

Long-term drivers and timing of accelerated vegetation changes in African biomes and their management implications

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Abstract

Aim: Owing to its diverse bioclimatic zones, long human history and intense anthropogenic impacts, Africa provides a model system for studying how global terrestrial ecosystems might respond to accelerated socio-environmental stress. Africa is particularly vulnerable to climate change and human impact, and insufficient baseline data hamper current environmental management efforts. Using palaeoecological data, we seek to identify the timing, pace and drivers of change in African biomes on a long-term scale to inform current ecosystem management frameworks on the continent.

Location: Africa.

Time period: 0–12 ka.

Major taxa studied: African biomes.

Methods: Sixty-four pollen records across Africa and nearby sites were retrieved from multiple databases/sources and grouped into biomes. Turnover (quantified using the squared chord distance dissimilarity metric) and rarefaction analyses were conducted on pollen records in each biome group to reconstruct regional temporal vegetation turnover and richness. Reconstructed vegetation turnover and richness were compared with independent records of climate, fire and human activity to identify possible drivers of change.

Results: We found that the most stable biomes were those with the greatest floristic richness. Southern Africa's mediterranean-type (SAM) ecosystems were the most stable and northern Africa's mediterranean-type (NAM) ecosystems were the most unstable (mainly owing to fire). Tropical savannas (TS) and SAM ecosystems expressed the most sensitivity to climatic shifts from ≥ 6 ka, whereas tropical forests (TF) were relatively stable before human activities intensified from c. 2 ka. Floristic richness also declined across the tropics from c. 2 ka.

Main conclusions: Our analysis pinpoints NAM ecosystems as undergoing the fastest acceleration in turnover on the continent in response to fire, whereas TF and TS have been undergoing unprecedented changes in biodiversity in the last 2,000 years. We expect further changes in biodiversity where climate becomes warmer and drier and where human impacts are novel and rapid in comparison to long-term baselines.

KEYWORDS

African biodiversity, African vegetation, beta diversity, climate change, diversity–stability hypothesis, human impact, palynological richness, vegetation turnover

1 | INTRODUCTION

Human impact continues to cause significant changes in global environments, and this is especially evident in the rapid changes resulting in high turnover in ecosystems and biodiversity over the last century (McGill et al., 2015; Pereira et al., 2012). While management efforts continue to respond to these changes in order to restore and maintain ecosystem health, the continuous emergence of novel anthropogenic ecosystems confounds these efforts (Manzano et al., 2020; Zeide, 1999). Travelling back in time to when human impact was minimal in comparison to today can help us to understand the direction and pace at which the planet's ecosystems naturally responded to different disturbances in the past (Cole et al., 2014). These insights can assist land managers to track and manage current changes in ecosystems better, with the aim of achieving long-term restoration and maintenance goals (Dietl & Flessa, 2011; Gillson et al., 2021). Palaeoecological records offer the opportunity to investigate these themes by providing snapshots of past environments and ecological changes (Słowiński et al., 2019; Wingard et al., 2017). In this study, we take an palaeoecological approach to investigate the pace of ecosystem change and taxonomic turnover in key African biomes for the first time, highlighting implications for present and future management on the continent.

Africa has the largest tropical landmass, which hosts the second largest global vegetation carbon sink (after South America) and c. 25% of Earth's biodiversity, with thousands of endemic species (FAO, 2020; The State of Biodiversity in Africa, 2016). Unfortunately, ecosystems and biodiversity on the continent continue to face degradation and extinction threats owing to the rapidly growing human population and resource over-exploitation (Malhi et al., 2013; Mayaux et al., 2013). These threats are magnified by major changes in climate patterns (extreme temperatures, heavy precipitation events and intense drought), as reflected in the Intergovernmental Panel on Climate Change's Sixth Assessment Report for African regions (IPCC, 2021). Current management efforts are based mainly on short-term studies that capture ecological patterns created by modern human impacts, which might be unreliable, considering the time required for ecosystems such as forests to respond fully to disturbance, especially climate change (Dirk & Gillson, 2020; Wangai et al., 2016). Combining short-term contemporary ecological information with knowledge of long-term (millennial-scale) ecosystem changes under different disturbance regimes will assist management agencies to channel resources into appropriate strategies to conserve Africa's ecosystems and biodiversity better (FAO, 2020; The State of Biodiversity in Africa, 2016).

Using a large palaeoecological dataset (for dataset details, see Supporting Information Appendix S1.1), our aims in this study are to identify the timing and drivers of both vegetation compositional change (vegetation turnover) and floristic richness (taxonomic

diversity) in key African biomes during the Holocene and to highlight what this means for future ecosystem management. Without biome-specific information, conservation and management efforts might be misdirected when continental-scale observations are applied in areas that respond in unique ways to environmental change. The existing continental-scale vegetation turnover reconstruction for Africa is based on relatively few sites (21 suitable sites that span the Last Glacial Maximum to the present) and does not take into account the unique ecological responses of different biomes on the continent (Mottl, Flantua, et al., 2021). Here, we are able to use an expanded site network of fossil pollen records (62 suitable sites) by selecting a shorter timespan (the last 12,000 years) to estimate turnover and floristic richness changes in three key biomes: African tropical forests, tropical savanna and bushland, and southern and northern mediterranean-type forest-woodland-scrub (Figure 1). Sites with records spanning at least the last 4,000 years with a sample resolution of $\leq 1,000$ years were selected for our analyses. Vegetation turnover and floristic richness estimates were compared with independent records of climate (e.g., elemental ratios and isotopes) and fire regimes (i.e., charcoal records) using generalized additive modelling (Wood, 2021) to identify the major drivers of vegetation change.

