Ecosystem change in the South Pare Mountain bloc, Eastern Arc Mountains of Tanzania

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Abstract
Palaeoecological evidence is used to investigate climatic and anthropogenic drivers of vegetation and fire dynamics through the past ~1200 years in the Eastern Arc Mountains, Tanzania. Pollen and charcoal analyses are supported by a chronology derived from five accelerator mass spectrometry ages, a 137Cs activity profile and marker horizons from two exotic pollen taxa. Pollen indicator taxa are used to develop a series of environmental indices, and compared with fluctuations in key timber species, and a fire history reconstruction. Prior to AD 1274, the ecosystem is characterised by moist montane forest that is somewhat anomalous with other East African records, providing evidence for the persistence of a mesic environment and ecosystem resilience of the Eastern Arc Mountains. An open drier forest type is recorded from AD 1275 to 1512, resulting from regional aridity; when the aforementioned buffering ability was exceeded and ecosystem resilience curtailed. Maize appears from ~AD 1737, possibly associated with the regional expansion of agriculture to supply the ivory trade. The peak of the caravan trade in the mid-19th century, and later colonial administration, coincides with intensified human impacts, specifically forest clearance suggested by substantial declines in the timber tree Ocotea. Following independence, there are tentative signals of montane forest recovery, which coincide with the establishment of forest reserves, and associated timber bans. Palaeoecological understanding of historical ecosystem change in the Eastern Arc Mountains biodiversity hotspot is vital to build informed conservation and forest management policies for a future characterised by growing human populations coupled with changing climate–ecosystem relationships.

Introduction
Palaeoecological studies provide a long-term perspective on climate–human–ecosystem interactions. Such insights are vital for informing current conservation and management, which requires in-depth understanding of long-term variability and change (Gillson, 2015; Gillson and Marchant, 2014). ‘Deep time’ perspectives are key for addressing priority biogeographical and conservation questions, such as identifying locations that remain buffered under the present climate change trends, and how linking past and future ecosystem response to such changes can help mitigate biodiversity loss (Pfeifer et al., 2012). Long-term palaeoecological records provide an opportunity to observe conditions prior to major human impacts, thereby helping to establish natural reference states, and determine how human activity has influenced ecosystem composition and distribution (Dearing et al., 2015). The need to understand long-term human–ecosystem interactions is perhaps most pressing in the African context, where human–ecosystem interactions extend over long timescales, and where close reliance on natural capital is central to ongoing development. The Eastern Arc Mountains of East Africa (Lovett, 1990; Figure 1) constitute an area of global conservation importance (Burgess et al., 2007; Mittermeier et al., 2004), yet lack good spatial and temporal coverage of palaeoecological records (Finch et al., 2009, 2014; Finch and Marchant, 2010; Heckmann, 2014; Heckmann et al., 2014; Mumbi et al., 2008). The nature and timing of human impacts in the Eastern Arc Mountains is uncertain during the late-Holocene. Evidence for regional iron production and agriculture is provided by iron smelting furnaces, stone built terraces and extensive irrigation furrows, in addition to local oral traditions (Chami, 1995; Odner, 1971; Soper, 1967). In the South Pare Mountain bloc of the Eastern Arc, several iron smelting sites have been recorded (Figure 2), ranging in altitude from 500 to 1100 m a.s.l., and according to Soper (1967), ‘smelting remains are very common around the Pare Hills’ (p. 27). Iron Age sites are testament to long-term human activity in the Eastern Arc Mountains, although assertions that iron smelting resulted in significant deforestation over the past 2000 years (e.g. Schmidt, 1989) require palaeoecological verification (Heckmann et al., 2014). The Eastern Arc montane forests have been subjected to human exploitation for farmland, fuelwood and charcoal for many centuries, with anthropogenic clearance resulting in extensive forest...
loss and fragmentation (Newmark, 1998), with Hall et al. (2009) estimating an 80% loss in past forest extent for the Eastern Arc mountain range (Figure 1) and 82% loss for the South Pare Mountain bloc (Figure 2). By the late 19th century, early European visitors to the North Pare Mountains described the landscape as deforested (Gillson et al., 2003). Similarly, by 1898 there was concern about the extent of deforestation in the East Usambara Mountains (Schabel, 1990), suggesting wide-scale human impacts prior to colonial influence.

Palaeoecological data, such as that derived from pollen, charcoal, diatoms and other microfossils, offer an unrivalled source of long-term information on ecosystem change. This can

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**Figure 1.** Map of the Eastern Arc Mountains (after Platts et al., 2011), which extend from the Taita Hills of southern Kenya to the southern Udzungwa Mountains of Tanzania, and comprise 13 isolated mountain blocs, namely, Taita, Pare, Usambara, Ngulu, Nguru, Uluguru, Ukaguru, Rubeho, Malundwe, Mahenge and Udzungwa. Current forest extent (Platts et al., 2011) is compared with estimated palaeoecological forest extent for >2000 years BP (Hall et al., 2009).

**Figure 2.** (a) Position of Mt Shengena within the Chome Forest Reserve in the South Pare Mountain bloc, indicating iron smelting sites (Soper, 1967) and (b) catchment area of the Kwasebuge peat bog, indicating proximity of the montane forest boundary.
be used to provide baseline data over ecologically meaningful timeframes on forest response to climate change and human interactions. In this paper, we present a high temporal resolution, multi-proxy record of montane forest history from the Kwasebugo peat bog on the slopes of Mt Shengena in the Chome Forest Reserve (South Pare Mountain bloc; Figure 2), an area threatened by historical and ongoing human modifications, particularly illegal logging (Richard et al., 2014; Figure 3). The record covers the last 1200 years: a period in East African history characterised by population growth, establishment of sedentary agriculture, arrival of exotic staple crops and associated ecosystem impacts. We use indicator pollen taxa to develop an index of forest disturbance, and compare this with robust evidence of human activity and fire, to understand drivers of ecosystem change.

