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Evenness peaks in fire-resilient vegetation preceded ecosystem shifts in East Africa

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E-mail: aleman@cerege.fr and christopher.carcaillet@ephe.psl.eu**Keywords:** fire regime, diversity indices, richness, savanna, tropical forest, rate-of-change, Miombo woodlandsSupplementary material for this article is available [online](#)**Abstract**

Fire is often assumed to be a key driver in shaping tropical vegetation structure and composition in grass-dominated ecosystems, while forests experience infrequent but impactful fires that influence ecosystem resilience. Although short-term interactions between fire and vegetation are well-documented, long-term dynamics remain underexplored. This study examines fire regimes, vegetation dynamics, and its biodiversity over the past 17 000 years in southwest Tanzania, using sedimentary charcoal and pollen. Major ecological transformations of vegetation and fire regimes were recorded, with vegetation changes consistently preceded shifts in fire regimes. Increased grass pollen correlated with more frequent or larger fires, while high tree cover in Miombo woodland reduced fire activity. Interestingly, pollen evenness was a precursor to major ecological transformations as peaks preceded changes in ecosystem states. Changes in precipitation and moisture seems the major top-down drivers of these changes in vegetation and fire. Fire regimes were indirectly controlled by water availability, and vegetation exhibited resilience to fire at centennial timescales before reaching ecosystem shifts at 12 400 and 1700 cal BP. Our results emphasize the critical role of tree and grass cover in shaping fire regimes and highlight the interplay between climate, vegetation structure, and fire in East African ecosystems.

1. Introduction

The vegetation structure and composition of African grass-dominated ecosystems, such as savannas and Miombo woodlands, are assumed to be influenced by fire, which interacts with precipitation and water deficit [1, 2]. Fire regimes—frequency, intensity, or extent—are sensitive to changes in precipitation and its seasonality, which modulate fuel accumulation and flammability [3, 4]. In tropical forests with denser tree cover, fire is rare or naturally almost absent [5, 6] but, when it occurs, can deeply impact biodiversity and ecosystem resilience [7, 8].

Changes in climate and fire regimes are expected to modify tree and grass cover, impacting biodiversity, biogeochemistry [9, 10], and ecosystem services [11]. While short-term interactions between fire, climate, and vegetation are relatively well understood [12], the timing, duration and pace of these changes remain poorly resolved. Understanding how biodiversity, including composition and evenness, which reflects the even distribution of species within a community, responds to fire and climate shifts over centuries is critical, unless fire regimes respond to changes in vegetation composition, which controls fuel quality and biomass.

Long-term data are essential to assess whether biodiversity shifts align with environmental changes or lag behind, providing insights into ecosystem resilience [13].

Since the Last Glacial Maximum (LGM), East Africa underwent climate and vegetation transformations [14], likely influencing fire regimes (details in Supplementary data). Post-LGM warming was accompanied by increased precipitation [15, 16], driving shifts from Afromontane to lowland tropical forests and Miombo woodlands [17, 18]. Precipitation peaked around 13 500 calibrated years before present (cal BP) then declined between 12 900 and 11 800 cal BP [19], with varied regional aridity [20]. The East African Humid Period (AHP) at the Holocene onset \sim 11 700 cal BP [21] regionally featured increased precipitation but prolonged local dry seasons [22], likely altering fire activity, disrupting vegetation and resulting in ecosystem state changes. During the late Holocene (1800–1500 cal BP), Iron Age farming triggered land-use changes and technology diffusion to the eastern plateaus [23–25]. Although human activity contributed to biomass burning for agriculture and grazing [26], its influence remains debated, with some attributing tree cover and fire changes mainly to climate until the 20th century [27, 28].

These environmental changes have likely influenced biodiversity with aftermaths on ecosystem resilience. While tropical forests exhibit higher plant diversity than grasslands [29], fire regimes and their interactions with landscape, soil, precipitation and grazing, influence species richness, diversity and evenness ([30–33] see development in Supplementary data). Evenness, alongside richness, is a key component of biodiversity [34, 35], providing insights into species dominance and community structure (figures SI2 and SI3 in Supplementary data). Communities typically consist of a few dominant species, numerous subordinate species (secondary), and many rare ones [36, 37]. While perfect evenness is naturally unattainable, it can rise during transitional phases, when communities shift between stable states, in response to changes in climate or disturbance regimes (figure SI4). We hypothesize that such transitions, marked by higher evenness, occurred before the Miombo woodland expansion and following the Iron Age peoples arrival, aligning with significant shifts in ecosystems and fire regimes.

To test this hypothesis, we used an original charcoal record and published sedimentary pollen [17, 38] record from Lake Masoko, southwest Tanzania, to reconstruct vegetation, plant diversity and fire regimes since 17 000 years. Past biomass burning was assessed using sedimentary charcoal [39], but interpreting charcoal records to infer fire regimes remains challenging [40], especially in tropical Africa where high-resolution charcoal data are scarce [41] and studies linking charcoal accumulation to fire

parameters limited [42, 43]. Overall, fire intensity and burned area influence charcoal deposition in grasslands, with larger, intense, or nearby fires contributing more [42, 44, 45]. However, paleo-fire frequency is constrained by analytical resolution, often exceeding short fire intervals typical of grasslands [46]. To address these complexities, we interpret charcoal accumulation rates (CHAR) as a proxy for biomass burning, with peaks indicating very frequent or large fires (figure 1).

These reconstructions were contextualized within regional climatic changes and human activity. While precipitation shifts and land-use expansion likely influenced ecosystems, abrupt vegetation changes are expected to align with shifts in fire regimes. Understanding these long-term interactions provides insights into the resilience of tropical ecosystems under climatic and anthropogenic pressures.