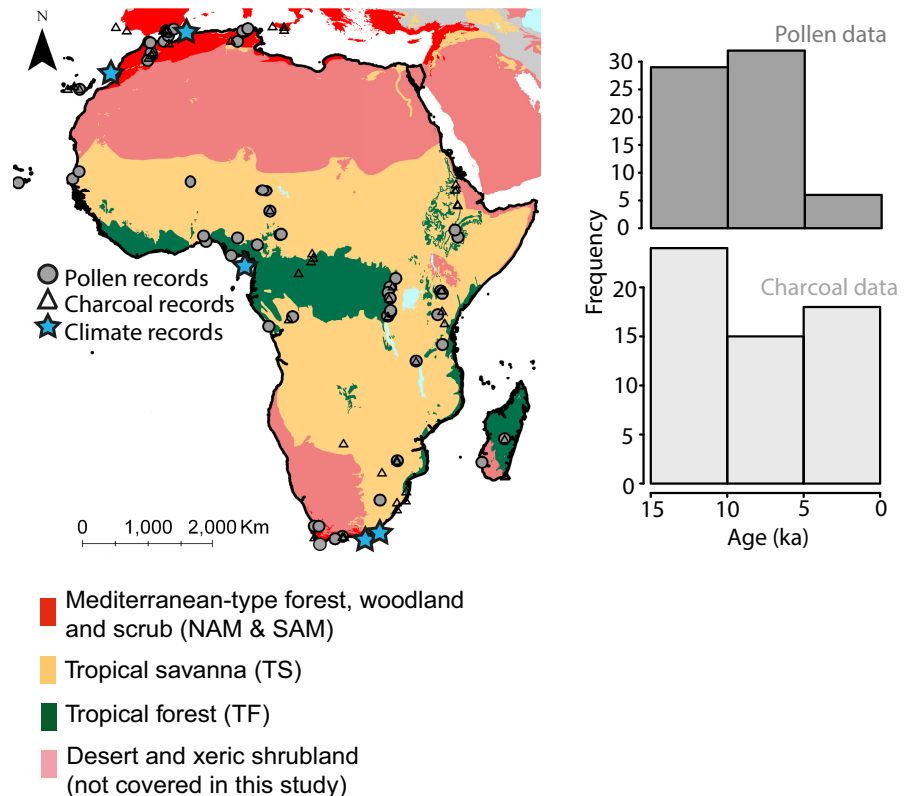
The number of species in ecosystems is thought to play a major role in the maintenance of long-term ecosystem stability in response to disturbance, with greater stability in more diverse systems (Lucini et al., 2020; Tilman et al., 2006). We also test this diversity–stability hypothesis in Africa by comparing the overall turnover among African biomes with the overall floristic richness gradient. Understanding long-term relationships between vegetation stability and diversity in African biomes will help in better prediction and tracking of potential future large-scale impacts of biodiversity changes on the continent's biomes.

2 | MATERIALS AND METHODS

2.1 | Pollen records as a proxy for vegetation change and floristic richness

Limitations associated with pollen as a proxy (e.g., low pollen taxonomic resolution of some plant families, differential pollen productivity and dispersal) affect vegetation information obtained from pollen assemblages. Despite these limitations, previous studies have empirically validated significant relationships between modern pollen rain and modern vegetation communities, in terms of both compositional change (turnover) and floristic richness (e.g., Adeleye et al., 2021; Birks et al., 2016; Connor et al., 2021; Gosling et al., 2018; Hély et al., 2014; Plumpton et al., 2019; Schüller et al., 2014). Adeleye et al. (2021) and Felde et al. (2016) also found significant relationships between pollen assemblages and vegetation communities using targeted pollen

FIGURE 1 Major African biomes (Olson et al., 2001) and data distribution. Locations of pollen (grey filled circles), charcoal (open triangles) and climatic records (blue filled stars). Five high-resolution pollen and charcoal records from sites neighbouring northern Africa in the Mediterranean basin were included in northern African mediterranean-type (NAM) reconstructions to increase result robustness. Sixty-one pollen records were obtained from the Neotoma database (Williams et al., 2018) and one from PANGAEA (Cheddadi et al., 2021). Fifty-eight charcoal records were drawn from the global Paleofire database (Hawthorne et al., 2018). See Figure 2 for climate record sources. Also shown is the temporal (earliest age) frequency distribution of pollen and charcoal records, with most records spanning from 0 to >5,000ka



taxa corrected for cover, distance, productivity and dispersal. The positive relationship is stronger when the study is restricted to a particular climatic/ecological zone (Meltsov et al., 2013) or involves comparison between ecological regions (Gosling et al., 2018). For this reason, in our study we have divided our study area into tropical and mediterranean-type biomes, increasing the reliability of our pollen-based reconstructions. Tropical biomes include tropical forests (TF) and tropical savannas (TS); the latter consists of a spectrum of seasonally dry vegetation types with variable canopy covers, including tropical and subtropical savanna, bushland and woodland. However, for simplicity, we use TS throughout the manuscript. The mediterranean-type biomes include forest, woodland, scrub and heathland of the southern and northern tips of Africa.

