Distinct phases of natural landscape dynamics and intensifying human activity in the central Kenya Rift Valley during the past 1300 years

Running head: Past human influence on a Kenya Rift Valley landscape

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Abstract

Socio-ecological stresses currently affecting the semi-arid regions of equatorial East Africa are driving environmental changes that need to be placed in a proper context of long-term human-climate-landscape interaction. Here we present a detailed reconstruction of past human influences

on the landscape of the central Kenya Rift Valley, against the backdrop of natural climate-driven ecosystem dynamics over the past 1300 years. Proxy records of vegetation dynamics (pollen), animal husbandry (fungal spores), biomass burning (charcoal) and soil mobilization (clastic mineral influx) extracted from the continuous depositional archive of Lake Bogoria reveal six distinct phases of human activity. From *ca* 700 to 1430 CE, strong primary response of savanna woodland ecotonal vegetation to climatic moisture-balance variation suggests that anthropogenic influence on regional ecosystem dynamics was limited. The first unambiguous ecological signature of human activities involves a mid-15th century reduction of woodland/forest trees followed by the appearance of cereal pollen, both evidence for mixed farming. From the mid-17th century, animal husbandry became a significant ecological factor and reached near-modern levels by the mid-19th century, after severe early-19th century drought had substantially changed human-landscape interaction. A short-lived peak in biomass burning and evidence for soil mobilization in low-lying areas of the Bogoria catchment likely reflects the known 19th-century establishment of irrigation agriculture, while renewed expansion of forest and woodland trees reflect the return of a wetter climate and abandonment of other farmland. Since the mid-20th century, the principal signature of human activity within the Lake Bogoria catchment is the unprecedented increase in clastic sediment flux, reflecting widespread soil erosion associated with rapidly intensifying land use.

Keywords: Anthropocene, climate-human interaction, disturbance ecology, East Africa, Kenya Rift Valley, Lake Bogoria, landscape ecology, paleoecology, vegetation dynamics

Paper type: Primary research

1. Introduction

The ever-increasing influence of human activity on virtually all aspects of the natural world has underlined the need for better understanding of longer-term climate-human-ecosystem interaction, knowledge that is essential for the sound and sustainable management of cultural landscapes. Establishing this long-term historical context is especially problematic in Africa, where hominin influence on the environment, through use of tools and fire, may even predate the origin of modern humans as biological species ~300,000 years ago (Gowlett, 2016; Schlebusch et al., 2017). Many authors suggest that human influence on the East African landscape must have become substantial with the introduction of food production (e.g. Taylor, 1990; Jolly et al., 1997; Heckmann et al., 2014). But, while archaeological evidence indicates that crop agriculture has been practiced in eastern equatorial Africa for roughly 2500 years (Fuller & Hildebrand, 2013; Lane, 2015), paleoecological signatures for marked landscape transformation have so far mostly been documented only from a few small regions where suitable natural archives, such as lake and bog deposits, can be found (Marchant et al., 2018). The combined evidence suggests that human impact visible in proxy records may have been limited to 'niche' environments or 'islands' within a mosaic landscape that offered early farmers a fortuitous combination of climate, topography, and soils (Marshall & Hildebrand, 2002; Widgren & Sutton, 2004), while people practicing nomadic or transhumant lifestyles exerted a relatively light footprint on the region's savanna environments (Lane, 2016). Some studies of ancient land-use patterns in tropical Africa, based on extrapolation from historical population trends (e.g. Ramankutty & Foley, 1999; Houghton & Hackler, 2006) even suggest that disruptive human impacts on East Africa's ecosystems must have been very limited prior to two-three centuries ago, due to the very low demographic pressure of its ancient inhabitants compared to their present-day counterparts. Substantial differences exist between various reconstructions (e.g., Kaplan et al., 2011; Klein Goldewijk et al., 2011) of the spatial extent of land areas subject to farming and grazing prior to

industrialization or the era of colonial governance. This situation translates into significant uncertainty about the magnitude of anthropogenic climate forcing attributable to (pre-) historical greenhouse-gas emissions (Stocker et al., 2018); and calls for improved documentation of land-use change during recent millennia worldwide (Harrison et al., 2018).

Documenting the long-term history of climate-human-landscape interaction in East Africa is complicated by the challenge of discriminating between the paleoecological signatures of human activities and the response of local vegetation ecotones and fire regimes to the variation in available moisture associated with natural climate variability (Colombaroli et al., 2014). A second challenge is the relative scarcity of paleoenvironmental archives with demonstrated continuity throughout the last few millennia, because large natural climate variability has repeatedly caused the (near-) desiccation of many lake and bog sites, and hence partial loss of their sedimentary archives, in the relatively recent past (Verschuren, 2003). Nevertheless, increased availability of continuous paleoclimate and paleohydrological records with high temporal resolution, and regional syntheses thereof (Verschuren, 2004; Verschuren & Charman, 2008; Tierney et al., 2013; Nash et al., 2016), have greatly improved our insight into the spatiotemporal patterns of environmental change in East Africa at decadal to century timescales. These records can now be compared directly with the reconstructions of human activity.

This study aims to elucidate historical changes in the relative role of natural and anthropogenic processes in East Africa through a detailed paleoecological analysis of vegetation and landscape dynamics in the tropical semi-arid Rift Valley region of central Kenya over the last 1300 years. Multi-proxy data extracted from the sediment record of Lake Bogoria are set within a tight reference frame of the region's hydroclimatic history, as reconstructed from sedimentological and geochemical moisture-balance proxies in the same sediment record (De Cort et al., 2018). Further

we compare the paleoecological data with regional archaeological evidence, in order to assess discipline-specific perspectives on past landscape change (cf. Caseldine & Turney, 2010). Importantly, our proxy data represent continuous time series from *ca* 700 CE (*ca* 1250 calendar years BP) until the present (2014 CE). This allows for direct comparison of the relative magnitude of ancient landscape changes with those that occurred during the colonial period (i.e., from *ca* 1900 CE) and after Kenya attained political independence in 1963. By quantifying those recent changes independently using historical data, issues of interpretation related to the sensitivity of proxies used to reconstruct the more ancient changes can be circumvented (cf. Dearing et al., 2006).

2. Regional setting

2.1 Geographical location, climate and hydrology

Lake Bogoria (0°15'N, 36°06'E; *ca* 17 x 3.5 km) is a hypersaline closed-basin lake occupying the southern end of a half-graben depression in the central Kenya Rift Valley (Fig. 1a). Its 705 km^2 catchment is bounded to the east by the Laikipia Plateau. The Tugen Hills and Elgeyo Escarpment, which form the valley's western flank, are located *ca* 35 km to the west.

Rainfall seasonality in equatorial East Africa is linked to latitudinal migration of the tropical rain belt (Nicholson, 1996, 2018; Yang et al., 2015), which passes across the region twice each year and thus produces two rainy seasons: the long rains (March to May) and short rains (October and November). Both long and short rains are brought in from the Indian Ocean by, respectively, south-easterly and north-easterly monsoon winds. Located in the rain shadow of the eastern escarpment, Lake Bogoria's catchment receives rather little of this rainfall (500-1000 mm). This is however compensated by frequent late-afternoon cloud-bursts during the so-called dry season

(June to September), which deliver considerable amounts of precipitation from moist westerly air (Davies et al., 1985). Although its water budget is climate-controlled, geothermal springs fed by percolated rainwater provide the lake with 30-35% of its annual inflow and buffer the lake's surface level against short-term rainfall anomalies. Over longer time scales, this continuous geothermal inflow has also protected Lake Bogoria against complete desiccation during past episodes of severe climatic drought (Renaut & Tiercelin, 1994; Onyando et al., 2005). As a result, its bottom sediments have preserved a regionally unique continuous record of climate and landscape history throughout at least the last 1300 years (De Cort et al., 2013, 2018). Lake Bogoria is divided into three basins along its length, separated by sills that are currently submerged. About two-thirds of its catchment is drained by the Sandai-Waseges River, which enters the lake from the north via a broad floodplain. It is a mostly seasonal river, but can be perennial during exceptionally wet years (Renaut et al., 1986). In recent years water from the river has been diverted for crop irrigation immediately north of the lake. The narrow western and southern portions of the catchment are drained by small ephemeral streams which flow into the central and southern basins. The Lake Bogoria National Reserve (107 km²; Fig. 1a) protects the lake and immediately adjacent catchment areas from anthropogenic impact, but not the large upstream portions of the Sandai-Waseges drainage, which are thus more susceptible to disturbance.

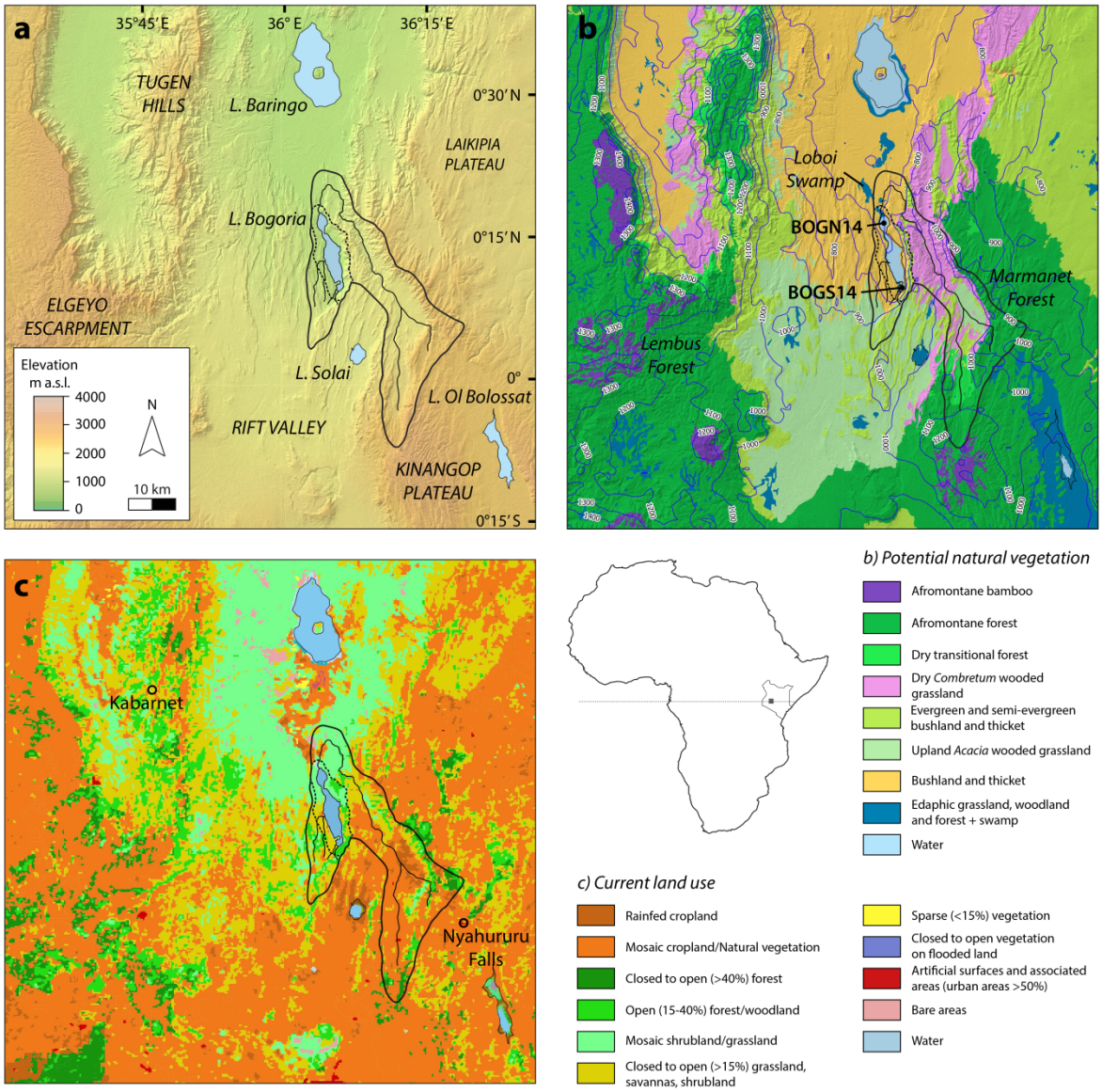


Fig. 1 (a) Location of Lake Bogoria, its drainage basin (bold line), major rivers feeding into the lake (thin lines) and the Lake Bogoria National Reserve (boundary as stippled line), in relation to other regional lakes and surrounding topography. Topography data are from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) data set (NASA LP DAAC, 2011). (b) Potential vegetation of the study region, simplified from the VECEA classification (van Breugel et al., 2015). Superimposed on this map are the isolines of mean annual rainfall for the period 1970-2000 based on the Worldclim 2.0 dataset (Fick & Hijmans, 2017) shown to highlight the moisture dependence of vegetation distribution. (c) Map of current land cover and land use, derived from Globcover data for 2009 (Bontemps, 2011) using a regional model by the Food and Agriculture Organization of the United Nations (FAO, 2015). The skeleton map shows the location of the study area in eastern equatorial Africa.

144 2.2 Modern-day vegetation

145 Modern-day vegetation around Lake Bogoria falls within the Somalia-Masai phytogeographic
146 region as defined by White (1983). According to Vincens et al. (2006), vegetation in the direct
147 vicinity of the lake can all be broadly classified under the biomes of tropical savanna and dry
148 forest. At mid-elevations on the eastern escarpment these authors report the occurrence of *Acacia*
149 wooded grassland with *Combretum*, *Tarchonanthus*, *Dodonaea* and *Justicia* as other principal
150 arboreal taxa (i.e., trees) and Amaranthaceae as most common herbaceous taxa (i.e., herbs).
151 Somewhat less open woodland occurs on the low ridge along on the west side of the lake with
152 *Dodonaea* as the dominant tree species together with *Terminalia* and sparse thickets of *Acacia*
153 *brevispica*, while south of the lake *Tarchonanthus* is the most abundant tree (Vincens et al.,
154 2006). In the wider region of the central Rift Valley, wooded grassland dominated by *Combretum*
155 and *Terminalia* tends to occur mostly on westward slopes, whereas evergreen bushland with
156 *Dodonaea*, *Euphorbia*, *Olea* and *Tarchonanthus* occurs more on eastward slopes (Fig. 1b; Kindt
157 et al., 2011b; Van Breugel et al., 2015). Closed-canopy Afromontane forest is mostly lacking
158 within the Bogoria catchment (Fig.1c), and found only within Marmanet Forest in the southeast
159 (Vincens et al., 1986) and in dry coniferous forest dominated by *Podocarpus*, *Juniperus, Olea*
160 and *Dodonaea* in the south. Outside the Bogoria catchment, Afromontane forest is found above
161 2000 m elevation in Lembus Forest near Kabarnet, *ca* 45 km west of the lake; and on the Laikipia
162 Plateau, from *ca* 25 km to the east, where it consists mostly of *Juniperus*, *Olea* and *Croton*
163 (Taylor et al., 2005). Dry transitional forest consisting of *Calodendrum*, *Croton, Euclea, Olea*
164 and a mix of other Afromontane and savanna trees used to rise from the woodlands up dry
165 escarpment slopes, but very little of this biome remains in Kenya today (Kindt et al., 2011a).
166 Today *Dodonaea viscosa*, native to the area but with a tendency to encroach into disturbed

vegetation (Becker et al., 2016), is common throughout the region's grassland-forest ecotone. Timber plantations with pine (*Pinus patula* and *P. radiata*) and cypress (*Cupressus arizonica, C. torulosa*, *C. macrocarpa,* etc.), both introduced since the early 1900s, now replace part of the region's indigenous forests (Troup, 1932; Ofcansky, 1984; Kokwaro, 2015).

3. Materials and methods

3.1 Sediment sampling and chronology

The sediment cores analyzed in this study were collected from the deepest points of the southern and northern basins of Lake Bogoria in 2014, using gravity- and piston-coring equipment. Overlapping core sections were assembled in two composite sediment sequences labelled BOGS14 and BOGN14 (Fig. 1b), through cross-correlation using visual lithostratigraphic markers and magnetic-susceptibility scanning data (De Cort et al., 2018). The chronology of Lake Bogoria's sediment record is based on 16 ^{14}C-dated levels, together with ^{210}Pb-dating of recent sediments and a comprehensive set of tie points between the respective sediment sequences (De Cort et al., 2018). Radiocarbon dating targeted terrestrial plant material, mostly small grass-charcoal fragments, but also terrestrial seeds and charred wood. Tie points between cores were established using visual characteristics, charcoal counts and geochemical data. Age-depth modelling was performed using Bacon software in R (Blaauw & Christen, 2011), after calibrating the ^{14}C ages with the IntCal13 calibration curve (Reimer et al., 2013). There is a sizable analytical error on individual ^{14}C dates compared to the total time period covered by the record. Combined with wide calendar-age windows associated with ^{14}C dates younger than 700 years (Reimer et al., 2013), and short-term variation in the rate of sediment accumulation associated with lake-level fluctuations (Verschuren, 1999, 2001) this translates into relatively

high age uncertainty on all sediment intervals beyond the ^{210}Pb-dated range (De Cort et al., 2018; Supplementary Fig. S1). In turn, this places an unavoidable upper limit to dating precision in natural paleoenvironmental archives of this type and time range, even when applying state-of-the-art Bayesian age-modelling techniques (e.g., Blaauw et al., 2011). These age uncertainties (Table 1) must be taken into account when comparing the results of this study with paleoecological evidence from other sites, or with independently constrained historical data. However, since our proxy evidence for past landscape changes is drawn from the same sediment archive as the proxy evidence for hydroclimate change (De Cort et al., 2018), temporal relationships between the reported sedimentary signatures of the respective events are secure.

