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“Sensitivity of the grassland-forest ecotone in East African open woodland savannah to historical rainfall variation” by I. Ssemmanda et al.

Overview of revisions to the manuscript, and response to reviewer comments

We greatly appreciate the generally positive evaluation of our submitted work by the reviewers and the editor, and the opportunity to submit a revised manuscript which incorporates (most of) their suggestions for improvement. A summarized overview of the changes made is given below. In those cases where we are inclined not to follow specific recommendations for alteration, we present further arguments supporting our approach.

Reviewer 1 general comments:

We acknowledge the reviewer’s recommendation for a more quantitative approach at reconstructing vegetation change, and indeed also see this as an important long-term objective. However, it is no coincidence that “there are only few (if any) studies describing such high-resolution pollen record in tropical Africa”, and none so far presents a “highly valuable quantitative reconstruction for the region”. The methods employed by Lebamba et al. (2012 CP), while being clearly state-of-the-art for vegetation-based climate reconstruction at multi-millennial time scales, would doubtfully succeed in producing a robust signal of the modest decade-scale vegetation changes that are the subject of our study. The average time interval between two consecutive pollen spectra at their Barombi Mbo study site (400 years: 82 samples over 33,000 years) is twice as long as our entire record; and the regional vegetation gradient from forest to savanna that provides the modern samples for their vegetation-climate calibration spans more than 1000 km. Even at such large temporal and spatial scales, Lebamba et al. conservatively discuss only the main, multi-millennial trends that can be considered robust (and which represent full-scale biome shifts), not the individual climate ‘spikes’ apparent in the reconstructions (their Fig.6) that are only supported by single data points. These spikes are not likely to reflect real short-term climate fluctuation, but result from unavoidable imperfection in the transfer function and in the relationship between modern-day vegetation (actually its representation in pollen rain) and climate. Indeed, the width of their late-Holocene uncertainty envelope for quantified precipitation equals the entire range of mean annual rainfall across our study region. If we tried to apply the Lebamba et al. methods to our pollen sequence situated in a small-scale mosaic landscape, we would almost certainly reconstruct mostly noise, while missing the pertinent, taxon-specific trends that are central to the story.

Second, we acknowledge the fact that the instrumental and diatom-inferred lake-level records used to represent ‘historical rainfall variation’ are actually an integrated climate proxy representing general ‘moisture balance’ or ‘moisture availability’, in which (multi-) decadal trends are created by the cumulative effects of annual surpluses and deficits. In that sense, lake records are a more appropriate proxy to compare with pollen records than historical time series of annual rainfall. In addition, GHCN data series for any particular area interpolate between the data available from regional weather stations. In our case, the two closest weather stations (Kasese and Fort Portal) are outside of the map region of Fig. 1, and thus well outside the probable effective pollen source area for Lake Chibwera. Finally, the semi-quantitative rainfall anomaly time series presented by Nicholson et al. (2012 QR) for western Uganda (region 31, with regions 27, 32, 33 and 87 as acceptable substitutes) is heavily dominated by Nicholson’s earlier reconstruction of historical rainfall anomalies over the Lake Victoria catchment (Nicholson & Yin, 2001), as derived from the Nicholson (1998) lake-level record shown in our

Fig. 2 (now Fig. 3). Therefore, using as hydrological indicator, for our study area, the precipitation field data series for region 32 from Nicholson et al. (2012) would be no different than using the Lake Victoria record that we present in Fig. 3. We do take heart in the latter authors' assessment, now cited in our paper (lines 122-126), that "[tropical African] lakes integrate rainfall over their catchment" and "Lake Victoria's level primarily reflects catchment rainfall" (Nicholson et al., 2000, 2012). At the same time, we note that the pre-1840 AD portion of the Lake Victoria curve (first presented by Nicholson, 1998) is very uncertain, given that the lake was discovered only in AD 1858. For that reason, we give greater credence to the early-19th century portion of the diatom-based reconstruction by Stager et al. (2005), which indicates that its lowest level was reached around 1810. This is consistent with the early 19th century lowstand of Lake Chibwera and many other lakes throughout East Africa (Verschuren, 1999; Bessems et al., 2008; De Cort et al., 2013), as well as with the continent-wide synthesis of Nicholson et al. (2012).

Reviewer 1 specific comments (in succession):

We concur with reviewer 1 (and the editor) that comparison between Figs. 2 and 4 was complicated by the different orientation and different axis scales. To correct this, we added to Fig. 2 (now Fig. 3) curves of pollen sums for the three main categories of trees that comprise the arboreal pollen (AP) component.

While we entirely agree with the reviewer on the interest of a possible lag in vegetation response, we deliberately refrained from focusing too much attention an discussion on it because for most of these episodes the magnitude of the lag is comparable to the uncertainty on the ages of the respective pollen intervals (which is larger than the uncertainty on individual ^{210}Pb dates, due to additional uncertainty on anchoring the ^{210}Pb chronology in the ^{137}Cs-derived age marker for AD 1963). The simple reality is that only varved sediment records (cf. Hughen et al., 2004 Science) are suited for study of a vegetation lag at this time scale. Note also that Maslin (2004 Science) quickly resolved the mentioned debate on the variable speed of vegetation change. He stressed that the apparent vegetation lag of 1000 years reported by Jennerjahn et al. (2004 Science) was actually due to a threshold effect: an early climate change (increased rainfall) was large enough to promote pioneer vegetation, but not large enough to completely annihilate the seasonal drought that prevented development of gallery and montane forest.