2. Material and methods

2.1. Study site

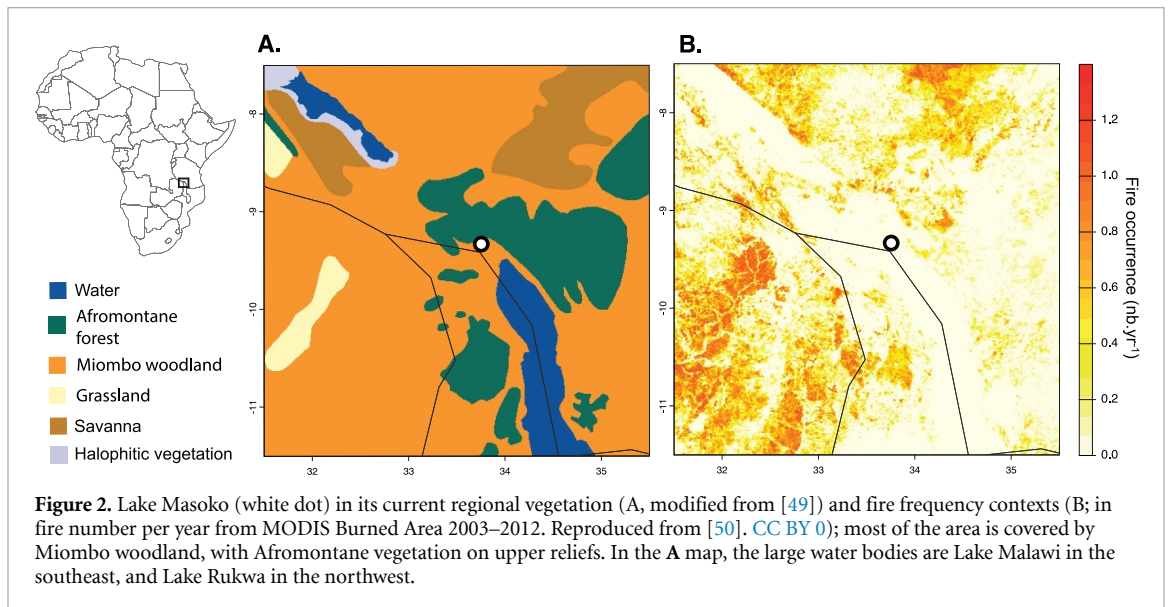
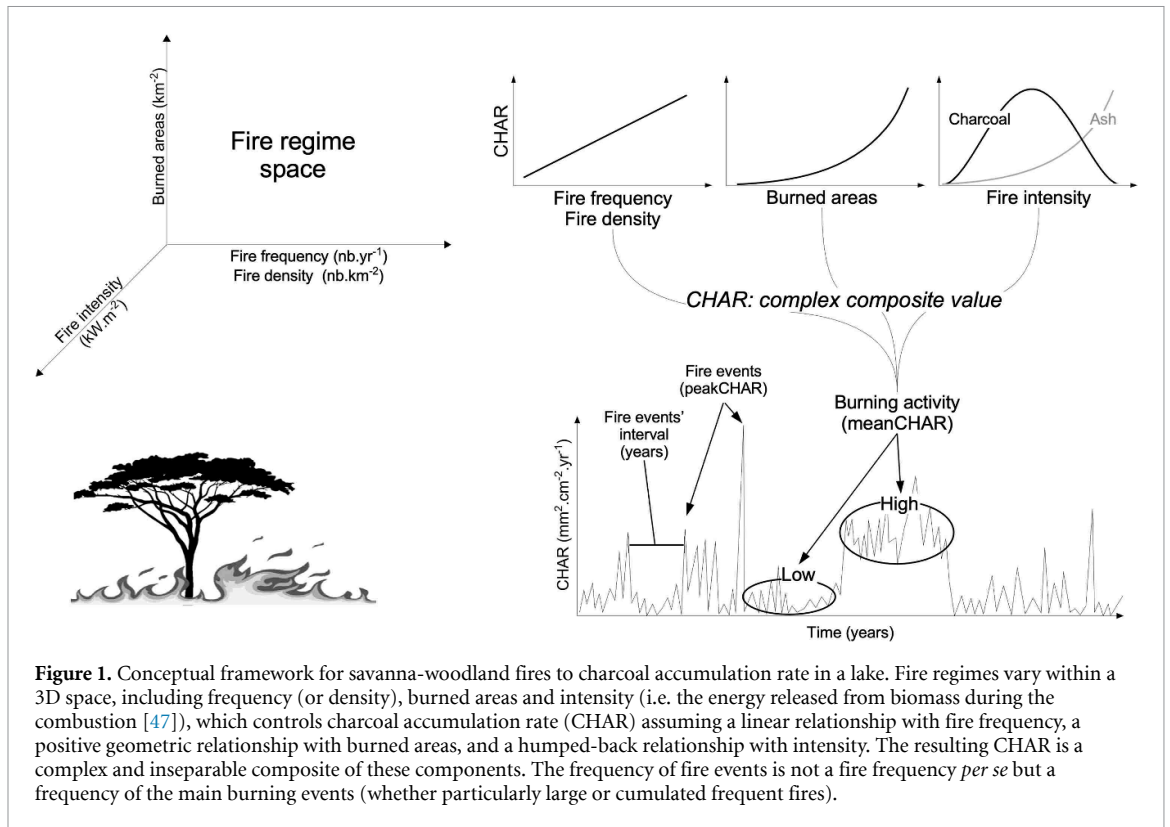
Lake Masoko, located in southern Tanzania ($9^{\circ}20.0' S$, $33^{\circ}45.3' E$, 840 m asl; figure 2) in the Rungwe volcanic area, lies between Mount Rungwe and Lake Malawi. This circular volcanic crater lake, formed 50 000 years ago [48], has a diameter of 900 m, a U-shaped topography with steep slopes and a flat bottom (maximum depth 38 m). Its catchment area (0.22 km^2) is small relative to its surface area (0.36 km^2).

The region's rainy season (November–May) aligns with Southern Hemisphere trade winds; the dry, windy season spans May–October [51]. Southern Rungwe receives higher precipitation ($\sim 2400 \text{ mm yr}^{-1}$) than the regional average ($\sim 1200 \text{ mm yr}^{-1}$) due to orographic uplift of humid air masses from Lake Malawi, which condense over highlands [52].

The surrounding plateau is currently dominated by dense dry tropical woodlands called Miombo [49], primarily composed of *Brachystegia* and *Uapaca* species, along with *Isobertinia* and *Julbernardia*, with grass understories burning regularly (figure 2), maintaining the woodland's ecological balance [53, 54]. The crater rim and southern depression are cultivated, while lowland forests persist in less disturbed areas. Above 1500 m asl, vegetation transitions to Afromontane ecosystems, ranging from montane evergreen forests to grasslands [49]. Moist montane areas ($1500\text{--}2000 \text{ mm yr}^{-1}$; 0–3 dry months) are dominated by *Olea capensis*, while drier zones above 2000 m ($800\text{--}1700 \text{ mm yr}^{-1}$; ~ 4 dry months) feature *Podocarpus*, *Juniperus procera*, *Olea africana* and Ericaceae.