Methods

Environmental setting

The Eastern Arc Mountains comprise block faults of crystalline Precambrian granulite, gneiss and migmatite rocks (Schlüter, 1997), up to a maximum altitude of 2635 m a.s.l. This chain of 13 mountain blocks ranges from southeast Kenya to eastern Tanzania, with the northernmost blocs in closest proximity to the coastline (Figure 1). Regional average annual temperatures range from 15°C to 20°C and the Pare mountain bloc is characterised by bimodal rainfall linked with the migration of the Inter-tropical Convergence Zone (Nicholson, 2000). Short rains fall between October and December, with long rains between March and May. Rainfall variability is influenced by the El Niño-Southern Oscillation, Indian Ocean sea-surface temperature variability and land-atmosphere feedbacks (Nicholson, 2000). The windward slopes of the eastern Pare Mountains receive maximum orographic rainfall estimated at 3000 mm yr\(^{-1}\) while the drier western slopes receive up to 2000 mm yr\(^{-1}\) (Lovett and Pócs, 1993). Present forest composition and distribution in the Eastern Arc Mountains is determined by climate, particularly temperature, rainfall and dry season length (Platts et al., 2010), in addition to anthropogenic activities (Hall et al., 2009). Discrete altitudinal vegetation belts are not as well-defined in the Eastern Arc Mountains as in many other East African montane areas.

The Chome Forest Reserve covers the highest ridge of the South Pare Mountains, encompassing a gazetted area of 14,283 ha. The current human impacts within the reserve include extensive illegal pit-sawing for Ocotea usambarensis on the western slopes of Mt Shengena (Figure 3) and uncontrolled fires, which result in the encroachment of heathland at the forest edge (Lovett and Pócs, 1993). Lovett and Pócs (1993) provide the following vegetation description for the Chome Forest Reserve.

Upper montane forest zone (>2300 m). Ericaceous heathland is distributed in rocky areas typified by shallow, acidic soils. At lower altitudes, secondary ericaceous heath has colonised areas following fire. Upper montane forest is characterised by a canopy covered in epiphytic bryophytes, ferns and orchids such as Campylopus jamesonii, Neorutenbergia usagarae and Stolzia repens. Common forest tree species include Cornus volkensii, Ilex mitis, Rapanea melanophloes, Schefflera myriantha and Syzygium cordatum.

Montane forest zone (1500–2300 m). The dominant emergent tree is O. usambarensis with Podocarpus latifolius subdominant (Figure 3). Montane forest species include Albizia gumifera, Chrysophyllum gorongosanum, Macaranga kilimandscharica, Teclea nobilis and Xymalos monospora. Polyscias fulva and the fire-adapted Morella salicifolia (Hemp, 2006a, 2006b; Livingstone, 1967, 1975) are commonly found in clearings in the montane forest. Smaller trees include Balthasaria schleibernii, Ekebergia capensis, Maesa lanceolata and R. melanophloes.

Lowland forest zone (<1500 m). Lowland forest is found on the lower slopes of the Chome Forest Reserve at altitudes from 1250 to 1500 m and is dominated by forest species Parinari excelsa. Other typical lowland forest genera occurring in the reserve include Acacia, Brachystegia, Celtis, Commiphora, Croton, Euphorbia and Hymenocardia acida.
Core extraction, chronology and stratigraphy

Kwasebuge (2000 m a.s.l.; 4°17.52'S; 37°55.37'E) is a small (~1 ha) peat bog on the Chomessui Plateau, ~400 m from the western slopes of Mt Shengena (Figures 2 and 3). The vertically accumulating peat bog is fed hydrologically by a small stream channel and drainage from surrounding slopes (perched; Figure 2). Kwasebuge is situated within a mosaic of 1–2.5 m tall Erica spp., heath and Sporobolus grassland, in close proximity to the current lower montane forest boundary.

In July 2007, a 50-cm-long, 5-cm-diameter Russian corer (Jowsey, 1966) was used to extract a 3.18-m sediment core from parallel boreholes with overlapping sections. Core stratigraphy (Troels-Smith, 1955) was described in the field and again in the laboratory and used to select appropriate horizons for dating. Five bulk-sediment samples were subsampled in the laboratory at York, dried overnight at 100°C and sent by courier to Waikato Radiocarbon Laboratory, New Zealand, for accelerator mass spectrometry (AMS) radiocarbon dating. An age-depth model was developed using the ‘classical’ age-depth modelling source code (clam; Blaauw, 2010) in R (R Core Team, 2015). The model was presented as calendar years AD using a smooth spline of the IntCal13 calibrated radiocarbon dates (Reimer et al., 2013). Uncalibrated radiocarbon ages cited from the supporting literature were calibrated using the same methodology for standardisation (original ages are provided in parentheses). Marker horizons (exotic pollen and 137Cs activity) were plotted alongside the age model but did not contribute to the model.

To detect peak atmospheric 137Cs fallout produced from nuclear weapons testing (AD 1963; Appleby, 2001), samples from the upper 75 cm of the core were selected for non-destructive gamma spectrometry (Appleby and Oldfield, 1992), on a Canberra well-type ultra-low background HPGe gamma ray spectrometer at the National Oceanography Centre, Southampton, UK, and counted for >8 h.

The consistent presence of neophytic maize (Zea mays) and pine (Pinus) is used as time markers based on the following age constraints. Although the first introduction of maize in Africa is dated as early as AD 1554 (Gallagher, 2016), a maximum probable age for eastern Africa is derived from the first historical account of maize in the region (AD 1643), ascribed to Portuguese settlers growing maize on Zanzibar and Pemba, with trade links to the coastal mainland (Freeman-Grenville, 1962; Miracle, 1965). Baumann (1891, summarised in Håkansson, 2008) reports that maize was widely cultivated in the South Pare Mountains around AD 1850, constraining the introduction of maize to between AD 1643 and 1850. There is no available documentation of early pine planting in South Pare; however, it is likely that pine was only planted in this area following the AD 1903 establishment of the Amani Biological-Agricultural Research Station in the Usambara Mountains approximately 120 km away from the coring site, which was the main distributor of seed and seedlings for Tanganyika Territory (Schabel, 1990).