Table 1 Sediment depth, weighted-mean modelled age and the lower and upper boundaries of 95% confidence envelopes (Min/Max Age) of pollen-zone boundaries in composite sequence BOGS14 from the southern basin of Lake Bogoria, based on ^{210}Pb- and ^{14}C-dating by De Cort et al. (2018).

	Depth (cm)	Mean Age (year CE)	Min. Age (year CE)	Max. Age (year CE)
Top of record	0	2014.6	2014.6	2014.6
BOGS-5/BOGS-6 transition	13.8	1965	1958	1973
BOGS-4b/BOGS-5 transition	30.4	1910	1876	1935
BOGS-4a/BOGS-4b transition	66.5	1670	1586	1750
BOGS-3/BOGS-4a transition	107.1	1430	1399	1472
BOGS-2b/BOGS-3 transition	127.1	1330	1282	1373
BOGS-2a/BOGS-2b transition	148.1	1250	1199	1296
BOGS-1/BOGS-2a transition	176.4	1175	1127	1216
Base of record	300	686	623	767

203

204 3.2 Pollen and fungal-spore analysis

205 Pollen samples for vegetation reconstruction were prepared according to standard procedures
206 (Faegri & Iversen, 1964; Moore et al., 1991; see Supplementary Information for details). The
207 targeted minimum pollen sum was 400 pollen grains of terrestrial plants (BOGS14: range 225-
208 872, mean 567; BOGN14: range 111-576, mean 429). This sum excludes pollen of aquatic plants,
209 Cyperaceae (sedges, in this environment also mostly aquatic or riparian), and all non-pollen
210 palynomorphs (NPPs) such as fern and fungal spores. It does include cultivated plants such as
211 pine (*Pinus*), a prolific pollen producer (see Supplementary Information for further comment).
212 Most Cupressaceae pollen encountered in this study probably derives from the native *Juniperus*
213 *procera*, an important element in the Afromontane forest of central Kenya (Lamb et al., 2003).
214 However, post-1900 CE samples must also contain introduced cypress (*Cupressus*) species.

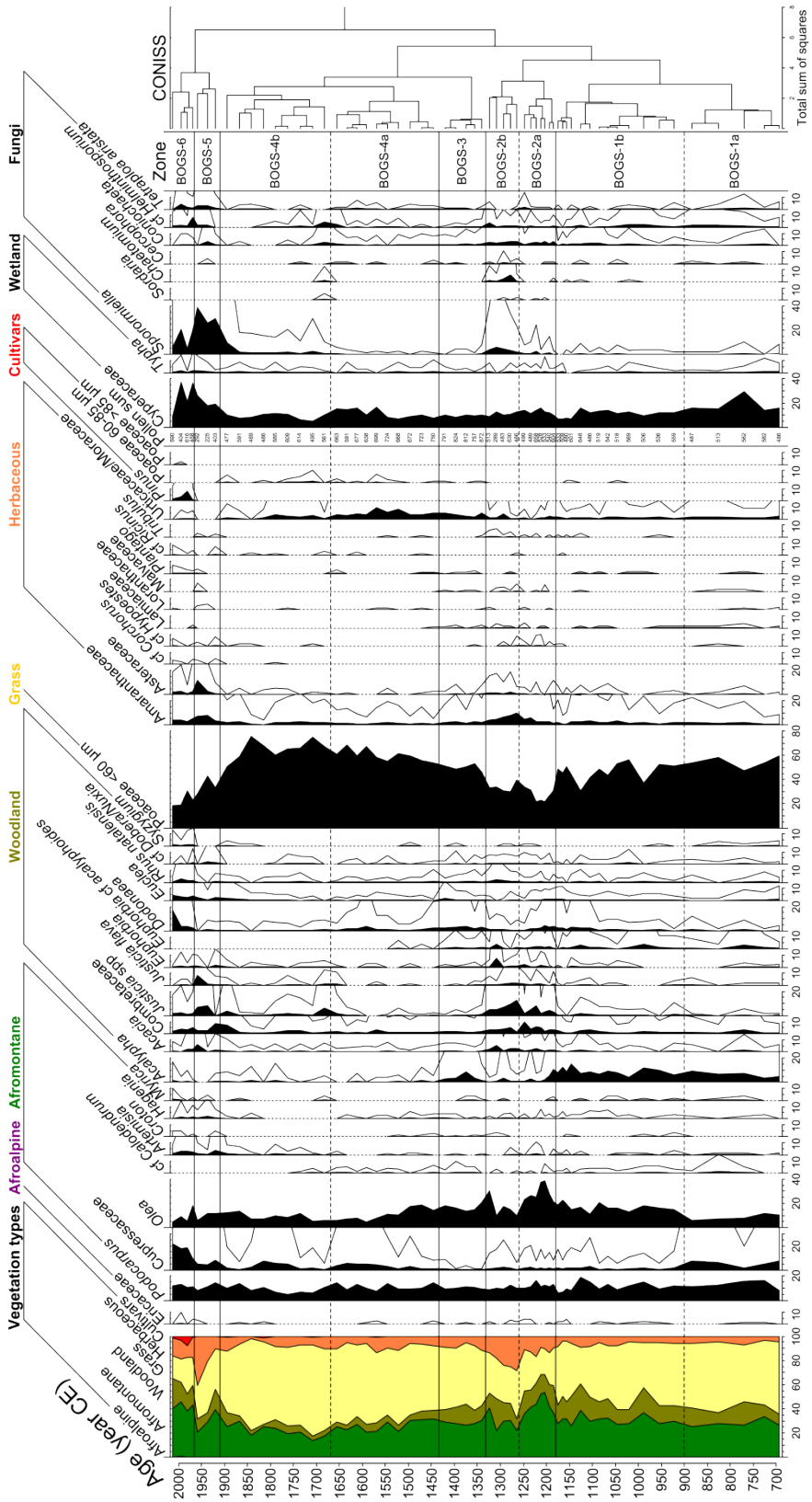
215 Analysis of fungal spores focused on coprophilous fungi, i.e. fungi growing either obligately or
216 facultatively on the excrements of large herbivores (Baker et al., 2013), and selected other taxa
217 such as *Glomus*, cf. *Helminthosporium* and *Tetraploa*. However, all spores were counted to
218 assess their overall abundance relative to vascular-plant pollen. We used atlases of African NPPs
219 (van Geel et al., 2011; Gelorini et al., 2011) as main reference for fungal-spore identification.
220 Among the fungal spores recovered, we considered only *Sordaria* and *Sporormiella* as obligate
221 coprophiles (Gelorini et al., 2012; Baker et al., 2013); this record yielded no *Delitschia* or
222 *Podospora*. C*ercophora*, *Chaetomium* and the widespread saprotrophic *Coniochaeta* are
223 considered facultative coprophiles, and thus less persuasive as proxies for past animal husbandry.
224 The percent abundance of individual fungal spore taxa is expressed relative to the terrestrial
225 pollen sum.

Constrained incremental sum-of-squares cluster analysis (CONISS; Grimm, 1987) of the fossil pollen assemblages was used to delineate stratigraphic pollen zones. This zonation is based only on the terrestrial pollen sum. Since fungal spores are not part of the pollen sum they are treated as an independent environmental variable. Stratigraphic changes in pollen-assemblage composition were visualized using TILIA 2.0.41 (Grimm, 2015). Indirect gradient analysis was used to extract the underlying comprehensive changes in pollen-assemblage composition. As the overall variability in our pollen data fits a linear model rather than a unimodal model, PCA was preferred over DCA (DCA axis 1 < 2 SD; Ter Braak & Prentice, 1988). To estimate how much of the variance in the response variable (vegetation) can be explained by variation in fire regime, Redundancy Analysis (RDA; preferred above the unimodal response model CCA, cf. above) was performed on the pollen data, using charcoal accumulation rate (CHAR) as the explanatory variable (Davies & Tso, 1982; Ter Braak & Prentice, 1988). In this approach, only the first canonical axis is constrained, whereas the other axes remain unconstrained ('hybrid redundancy analysis'; Colombaroli et al., 2009). All gradient analyses were performed using Canoco 5 (Ter Braak, 1988).

3.3 Size classes of Poaceae pollen grains

The traditional method to distinguish Poaceae pollen derived from cereals (i.e., domesticated grasses) from wild-type grass pollen is that grains <37 μm are counted as wild type while grains >37 μm are counted as cereals (Andersen, 1979). Developed for tracing European and Middle Eastern cereals, this criterion does not necessarily apply to the pollen of indigenous African cereals and wild-type grasses (Bonnefille 1972). Moreover, preparation methods using potassium hydroxide and acetolysis, as well as mounting of the pollen residue in glycerol, can cause swelling of the pollen grains (Moore & Webb, 1978; Dickson, 1988). Pollen grains of *Zea mays*

(maize, corn) are normally discriminated by their very large size (>85 μm; Eubanks, 1997). However, ancient maize pollen grains are sometimes found to be smaller than modern grains (60–85 μm instead of the modern 85–125 μm; Tsukada & Rowley, 1964). Following Colombaroli et al. (2018), we opted for a conservative approach and divided Poaceae pollen into three size categories. Grains <60 μm are considered to be derived from wild-type grass, although significant overlap with the indigenous cereals finger millet (*Eleusine coracana*) and sorghum (*Sorghum bicolor*) cannot be excluded (Chaturvedi et al., 1994). Grains >85 μm are all assumed to be *Z. mays*; and grains in the 60-85 μm range are assumed to be disproportionally derived from indigenous cereals, as opposed to wild-type grasses. Another complication is that the probability of finding wild-type grass pollen grains large enough to be misclassified as cereal pollen increases in proportion to the percentage (%) of Poaceae in the total pollen sum. To control for this artefact, we calculated the fraction of 60-85 μm Poaceae grains relative to the total Poaceae pollen abundance in each sampling interval, and compared the average 60-85 μm fraction for each pollen zone with the record-wide mean value.


CONISS
Total sum of squares
Zone
BOGS-6
BOGS-5
BOGS-4b
BOGS-4a
BOGS-3
BOGS-2b
BOGS-2a
BOGS-1b
BOGS-1a
Vegetation types
Age (year CE)
Afroalpine
Afromontane
Woodland
Grass
Herbaceous
Cultivars
Wetland
Fungi

263

Fig. 2 Stratigraphic distribution of selected pollen taxa (most, but not all >1% of the terrestrial pollen sum) in the BOGS14 sediment sequence from the southern basin of Lake Bogoria, in relation to sediment age (De Cort et al., 2018) and pollen-based stratigraphic zonation (CONISS; Grimm, 1987). Taxon abundance is presented as percentage (%) of the terrestrial pollen sum (black curves; 10x exaggeration in white), with taxa grouped per vegetation type and summary diagram on the left. Pollen from wetland taxa and fungal spores are expressed as percent of the terrestrial pollen sum but not included in it.

4. Results

4.1 Landscape history as recorded in the southern basin of Lake Bogoria

4.1.1 Evidence from vascular-plant pollen

The 1300-year record of terrestrial vegetation dynamics revealed by sediment sequence BOGS14 comprises six pollen zones as defined by CONISS (Fig. 2). A detailed description is provided in Supplementary Information; here we summarize the main trends. On the whole in pollen zone BOGS-1 (*ca* 700-1175 CE), the pollen assemblage indicates that much of the catchment was covered by a relatively open grassland-woodland ecotone, with stands of closed-canopy forest relatively nearby. The grass pollen fraction is relatively high, fluctuating around 50% with two short-lived declines around 960 and 1130 CE (Fig. 2). The Afromontane forest component is substantial (mean 30%) and dominated by *Podocarpus*, *Olea* and Cupressaceae (at this time, the native *Juniperus procera*). The woodland fraction (mean 16%) is relatively stable through time and consists primarily of *Acalypha* with smaller contributions from Combretaceae, *Dodonaea*, *Euphorbia* and *Acacia*. The herbaceous component is relatively modest (mean 6%). In zone BOGS-2 (*ca* 1175-1330 CE), grass and *Acalypha* pollen decrease to levels well below those in BOGS-1 during two multi-decadal episodes centered around 1220 and 1280 CE. During the first episode (sub-zone BOGS-2a) this is mainly compensated by an increase of the forest component

289 (mean 38%) carried in large part by *Olea*. During the second (sub-zone BOGS-2b) there are
290 major increases in diverse trees and herbs associated with *Acacia* wooded grassland. In zone
291 BOGS-3 (*ca* 1330-1430 CE), grass pollen percentages increase again to a mean value of 50%.
292 Taxa associated with *Acacia* wooded grassland are reduced, largely compensated by re-expansion
293 of *Acalypha* to a level approaching that of BOGS-1. The total woodland and forest fractions
294 remain similar to those in BOGS-1 and BOGS-2b.

295 Pollen zone BOGS-4 (*ca* 1430-1910 CE) encompasses a *ca* 500-year period of Rift Valley
296 history. Grass percentages mostly exceed 60% and reach peak values of *ca* 75% around 1710 CE
297 and 1840 CE, but decrease to *ca* 50% at the top of this zone. In the forest component, *Olea*
298 maintains the mean level of 20% it had in BOGS-3 only until *ca* 1500 CE, after which it drops to
299 *ca* 10%. Simultaneously, Poaceae grains in the size range 60-85 μm start appearing more or less
300 continuously and in significant numbers. Overall, the woodland component is strongly reduced to
301 a mean value of 6% between *ca* 1480 and 1870 CE, coincident with the period of low *Olea*
302 abundances (Fig. 2). Cf. *Ricinus* (castor oil plant), only occasionally present before, appears more
303 regularly from *ca* 1600 CE onwards (Fig. 2). A concentration of percent-abundance shifts around
304 1670 CE divides this zone in two sub-zones (BOGS-4a and BOGS-4b). Among forest taxa cf.
305 *Calodendrum* and *Hagenia* decrease to the benefit of *Artemisia*, while among the woodland taxa
306 *Dodonaea* decrease to the benefit of *Justicia* and *Euphorbia*.

307 In zone BOGS-5 (*ca* 1910-1965 CE), which broadly encompasses the period of European
308 colonial governance, Poaceae pollen decrease further to reach a low value of *ca* 30% around
309 1960 CE. Trees of *Acacia* wooded grassland all increase, suggesting a recovery of the woodland
310 component (range 8-17%). This woodland recovery is also reflected in marked increases of
311 herbaceous taxa belonging to the Amaranthaceae and Asteraceae, cf. *Ricinus* and *Tribulus*, and

312 diverse rare taxa (< 1% of the pollen sum) such as cf. *Corchorus,* cf. *Hypoestes,* Loranthaceae
313 and Malvaceae (Fig. 2). The Afromontane forest component expands only temporarily in the
314 lower part of this zone, representing the early 20th century. Finally, in zone BOGS-6 (*ca* 1965 –
315 2014 CE), which broadly encompasses the post-colonial period, the fraction of Poaceae pollen
316 declines further to reach a record low value of 18% in the pollen assemblage representing
317 modern-day vegetation. However, the now strong Afromontane (38-46%), woodland (14-25%)
318 and herbaceous (9-16%) components mostly benefit from the unprecedented increases in
319 Cupressaceae, now to be attributed largely to exotic cypress species planted for timber
320 production; as well as *Dodonaea* and ruderal herbs such as *Plantago* and cf. *Ricinus.* Also the
321 exotic *Pinus* makes a strong appearance. Only a single Poaceae grain >85 µm (maize) was
322 recovered from BOGS-6, and none in the 60-85 µm range.

323 *4.1.2 Spores of coprophilous and other fungi*

324 During the period 700–1175 CE (pollen zone BOGS-1) the most abundant fungal spores belong
325 to cf. *Helminthosporium*, which occurs on grasses (Shoemaker, 1959); and *Coniochaeta*, a
326 general saprotrophic taxon (Gelorini et al., 2011, 2012; Baker et al., 2013; Fig. 2). Also almost
327 continuously present is *Tetraploa aristata*, a fungus found on the leaf bases and stems of living
328 plants, including Poaceae and Cyperaceae (Ellis, 1971). The obligate coprophilous fungus
329 *Sporormiella* and a few other taxa are present at very low abundances only. In BOGS-2
330 *Sporormiella* is more common, especially during 1250–1330 CE. Also the obligate coprophile
331 *Sordaria* is found, albeit in low percentages; and *Chaetomium*, a facultative coprophile. In
332 BOGS-3 and BOGS-4a (*ca* 1330–1675 CE), fungal spore assemblages and abundances are
333 similar to those recorded in BOGS-1. Starting from the base of BOGS-4b, *Sporormiella*
334 abundances increase again to those attained in BOGS-2, and remain at that (overall still relatively

modest) level until near the top of BOGS-4b (Fig. 2). Early during this period there are also temporary peaks in cf. *Helminthosporium* and *Coniochaeta,* and brief appearances of *Chaetomium* and *Sordaria* but the two latter taxa disappear again shortly thereafter. From *ca* 1890 CE until the 1960s (largely corresponding with BOGS-5) *Sporormiella* increase dramatically, together with modest but still significant increases in cf. *Helminthosporium*, *Coniochaeta* and *Tetraploa aristata*. In BOGS-6 (the last 50 years) the total abundance of fungal spores delivered to southern Lake Bogoria sediments is reduced, with notable decreases in *Sporormiella*, cf. *Helminthosporium* and *Coniochaeta*.