Following the reviewer's suggestion we have added a table (Table 1) with lake and catchment area information on Lake Chibwera and all reference lakes. This shows that these are all small lakes with limited catchments, and thus can be expected to have a broadly similar effective pollen source area with a comparable ratio between local and long-distance inputs.

We also added a landscape photo of the study region (new Fig. 2), showing the transition zone between open grassland and wooded savanna in the Rift Valley near Lake Chibwera.

Reviewer 2 general comments:

These are similar to the general comments of reviewer 1, allowing us to refer to our rebuttal above.

Reviewer 2 specific comments:

a) To avoid confusion about terminology, we replaced 'diversity' by 'taxonomic richness', and 'pollen influx' by 'pollen input'. In our opinion, adding traditional data on pollen influx is ill-advised in this hydrologically sensitive lake, and at this time scale, because it would require corrections for the compaction gradient and for changes in sedimentation rate (and thus pollen dilution/concentration) that even a robust ^{210}Pb-chronology does not capture very well (cf. Verschuren, 1999). These issues would further compound the already substantial noise in the method of spiking samples with a 'fixed' quantity of exotic pollen to derive absolute concentrations. The reality is that this and other traditional palynological methods were designed for vegetation reconstructions at millennial time scales, and from pollen records in hydrologically stable lake basins. They hit a wall of (generally under-appreciated) compounded uncertainty when applied to high-resolution records from unstable systems. The only way to get around this problem would be to count all the pollen contained in samples of known dry weight, something we are considering to do in future work.

b) We added a second panel to the map of the study region in Fig. 1, showing contour lines of mean annual rainfall on top of a digital elevation map. Given the small study area and relative scarcity of weather stations, these contour lines (taken from one of several available Uganda atlases) are no doubt partly based on a general relationship between rainfall and elevation, modified by topography. For vegetation, the traditional map of White (1983) provides insufficient detail, and both the latter and that of Langdale-Brown et al. (1964) do not show the extent of human landscape modification. We have opted to show the vegetation classification from the Uganda Forest Department's National Biomass Study (1996), which distinguishes land cover classes that are each broadly comparable to the principal natural vegetation types plus two anthropogenic land cover types (degraded forest and small-scale farmland). The main alternative classification is that of the FAO, but this divides up woodland and bushland into multiple additional categories of tree height and canopy cover with no straightforward relationship to the pollen assemblages.

c) We replaced the term 'calibration lakes' with 'reference lakes', and avoid using the term 'calibration'. Also here we note that the spatial scale of the study area is quite small (compared to the mosaic structure of the vegetation) for successful multivariate analysis of environmental controls; and that with the exception of elevation, site-specific information on key environmental controls such as rainfall and temperature is lacking. We argue that this should not prevent us from deriving pertinent information from modern pollen spectra of the reference lakes, given that we have replicate reference lakes for each major vegetation type.

d) We concur with the value of charcoal data, but also here traditional methods are not up to the task. Given large differences in sedimentation rate among hydrologically-sensitive lakes (particularly when also the intensity of local human impact is variable), charcoal concentrations in surface sediments cannot be compared between sites with the aim to discern a burning gradient. To do this properly, one would have to radiometrically date the recent sediments of all reference lakes (quite costly…), or do a long-term (>5 years) sediment-trap analysis, so that trustworthy mean fluxes can be calculated.

e) OK, this reference is now added.

f) See lines 199-201.

g) The age model is now shown in the new Fig. 4.

h) The dry and wet periods shown in Fig. 4 (now Fig. 5) are inferred from increasing or decreasing Poaceae percentages, as now mentioned in the caption.

i) With respect for the reviewer's opinion, we consider our age model on the Lake Chibwera record to be as good as one can possibly hope to obtain from an African savanna lake; in fact the (uniquely) good dating control on our sequence was noted by reviewer 3. As mentioned above, we fully acknowledge that its dating precision is not good enough to unequivocally establish the magnitude of leads and lags, which is why we discuss it only in passing. What we are saying with greater certitude is that the number and approximate timing of decade-scale vegetation changes matches the number and approximate timing of decade-scale variation in regional rainfall (or moisture balance, as reflected in the Lake Victoria record), and that this is indicative of a cause-and-effect relationship.

j) We are uncertain about which statistical tests the reviewer refers to.

k) Consideration of the effective pollen source is important to discern apparent vegetation shifts caused by changes in pollen source area through time, from the modest but real shifts in plant community composition on the surrounding landscape.

Reviewer 3 general comments:

We thank the reviewer for his/her appreciation of our effort to reconstruct vegetation shifts within the historical period and with high temporal resolution, and for confirming the validity of our method to use modern pollen spectra from regional reference lakes to infer the nature and magnitude of those shifts.