2.2 | Data selection

Pollen records spanning at least the last 4,000 years (with maximum 1,000-year dating resolution) were selected across Africa. We included five sites on the African margin in the Southern Mediterranean, where the vegetation is floristically and functionally equivalent to that of North Africa. In total, our criteria yielded 62 records, 61 from the African Pollen Database holdings within the Neotoma Paleocology Database (Ivory et al., 2020; Williams et al., 2018) and one site from PANGAEA (Cheddadi et al., 2021). The majority (c. 70%) of the selected sites span at least the last 12,000–8,000 years, while 18 sites span the last 7,000–5,000 years, and five sites span the last 4,000 years (Figure 1). Out of the total 64 records, 59 were from Africa and five were from the coast of the Iberian

Peninsula adjacent to north-east Africa (see Supporting Information Appendix S1.1 for all pollen site details). Holocene charcoal records (macroscopic and microscopic particles) were drawn from the Global Paleofire Database using the same criteria as for the pollen records (Hawthorne et al., 2018; see Supporting Information Appendix S1.2).

Palaeoclimatic proxy records were selected based on their temporal resolution and proximity to each biome and the selected pollen records. We selected non-pollen-based proxies to ensure data independence and used the single longest temperature and precipitation/moisture records closest to a particular biome. For the northern African mediterranean-type (NAM) biome, a precipitation record from off the coast of Morocco (Tierney et al., 2017) and Alboran Sea surface temperatures (SST) (Cacho et al., 2001) were selected. For the tropics, although precipitation drivers at present differ between Western and Eastern Africa (Shanahan et al., 2015; Tierney et al., 2013), the long-term precipitation trends are similar during the Holocene in both regions (Gasse, 2006). Therefore, we opted for a single high-resolution climatic record in the region, which includes river runoff (Ba/Ca) as an indicator of rainfall and SST records from the Gulf of Guinea (Weldeab et al., 2007). For the southern African mediterranean-type (SAM) biome, climatic records include a $\delta^{13}\text{C}$ record of hyrax middens from Seweweekspoort, a proxy for humidity changes (Chase et al., 2013), and a speleothem-based temperature record from Cango cave (Talma & Vogel, 1992) with updated chronology (Chase et al., 2013). Human land use is inferred from the density of radiocarbon-dated archeological materials of human occupation in Central-Western African rain forest (Garcin et al., 2018) and the northern African Mediterranean area (Lucarini et al., 2020). Currently, continuous, high-resolution

Holocene archeological datasets for the tropical savanna (TS) and SAM biomes are lacking.

2.3 | Data preparation and analysis

Before analysis, unknown/indeterminate and aquatic pollen types were excluded from all pollen data, because our focus was on terrestrial vegetation. Thus, the pollen data included all terrestrial taxa including fern. Pollen taxa were also harmonized using the taxonomic harmonization table for Africa developed by Mottl, Flantua, et al. (2021). Pollen records were then grouped into biomes, following WWF global biome classification (Olson et al., 2001), covering tropical forest (TF), tropical savanna (TS) and mediterranean-type forest-woodland-shrubland (Supporting Information Table S1). An additional analysis was conducted by separating the Western and Eastern African tropical regions to identify potential spatial heterogeneity in patterns of drivers that might not have been captured at the biome level. We separated mediterranean-type forest-woodland-shrubland into northern and southern African mediterranean types (NAM and SAM) because they are characterized by different climatic modes, floristics and vegetation physiognomies.

There are various dissimilarity metrics used in computing compositional turnover based on pollen records, some of which include chord distance, squared chord distance (SCD) and χ^2 coefficient; however, different metrics produce similar results (Mottl, Grytnes, et al., 2021; Overpeck et al., 1985). We opted for SCD owing to its better handling of signal-to-noise effects (Overpeck et al., 1985). Before conducting turnover analysis, pollen data were binned into 1,000-year intervals owing to the low temporal resolution of some pollen records. The binning approach, which produces results similar to other robust methods, reduces the effect of age uncertainties and the potential for statistical artefacts in turnover results (Connor et al., 2019, 2021; Mottl, Grytnes, et al., 2021; Seddon et al., 2015). Turnover was then calculated using the fossil pollen records based on the average SCD between adjacent time bins after randomly resampling 50 times (Connor et al., 2019; Seddon et al., 2015).

Rarefaction analysis was conducted on pollen records to estimate palynological richness, which we used as a proxy for floristic richness. This analysis was based on the minimum pollen sum in each record in order to reduce the effect of different sampling efforts (Birks et al., 2016; Connor et al., 2021). Turnover and richness results from individual pollen records were averaged for each biome, and the resulting averages were taken to represent biome turnover and richness. All analyses were conducted in R using the “analogue” and “vegan” packages (Oksanen et al., 2020; R Core Team, 2021; Simpson, 2007).

To reconstruct an estimate of the amount of biomass burned in each biome in the past, composite analysis was performed on charcoal influx records for each biome using the “pfCompositeLF” function in the R “paleofire” package, with Box-Cox and z-score transformations (Blarquez et al., 2014; R Core Team, 2021). There are various approaches for creating charcoal composites (e.g., Mariani et al., 2022; McMichael et al., 2021); here, we opted for the z-score transformation method owing to the heterogeneity of charcoal quantification methods in the Global Paleofire Database.