4.1.3 Charcoal

The influx of charcoal to the southern basin of Lake Bogoria exhibits high temporal variability at the (sub-)decadal time scale during the past 1300 years (Fig. 3d). Initially, charcoal influx displays an inverse relationship with local hydroclimatic variability (Fig. 3a; De Cort et al., 2018). This is the case in pollen zones BOGS-1 through BOGS-3 (the period from *ca* 700 to 1430 CE), with the exception of BOGS-1a when charcoal influx is low while climate conditions are inferred to have been dry. On average, the highest sustained charcoal influx in this *ca* 700-year period (>500 particles $cm^{-2}yr^{-1}$) occurred from *ca* 880 to 1070 CE, with a peak of 1300 particles $cm^{-2}yr^{-1}$ around 1040 CE. The lowest charcoal influx occurred in the second half of the 8th century CE (<250 particles $cm^{-2}yr^{-1}$) and around 1110 CE and 1320 CE (<100 particles $cm^{-2}yr^{-1}$). In BOGS-4a, fluctuating but mostly high charcoal influx values averaging 300-400 particles $cm^{-2}yr^{-1}$ are sustained throughout the 15th and 16th century. They reach a peak of >600 particles $cm^{-2}yr^{-1}$ around 1580 CE before decreasing to very low levels (<100 particles $cm^{-2}yr^{-1}$) toward the top of BOGS-4a and the base of BOGS-4b, dated to the late 17th century CE. Charcoal influx remains very to moderately low (most often <200 particles $cm^{-2}yr^{-1}$) throughout the 18th and 19th

centuries, with the exception of a pronounced but short-lived maximum (1345 particles $cm^{-2}yr^{-1}$) dated to *ca* 1820 CE, just after the start of a progressive rise in reconstructed lake level. At the top of BOGS-4b, i.e. the turn of the 20th century, charcoal influx values reach an extreme low point (5 particles $cm^{-2}yr^{-1}$) after which they remain low (usually <100 particles $cm^{-2}yr^{-1}$) until the present-day.

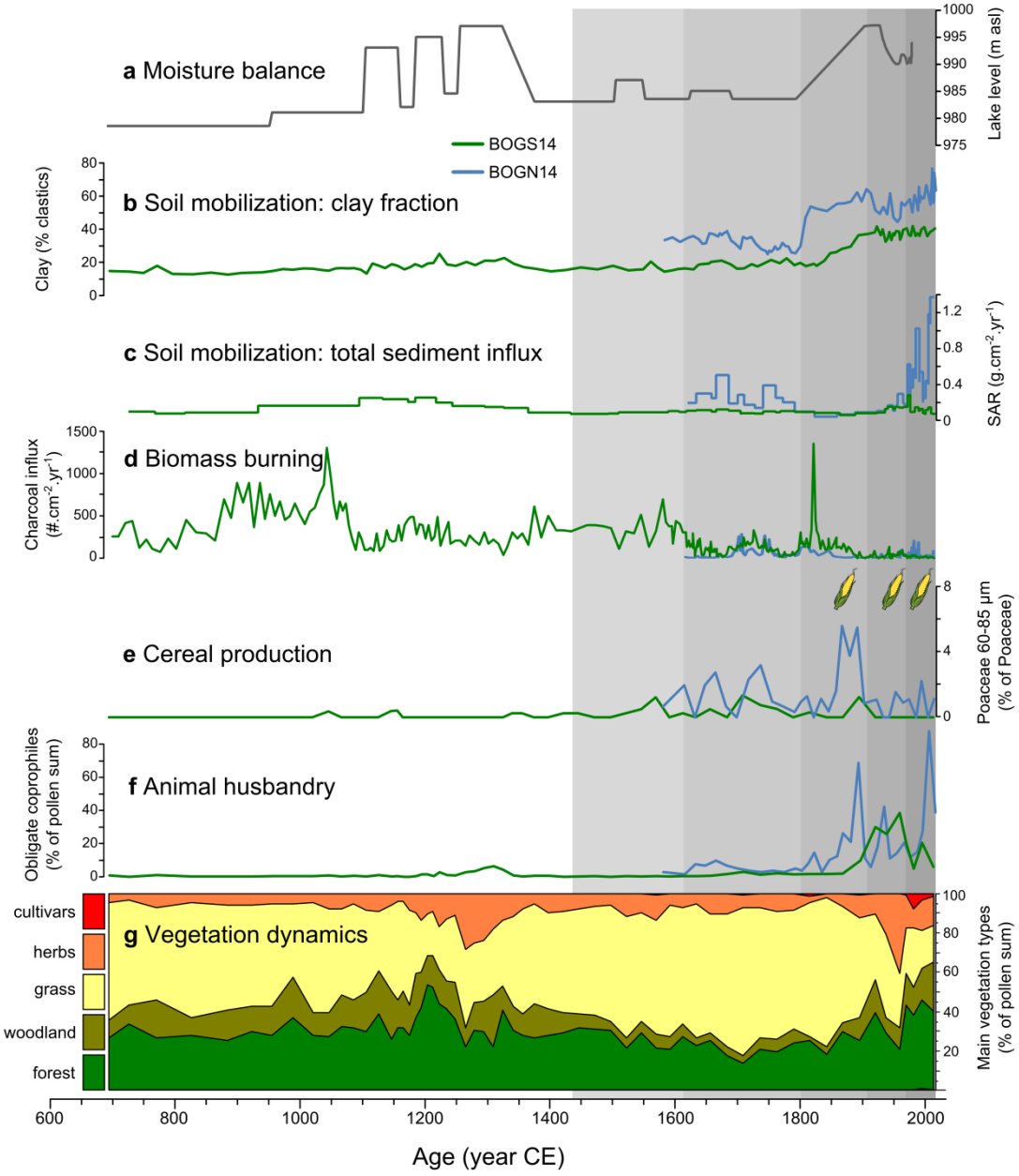
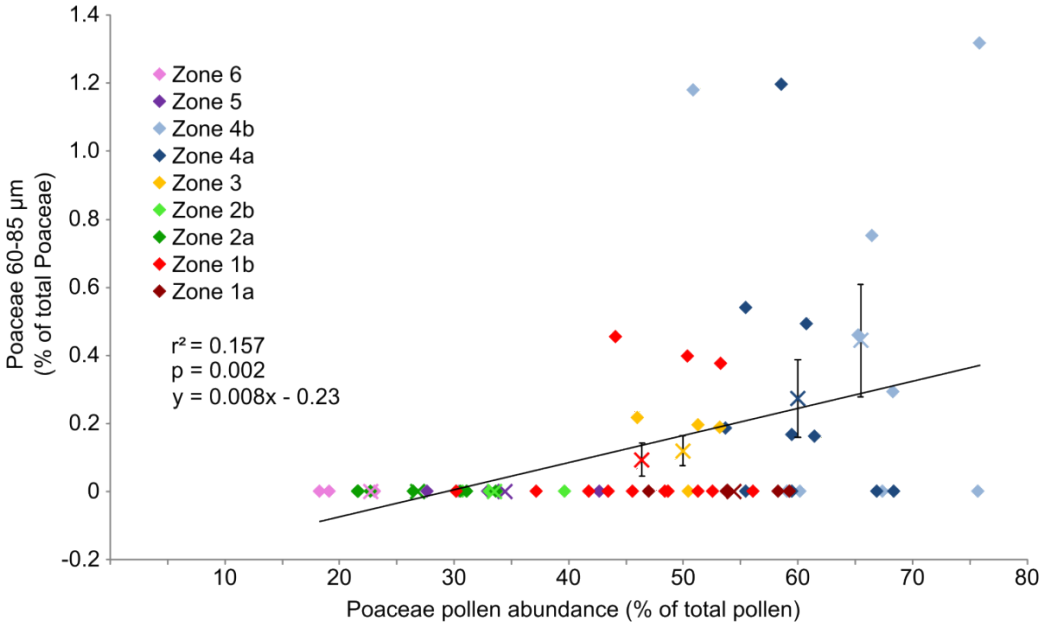


Fig. 3 Synthesis of proxy data from the southern (BOGS14, green) and northern (BOGN14, blue) sediment record of Lake Bogoria, with indication of the five phases of intensifying ecological influence of human activity (light to dark grey shading). The panels show (a) climatic moisture-balance variation inferred from lake-level change, simplified from De Cort et al. (2018); (b) clay fraction as % of clastic mineral sediment; (c) total lake-sediment accumulation rate (SAR); (d) biomass burning inferred from charcoal influx; (e) cereal production inferred from the fraction of Poaceae pollen grains sized 60-85 µm, with isolated finds of maize pollen (Poaceae grains >85 µm) indicated with pictograms; (f) Animal husbandry (plus wild herbivores; see text), inferred from the relative abundance of spores from obligate coprophilous fungi (*Sporormiella* + *Sordaria*); (g) summary diagram of temporal shifts in the composition of terrestrial vegetation, based on BOGS14 data.

4.1.4 Cereals versus wild-type grasses

Over the entire 1300-year record, the fractional abundance of 60-85 µm grass-pollen grains (as % of total Poaceae) is positively correlated with % total Poaceae pollen ($r^2 = 0.157$, $p < 0.01$, $n = 90$; Fig. 4). No such correlation is found within zone BOGS-4 ($r^2 = 0.002$, $p = 0.87$, $n = 25$), and the average fractional abundance of 60-85 µm grass-pollen grains within that zone (0.36%) is well above that predicted by the full-record regression (0.27%). This indicates that although the 60-85 µm fraction may always contain a certain amount of wild-type grass pollen, its near-continuous presence in above-average amounts within zone BOGS-4 does indeed reflect the occurrence of indigenous cereal farming in the wider Lake Bogoria region.



385

386 **Fig. 4** Percentage (%) of 60-85 µm Poaceae pollen grains versus the total % abundance of
387 Poaceae pollen, with symbol colors representing the successive pollen zones. Also shown are the
388 linear regression for all pollen zones (black line), and the average values (± SE) of each pollen
389 zone separately (colored crosses).
390

391 4.2 Multivariate analyses of vegetation and fire dynamics

392 *4.2.1 Temporal dynamics in vegetation composition*

393 PCA ordination biplots show the first two dimensions of the stratigraphic distribution of the 30
394 most diagnostic terrestrial pollen taxa in multivariate space (Fig. 5a), and changes in terrestrial
395 vegetation composition through time (Fig. 5b). Together these two dimensions represent almost
396 half (48.14%) of the observed variation in pollen assemblages. Dominant arboreal woodland taxa
397 (*Acacia,* Combretaceae, *Euclea, Euphorbia, Justicia spp.* incl. *J. flava,* cf. *Rhus natalensis,*
398 *Syzygium*), as well as several important herbs (Amaranthaceae, cf. *Corchorus,* cf. *Hypoestes*)
399 show close association with the *Acacia* wooded grassland. However, they are also associated with
400 the cultivated trees *Pinus* and Cupressaceae (partim) and herbs such as Asteraceae, cf. *Ricinus*

401 and *Plantago*, commonly interpreted as "disturbance" indicators (either natural or
402 anthropogenic). The important Afromontane trees *Olea* and *Podocarpus* plot separately. Poaceae,
403 cereals (Poaceae 60-85 μm), Urticaceae/Moraceae and cf. *Calodendrum* are also plotted in a
404 separate group. With Poaceae being the dominant vector along PCA axis 1 (27.6% of the total
405 variation), this first dimension of historical changes in pollen assemblages seems to reflect the
406 gradient between open grassland (negative PCA 1 scores) and the more wooded biomes (positive
407 PCA1 scores). The dominant vectors along PCA axis 2 (20.5% of total variation) are *Acalypha*
408 and *Olea* on the negative side and Cupressaceae along with various "disturbance" indicators on
409 the positive side, reflecting a gradient of increasing alteration of the vegetation. In the samples
410 biplot (Fig. 4b), we note a shift along PCA axis 1 from the dry-phase open grassland vegetation
411 of pollen zones BOGS-1a and BOGS-1b (mostly negative PCA1 scores) to the more wooded
412 wetter-phase vegetation prevalent during BOGS-2a and BOGS-2b (positive PCA1 scores), and
413 back to the dry-phase vegetation of BOGS-3, with all these assemblages having negative to
414 neutral PCA2 scores. These shifts in PCA1 scores are mainly driven by abundance changes in
415 Poaceae and in the savanna woodland taxa *Acacia*, *Justicia* spp., *J. flava*, Combretaceae and
416 Amaranthaceae. Minor shifts along PCA2 mainly reflect variation in percent abundance of the
417 Afromontane tree *Olea*. From BOGS-4 onward we see movement toward the positive side of
418 PCA2, starting with the increase in Poaceae 60-85 μm and declines in *Acalypha* and *Olea* (upper
419 portion of BOGS-4a, and BOGS-4b) and followed by the increase in Cupressaceae and
420 appearance of *Pinus* (BOGS-5 and BOGS-6). Simultaneously, the pollen assemblages also shift
421 again from a dry-phase vegetation type (BOGS-4; negative PCA1 scores) to wetter-phase
422 vegetation types (BOGS-5 and BOGS-6; positive PCA1 scores).

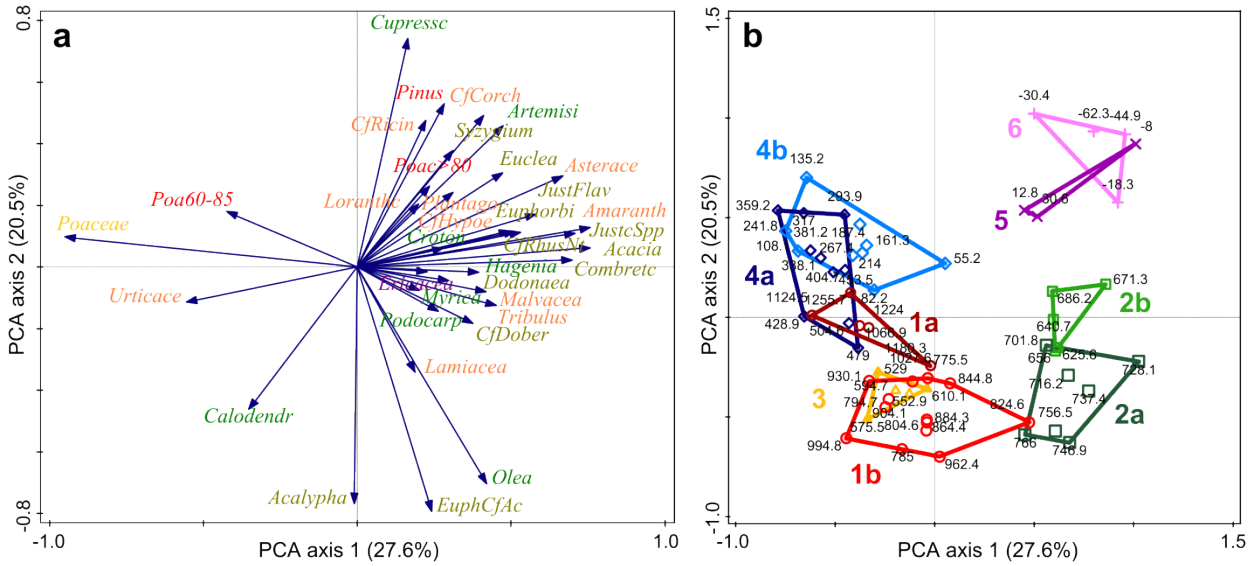


Fig. 5 Principal Component Analysis (PCA) of the temporal distribution of pollen taxa in sediment sequence BOGS14. (a) Species plot with color coding according to vegetation type, as in Fig. 2. (b) Sample plot with samples labelled by age, and grouped using colored polygons to demarcate the pollen zones, as in Fig. 3.

4.2.2 Fire-vegetation interaction

RDA analysis of the pollen-assemblage data with charcoal influx as single explanatory variable indicates that fire (frequency and/or intensity) is responsible for only up to 10.5% of total observed variance in past vegetation composition, which is modest but still significant ($p < 0.01$). The level of variance is in agreement with variance explained by fire elsewhere in Kenya and in other fire-prone ecosystems (Colombaroli et al., 2009, 2018). Charcoal influx, interpreted here as proxy for the magnitude of biomass burning, is positively associated with the percent pollen abundances of the Afromontane forest tree cf. *Calodendrum* ($r^2 = 0.25$, $p < 0.001$) and woodland tree *Acalypha* ($r^2 = 0.25$, $p < 0.001$), and negatively with Cupressaceae ($r^2 = 0.27$, $p < 0.001$) and cf. *Ricinus* ($r^2 = 0.28$, $p < 0.001$). Considering the low explanatory power of charcoal in our analysis these associations may however be fortuitous. Charcoal influx is also positively associated with temporal variation in the percent Poaceae pollen, as could be expected, but this

441 correlation is modest at best ($r^2 = 0.06$, $p = 0.05$). Notably, charcoal influx has no relationship
442 with the fraction of cereal-derived grass-pollen grains ($r^2 = 0.00$, $p = 0.93$).

