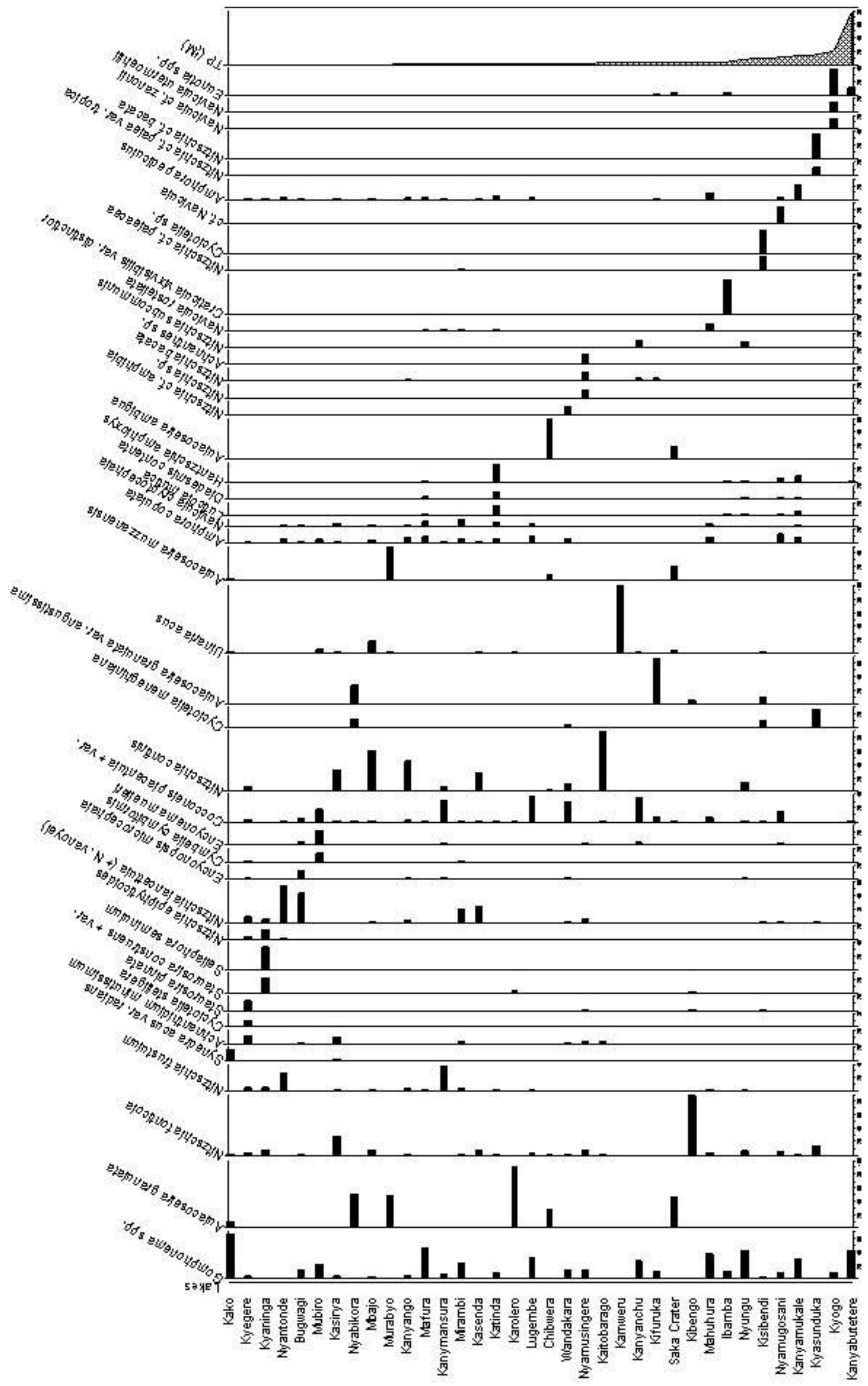


Fig. 16. Species composition of diatom algal communities in 36 Uganda crater lakes, analyzed in recently deposited surface sediments, which integrate seasonal variability. Lakes are arranged from top to bottom in order of increasing total phosphorus concentration (TP), a measure of lake productivity.

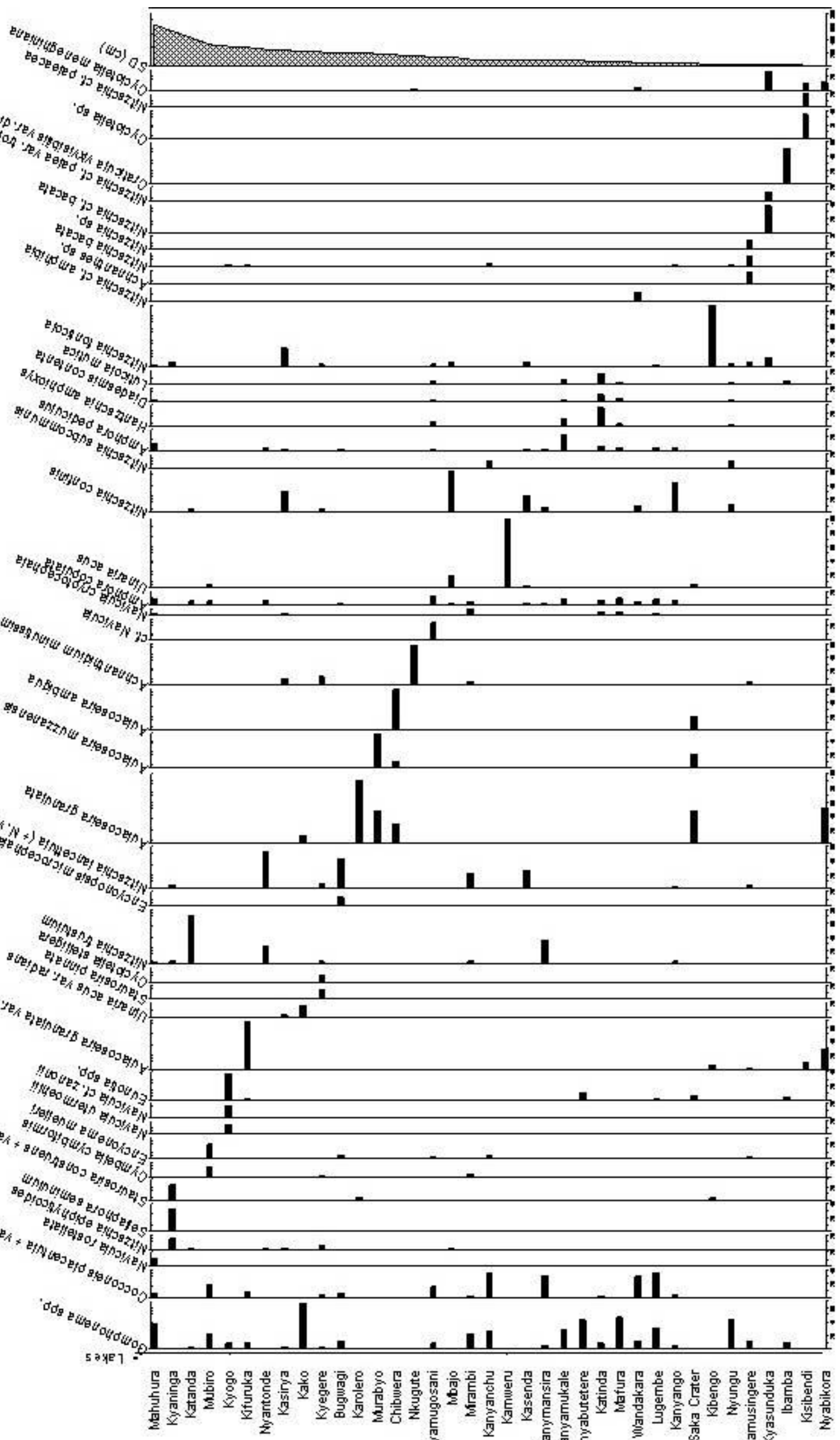


Fig. 17. Species composition of diatom algal communities in 37 Uganda crater lakes, as analyzed in recently deposited surface sediments, which integrate seasonal variability. Lakes are arranged from top to bottom in order of decreasing Secchi disk transparency (SD), a measure of lake productivity.

Lakes	Katanda	Mwengenyi	Bugwagi	Lugembe	Katinda	Kyaninga	Nkugute	Karolero	Saka-Crater	Mahuhura	Kyogo
Cyanobacteria											
Anabaena cf. verrucosa											
Anabaena sp.						xx	xx	x			xxx
Aphanizomenon flos-aquae						xx					
Aphanocapsa		x	xx		x		x	xxx	x		x
Aphanothece	x		xx	xx			x		x	x	x
cf. Cylindrospermum	xx										
Chroococcales			xx	xx	xxxx		xx				xx
Chroococcus spp.		xx	xx			xx		xx	xx	xx	
Coelosphaer. cf kuetzingianum					x						
Coelosphaerium cf. lacustris			xxx				x	xxxx	xx		
Cylindrospermopsis sp.	xxxx	xx	xx	xxxxx	xx	xx	xxx			xx	
Gomphosphaeria sp.									xx		
Gomphosphaeria cf. aponina											
Merismopedia minima			xx	xx	xxxx	xx	xxxx		xxx		
Merismopedia tenuissima					xx		xx				
Microcystis aeruginosus					x						
Microcystis sp.				x					x		
Oscillatoria agardhii					x				xxxxx		
Oscillatoria sp.			xx								
Planktolyngbya cf. limnetica	x	xx							xxx		
Planktolyngbya contorta			xxx	xx	xxxx	xx	xx	xxxxx	xxx		
Planktolyngbya limnetica	xxxx	xxxx	xxx	xxxx	xxx	xxx	xx	xxx	x	xxxx	xxx
Spirulina sp.				xx							
Synechococcus sp.					xxx				xx	x	
Synechocystis sp.		x									
Chlorophyta											
Chlorococcales (coccoid spp.)			xx	xx							
Actinastrum sp.								x			
Ankistrodesmus falcatus							x				xx
Ankyra sp.							x				
Botryococcus braunii						x			x		
Chlorella sp.	xx	xx	xx		xx	xx	xx	xx	xx	xx	xx
Chodatella sp.			x								
cf. Astroideum sp.									x		
Crucigenia sp.				xx				xx	x		
Crucigeniella crucifera											
Dictyosphaer. ehrenbergianum						x	x				
Dictyosphaerium pulchellum						x	xx				
Dictyosphaerium sp.									x		
Didymocystis bicellularis				xx			xx	xx	xx		
cf. Didymocystis bicellularis		xx								xx	
cf. Eremosphaeria		x					x				
Kirchneriella cf. irregularis		x						xx	xx		
Kirchneriella obesa			x	xx							
Lagerheimia sp.								x			
Monoraphidium cf. arcuatum								x			
Monoraphidium circinale									xx		xx
Monoraphidium contortum		x	xx	xx							
Monoraphidium dybowskii						x					
Monorap. flexuosum/irregulare	xxx	xxx	xxx	xx		xxxxx	xx		xx	xxx	xx
Monoraphidium komarkovae	xx	x	x			xx		x	x	xx	
Monoraphidium skujae			x				xx				
Monoraphidium minutum			x				x	x			x
Oocystis sp.											

Pediastrum duplex								x			
Ped. duplex var. gracillimum									x		
Pediastrum tetra											
Quadrigula lacustris									x		
Scenedesmus acuminatus							x		xx		
Sc. acuminatus var. elongatus									x		
Scenedesmus ecornis							xx	x			
Scenedesmus cf. ginzbergeri											x
Scenedesmus cf. obliquus								x	xx		x
Sc. opoliensis var. bicaudatus									x		
Scenedesmus cf. platydiscus							xx				
Scenedesmus quadricauda									x		
Scenedesmus sp.				xxx			xx				
Schroederia setigera									x		
Tetraedron triangulare			x	x			x		x	x	
Tetraedron minimum	x	x	xx	x		xx	xx	x	x	x	x
Closterium sp.							x				x
Cosmarium spp.	x	x	xx			x	xx				
Staurastrum spp.						x	x				x
Dinophyta											
Gymnodinium sp.	x	x	x	x				x			x
Peridinium cf. africanum			x			x	x	x			xx
Peridinium sp.	x			x	x						x
Euglenophyta											
Euglena sp.						x			x		
Lepocinclis sp.							x				
Bacillariophyta											
Achnanthidium minutissimum							xx				
Amphora copulata										x	
Aulacoseira granulata									x		
Navicula sp.				x		x	x				
Nitzschia cf. gracilis							x				
Nitzschia spp.				x		x					x
Chrysophyta & Cryptophta											
cf. Mallomonas		x									x
Chromulina sp.										x	
Chroomonas sp.		xx									
Ochromonas sp.											x
Dinobryon sp.											xx
unidentified sp. 1				xx							
unidentified sp. 2				xx							
unidentified sp. 3						x					
unidentified sp. 4								x			
unidentified sp. 5											
unidentified sp. 6					x				xx		
unidentified sp. 7											x

Table 4. Species composition of pelagic phytoplankton communities in a selection of 11 Uganda crater lakes, as sampled in February 2008 (Kyogo) or July/August 2008 (all other lakes). Relative abundance classes from sporadic (x) over rather common (xx), common (xxx), and very common (xxxx) to abundant (xxxxx). CLANIMAE produced such phytoplankton composition data for 27 Uganda crater lakes.

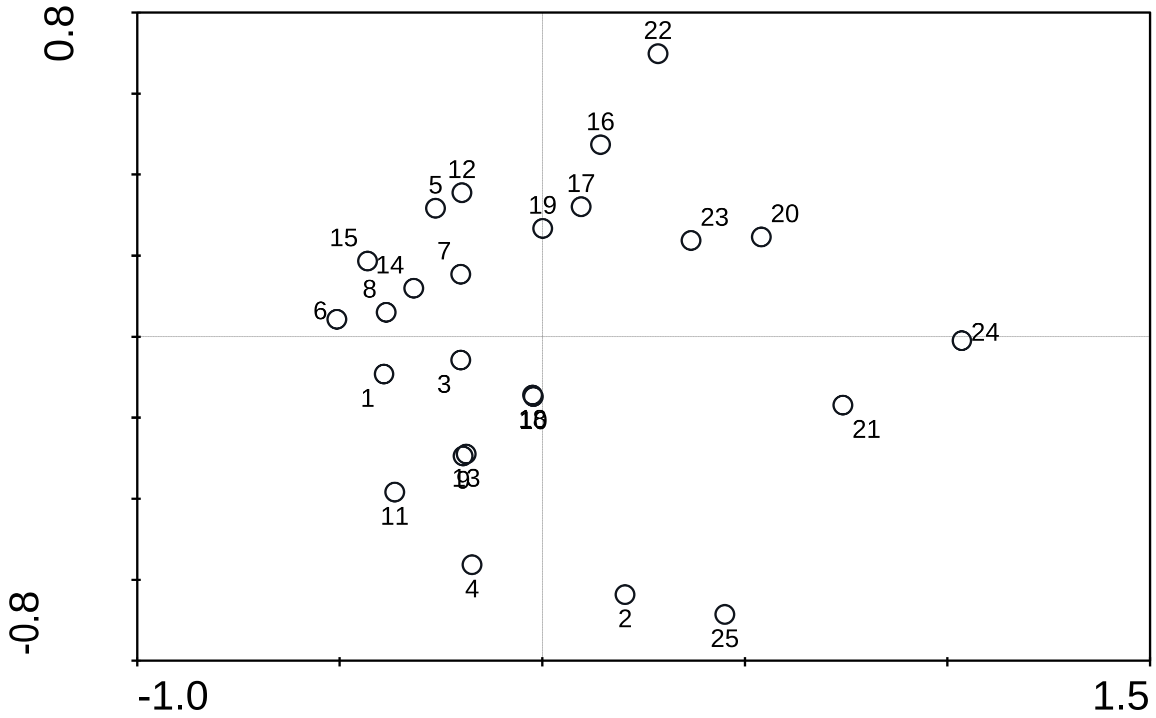


Fig. 18. PCA axes 1 and 2 of the ordination of 49 genera (groups) of phytoplankton in 25 Uganda crater lakes. Lakes numbered 1-7 are oligotrophic, 8-14 are mesotrophic and 15-25 are eutrophic. The phytoplankton data are log-transformed percent abundances of cell volumes.

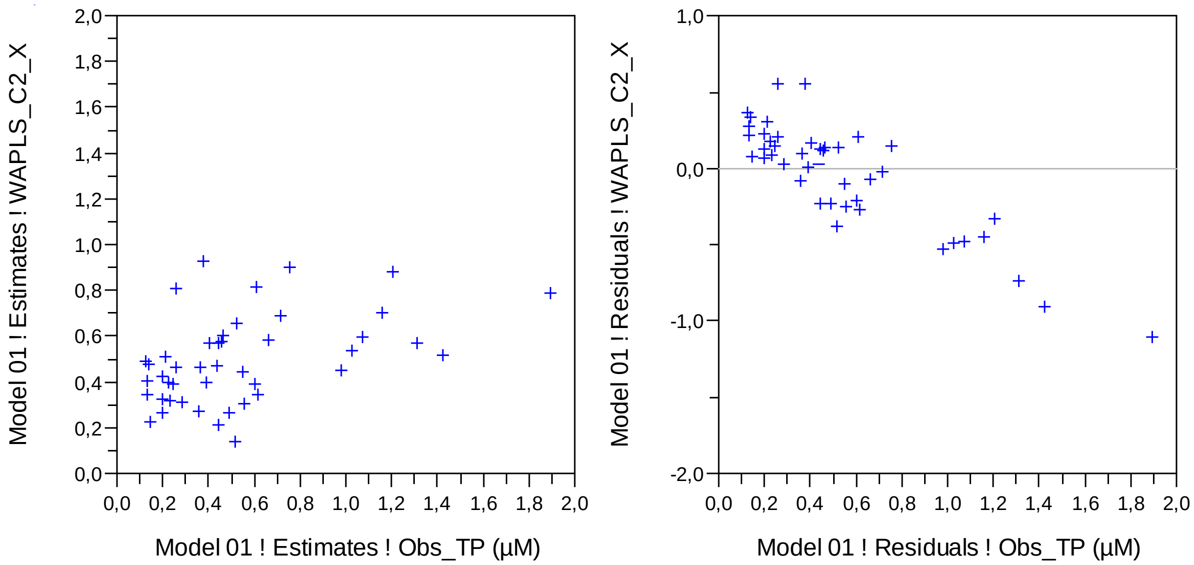


Fig. 19. Estimates (left) and residuals (right) of a diatom-based, WA-PLS type total phosphorus (TP) inference model versus the corresponding observed values (x-axes).

Data quality screening reduced the data set for model development to 44 lakes and the 56 most common diatom taxa, TP values (in µg/liter) were log-transformed, and the analysis was done in C2 (Juggins et al.). The result (**Fig. 19**) is unimpressive: with jack-knifing the best-performing transfer function (WA-PLS) has a R^2 value of only 0.204 between inferred and observed TP values, and a root-mean-square error of prediction of 0.355 log TP units. Presumably, model performance is compromised by the apparent scarcity of diatoms in the living phytoplankton of most Ugandan crater lakes, as much of the aquatic productivity is contributed by other groups of algae.