2.2. Stratigraphy and chronology

The Masoko composite core [55] spans the entire 50 000 year history of the crater, with its chronology



established using 25 AMS radiocarbon dates of organic matter [48]. Layers of tephra and turbidites thicker than 1 mm were removed from the original depth scale and the radiocarbon ages were assigned to turbidite- and tephra-free layers [56]. These radiocarbon ages were calibrated using the latest calibration curve (figure SI1 [57]). Here we focused on the last 17 000 cal BP, for which the median chronological resolution is ~ 30 years \cdot cm $^{-1}$.

2.3. Sampling and charcoal analysis

Sediments subsamples of 2 cm 3 were taken continuously at every 1 cm-depth, soaked in a 5% KOH solution, bleached in a 10% aqueous solution of NaOCl, and sieved through a 160 μ m mesh [58, 59]. The samples were then washed into a Petri dish for area assessments of individual charcoal under a microscope at 40 \times magnification. In total, 715 samples were measured [60]. Due to the small

catchment area of Lake Masoko, most charcoal fragments are likely wind-transported [42, 43].

2.4. Numerical and statistical analyses of charcoal and pollen data

Charcoal concentration were converted to charcoal accumulation rate (CHAR, $\text{mm}^2 \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$) and resampled to the median resolution ($30 \text{ years} \cdot \text{cm}^{-1}$) using the 'pretreatment' function of the *tapas* R package [61]. Peak detection analysis [62] was applied by decomposing the record into a long-term background trend and short-term peaks using a 1000 year locally weighted polynomial regression. The optimal window size was selected using the signal-to-noise index [63]. Peaks were isolated by subtracting the background from the smoothed series, with a 95th-percentile threshold determined via a Gaussian mixture model. Interpretation of charcoal series in paleo-fire regimes is based on the rationale developed in Supplementary data and illustrated in figure 1: in grass-dominated ecosystems, charcoal peaks likely represent aggregated fire events rather than individual fires and illustrate periods of elevated fire activity.

The frequency of these peaks was estimated using a Gaussian kernel density approach with a 500 year bandwidth and pseudo-replicated values to correct edge bias, applying a modified 'kdfreq' function from the *paleofire* R package [64]. Change points in CHAR, reflecting changes in biomass burning, were detected using the *beast* R package employing Bayesian estimation of change-points in the slope of multivariate time-series, selecting points with a probability >0.9 . To enhance visualization of biomass burning trends, CHAR values were standardized using a Box-Cox power transformation: (1) rescaling via a minimax transformation, (2) homogenizing variance using the Box-Cox method, and (3) converting to z-scores [65].

To analyze vegetation dynamics, we applied non-metric multidimensional scaling (NMDS) on a Bray-Curtis dissimilarity matrix [66], using the total pollen assemblage [17, 38] and the *vegan* R package [67]. The NMDS coordinates were averaged every 1000 years, millennium centered and plotted to summarize vegetation trajectory over the last 17 000 years.

We also computed five indices: rate-of-change (RoC, [68]), taxonomic richness, two biodiversity indices (N_1 , N_2), and evenness (formula in Supplementary data). RoC quantifies the magnitude of changes between two adjacent pollen spectra per time unit. RoC was calculated using the *R-Ratepol* package [69] with a χ^2 dissimilarity coefficient and a Shepard's 5-term smoothing filter. Pollen data were standardized to a maximum of 150 terrestrial pollen per sample, and RoC was estimated using a 250 year moving window, repeated 1000 times to generate confidence intervals, reducing age uncertainties and statistical artifacts [69, 70]. Pollen richness N_0 [71, 72], biodiversity indices (N_1 , N_2), and evenness were

assessed via rarefaction to correct for sample size biases [73, 74]. N_2 (Simpson diversity index) was used in line with the mass:ratio hypothesis [37], which emphasizes the role of dominant taxa (in abundance or mass) in controlling ecosystem functioning. In contrast, N_1 (Shannon diversity index) gives more weight to less abundant taxa, which have low functional redundancy in tropical forest ecosystems [75]. Using the *rrarefy* function from the *vegan* R package, we resampled pollen counts 1000 times to the smallest sample size ($n = 321$) to estimate mean pollen richness (N_0) and evenness ($N_2:N_0$) with 95% confidence intervals [76].

Although richness and evenness describe the number and distribution of taxa, they do not capture taxonomic identity. Distinct communities can have similar richness and evenness but differ in composition. In contrast, the compositional rate-of-change (RoC) accounts for taxa identity, detecting shifts in community type. Evenness specifically reflects the structure of a community by quantifying the number and relative abundance of taxa. Evenness and RoC are thus complementary to assess plant community changes, potentially revealing different trajectories.

The original resolution of both datasets was maintained for the analysis of temporal trends. For biplot comparison of vegetation and fire parameters, charcoal data were aggregated into 300 year bins to align with the lower temporal resolution of the pollen data. When multiple pollen samples were present within a 300 year interval, their values were also averaged. This binning approach smoothed fire activity data, reducing short-term variability and improving comparability with the averaged pollen data.

A regime shift refers to a substantial, often abrupt, and persistent reorganization in the structure and function of an ecosystem, typically resulting from a change in the dominant internal feedbacks that maintain the system's stability [77]. Such shifts differ from gradual transitions and are characterized by the system crossing a critical threshold, beyond which it reorganizes into a state with distinct structural and functional attributes. In our study, we identify these shifts by detecting sharp peaks in ecological indicators followed by rapid declines. These abrupt changes were identified using peaks in RoC and evenness, which we used to pinpoint the timing of ecosystem transitions.