443 4.3 Landscape history as recorded in the northern basin of Lake Bogoria

444 The pollen record of the northern basin (BOGN14) covers only the last 440 years, but has a
445 higher temporal resolution than BOGS14 because of the higher rate of sediment accumulation,
446 particularly since the mid-20th century (De Cort et al., 2018). CONISS defines four pollen zones
447 (Fig. 6), of which the boundary ages generally correspond well to those of the BOGS14 sequence
448 (Fig. 2). The transition between BOGN-1 and BOGN-2 is placed around 1690 CE, almost coeval
449 with the BOGS-4a/BOGS-4b transition dated to *ca* 1670 CE. The BOGN-2/BOGN-3 transition
450 reflects the start of the savanna woodland expansion around 1850 CE evident at the top of
451 BOGS-4b, shown through increases in *Acacia*, Combretaceae, *Justicia* spp. and Amaranthaceae.
452 There is also a deep split in the CONISS cluster diagram around 1910 CE, i.e. coeval with the
453 BOGS-4/BOGS-5 transition, justifying the division of BOGN-3 in two sub-zones. One of the
454 prominent changes creating this sub-division is the abrupt rise in Cupressaceae, which also
455 display a prominent increase across the BOGS-4/BOGS-5 transition. The most recent significant
456 change in the north-basin pollen assemblage, the BOGN-3/BOGN-4 transition, is placed at *ca*
457 2000 CE, several decades later than the BOGS-5/BOGS-6 transition, which is dated to *ca* 1965
458 CE. Nevertheless, the main temporal trends in the pollen record of Lake Bogoria's northern basin
459 are similar to our findings from the south-basin record 15 km away. Grasses (Poaceae) peak
460 around 1800 CE at both sites, in BOGN14 with values up to 70%. *Sporormiella* displays its first
461 notable increase *ca* 1630 CE (~50 years earlier than in BOGS14), followed by a strong increase
462 ~200 years later from around 1850 CE, similar to BOGS14. Contrasting with BOGS14, also

463 *Sordaria* is recorded almost continuously since its first appearance in the late 17th century CE
464 (Fig. 6).

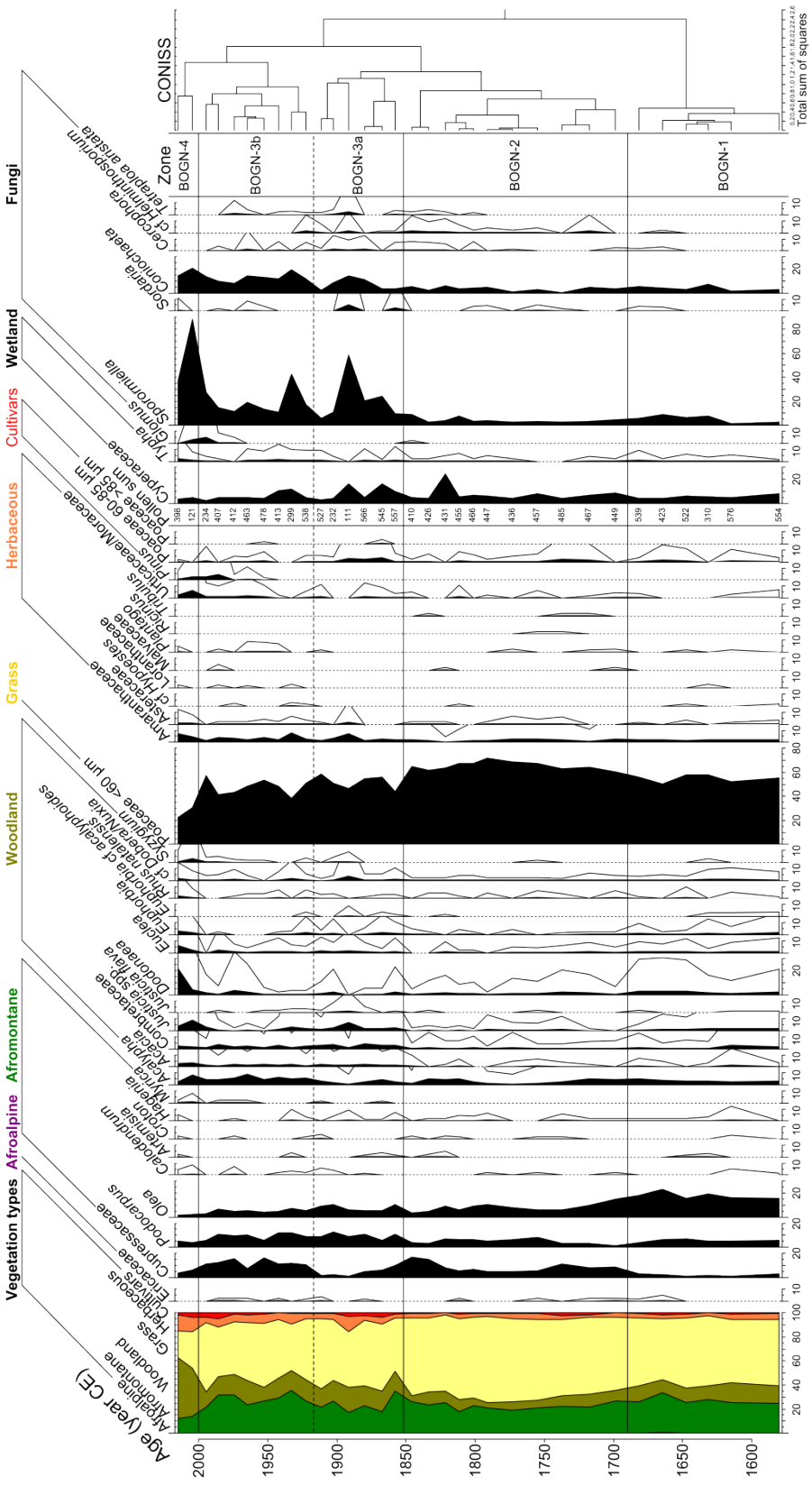

CONISS
Total sum of squares
Zone
BOGN-4
BOGN-3b
BOGN-3a
BOGN-2
BOGN-1
Fungi
Wetland
Cultivars
Herbaceous
Grass
Woodland
Afromontane
Afroalpine
Vegetation types
Age (year CE)
2000
1950
1900
1850
1800
1750
1700
1650
1600

Fig. 6 Stratigraphic distribution of selected pollen taxa (all >1% of the terrestrial pollen sum) in the BOGN14 sediment sequence from the northern basin of Lake Bogoria, in relation to sediment age (De Cort et al., 2018) and pollen-based stratigraphic zonation (CONISS; Grimm, 1987). Taxon abundance is presented as percentage (%) based on the terrestrial pollen sum (black curves; 10x exaggeration in white), with taxa grouped per vegetation type. A summary diagram is shown on the left. Pollen from wetland taxa and fungal spores are expressed as percent of the terrestrial pollen sum but not included in it.

The pronounced maxima in *Sporormiella* and *Sordaria* (and also *Coniochaeta*) dated to *ca* 1900 CE are recorded in a depth interval with low total pollen count (Fig. 6), thus these particular peaks are likely an artifact of poor pollen preservation at that level. Poaceae grains of 60-85 µm are (almost) continuously present throughout the BOGN record (i.e., since at least *ca* 1575 CE), again consistent with BOGS, except that they persist into the 20th-century sediments (BOGN-3b) and become rare only after *ca* 2000 CE (BOGN-4). The cultivated taxa maize (i.e., Poaceae >85 µm) and *Pinus* both appear in this record from around 1950 CE; in the south-basin record *Pinus* appears in the late 1960s, whereas the only identified maize grain is dated to the 1990s. Finally, *Dodonaea* increases sharply in the last two decades (BOGN-4), a pattern highly similar to that in the south-basin record (top of BOGS-6). One notable difference between the recent portions of the two records concerns the Cupressaceae. In the south basin, the sharp and uniquely prominent increase in Cupressaceae from the 1960s onwards helps define the BOGS-5/BOGS-6 transition, whereas in the north basin Cupressaceae never exceed their pre-20th century abundances, and even experience a significant decrease since *ca* 2000 CE. Another notable difference is the presence of spores of the arbuscular mycorrhizal fungus *Glomus* in the north basin, first in a sediment layer deposited around 1850 CE and then more commonly in sediments deposited since the 1970s and until the present (Fig. 6). Living symbiotically in the root systems of terrestrial plants, the fossil spores of *Glomus* are indicative of soil erosion (van Geel et al., 1989). Its

occurrence at the top of the north-basin pollen record (top of BOGN-3b plus BOGN-4) is directly associated with the exponential increase in the rate of sediment accumulation in that basin (De Cort et al., 2018; Fig. 3c), reflecting rapidly accelerating soil erosion in the Sandai-Waseges River drainage since the 1970s. *Glomus* spores are lacking from BOGS14 (Fig. 2), because this plume of excess sediment enters Lake Bogoria from the north (Fig. 1a) and settles mostly within the north basin (Fig. 6). Because the areas drained by the ephemeral streams which enter the south basin are largely situated within the boundaries of Lake Bogoria National Reserve (Fig. 1a) they carry very little eroded soil. Excepting these topical differences, overall the north-basin pollen record of Lake Bogoria is equivalent to the last four centuries of its longer south-basin record, and can be considered to provide a close-up view of the latter.

5. Discussion

5.1 Vegetation response to climate variability

Modern-day potential natural vegetation in the wider Lake Bogoria region (Fig. 1b) consists of a mosaic of grass and shrub savanna, woodland, and open and closed canopy forest (Bontemps et al., 2011), i.e. it covers a wide portion of the East African grassland-to-forest ecotone. Our 1300-year pollen record documents past vegetation dynamics around Lake Bogoria covering the same range of vegetation types. Using percent Poaceae pollen as proxy for the degree of canopy openness in the grass-dominated ecosystems, the values between 40% and 75% found in this record are indicative of vegetation ranging from savanna woodland with relatively closed canopy to open grassland with isolated trees (Vincens et al., 2006; Ssemmanda et al., 2014). Many savanna trees and shrubs are insect-pollinated and therefore underrepresented in pollen records (Hamilton, 1972). However, the regionally important *Acacia*, *Dodonaea* and Combretaceae are

514 all sufficiently well-represented in the Lake Bogoria record to trace changes in their populations
515 through time.

516 Previous reconstructions of past vegetation dynamics in the Lake Bogoria region documented a
517 vegetation structure broadly similar to our findings. The only existing long pollen record from
518 Lake Bogoria (Vincens, 1986) lacks sufficient temporal resolution to trace detailed landscape
519 changes over the last few millennia, but shows comparable regional vegetation dominated by
520 grasses (50-80%) with *Podocarpus, Juniperus* and *Olea* as dominant Afromontane trees; and
521 typical Somalia-Masai savanna vegetation with *Acacia*, *Dodonaea* and a strong presence of
522 *Justicia.* Pollen records from nearby locations such as Loboi Swamp (Ashley et al., 2004; Driese
523 et al., 2004), Lake Baringo (Kiage & Liu, 2009) and Lake Solai (Goman et al., 2017) cover only
524 part of the last millennium and/or suffer from stratigraphic hiatuses. Due to the depositional
525 nature of these sites, the vegetation reconstructions also mainly reflect local to extra-local
526 ecosystem dynamics and do not shed much light on climate-human-landscape interaction in the
527 wider region. A reconstruction of vegetation history on the Laikipia plateau to the east of Lake
528 Bogoria shows that it was covered by *Podocarpus* forest and *Acacia* bushland until about 2000
529 years ago, which was gradually replaced by fire-adapted grassland with *Justicia* so that only
530 fragments of the earlier vegetation remain today (Taylor et al., 2005).

531 Our 1300-year pollen record reveals two major periods of regional forest and woodland
532 expansion, first from *ca* 1100 to 1330 CE and more recently from *ca* 1870 CE until the present.
533 Both periods see net increases of woody taxa within the local *Acacia* wooded grassland and in
534 more distant areas of Afromontane forest. There is also a large concurrent increase in herbaceous
535 taxa, at the expense of Poaceae. The older period comprises three distinct episodes of
536 woodland/forest expansion, one near the top of pollen zone BOGS-1b and two forming the bulk

of BOGS-2. All three episodes, respectively peaking around 1125, 1220 and 1280 CE, correspond with phases of high lake level (De Cort et al., 2018; Fig. 3a), strongly suggesting a primary vegetation response to temporary increase of the region's climatic moisture balance. Notably, the only tree that consistently increases during all three moist-climate episodes is *Acacia*. Otherwise, a different combination of woody taxa respond to increased moisture during each individual episode. During the first, the greatest increases are in *Podocarpus*, Combretaceae and *Dodonaea* followed by *Acalypha*; during the second, increases of *Olea*, *Justicia* and *Dodonaea* are followed by Combretaceae; and during the third, a further rise in *Justicia* is accompanied first by *Euphorbia* and then by *Olea* (Fig. 2). Previously, a brief episode of forest/woodland expansion had also occurred in the late 10th century CE, with increases in *Podocarpus*, *Acalypha* and *Euphorbia* cf. *acalyphoides* (Fig. 2) also at that time coinciding with a (modest) positive lake-level shift (Fig. 3a). The expansions of *Acacia* and *Euphorbia* cf. *acalyphoides* suggest a thickening of woody vegetation in savanna proper, whereas those of *Acalypha* and *Podocarpus* may reflect a temporary shift in the forest/woodland ecotone. A positive response of herbaceous taxa to moister climatic conditions seems to have occurred only during the two lake high-stands between *ca* 1175 and 1330 CE, and involved the Amaranthaceae as well as Asteraceae and Lamiaceae, many of which constitute savanna woodland understory (Vincens et al., 2006); this strong display of herbaceous taxa helps delineate pollen zone BOGS-2. The notably modest responsiveness of *Podocarpus* to both climatic (and anthropogenic) pressures over the 1300-year record (mean abundance 11 ± 2% throughout BOGS14) may indicate that its pollen has always predominantly been delivered to Lake Bogoria by long-distance transport, from areas of adjacent highlands (perhaps as far as the Aberdare Range, 80-100 km to the southeast) that are topographically sufficiently diverse to generate compensating positive and negative responses of the dry-forest biome to regional moisture-balance changes.

561 The younger period of forest/woodland expansion (*ca* 1870 until today), represented by the top of
562 pollen zone BOGS-4b plus BOGS-5 and BOGS-6 (Fig. 2), similarly correlates with generally
563 high lake levels of Lake Bogoria since the start of the 19th century (De Cort et al., 2018; Fig. 3a).
564 Among forest trees, the responses of *Podocarpus* and *Olea* are relatively weak; instead the
565 strongest increases from early in this period are in Cupressaceae (still on account of native
566 *Juniperus procera*) and the relatively uncommon *Artemisia* and *Hagenia* (Fig. 2). Otherwise the
567 initial vegetation changes follow the same general pattern as in the previous wet period, with
568 strongest increases in taxa associated with *Acacia* wooded grassland: *Acacia* itself, *Justicia* spp.
569 and Amaranthaceae. Toward the top of BOGS-5 the pollen record seems to reveal a temporary
570 decline in forest and woodland components dating to the early 20th century. Coeval with a
571 prolonged regression of Lake Bogoria (Fig. 3a) and other lake-level declines throughout Kenya
572 (Verschuren, 2004), this episode of climatic drying coincided with a period of colonial land
573 expropriation in the former 'White Highlands' of central Kenya (Verschuren et al., 1999).
574 However, apparent reduction in the forest/woodland component at that time may also, at least in
575 part, be a statistical effect resulting from strong increases in the disturbance indicators
576 Amaranthaceae and Asteraceae (Fig. 2). In any event, starting *ca* 1965 CE (pollen zone BOGS-6)
577 a last forest/woodland expansion is recorded, this one almost entirely due to increases in
578 Cupressaceae (most certainly the introduced timber cypress) and the encroaching native shrub
579 *Dodonaea*. With planted *Pinus* also appearing in the record, Poaceae are reduced to all-time low
580 values of respectively 20% and 23% in the modern-day pollen assemblages of Lake Bogoria's
581 southern and northern basins.

582 Corroborating the above interpretation of vegetation history, the results of PCA analysis show
583 that the greatest portion of explained variation in pollen-assemblage composition over the past

584 1300 years (PCA1 = 27.6%) is related to shifts between open grassland and more closed-canopy
585 dry vegetation, driven mainly by abundance changes in Poaceae and the savanna woodland taxa
586 *Acacia*, *Justicia*, Combretaceae and Amaranthaceae in response to climate-driven changes in
587 available moisture (Fig. 3a). Importantly, the PCA results show that after the first documented
588 period of forest/woodland expansion between *ca* 1100 and 1330 CE, regional vegetation returned
589 to its pre-existing composition associated with somewhat drier climate conditions.

590 Closed-canopy dry Afromontane forest can be found today on the Laikipia Plateau (Taylor et al.,
591 2005), in Lembus Forest on the western escarpment, and in small patches within the Bogoria
592 catchment (Vincens et al., 1986; Fig. 1c). Excluding Cupressaceae, the Afromontane component
593 represents 9% and 12%, respectively, of the modern-day pollen assemblage in the northern and
594 southern basins, and in the latter it has varied between 14% and 54% during the past 1300 years
595 of recorded history. This is because its prominent tree taxa *Podocarpus* and *Olea* tend to be over-
596 represented in pollen assemblages, as their pollen is delivered to lakes and swamps by long-
597 distance aerial transport (Taylor et al., 1999). Thus, the percent abundance of the Afromontane
598 component should not be taken to reflect the percent areal cover of closed-canopy forest on the
599 regional landscape (Prentice & Webb, 1986; Ssemmanda et al., 2014). Nevertheless, as long as
600 the magnitude of this over-representation can be considered constant through time, temporal
601 changes in percent abundance of the Afromontane component can be considered to reflect true
602 shifts of the forest-woodland ecotone across the regional landscape. One important caveat is that
603 pollen can also be transported over large distances by rivers, so that temporal changes in the
604 hydrography of lake catchments can create signatures of apparent vegetation change without any
605 real change in areal coverage (Prentice, 1985). Specifically, in our record the correlation between
606 forest/woodland expansion and high lake-level stands might be due partly to enhanced influx of

607 forest and woodland pollen from highland areas within the Lake Bogoria catchment during
608 episodes of greater streamflow. We consider the impact of this long-distance transport as
609 relatively minor, for three reasons. First, past vegetation changes reconstructed from BOGN14
610 for the most part echo the results from BOGS14, highlighting the robustness of common
611 temporal trends in the region's vegetation revealed by both records, notwithstanding the distance
612 of 15 km between these sites. Second, since inflow via the Sandai-Waseges River enters Lake
613 Bogoria from the north (Fig. 1a) and reaches the southern basin only during high-stands (De Cort
614 et al., 2018), the ratio between forest/woodland and Poaceae pollen, if it has a strong riverine-
615 influx signature, should on average be higher in BOGN14 than in BOGS14, which is not the case
616 (80% versus 100% ($p = 0.4$) over the past 440 years). Finally, vegetation response to the inferred
617 shift toward a wetter climate between *ca* 1100 and 1330 CE displays distinct differences during
618 each separate episode of forest/woodland expansion, with different forest and woodland taxa
619 enjoying the most prominent increases. Had the increases in forest/woodland been due mostly to
620 higher influx rather than vegetation change, we would expect the patterns to be more similar to
621 each other. Thus, the combined evidence suggests that although the influence of changing river
622 influx cannot be dismissed, the largest portion of documented increases in woodland and forest
623 pollen reflects shifts in vegetation ecotones both within and beyond the Lake Bogoria catchment.