Environmental regulation of aquatic macrophyte communities. Also in work package 1, CLANIMAE studied environmental controls on the distribution of aquatic macrophyte species in Ugandan crater lakes, similarly to explore their value as environmental indicators. This involved a total of 216 survey plots in 36 lakes, where a total of 140 terrestrial, semi-aquatic and aquatic plant species were identified along transects between the lakeshore and the depth limit of aquatic plant development. Local species abundance was scored visually on the DAFOR scale (Kent & Coker, 1995). Submerged macrophytes in deeper water were sampled using a 4-m long rake. At each plot, water depth, bottom slope, sediment type (soft or compact) and distance from shore were recorded. Turbidity was measured with a Hach turbidimeter, and physical variables (pH, conductivity, temperature and dissolved oxygen) were measured with a Hydrolab Quanta multi-probe. Prior to analysis, floristic data were transformed to ordinal coefficients using the van der Maarel scale (Jongman *et al.*, 1995).

The habitat requirements of individual plant species were reflected in distinct ranges of distribution along gradients of 13 relevant physical and chemical habitat characteristics (**Figs. 20-21**). Clustering analysis revealed eight major ecological communities (groups), each with particular indicator species (**Fig. 22**). Group I is dominated by *Phragmites mauritianus* and lianas growing in association with it. Group II is characterized by the co-dominance of the emergent aquatic plants *Cladium mariscus* subsp. *jamaicense*, *Cyperus alternifolius* and *Cyperus dives*. Group III is heterogeneous and contains many plots which were difficult to associate to a particular group. It is characterized by lake-edge species (*Phoenix reclinata*, *Hibiscus diversifolius*) and re-colonization stage species (*Penisetum purpureum, Hyparrhenia* sp.).

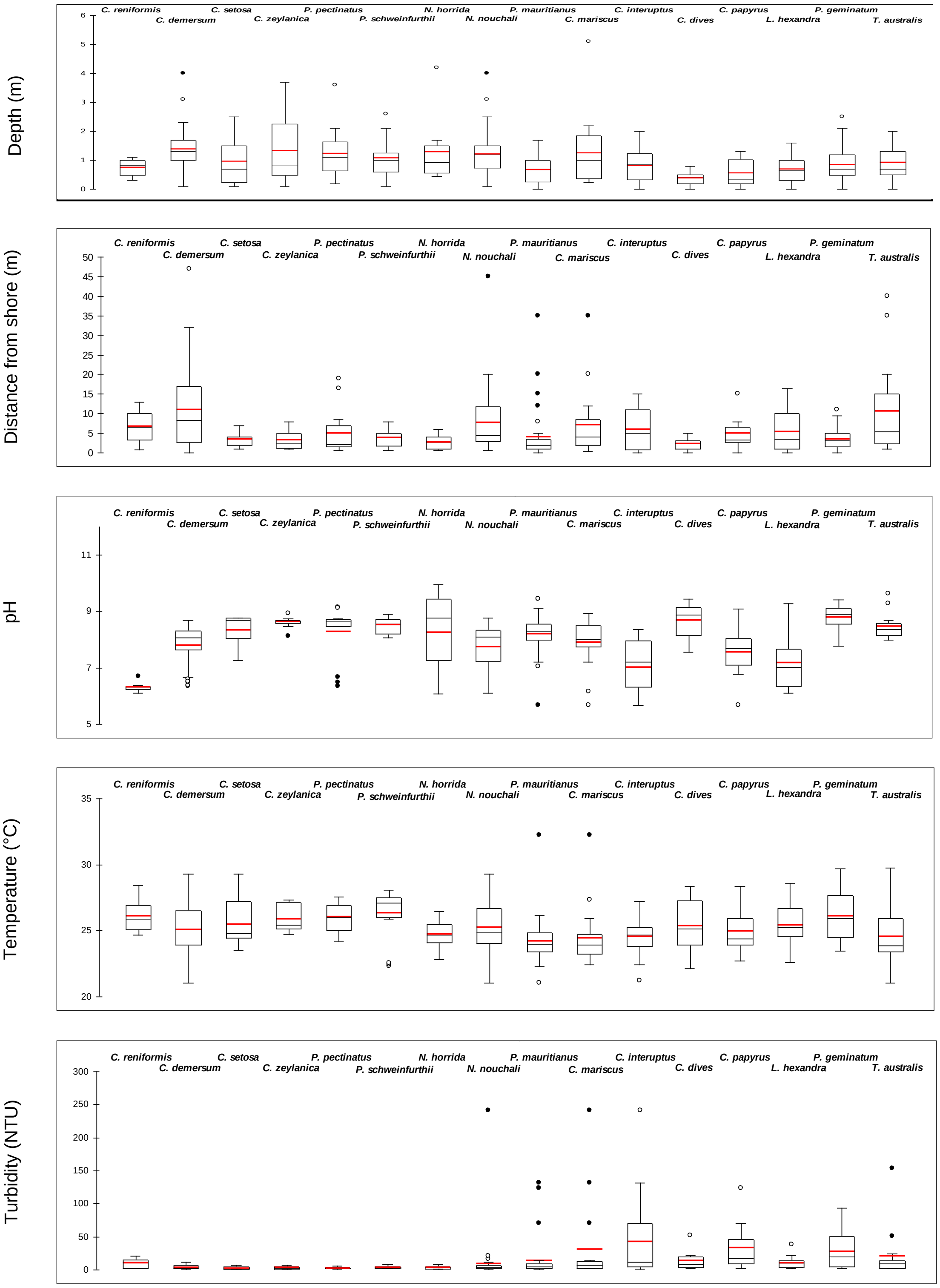


Fig. 20. Box plots (mean, standard deviation SD, minimum and maximum values) of the distribution range of 16 aquatic macrophyte species in 36 Uganda crater lakes, in relation to the habitat variables (from top to bottom) water depth, distance to shore, water temperature, pH and turbidity.

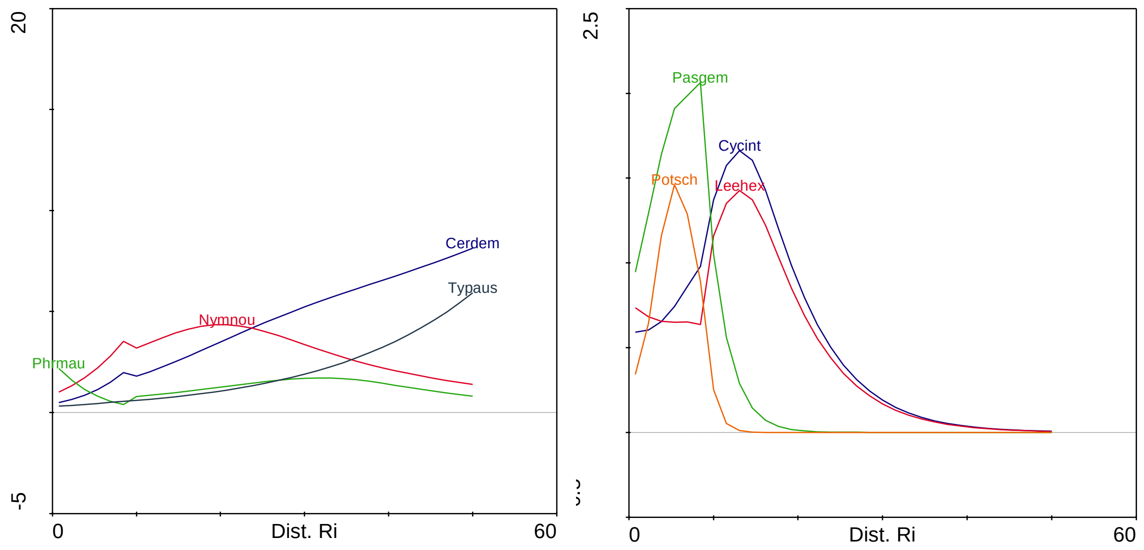


Fig. 21. Distribution of aquatic macrophyte species in relation to distance to shore (x-axis, in m) in 36 Ugandan crater lakes; CLANIMAE produced similar response curves for dissolved ion content and oxygen, temperature, turbidity (1/~ transparency), pH and local water depth. Cerdem = *Ceratophyllum demersum*, Cycint = *Cyclosorus interruptus*, Leehex = *Leersia hexandra*, Nymnou = *Nymphaea nouchali*, Pasgem = *Paspalidium geminatum*, Phrmau = *Phragmites mauritianus*, Potsch = *Potamogeton schweinfurthii*, Typaus = *Typha australis*.

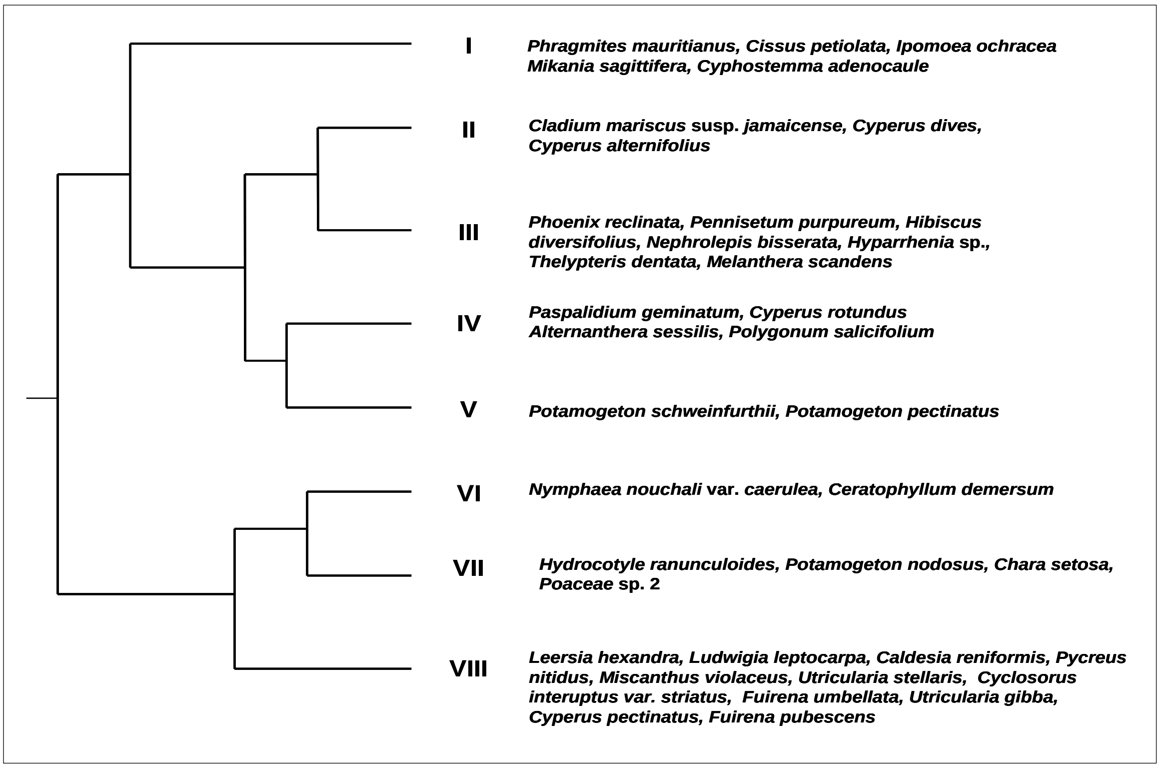


Fig. 22. Cluster diagram of 216 vegetation sampling plots in 36 Uganda crater lakes reveals eight distinct communities of aquatic macrophytes (groups I-VIII). Clustering is based on squared Euclidian distance, with Ward linkage. Selection of the listed indicator species is based on IndVal (Dufrêne & Legendre, 1997). Clustering, analysis of variance and statistical tests were performed with Minitab 15 (Minitab Inc., 2006).

The dominant species of Group IV is *Paspalidium geminatum*, an aquatic herb. Submerged vegetation is represented by group V, which is dominated by *Potamogeton pectinatus* and *Potamogeton schweinfurthii*. Group VI is dominated by the aquatic macrophytes *Nymphaea nouchali* var. *caerulea* and *Ceratophyllum demersum*, and Group VII by *Hydrocotyle ranunculoides*, *Chara setosa* and the rare *Potamogeton nodosus*. Group VIII was largely restricted to Lake Ibamba, which is occupied by a *Miscanthus violaceus* swamp with rare *Utricularia* spp. and *Caldesia reniformis*. Other, more common species in this group (*Leersia hexandra*, *Ludwigia leptocarpa*) were sampled in several lakes. We stress that all these plant communities are part of a continuum and overlap with each other.

ANOVA tests showed that ecological groups had distinct requirements with regard to local water depth, distance from shore, transparency (or its inverse, turbidity), temperature, dissolved ion content and dissolved oxygen (**Table 5**). Group I and III share their restriction to shallow water, exemplified by *Phragmites* which stays above the water table and does not tolerate frequent flooding. These groups prevail near the shore, often in relatively cold water (due either to shading or higher elevation). Group I (and IV) further occurs in lakes with slightly elevated dissolved ion content. Emergent macrophytes of group II can also colonize deeper parts of the littoral zone. This plant community is associated with high pH and turbidity, which here are often the highly productive lakes. It is exemplified by *C. mariscus*, well known to have high nutrient requirements (Denny, 1985). Group IV (exemplified by *P. geminatum*) is associated with high dissolved ion content in addition to high turbidity and pH. The mostly submerged aquatic macrophytes constituting groups V, VI and VII share their obvious need for high transparency (low turbidity); group VIII species tolerate less transparent conditions. Group VI and VIII communities share a requirement for low pH and low dissolved ion content. Among the submerged water plants, Group VI (with *Nymphaea* and *Ceratophyllum*) tend to occur in habitat with the greatest mean water depth.

The eight aquatic macrophyte communities in Ugandan crater lakes are also distinct in a Correspondence Analysis (CA) ordination (CANOCO 4.5: Ter Braak & Šmilauer, 2002), with axes 1 and 2 together explaining 35% of floristic variability among sampling plots (**Fig. 23**). CA axis 1 mostly reflects a gradient from shallow near-shore to deeper offshore habitat; CA axis 2 appears to reflect the gradient of increasing productivity, temperature and pH. Between lakes (results not shown), only pH and total nitrogen are significant environmental predictors of aquatic macrophyte distribution in the Ugandan crater lakes.

Groups	I	II	III	IV	V	VI	VII	VIII
Number of survey plots	28	51	21	25	21	23	30	17
Depth (m)	0.61^{c}	1.02^{abc}	0.66^{c}	0.82^{bc}	1.13^{abc}	1.50^{ab}	1.22^{ab}	0.78^{abc}
Distance from shore (m)	2.56^{ac}	5.46^{c}	0.67^{a}	4.01^{c}	3.56^{c}	13.12^{b}	5.88^{c}	5.98^{c}
Bottom slope (°)	19.0	18.3	30.1	13.4	19.8	11.6	17.2	12.9
Turbidity (NTU)	15.53^{ac}	34.95^{ab}	14.55^{ac}	30.78^{ab}	3.73^{c}	3.45^{c}	4.38^{c}	11.68^{ab}
Temperature (°C)	24.16^{b}	24.94^{b}	24.81^{abc}	26.31^{c}	26.21^{ac}	25.16^{b}	24.77^{abc}	25.29^{abc}
pH	8.11^{c}	8.37^{b}	8.03^{c}	8.80^{b}	8.61^{b}	7.74^{ac}	8.03^{c}	7.10^{ac}
Conductivity (µS/cm)	633.0^{b}	522.8^{bc}	434.6^{bc}	618.9^{b}	535.4^{bc}	357.7^{ac}	391.5^{c}	208.2^{a}
Dissolved oxygen (mg/L)	3.26^{ab}	5.06^{bc}	4.54^{bc}	6.29^{c}	5.67^{c}	5.25^{bc}	5.13^{abc}	3.68^{ab}

Table 5. Average values for diverse environmental parameters recorded in each of the eight recognized ecological communities of aquatic macrophytes in Uganda crater lakes, as identified by cluster analysis. Averages sharing the same superscript letter are not significantly different (P<0.05, Tukey's test). To improve the normality and homoscedasticity of plot data, values for depth, distance from shore, turbidity and temperature were log-transformed and bottom slope was square-root transformed.

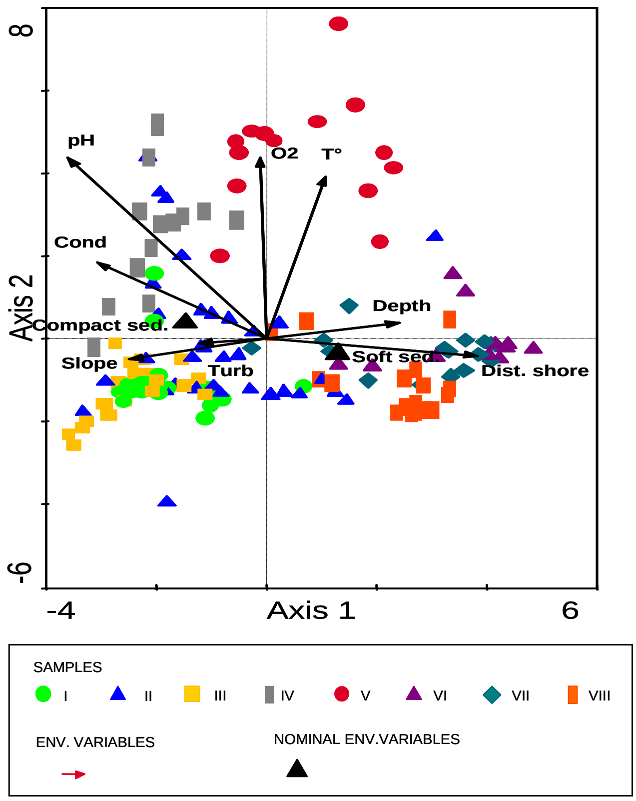


Fig. 23. Correspondence analysis of aquatic macrophyte species composition at 216 plots in 36 Uganda crater lakes, colour-coded according the eight ecological groups identified by cluster analysis. Arrows show the main direction of variation in the relevant environmental parameters: CA axis 1 arranges plots along a gradient from nearshore to offshore; CA axis 2 arranges plots along a productivity gradient.

Representation of aquatic macrophyte communities in Uganda crater lakes by macrofossil assemblages extracted from the lake sediments. Fossil plant remains are commonly used to reconstruct climate-driven and anthropogenic changes in lake hydrology and water quality. However a direct link between past and modern-day communities is hampered by the small fraction of aquatic plant species preserving well in lake-sediment records. To help improve the methodology of plant macrofossil studies in Africa, we analyzed fossil assemblages of aquatic macrophytes in the surface sediments of 13 Uganda crater lakes, linked to our data on the modern-day distribution of aquatic macrophytes within and among lakes. Together these transects represent six of the eight aquatic plant communities recognized to occur in western Uganda crater lakes along habitat gradients in bottom slope, temperature and pH. Our scans of the fossil material at low magnification (25-40x) allowed differentiation between 11 plant macrofossil types, of which seven types correspond with individual plant species (Nymphaea nouchali, Ceratophyllum demersum, three Potamogeton spp., Chara setosa and Najas horrida) and four with genera or larger taxonomic groups (Cyperaceae, Nitella spp., Potamogeton spp., Typha spp.). Analysis of vegetative remains improved ecological characterization of past aquatic macrophyte communities as compared with exclusive reliance on seeds, but poor preservation of several common species clearly introduces bias in paleo-environmental interpretation. This can be partly resolved by using well-preserved taxa as proxy indicator for particular communities. Nevertheless, fossil assemblages derived from habitat characterized by abundant reeds (Phragmites) and papyrus (Cyperus) and/or submerged pennywort (Hydrocotyle) can be erroneously inferred to represent a waterlily-hornwort (Nymphaea-Ceratophyllum) community.