3. Results

3.1. Charcoal-based fire activity history

CHAR exhibits significant variability over the past 17 000 years. A prolonged period of low fire activity occurred between 17 000 and 11 000 cal BP (figure 3(A) and (B)). CHAR began rising at the Holocene's onset, peaking between 10 700 and 9400 cal BP. A minimum was reached at 6400 cal BP, followed by an increase at 5800 cal BP with intermediate fluctuations until 1600 cal BP. Around 1500 cal BP,

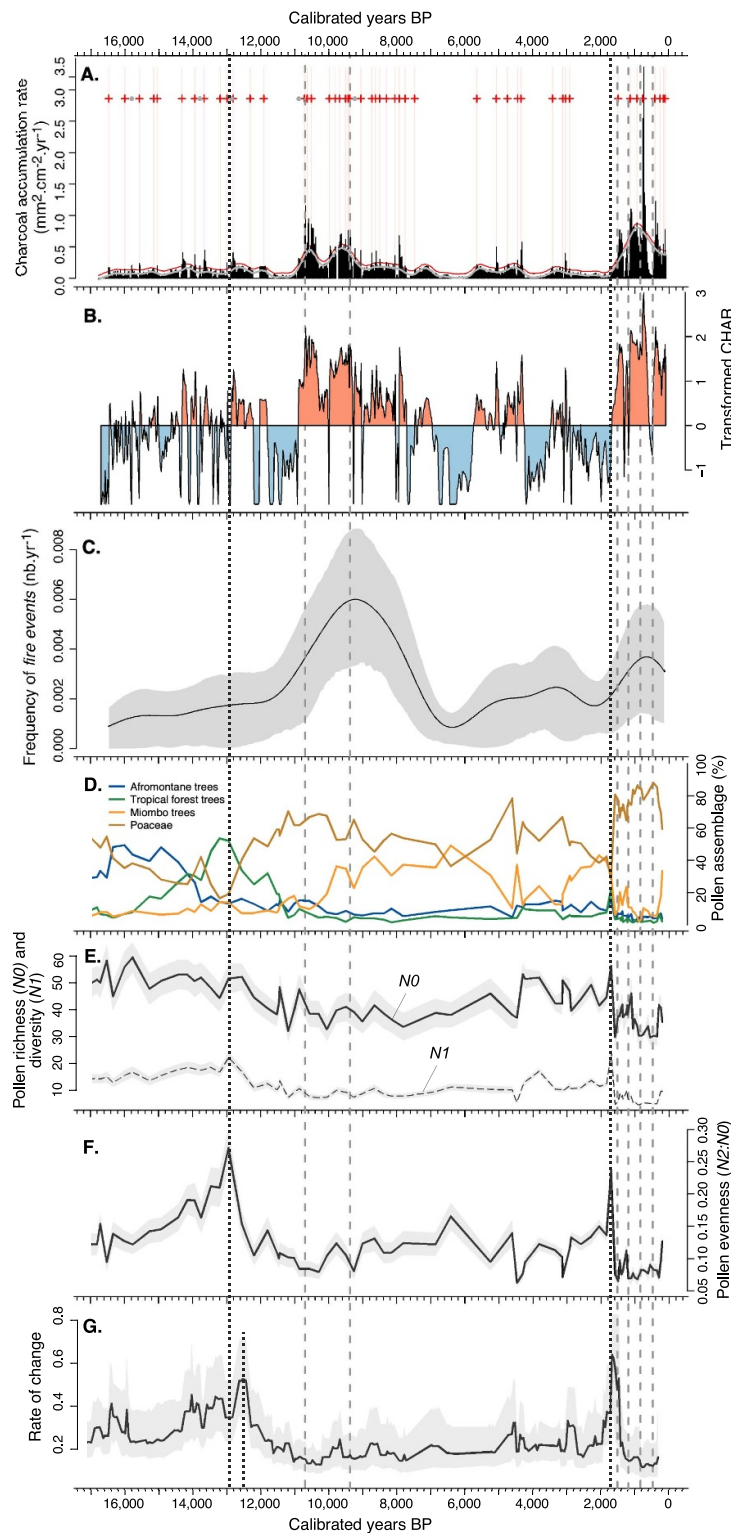


Figure 3. Fire history reconstructions and pollen-based vegetation and biodiversity trajectories at Lake Masoko, SW Tanzania. (A) Charcoal accumulation rate or CHAR (black histograms) and resulting main *fire events* (red crosses) from peak analysis, (B) Box–Cox-transformed CHAR highlighting biomass burning trends where positive values (red) indicated periods of increased fire activity relative to the mean, and negative values (blue) indicate reduced fire activity; and (C) frequency of *fire events* estimated from peak analysis and smoothed using a Gaussian kernel density (500 year bandwidth) with a 95% confidence interval. (D) Synthetic pollen record (original data: [17, 38]), organized in four pollen groups, and according to the new age~depth model. (E) Rarefied pollen richness (N_0 , the total number of taxa as the full black line, and N_1 , the exponential of Shannon diversity index as the dashed gray line) and (F) evenness ($N_2:N_0$), where N_2 corresponds to the Simpson diversity index (cf. Supplementary data). (G) Rate-of-change (RoC, pollen data bin: 250 years). Vertical dashed gray lines represent significant CHAR changes based on change point analysis: 10 700, 9400, 1550, 1200, 850, and 500 cal BP. Vertical dotted black lines pinpoint the date of the maximal evenness values (12 950 and 1700 cal BP) and RoC (12 400 and 1650 cal BP).

CHAR sharply rose, showing a pattern similar to the period between 10 700 and 9400 cal BP but reaching the highest values in 17 000 years (figure 3(B)).

The frequency of *fire events* ('frequency') was initially low until 11 500 cal BP, then increased six-fold by 9000 cal BP (figure 3(C)). From 9000 to 6500 cal BP, frequency decreased to a steady period between 6000 and 1800 cal BP. After 1500 cal BP, frequency rose again but remained below levels between 11 000 and 8000 cal BP (figure 3(C)), despite higher overall CHAR.

3.2. Vegetation change inferred from pollen analysis

Vegetation reconstructions reveal transitions between ecosystem types (figure 3(D)). Between 17 000 and 14 000 cal BP, open Afromontane vegetation dominated, with Poaceae exceeding 50% and a minor tropical forest trees presence. By 15 000 cal BP, tropical forest trees started to expand, peaking at 13 200 cal BP, before declining steadily until 11 000 cal BP. Concurrently, Poaceae increased (>60%) followed by a rise in Miombo trees around 10 000 cal BP marking a major ecological shift. Poaceae peaked near 11 000 cal BP, while Miombo trees reached a plateau of higher abundance between 10 000 and 5500 cal BP. From 10 000 to 1800 cal BP, assemblages reflected fluctuating proportions of Poaceae and Miombo trees. Since 1800 cal BP, grasses dominated (>70%), characterizing the most recent vegetation state.

Throughout the 17 000 year sequence, the diversity index $N1$ closely mirrors $N0$ (figure 3(E); $r^2 = 0.74$; $p < 0.0001$), as expected given $N1$ accounts for rare and poorly abundant taxa. Additionally, $N2$, which emphasizes more abundant taxa and was used for the calculation of evenness (figure 3(F)), strongly correlates with $N1$ ($r^2 = 0.91$; $p < 0.0001$), highlighting consistent patterns across diversity metrics.