624 5.2 History of human influence on Kenya Rift Valley ecosystems

625 The history and archaeology of human occupation in central Kenya has been studied in some
626 detail. Pastoralist communities are thought to have been present in East Africa from *ca* 4800 BP,
627 extending from Lake Turkana into the Rift Valley (Hildebrand et al., 2018), but the
628 archaeological record of this southward expansion remains scarce until *ca* 3000 years ago (Lane,
629 2013; Petek, 2018). Agriculture is thought to have spread from the Lake Victoria region into the

central Rift Valley by the mid-first millennium CE, first evidenced by botanical remains found *ca* 30 km west of Lake Nakuru (Ambrose et al., 1984). The area around Lake Baringo, probably including Lake Bogoria, was at that time occupied by producers of Turkwel ceramics, who were principally herders who also hunted and fished. From around the time that human influence can first be discerned in the Bogoria pollen record (cf. below), archaeological sites south of Lake Baringo indicate that well-watered locations surrounding lakes Baringo and Bogoria were most likely inhabited by farming and/or hunting-gathering groups. Pastoral communities mostly occupied drier Rift Valley areas to the south and west, utilizing pasture and swamps near the lakes only seasonally (Petek, 2018). Pastoralism was also well established eastward of the lakes, on the Laikipia Plateau (Lane, 2013). As indicated by our 1300-year paleo-environmental reconstruction, the magnitude and diversity of influences on the region's natural resources exerted by the various people inhabiting the Bogoria drainage basin has steadily increased through time, in six more or less distinct phases.

5.2.1 First phase: limited human influence pre-1430 CE

In the PCA biplot showing the compound trends in pollen-assemblage composition through time (Fig. 3b), shifts along PCA axis 1 reflects vegetation response to changes in climatic moisture balance while shifts along PCA axis 2 reflects the relative intensity of human influence. In the first *ca* 700 years of the Lake Bogoria record, vegetation changes from a dry-phase open grassland (zone BOGS-1) to more wooded wet-phase vegetation (BOGS-2) and back to dry-phase open grassland (BOGS-3), with all these pollen assemblages having negative to neutral PCA2 scores, and thus little evidence of anthropogenic disturbance. Also in the other proxies, the pre-1430 CE portion of the record shows little evidence of human landscape modification. Charcoal influx has a mostly inverse relationship with hydroclimatic variation in zones BOGS-1

through BOGS-3 (Figs. 3d and 3a), indicating that savanna fires were predominantly under climatic control; and that biomass burning was promoted by relative drought, as is expected to occur in areas near the forest/grassland boundary (Colombaroli et al., 2014). The first modest presence of *Sporormiella* between *ca* 1175 and 1330 CE postdates archaeological sites associated with Turkwel herders (*ca* 200-1100 CE; Petek, 2018), while no recorded sites date specifically to the period 1175-1330 CE. In the absence of other proxy indicators of human activity in this part of the record, the most conservative explanation for the early appearance of *Sporormiella* is a greater proliferation of fungi on wildlife rather than domesticated herbivore dung during the relatively moist climate conditions which then prevailed (Fig. 3a).

5.2.2 Second phase: expanding agricultural activity and landscape clearing

The first suspected ecological indication of humans being present in the landscape surrounding Lake Bogoria is the general shift in pollen-assemblage composition along PCA axis 2 (Fig. 5b), starting modestly in zone BOGS-4 (of which the base is dated to *ca* 1430 CE) and becoming stronger in BOGS-5 (from *ca* 1910 CE) and BOGS-6 (from *ca* 1965 CE). The first unambiguous proxy evidence of agricultural activity is the continuous presence, from *ca* 1500 CE, of Poaceae pollen in the size range 60-85 μm, which we argue is disproportionally derived from indigenous cereals such as finger millet and sorghum and therefore indicative of farming being practiced in the Lake Bogoria region (cf. Results, section 4.1.4). Note that because of the positive correlation between the fraction of 60-85 μm Poaceae grains and total Poaceae pollen (Fig. 4), elevated amounts of 60-85 μm grass pollen are not *by themselves* an unambiguous indicator for cereal farming. Conversely, we cannot claim that the 60-85 μm 'cereal-type' grains occurring earlier in the record, specifically during the relatively dry climatic periods represented by zones BOGS-1b and BOGS-3 (Figs. 2 and 4), are anything other than very large wild-type grass pollen.

676 Strikingly, between *ca* 1500 and 1870 CE, broadly the period when 60-85 μm Poaceae pollen is
677 more abundant than expected from wild-type distribution, the combined fraction of arboreal
678 woodland pollen is only 4-8% (mean value 5%) whereas it is mostly >15% (7-25%) in the rest of
679 the record, during both wet and dry climate phases (Fig. 2). This pattern is mostly due to a near-
680 total loss of *Acalypha* after 1430 CE. Also during this same period the forest tree *Olea* is reduced
681 to <10%, while it exceeds 15% in much of the rest of the record, again during both wet and dry
682 climate phases. These patterns suggest that indigenous land-use practices in the Lake Bogoria
683 region between the 15th and 19th centuries CE led to a general reduction of land covered by
684 grassland-to-forest ecotonal vegetation – where *Acalypha fruticosa* can be found – due to
685 clearance of mid-elevation areas with fairly densely wooded savanna and the fringe of closed-
686 canopy dry forest. *A. fruticosa* having many useful applications, it may have been removed
687 selectively. Considering the responsiveness of *Olea* to climate-driven moisture-balance changes
688 in the early part of the record, this tree may have been particularly common in the patches of
689 forest within the Bogoria catchment that were cleared for farming or wood collection.

690 *5.2.3 Third phase: increased animal husbandry, and modification of the fire regime*

691 Our dung-fungus evidence indicates that animal husbandry, as a livelihood strategy with
692 significant ecological impact in the Lake Bogoria region, is attested from the mid-17th century
693 onwards. In temporally dynamic ecosystems, such as our semi-arid tropical study area, natural
694 processes can exert substantial control on dung-fungus growth and distribution (Gelorini et al.,
695 2012; Baker et al., 2013). Specifically, past episodes of wetter/drier climate likely
696 increased/decreased the prevalence of damp micro-habitat conditions which tend to
697 promote/restrict the growth of fungi. Consequently we surmise that the contrast between
698 moderately high abundances of obligate coprophilous fungi in pollen zone BOGS-2, versus very

low abundances in pollen zones BOGS-1, BOGS-3 and the base of BOGS-4, is within the expected variability resulting from entirely natural variation in local habitat suitability for the fungi themselves, rather than from changes in herbivore populations. Only spore abundances clearly exceeding this natural variability can be considered as created by livestock present along the shores of Lake Bogoria. From *ca* 1630-1670 CE onwards, the abundances of *Sporormiella* (and of *Sordaria*, in the north basin) increase above their previous mean dry-phase abundance (cf. pollen zone BOGS-2; Fig. 2), and are therefore interpreted as being linked to domestic cattle. Further, as this mid-17th century *Sporormiella* rise coincides with the certified presence of cereal grains, it most likely reflects mixed farming and animal husbandry, the latter partly by pastoralists utilizing the lake area on a seasonal basis (Lane, 2013; Petek, 2018).

The broadly inverse relationship between charcoal and moisture balance culminates in a broad charcoal maximum dated to *ca* 1550-1600 CE (Fig. 3d). This is consistent with the prevailing dry climate conditions (Fig. 3a) but may also be attributed to, or enhanced by, the clearance of natural vegetation due to the then expanding farming practices. Notably, the inverse correlation between fire and moisture balance continues for another ~200 years until *ca* 1800 CE, but with overall lower amounts of biomass burning both during wetter and drier climatic episodes (Fig. 3d). Coeval with the now firm proxy evidence for farming activity, we surmise that this reduction in overall biomass burning reflects the suppression of fire which occurs when land conversion for agriculture becomes significant at the landscape scale (Colombaroli et al., 2014). Any human-assisted burning that did occur was most likely associated with additional plot clearance for farming, not burning by pastoralists to improve fodder (e.g., Bird & Cali, 1998). In fact, the contemporaneous groups of specialized pastoralists probably dwelled mostly in Rift Valley areas too dry to make deliberate burning useful.

722 *5.2.4 Fourth phase: establishment of irrigation agriculture*

723 Historical information and archaeological evidence indicate that from the 1830s CE onwards,
724 Ilchamus groups occupying the land between lakes Baringo and Bogoria established a large-scale
725 irrigation agriculture system with the intention of surplus food production, while more traditional
726 rain-fed agriculture was restricted to wetter zones on the Rift Valley flanks (Anderson, 2016;
727 Petek & Lane, 2017; Petek, 2018). In the Lake Bogoria record, this development appears to be
728 reflected in the much greater abundance of cereal pollen being recovered from north-basin
729 sediments dated to the second half of the 19th century, compared to south-basin sediments (Fig.
730 3); and the first appearance of certified maize pollen *ca* 1880 CE. The charcoal record is also
731 broadly consistent with increased agricultural activity. The prominent but short-lived charcoal
732 peak dated to *ca* 1820 CE coincides, within dating precision, to the end of a severe early 19th
733 century drought that affected much of East Africa (Verschuren et al., 2000; Bessems et al., 2008;
734 Nash et al., 2016). Attracting Maa and Kalenjin pastoralists to the area immediately north of Lake
735 Bogoria, the resulting increase in demographic pressure caused social upheaval and
736 reconfiguration (Anderson, 2016). We therefore surmise that the 1820 CE charcoal peak is most
737 likely anthropogenic, and reflects land clearance by Il Chamus farmers in low-lying valley areas
738 for the purpose of irrigation agriculture (Anderson & Bollig, 2016). The characteristic pattern of
739 an initial peak of biomass burning followed by strong reduction of fire has also been commonly
740 reported from episodes of vegetation clearance in extra-tropical regions, at local (e.g., Bradshaw
741 & Lindblath, 2005; Colombaroli et al., 2013) to near-global scales (Marlon et al., 2008). This
742 particular charcoal peak is accompanied by a prominent shift to more fine-grained clastic
743 sedimentation, the first indication of soil loss in clay-rich areas of the Sandai River catchment
744 (De Cort et al., 2018; Fig. 3b). In the north basin this shift is abrupt, as expected given its direct

hydrographic connection with the source area of this clay. In the south basin the shift starts around 1820 CE but ramps up gradually to peak around 1900 CE (Fig. 6), likely because the lake level was initially too low for effective inter-basin redistribution of suspended clays. Importantly, excluding this brief peak around 1820 CE, 19th-century biomass burning never reached the levels commonly attained during the earlier part of the Bogoria record.

Not only crop agriculture but also animal husbandry expanded through much of the 19th century CE. The prominent rise in *Sporormiella* from *ca* 1850-1870 CE onwards, to abundances well above their previous mean wet-phase abundance (Fig. 6), is consistent with historical evidence for strong expansion of cattle pastoralism between the 1830s and 1870s (Anderson & Bollig, 2016). However, at least in its initial phase the dung-fungus rise may have been produced partly by wild herbivores, since large herds of buffalo, wildebeest and other large ungulates are historically well attested for the late 19th century while the cattle population tended to fluctuate due to diseases such as rinderpest (Little, 1996). This period was also marred by inter-community conflict; in particular the Loikop wars between different Maasai sections competing for the best grazing land (Anderson, 2016).

5.2.5 Fifth phase: return of wetter climate and reduction of crop agriculture

With the return of wetter climate conditions in the mid-19th century, there was renewed expansion of forest/woodland ecotone vegetation, signifying an overall reduction of crop agriculture on the Rift Valley flanks (i.e., higher-elevation portions of the Bogoria catchment). *Acalypha*, which had become scarce coincident with the appearance of cereal pollen four centuries before, failed to recover (Fig. 2). However, this was compensated by notable increases in Combretaceae, *Justicia* spp. and cf. *Dobera/Nuxia* from the mid-19th century onwards (Fig. 2).

As regards the former two taxa, the resulting higher percent abundances are largely sustained until the present (top of BOGS-4, plus BOGS-5 and BOGS-6), notwithstanding the three- to fourfold expansion of Cupressaceae (cypress plantations) and invasive *Dodonaea* in recent decades (Fig. 2). Complete lack of 60-85 µm Poaceae grains from *ca* 1910 CE onward in the south-basin record probably also reflects this reduction farming compared with earlier times, except that also the amount of total Poaceae pollen counted in this section of the sequence is too low to state this with certainty. In notable contrast, 60-85 µm grass pollen is persistently present throughout 19th and 20th century sediments deposited in the north basin (Figs. 3 and 6), testifying to a general shift of cereal farming to the irrigated cropland in low-lying portions of the Bogoria catchment. By the start of British colonial rule around the turn of the 20th century, cattle pastoralism had become the dominant production system in the wider Baringo-Bogoria region, including areas to the south of Lake Bogoria (around Lake Solai; Fig. 1a) occupied in the 1910s and 1920s by specialized pastoralists migrating from the Tugen Hills area west of Lake Baringo (Little, 1992; Anderson, 2002; Petek, 2018),

5.2.6 Sixth phase: intensive land use leading to widespread soil erosion

Following over half a century of rapid growth in cattle herding (i.e. the period of persistently high *Sporormiella* abundances in zone BOGS-5; Figs. 2 and 3), livestock numbers eventually exceeded the carrying capacity of the land, resulting in widespread vegetation degradation (Johansson & Svensson, 2002). Most pertinently, since the 1950s open grassland in the Baringo rangelands was increasingly replaced by *Acacia* bushland, exacerbated by a burning prohibition (Vehrs, 2016; Vehrs & Heller, 2017). This expansion of *Acacia* bushland is likely responsible for the strong reduction in Poaceae pollen and rises in *Acacia*, *Justicia flava* and Asteraceae from the 1930s onwards (Fig. 2). Moreover, apparent reduction of the latter three taxa in the pollen

assemblages after *ca* 1965 CE may well be an artefact of the strong expansions of exotic *Pinus* and Cupressaceae, and of native disturbance taxa such as *Plantago*, *Ricinus* and *Dodonaea* (Fig. 2). In recent decades many low-lying areas around Lake Baringo and Loboi Swamp (immediately to the north of Lake Bogoria; Fig. 1b) have also suffered from encroachment by the exotic shrub *Prosopis juliflora* (mesquite; Mwangi & Swallow, 2008), an insect-pollinated plant related to *Acacia* but largely invisible in the pollen record.

Bond & Midgley (2000) implicated the anthropogenic rise in atmospheric CO_2 since the early 19th century CE, and accelerating since the 1950s, in the historical trend toward greater tree cover observed in many tropical savannas. This trend specifically applies to mesic wooded savannas of the forest/grassland ecotone where fire is drought-controlled (Bond & Midgley, 2012), as is the case in our study area (sections 4.1.2 and 5.2.1). The question then arises whether rising CO_2 may have contributed to the historical expansion of tree cover across the Rift-Valley landscape as inferred from our Bogoria record. Combretaceae, *Justicia* spp. and cf. *Dobera/Nuxia* expanded from the mid-19th century onwards, followed by *Acacia* bushland from the mid-20th century. However, given the magnitude of alternative ecological drivers, i.e. an improving moisture balance from the 1830s onwards and 20th-century rangeland degradation due to overgrazing, we refrain from attributing any recorded changes in pollen-assemblage composition uniquely to the rise in atmospheric CO_2.

Scarcity of open grassland prompted the region's pastoralists to switch from cattle to browsers such as goats and camels (Vehrs, 2016). Browsing by goats, in particular, further increased the pressure on this fragile valley-floor landscape by over-eating the vegetation and trampling its root systems. The logical consequence, then, was severe soil erosion and gully formation throughout the riparian lands surrounding Lake Baringo, including the lower Sandai River drainage towards

Lake Bogoria (Johansson & Svensson, 2002). Meanwhile in higher-elevation portions of the Sandai-Waseges drainage, where mixed subsistence farmers used to concentrate, rapid demographic growth and increased development of timber plantations reduced the acreage available for individual small-holdings (Anderson, 2002), so that land use intensified, few plots lay fallow at any one time, and also those soils became increasingly destabilized. Sedimentological analyses by De Cort et al. (2018) suggest that soil erosion in the upper Bogoria catchment, entirely outside Lake Bogoria National Reserve, is the principal cause for the order-of-magnitude increase in terrestrial sediment supply to Lake Bogoria since the 1970s (Fig. 3c). Soil eroded from such agricultural land is likely to contain elevated concentrations of coprophilous fungal spores derived from locally applied domestic herbivore dung. We surmise that the most recent peak in *Sporormiella* spores recorded in Lake Bogoria's north basin (but not south basin; Fig. 3c) may reflect this process rather than changes in large herbivore density nearby the lake, which grew slowly or stagnated at that time (Little, 1992; Anderson, 2002). This inference is supported by the coincidence of this *Sporormiella* peak with maximum abundance of *Glomus* spores, a root symbiont indicative of soil erosion (van Geel et al., 1989).