Environmental regulation of the distribution and species richness of Cladocera (water fleas *sensu lato**) and Ostracoda (mussel shrimps) in East African lakes.*** Parallel studies of the species distribution of Cladocera and Ostracoda in 62 Uganda crater lakes, the focus of a UGent PhD project using CLANIMAE materials, demonstrated their potential as biological indicators for water quality and ecosystem health in East African lakes. Both groups of aquatic invertebrates play an important role in aquatic food webs, and as such contribute to the ecological integrity of aquatic ecosystems. Understanding the environmental controls underlying their distribution can thus provide valuable information on aquatic ecosystem functioning needed for management and conservation. In total, 36 species of Cladocera were encountered in the fresh Ugandan crater lakes (< 1500 µS/cm), whereas only a single species, *Moina belli*, was found in the true saline lakes (> 10 000 µS/cm). The species richness of Cladocera in the fresh lakes was found to be determined primarily by the presence of a well-developed littoral belt of submerged and emergent aquatic macrophytes, and pH. The highest species richness occurred in fresh but eutrophic shallow waters, with relatively low pH (6.5-7) and dense aquatic macrophyte growth. The distribution of Cladocera among lakes was strongly determined by nutrient availability (total phosphorus concentration), the diversity of aquatic macrophytes, pH, mean annual temperature, and the fraction of the crater catchment under agriculture. This influence of agriculture is probably due to its effect on transparency and aquatic macrophyte growth. The significant turnover of Cladoceran species along the sampled environmental gradients demonstrates their potential as biological indicators for water quality and ecosystem health in East African lakes.

We further analyzed the species composition of Ostracoda communities in the same set of 62 Uganda crater lakes. We found 33 ostracod species, 29 of which had not previously been reported from Uganda. We produced scanning electron microscopy (SEM) images of the valve morphology of all encountered taxa to aid their identification in paleo-ecological applications. Based on analysis of species records of at least two live specimens per sampled lake, the species composition of ostracod faunas in Uganda crater lakes is primarily controlled by the structural diversity of submerged vegetated habitat, dissolved ion content and aquatic productivity. An expanded analysis which also included species records of single live specimens and by-catch of sub-recent ostracod valves did not significantly alter which habitat variables determine most strongly ostracod distribution. However, it dramatically increased the fraction of lakes in which species were recorded as present, suggesting significant seasonal patterns of local population development.

Also in Kenya, use of Ostracoda in ecological and management applications is hampered by a general lack of accurate information on the habitat requirements of individual species. To correct this situation, we analyzed the species composition of ostracod communities in 37 shallow lakes and ponds in southern Kenya, along with an assessment of abiotic and biotic habitat characteristics. Our study sites comprise a wide variety of standing-water

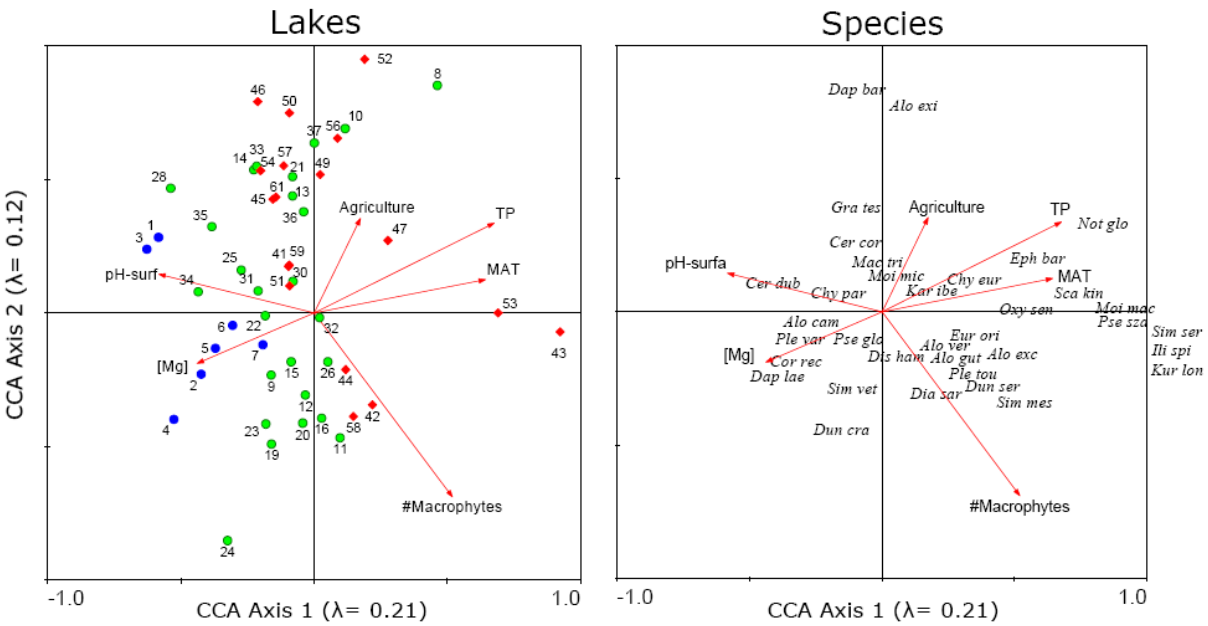


Fig. 24. CCA of the distribution of aquatic invertebrate habitat in lakes, and of the distribution of Cladoceran species in relation to particular habitat types.

aquatic habitats ranging from small, mostly dilute ephemeral pools to large permanent lakes, both fresh and saline, situated between 700 and 2800 m elevation. We encountered a total of 34 species of Ostracoda, among which *Physocypria* sp., cf. *Sarscypridopsis elizabethae* and *Oncocypris mulleri* were both the most widely distributed and often locally most abundant species. Species richness indices and comparison with previous studies indicates that we often sampled only part of the locally present ostracod community, which can be explained in part by the highly dynamic nature of the sampled ecosystems, both seasonally and inter-annually. Canonical correspondence analysis of species-environment relationships indicates that littoral vegetation cover, elevation (a proxy for mean annual air temperature) and surface-water temperature best explain the observed variation in ostracod community composition in Kenyan lakes. Fish presence and lake depth also strongly influence species composition, with large (>1.5 mm) species being more common in shallow, often ephemeral waters lacking fish. The distinct distribution of ostracod species in relation to aquatic habitat variability both in Uganda en Kenya indicate that fossil Ostracoda preserved in lake sediments are excellent paleo-environmental indicators for past climatic and human impacts on aquatic ecosystems in equatorial East Africa.

Taphonomic controls on the composition of fossil aquatic invertebrate assemblages across a wide environmental gradient of East African lakes. Lake-sediment records of past climate and environmental change are often based on analyses of biological remains preserved in a single, mid-lake sediment core, which is assumed to represent a relatively stable integration, in space and in time, of the local aquatic community at the time of burial. We compared the composition of aquatic invertebrate assemblages (Cladocera, Ostracoda, Acari, Bryozoa, Thecamoeba, Turbellaria and several groups of aquatic insect larvae) from recently deposited surface sediments of 61 Uganda crater lakes with surveys of the living communities in those lakes to determine i) the relative preservation potential of these groups and their constituent species, and ii) the extent to which the surface-sediment assemblages from the centre of the lake reflect the lake-wide living aquatic invertebrate community. Using indirect and direct ordination methods, we related species composition to environmental gradients, and determined which environmental parameters influenced both fossil and live assemblages. A total of 96 distinct types of aquatic invertebrate remains were encountered in the surface-sediment samples, whereas 139 taxa were encountered in the live samples. Despite their relatively abundant occurrence in live samples, many species of pelagic Cladocera left few recognizable remains, whereas chydorid (mostly epibenthic) Cladocera were nearly always more common in the fossil assemblages. For most ostracod species, fossil valves were encountered less frequently than live specimens, with the exception of the pelagic *Oncocypris* spp. and the numerically abundant *Zonocypris costata*.

Environmental controls on the isotopic composition of dissolved silica. This component of the CLANIMAE project aimed to develop the silicon-isotope signature of diatom opal as a geochemical tracer of past changes in lake productivity, using MC-ICP-MS instrumentation for high-accuracy δ^{30}Si measurements. We showed earlier that Si-isotope fractionation during uptake by diatoms in lakes Tanganyika and Baikal (Alleman *et al.* , 2005; Cardinal *et al.*, 2006) closely follows that observed in tropical marine (De La Rocha *et al.,* 1997) and polar marine diatoms (Fripiat *et al.,* 2010). This fractionation is species- and temperature-independent (Alleman *et al.,* 2005), making δ^{30}Si measurements in fossil diatoms a potentially powerful tool to quantify past Si utilization (and thus diatom productivity) in lakes. To reach this objective, we needed to gather linked data on dissolved silicon (DSi) concentration and isotopic ratios in the water column of lakes situated in climate zones with mild to strongly negative local water balance, and in landscapes with no to intense human impact.

Methods. For this study, water samples were collected at different depths in 14 Ugandan crater lakes and one Kenyan lake (Lake Challa) representing a large range of ecological conditions including pristine oligotrophic lakes as well as eutrophic lakes with heavy human impact (deforestation, soil erosion, etc.), and deep as well as shallow lakes. In all the lakes, samples were collected just below the water surface and close to the maximum depth of each lake. In some lakes, intermediate depths were also sampled. In all lakes, major element concentrations were measured in the entire water column. Silicon isotopes in the dissolved phase were measured in the sample from maximum depth only, to avoid influence of seasonal events (e.g. diatom blooms) and to measure isotopic ratios that are representative for the mean value of each lake. The water samples were filtered immediately after collection through 0.45µm polycarbonate filters and kept in the dark until analyses in the laboratory. Particulate silicon in particles retained on the filters were measured following a double wet-alkaline digestion method (Rageneau *et al.,* 2005) but were found to be under detection limit. Consequently the estimation of diatom biomass is based on diatom counts and chlorophyll *a* values. Silicon isotopes in the dissolved phase were measured after quantitative co-precipitation using a Triethylamine Molybdate technique (De La Rocha *et al.*, 1996). Isotopic analyses were carried out under dry plasma conditions using a multi-collector mass spectrometer (Nu Plasma) with a desolvator to minimize polyatomic interferences. This involved upgrading the Nu (MC)-ICP-MS with a new adjustable entrance slit as well as a stronger primary pump and newly designed sampler and skimmer cones (Abraham et al., 2008). These settings, combined with the use of collector slits, allowed an isotopic resolution sufficient to overcome the $^{14}N^{16}O$ and $^{14}N_2$ interferences overlying the ^{30}Si and ^{28}Si peaks (Cardinal et al., 2003). This enabled more accurate measurements of $\delta^{30}Si$ and $\delta^{29}Si$ (Abraham et al., 2008). $\delta^{30}Si$ values express the $^{30}Si/^{28}Si$ ratio as deviation in ‰ from the $^{30}Si/^{28}Si$ ratio of the NBS28 standard reference (Cardinal *et al.,* 2003; Abraham et al., 2008).

Results. The range of silicon concentrations observed in the lakes is extremely large, from 0.85 ppm up to 27.85 ppm. Most of the lakes (12 out of 15) show an increase of Si concentration with depth, reflecting the uptake of silicon by diatoms in surface. The increase of the dissolved Si with depth is also probably the consequence of the dissolution of settling biogenic silica (BSi) particles and/or dissolved Si diffusion from sediments. Regarding the $\delta^{30}Si$ values, we observe that contrary to what had been suggested by preliminary analyses there is no link between the degree of human impact on the lake and the isotopic ratio. However, two main observations have to be drawn. First, a

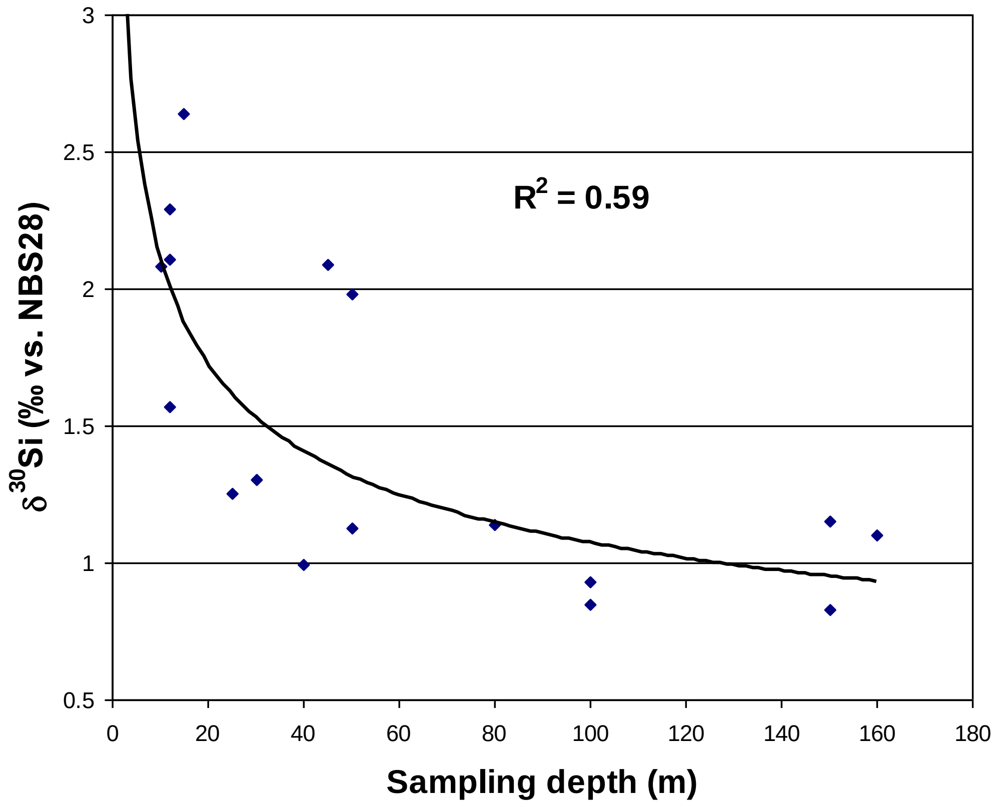


Fig. 25. Correlation between δ^{30}Si and near-bottom (deep-water) sampling depth.

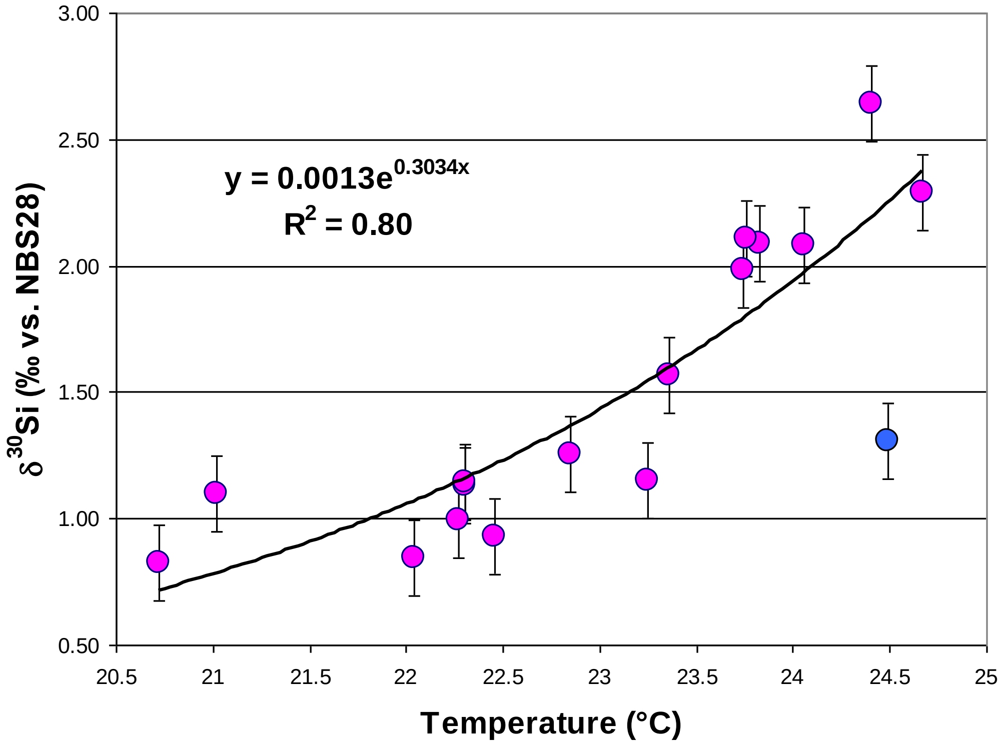


Fig. 26. Correlation between δ^{30}Si and deep-water temperature of 15 East African lakes. The blue dot (Lake Karolero) is an outlier and not included in the analysis.

good link (R^2=0.59) exists between δ^{30}Si and lake depth (**Fig. 25**): in deeper lakes, the near-bottom water sample is enriched in light silicon isotopes. This is consistent with the hypothesis that dissolved Si uptake by diatoms enriches the surface water in the heavy isotope while deeper water gets progressively enriched in the light isotope by the dissolution of settling diatoms (cf. De La Rocha, 1997). Secondly, we observe an excellent exponential correlation (R^2=0.80) between δ^{30}Si and deep-water temperature over the entire regional range of temperatures (~5 °C, **Fig. 26**). Deep-water temperature reflects the lowest annual surface-water temperature. Some analyses are still in progress in order to clarify the nature of this link between temperature and δ^{30}Si. One possible explanation is an increase of diatom productivity with increasing temperature. Understanding this phenomenon is of primary importance in order to understand the silicon cycle within the lakes.

In preparation of developing δ^{30}Si as diatom productivity indicator we engaged subcontractor Lancaster University to produce pure diatom isolates (Morley et al. 2004) from surface-sediment samples of five lakes with contrasting algal productivity and human impact. These isolates were to be used for paired measurement of diatom δ^{18}O at the NERC Isotope Geosciences Laboratory (Keyworth, UK), and δ^{30}Si by MRAC (partner 2). However, only two of the selected lakes contained sufficiently high abundance of intact fossil diatoms and few other opal components (phytoliths, volcanic glass) suitable for analysis of fossil diatom isotopes, despite generally very good diatom preservation (88-98% full valves on microscope slides). Therefore these measurements could not be carried out.

Work package 2 focused on reconstructing past climatic variation in East Africa during recent millennia. Climate-proxy data sets from principal CLANIMAE study sites were already available prior to the start of this project or became available through complementary projects and PhDs.

Until recently, climate reconstructions for equatorial East Africa with at least century-scale resolution and age control were available only for the central Kenya Rift Valley (Naivasha, 1800 years; Verschuren et al., 2000a; Verschuren, 2001), the northern Lake Victoria region (1000 years; Stager et al., 2005) and the western Rift Valley at Lake Edward (5400 years; Russell & Johnson, 2005, 2007). These combined records suggested that equatorial East Africa was relatively dry from about 1000 and 1250 AD and in the late 18th century up to about 1820 AD, and relatively wet from about 1250 to 1500 AD. Between 1500 AD and the late 18th century an interesting climatic gradient appears to have developed over our study region, with drier-than-normal conditions in the west and wetter-than-normal conditions in the east. As a result, during that time the climatic gradient from humid western Uganda to semi-arid eastern Kenya was less pronounced than today (Verschuren & Charman, 2008). New lake-based climate reconstructions by UGent (partner 1) and other workers on crater lakes in western Uganda (Kitagata, Kibengo: Russell et al., 2007; Kasenda, Wandakara, Katinda: Bessems, 2007), Rift Valley lakes in central Kenya (Bogoria, Baringo: Bessems, 2007) and Lake Challa in southeast Kenya (Verschuren et al., 2009) confirm these general temporal and spatial patterns, indicating that the Lake Edward and Lake Naivasha moisture-balance records correctly describe the long-term climate history of respectively western and eastern portions of the East African Plateau. The Lake Challa moisture-balance record also confirms the widespread occurrence of late 18th-century drought (Bessems et al., 2008), which was more severe than any drought in recorded history and most probably the most severe drought in at least the last 800 years (Verschuren, 2004).