In order to identify potential drivers of vegetation turnover and floristic richness changes, we compared SCD and rarefaction results for each biome with independent records of past climate, biomass burned and human land use. Generalized additive modelling (GAM) was used for the comparison between the drivers (climate, fire and human land use) and response (turnover and richness). Significant ($p < .05$) predictors were then selected as the major drivers of turnover and richness. The GAMs were performed in R using the “mgcv” package (Wood, 2021).

3 | RESULTS

Among the biomes captured by our data, the NAM and TS biomes showed the greatest vegetation compositional change (turnover) during the Holocene, whereas the SAM and TF biomes showed the least turnover (Figure 2a). In terms of floristic richness, the reverse was the case. Turnover was greatest in all biomes after 4 ka, whereas floristic richness patterns varied temporally and spatially. Floristic richness was generally stable for most of the Holocene in the Mediterranean-type biomes and

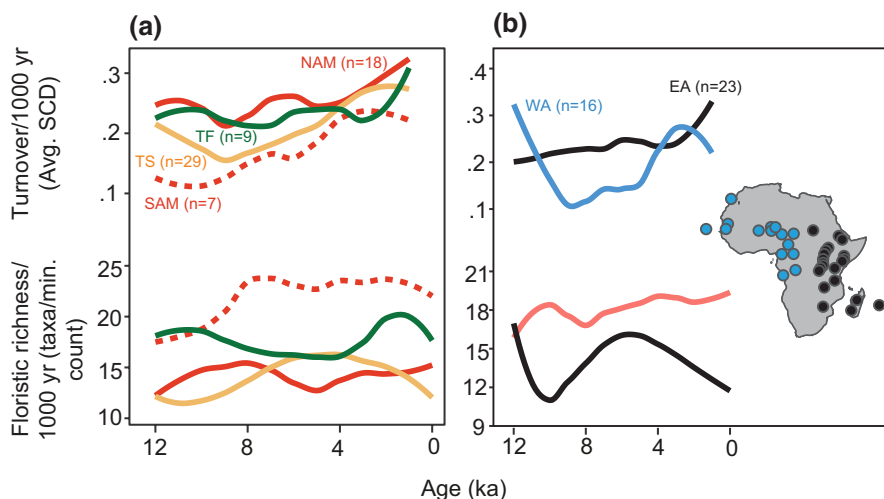


FIGURE 2 (a) Vegetation turnover and floristic richness reconstructions for all African biomes. (b) Turnover and floristic richness reconstructions for Western (WA) and Eastern African (EA) regions. See the Supporting Information (Appendix S2) for individual site turnover and richness results and the Supporting Information (Appendix S3) for individual site turnover and richness curves. NAM = northern Africa mediterranean-type; SAM = southern Africa mediterranean-type; SCD = squared chord distance; TF = tropical forest; TS = tropical savanna

followed opposing trends in TF and TS before c. 2 ka. Floristic richness decreased markedly in both TF and TS from c. 2 ka. The onset of an acceleration in Holocene turnover differed substantially between biomes. The increasing trend of vegetation change began earlier (≥ 8 –6 ka) in mediterranean-type (NAM and SAM) and TS biomes, and later (after c. 4 ka) in TF. The overall late Holocene (between 4 ka and the present) acceleration of turnover and decline in floristic richness in the tropical biomes occurred mainly in Western Africa (Figure 2b).

Comparing records of potential drivers, such as past climate, biomass burned and land use, with vegetation turnover showed that changes in biomass burned were most important for driving turnover and richness changes in NAM. For TS, temperature and precipitation changes best predicted turnover changes, whereas changes in biomass burned and precipitation best predicted richness changes. In TF, changes in biomass burned and land use were significant predictors of turnover changes, whereas precipitation and land-use change best explained floristic richness changes. In SAM, temperature and precipitation change best explained turnover changes, whereas all predictors explained richness poorly (Table 1; Figure 3).

4 | DISCUSSION

4.1 | The timing of significant turnover in African biomes

An empirically derived threshold for significant turnover is currently available only for temperate ecosystems, with SCD generally $< .2$ when the vegetation remains stable through space and time (Adeleye

et al., 2021; Davis et al., 2015; Overpeck et al., 1985). Given that such a threshold has not been evaluated for tropical ecosystems, we apply the 0.2 SCD threshold to NAM and SAM, and this shows significant turnover in NAM throughout the Holocene, whereas SAM experienced significant turnover only in the last c. 5,000 years (Figure 3). Additional study focused on the validation of a modern vegetation–pollen turnover threshold in the African tropics or other tropical systems will help to pinpoint the timing of significant turnover in TF and TS better.