The Late Glacial period is marked by high pollen richness ($N0$), which declines around 12 500 cal BP (figure 3(E)). While $N0$ decreases, $N1$ increases slightly, reflecting a better balance of taxa proportions. This decline in richness, but not in $N1$, coincides with reduction in Afromontane and tropical forest trees, and the establishment of grass-dominated ecosystems. At 12 950 cal BP, evenness ($N2:N0$) and diversity ($N1$) peaked, reaching their climax over the past 17 000 years (figure 3(F)). Following this peak, evenness dropped sharply, halving by 12 200 cal BP, and remained low until 2000 cal BP. Around 1700 cal BP, evenness and diversity abruptly and shortly peaked again, before reaching their lowest levels with a decline in richness at 1500 cal BP (figure 3(E) and (F)).

The rate-of-change (RoC) peaked at 12 400 cal BP, 500 years after the evenness climax (figure 3(G)). RoC then decreased until 11 000 cal BP and remained low for the following 9000 years, indicating a prolonged

stability in plant communities compared to the unstable 14 000–11 000 cal BP period. At 1650 cal BP, RoC surged again during a 250 year phase of vegetation instability, before steadily declining to its lowest levels over the past 17 000 years (figure 3(G)).

The NMDS analysis highlights a dynamic and unstable Late Glacial period (17 000–11 000 cal BP; figure 4, positive side of NMDS1-axis), marked by a major shift in pollen assemblages from Afromontane trees and shrubs (e.g. *Podocarpus*, *Ilex*, *Juniperus*, Ericaceae), to tropical forests taxa (*Macaranga*, *Celtis* and Moraceae). The entire Holocene lies on the negative side of the NMDS1-axis. Between 10 000 and 6000 cal BP, a stable period is recorded, characterized by *Uapaca nitida*, *U. kirkiana*, *Brachystegia*, *Protea*, *Allophylus* and *Apodytes dimidiata*. Assemblages shifted again around 6000–5000 cal BP but stabilized until 3000 cal BP, followed by a 2000 year major shift (figure 4) characterized by Poaceae and Asteraceae, with some taxa linked to cultivation (i.e. *Ricinus*).

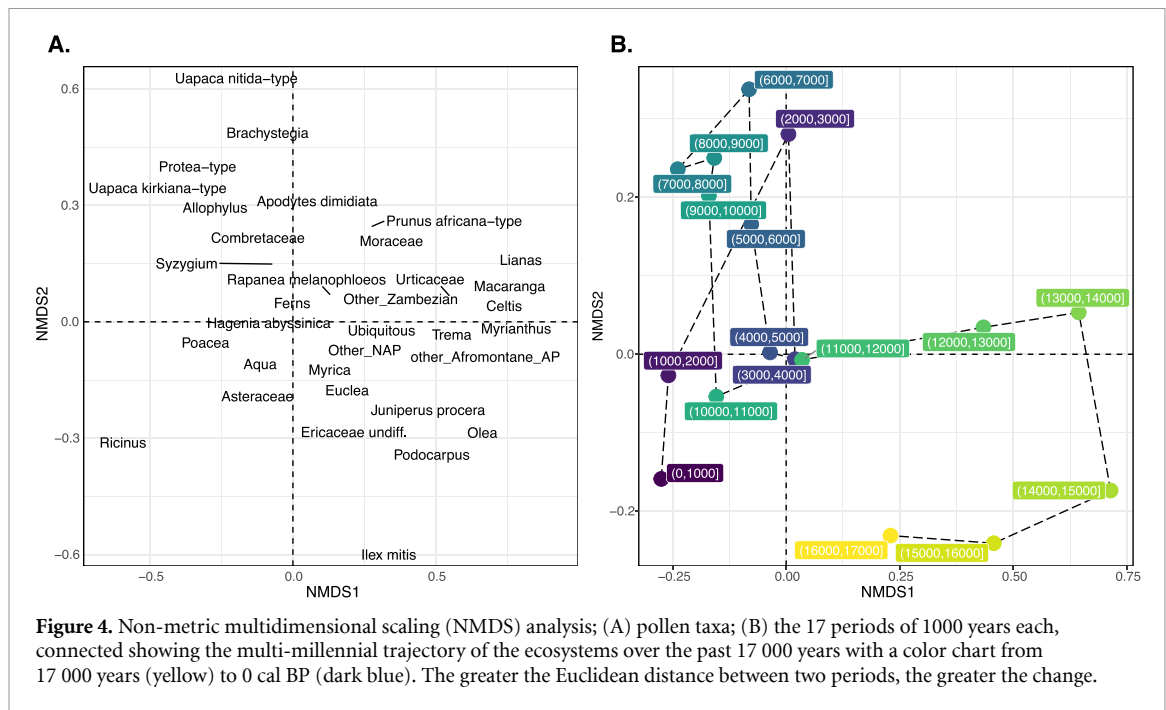
3.3. Relationships between vegetation and fire regime

The trajectory analyses (figures 3 and 4) indicate that vegetation changed before fire activity. Therefore, biplots in figure 5 compare fire parameters in relation to vegetation. Frequency and biomass burning, inferred from CHAR (figure 1), were negatively correlated with pollen richness $N0$ (figure 5(A) and (C)), with the highest frequency occurring during periods of low pollen richness, and vice versa ($p < 0.001$). The lowest frequencies corresponded to periods dominated by Afromontane and tropical forest, while Miombo woodland showed high pollen richness variability, which correlated with fire fluctuations (figure 5(A) and (C)). This contrasts with the more stable low-fire regimes of Afromontane and tropical forests.

However, frequency and CHAR did not follow the same patterns with tree cover in Miombo woodland, measured by Miombo trees to Poaceae pollen ratio (figure 5(B) and (D)). While frequency showed no clear trend (figure 5(B)), CHAR exhibited an inverse J-shaped relationship ($pseudo-r^2 = 0.44$, $p < 0.05$, fitted on Holocene data only, 11 000–0 cal BP), suggesting a threshold beyond which high Miombo tree cover suppressed fire activity (figure 5(D)).

4. Discussion

This study reveals significant ecological transformations in southwest Tanzania over the past 17 000 years, including changes in fire regimes, vegetation cover and biodiversity. While fire and vegetation changes can occur concomitantly, chronological lags were also observed with these major changes. The discussion examines fire-vegetation relationships in the context of modern processes, emphasizing biodiversity and time lags, explores the impact of these dynamics on



ecosystem stability, and finally places these findings within the broader East African context of paleo-burning, climate and human activity.