Considering the evident causal relationship between accelerated sedimentation in the north basin and land-use intensification over the past *ca* 50 years, it is tempting to link the elevated rate of sedimentation which occurred between *ca* 1600 and 1800 CE (Fig. 3c) with the multi-proxy evidence for indigenous farming during this period (Fig. 3d-f). However, as the texture of sediments deposited at the offshore core site remains unchanged throughout this period (Fig. 3b), we interpret these data as reflecting the focusing and re-deposition of sub-lacustrine mud during the contemporaneous low-stand episode (Fig. 3a; Verschuren, 1999). This low-stand impacted water depth (and hence sedimentation dynamics) in the north basin more strongly than in the

836 south basin because of its shallower lake bottom, while also restricting any new sediment load
837 from the Sandai-Waseges entirely to the north basin (De Cort et al., 2018).

838 **6. Conclusion**

839 The regionally unique situation of depositional continuity, undisturbed accumulation and well-
840 constrained chronology of the Lake Bogoria sediment record (De Cort et al., 2018) has permitted
841 a detailed reconstruction of the history of human influences on the landscape of Kenya's central
842 Rift Valley against the backdrop of natural, climate-driven ecosystem dynamics over the past
843 1300 years. Our multi-proxy reconstruction reveals a succession of five phases of distinct human
844 activity since *ca* 1430 CE, following a period of (at least) *ca* 700 years when the region's
845 landscape consisted of a savanna-forest ecotone responding primarily to climate-driven shifts in
846 moisture balance. The first unambiguous ecological signature of human activity occurs long after
847 human presence is first attested archaeologically; and landscape evolution during the last six
848 centuries reflected the continually shifting interplay between human activity, climate, and locally
849 available land and water resources. Our results show that ecological impacts by indigenous
850 human activity in this tropical African landscape became significant already *ca* 500 years before
851 the start of the colonial period; however in contrast to many Mediterranean, temperate and boreal
852 ecosystems (Lewis & Maslin, 2015), they supplanted natural processes as the dominant driver of
853 vegetation dynamics only in the course of the 20th century, through the introduction of exotic
854 trees and crops, fire suppression, scrub encroachment, and eventually widespread soil erosion
855 since the 1960s resulting from intensified agriculture and overgrazing.

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Distinct phases of natural landscape dynamics and intensifying human activity in the central Kenya Rift Valley during the past 1300 years

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SUPPLEMENTARY INFORMATION

1. Sediment sampling and chronology (supplement to section 3.1)

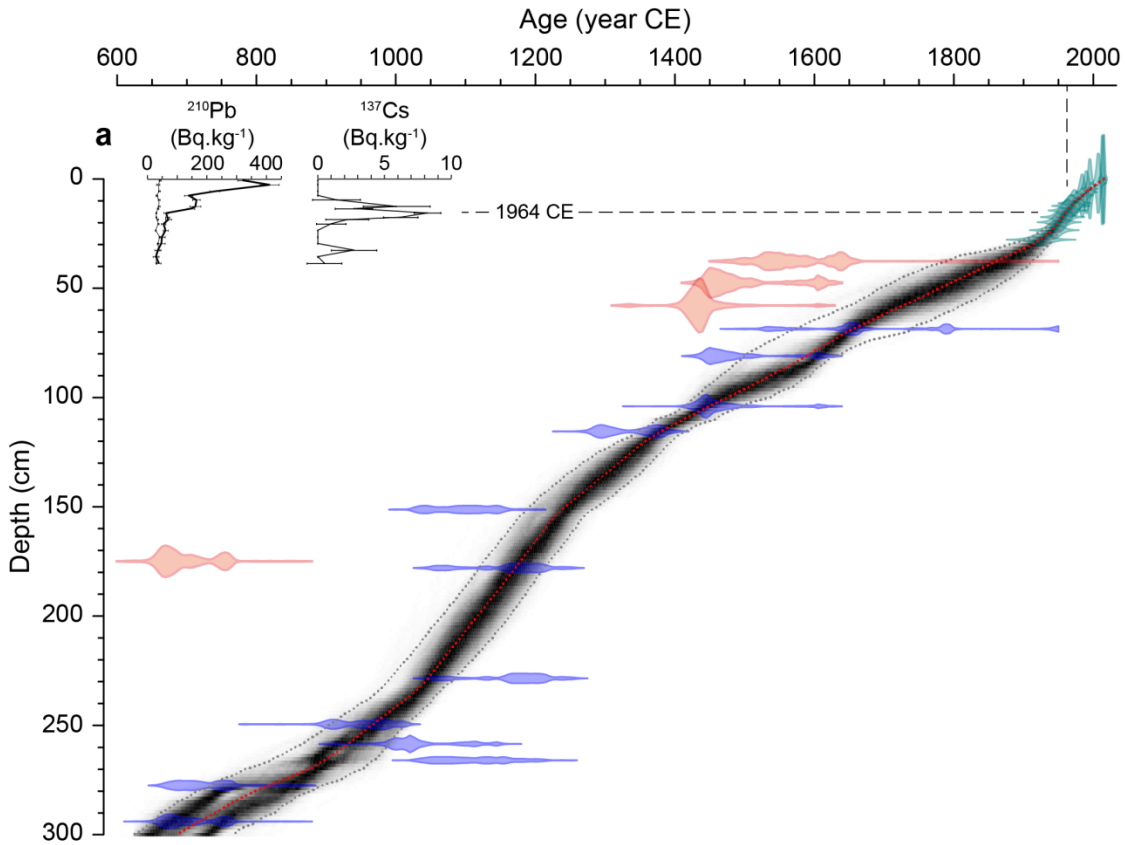

Fig. S1 Age–depth model for composite core BOGS14 from the southern basin of Lake Bogoria, generated with the Bacon software package for R (Blaauw & Christen, 2011). 'Mirrored' calendar-age distributions, with height proportional to probability, are shown for both ^{210}Pb-derived ages (green) and ^{14}C-dated intervals (blue if incorporated in the age model; pink if not retained). The 12 incorporated ^{14}C dates infer realistic changes in age with depth, even in core sections with syn-sedimentary growth of large nahcolite crystals (255-210 cm depth) or high rates of clastic sediment input. The red dotted line depicts the modelled age–depth relationship (weighted mean of model iterations), with grey dotted lines indicating the upper and lower boundaries of the 95% confidence interval. Insert plots show the depth profile of total (thick line) and supported (thin line) ^{210}Pb activity in the uppermost sediments, as well as ^{137}Cs activity which displays a peak at AD 1964. Modified from De Cort et al., (2018).

2. Pollen and fungal-spore analysis (supplement to section 3. 2)

Raw sediment was treated with hydrochloric acid, warm 10% potassium hydroxide, 96% acetic acid, and an acetolysis mixture of 1:9 sulphuric acid and acetic anhydride boiled to 100 °C. Heavy liquid separation using sodium polytungstate with a specific gravity of 2.0 was used to separate the pollen from mineral components. For pollen identification, we referred to photographs of voucher specimens in standard atlases (Bonnefille & Riollet, 1980; Schüler & Hemp, 2016); our nomenclature follows the African Pollen Database (Vincens et al., 2007). Slides from BOGS14 were most often counted completely. After reaching the desired pollen sum in BOGN14 slides, the remainder of the slides was scanned for rare plant taxa to confirm their presence or absence in that particular time window. Pollen preservation was generally good to excellent, with the exception of a short section of BOGN14 covering four sampling intervals (125.5-126.5, 128-129, 131-132, 137.5-138.5 cm composite depth), where sample processing proved problematic and the resulting pollen count was atypically low (with a minimum of only 111 grains at 131-132 cm depth). Because of these difficulties, fungal-spore counts in these intervals required correction through additional pollen analysis. This correction was not possible for fungal spore taxa with only sporadic appearances, and hence these rare taxa were omitted from the BOGN14 diagram (Fig. 6).

Besides being more or less continuously present in Lake Bogoria sediments dated to the last *ca* 70 years, a few *Pinus*-type pollen grains were also recovered from isolated core intervals dated to *ca* 1800 CE in BOGS14, and *ca* 1850 CE in BOGN14. Although pine trees have been planted in South Africa since the early 18th century (Burgess & Wingfield, 2001), there is no record of pine being present in East Africa before the early 20th century. Considering the methods of core collection and processing (De Cort et al., 2018) and the permanently anoxic bottom environment of Lake Bogoria (translated in the sediments being finely laminated), we can exclude the possibility of cross-level contamination or post-depositional movement of pollen grains through the sequence. We therefore treated these old *Pinus*-type grains as aberrant *Podocarpus* pollen, and excluded them from all analyses.

3. Landscape history as recorded in the southern basin of Lake Bogoria (suppl. to section 4. 1)

Zone BOGS-1 (ca 700 – 1175 CE). The grass pollen fraction is relatively high (Fig. 2), fluctuating around 50% with two pronounced but short-lived dips around 960 CE (38%) and 1130 CE (31%). The Afromontane forest component is substantial (26-39%, mean 30%) and dominated by *Podocarpus*, *Olea* and Cupressaceae (at that time, *Juniperus procera*). The decrease in Cupressaceae and increase in *Olea* around 900 CE drives the division of this zone in sub-zones BOGS-1a and BOGS-1b. The smaller woodland fraction (9-25%, mean 16%) is relatively stable through time and consists primarily of *Acalypha* with smaller contributions from Combretaceae, *Dodonaea*, *Euphorbia* (mostly *E.* cf. *acalyphoides*) and *Acacia*. Also the herbaceous component is relatively modest (3-9%, mean 6%). On the whole the pollen

assemblage indicates that much of the catchment was covered by relatively open grassland-woodland ecotonal vegetation, with stands of closed-canopy forest relatively nearby.

Zone BOGS-2 (ca 1175 – 1330 CE). Grass pollen (22-40%) decreases to levels well below those in BOGS-1 during two multi-decadal episodes centered around 1220 CE (22%) and 1280 CE (30%). The compensation by other elements of the vegetation, however, differs between the two episodes, resulting in a division into sub-zones BOGS-2a (1175 – 1250 CE) and BOGS-2b (1250 – 1330 CE). BOGS-2a is characterized by an increase of the forest component (36-54%, mean 38%) carried in large part by *Olea* (up to 39%). In BOGS-2b there are major increases in *Justicia* spp., *Acacia*, Asteraceae and Amaranthaceae, which are all trees and herbs associated with *Acacia* wooded grassland (Vincens et al., 2006). However, one characteristic woodland shrub with generally reduced prominence throughout BOGS-2, compared to BOGS-1, is *Acalypha*. Overall the woodland fraction varies between 14-22% (mean 17%) in BOGS-2a and 10-26% (mean 15%) in BOGS-2b. The forest component in BOGS-2b ranges between 22 and 40% (mean 29%), i.e. similar to the situation in BOGS-1.

Zone BOGS-3 (ca 1330 – 1430 CE). Grass pollen percentages increase again, reaching 46-53% within this zone. The taxa associated with *Acacia*-wooded grassland decrease again, but this is largely compensated by re-expansion of *Acalypha*. The total woodland (10-18%, mean 13%) and forest (27-31%, mean 28%) fractions remained mostly constant relative to BOGS-2b, and in the latter *Olea* and *Podocarpus* remain prominent at mean values of 20% and 12%.

Zone BOGS-4 (ca 1430 – 1910 CE). This pollen zone encompasses a *ca* 500-year period of Rift Valley history, ending in the early 20th century. Grasses are abundant throughout most of this period, with percentages mostly exceeding 60% and reaching peak values of 75-76% around 1710 CE and 1840 CE. After this most recent peak, Poaceae decrease again to *ca* 50% at the top of this zone. In the forest component, *Olea* can maintain its 20% level only until *ca* 1500 CE, after which it decreases mostly to the benefit of Cupressaceae. From *ca* 1500 CE, Poaceae grains in the size range 60–85 μm start appearing more or less continuously and in significant numbers, although they were occasionally present already in BOGS-1 and BOGS-3 (but not in BOGS-2). Also cf. *Ricinus* (castor oil plant), previously showing only erratic occurrences, makes more regular appearances from *ca* 1600 AD onwards although it remains rare (Fig. 2). Although this 500-year period is delineated as a single zone by CONISS, by no means vegetation composition in the southern Bogoria catchment (and beyond) remained stable throughout. Marked percent-abundance shifts are more or less concentrated around 1670 CE, resulting in a division between sub-zones BOGS-4a and BOGS-4b at that level. In the forest, cf. *Calodendrum* and *Hagenia* decreased to the benefit of *Artemisia*; in the woodland, *Dodonaea* decreased to the benefit of *Justicia* and *Euphorbia*. Other woodland trees such as *Acacia* and Combretaceae maintain relatively stable populations throughout BOGS-4. Overall, however, the total woodland component was strongly reduced, with a mean low value of 6% between *ca* 1480 and 1870 CE (Fig. 2). Meanwhile *Podocarpus* mostly maintains stable values of *ca* 15%, falling to values consistently <10% only between *ca* 1700 and 1780 CE. Coincidence with low *Olea* abundance

around the start of this period reduces the total Afromontane forest component to less than 20% around 1700 CE, its lowest level of the entire record.

Zone BOGS-5 (ca 1910 – 1965 CE). During this period, which broadly encompasses the period of European colonial rule, Poaceae pollen decreased further to reach a low value of *ca* 30% around 1960 CE. The wooded savanna arboreal taxa *Acacia*, Combretaceae, *Justicia* spp., cf. *Dobera/Nuxia* and *Euclea* all increase, realizing a recovery of the woodland component to 8-17% (in the case of *Euclea*, expansion had already started in the upper part of BOGS-4). This woodland recovery is also reflected in marked increases of herbaceous taxa belonging to the Amaranthaceae and Asteraceae. Other herbaceous taxa that increase are cf. *Ricinus* and *Tribulus*, and diverse rare taxa such as cf. *Corchorus*, cf. *Hypoestes*, unidentified Loranthaceae and Malvaceae. The Afromontane forest component expands (to a peak value of 40%) only temporarily in the lower part of this zone, representing the early 20th century. Notably, whereas the previous episode of forest expansion (in BOGS-2) was mostly on account of *Olea*, Afromontane taxa that increase now are the Cupressaceae, *Artemisia*, *Croton*, *Hagenia* and *Myrica*. No Poaceae grains >60 μm (either 60–85 μm or >85 μm) were recovered from this pollen zone.

Zone BOGS-6 (ca 1965 – 2014 CE). This most recent period, which broadly encompasses the post-colonial period, sees the fraction of Poaceae pollen decline further still to reach its lowest value of the entire record (18%) in the pollen assemblage representing modern-day vegetation. This is not only due to the strong Afromontane (38-46%) and Herbaceous (9-16%) components but also the relatively high values (14-25%) for Woodland (due to unprecedented increases in *Dodonaea* and *Syzygium*), and appearance of the exotic cultivar *Pinus*. Likely, the unprecedented increase in Cupressaceae in this zone must be attributed largely to the planting of exotic cypress species for timber production. Noteworthy herbs include *Plantago*, cf. *Ricinus*, cf. *Corchorus* and cf. *Hypoestes*. Only a single Poaceae grain >85 μm (maize) was recovered from BOGS-6, and none in the 60-85 μm range.

4. Additional reference

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Figure captions

Fig. 3 (a) Location of Lake Bogoria, its drainage basin (bold line), major rivers feeding into the lake (thin lines) and the Lake Bogoria National Reserve (boundary as stippled line), in relation to other regional lakes and surrounding topography. Topography data are from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) data set (NASA LP DAAC, 2011). (b) Potential vegetation of the study region, simplified from the VECEA classification (van Breugel et al., 2015). Superimposed on this map are the isolines of mean annual rainfall for the period 1970-2000 based on the Worldclim 2.0 dataset (Fick & Hijmans, 2017) shown to highlight the moisture dependence of vegetation distribution. (c) Map of current land cover and land use, derived from Globcover data for 2009 (Bontemps, 2011) using a regional model by the Food and Agriculture Organization of the United Nations (FAO, 2015). The skeleton map shows the location of the study area in eastern equatorial Africa.

Fig. 4 Stratigraphic distribution of selected pollen taxa (most, but not all >1% of the terrestrial pollen sum) in the BOGS14 sediment sequence from the southern basin of Lake Bogoria, in relation to sediment age (De Cort et al., 2018) and pollen-based stratigraphic zonation (CONISS; Grimm, 1987). Taxon abundance is presented as percentage (%) of the terrestrial pollen sum (black curves; 10x exaggeration in white), with taxa grouped per vegetation type and summary diagram on the left. Pollen from wetland taxa and fungal spores are expressed as percent of the terrestrial pollen sum but not included in it.