4.2 | Drivers of vegetation turnover in African biomes: Climate and human impact

Changing climate and human land use are key threats to the ecosystems of Africa (Niang et al., 2014). Drier, warmer and more variable conditions are driving rapid changes in vegetation biomass, structure, composition and species distributions, and human activities are magnifying/accelerating these changes (Bond & Midgley, 2012; Goldammer & Mutch, 2001; Gonzalez et al., 2012; Réjou-Méchain et al., 2021). In agreement with existing views, our results show that climate was a key driver of vegetation compositional change in Africa in the past 12,000 years (Willis et al., 2013). However, our results also show that human activities and fire have been significant drivers of vegetation turnover and floristic richness for millennia in some areas (Table 1). Following the late glacial–early Holocene climate transition, the timing of accelerated changes varied between biomes, with an earlier timing of ecosystem change in mediterranean-type and TS biomes and a later onset in TF (Figure 2a). We focus here on the

TABLE 1 Generalized additive models showing climate (precipitation and temperature), fire and human activities as predictors of vegetation turnover and floristic richness in tropical forest (TF) and northern African mediterranean-type (NAM), tropical savanna (TS) and southern African mediterranean-type (SAM) biomes

Biomes	Predictors	Vegetation turnover			Floristic richness		
		Percentage deviance	Adjusted r^2	p -value	Percentage deviance	Adjusted r^2	p -value
NAM	Precipitation	35.5	0.26	.13	22.6	0.15	.12
	Temperature	55.4	0.38	.16	27.2	0.20	.08
	Fire	69.3	0.62	.01	55.4	0.54	.05
	Humans	0.03	−0.11	.96	0.04	−0.11	.96
TS	Precipitation	71.3	0.68	.0004	67.2	0.56	.043
	Fire	23.2	0.08	.52	56.4	0.52	.005
	Temperature	36.2	0.30	.04	0.06	−0.10	.94
TF	Fire	88.3	0.81	.003	54.1	0.43	.07
	Precipitation	70.0	0.52	.08	89.9	0.86	.0002
	Temperature	0.23	−0.10	.87	0.32	−0.10	.86
	Humans	79.3	0.73	.01	98.6	0.97	.0003
SAM	Precipitation	85.1	0.82	.002	8.94	−0.04	.43
	Temperature	49.6	0.42	.034	30.2	0.20	.14
	Fire	9.1	−0.04	.43	16.3	0.04	.28

Note: Significant ($p < .05$) predictor values are in bold.