4.1. No linkage between vegetation and fire during the Late Glacial

Between 17 000 and 11 000 cal BP, vegetation underwent two major transitions: from Afromontane forest coexisting with grasslands, favored by low $p\text{CO}_2$ and temperature at the elevation of Lake Masoko [78], to lowland tropical forest around 14 000 cal BP, and then to a grass-dominated ecosystem by 12 600 cal BP (figures 3(D) and 4(B)). These transitions were characterized by a gradual increase in both evenness and rate-of-change (RoC), with evenness peaking at 12 950 cal BP, i.e. 500 years before the peak in RoC (figure 3(E)–(G)). This suggests a significant community reorganization before transitioning to a stable state. During this unstable period lasting until 11 000 cal BP (figure 4), richness declined gradually, when the system stabilized as grass-dominated, without changes in diversity (N_1), evenness or RoC (figure 3(D)–(G)).

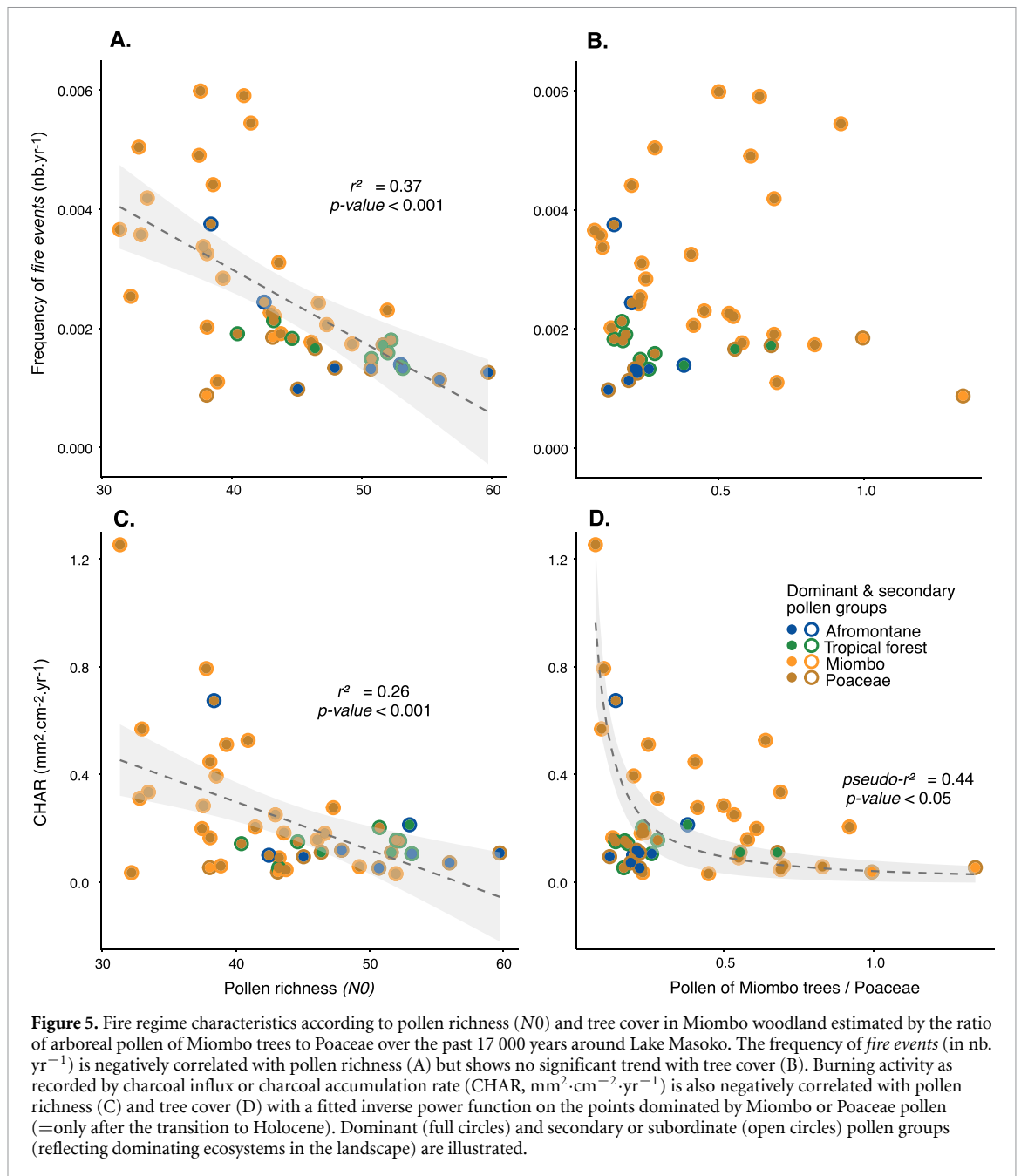
None of these changes were linked to significant shifts in fire regimes; even low burning was recorded between 12 000 and 11 000 cal BP, while grasslands expanded (figure 3). This challenges the widely held assumption that fires, in combination with climate, drive vegetation changes and patterns in such African ecosystems [33, 79, 80]. It suggests that fire may not have played a key role in the macroecological transformations between 17 000 and 11 000 cal BP, which were likely driven primarily by climate change, as assumed but without having tested for the potential effect of fire [17]. This also

implies that forest-savanna transitions at this macro-scale may not be driven by fire, despite previous assumptions [81, 82].

4.2. Vegetation and diversity interacted with fire during the Holocene

The first major change in burning activity occurred at 11 000 cal BP, coinciding with a stable grass-dominated ecosystem (figure 3). While the frequency of *fire events* steadily increased, CHAR fluctuated, likely indicating changes in burned areas or fire intensity [42]. Pollen richness declined alongside the reduction in tree components, as tropical grass-dominated ecosystems typically exhibit lower plant richness than forests [29]. This decline may also reflect the underrepresentation of savanna herbaceous diversity in the pollen record, as forbs, which are primarily insect-pollinated, are less represented compared to wind-pollinated grasses [83]. This is a limitation in paleo-diversity studies, because forb richness in savanna is today higher than grass richness [84], whereas grass cover largely dominates forb cover [85]. Despite increased fire activity, stable evenness and RoC suggest that plant communities remained resilient (figure 3), with savanna structure likely shaping fire regimes (figure 5), as plant biomass and traits drive savanna flammability [86].