Work Package 3 focused on reconstructing past vegetation dynamics based on analysis of fossil pollen in the same, well-dated lake-sediment records. In addition we calibrated the magnitude of terrestrial ecosystem response to climate change as recorded in fossil pollen data, through comparison of reconstructed vegetation history near two Ugandan crater lakes situated in a relatively pristine and an anthropogenically disturbed landscape, respectively. All CLANIMAE pollen analytical work was tendered to sub-contractors in Kenya (Stephen Mathai Rucina, National Museums of Kenya, Nairobi) and Uganda (Dr. Immaculate Ssemmanda, Makerere University, Kampala), who produced reconstructions of vegetation history at five sites: Simbi (Fig. 25) and Challa (Fig. 26) in Kenya, Chibwera (Fig. 27), Kanyamukali and Katinda (both not shown) in Uganda. Preparation of sediment samples for pollen analysis followed Faegri *et al.* (1989). Scanning and counting of pollen and spores was done using a compound microscope at 400x and 1000x magnification. The relative abundance of plant species in the landscape is expressed as percentages of the pollen sum, which besides plant taxa found in the crater catchment and near surroundings also includes a varying degree of long-distance pollen from plant species occurring farther away. Aquatic plants and ferns are excluded from the pollen sum due to local over-representation in lake environments; their abundance is expressed as a % of the pollen sum, hence can exceed 100%.

The Simbi vegetation reconstruction for sub-humid western Kenya can be linked to the diatom-inferred Lake Victoria lake-level record (Stager et al. 2005). The Challa reconstruction covers the last 2700 years and can be directly related to the regional moisture-balance record produced by the ESF-EuroCLIMATE project CHALLACEA (Verschuren et al., 2009). The Chibwera reconstruction for pristine savanna in the western Rift Valley covers the last ~250 years, starting with desiccation resulting from severe late 18th-century drought. The Chibwera vegetation reconstruction for the pristine savanna presently occupying the floor of the Rift Valley in western Uganda covers the last ~250 years, and starts in a phase of severe late 18th-century drought. Its record of regional vegetation history can be related directly to reconstructions of climate-driven lake-level change based on sedimentological characteristics (Bessems et al. 2008), fossil diatom assemblages and aquatic invertebrates (Audenaert et al., in prep.).

Vegetation reconstruction for sub-humid western Kenya. The Simbi pollen diagram (**Fig. 27**) comprises three vegetation zones (Sim I-III) that can be related to minor vegetation disturbances caused by climate-driven moisture-balance changes and historical land-use practices. In Sim I (140-104 cm core depth) the pollen assemblage is characterised by high abundance of grasses (Poaceae, ~80%) and *Podocarpus* (~20%). Pollen from other trees and herbs (*Acacia, Artemisia, Juniperus*, *Myrica, Olea*) are barely present. This suggests open savanna vegetation typical of a rather dry climate regime. The relatively high *Podocarpus* pollen presence is probably due to long-distance pollen dispersal from wetter highland regions (Lamb *et al.* 2003; Ashley *et al.* 2004), in this case the Mau Range and Nandi Hills.

At the start of Sim II (104-22 cm) *Acacia,* Asteraceae, *Euphorbia, Juniperus* and *Olea* become more prominent. Grass pollen continues to dominate, but at a slightly lower mean abundance of ~75%. The greater prominence of montane forest taxa, *Juniperus* and *Olea*, and very high peaks in Cyperaceae may reflect an overall improvement of regional moisture balance (higher rainfall) during the period represented by Sim II, however with much temporal variability. The rise in Asteraceae pollen may also be related to improved moisture, but since its onset is situated within the drier period preceding Sim II, we favour the alternative possibility that it reflects increasing

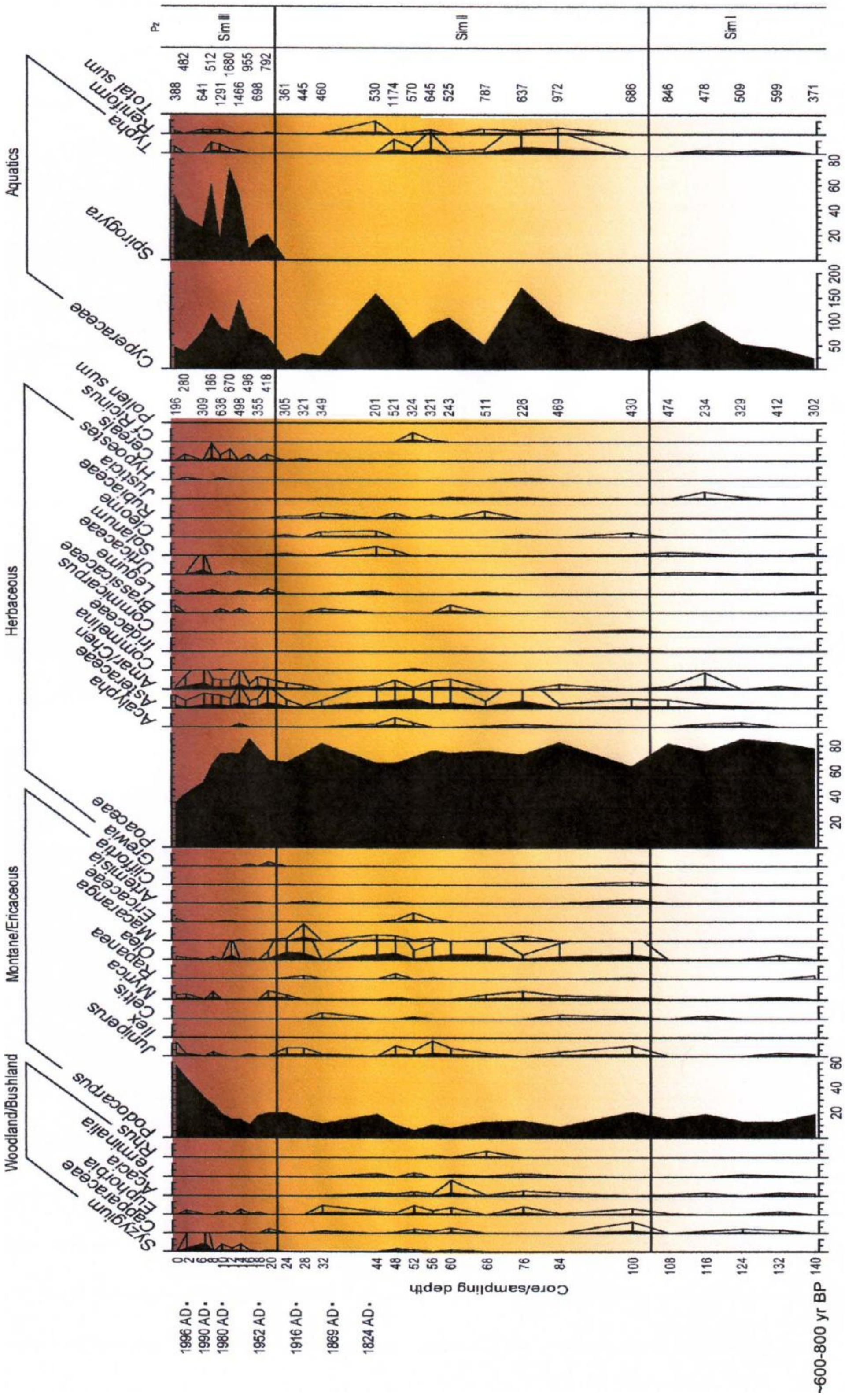


Fig. 27. Fossil pollen record of Lake Simbi, showing vegetation history near the shore of Lake Victoria in western Kenya over the last 600-800 years. Natural, climate-driven vegetation shifts are hard to discern, except for a greater proportion of moist indicator plant taxa in pollen zone Sim II than in Sim I. The increase in Asteraceae starting halfway zone Sim I may reflect increasing pastoralist impact (orange highlight). Onset of sedentary agriculture in the early 20th century (brown highlight) is clearly marked by arrival of cereal grasses. Pz: Pollen Zonation.

vegetation disturbance due to more intense land use by pastoralists. The exact timing of this increasing human occupation of the Simbi area is uncertain, pending ^{14}C dating of the lower section of the record. Judging from average sedimentation rates in the ^{210}Pb-dated upper section, we surmise that the Sim I-II zone boundary correlates with the climatic transition ~1250 AD which ended the medieval drought episode known to have affected the entire East African Plateau (Verschuren & Charman, 2008).

Sim III (22-0 cm), which covers the last 60-70 years, records marked vegetation changes which likely result mostly from intensifying human impact. Pollen of cultivated cereals appear slightly below the Sim II-III zone boundary in sediments dated to the early 20th century. Also characteristic is the appearance around this time of *Spyrogira*, a cyanobacterium indicative of high nutrient availability and thus possibly reflecting the soil erosion resulting from vegetation clearance for crop cultivation. Intensifying anthropogenic vegetation disturbance is also indicated by the rise in ruderal plants of the families Amaranthaceae and/or Chenopodiaceae (pollen from these families is hard to differentiate). The marked reduction in grass pollen from ~70% at 12 cm depth (~1980) to ~35% at the surface (1999) should not be interpreted as a drastic recent reduction in grassy ecosystems. It is mainly due to a parallel increase in *Podocarpus* pollen (~15% to 45%), which may reflect current forest management practices in which *Podocarpus* is protected from cutting. Other montane forest taxa, such as *Juniperus* and *Olea*, decrease from the base of zone III, consistent with rather dry climatic conditions in Kenya since the 1930s.

Long-term dynamics of semi-arid savanna vegetation in southeastern Kenya. High-resolution pollen analyses on well-dated sediments recovered from Lake Challa in southeastern Kenya document the response of lowland savanna and dry forest ecosystems to climate variability in the Mt. Kilimanjaro region over the past 2700 years. Century-scale episodes of climatic drought are recorded by local increases in the % pollen abundance of grasses (Poaceae) and certain dry savanna trees, shrubs (*Combretum*, *Commiphora*, *Salvadora* and *Rhus*) and herbs (*Corchorus* and Urticaceae), and reductions in other common savanna trees and shrubs such as *Maerua* and *Sideroxylon* (**Fig. 28**). Dry climatic conditions are further recorded by increased pollen from aquatic plants, as lowstands of shallow lakes nearby exposed extensive lake margins to be colonized by sedge (Cyperaceae) swamp. Based on the Challa pollen evidence, climate conditions appear to have been drier than today from

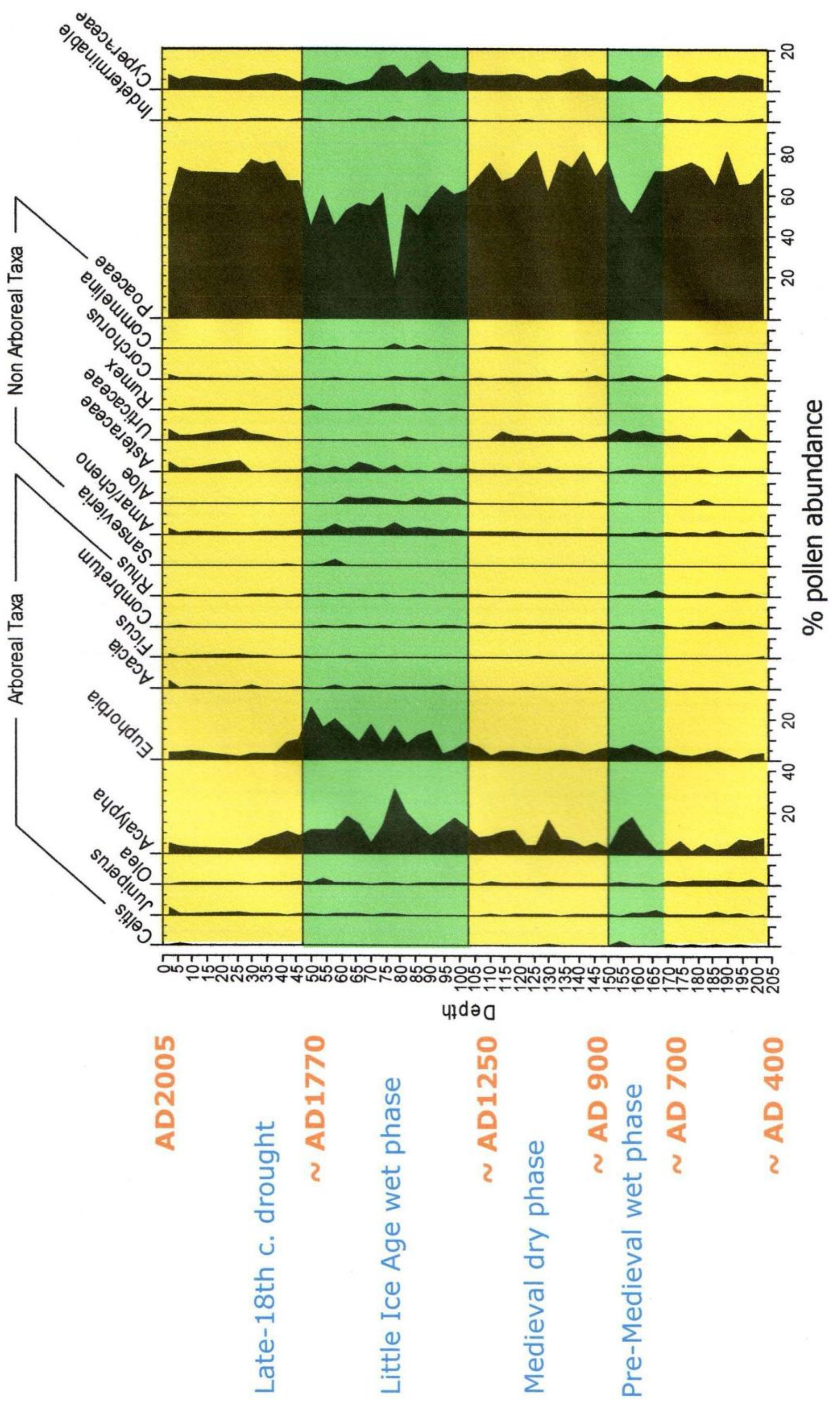
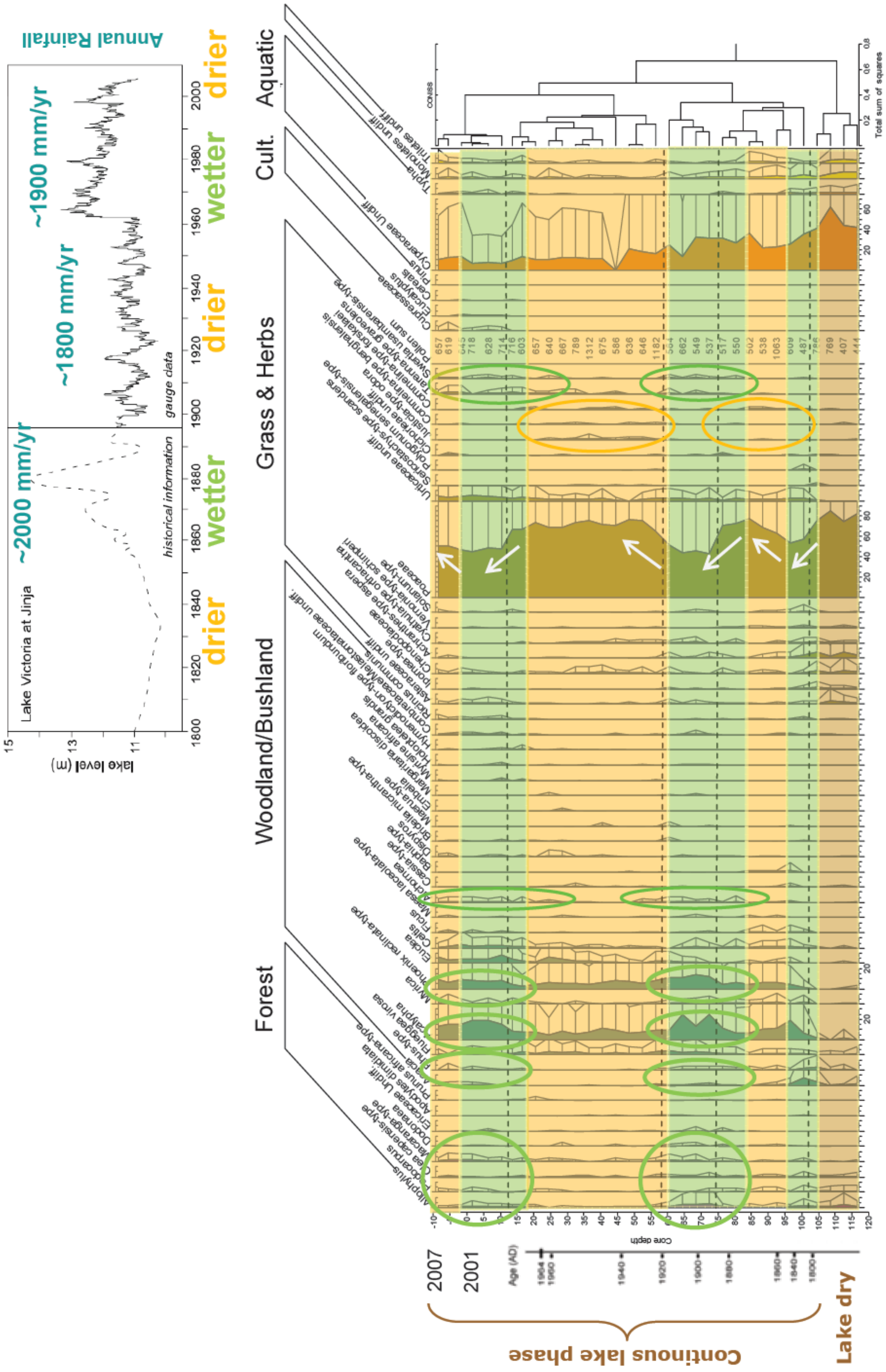


Fig. 28. Vegetation reconstruction (1600 cal year BP to Present) for southeastern Kenya based on the % abundance of 19 selected plant taxa, as recorded in fossil pollen assemblages preserved in sediments of Lake Challa (Taita-Taveta district).

2700 to 2300 cal yr BP, 1800 to 1500 cal yr BP, 1300 to 800 cal yr BP and from ~250 to 70 years ago. The wettest regional climate of the last 2700 years occurred from ~600 to 300 years ago, i.e. coeval with the main phase of the Little Ice Age in Europe. Erratic occurrences of large Poaceae pollen, presumably originating from indigenous cereal crops, is suggestive of intermittent agricultural activity in the Mt. Kilimanjaro region as early as ~2650 cal yr BP. Sustained presence of cereal pollen, presumably mostly maize, starting around 150 years ago is associated with increases in herbaceous plants indicative of more widespread ecosystem disturbance, and reflect intensifying farming activities in an increasingly human-impacted landscape.