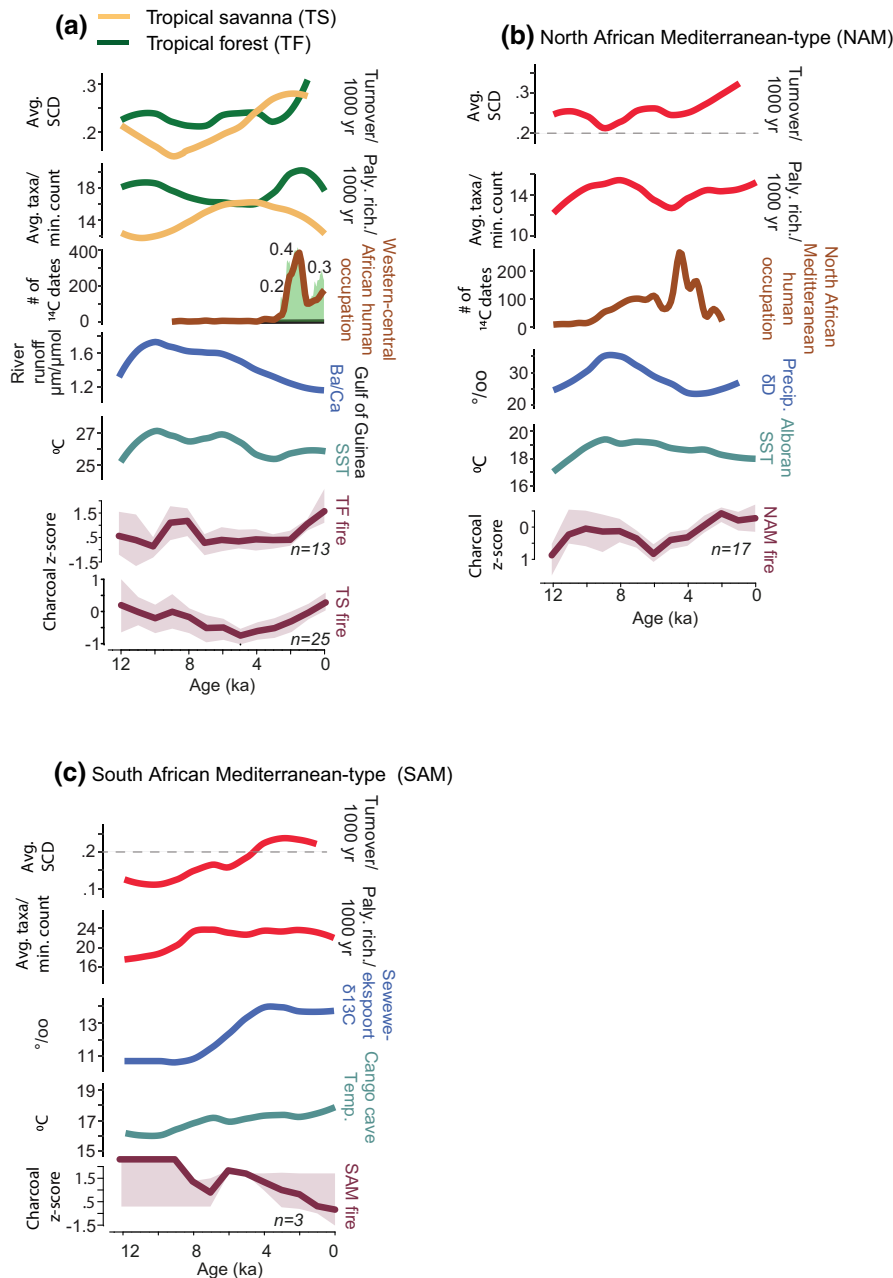


FIGURE 3 Vegetation turnover and palynological richness in relationship to changes in climate, biomass burned and human land use. Turnover is the average squared chord distance (SCD) across biomes, and palynological (floristic) richness is the average taxa/minimum count or sum across biomes. The grey dashed line in NAM and SAM indicates the empirically validated turnover threshold ($\text{SCD} = .2$) for temperate ecosystems (Adeleye et al., 2021; Overpeck et al., 1985). Northern African mediterranean-type (NAM) climate records include a precipitation record from the coast of Morocco (Tierney et al., 2017) and Alboran Sea surface temperatures (SST) (Cacho et al., 2001). For the tropics, high-resolution climatic records include river runoff (Ba/Ca) and SST records from the Gulf of Guinea (Weldeab et al., 2007). Southern African mediterranean-type (SAM) climatic records include a $\delta^{13}\text{C}$ record of hyrax middens from Seweweekspoort, a proxy for humidity changes (Chase et al., 2013), and a speleothem-based temperature record from Cango cave (Talma & Vogel, 1992) with updated chronology (Chase et al., 2013). Human land use is inferred from radiocarbon-dated archeological evidence of human occupation in central African rain forest (Garcin et al., 2018) and the northern African Mediterranean area (Lucarini et al., 2020). Also shown is the probability of population growth (green-shaded area) in central African rain forest (Seidensticker et al., 2021)

NAM and tropical biomes, given the relative lesser amount of pollen and charcoal records publicly available from the SAM biome.

Our GAM results identified changes in biomass burned as the major driver of turnover in NAM during the Holocene (Table 1). Human impact on vegetation and fire activity was pronounced in the Mediterranean during the mid- to late Holocene (Connor et al., 2019); however, the role of climate was thought to be stronger in shaping fire regimes during this period (Vannière et al., 2008). Anthropogenic burning might have contributed to increasing turnover in NAM; however, the turnover peak and reduced land use after 4 ka suggest that climate-driven fires were the primary driver of vegetation compositional change at this time. The onset of drought is thought to have facilitated southward spread of Iron-Age farmers from northern to Western and Central Africa around 2.8–1.9 ka

and after 1 ka (Garcin et al., 2018; Malhi et al., 2013; Seidensticker et al., 2021), leaving climate as the most plausible primary driver of fire regimes in NAM during the late Holocene (Figure 3).

Climate change was the major driver of turnover changes in TS, whereas changes in fire regimes and land use were the most important drivers in TF (Table 1). The earlier increasing turnover trend in TS, especially after 6 ka, might reflect the greater sensitivity of the biome to drier conditions and greater seasonality during the concluding phase of the African Humid Period (AHP) (Hély et al., 2009; Neumann et al., 2012; Shanahan et al., 2015). Meanwhile, TF remained generally stable (low turnover) at this time and until c. 2 ka (Neumann et al., 2012), reflecting the long-term resilience of TF to climatic forcings (Cole et al., 2014; Figure 3). Rain forest plants have been shown to recover rapidly even in dry conditions. However, this resilience is

significantly reduced when anthropogenic burning and forest clearance are introduced (Cole et al., 2014; Fauset et al., 2012) and is likely to explain the high turnover in TF in the last 2,000 years, when human land use and burning intensified in Central and Western Africa (see 'Drivers of floristic richness changes in African biomes: Fire, human impact and climate' below). Conversely, inter-seasonal rainfall variability drives tree and grass distribution and long-term mortality in TS (D'Onofrio et al., 2019; Sankaran, 2019) and might explain high compositional changes in TS, especially during the last 4,000 years (Figure 3). TF expanded beyond their present limit into TS during the AHP (Malhi et al., 2013), and the high turnover observed in TS, especially in the last 4,000 years, is likely to reflect the collapse of forest to open vegetation communities owing to the increasingly variable and drier climatic conditions that succeeded the AHP. For instance, in the Western African Sahel region, Guinean forest communities that expanded in the ecoregion during the humid early to mid-Holocene gave way to Sudanian and Sahelian open communities in the drier, more variable late Holocene (Salzmann, 2000).

Major population growth, land-use change and technological advancement occurred in many parts of Africa, especially in central and northern parts, from c. 3 ka, and human activities would have been a major source of ignition and fire activity at this time, especially in the tropics (Malhi et al., 2013; Mercuri et al., 2011). Although a period of population collapse is thought to have occurred in African rain forest between c. 1.5 and 0.7 ka, human land use after 0.7 ka would have at least contributed to changes in TF in the last millennium (Seidensticker et al., 2021; Figure 3). It is also possible that the existing effect of human forest fragmentation related to Bantu population expansion in Central-Western Africa at c. 2.6 ka contributed to the later forest transformation from c. 2 ka (Garcin et al., 2018; Seidensticker et al., 2021). The legacy of widespread intensive selective logging and crop cultivation would have contributed to long-term changes in TF composition, with the expansion of secondary regrowth and pyrophytic grasslands (Aleman et al., 2020; Malhi et al., 2013; Neumann et al., 2012).