Around 9000 cal BP, frequency declined gradually until 6000 cal BP, a period of ecosystem stability marked by increasing Miombo tree cover. Fire activity reached its lowest level between 6600 and 6200 cal BP, coinciding with a peak in Miombo trees. After 6000 cal BP, as Miombo trees declined and grasses increased, fire activity rose, highlighting the



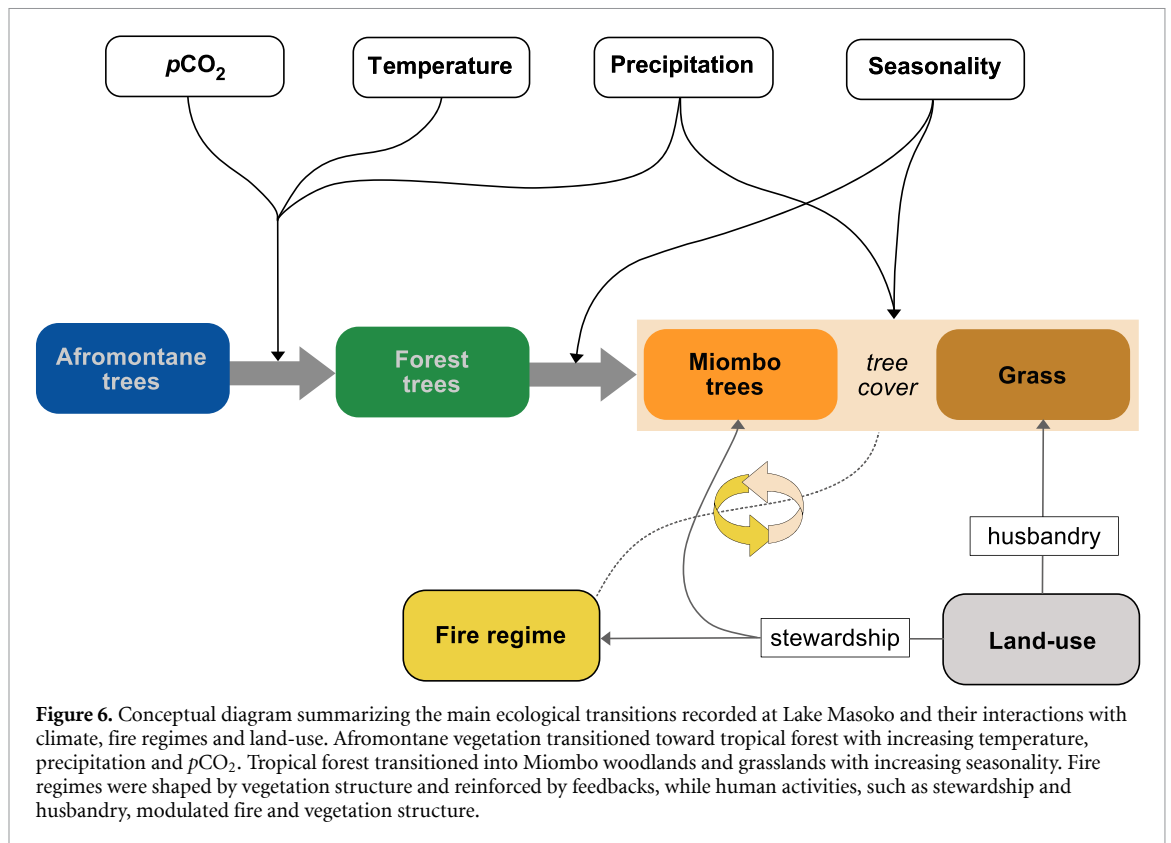
opposing influence of grasses and Miombo trees in fire dynamics [87].

4.3. Human influence on fire and vegetation in the Late Holocene

The late Holocene marks a significant ecological transition, with shifts in vegetation composition and fire regimes (NMDS, figures 3 and 4), likely influenced by human activity. Around 1700 cal BP, simultaneous peaks in pollen richness (N_0), diversity (N_1) and evenness ($N_2:N_0$), followed by a peak in RoC at 1650 cal BP, indicate significant reorganization of plant communities. This period coincides with the expansion of grasses, a decline in Miombo trees and the collapse of Afromontane and tropical forest trees. By 1550 cal BP, fire activity increased, yet with

a 150 year lag after the main vegetation changes, as indicated in RoC and diversity values. This delay suggests that vegetation restructuring, likely influenced by human land-use, preceded and ultimately facilitated changes in fire regimes (figure 6).

Archaeological evidence from East Africa indicates increased human activity between 3500–1500 cal BP, peaking around 1500 cal BP (figure SI5(A)). This trajectory aligns with intensified biomass burning, suggesting that land clearing, agricultural practices, or controlled burning might have regionally played an important role in shaping fire regimes [25, 88] and plant biodiversity. This regional effect aligned with studies showing that human impact can significantly affect plant diversity over distances of several hundreds of kilometers [89].



The expansion of Iron Age farming communities brought landscape transformations, including fire use to clear land, enhance soil fertility and promote pasture regrowth, which impacted plant richness, diversity and evenness (figure 3). These practices likely altered fire regimes by increasing fine fuel availability, artificially extending the fire season, and shifting fire intensity [26]. Similar fire regime transformations have been documented in other regions, such as Australia, where Indigenous fire management transformed forested landscapes into more fire-adapted savannas by reducing tree cover and increasing grasses and shrubs [90, 91]. However, unlike in Australia, where fire was primarily used as a hunter-gatherer management tool, in East Africa, fire use was closely linked to agriculture and pastoralism [92, 93], intensifying over the past 2000 years. At Masoko, the socio-ecosystem (*sensu* [94]) began at 1700 cal BP.

4.4. Climatic, vegetation and biotic drivers of fire regimes

Over the past 17 000 years, fire regimes shifted in response to climate variability, vegetation changes, and biotic processes. During the cool, dry period between 17 000 and 15 000 cal BP [14], fire activity was low despite abundant grass pollen, suggesting that fuel availability, rather than vegetation type alone, constrained fire regimes. Limited grass biomass, low fuel connectivity and reduced flammability prevented large, frequent fires. After 15 000 cal BP, rising precipitation, temperatures, and $p\text{CO}_2$ (figure

SI5(B), [15, 78, 95]), associated with a shorter dry season [17, 18], promoted tropical forest expansion (figure 6), potentially reducing fire spread by limiting fuel and narrowing the effective burning window. Even as forests retreated and grasslands expanded after 12 600 cal BP, humid microclimates created by forests [96, 97] and local groundwater around Masoko [98], along with increased grass fuel moisture from high precipitation [99], may have continued to limit fire spread.