Pollen analysis

Subsamples were extracted at 5 cm intervals and processed for pollen analysis using the ‘swirling technique’ (Hunt, 1985). Samples were boiled in a 5% potassium hydroxide and sodium pyrophosphate solution for sediment disaggregation and sieved through a 140-µm nylon mesh. Silt and sand were removed by swirling samples on a 35-cm clock-glass. The suspended portion was poured through a 6-µm mesh and rinsed with water to remove solutes and fines.

Pollen counts on 44 samples were conducted using a Leica DM4000B microscope at a magnification of 400× with a minimum tally of 600 pollen and spores per sample. Identifications were confirmed using a reference collection derived from pollen and herbarium specimens from the National Museums of Kenya and the University of Dar es Salaam, supplemented by published works on East African pollen morphology (African Pollen Database (APD), 2004; Association des Palynologues de Langue Francaise (APLF), 1974; Bonnefille, 1971; Bonnefille and Riollet, 1980).

Palynomorphs were grouped into ecological units: upper montane herbs and shrubs, upper montane forest, montane forest, lower montane forest, ericaceous heath, neophytes (exotics), locally common and undetermined taxa (Table 1). These are not intended as discrete categories, particularly in light of limited taxonomic resolution associated with pollen identifications, and the fact that many taxa have broad ecological tolerances. Nevertheless, the units serve to aid interpretation and inter-comparison with previously published pollen studies from the Eastern Arc Mountains (Finch et al., 2009, 2014; Finch and Marchant, 2010). Interpretation was aided by calculating percentages in two pollen sums: regional and total (Table 1). The regional sum excludes locally dominant taxa that otherwise dominate the pollen signal because of over-representation. Thus, the regional sum is used for interpreting extra-local vegetation changes.

We calculated three ecological indices by summing regional pollen percentages of indicator taxa (Table 2). Pollen types for which parent taxa are associated with secondary, disturbed or degraded forest types were summed to create a forest disturbance index. The pioneer index comprised pollen types from pioneer taxa colonising disturbed ground. The anthropogenic index was based on exotic pollen types.

Pollen diagrams were plotted using Psimpoll 4.26 (Bennett, 2005). The Constrained Incremental Sum of Squares (CONISS) cluster technique (Grimm, 1987) was used to delimit statistically significant pollen assemblage zones through a broken stick test (Bennett, 1996) based on regional pollen data.

Macroscopic charcoal analysis

Subsamples of 1 cm³ of wet sediment were removed at a continuous 1-cm resolution for macroscopic charcoal analysis. Samples were soaked in a sodium metaphosphate solution (Bamber, 1982) for >24 h and then wet sieved through a 125-µm mesh and the larger fraction was transferred to a gridded Petri dish. Charcoal pieces were identified and total charcoal was tallied through visual inspection and manipulated with a metal probing needle under a Zeiss Stemi 2000-C optical stereomicroscope at 10–40× magnifications. This macroscopic charcoal size represents charcoal produced locally during fires within the catchment area (Lynch et al., 2004; Peters and Higuera, 2007). Macroscopic charcoal concentrations (pieces cm⁻³) were converted to charcoal accumulation rates (CHAR, pieces cm⁻³ yr⁻¹) for comparison through time and 13 samples were linearly interpolated because of a lack of available core material. CHAR values from 0 to 230 cm depth were linearly resampled to the mean sampling interval of 6 years and transformed with a univariate bias-corrected continuous Morlet wavelet (Liu et al., 2007) using the biwavelet package in R (R Core Team, 2015) to visualise persistent periodicities within the time series. Resampling to the maximum sampling interval for charcoal (20 years) produced very similar results and identical interpretations.

Results

Stratigraphy and chronology

All analyses were restricted to the upper 220 cm of the core because of a complex stratigraphy and poor dating control in the lower section of the core and focal interest on ecosystem history over the past millenium. The basal sediments (220–213 cm) are characterised by smooth, dark and well-humified peat (Figure 4). Above this (213–200 cm), there is a bed containing light grey sand. Sediments from 200 to 171 cm are dark brown and
Table 1. Palynomorphs and non-pollen types identified from the Mt Shengena site, and associated ecological groupings (R: regional pollen sum; T: total pollen sum). Rare types hidden from the pollen diagrams are denoted with an asterisk.