4.3 | Drivers of floristic richness changes in African biomes: Fire, human impact and climate

The amount of biomass burned on the landscape was a key driver of floristic richness changes in the TS and NAM biomes during the Holocene (Table 1), and periods of low- to moderate burning supported maximum floristic richness in TS, whereas periods of high fire activity promoted richness in NAM (Figure 3). This might reflect the important role of intermediate fire levels in maintaining diversity in these biomes (Bongers et al., 2009; Lazarina et al., 2019), and fire exclusion, especially in NAM, can potentially result in long-term biodiversity decline (Fernandes et al., 2013). The role of climate was also important in TS floristic richness changes, where periods of intermediate precipitation/moisture levels in the mid-Holocene might have supported both wet (closed) and dry (open) vegetation (i.e., forest-savanna mosaics; Aleman et al., 2020), increasing floristic

richness, whereas the wetter early Holocene and drier late Holocene supported low richness.

Precipitation and land-use change mainly drove floristic richness changes in the TF, and richness mostly follows a decreasing trend during the Holocene until c. 4 ka. High floristic richness in the early Holocene is likely to reflect the afforestation of TF in warm and wet climates, with a declining trend as drier conditions set in later (Figure 3). Although climatic changes might have contributed to TF richness changes in the Holocene, the late Holocene increasing richness trend between 3 and 2 ka is likely to be related primarily to land-use intensification that opened forests and promoted open vegetation communities at this time (Garcin et al., 2018; Neumann et al., 2012). The later decline after c. 2 ka might be linked to persistent land use or/and drought during this period, with a major decline in rain forest plant specialists. The observed Holocene climate-floristic richness relationships have implications for biodiversity management in the African tropics under projected future climates. As in the Holocene, current and future changes in precipitation regime (especially drought) are likely to drive biodiversity decline in TF and TS biomes.

4.4 | Turnover and richness changes in tropical Western and Eastern Africa

It is likely that climate, fire and land use-driven changes in vegetation turnover and floristic richness in tropical biomes differ, not only between forest and savanna systems, but also between geographical regions. Spatial heterogeneity in climatic and land-use patterns between Western Africa (WA) and Eastern Africa (EA) might also have contributed to turnover changes in tropical Africa during the Holocene. The overall stable (low/decreasing turnover) vegetation in WA and EA before c. 4 ka might have been linked to more humid conditions in Africa during the early-mid-Holocene, whereas higher turnover in EA from c. 10 to 4 ka and in WA after 4 ka might be linked to climatic phasing between WA and EA (Figure 4). The Walker circulation, which is associated with El Niño–Southern Oscillation (ENSO), also modulates African climate. In El Niño years (weaker Walker circulation), dryness increases in WA and wetness increases in EA, and the reverse is the case in La Niña years (stronger Walker circulation) (Kabothe-Bahr et al., 2021). Stronger Walker circulation associated with wetness in WA before 4 ka might have promoted more stable vegetation in WA, with an opposite effect in EA (i.e., dryness and unstable vegetation). Drier conditions associated with weaker Walker circulation and ENSO intensification would have contributed to vegetation instability in WA after c. 4 ka (Barr et al., 2019). High vegetation turnover in EA after c. 4 ka, despite weaker Walker circulation (wetter), might indicate the dominant role of human land use in shaping the vegetation of the region, as population expansion and agricultural practices intensified in EA during this period, especially from c. 3 ka (Marchant et al., 2018). Intense land use during the Bantu expansion in Central-Western Africa at c. 2.6 ka would also have contributed to high vegetation turnover in WA (Garcin et al., 2018).

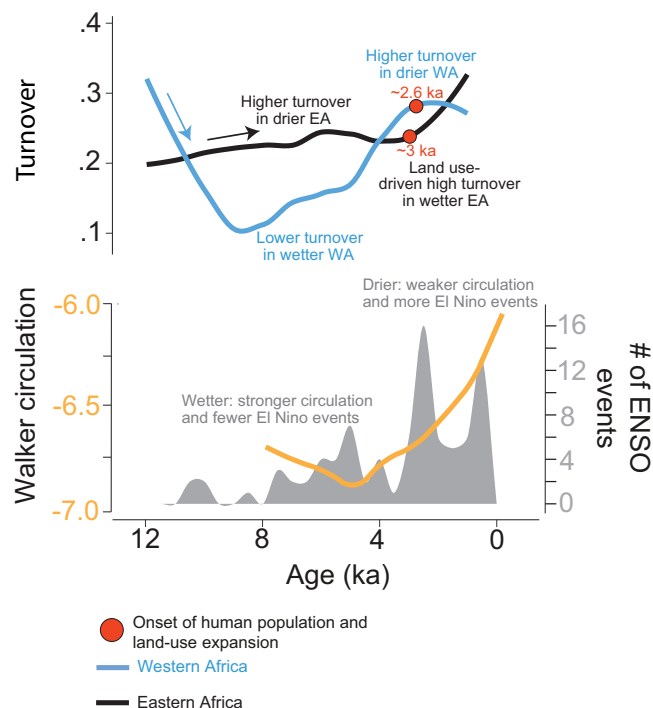


FIGURE 4 Western (WA) and Eastern African (EA) vegetation turnover in relationship to climatic phasing and the onset of major land use and population expansion in the regions. The Walker circulation record is a simulation based on the SIRO Mk3L climate system model (Barr et al., 2019), and the El Niño–Southern Oscillation (ENSO) event record is based on lake sediment analysis of Laguna Pallcacocha (Moy et al., 2002). The onset of human population and land-use expansion is based on the timing of Bantu expansion in Central–Western Africa (Garcin et al., 2018) and population and crop land cover expansion in Eastern Africa (Marchant et al., 2018)