At the onset of the Holocene (~10 700 cal BP), Miombo woodland expanded while grasses remained dominant, a pattern observed regionally [18, 20]. The northward displacement of the Intertropical Convergence Zone (ITCZ) extended the dry season [17, 100], and the combination of high grass biomass with prolonged drought may have supported large, frequent fires, as indicated by the alignment of CHAR with frequency. Between 9000 and 6000 cal BP, fire activity declined as tree cover increased (figure 5(D)), consistent with patterns in wetter savannas where high tree cover reduces fire spread by limiting grass biomass and fuel continuity, despite favorable climatic conditions [28]. The end of the AHP (6000–5000 cal BP [95], figure SI5(B)), brought drier conditions, shifting vegetation toward lower tree cover and more fire-prone grasslands, increasing fire activity (figure 6). These patterns indicate that fire regimes emerged not solely from climate [27] but from interactions between vegetation traits, fuel properties, and moisture availability. While grass biomass promoted fuel continuity and fire spread, increased tree cover

disrupted it. Fire-tolerant, resprouting trees (many Miombo species) persisted despite burning [54], whereas fire-intolerant trees were gradually excluded, reinforcing vegetation-fire feedbacks [4, 26, 101]. Such feedbacks characterize forests and savannas as potential alternative stable states [102].

Moreover, we observed that vegetation changes consistently preceded shifts in fire activity (figure 3). This contrasts with findings from West Africa [103], where fire was considered a primary driver of vegetation changes, with forest expansion occurring during a period of declining fire activity, likely due to increasing atmospheric humidity (15 500–14 500 cal BP). While fire is often seen as a driver of vegetation change, our results suggest that fire regimes are primarily controlled by grass biomass and vegetation structure, as observed today in southern Africa [4]. Similar patterns have been documented in North American forest-grassland transitions during the Holocene, where changes in grass biomass likely regulated fire regimes [104], in Mediterranean fire simulations [105, 106], and in southwestern USA, where wetter El Niño years increased biomass and fire activity [107, 108]. These examples show that while climate influences fire regimes, vegetation structure and fuel dynamics ultimately control fire frequency and extent in ecosystems with strong vegetation-fire feedbacks.

Beyond vegetation, biotic factors such as grazing likely influenced fire regimes but remain difficult to quantify in paleoecological records [109]. Large herbivores reduce fine fuel accumulation by consuming grasses, thereby lowering fire intensity and frequency, a process documented in modern African savannas [110] that may reflect similar shifts in Holocene herbivores populations.

4.5. Evenness as a potential early warning signal of ecological change

Our results indicate that evenness peaks preceded major ecological transitions at Masoko, suggesting that shifts in community structure may occur before broader changes in ecosystem state. However, multiple processes could contribute to evenness fluctuations in response to environmental pressures.

The first peak in evenness at 12 950 cal BP followed a gradual increase in evenness and repeated vegetation dominance shifts from Afromontane to tropical forest, before the establishment of Miombo woodland. This pattern may reflect progressive weakening of dominant taxa due to changing climate conditions, which could have temporarily reduced competitive exclusion and allowed for greater species co-occurrence. The transition from Afromontane to tropical forest driven by warming, increasing precipitation and rising $p\text{CO}_2$ may have allowed secondary species to persist for longer periods before the system reorganized into a new stable state dominated by Miombo woodland species. The transient

increase in evenness may signal ecological reorganization with high initial biodiversity buffering the transition and allowing evenness to rise gradually. This aligns with ecological theory suggesting that environmental stress can disrupt competitive hierarchies, allowing suppressed species to occupy available niches [111, 112], temporarily increasing evenness before reorganization [113].

In contrast, the second evenness peak (1700 cal BP) was more abrupt and coincided with the beginning of fire activity increase, likely driven by human disturbances such as land clearance and fire use. These disruptions may have temporarily reduced dominance, elevating evenness before new dominant vegetation emerged and restored competitive hierarchies. This pattern is consistent with studies showing that disturbances create transient windows of opportunity for species establishment or expansion before ecosystems reorganize [114, 115].

Differences in proxy resolution may hide the exact timing of vegetation and fire shifts, complicating the determination of lag times identified in figure 3. Charcoal provides the highest resolution, making fire history more precise. Regardless of the exact timing, the second transition is clearly linked to human influences, as both vegetation and fire regimes experienced significant changes during this period (figure 3).

These results support the idea that evenness peaks can indicate impending ecological change but emphasize the importance of considering environmental context. In relatively stable or competitively structured systems, external disturbances (e.g. fire, deforestation) can temporarily elevate evenness by disrupting dominant species. In already dynamic environments, increasing instability can gradually erode dominance, allowing greater species turnover and enhancing evenness.

5. Conclusion

Over the past 17 000 years around Lake Masoko in SW Tanzania, vegetation and fire regimes fluctuated, with vegetation shifts preceding changes in fire activity. These vegetation changes were driven by climatic shifts, particularly precipitation and moisture availability, which indirectly controlled fire regimes. However, no abrupt transition in vegetation were driven by fire, indicating that vegetation was resilient to fire over centennial timescales. Tree-dominated ecosystems had higher pollen richness, while transitions to grasslands saw declines in richness but notable peaks in evenness during ecological shifts; these peaks likely acted as early warning signals of vegetation changes. The last evenness peak occurred 1700 years ago, before the establishment of the present-day savanna and the sustained high fire regime during the increasing land-use period. Periods of high tree cover correlated with reduced fire activity, while grasslands expansion led to increased

fire activity. This study shows that fire responded to, rather than drove, ecological shifts triggered by climate, land-use and vegetation in a top-down cascading process. The resilience of vegetation to fire at centennial scales suggests a robust capacity for recovery, as fire regimes did not irreversibly disrupt ecosystems. However, fire regimes were less resilient to vegetation changes, particularly during transitions like the end of the AHP and the establishment of Iron Age populations. These findings provide insights into the long-term interactions shaping tropical ecosystems and suggest that fire could be managed through vegetation structure, particularly by preserving Miombo tree cover.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.pangaea.de/10.1594/PANGAEA.982402>.

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