Reviewer 3 specific comments:

1) Methodology

We have not cited the 1970s and 1980s studies by the groups of Margaret Davis, George Jacobson and others, but are aware of their main findings as reflected in more recent literature (e.g., Mathias and Giesecke, 2004; Sugita, 2013). What seems to be most important is that all reference lakes are small crater lakes with limited catchments, and thus broadly comparable 'pollen collectors' as the target study lake. The exact dimension of their effective pollen source area remains uncertain (even for small lakes, published estimates range by an order of magnitude), which hampers evaluation of how well a pollen spectrum reflects the mosaic of surrounding vegetation. But given their similar setting, we argue that their pollen source areas are broadly comparable, and thus that differences in pollen spectra across space in the reference lakes are equivalent to differences through time in Lake Chibwera. The one exception is that Lake Chibwera was likely fed by an upland stream several times in the past, at which times its pollen source area must have been substantially greater; the implications of this are discussed in section 5.2.

We added site info on the reference lakes as requested, in an amended Fig. 1 and new Table 1. The regional vegetation description is improved (largely avoiding the terms 'biome', 'ecotone' and 'pristine'), and we hope that the juxtaposition of panels A and B in Fig. 1 now clarify the dependence of vegetation distribution on elevation and rainfall. Other reviewer comments have been accommodated by text alterations. The term 'biome' has mostly been replaced by 'vegetation type'. However in the final paragraph of section 4.1 (lines 281-291), we still relate the modern pollen spectra of our reference sites to the regional biome and plant functional type classifications by Vincens et al. (2006) so as to make a link with pollen-based vegetation reconstruction at larger spatial (and temporal) scales.

Cyperaceae pollen was recorded at all reference lakes. As now explained in the caption, we left this local semi-aquatic vegetation out of Fig. 3 (now Fig. 6) because it is not part of the terrestrial pollen sum, and varies widely between sites depending on basin slope. Adding it in the plot would also necessitate a further reduction of this figure's scale, making the differences between samples more difficult to see. All three forest lakes have steep shores with overhanging trees, therefore local grasses are unlikely to represent a significant component of Poaceae pollen at these sites.

2) Interpretation

Most of the reviewer's comments have been accommodated by text alterations; a total AP curve is added to Fig. 2 (now Fig. 3); and the new panel B of Fig.1 shows the situation of Lake Chibwera and the reference lakes in relation to regional topography.

The sedimentation rate in Lake Chibwera is substantially higher than in typical African forest lakes, but not unlike that of other small lakes situated in rather dry open landscapes. Stream input from the escarpment flows through a swampy area before entering Lake Chibwera, therefore we do not expect a significant contribution of escarpment soils to Lake Chibwera sediments.

We agree with the reviewer that part of the inferred changes in forest composition may be real. However, although episodes of relative drought are expected to favour *Celtis* as a component within (semi-) deciduous forest, its % in the entire terrestrial pollen assemblage decreases rather than increases during the inferred dry periods. We therefore surmise that its increases during wet periods are part of a signal signifying forest and woodland expansion relative to open grassland.

We are not aware of a study by J. Lebamba on a pollen record from Gabon. Perhaps the reviewer refers to Lake Barombi Mbo in Cameroon?

3) Missing points

The possibility of differential pollen production possibly exaggerating inferred vegetation shifts is a good point, and now mentioned in the text (lines 470-472).

Fig. 4 (now Fig. 5) shows all 33 pollen samples analyzed at 4-cm intervals, not 25 at 5-cm intervals as suggested by the reviewer. Also, all samples contained adequate amounts of pollen: counts ranged between 275 and 1313. Each 1-cm pollen sample represents on the order of 1 year deposition near the sediment surface, and 2 to 4 years lower down. Bioturbation will certainly have caused some mixing over a greater interval, but its average effect is likely smaller than in lakes with a (seasonally) oxygenated bottom but lower sediment accumulation rate.

As indicated on the legend of Fig. 4 (now Fig. 5), the peat of Unit III is a peaty organic clay, i.e. a clay with abundant macroscopic plant debris. It is not real bog peat with low clastic mineral content, as is found at high elevation on East Africa's mountains.

We appreciate the reviewer's suggestion to use the % grass or AP pollen from Fig. 3 (now Fig. 6) as a vegetation-based rainfall proxy for comparison with the Lake Victoria record in Fig. 2 (now Fig. 3). However we deem this as too audacious for even a rough estimate of past rainfall variation, considering the modest number of reference sites in relation to (elevation-inferred) values for local rainfall. We therefore opt to compare the %AP curve from Chibwera directly with the Lake Victoria record.

4) Introduction, figures, title and references

The introduction has been shortened (previously 47, now 38 lines) with deletion of some parts, and other parts moved to the site description.

Fig. 1 is redrawn according to all reviewer recommendations.

The title is revised following the recommendation by reviewer 3.

Associated with the text and figure alterations, we added eleven references to the bibliography, and deleted two.