Fig. 3 Synthesis of proxy data from the southern (BOGS14, green) and northern (BOGN14, blue) sediment record of Lake Bogoria, with indication of the five phases of intensifying ecological influence of human activity (light to dark grey shading). The panels show (a) climatic moisture-balance variation inferred from lake-level change, simplified from De Cort et al. (2018); (b) clay fraction as % of clastic mineral sediment; (c) total lake-sediment accumulation rate (SAR); (d) biomass burning inferred from charcoal influx; (e) cereal production inferred from the fraction of Poaceae pollen grains sized 60-85 μm, with isolated finds of maize pollen (Poaceae grains >85 μm) indicated with pictograms; (f) Animal husbandry (plus wild herbivores; see text), inferred from the relative abundance of spores from obligate coprophilous fungi (*Sporormiella* + *Sordaria*); (g) summary diagram of temporal shifts in the composition of terrestrial vegetation, based on BOGS14 data.

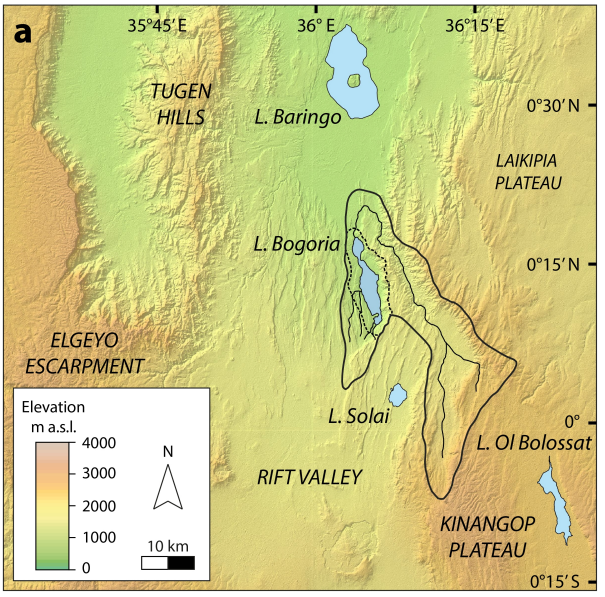
Fig. 4 Percentage (%) of 60-85 μm Poaceae pollen grains versus the total % abundance of Poaceae pollen, with symbol colors representing the successive pollen zones. Also shown are the linear regression for all pollen zones (black line), and the average values (± SE) of each pollen zone separately (colored crosses).

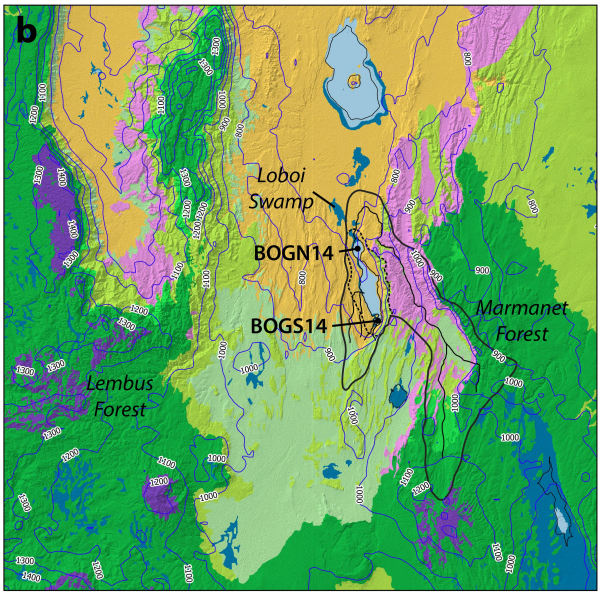
Fig. 5 Principal Component Analysis (PCA) of the temporal distribution of pollen taxa in sediment sequence BOGS14. (a) Species plot with color coding according to vegetation type, as in Fig. 2. (b) Sample plot with samples labelled by age, and grouped using colored polygons to demarcate the pollen zones, as in Fig. 3.

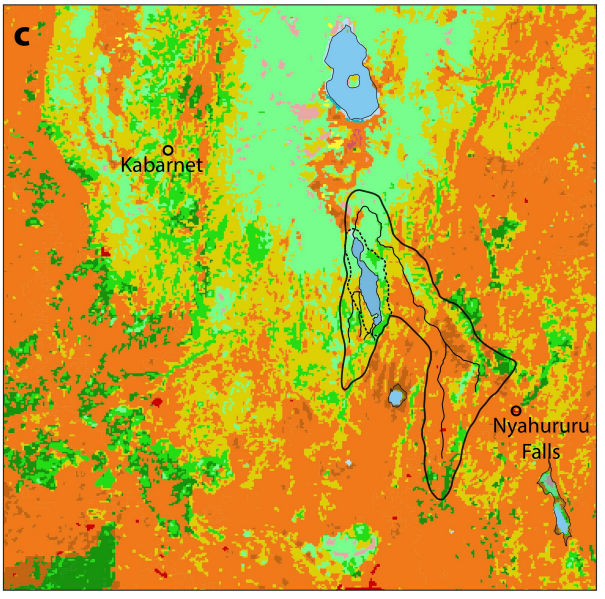
Fig. 6 Stratigraphic distribution of selected pollen taxa (all >1% of the terrestrial pollen sum) in the BOGN14 sediment sequence from the northern basin of Lake Bogoria, in relation to sediment age (De Cort et al., 2018) and pollen-based stratigraphic zonation (CONISS; Grimm, 1987). Taxon abundance is presented as percentage (%) based on the terrestrial pollen sum (black curves; 10x exaggeration in white), with taxa grouped per vegetation type. A summary diagram is shown on the left. Pollen from wetland taxa and fungal spores are expressed as percent of the terrestrial pollen sum but not included in it.

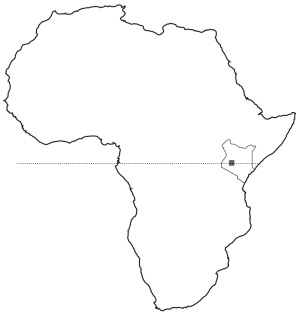
Table captions

Table 2 Sediment depth, weighted-mean modelled age and the lower and upper boundaries of 95% confidence envelopes (Min/Max Age) of pollen-zone boundaries in composite sequence BOGS14 from the southern basin of Lake Bogoria, based on ^{210}Pb- and ^{14}C-dating by De Cort et al. (2018).







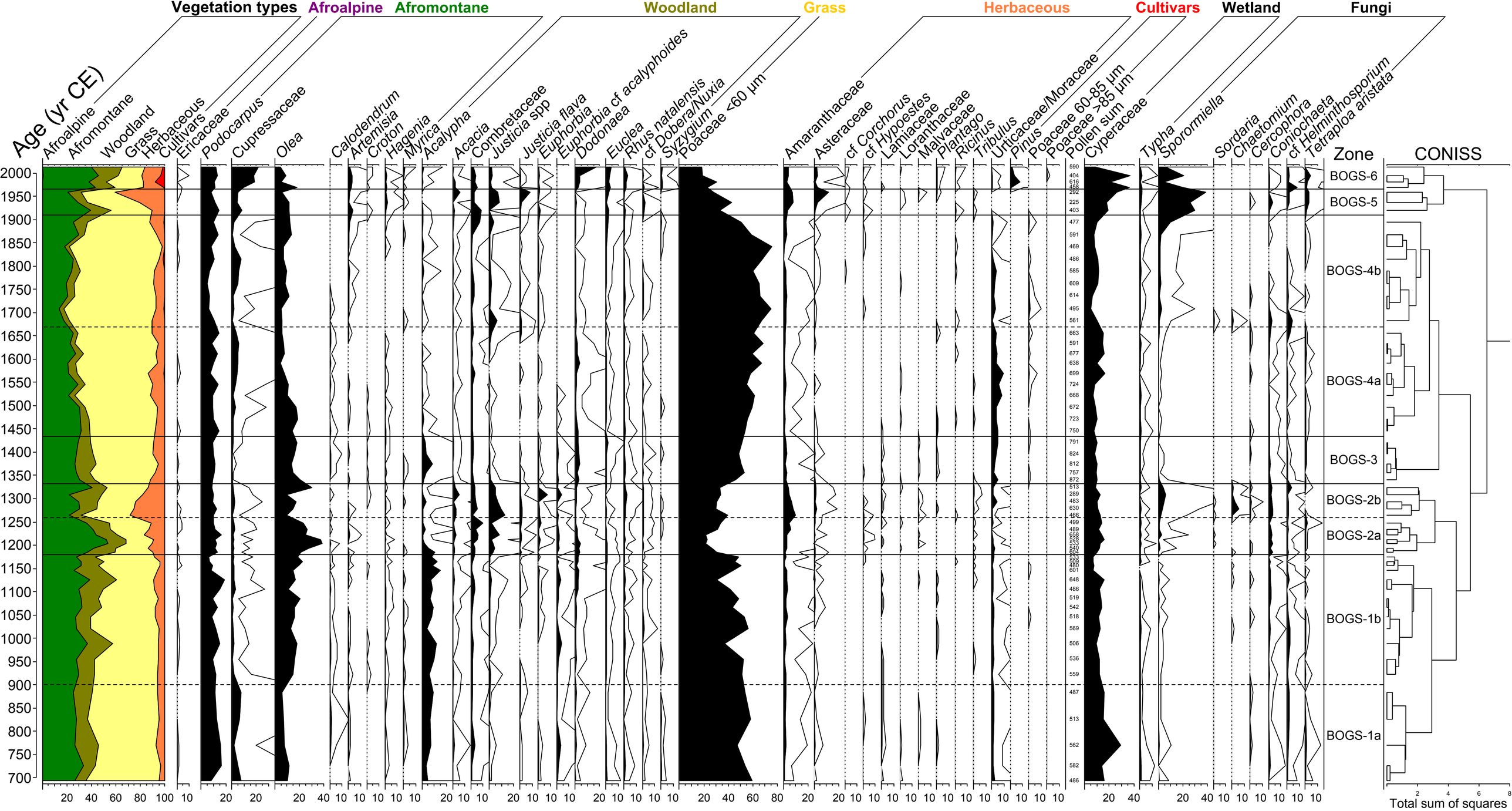


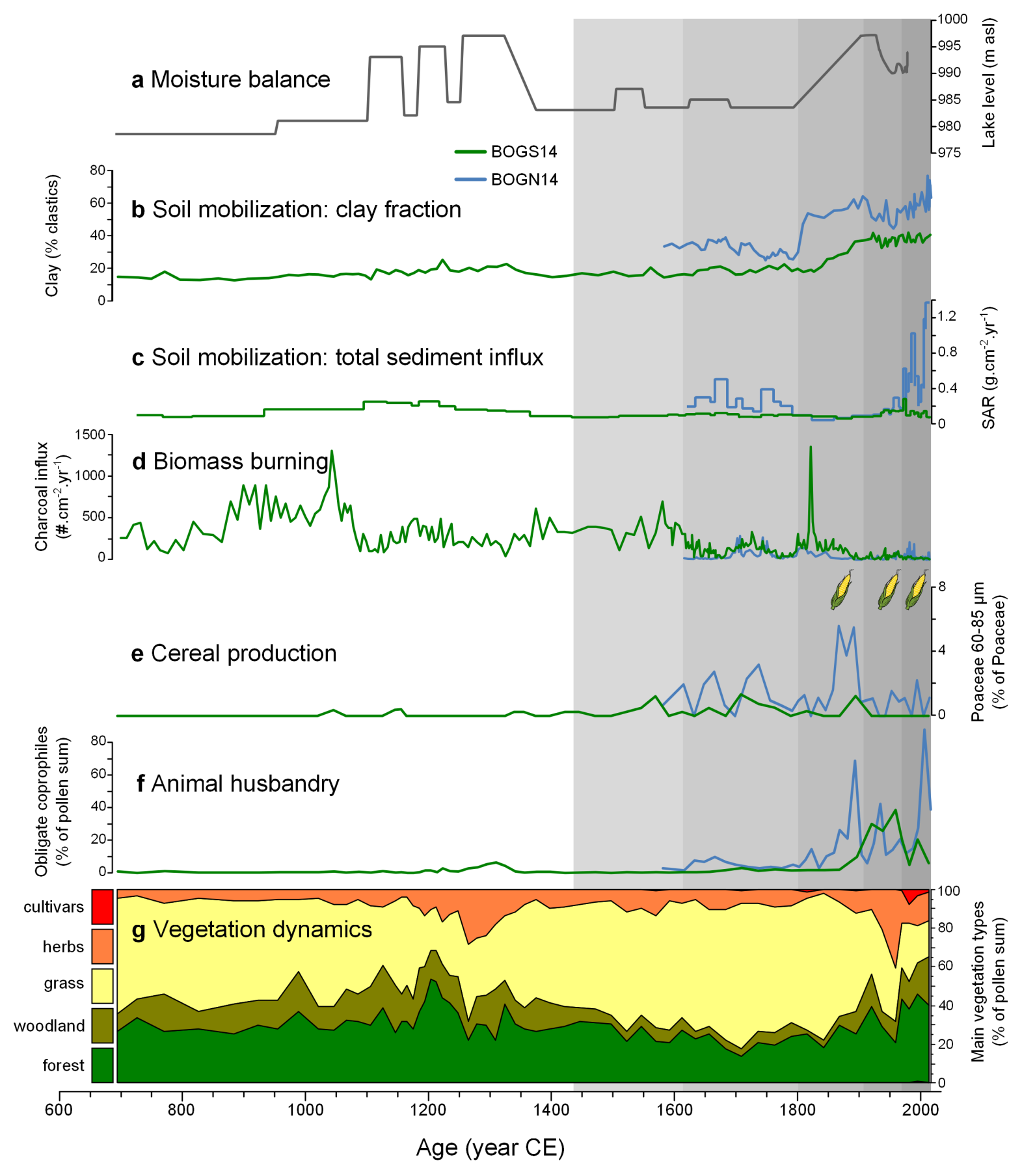
b) Potential natural vegetation

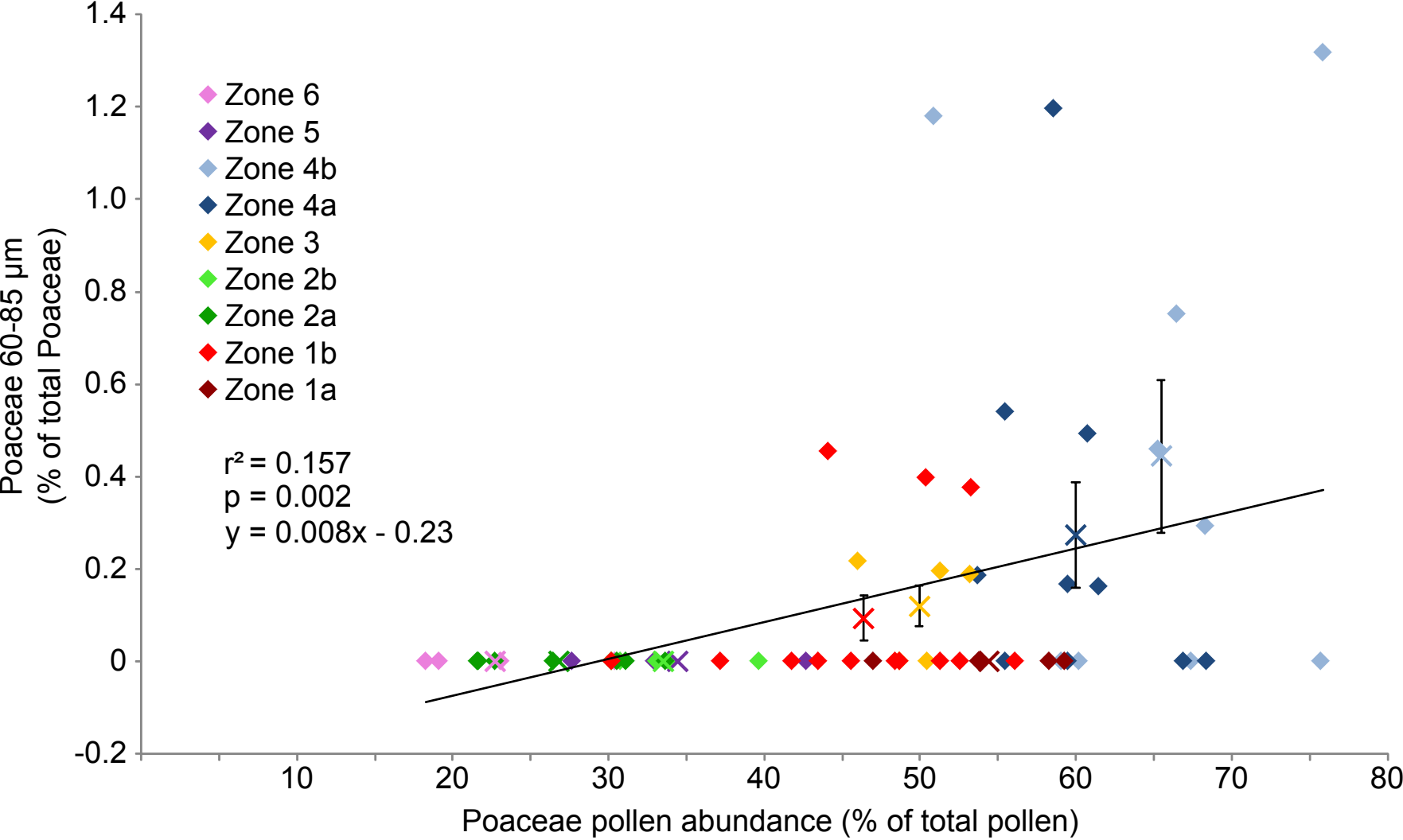
- Afromontane bamboo
- Afromontane forest
- Dry transitional forest
- Dry *Combretum* wooded grassland
- Evergreen and semi-evergreen bushland and thicket
- Upland *Acacia* wooded grassland
- Bushland and thicket
- Edaphic grassland, woodland and forest + swamp
- Water