Sensitivity of the forest-grassland ecotone to historical rainfall variation in pristine open woodland savanna of western Uganda. Contrary to the Simbi reconstruction, where modest vegetation response to past climate change is overprinted by strong signatures of human impact, our Chibwera data indicate a clear dominance of climate-driven vegetation change in the pristine (or at least semi-natural) landscape of Queen Elisabeth National Park. The Lake Chibwera record (**Fig. 29**) documents the sensitivity of natural vegetation spanning the lowland tropical forest-grassland ecotone to historical trends in annual rainfall between 1800 and 2000 mm/yr (i.e., on the order of 10%) lasting several decades. Specifically it traces regional vegetation response to increased rainfall during the periods ~1865-1885 (modestly persisting until ~1920) and 1962-1985. During these wetter episodes we find an immediate increase in pollen influx from woodland shrubs *Myrica*, *Rhus*, *Celtis*, *Macaranga* and *Alchornea*, and herbs such as Asteraceae and *Swertia usumbarensis*-type. Conversely, herbs such as *Commelina* and *Justicia* expanded during the intervening mid-20th century dry episode ~1920-1962. The strong positive response to increased moisture of *Acalypha* and *Phoenix reclinata*-type, two important woodland taxa with strong influence on grass pollen percentage, is delayed on the order of 20 years, suggesting that it represents a real but short-lived expansion of woodland relative to grassland. Long-distance influx of pollen from cultivated plants and exotic trees appears from the 1970s onwards, but their influence fails to mask regional vegetation response to natural rainfall variability.

Fig. 29 (next page). Fossil pollen record of Lake Chibwera, showing vegetation shifts in the southern Lake George area of western Uganda between the late 18th century and 2007 AD in relation to regional variation in annual rainfall (inset, from Nicholson & Yin, 2001). This lake dried out completely during severe late-18th century drought (brown shade). Since then, wet episodes (green shade) have alternated with modestly dry episodes (orange shade). Pz: Pollen Zonation; Lz: Lithological zonation. Ellipses highlight drought-tolerant (orange) and drought-intolerant (green) plant taxa.



The Chibwera record also illustrates how availability of solid independent data on climate-driven moisture-balance change can improve the information extracted from pollen data. For example, the herb *Solanum* appears to be naturally scarce in the Chibwera area, reaching significant abundances only during brief episodes of unusually wet conditions. It may thus be considered a trustworthy indicator of such conditions in an East African grass savanna habitat. In contrast, Asteraceae reached peak abundances both during a known dry period and a known wet period, suggesting that this pollen type comprises species with contrasting ecological requirements. If true, this would limit the use of this pollen type as a paleo-environmental indicator of specific habitat conditions. The families Amaranthaceae and Chenopodiaceae are commonly used as indicators of vegetation disturbance by humans. However, restriction of their pollen to Zone Chib Ia suggests that these plants responded naturally to severe late 18th-century drought by colonizing the dry lake bed.

Fossil phytolyths as indicators of past human impact on vegetation. Some important African food staples such as banana (*Musa*) produce insufficient pollen to be recorded in pollen preparations, but can be traced by means of their fossil phytoliths (Lejju et al. 2005), glass bodies that plants incorporate in their tissue to, among others, prevent consumption by insects. CLANIMAE has validated fossil *Musa* phytoliths as paleoenvironmental indicator of banana cultivation by quantifying the relationship between *Musa* phytolith abundance in the surface sediments of 25 Ugandan crater lakes, and the relative cover of banana plantations in their catchments. This test is being conducted by phytolith expert Dr. J.B. Lejju of Mbarara University of Technology (Uganda), using CLANIMAE surface-sediment samples and February 2007 land-cover survey. This survey estimated the % land cover occupied by 6 types of natural vegetation, 16 types of cultivated crops or plantations, and 4 types of fallow agricultural land. These classifications were transformed into human-impact index Hi, the summed product of land-cover fractions and a 'soil erosion susceptibility' factor specific to each type of vegetation (**Table 6**). This level of detail also allows to calibrate the distribution of phytolith types derived from other cultivated plants (e.g., maize, oil palm) and natural vegetation difficult to differentiate in pollen preparations (e.g., *Phragmites*).

Exploratory phytolith analyses during phase 1 of the CLANIMAE showed great promise, but found that large numbers of phytoliths must be counted from each site to achieve statistically meaningful results on the phytolith types of greatest interest. This more detailed study is carried out in the context of a BelSPO-funded visiting postdoctoral fellowship to Dr. Lejju, which he will take up at Ghent University (partner 1) during the periods October-December 2011 and February-April 2012.

Lake	**Kifuruka**	**Nyantonde**	**Kanyanchu**	**Kanyango**	**Mubiro**	**Kaitabarago**	**Ekikoto**	**Kanyamansira**	**Wandakara**	**Wankenzi**	**Kanyamukali**	**Mbajo**	**Njarajabana**	**Katinda**	**Mirambi**	**Kyasunduka**	**Nyamunsingere**	**Kyogo**	**Kako**	**Murabyo**	**Ibamba**	**Nyungu**
palm trees	-	-	40	-	-	-	-	8*	-	-	-	-	-	-	-	-	*few*	*few*	-	*few*	-	-
other trees	-	-	40	-	-	-	-	87	-	-	-	-	-	-	-	82	100	100	-	100	-	-
shrubs	-	-	13	-	-	-	-	8*	-	-	-	-	-	-	-	-	*few*	*few*	-	*few*	-	-
lianas	-	-	5	-	-	-	-	8*	-	-	-	-	-	-	-	-	*few*	*few*	-	*few*	-	-
ferns	-	-	2,5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*few*	-	*few*	-	-
grass savannah	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-
Total pristine or secondary vegetation	**20**	**18**	**100**	**33**	**40**	**75**	**70**	**95**	**0**	**55**	**18**	**59**	**60**	**5**	**10**	**90**	**100**	**100**	**0**	**100**	**0**	**0**
banana	25	8	-	6	-	-	-	-	15	11	3	3	-	15	40	-	-	-	10	-	58	60
cassava	4	1	-	1*	2	-	-	-	*few*	-	-	-	-	2*	1*	-	-	-	30	-	2*	4
maize	4	40	-	2	1	-	-	-	17	10	1	2	5	8	9	1	-	-	4	-	2*	1*
potatoes	1*	1*	-	1*	-	-	-	-	5	1	*few*	-	-	2*	1*	-	-	-	20	-	2*	-
tea	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
gabbage	-	1*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
beans	1*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*few*	-	-	-
Eucalyptus	1	2	-	1	-	-	*few*	-	-	5	15	1	-	-	-	-	-	-	4	-	5	-
pine	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-
sugar cane	-	-	-	-	-	-	-	-	8	3	*few*	-	-	-	-	-	-	-	-	-	-	-
papaya	-	-	-	-	-	-	-	-	*few*	-	-	-	-	-	-	-	-	-	-	-	-	-
coco yam	-	-	-	-	-	-	-	-	-	-	*few*	-	-	-	-	-	-	-	-	-	2*	1*
cotton	-	-	-	-	-	-	-	-	-	-	-	-	-	45	-	4	-	-	-	-	-	-
sorghum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*few*	-	-	-
millet	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
coffee	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2*	-
Total cultivated crops +plantations	**35**	**52**	**0**	**11**	**3**	**0**	**0**	**0**	**45**	**30**	**19**	**6**	**5**	**70**	**50**	**5**	**0**	**0**	**70**	**0**	**65**	**65**
elephant grass/shrubs	39	*few*	-	45	20	-	-	-	55	-	45	25	34	25	30	5	-	-	25	-	20	35
recently cleared	5	22	-	8	-	16	-	5	-	14	-	-	1	-	10	-	-	-	-	-	13	-
burned	1	8	-	*few*	-	8	*few*	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-
pasture	-	-	-	3	37	1	30	-	*few*	-	18	10	-	-	-	-	-	-	5	-	-	-
Total fallow land	**45**	**30**	**0**	**56**	**57**	**25**	**30**	**5**	**55**	**15**	**63**	**35**	**35**	**25**	**40**	**5**	**0**	**0**	**30**	**0**	**35**	**35**

Table 6. Percent land use/land cover in 22 Uganda crater lake basins, recorded in August 2007 or February 2008.

Paleoenvironmental calibration of non-pollen palynomorph microfossils (NPPs), including fossil fungal spores. Non-pollen palynomorph microfossils (NPPs) are much used as paleo-ecological indicators in Europe and North America, but prior to this project their value as such in tropical Africa had not been thoroughly explored. We calibrated the ecological indicator value of African NPPs in relation to landscape variables (vegetation, land use, erosion, burning practices) and lake characteristics (depth, productivity), again through analysis of surface sediments in 24 Ugandan crater lake basins located along environmental gradients of vegetation (moist evergreen and semi-deciduous forest, wooded and open grass savanna), land use (pastoralism, crop agriculture, plantations) and lake characteristics (basin morphometry, water chemistry and aquatic production). For this purpose the CLANIMAE land-cover classification (**Table 6**) was supplemented by data on domestic herbivore abundance. This analysis produced 311 distinct types of NPP, for a large part (230 types) spores and other remains of fungi. About 31% of these could be identified at the family, genus or species level, but the affinity of the majority of NPP types, specifically fungal spores, remains unknown. This high biodiversity coupled with a restricted distribution of NPP types among sites suggests high ecological specificity of the fungal species producing the NPPs.

Direct gradient analysis of the distribution of 30 major terrestrial NPP morphotypes showed that the distribution of fungi generally associated with human landscape disturbance indeed correlates with anthropogenic land-cover variables such as crop agriculture and pasture. For example, *Glomus* (a mycorrhizal fungus living symbiotically in plant roots) is positively related to soil erosion from agricultural activity. Redundancy Analysis (RDA) was used to determine which environmental variables most strongly structure the fungal community. The first two RDA axes captured 33.8% of the variance in the species data, and 49.3% of the cumulative species-environment relation (**Fig. 30**). RDA axes 1 and 2 appeared to be strongly oriented by the Anthropic Impact index, perennial agriculture and natural vegetation (plus plantations). These three variables accounted for a statistically significant portion of the variance in the NPP data (11.5%, 12.8% and 12.2%, respectively), together with Chl a (8.8%). The distribution of *Delitschia* sp. (T1066), cf. *Sordaria* sp. (T1178), *Gelasinospora cf. cratiphora* (T1093) and *Sporoschisma* spp. (T1002) is strongly determined by land-use practices, such as annual and perennial crop cultivation. Apparently, the distribution of *Cercophora* (T1013), mostly living on dung, appears to be more strongly linked to Chl a, which is indicative of high nutrient inflow (plant debris, dung) to the lake. These preliminary findings question the common assumption in European NPP studies that certain fungal spores are strictly associated with cattle dung and pastoralism,. In fact most so-called coprophilous fungi do not live exclusively on dung, but also occur on other organic substrates (plant debris, decaying wood).

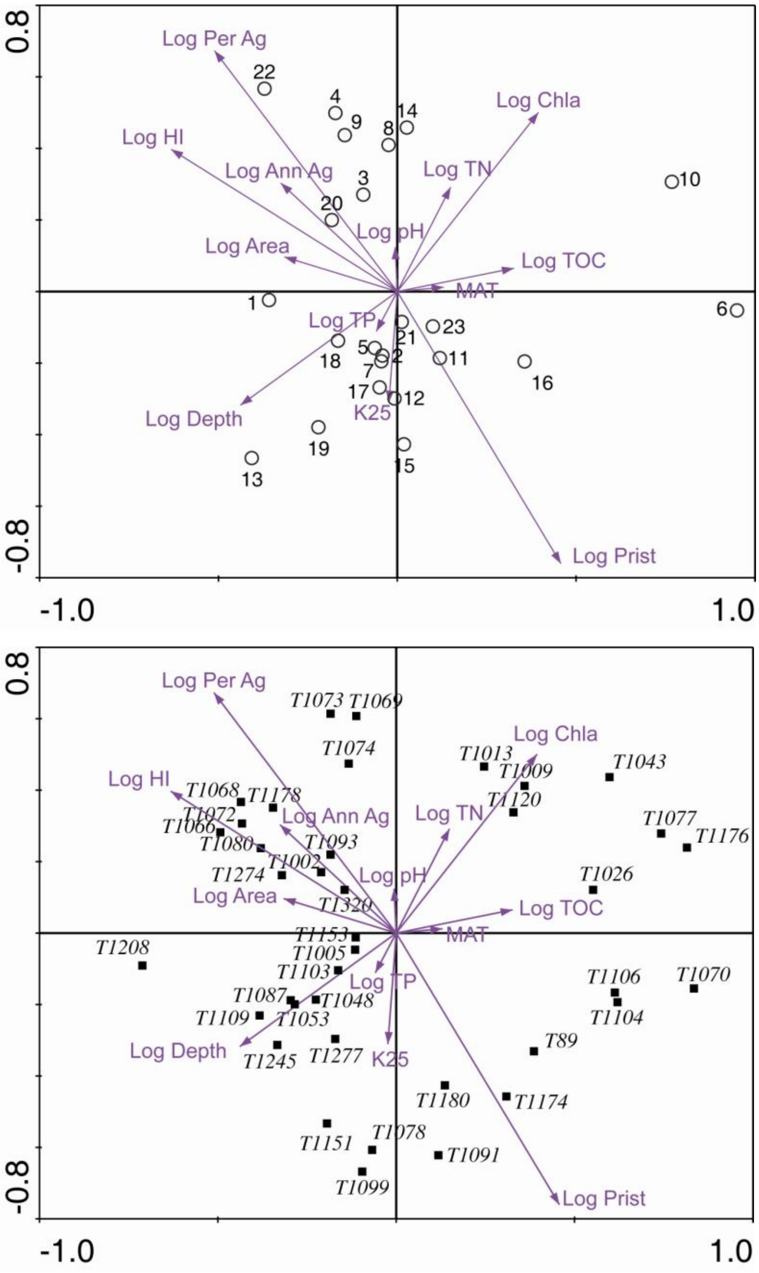


Fig. 30. RDA correlation biplots illustrating the relationship between (a) 23 study sites (i.e. all freshwater lakes), and (b) 38 dominant fungal species (each accounting for > 0,2 % of total fungal spore counts), and selected lake and landscape/climate-related variables: ake depth and area, pH, total phosphorus (TP), total nitrogen (TN), conductivity (K25), total organic carbon (TOC) chlorophyll a (Chl a), pristine/secondary forest, annual agriculture, perennial agriculture, human impact index (HI) and mean annual temperature (MAT).

We also investigated the relationship between fungal species richness, land use intensity and habitat differentiation. As traditional test statistics may be confounded by col-linearity between lake and catchment characteristics, we applied model selection based on AIC values to select models that explained variation in fungal diversity in the most parsimonious way. The raw number of fungal taxa per lake varied from 14 in Lake Kikorongo to 72 in Lake Wankenzi, with a mean of 38. We calculated several diversity indices (ES200, Margalef, Shannon-Wiener), from which we selected ES200 (range: 14-44, mean: 29) for a multi-model test on the effects of land cover on fungal spore diversity. Across our 24 lake sites no significant correlation could be observed between fungal spore diversity and the relevant land-use variables. However, when restricting the analysis to the 17 disturbed lakes only, fungal diversity decreased significantly with increasing land use intensity ($F_{1,14}$=14.39, P=0.002; **Fig. 31**). These preliminary findings strongly support the general idea that conversion of tropical forest to agricultural land causes biodiversity loss in fungi, whose habitat is largely determined by vegetation diversity and composition. This is certainly true for saprotrophic fungi, which mainly rely on plant debris and decaying wood for obtaining nutrients, and mycorrhizal fungi, which live in symbiotic association with their host plants.

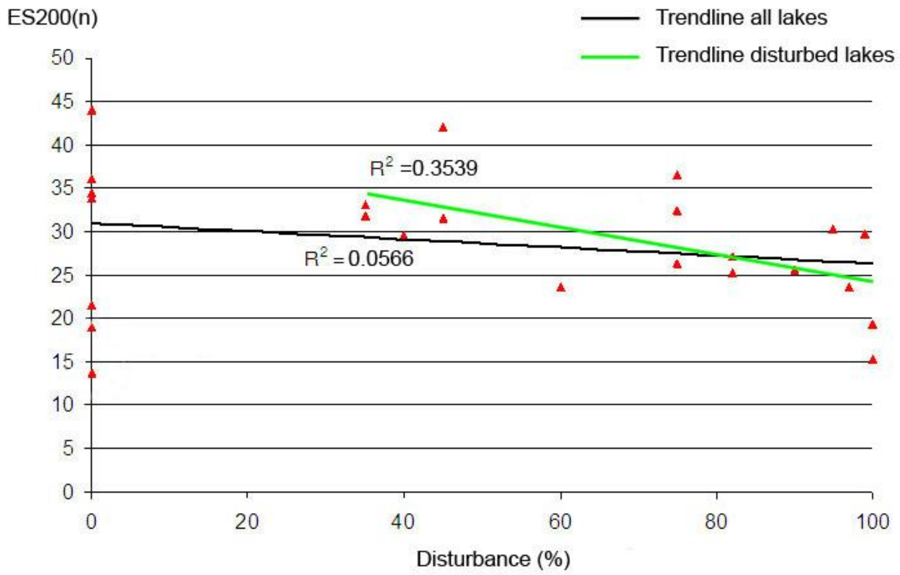


Fig. 31. Linear model of the effects of human disturbance (%) on the diversity (ES200) of fungi, applied on all lake catchments (24, black trendline) and only the disturbed lake catchments (17, light green trendline). In a simple linear regression on all 24 lake data sets, the correlation is probably partly biased by the variability in natural local environments (i.e. saline lakes vs. freshwater lakes; tree savanna vs. tropical forest).

Work Package 4 focused on reconstruction of past water-quality changes. This was planned to include applications of the new CLANIMAE productivity-inference model to fossil diatom assemblages extracted from long lake-sediment records. Our principal target study site for this reconstruction is Lake Katinda (Bunyaruguru district) in western Uganda, where sedimentological proxies (Magnetic Susceptibility, percent mineral matter) suggest human occupation as early as ~1800 years BP (Bessems, 2007). Given the poor performance of the current diatom-based phosphorus inference model (see under Work package 1), we limit the present assessment of past variations in aquatic productivity to a qualitative, indicator-species approach.