<table>
<thead>
<tr>
<th>Category</th>
<th>Local Ecological Groupings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper montane herbs and shrubs (R, T)</td>
<td>Lowland forest (R, T)</td>
</tr>
<tr>
<td>Aceraceae: <em>Hyperestes</em>-type</td>
<td>Amaranthaceae: <em>Achyranthes</em>-type aspera*</td>
</tr>
<tr>
<td>Aceraceae: <em>Sclerociton</em></td>
<td>Anacardiaceae: <em>Lannea</em>-type</td>
</tr>
<tr>
<td>Asteraceae: <em>Carduus</em>-type</td>
<td>Anacardiaceae: <em>Rhus</em> undiff.</td>
</tr>
<tr>
<td>Asteraceae: <em>Crascocephalum</em>-type montuosum*</td>
<td>Anacardiaceae: <em>Rhus</em>-type natalensis*</td>
</tr>
<tr>
<td>Asteraceae: <em>Tubuliflorae</em> undiff.</td>
<td>Boraginaceae: <em>Heliotropium</em></td>
</tr>
<tr>
<td>Polygalaceae: <em>Polygala</em>-type*</td>
<td>Burseraceae: <em>Commiphora</em></td>
</tr>
<tr>
<td>Upper montane forest (R, T)</td>
<td>Caryophyllaceae: <em>Silene</em>/<em>Helianthea</em>-type</td>
</tr>
<tr>
<td>Aquifoliaceae: <em>ilex</em> <em>mitis</em></td>
<td>Caryophyllaceae: <em>Stellaria</em> manni-type</td>
</tr>
<tr>
<td>Cornaceae: <em>Cornus</em> <em>volkensii</em></td>
<td>Convolvulaceae undiff.*</td>
</tr>
<tr>
<td>Loganiaceae: <em>Nuxia</em>-type</td>
<td>Euphorbiaceae: <em>Coca</em>-type undiff.*</td>
</tr>
<tr>
<td>Oleaceae: <em>Olea</em></td>
<td>Euphorbiaceae: <em>Clitandra</em></td>
</tr>
<tr>
<td>Rosaceae: <em>Punus</em> <em>africana</em>-type</td>
<td>Euphorbiaceae: <em>Croton</em>-type</td>
</tr>
<tr>
<td>Montane forest (R, T)</td>
<td>Euphorbiaceae: <em>Euphorbia</em>-type*</td>
</tr>
<tr>
<td>Araliaceae undiff.*</td>
<td>Euphorbiaceae: <em>Shirakia</em>-type elliptica*</td>
</tr>
<tr>
<td>Araliaceae: <em>Polyscias</em></td>
<td>Fabaceae (C): <em>Brachystegia</em></td>
</tr>
<tr>
<td><em>fulvo</em>-type*</td>
<td>Hymenocardiaaceae: <em>Hymenocardia</em> acid-type</td>
</tr>
<tr>
<td>Asteraceae: <em>Vernonia</em>-type</td>
<td>Lentibulariaceae undiff.*</td>
</tr>
<tr>
<td>Brassicaceae undiff.</td>
<td>Mimosaceae: <em>Acacia</em> undiff.*</td>
</tr>
<tr>
<td>Celastraceae: <em>Cassine</em>-type</td>
<td>Mimosaceae: <em>Acacia</em>-type III*</td>
</tr>
<tr>
<td>Combretaceae: <em>Combretum</em>-type</td>
<td>Ulmaceae: <em>Celtis</em></td>
</tr>
<tr>
<td>Ebenaceae: <em>Euclea</em></td>
<td>Euphorbiaceae: <em>Achmea</em>-type*</td>
</tr>
<tr>
<td>Euphorbiaceae: <em>Macaranga</em></td>
<td>Euphorbiaceae: <em>Derris</em>-type</td>
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<tr>
<td>Euphorbiaceae: <em>Neoboutonie</em>-type*</td>
<td>Euphorbiaceae: <em>Derris</em>-form type</td>
</tr>
<tr>
<td>Lamiaceae: <em>Satureja</em></td>
<td>Lycopodiaceae: <em>Lycopodium</em> <em>vagum</em>-form type</td>
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<tr>
<td>Lauraceae: <em>Ocotea</em></td>
<td>Lycopodiaceae: <em>Lycopodium jussiieae</em>-form type</td>
</tr>
<tr>
<td>Meliaceae: <em>Ekebergia</em>-type capensis</td>
<td>Poaceae undiff.</td>
</tr>
<tr>
<td>Myrtaceae: <em>Syzygium</em>-type</td>
<td>Pteridophyta: <em>Triletes</em> undiff.</td>
</tr>
<tr>
<td>Palmae: <em>Borassus</em>-type oethipum*</td>
<td>Undetermined (T)</td>
</tr>
<tr>
<td>Podocarpaceae: Podocarpus</td>
<td>Indeterminable (corroded/broken)</td>
</tr>
<tr>
<td>Proteaceae: Protea*-type*</td>
<td>Indeterminable (obsured)</td>
</tr>
<tr>
<td>Pteridophyta: <em>Cyathaea</em></td>
<td>Undetermined</td>
</tr>
</tbody>
</table>

well-humified. Between 171 and 110 cm, smooth dark peat containing fibrous patches occurs. The peat becomes increasingly fibrous between 110 and 54 cm, containing herbaceous and fine detritus. A section of densely fibrous, medium-dark brown peat containing matted roots and Cyperaceae fragments occur above 54 cm. The topmost part of the core (0–13 cm) is dominated by fibrous, decomposing Cyperaceae material.

The radiocarbon results place the record within the late-Holocene, with a basal date of AD 423–569 (Table 3). The AMS determination at 200 cm (AD 1337–1398) was designated an outlier by the smooth spline age model (Figure 4). In a peatland system, contamination by rootlets bringing younger material down the profile can produce younger radiocarbon results than the stratum. At 182 cm, a result of AD 1256–1303 suggests higher sedimentation rate for the upper part of the core than below this depth. The remaining two AMS results fall along a fairly linear age–depth curve to the top of the core, with a sample at 121 cm yielding a result of AD 1622–1673, and at 64 cm a result of AD 1800–1894. 

Pollen and charcoal

Pollen preservation was excellent throughout the Mt Shengena core sequence, with relatively few broken and damaged grains encountered. A total of 67 taxa were identified (Table 1). Pollen data are presented as regional (Figure 5) and total (Figure 6) pollen diagrams and CHAR data are presented in Figure 6. CONISS yielded five pollen zones: S-1 (220-188 cm), S-2 (188-158 cm), S-3 (158-113 cm), S-4 (113-62 cm) and S-5 (62-0 cm).

Zone S-1 (AD 790–1275). The pollen assemblage is dominated by montane forest taxa; notably the tree *Podocarpus*, although the diversity of palynomorphs recorded in this zone is low relative to the remainder of the sequence. *Podocarpus* reaches highest values in the sequence (75%), dropping gradually after AD 970 to reach 40% by the upper zone boundary. The montane forest tree *Ocotea* records a steady increase from 5% to 30% over the course of Zone S-1. The upper montane forest sum is prominent in this zone, because of high values of *I. mitis* (2–5%) relative to the remainder of the sequence. Eriocaceae heath records a gradual expansion (20–35%), although percentages are generally very low. Lowland forest is poorly represented in this zone. Cyperaceae and Poaceae dominate the local pollen signal, with trilite fern spores subdominant. Macroscopic charcoal is generally low with mean CHAR of 61 pieces cm$^{-2}$yr$^{-1}$.

Zone S-2 (AD 1275–1513). Montane forest remains well represented by *Podocarpus* and *Ocotea*, which remain prominent in this zone. *Podocarpus* increases initially from 40% to 55%, dropping to 20% after AD 1460. *Ocotea* records the opposite trend, initially decreasing, and then increasing by 20%. Eriocaceae heathland continues to expand through this zone. Upper montane forest taxa, including *I. mitis*, are relatively poorly represented. Lowland forest taxa *Cluita*, *Commiphora* and *Croton* make an appearance, albeit at low percentages. Cyperaceae record an increase in this zone, while Poaceae remain relatively stable at 20%. CHAR increases to a mean value of 130 pieces cm$^{-2}$yr$^{-1}$.