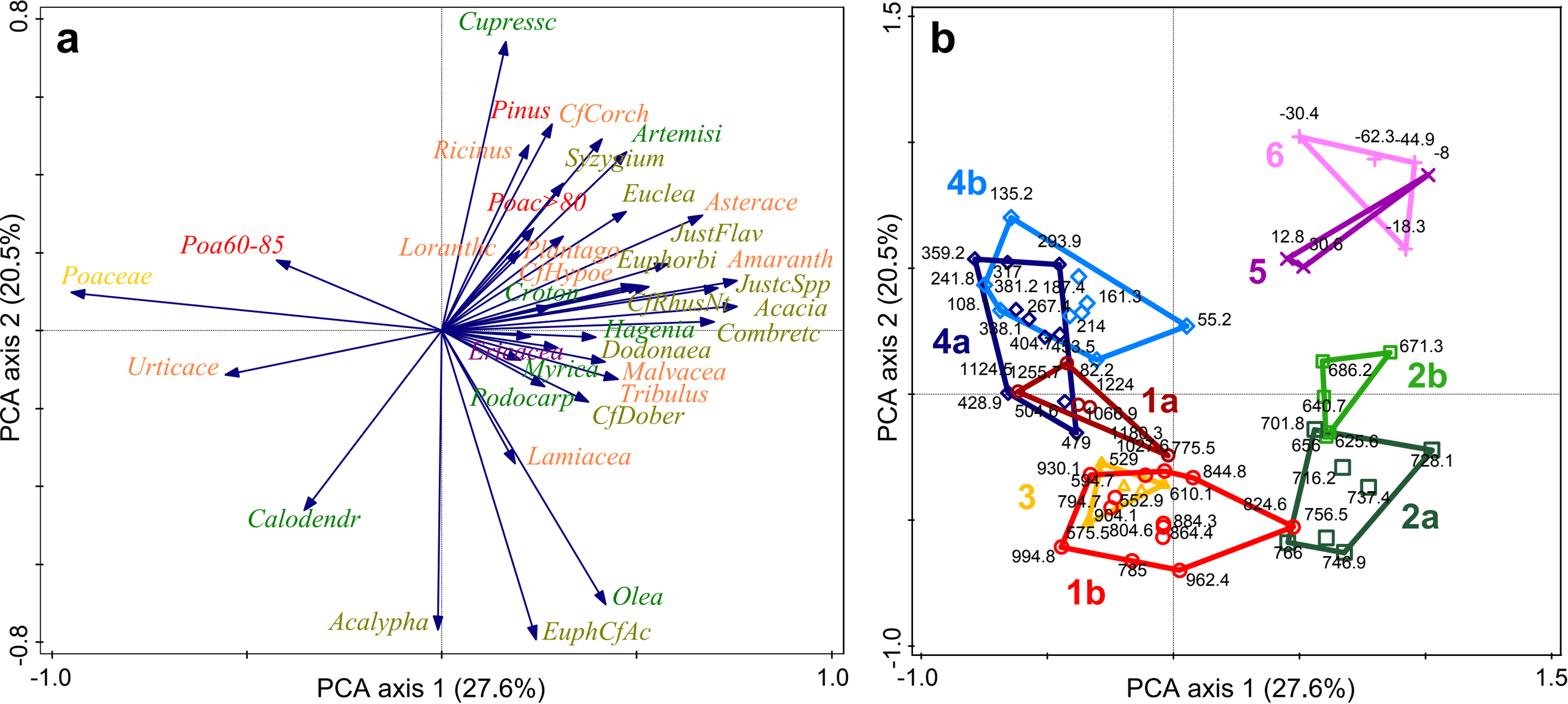
c) Current land use

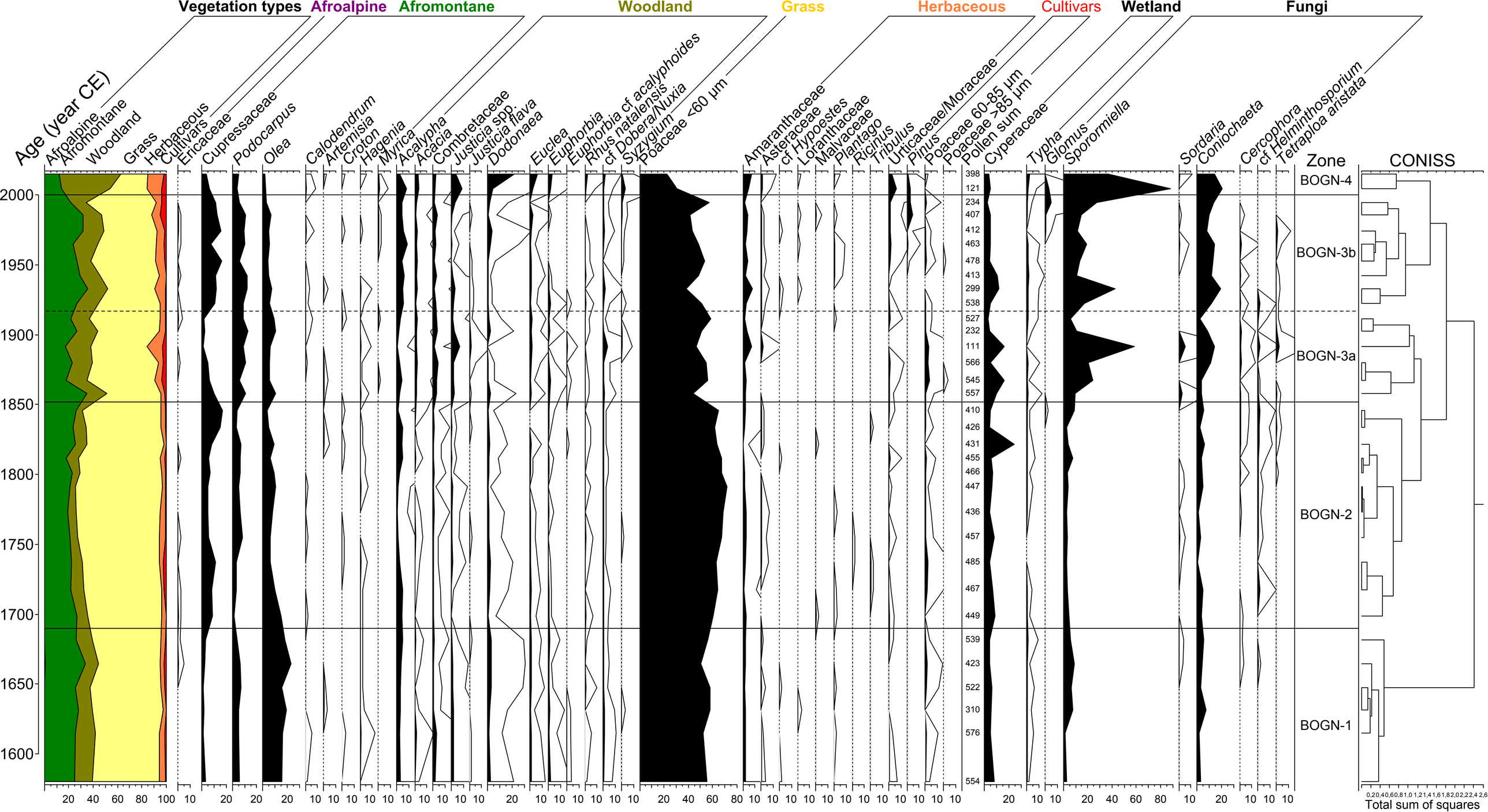
- Rainfed cropland
- Mosaic cropland/Natural vegetation
- Closed to open (>40%) forest
- Open (15-40%) forest/woodland
- Mosaic shrubland/grassland
- Closed to open (>15%) grassland, savannas, shrubland
- Sparse (<15%) vegetation
- Closed to open vegetation on flooded land
- Artificial surfaces and associated areas (urban areas >50%)
- Bare areas
- Water

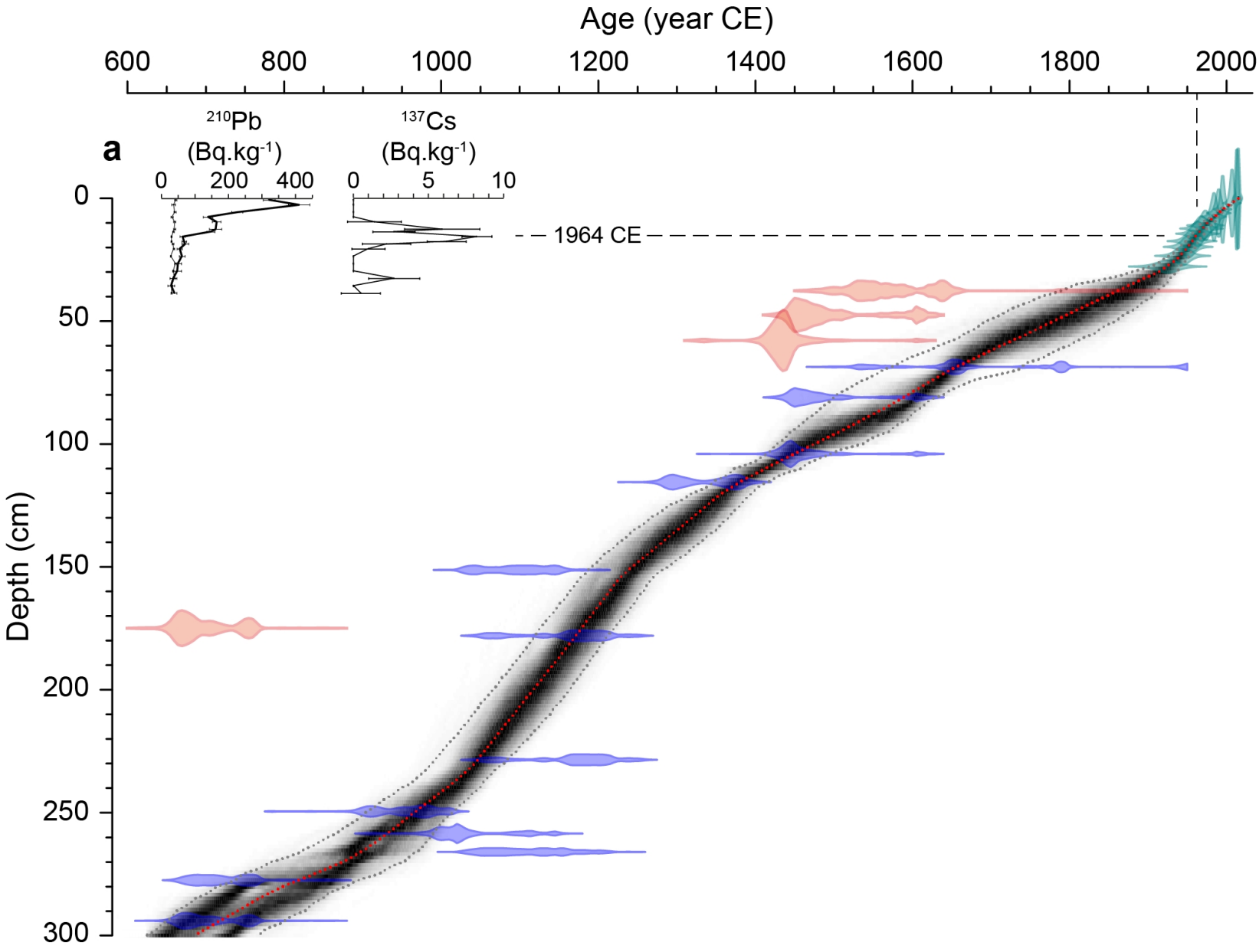

Vegetation types
Afroalpine
Afromontane
Woodland
Grass
Herbaceous
Cultivars
Wetland
Fungi
Age (yr CE)
Afroalpine
Afromontane
Woodland
Grass
Herbaceous
Cultivars
Ericaceae
Podocarpus
Cupressaceae
Olea
Calodendrum
Artemisia
Croton
Hagenia
Myrica
Acalypha
Acacia
Combretaceae
Justicia
Justicia flava
Euphorbia
Euphorbia cf acalyphoides
Dodonaea
Euclea
Rhus natalensis
cf Dobera/Nuxia
Syzygium
Poaceae <60 µm
Amaranthaceae
Asteraceae
cf Corchorus
cf Hypoestes
Lamiaceae
Loranthaceae
Malvaceae
Plantago
Ricinus
Tribulus
Urticaceae/Moraceae
Pinus
Poaceae 60-85 µm
Poaceae >85 µm
Pollen sum
Cyperaceae
Typha
Sporormiella
Sordaria
Chaetomium
Cercophora
Coniochaeta
cf Helminthosporium
Tetraploa aristata
Zone
CONISS
BOGS-6
BOGS-5
BOGS-4b
BOGS-4a
BOGS-3
BOGS-2b
BOGS-2a
BOGS-1b
BOGS-1a
Total sum of squares


a Moisture balance
Lake level (m asl)
1000
995
990
985
980
975
BOGS14
BOGN14
b Soil mobilization: clay fraction
Clay (% clastics)
80
60
40
20
0
c Soil mobilization: total sediment influx
SAR (g.cm-2.yr-1)
1.2
0.8
0.4
0
d Biomass burning
Charcoal influx (#.cm-2.yr-1)
1500
1000
500
0
e Cereal production
Poaceae 60-85 µm (% of Poaceae)
8
4
0
f Animal husbandry
Obligate coprophiles (% of pollen sum)
80
60
40
20
0
g Vegetation dynamics
cultivars
herbs
grass
woodland
forest
Main vegetation types (% of pollen sum)
100
80
60
40
20
0
600
800
1000
1200
1400
1600
1800
2000
Age (year CE)


Zone 6
Zone 5
Zone 4b
Zone 4a
Zone 3
Zone 2b
Zone 2a
Zone 1b
Zone 1a
r² = 0.157
p = 0.002
y = 0.008x - 0.23
Poaceae 60-85 µm (% of total Poaceae)
Poaceae pollen abundance (% of total pollen)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
-0.2
10
20
30
40
50
60
70
80


a
Cupressc
Pinus
CfCorch
Artemisi
Ricinus
Syzygium
Euclea
Asterace
Poac>80
JustFlav
Poa60-85
Loranthc
Plantago
Euphorbi
Amaranth
Poaceae
CfHypoe
JustcSpp
Croton
CfRhusNt
Acacia
Hagenia
Combretc
Urticace
Dodonaea
Myrica
Malvacea
Podocarp
Tribulus
CfDober
Lamiacea
Calodendr
Olea
Acalypha
EuphCfAc
PCA axis 2 (20.5%)
PCA axis 1 (27.6%)
0.8
-0.8
-1.0
1.0
b
4b
135.2
293.9
359.2
241.8
317
381.2
187.4
108.1
267.4
161.3
55.2
338.1
214
4a
404.7
453.5
1124.5
1255.7
82.2
1224
428.9
504.6
1066.9
1a
479
1180.3
1027.6
775.5
529
930.1
844.8
594.7
610.1
3
794.7
552.9
904.1
884.3
575.5
804.6
864.4
994.8
785
962.4
1b
6
-30.4
-62.3
-44.9
-8
5
12.8
30.6
-18.3
671.3
686.2
2b
640.7
701.8
656
625.6
728.1
716.2
737.4
824.6
756.5
2a
766
746.9
PCA axis 2 (20.5%)
PCA axis 1 (27.6%)
1.5
-1.0
1.5


Vegetation types
Afroalpine
Afromontane
Woodland
Grass
Herbaceous
Cultivars
Wetland
Fungi
Age (year CE)
Afroalpine
Afrohontane
Woodland
Grass
Herbaceous
Cultivars
Ericaceae
Cupressaceae
Podocarpus
Olea
Calodendrum
Artemisia
Croton
Hagenia
Myrica
Acalypha
Acacia
Combretaceae
Justicia spp.
Justicia flava
Dodonaea
Euclea
Euphorbia
Euphorbia cf acalyphoides
Rhus natalensis
cf Dobera/Nuxia
Syzygium
Poaceae <60 µm
Amaranthaceae
Asteraceae
cf Hypoestes
Loranthaceae
Malvaceae
Plantago
Ricinus
Tribulus
Urticaceae/Moraceae
Pinus
Poaceae 60-85 µm
Poaceae >85 µm
Pollen sum
Cyperaceae
Typha
Glomus
Sporormiella
Sordaria
Coniochaeta
Cercophora
cf Helminthosporium
Tetraploa aristata
Zone
CONISS
BOGN-4
BOGN-3b
BOGN-3a
BOGN-2
BOGN-1
2000
1950
1900
1850
1800
1750
1700
1650
1600
398
121
234
407
412
463
478
413
299
538
527
232
111
566
545
557
410
426
431
455
466
447
436
457
485
467
449
539
423
522
310
576
554
20 40 60 80 100
10 20
20 20
10 10 10 10 10 10 10 10 10 10
20
10 10 10 10 10 10
20 40 60 80
10 10 10 10 10 10 10 10 10 10 10 10 10 10
20
10 10
20 40 60 80
10 20
10 10 10
0,20,40,60,81,0 1,21,41,61,82,02,22,4 2,6
Total sum of squares


Age (year CE)
600
800
1000
1200
1400
1600
1800
2000
a
^{210}Pb
(Bq.kg^{-1})
0
200
400
^{137}Cs
(Bq.kg^{-1})
0
5
10
1964 CE
Depth (cm)
0
50
100
150
200
250
300