We first summarize fossil-diatom data from one of our method-validation lakes, the pristine savanna lake Chibwera in western Uganda, covering the last ~250 years (**Fig. 32**). Diatom zone Chib D1 at the base of the Chibwera sequence, deposited during severe late 18th-century drought, is characterized by a diverse community of benthic-epiphytic diatoms (taxa belonging to *Diadesmis*, *Achnanthes*, *Eunotia*, *Luticola*, *Gomphonema*), consistent with a swampy remnant aquatic ecosystem surviving through this drought in the centre of a dried-out lake bed. Immediately following the early 19th lake-filling phase (starting ~1810 AD) most of these benthic-epiphytic diatoms either disappeared or reduced to very low abundances, indicating that Lake Chibwera never came close to drying completely again. In the past 200 years (diatom zones Chib D2-D5), the local diatom flora has been dominated by planktonic species (*Synedra ulna* var. *radians* and *Aulacoseira* spp.). Most notably we document a striking succession of species within the genus *Aulacoseira*, with *A. granulata* (sum of vars. *muzzanensis* and *angustissima*) fully dominant during known episodes of wetter climate (1890s-1930s; 1960s-1980s), and *A. italica* usually less common but approaching co-dominance during known episodes of drier climate (1870s; 1940s-1950s). A third species, *A. ambigua*, inhabited Lake Chibwera during the early 19th-century lake filling, and again briefly in the 1950s, possibly coincident with the driest period of the 20th century. The Chibwera diatom record shows no evidence of increasing productivity or water-quality loss in recent decades, consistent with the undisturbed condition of savanna vegetation in Queen Elisabeth National Park. The recorded changes in diatom community composition can all be explained by changes in aquatic productivity due to natural, climate-driven lake-level fluctuation. This dynamic nature of aquatic productivity in shallow lakes occurs because during lake lowstands new nutrient imports from the

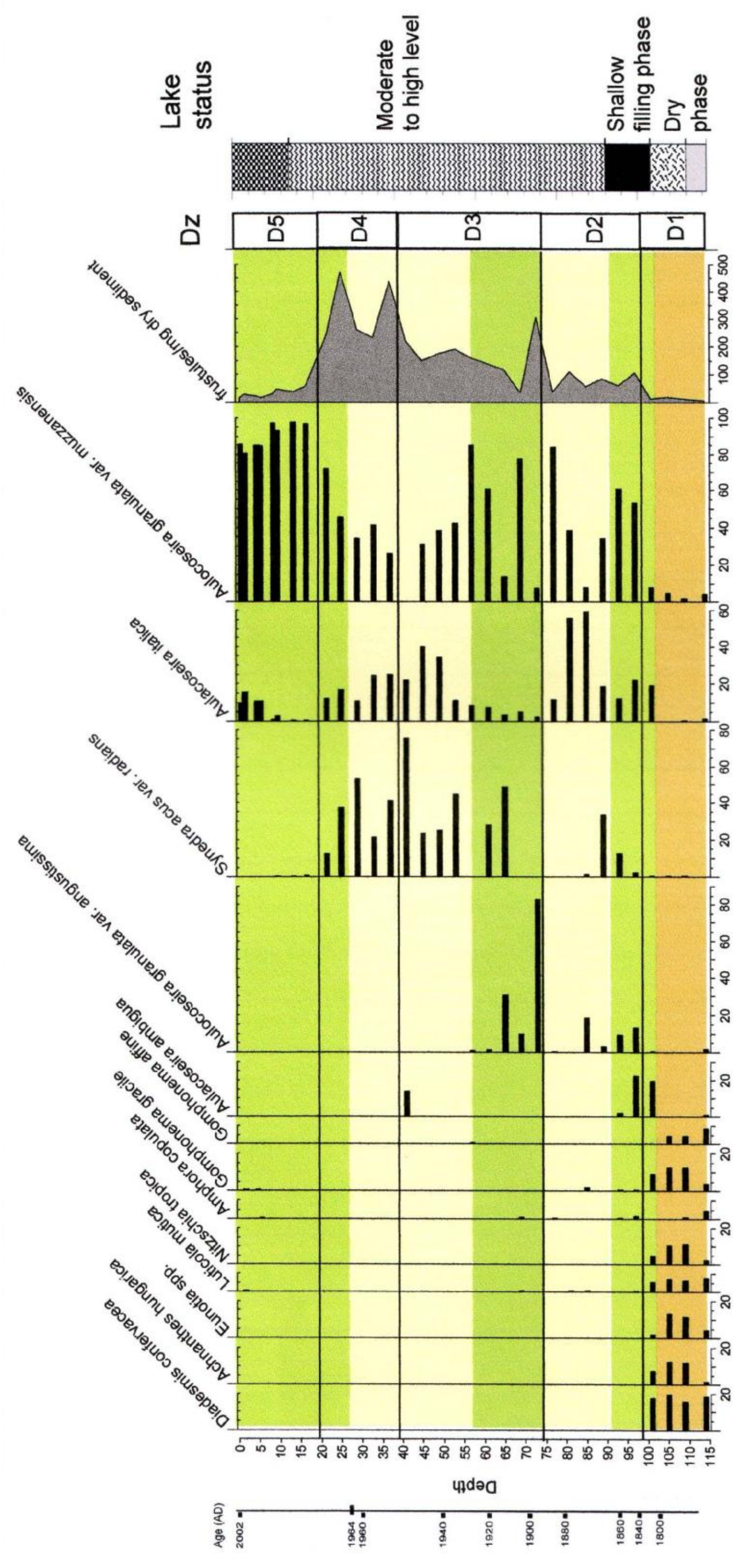


Fig. 32. Fossil record of diatom communities in the pristine Lake Chibwera (southern Lake George, western Uganda) from the late 18th century to present. Highlights show wet and dry episodes as in **Fig. 29**. During the late 18th-century drystand the local diatom flora was dominated by epiphytic species inhabiting freshwater swamps and ephemeral ponds. Since then the diatom flora has been dominated by planktonic species, indicating a large open-water area. Dz: Diatom Zonation.

catchment are concentrated in a smaller water volume (Harper et al. 1993), or because nutrients stored in the lower water column and lake bottom are more efficiently recycled (Verschuren et al. 1999).

The evolution of diatom communities in the ~4000-year sediment record of Lake Katinda can be divided in seven periods or diatom Zones (**Fig. 33**). Zone D7 (786-729 cm) is typified by co-dominance of *Aulacoseira granulata* (including transition forms to *A. muzzanensis*), *Staurosira construens* and its f. *venter*, *Fragilaria leptostauron* and *Nitzschia lancettula*. It is also characterized by a high density of fossil diatoms (365-685 x10^3 frustules per mg dry weight) compared to the other zones, except zone D5. Zone D6 (729-353 cm) is typified by dominance of *Aulacoseira granulata* (including transition forms to *A. muzzanensis*), but several depth intervals show peaks of *Nitzschia fonticola*, *A. granulata* var. *angustissima* and *A. italica*. Zone D5 (353-280 cm) is typified by peak abundance of *Nitzschia confinis* and a decrease of *A. granulata* (including transition forms to *A. muzzanensis*). *Cyclotella meneghiniana*, *Gomphonema affine* and its var. *rhombicum* are important temporally reaching up to 13, 16 and 13 % of the relative diatom abundance. This zone is characterized by its high density of fossil diatoms (up to 1180 x10^3 frustules per mg dry weight), almost all *Nitzschia confinis.* Zone D4 (280-179 cm) is characteristically dominated by epiphytic taxa, such as *Gomphonema affine*, its var. *rhombicum*, *G. gracile*, *G.* cf. *gracile*, *G. parvulum*, *Navicula cryptotenella* and some aerophilic taxa, namely *Hantzschia* spp. and *Luticola mutica*. Overall fossil diatom density is low, except at 240 cm were a small peak of 250 x10^3 frustules per mg dry weight occurs. Zone D3 (179-123 cm) is dominated by *Cyclotella meneghiniana*, *Nitzschia palea* var. *tropica* and *Synedra rumpens* vars. *rumpens* and *oxyrhynchus*. The latter two taxa are especially important in the upper part of this zone, which is otherwise characterized by low density of fossil diatoms. Zone D2 (123-50 cm) is dominated by *Aulacoseira italica*, reaching up to 82 % of all diatoms, and the high relative abundance of *Gomphonema gracile* and *G.* cf. *gracile*. The number of frustules per mg dry weight is relatively high. Finally, Zone D1 (50-0 cm) is typified by co-dominance of the epibenthic taxa *Amphora minutissima* var. *africana*, *A. pediculus*, *A. copulate*, *Gomphonema gracile*, *G. parvulum*, *G. affine* and its var. *rhombicum*, *Navicula cryptotenella* and some aerophylic taxa of the genera *Hantzschia* and *Luticola*. Fossil diatom abundance is again low, with a mean of 4000 frustules per mg dry weight.

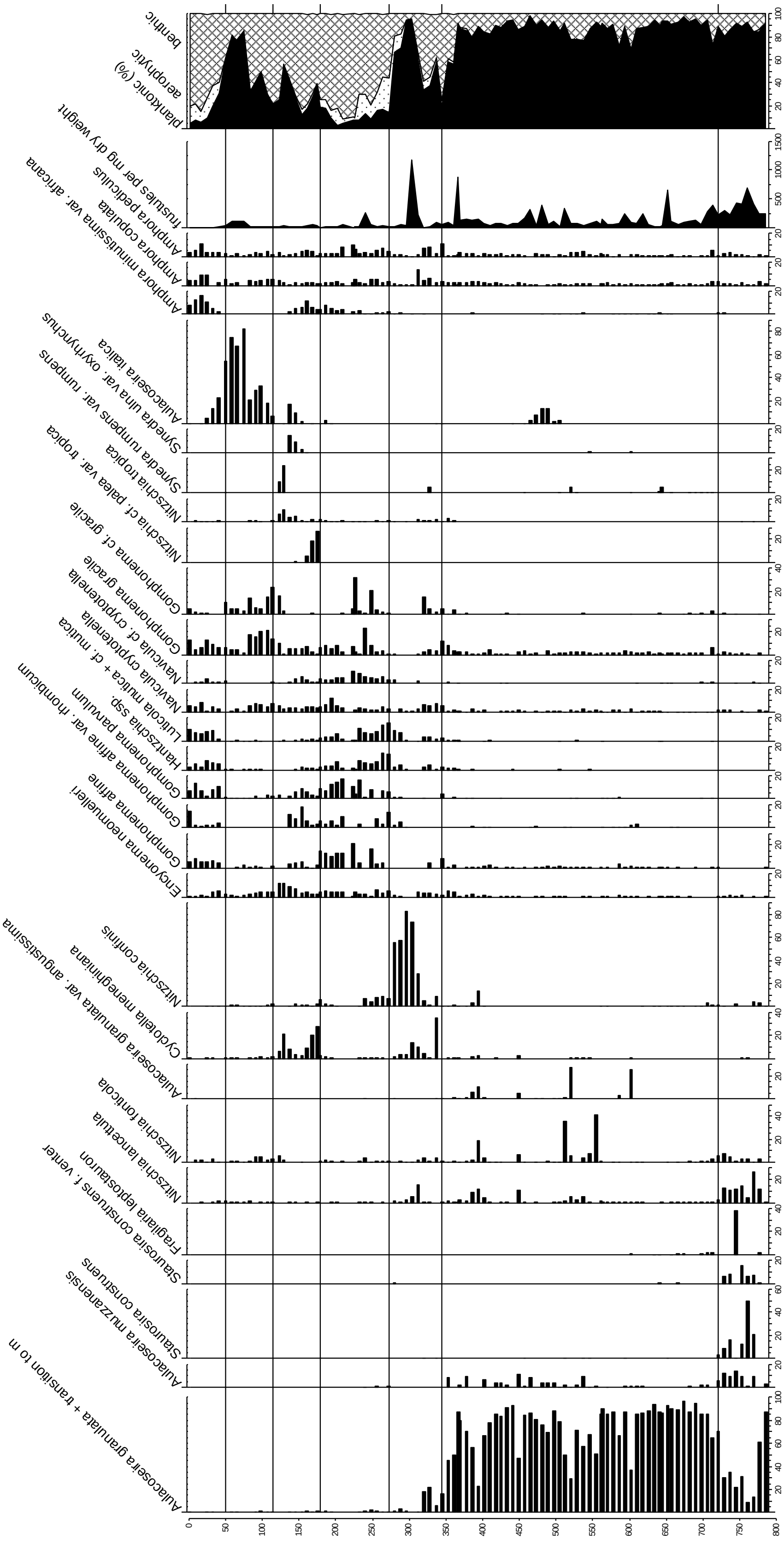


Fig. 33. Fossil record of diatom communities in Lake Katinda (Bunyaruguru area, western Uganda) with indications of diatom zones D1-D7 as defined by cluster analyis CONISS.

The fossil diatom zonation in Lake Katinda defined by the cluster analysis CONISS (**Fig. 33**) corresponds rather well with the zonation based on the fossil stratigraphy of aquatic invertebrates (Rumes, 2010), with the exception of fossil chironomid (midge) assemblages. Between ~3740 and 3400 cal. yr BP (Zone D7), high abundance of the chironimid *Tanytarsini* indet. type points to a productive lake at that time (Rumes, 2010). High percentages of the diatom taxa *Staurosira construens* and its f. *venter* confirm that the lake was not necessarily oligotrophic. According to Gasse (1986) these two taxa are indicative for shallow lake areas. The ecological optimum of *Fragilaria leptostauron* is difficult to define (Krammer & Lange-Bertalot 1991). Presence of the euplanktic species *A. muzzanensis* points to little eutrophic water. Dominance of *Nitzschia confinis*, a planktonic species described from deep water in Lake Kivu (Hustedt 1949), in Zone D5 indicates that it may represent a period of increasing lake level. Zone D2, with the dominance of *Aulacoseira italica*, indicator for more or less eutrophic waters, points to lake-level decrease, as this tropical species is known to be associated with near-shore habitat (Gasse 1986). Agricultural activity inside the Katinda crater during the last 100 years is evident by the presence of *Amphora pediculus*, an indicator of eutrophic conditions (cf. its occurrence in Lake Oloidien in central Kenya; Verschuren et al., 1999). Overall, these fossil diatom data from the (now) strongly disturbed Lake Katinda appear to indicate that anthropogenic water-quality loss started ~700 years ago. Evidence for increased productivity as early as ~1800 years ago can also be explained by temporary, climate-driven episodes of low lake level.

Work Package 5 focused on integrating regional patterns and processes of past climate and human impact. The relationship between each individual climate-proxy indicator and climate is typically complex, hence reliability of reconstructed climate and environmental history is improved by integrating data from different climate proxies (the multi-proxy indicator approach: Battarbee 2000). The diverse specialist expertise among CLANIMAE partners has produced adequate redundancy in climate-proxy information from each of the studied sediment records, ensuring reliability and internal consistency of the resulting reconstructions. Comparative analysis of local reconstructions across the study region (including published and unpublished information from sites not studied by CLANIMAE) is an iterative process in which site-specific time series and the linked age models are progressively integrated to allow evaluation of the patterns, synchrony, and geographical coherence of past climate variation. The amplitude of rainfall and drought variability during the last few millennia can be estimated from comparing the relative magnitude of reconstructed long-term lake-level changes with those which have resulted from historical (20th-century) rainfall variability. Integration of climate history with the vegetation and water-quality reconstructions at each study site then allows to trace the evolution of human impact on East African terrestrial and aquatic ecosystems through space and time. From this, patterns in the timing and relative magnitude of pre-colonial (indigenous) impact can be related to regional patterns in water-resource availability and environmental stability.

Scientists studying global patterns of past land use and land-cover change tend to assume that prior to 300 years ago human impact on the East African landscape was limited, mainly because of very low population density (on average ~3% of today's value; Klein Goldewijk 2001). Also after AD 1700 the area of land under agriculture is thought to have expanded only very gradually. Strongly exponential increase in additional land clearance is a phenomenon of the past 60-70 years (Ramankutty & Foley 1999), primarily associated with the post-independence redistribution of land ownership and explosive population growth in recent decades (**Fig. 1a**). This contrasts with the position held by many archaeologists and paleoecologists (e.g., Runge 1996; Robertshaw et al. 2004), who situate the start of anthropogenic forest clearance in equatorial East Africa about 2500 years ago, linked to the introduction of iron smelting by Bantu-speaking immigrants. Their evidence would suggest that the procedure of land-use researchers to hind-cast past land-use patterns in tropical countries using (poorly constrained) historical population estimates (e.g., Houghton 2003; IPCC 2007) must be re-evaluated. However, many pollen-based vegetation reconstructions that were claimed to indicate early anthropogenic deforestation in East Africa are ambiguous, because analysts failed to adequately consider the possibility that natural, climate-driven episodes of prolonged drought would also reduce forest cover and expand grassland (Verschuren 2004; Ngomanda et al. 2005). Now that this natural climatic variability in rainfall and drought over the past several thousand years has been documented for both eastern and western portions of the East African plateau (Verschuren et al., 2000, 2009; Stager et al., 2005; Russell & Johnson, 2005, 2007), we can attempt to separate the effects of past human activities and natural climate variability on the terrestrial and aquatic ecosystems of East Africa.

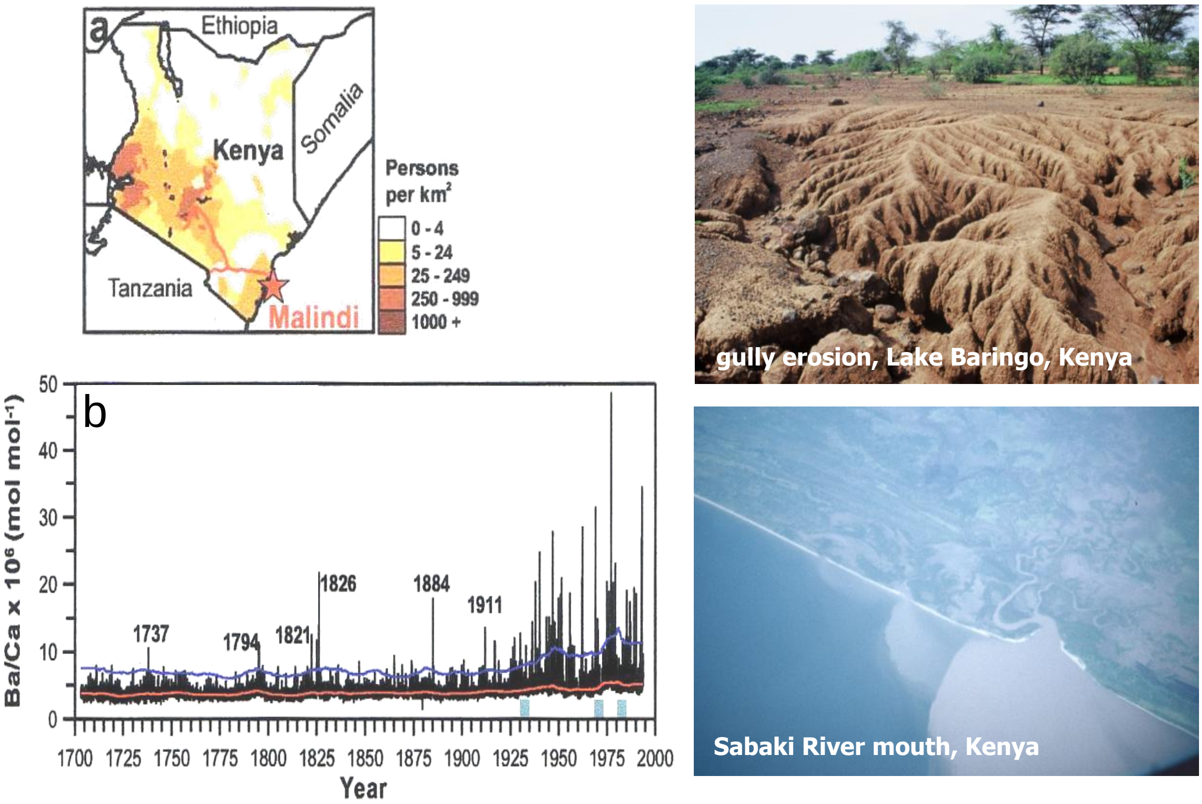


Fig. 34. Barium/Calcium ratio in a *Porites* coral growing near the mouth of the Sabaki River in Malindi (Kenya) shows episodes of increased soil erosion in the Athi-Sabaki River watershed, initially only during high rainfall events terminating climatic drought (e.g., the 1820s) but since the early 20th century mostly reflecting increasing population density and unregulated land use. From Fleitmann et al. (2006).