Zone S-3 (AD 1513–1700). The S-2/S-3 zone boundary sees a shift in the relative dominance of *Ocotea* and *Podocarpus*, with *Ocotea* recording a sustained increase until AD 1837, and *Podocarpus* a corresponding decrease. A marked increase is recorded in the montane forest understory herb *Impatiens*. The upper montane forest tree *I. mitis* is well represented in this zone. A single
presence of *Pinus* is recorded at AD 1641, which may be attributed to contamination. Zones S-3, S-4 and S-5 record a noticeable increase in the diversity of taxa represented in the upper montane forest, montane forest and lowland forest groupings. Lowland forest is represented by a wide variety of taxa, including *Celtis*, *Clutia*, *Commiphora*, *Croton*, *Heliotropum* and *Silene-Uebelina*. A decline in Cyperaceae is observed. CHAR further increases to a mean value of 216 pieces cm$^{-2}$ yr$^{-1}$. The Holocene

Electronic supplementary material (ESM) Figure 4. Troels-Smith (1955) stratigraphy and calibrated age model for the Mt Shengena record based on radiocarbon age determinations. Time markers plotted include first introduction of maize (*Zea mays*; AD 1645–1850) and pine (*Pinus*; after AD 1902) pollen. A single outlier date at 200 cm is denoted with an X. 137Cs activity profile is included as an inset.

Dominant *Ocotea* records percentages of up to 40%. *Impatiens* records continued high percentages from the previous zone. *Morella* appears for the first time in the profile after AD 1830. Maize is recorded from AD 1737 onwards. Ericaceae percentages are high during this zone. Cyperaceae increase gradually, reaching 20% by the zone boundary, while aquatic weed *Laurembergia* becomes prominent for the first time in the profile. CHAR decreases in Zone S-4 to a mean value of 142 pieces cm$^{-2}$ yr$^{-1}$.

**Zone S-5 (AD 1837–present).** *Pinus* is a consistent feature in this zone. The zone also includes neophyte maize and potentially exotic palynomorphs (*Acacia*-type II and *Eucalyptus*-type). *Podocarpus* percentages increase initially and stabilise after AD 1900. *Ocotea* records an initial decline, peaks at AD 1930 and again towards the present day. *Impatiens*, *Tubuliflorae* and *Vernonia*-type are prominent during this zone. *Celtis* and *Morella* become prominent for the first time in the profile. Ericaceae percentages remain a dominant feature of the pollen assemblage. Among local taxa, Poaceae and Cyperaceae remain dominant. *Ocotea* records his highest values (30%) around AD 1860, followed by a decline towards the present day. *Laurembergia* percentages are consistently low. CHAR increases again to a mean value of 216 pieces cm$^{-2}$ yr$^{-1}$ and the variability, standard deviation of 201 pieces cm$^{-2}$ yr$^{-1}$, is the highest of the record.

**Environmental indices**

The forest disturbance index is characterised by relatively low values at the start of the profile, increasing and becoming more variable through the sequence, and finally reaching its highest values after AD 1837 (Figure 7). The pioneer index shows a gradual overall increase in pioneer species prevalence through the record. The anthropogenic index suggests clear evidence of human activity after AD 1837. By comparison, the timber taxon *Ocotea* shows an overall increase until AD 1837, declining sharply thereafter, and recovering after AD 1970. The prevalence of *Ocotea* in the regional pollen signal is unusual given that this pollen type is generally not well represented in East African pollen sequences possibly owing to poor dispersal, production or preservation characteristics. *Ocotea* pollen has, however, been recorded from other sites in the Eastern
Arc Mountains (Udzungwa Mountains, Mumbi et al., 2008; Uluguru Mountains, Finch et al., 2009; Finch and Marchant, 2010). The unusually high frequencies of Ocotaea pollen recorded within the Kwasebuge record may be attributed to the dominance of O. usambarensis in the Chome Forest Reserve, and proximity of the site to the montane forest boundary, possibly combined with preservation characteristics of the peatland sediments.

*Podocarpus* shows an overall decline through the sequence, reaching lowest abundances during the very recent past at the top of the sequence. CHAR values represent biomass burning within the swamp catchment area and are compared with the environmental pollen indices to examine the role of fire on the forest landscape. It is difficult to disentangle anthropogenic influences from natural controls on fire and the CHAR data are limited to being interpreted as an indicator of biomass burning within the swamp catchment.

**Discussion**

Late-Pleistocene climatic shifts would have impacted species in some regions less severely than in others, allowing for accumulation of new taxa in centres of endemism, such as the Eastern Arc Mountains. Consistent with the ‘long-term environmental stability’ hypothesis (Fjellå and Lovett, 1997: 325), pollen evidence suggests that Eastern Arc montane forests have been relatively stable throughout the late Quaternary (Finch et al., 2009; Mumbi et al., 2008). Mumbi et al. (2008) were the first to document palaeoecological evidence of such stability from Kissing’-a-Rugaro (2100 m a.s.l.) in the Udzungwa Mountain bloc, recording the presence of moist forest during the last glacial period. A continuous 48,000-year pollen sequence from Deva-Deva (2600 m a.s.l.) in the Uluguru Mountains recorded persistence of moisture-dependent forest taxa throughout the glacial period, lending further support to the stability hypothesis (Finch et al., 2009). This new record from the Eastern Arc Mountains, although not extending into periods of greater aridity such as the last glacial maximum, provides insight into late-Holocene ecosystem responses to environmental change and anthropogenic influences, with high temporal resolution.

**Moist closed forest phase (AD 790–1275)**

The initial 500 years of the record is dominated by *Podocarpus* and *I. mitis* pollen and is characterised by low palynomorph diversity relative to the remainder of the sequence. According to the guidelines proposed by Coetzee (1967), high *Podocarpus* frequencies (70%) recorded at this time indicate the presence of *Podocarpus* forest. As the dominant tree species characterising Chome montane forest (Lovett and Pocs, 1993; Richard et al., 2014), *P. latifolius* is characteristic of moist montane forest (Beentje, 1994) and is thus considered here to be the likely parent taxon. Moist environmental conditions inferred from *Podocarpus* are corroborated by high percentages of *I. mitis*, an indicator of wet climate (Van Zinderen Bakker and Coetzee, 1988). Environmental indices suggest low levels of vegetation disturbance during this phase. Low CHARs suggest low rates of biomass burning which may be attributed to reduced ignitions and/or fire spread because of moist conditions.

Conditions inferred from most East African lake pollen records contrast with moist conditions inferred from Mt Shengena. For example, dry conditions are indicated at Lake Masoko in southern Tanzania from AD 750 to 1450 (840 m a.s.l.; Vincens et al., 2003); Lake Naivasha experienced a lowstand from AD 980 to 1270 (1890 m a.s.l.; Verschuren et al., 2000); Lake Victoria from AD 1030 to 1350 (1133 m a.s.l.; Stager et al., 2005) and Lake Emakat, in northern Tanzania, from AD 800 to 1200 (2300 m a.s.l.; Ryner et al., 2008). A pollen record from the Amboseli Basin (1146 m a.s.l.) in southern Kenya reflects relatively dry conditions between AD 550 and 1150, although a rapid transition to wet conditions is indicated from AD 1150 to 1400 (Rucina et al., 2010). Site-specific characteristics may provide a possible explanation for apparently moist conditions at Mt Shengena while other East African sites reflect dry conditions. Mt Shengena is a moist montane site and quite distinct from low-altitude medium to large lake systems with markedly different climatic and topographical characteristics. Lake Emakat is one of the few higher altitude lake records in East Africa (2300 m a.s.l.); however, even this site differs remarkably in climate regime receiving between 600 and 1000 mm yr⁻¹ where Mt Shengena receives 2000–3000 mm yr⁻¹. Close proximity of the Eastern Arc Mountains to the Indian Ocean provides a stable moisture source in the form of orographic rainfall that continued to support moist montane forest persistence during this period, even though other sites record pronounced ecosystem shifts. Hence, as during the last glacial maximum, pollen records from the Eastern Arc Mountains are characterised by relative ecosystem stability (Finch et al., 2009; Mumbi et al., 2008), a situation that continued into the late-Holocene.
Figure 5. Regional pollen profile for the Mt Shengena record, indicating CONISS-derived zonations and regional pollen sums.
Dry episode (AD 1275–1513)

*Podocarpus* increases until AD 1400, followed by an abrupt decline. Coupled with noticeably low frequencies of *I. mitis*, this is suggestive of drier or more seasonal climatic conditions relative to the preceding phase. Dry conditions at Mt Shengena are broadly compatible with lowstands recorded at Lakes Masoko (AD 1340–1430; Vincens et al., 2003), Naivasha (AD 1380–1420; Verschuren et al., 2000) and Victoria (AD 1360–1380; Stager et al., 2005). The reduced presence of montane forest taxa is accompanied by an increase in lowland forest taxa *Commiphora*, *Clutia* and *Croton*, further supporting the prevalence of drier conditions than the previous phase of the pollen record. A sustained increase in Ericaceae, most likely from the tree heather *Erica arborea*, is accompanied by increased CHAR, indicating the expansion of fire-adapted ericaceous scrub perhaps owing to more prevalent high elevation fires under the drier climate.

Figure 6. Total palynomorph profile for the Mt Shengena record, indicating dominant regional taxa, locally common taxa and pollen sums. CONISS-derived zonations are based on the regional data.

Early disturbance phase (AD 1513–1837)

The period post AD 1500 is characterised by greater levels of forest disturbance, an increase in pioneer taxa and sporadic anthropogenic signals after AD 1737. A sustained decline in *Podocarpus* is recorded, with a corresponding increase in *Ocotea*. These changes are contemporaneous with an increase in palynomorph diversity, suggesting a diversification of the vegetation, a characteristic often associated with intermediate disturbance (e.g. Mpanda et al., 2011). In general, the changes in community diversity may reflect local-scale, regional-scale and historical processes (Birks and Line, 1992). CHAR values are also elevated during this phase, consistent with increased biomass burning and persistent increases of Ericaceae and declining *Podocarpus* abundances.

According to archaeological evidence, in the form of distinctive *Kwale ware* pottery, the South Pare Mountains were
occupied, at least by low density populations, as early as ~AD 290 (1730±115 14C yr BP; Soper, 1967). However, *Ocotea* records a gradual increase during this phase, which suggests that logging of this targeted timber species was probably only initiated in the more recent past associated with the onset of the colonial, initially German and subsequently British, administration.

The appearance of maize pollen after AD 1737 provides one of the earliest records of this exotic crop in Tanzania. Maize was introduced into East Africa by the Portuguese trading diaspora during the 16th century via Zanzibar and the wider Swahili coast (Maddox, 2006). The earliest pollen evidence of maize from East Africa is from Lake Naivasha at AD 1690 (Lamb et al., 2003), with a later record from Lake Baringo at AD 1800 (Kiage and Liu, 2009). An early phytolith record of maize was recorded from Munsa in Uganda at AD 1780 (Lejju et al., 2005). Maize pollen is poorly dispersed (Jarosz et al., 2003) and its presence at Mt Shengena provides robust evidence of food production in the catchment. Evidence of maize production in the early 18th century at Mt Shengena corresponds to the expansion of the ivory trade in East Africa (Håkansson, 2004) and signifies a change in land use practices in the Pare Mountains. The Pare Mountains, adjacent to the main Pangani caravan trade route, would have been a focus of increased agricultural production to feed the growing number of people moving in and out of the East African interior; this crop being intertwined with 19th-century trade and export (Gallagher, 2016). Such rapid and extensive transformation of land would have resulted in the largely deforested montane landscape as characterised in the adjacent East Usambara Mountains at the turn of the 19th century (Schabel, 1990).