Earlier studies integrating historical anthropogenic impact in East Africa on large regional scales, such as the geochemical record of soil erosion in the Athi-Sabaki river drainage preserved in corals along the Indian Ocean coast (Fleitmann et al. 2006; **Fig. 34**) indicated that large-scale stripping of natural vegetation is indeed a relatively recent phenomenon, which started in the 1920s-1930s when completion of transport infrastructure (the colonial railroad network) allowed industrial-scale production of food crops for export. This is supported by CLANIMAE data from Lake Simbi near Lake Victoria (**Fig. 27**), which show that sedentary agriculture in this region started in the 1920s, and was quickly followed by eutrophication and water-quality loss (inferred from the appearance of *Spirogyra* cyanobacteria) due to enhanced nutrient inputs associated with soil erosion. In the semi-arid eastern Rift Valley of central Kenya, major changes in aquatic productivity and water quality associated with natural water-balance fluctuation (Harper et al. 1993; Verschuren et al. 2000b) has long complicated the identification of unique human impacts on lake nutrient dynamics (Kitaka et al. 2001). A CLANIMAE analysis of changes in the rate of sediment accumulation in Lake Naivasha over the past 120 years (**Fig. 35**) shows that (only) since the mid-1980s mineral sediment deposition at the mid-lake coring site has been exceeding the natural variability associated with climate-driven lake-level change. This recent acceleration of sediment deposition points to a general loss of the vegetation buffers which until then had limited soil erosion in the Malewa River drainage. Bessems (2007) presents similar data on drastically increased soil erosion in the Lake Baringo drainage basin, further north in the Kenya Rift Valley, in recent decades. In Lake Naivasha, the resulting enhancement of lake turbidity (decreased water transparency) already has a clear impact on local algal and zooplankton communities (Mergeay et al. 2004), and possibly its fisheries (Hickley et al. 2001). In this context, we also re-confirm the finding by Verschuren (1999) that in Lake Naivasha, the minimum water level required to avoid high turbidity due to widespread wind-driven re-suspension of offshore bottom sediments is 1885 m a.s.l.

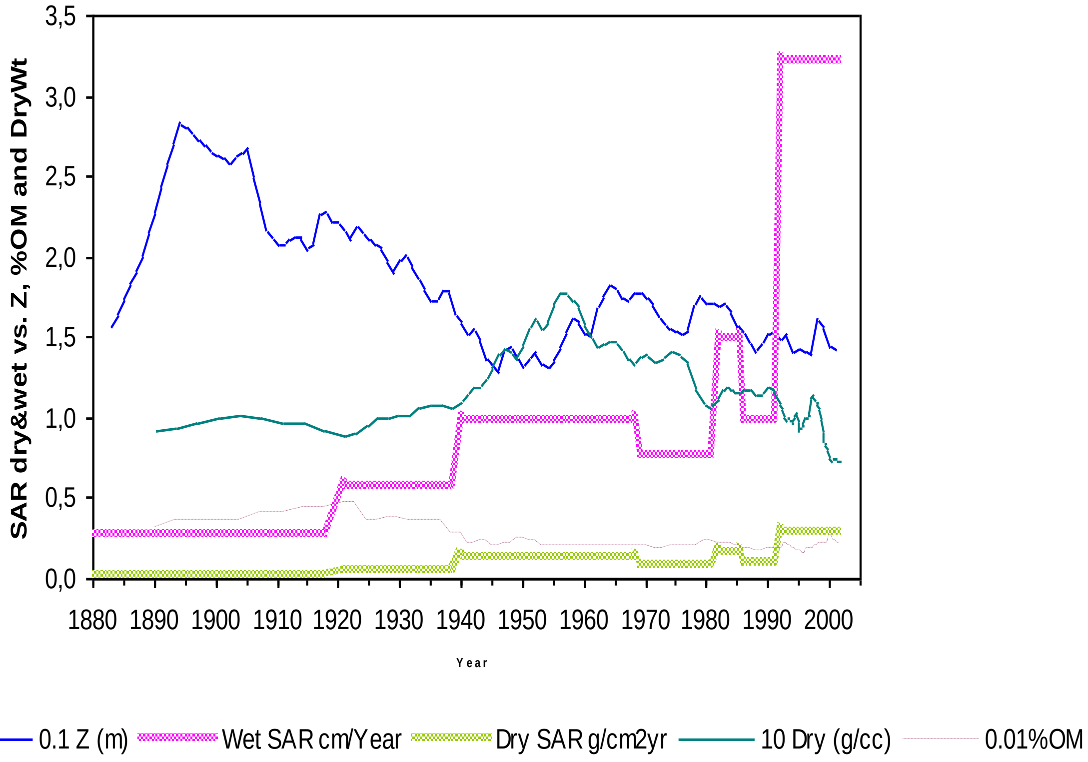


Fig. 35. Dry and wet (i.e., linear) sediment accumulation through time in Lake Naivasha (Kenya) in relation to 20th-century lake-level fluctuations. Natural lake-level fluctuation (thin blue line) causes major variability in sedimentation rate (and turbidity), due to greater sediment focusing during lowstands (e.g., 1950s peak sedimentation). Sediment accumulation has exceeded natural variability only in recent decades, due to intensifying agriculture and removal of soil-erosion barriers in the Malewa River drainage.

Pollen-based reconstruction of past vegetation dynamics in the central Kenya Rift Valley (Lamb et al. 2003), coupled with the climatic water-balance reconstruction for Lake Naivasha (Verschuren et al., 2000) indicates that significant impact by agriculturalists (sedentary farming) on forest and woodland previously covering the humid Rift Valley shoulders dates back to the 17th century AD, and was possibly related to population increases following the adoption of imported maize as a new staple food. New vegetation reconstructions from CLANIMAE study sites in drier regions of Kenya (Simbi, Challa) do not show clear signatures of sedentary farming prior to the early 20th century. The preliminary pollen diagram from Lake Challa (**Fig. 28**) shows the evident dominance of climate-driven moisture-balance changes on the semi-arid, and until recently sparsely populated landscape of southeastern Kenya. In the Lake Simbi record (**Fig. 27**) from western Kenya such climatic forcing of long-term vegetation dynamics is less evident, perhaps because the local terrestrial ecosystem was buffered against episodic drought by the shallow groundwater table surrounding Lake Victoria. What we do see are tentative signatures of intensifying land use by pastoralists starting perhaps 600 to 800 years ago.

In sub-humid regions of western Uganda, significant forest clearing by agriculturalists has been established to date back at least 900-1000 years (e.g., Taylor et al. 2000, Ssemmanda et al. 2005). New data by CLANIMAE collaborators at Brown University (USA), based on biogeochemical proxies extracted from the sediment record of Lake Wandakara (Kasenda lake district; Russell et al., 2009) support this timing, and highlight the relatively abrupt switch from pristine to heavily impacted vegetation in the immediate vicinity of this crater lake. Our own pollen and fossil-diatom data from Lake Chibwera showed no evidence of either recent or historical vegetation disturbance and water-quality loss, consistent with the relatively undisturbed present-day condition of savanna vegetation in Queen Elisabeth National Park. In contrast, data from the heavily impacted Lake Katinda (and Kanyamukali) indicate that anthropogenic water-quality loss started ~700 years ago. Earlier evidence for increased aquatic productivity can also be explained by temporary, climate-driven episodes of low lake level. During long periods of severe drought, the reduction in lake depth can be expected to have a positive impact on aquatic productivity; during very wet periods the opposite situation is likely to develop. This strong productivity response to lake-level fluctuation in East African lakes may be explained by the exponential relationship between temperature-driven stability of the water column and lake depth (**Fig. 36**).

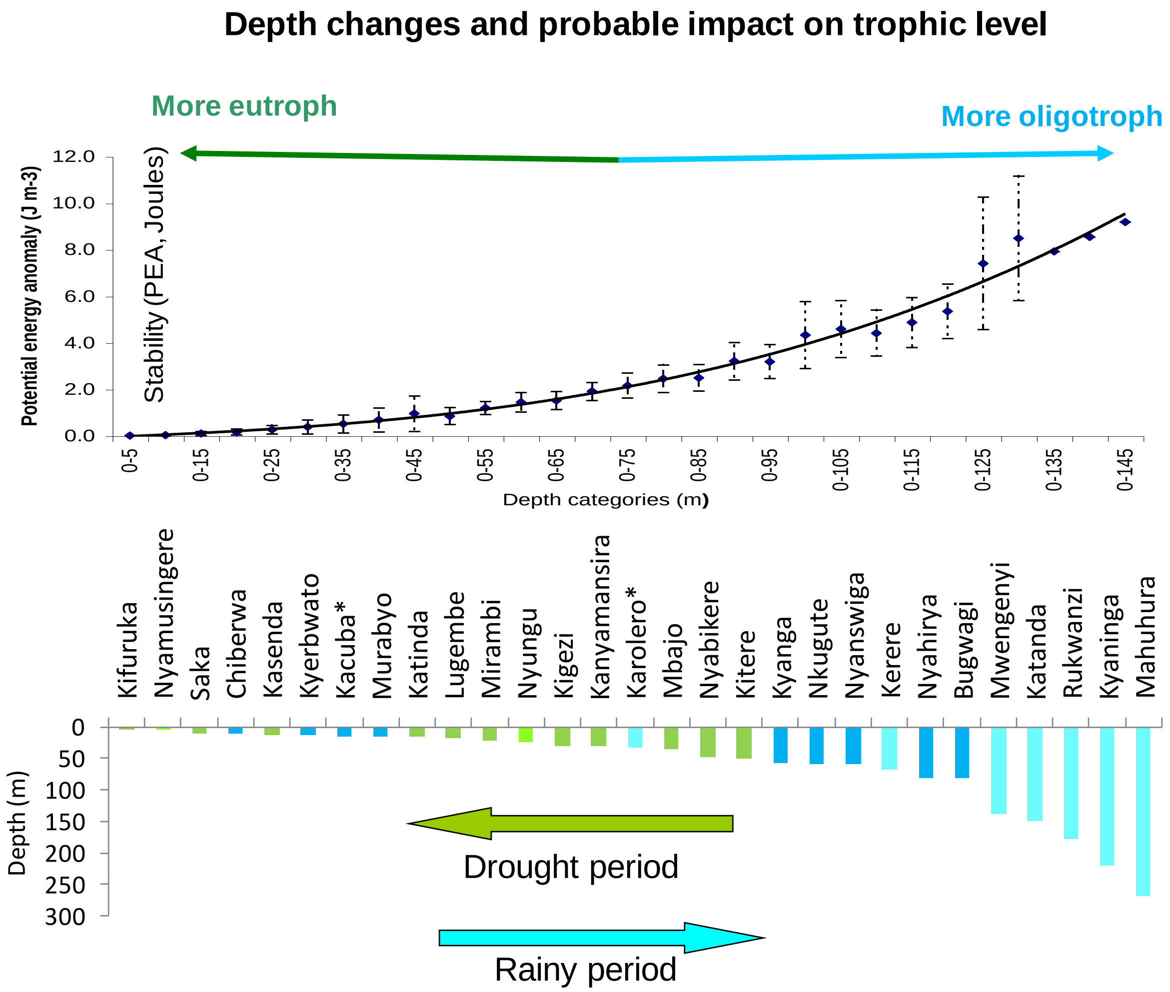
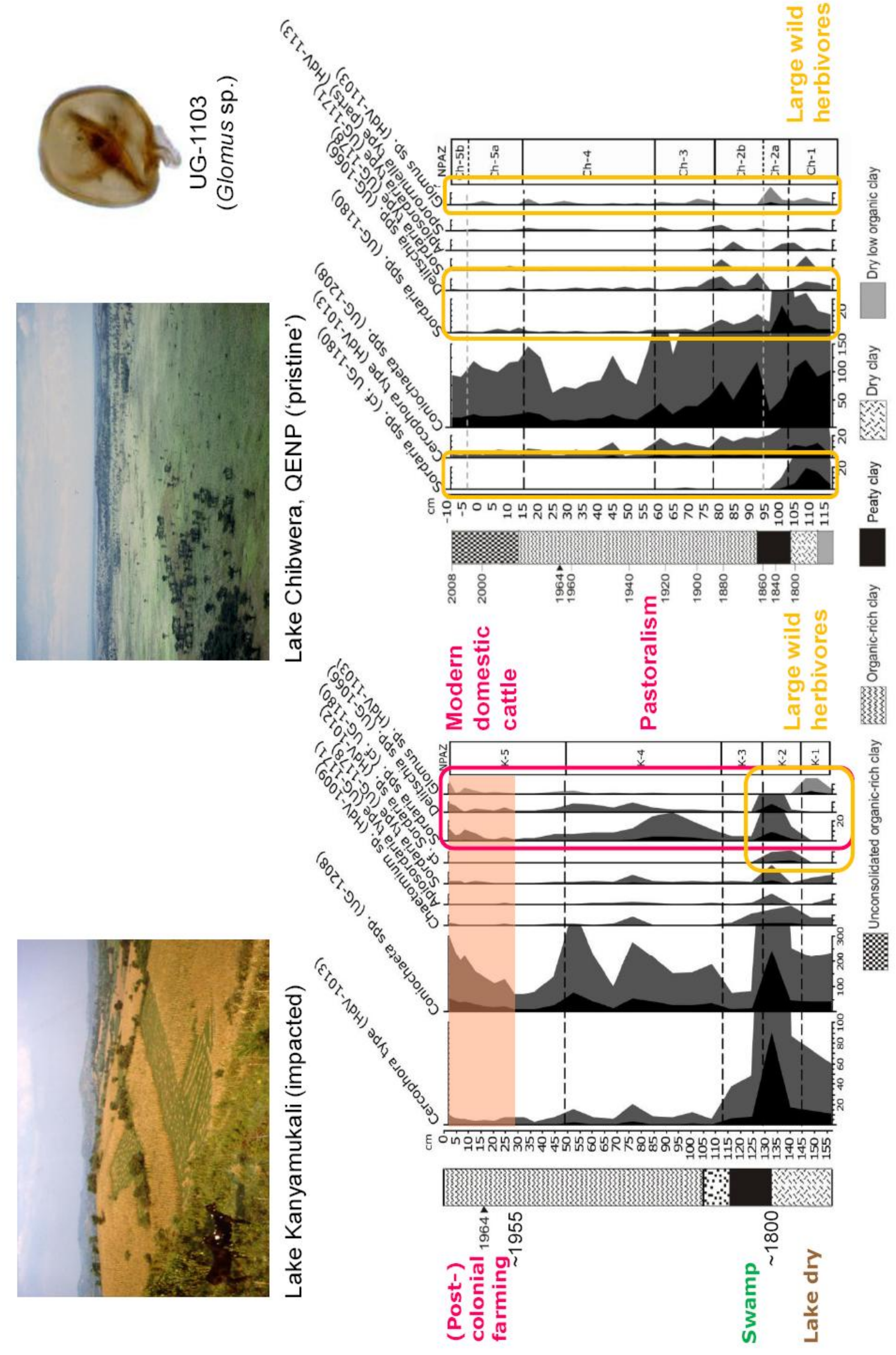


Fig. 36. Potential energy anomaly (top, PEA in J/m³) in relation to lake depth, compared with lake productivity in relation to lake depth (**Fig. 8**). PEA was calculated for each 5 m depth segment (from 0-5 m to 145-150 m) from all available lake temperature profiles (cf. **Fig. 4**). The exponential relationship between PEA and lake depth suggests that changes in lake depth due to climate change (more rain or more drought) and/or water abstraction can result in a strong response in aquatic productivity.

Finally, integration of paleoenvironmental evidence from the analysis of fossil non-pollen palynomorphs (NPPs) in the sediment records of lakes Chibwera and Kanyamukali with the above-mentioned evidence on water-quality changes from fossil diatoms (**Fig. 32**) and the history of vegetation change from fossil pollen (**Fig. 29**) reveals that during the late-18th century episode of severe climatic drought, when these and many other shallow crater lakes in western Uganda were reduced to ephemeral swampy pools, exploitation of the then scarce surface waters by large wild herbivores drastically increased (**Fig. 37**); possibly also by transhumant pastoralists herding their cattle. In the case of Lake Chibwera, the moister climate which occurred from the early-19th century reduced the animals' dependence on this particular lake for their water needs. In the case of Lake Kanyamukali, our NPP data indicate continued presence of large herbivores, most probably because it was situated along a route of pastoralist migration which later evolved into the trade route between Fort Portal and Kasese. The records of *Sordaria* and *Delitschia* fungal spores further show how sedentary agriculture in and around the Kanyamukali crater basin, which started in the late-1950s, again increased the prevalence of cattle watering after a period of relative disuse. Following independence, the lake's incorporation into the area of crop agriculture developing along the Fort Portal – Kasese road also brought about soil erosion at a scale which had not occurred previously (**Fig. 37**: *Glomus* fungal spores), consistent with our fossil diatom evidence for the loss of water quality in Lake Kanyamukali during recent decades.

Fig. 37 (next page). Fossil distribution of selected non-pollen palynomorphs (NPPs) derived from fungal spores in the sediment record of lakes Kanyamukali (impacted by human activity) and Chibwera (relatively undisturbed) in the Lake George area of western Uganda, with focus on coprophilous fungi obligately (*Sordaria, Delitschia*) or facultatively (e.g., *Coniochaeta*) associated with the excrements of large herbivores, and on Glomus sp., an indicator of soil erosion. Highlights show the taxa and patterns associated with use of the lake by wild herbivores (orange) or domestic cattle (fuchsia).


Lake Kanyamukali (impacted)
Lake Chibwera, QENP ('pristine')
UG-1103
(Glomus sp.)
(Post-) colonial farming
1964
~1955
Swamp
~1800
Lake dry
Modern domestic cattle
Pastoralism
Large wild herbivores
Large wild herbivores
cm
NPAZ
K-1
K-2
K-3
K-4
K-5
Ch-1
Ch-2a
Ch-2b
Ch-3
Ch-4
Ch-5a
Ch-5b
Cercophora type (HdV-1013)
Coniochaeta spp. (UG-1208)
Chaetomium sp.
Apiosordaria sp.
cf. Sordaria type (UG-1009)
Sordaria type (HdV-1178)
Sordaria spp. (cf. UG-1171)
Delitschia spp. (UG-1012)
Glomus sp. (HdV-1103)
Sordaria spp.
Cercophora type (cf. UG-1180)
Coniochaeta spp. (HdV-1013)
Sordaria spp. (UG-1208)
Delitschia spp. (UG-1180)
Apiosordaria type (UG-1066)
Sordaria type (UG-1178)
Sporormiella type (parts) (UG-1171)
Glomus sp. (HdV-1103)
(HdV-113)
2008
2000
1964
1960
1940
1920
1900
1880
1860
1840
1800
Unconsolidated organic-rich clay
Organic-rich clay
Peaty clay
Dry clay
Dry low organic clay

3. POLICY SUPPORT

Referring to stated priorities of the 'Science for a Sustainable Development' (SSD) programme, CLANIMAE directly addressed important unresolved research questions with critical relevance to the linked environmental policy issues of 1) sustainable economic development, 2) natural resource management, 3) biodiversity conservation, 4) adaptation of vulnerable communities to global change, and 5) a more humane globalisation. Project results particularly relevant to policy development on water and land resources in tropical Africa are:

1) The productivity of Uganda crater lakes can be estimated and monitored using simple, repeated measurements of water-column transparency with a Secchi disk.

2) The vulnerability of Uganda crater lakes to excess productivity (eutrophication) and water-quality loss for a given intensity of land use is strongly related to lake depth and the associated frequency of water-column mixing. Lakes shallower than 35 m are highly vulnerable, lakes deeper than 90 m are relatively resistant to water-quality loss. In their pristine condition, shallow crater lakes in Uganda are usually mesotrophic (with slightly elevated productivity), not oligotrophic (unproductive).

3) Clear-water, unproductive crater lakes (which today are almost without exception >90 m deep) are a most valuable source of drinking-quality water, and should be managed for ecotourism and modest recreation only. More productive lakes of shallow or intermediate depth (35-90 m) that are already subject to intensive land use can be managed for fisheries development and water extraction for agricultural use, the latter within limits determined by lake volume and water renewal rate. In both shallow and intermediate-depth lakes, runaway productivity leading to noxious algal blooms and frequent fish kills can be avoided by maintaining buffer strips of vegetation preventing soil run-off from reaching the lake. Fish farming is incompatible with most other uses of lake resources. It should be limited to productive shallow lakes where added nutrients and food have a high probability to be continually recycled to the water column.