**Recent anthropogenic disturbance phase (AD 1837–present)**

Intensification of human activity at Mt Shengena is interpreted from several lines of evidence, notably the presence of exotic

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**Figure 7.** Comparative pollen relative proportions of target timber species *Podocarpus* and *Ocotea* and fire-adapted taxa Ericaceae and *Morella*, with indices of anthropogenic impact (cumulative pine and maize), pioneer species (cumulative Ericaceae and *Morella*) and disturbance (cumulative *Celtis*, *Croton*, *Macaranga*, *Neoboutonia*, *Nuxia* and *Vernonia*). Data are smoothed and plotted against time rather than depth to aid interpretation. CHAR and a continuous wavelet transformation showing significant periodicities (95% CI) in the time series. Grey shaded area shows pollen Zone S-1, 1837–present, a period of intense anthropogenic modification of the Mt Shengena landscape.
pollen and a marked decline in the commercially important timber genus *Ocotea* after AD 1837. The exotic genus *Pinus* becomes prominent in the pollen record after AD 1860. Other potential indicators include *Acacia*-type II pollen, which could have been derived from exotic *Acacia mearnsii* (black wattle), a widely grown and readily observable exotic tree that has become an invasive in the Chome Forest reserve today. Similarly, *Eucalyptus*-type pollen may be derived from the exotic timber tree *Eucalyptus*; however, this pollen type could also be derived from *Eugenia, Psidium* or *Syzygium* which produce similar morphotypes. CHAR values are highest and most variable during this period, indicative of high biomass burning and the possibility that fire emerged as a management tool, intermittently used within an increasingly fragmented landscape. The very low CHAR values at the turn of the 20th century could reflect management decisions to reduce fire incidents as plantation forests expanded with a mosaic design to reduce fire risk and spread.

Following establishment of a forest office at nearby Lushoto in 1901, the Chome Forest Reserve was first demarcated by the German colonial government in 1910. By 1951, the reserve was officially gazetted under the National Forest Policy to promote soil, water and biodiversity conservation. However, exploitation of the forest reserve continued because of a logging concession to a British company and persistent pit-sawing by the local communities (Forestry and Beekeeping Division (FBD), 2002). These activities led to a Tanzanian government ban on all timber harvesting in 1984, although collection of firewood, building materials and non-timber products by the local communities was still permitted (FBD, 2002). Despite these regulations, illegal timber harvesting has continued, with burning and grazing posing a threat to the existing cover and regeneration of forests (Figure 3). Relative to the steeper slopes, the plateau areas of the Pare Mountains are more densely populated and have been subject to progressive forest clearance (Hall et al., 2009). Remnant forests are now almost entirely restricted to government forest reserves such as Chome, proposed forest reserves and sacred forests (Hall et al., 2009). Decreased forest extent has direct consequences for ecosystem service provision to local communities, particularly water and fuelwood (Rodgers, 1993).

From AD 1930, increases in pioneer and fire-adapted taxon Ericaceae (Hamilton, 1982) are recorded simultaneously with increases in trilete fern spores and increased CHAR. These indicators point towards an expansion of ericaceous heathland, increase in bracken scrub and elevated fire frequency and extent, respectively. Similar indications have been recorded in the adjacent Mount Kilimanjaro region (Hemp, 2005). The expansion of ericaceous scrubland and *Pteridium aquilinum* has been identified as a management concern in Chome Forest Reserve (Figure 3d), emphasising the need for fire management strategies in the reserve and information on long-term ecosystem–fire interactions.

Concurrent with these shifts in vegetation composition, *Morella* pollen increases in the most recent part of the record (S-5). *Morella* pollen is almost certainly derived from the tree/shrub *M. salicifolia*, the only species of *Morella* recorded from the Eastern Arc Mountains (Lovett et al., 2006), and prominent within the Chome montane forest zone (Lovett and Pocs, 1993). *M. salicifolia* is a fire-resistant species (Livingstone, 1967, 1975) with a thick, corky bark and can be considered a fire indicator as evidenced by its bimodal altitudinal distribution on Mt. Kilimanjaro (Hemp, 2006a, 2006b). Increases in fire-adapted *Morella* in the Mt Shengena record coincide with highest rate amplitudes of CHARs, reflecting increased burning immediately around the swamp. Such increases have been similarly observed from other Eastern Arc Mountain sites, specifically on the Uluguru Mountains (Finch et al., 2009; Finch and Marchant, 2010) and Udzungwa Mountains (Mumbi et al., 2008); albeit asynchronous with the Mt Shengena signal, these provide further support that this taxon is particularly resilient to increased levels of fire-related disturbance within extant forests.

### Fire–vegetation and anthropogenic interactions

Centennial-scale fire–vegetation interactions are evident through the long-term decreases in *Podocarpus* and increases in fire-adapted and forest disturbance indicator taxa *Ericaceae* and *Morella* (Hemp and Beck, 2001; Lovett and Pocs, 1993). The increasing trend of pioneer index taxa abundances also suggests that the disturbance regime is linked to interactions between changing fire regime, land use and climate. The changes in biomass burning by AD 1275–1510 during the drier phase show a consistent increase in CHAR values and much higher variability. This transition from low levels of biomass burning to increased and more dynamic activity is reflected by an increase in high-frequency variability and this ‘flickering’ signal preceded a new state (Wang et al., 2012) of increased burning and much higher variability from AD 1510 to present with lasting effects on forest composition. These changes are concomitant with increased anthropogenic pressures on the landscape that may have altered fire regimes further and modified the forest landscape as human population pressures on forest resources and forest-agriculture mosaics expanded. A complex interaction between human-modified and long-term climate-mediated land cover changes with the montane atmosphere could have impacted the local hydroclimatic regime (Salazar et al., 2016) to sustain a novel fire regime at this site. The changes in forest composition and structure in moist montane ecosystems alter the moisture balance and seasonality with implications on the pyrodiversity of a landscape and influences fire–vegetation interactions at multiple spatiotemporal scales (Parr and Andersen, 2006; Parr and Brockett, 1999). The wavelet transformation of CHAR shows persistent periodicity patterns in the time series data and can show periods of abrupt transition. Warm colours suggest stronger temporal patterns in the data of a given periodicity (in years) and the increasing regularity of burning, as well as an increase in the biomass burned (higher charcoal accumulation rates) persisting over the recent centuries. This suggests that fire activity on the Kwasebuge landscape increasingly exhibited underlying patterns at centennial to decadal scales, interpreted as increasing rates of biomass burning and greater cyclical temporal patterns since 1250 AD and becoming much more consistent since 1600 AD (Figure 7). The stepwise intensification of biomass burning at short (decadal) periodicities may suggest increasingly deliberate burning and more intensive land use and land cover changes (Colombaroli et al., 2014).