4) Aquatic macrophyte, diatom, zooplankton and zoobenthos communities display significant structured variation in species composition along gradients of abiotic habitat characteristics and intensity of human impact, confirming

their applicability as biological water-quality indicators in African lake management.

5) Paired reconstructions of past climate and ecosystem dynamics, with decadal to century-scale time resolution, from the sediment record of African lakes can help assess the relative vulnerability and resilience of these ecosystems to human impact.

6) Fossil pollen evidence for major terrestrial vegetation response to modest historical trends in natural rainfall variability in pristine East African landscapes demonstrates that strategies for sustainable economic development must take into account large natural, climate-driven variability in ecosystem conditions, which affect their carrying capacity and realized volume of ecosystem service to society.

7) The hydrological sensitivity of lakes to naturally large water-balance fluctuations in semi-arid regions (such as the central Kenya Rift Valley) should suffice for policy to adopt the precautionary principle in creating a water-resource buffer against intermittent severe drought. In strongly fluctuating lakes, studies of sedimentation dynamics can help set appropriate limits to water extraction by identifying the lake-level threshold below which a clear-water, healthy ecosystem state switches to a turbid state with poor water quality.

8) The crater lakes of western Uganda carry value well beyond their own economic significance as analogs of ecosystem functioning in the contrasting large lakes Victoria and Tanganyika, in their historical, present-day and possible future state.

4. DISSEMINATION AND VALORISATION

4.1. Knowledge transfer to local stakeholders and the general public

From 6 to 20 September 2010 we organized a CLANIMAE knowledge-transfer tour in Kenya and Uganda. The seven scheduled events (Taveta (**Fig. 36a**), Nairobi and Naivasha in Kenya; Jinja (**Fig. 36b**), Kampala, Kibale and Queen Elisabeth National Park in Uganda) were attended by a total of 143 people from diverse government agencies and ministries and a wide range of stakeholder groups; we also made a presentation at Kanyamukali parish (Fig. **36c-d**) for which no attendance list was made. Each event consisted of a formal PowerPoint presentation followed by a Question & Answer session; in Uganda we also showed a 20-minute film showing the diversity of crater-lake ecosystems, diverse types of human impact on those systems, and an overview of fieldwork methods.

Fig. 36. Presentation of CLANIMAE results to local stakeholder groups, September 2010. In Taveta near Lake Challa (Kenya, **a**) the audience included representatives of the Kenya Ministries of Agriculture, Water & Irrigation, Fisheries and Livestock Development; in Jinja (Uganda, **b**) the audience consisted mostly of the National Fisheries Resources Research Institute (NaFIRRI); in Kanyamukali parish (western Uganda, **c-d**) the audience included district and town council staff, the district environmental officer and the parish priest, and primary-school children.

The content of our presentations differed substantially between Kenya and Uganda, such that presented data pertained to the lakes of each region, and between the types of audience. We had to be selective in the data we showed; we focused on project results with most immediate relevance to water and land resource issues, and highlighted contributions by our African partners. In several venues the Question & Answer session evolved into lively debates between the stakeholder groups about preferred strategies for sustainable development of local water resources, which we can hope may develop into increased interaction between them, and in a joint planning of their activities. Representatives of government ministries, Kenya Wildlife Service and Uganda Wildlife Authority (including two members of the CLANIMAE follow-up committee) universally expressed their appreciation for our initiative to present and explain the results of our project to them in person: they are used to receiving technical final reports from which societal relevant information cannot easily be distilled. The type of questions varied greatly between events depending on the audience's perspective. PDF versions of the relevant presentation have been sent to selected staff members of the above-mentioned stakeholder groups, to be supplemented by the project summary and policy recommendations.

We also exploited multiple opportunities of knowledge transfer to specific stakeholder groups and the public. CLANIMAE data and ideas were featured in, or inspired the following initiatives:

1) Inaugural workshop (London, July 2008) for the PHAROS program, which integrates the IGBP-PAGES programs HITE, LUCIFS and LIMPACS into the overarching theme Past Human-Climate-Ecosystem Interactions, with links to the ESSP programs IHDP, WCRP and DIVERSITAS.

2) Tipping Point meeting of the EUNIC European Economic and Social Committee, December 2009.

3) Past Human-Climate-Ecosystem Interactions workshop on 'Regional integration of past records for management of modern resources and landscapes' (Southampton, UK, September 2010), the first activity in the 'Regional Integration' theme of the IGBP-PAGES Focus 4 program (http://www.pages-igbp.org/science/focus4.html), with strong and complementary links to the IGBP-IHDP-AIMES 'Integrated History and Future of People on Earth' program (http://www.aimes.ucar.edu/ihope/).

Final project deliverables will include all project data and meta-data, plus their interpretation and the discussion of their implications in the context of fundamental or more applied research questions. Having completed the project in July 2011 we are preparing to submit the 4-D CLANIMAE paleoclimate and paleoecological dataset (sites x time slices x proxy indicators x climate signal) to the database at the World Data Center for Paleoclimatology (NOAA/NCDC, Boulder, USA; www.ncdc.noaa.gov/paleo). This final report and associated dataset on the timing and magnitude of historical land use in East Africa is to be communicated to the IGBP-PAGES Focus 4 working group (http://www.pages-igbp.org/science/focus4.html). This transfer will initially be subject to restrictions on pre-publication data mining by people and organizations unrelated to this project, as appropriate to avoid premature public presentation or pre-emptive publication.

Further events which publicized the CLANIMAE project and disseminated project results included (at this time) 4 invited seminars for the general public or a non-scientific audience, and 33 active contributions to (mostly) international scientific meetings, four of which were also invited keynote presentations. Finally, a most effective strategy for wide dissemination of CLANIMAE project results will be to provide START-PACOM officials with this final report, so that the results of our research feature in the high-profile policy publications 'Africa Environment Outlook' and 'Global Environment Outlook' of the United Nations Environmental Program (UNEP).

4.2 Invited seminars for a non-specialist audience

Verschuren, D. (2007). Recent climate change in the context of natural climate variability: the African situation. Klimaatdag 'Wetenschappers aan het woord over klimaatverandering en wat we eraan kunnen doen', VUB en Erasmushogeschool, Brussel-Jette, 14/12/2007.

Verschuren, D. (2009). *Ghent University research in Uganda*. Presentation for the Ugandan Ambassador to Belgium. UGent Development Cooperation, Het Pand, Gent, 18/06/2009.

Verschuren, D. (2009). *Water and Climate*. Colloquium 'Essence of Water', LooktoFood & UGent, St.-Pietersabdij Gent. 13/11/2009.

Verschuren, D. (2010). Long-term ecosystem dynamics of Lake Naivasha, due to natural climate variability and human impact. Lake Naivasha research for sustainable development workshop, International Training Center, Enschede (Nederland), 22-24/10/2010.

4.3 Active contributions to (inter-)national research conferences (*= invited)

Cocquyt C., Plisnier P.-D. & Verschuren D. (2010) Lake Katinda, an eutrophic Ugandan crater lake: limnology, phytoplankton composition and diatoms. 4th Central European Diatom Meeting, Reichenau/Bodensee, Germany, 12-14 March 2010.

Cocquyt C. & D. Verschuren (2007). De bijdrage van fossiele diatomeeën aan multi-disciplinair onderzoek naar de lange-termijn dynamiek van Afrikaanse aquatische ecosystemen onderhevig aan klimaatverandering en historische antropogene invloed. Annual meeting of "Nederlands Vlaamse Kring van Diatomisten". Waternet, Amsterdam, The Netherlands, 8-9 June 2007.

Cocquyt C. & Verschuren D. (2009). The algal flora of Lake Kaitabarago, a small Ugandan crater lake, with special attention to the diatoms. 3rd Central European Diatom Meeting, Utrecht, The Netherlands, 7-13 March 2009.

Cocquyt C., Verschuren D., Eggermont H. Plisnier P.-D., (2008). Diatoms in Ugandan crater lakes as a tool to reconstruct past lake nutrient dynamics in East Africa. 20th International Diatom Symposium, Dubrovnik, Croatia, 7-13 September 2008.

Cocquyt C., Verschuren D. & Plisnier P.-D. (2009) The diatom flora of Lake Kyaninga, a freshwater crater lake in Western Uganda. "Diatom Taxonomy in the 21st Century, Symposium in honour of H. Van Heurck", National Botanic Garden of Belgium, Meise, Belgium, 23-26 August 2009.

Cocquyt C., Plisnier P.-D. & Verschuren D. (2011). The phytoplankton community of Lake Katinda, a eutrophic crater lake in the Edward-George extension of the East African Rift Valley, Uganda. 5th symposium of the Ghent Africa Platform, Gent University, Ghent, Belgium, 2 December 2011.

Colombaroli, D., Verschuren, D. (2011). Records of biomass burning in tropical ecosystems: linking biotic and climatic changes in East Africa over the last 4000 years. International Quaternary Association symposium, Bern, Switzerland, 20-27/07/2011.

Gelorini V., Verschuren D. & Van Geel B. (2007). Non-pollen palynomorphs as palaeoecological indicators for human impact on the East African landscape. Gents Afrika Platform Symposium 'Heritage and/as reproduction in Africa: outcomes and limits', 18 december 2007, Gent.

Gelorini, V., D. Verschuren en B. van Geel (2008). Evaluating modern non-pollen palynomorph diversity in East African lake deposits: a potential palaeoecological tool for tracing human and climatic impact through

time. 3rd International workshop on Quaternary Non-Pollen Palynomorphs. Università degli Studi di Padova, Padova (Italy), 25-28 juni 2008.

Gelorini, V., Verschuren, D., Eggermont, H., van Geel, B. (2009). Modern non-pollen palynomorph (NPP) diversity and distribution in East African lake sediments: evaluating a new palaeo-ecological tool for tracing human impact and climate change, EAQUA workshop, Addis Ababa (Ethiopia), 20-26 May 2009.

Gelorini, V., Verschuren, D., Eggermont, H., van Geel, B. (2009). Modern non-pollen palynomorph (NPP) diversity and distribution in East African lake sediments: evaluating a new palaeo-ecological tool for tracing human impact and climate change, Gents Afrika Platform Symposium 'Gendering Research in/on Africa', Gent (Belgium) , 18/12/2009.

Gelorini, V., Verschuren, D., Eggermont, H., van Geel, B. (2010). Non-pollen palynomorphs (NPPs) as paleoenvironmental indicators for tracing human impact and climate change in East Africa, 1st Landscape Archaeology Conference, Amsterdam (the Netherlands), 26-28 January 2010.

Gelorini, V., Eggermont, H., Lens, L., Verbeke, A., Verschuren, D. (2010). Effects of land use intensity and habitat differentiation on fungal spore diversity in small crater lakes of western Uganda, 4th International Non-pollen palynomorph workshop, Besançon (France) , 16-19 June 2010.

Gelorini, V., Ssemmanda, I., Verschuren, D. (2010). Validation of non-pollen palynomorphs (NPPs) as palaeoenvironmental indicators in tropical Africa: paired 200-year records contrasting pristine and disturbed crater lakes in western Uganda. 4th Belgian Geographers Days, KULeuven, 22/10/2010.

Gelorini, V., Ssemmanda, I., Verschuren, D. (2012). Validation of non-pollen palynomorphs (NPPs) as palaeoenvironmental indicators in tropical Africa: paired 200-year records contrasting pristine and disturbed crater lakes in western Uganda. Landscape Archeology Conference, Berlin, 6-9 June 2012.

Gelorini, V., B. van Geel, D. Verschuren (2012). Diversity and palaeoecological significance of non-pollen palynomorph assemblages in East African lake sediments. 5th International Non-pollen palynomorph workshop, Amsterdam, 2-4 july 2012.

Hughes, H., Plisnier, P.-D., André, L., Cocquyt, C., Cardinal, D. (2011). Dissolved Si isotopes as a tracer of diatom activity in Ugandan crater lakes, IBiS (Isotopes in Biogenic Silica) Congress, Antwerp (Belgium), 4-6 April 2011.

Lebrun J., Mahy G. (2008). Etude de l'écologie des communautés macrophytiques en vue de fournir des indicateurs paléo-environnementaux pour les lacs-cratères d'Afrique de l'Est. Oral communication at the Ecoveg 4 meeting, March 2008, Rennes (France).

Lebrun, J., & Mahy, G. (2009). Environmental Controls on the Distribution of Aquatic Macrophytes in Ugandan Crater lakes. Poster presented at the Symposium "La botanique africaine à Bruxelles", Brussels (Belgium), 27 March 2009.

Mergeay, J., De Meester, L., Verschuren, D. (2009). Species sorting, apparent neutrality and lasting priority effects: palaeoecological lessons from an inherently dynamic natural ecosystem in tropical Africa. European Geophysical Union General Assembly, Vienna (Austria).

Rumes, B., I. Bessems, G. Kabihogo, H. Eggermont & D. Verschuren. A four thousand year history of crater lakes in western Uganda: response of the aquatic invertebrate fauna to climatic and anthropogenic impacts. 31st Congress of the International Society of Limnology, Cape Town, South Africa, 15-20 August 2010.

Ssemmanda, I., Gelorini, V. & Verschuren, D. (2011). Sensitivity of the forest-grassland ecotone to historical rainfall variation in pristine open woodland savanna of equatorial East Africa. International Quaternary Association symposium, Bern, Switzerland, 20-27/07/2011.

*Verschuren, D. (2007). Climate-human interactions in equatorial East Africa during recent millennia. *Keynote*, East African Quaternary Research Association (EAQUA) Inaugural Symposium. Uganda Museum, Kampala, 7-8/06/2007.

*Verschuren, D. (2009). Moisture-balance variation in equatorial East Africa during the Medieval Climate Anomaly and Little Ice Age. ESF Exploratory Workshop on Synoptic-scale climate dynamics over the last millennium: a case study for the MCA-LIA transition. Kippel (Switzerland), 17-20 May 2009.

*Verschuren, D. (2009). Investigating Climate-Human-Ecosystem interaction in tropical Africa: the role of paleodata. Keynote, Darwin Center for Biogeology Annual Symposium, Veldhoven, 6-7/04/2009.

Verschuren, D. (2009). Investigating Climate-Human-Ecosystem interaction in tropical Africa: the role of paleodata. IMPETUS 'Global Change in Africa' symposium, 2-5 June 2009, Koeln.

*Verschuren, D. (2011). Investigating past Climate-Human-Ecosystem interaction in tropical Africa with an improved multi-proxy paleoecological toolbox. International Quaternary Association symposium, Bern, Switzerland, 20-27/07/2011.

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5. PUBLICATIONS

5.1 PhD theses

Bob Rumes (2010). *Regional diversity, ecology and paleoecology of aquatic invetebrate communities in East African lakes*. Unpublished PhD thesis, Ghent University, 257pp.

Vanessa Gelorini (2011). *Diversity and palaeoecological significance of non-pollen palynomorph assemblages in East African lake sediments*. Unpublished PhD thesis, Ghent University, 223 pp.

Harold Hughes (2011). *Si isotopes in tropical rivers as a proxy of the continental Si cycle*. Unpublished PhD thesis, Université Libre de Bruxelles.

5.2 Published, in press or submitted (*= included in Annex 1)

Cocquyt C., de Haan M., Jahn R., Kusber W.-H. & Hinz F. (2011). *Nitzschia epiphytica* O.Müll. versus *Nitzschia epiphyticoides* Hust., and *Nitzschia pseudepiphytica* spec. nov., three small *Nitzschia*'s from Central and East Africa. *Phycologia*, in press.

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*Mergeay, J., De Meester, L., Eggermont, H. & Verschuren, D. (2011). The ghost of environments past: neutral patterns of community composition fuelled by species sorting and priority effects. *Ecology*, in press.

*Rumes, B., H. Eggermont & D. Verschuren (2011). Environmental regulation of the distribution and faunal richness of Cladocera in western Uganda crater lakes. *Hydrobiologia* 676: 39-56.

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5.3 Manuscript in advanced stage of preparation

Audenaert L, C. Cocquyt, B. Rumes, H. Eggermont, V. Baetens & D. Verschuren (in prep.). Response of tropical African lake ecosystems to natural and anthropogenic habitat change: a 200-year paleoecological study contrasting pristine and disturbed crater lakes in western Uganda. *Journal of Paleolimnology.*

Bessems, I., Mees, Ph., Keppens, E. & Verschuren, D. (in prep.). Moisture-balance variation in the northern Kenya Rift Valley based on the mineralogy and oxygen-isotope ($\delta^{18}O$) variation in a 1600-year sediment record of Lake Bogoria. *Quaternary Research*.

Bessems, I., Verschuren, D. & Nowaczyk, N. (in prep.). Lake-level effects on sedimentation in Lake Baringo, central Kenya Rift Valley. *Catena*.

Hughes, H. Plisnier, P.-D., André, L., Cocquyt, C., Cardinal, D., Verschuren, D. (in prep.) Temperature dependence of deepwater dissolved silicon-isotope ($\delta^{29}Si$) variation in tropical African lakes. *Geochim. Cosmochim. Acta*.

Lebrun, J., Mahy, G. & Verschuren, D. (in prep.) Environmental regulation of the distribution of aquatic macrophytes in Ugandan crater lakes. *Aquatic Ecology*.

Plisnier P.D., B. Rumes, C. Cocquyt, H. Eggermont, J. M. Russell, H. Hughes, L. André, D. Verschuren (in prep.) Trophic levels and mixing of Ugandan crater lakes. *Limnology & Oceanography*.

Plisnier P.D., B. Rumes, C. Cocquyt, L. André & D. Verschuren (in prep.) Recent warming recorded in Uganda crater lakes. *Hydrobiologia*.

Rucina, S. M., Verschuren, D., Gelorini, V. & Marchant, R. M. (in prep.) Late-Holocene dynamics of a savanna ecosystem in equatorial East Africa. *Journal of Quaternary Science*.

Rumes, B. K. Martens & D. Verschuren (in prep.) Ostracod (Ostracoda, Crustacea) communities of shallow lakes and ponds in Kenya. *African Journal of Ecology*.

Rumes, B., H. Eggermont & D. Verschuren (in prep.) Ecological and taphonomic controls on the composition of fossil aquatic invertebrate assemblages across a wide environmental gradient of East African lakes. *Journal of Paleolimnology.*

Rumes, B., I. Bessems, H. Eggermont, G. Kabihogo & D. Verschuren (in prep.) Environmental history of a western Uganda crater lake during the last 4000 years: response of aquatic fauna to climatic and anthropogenic impacts. *Quaternary Science Reviews*.

Ryken, E. & Verschuren, D. (in prep.) Biased representation of aquatic macrophyte communities by plant macrofossil assemblages: a case study in Uganda crater lakes. *Journal of Paleolimnology.*

Ssemmanda, I., Gelorini, V. & Verschuren, D. (in prep.) Response of the East African woodland-savannah ecotone to natural moisture-balance variation: a palynological sensitivity study in the Rift Valley of western Uganda. *The Holocene*.

Verschuren, D., A. Bergner, M. Trauth, I. Bessems, M. De Batist, J. Mergeay and J. Richardson (in prep). Modern, historical and long-term sedimentation dynamics in Lake Naivasha (Kenya), due to climate-driven lake-level change and human impact. *Sedimentology*.

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8. ANNEXES

ANNEX 1: COPY OF THE PUBLICATIONS (116 pp.)

ANNEX 2: MINUTES OF THE FOLLOW_UP COMMITTEE MEETINGS (8 pp.)

The annexes are available on our website

http://www.belspo.be/belspo/ssd/science/pr_biodiversity_en.stm