### Anthropogenic signals in the pollen record

Disentangling fluctuations in pollen taxa as either climatically or human-induced is problematic (e.g. Hamilton et al., 1986; Perrott, 1987; Taylor et al., 2000), especially given the limited number of unambiguous indicators in East African records (Heckmann et al., 2014; Vincens et al., 2003). The presence of robust indicators, maize and pine has allowed for this limitation to be partially overcome in the case of Mt Shengena. Nevertheless, it remains difficult to attribute underlying drivers of ecosystem change, such as the dramatic decline in *Ocotea* pollen after AD 1837 to deforestation. It is tempting to attribute declines in forest taxa to forest clearance, particularly in the context of Chome Forest Reserve where deforestation is a long-standing issue (Figure 3c). For example, *Podocarpus* shows a sustained decline over the duration of the record; however, since forest disturbance, pioneer and anthropogenic signals only escatate later in the record, it seems unlikely that the primary driver of a long-term decline is
The environmental indices presented reveal an unmistakable increase in disturbance that falls within two main phases: (1) a relatively low level of disturbance from c. AD 1513 to 1837 and (2) a much more pervasive and high magnitude phase of disturbance in the latter part of the record from c. AD 1837 onwards (Figure 7). This second phase is characterised by an increase in pioneer, forest and anthropogenic indices, in addition to CHAR, with a corresponding decrease in the presence of key timber species such as Ocotea and Podocarpus (Richard et al., 2014; Figure 7). These changes provide evidence for the timing and character of human activity in the vicinity of Mt Shengena. Interaction between climatic, land cover and anthropogenic drivers was important to forest compositions changes, notably the long-term decreases in Podocarpus and increased Ericaceae and CHAR. The persistence of decadal- and centennial-scale periodicities in the CHAR time series also suggests changes to the regularity of burning and charcoal deposition into the bog sediments (Figure 7). The extensive encroachment of agriculture into the forested landscape led to a progressively more open environment as use of the forest intensified during the 19th century. Dramatic declines in Ocotea after AD 1837 are coincident with the onset of pollen taxa indicative of anthropogenic activity, in addition to high values for the pioneer and forest disturbance indices, suggesting Ocotea declines were anthropogenically induced. Large-scale removal of mature O. usambarensis trees would have resulted in a dramatic drop in pollen production, as testified by sharp declines in the fossil pollen of this taxon. Interestingly, Podocarpus percentages increase slightly after AD 1870, which may be attributed to a change in the relative abundance of these two dominant species. O. usambarensis is extremely slow growing (Bussmann, 1999), despite having good regeneration properties (Lovett and Pocs, 1993). Thus, removal of mature O. usambarensis trees may have facilitated proliferation of other species.

Regardless of the long history of regional human occupation (Heckmann et al., 2014), the Mt Shengena pollen record suggests that the intensification of human impacts on the forests of the South Pare Mountains has been largely restricted to the past 170 years. This corresponds to the peak of the caravan trade in the mid-19th century that paved the way for wide-scale exploitation and settlement by colonial administrations. East Africa became a key supplier of elephant ivory during the 19th century, serving a range of growing industries (e.g. cutlery, piano and billiard-ball manufacturing). Between AD 1840 and 1875, British demand alone escalated from ~200,000 to >800,000 kg of ivory per annum; estimates suggest that the trade would have required a supply of between 4000 and 17,000 elephants per year to fulfil this demand (Håkansson, 2004; Sheriff, 1987). Each of these tusks would have to be carried and the porters fed by a series of trade relationships; farming communities in proximity to long-distance trade routes would have been increasingly encouraged to produce an agricultural surplus to supply the caravans (Håkansson et al., 2008) in the developing market economy. Such massive demand to feed the large caravan trains would have led to forest clearance pressures in the South Pare Mountains for agricultural expansion, as evidenced by increased crop presence concomitant with decreases in forest cover. According to Håkansson (2008), the South Pare Mountains in the 1850s formed a key part of the regional economy of northern Tanzania including exchange of livestock, crops and tools. At this time, the rich iron ore deposits of the Pare provided a regional supply of iron (Håkansson et al., 2008), smelting of which would have further contributed to forest exploitation. It is difficult to judge whether evidence of forest clearance in the pollen record is due primarily to agricultural expansion or iron smelting; the most likely explanation is a combination of the two.

**Conclusion**

The Mt Shengena core provides a 1200-year sedimentary record of ecosystem history from the Eastern Arc Mountains, drawing on pollen, charcoal and radiocarbon analysis, and supported chronologically by marker horizons derived from exotic pollen and a 137Cs activity profile. The record allows for the following conclusions to be drawn: (1) prior to AD 1275, the record is characterised by fairly moist climatic conditions contrary to indicators from many East African sites; this discrepancy may be explained by the relative stability of the Eastern Arc montane ecosystems. (2) This stability was not sufficient to prevent dry forest expansion under more extreme regional aridity from AD 1275 to 1513. (3) The agricultural food crop maize appears in the pollen record from AD 1737 onwards indicating increased food production potentially linked with the growing caravan trade. (4) By applying a series of environmental indices, it is apparent that after AD 1837, anthropogenic activity and forest disturbance became the primary drivers of vegetation change, with sharp declines in Ocotea attributed to forest clearance in the area. The timing of anthropogenic intensification at Mt Shengena corresponds closely to the peak of the caravan trade around AD 1850, when the Pare Mountains would have played a critical role in supplying the Pan-gani trade route. (6) Palaeoecological techniques, as applied in this research, can improve our understanding of long-term ecosystem dynamics. Such information is vital to inform conservation and management strategies that are increasingly challenged to combine demands on ecosystem service provision from remaining forest remnants to a growing population under increasing impacts of climate change.

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