4.5 | Long-term diversity–stability patterns in Africa

Studies have shown that the more species that occur in an ecosystem, the higher the resilience of the system to environmental perturbations (Cardinale et al., 2012; Lucini et al., 2020; Tilman et al., 2006). High species diversity (species redundancy) in an ecosystem minimizes the overall impact of biotic interactions (e.g., competition) on species. Also, species tend to respond differently to different disturbances, and a decline in abundance or extirpation of a certain species is compensated by the increase in or the persistence of other species. In contrast, external factors are more likely to drive complete changes in species composition in less diverse ecosystems (Lucini et al., 2020; McCann, 2000; Shurin, 2007; Tilman et al., 2006). This diversity–stability pattern has been recorded mostly in community and ecosystem levels and on short-term scales. The results drawn from multiple pollen records in our study suggest that the diversity–stability pattern also operates at biome levels (and on millennial time-scales). “Stability” in this case is defined as low turnover or less change in vegetation floristic composition through time. We observe considerable differences in vegetation turnover and floristic richness

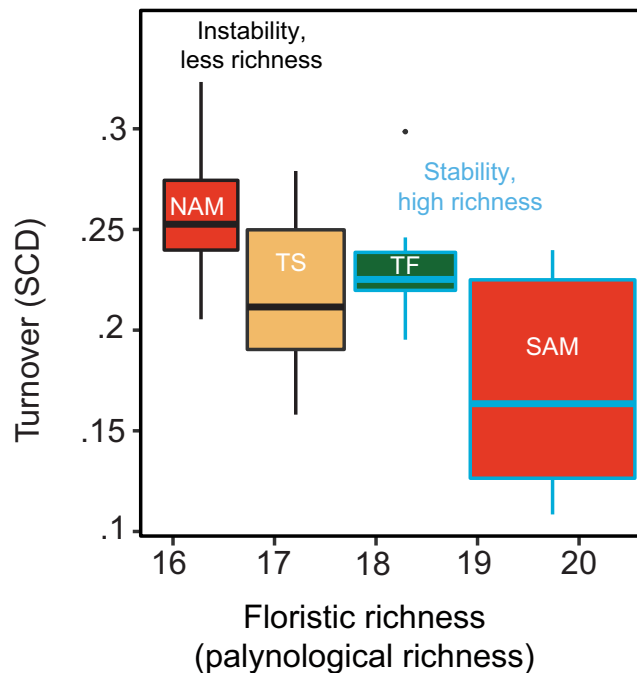


FIGURE 5 Testing the diversity–stability hypothesis using palaeoecology. Boxplot showing biome turnover along a diversity (floristic richness) gradient in Africa, with the greatest stability and diversity in southern Africa mediterranean-type (SAM) and tropical forest (TF) and least stability in northern Africa mediterranean-type (NAM) and tropical savanna (TS). SCD = squared chord distance

among African biomes (Figure 5). The greatest instability (turnover) during the last 12,000 years was observed in the NAM and SAM biomes where diversity (floristic richness) was lowest, and the greatest stability was observed in the SAM and TF biomes where diversity was greatest. This is likely to reflect changes in ecosystem resilience across the diversity gradient in Africa. The South African Fynbos and tropical forest are at present the most floristically diverse biomes in Africa and among the most diverse globally (Mittermeier et al., 1999). Our results suggest that the characteristic diversity of these biomes dates to at least the last 12,000 years and has contributed to the overall relative stability observed over the long term. Maintaining the diversity of African biomes, especially in SAM and TF, might prove critical to preservation of vegetation resilience into the uncertain future. The relatively low diversity in TS and NAM might explain, in part, the earlier timing of increasing turnover trend in the biomes in response to climate and fire disturbance from ≥ 6 ka (Figures 2a and 3).

5 | Conclusion

5.1 | The future of African biomes and potential way forward

The results presented in this study suggest that climatic and anthropogenic influences on African biomes are ancient features (Garcin et al., 2018), which started ≥ 2 ka and perhaps much earlier

in some biomes. Although the future of Africa's climate might be uncertain (Malhi et al., 2013), current climate projections suggest warmer climates and precipitation regime changes, and ecological assessments project major changes in species composition, distribution and diversity owing to habitat loss/alterations (Niang et al., 2014; State of the climate in Africa 2019, 2020). This projected pattern is consistent with past millennial-scale changes in African biomes, as reflected in our results, showing continuous accelerated turnover in vegetation and floristic richness changes in response to changes in precipitation, temperature, fire regimes and human land-use intensification during the Holocene. However, our results suggest that the direct influence of future climatic changes might be greatest in southern African mediterranean-type and tropical savanna ecosystems, considering how quickly these biomes responded to climatic shifts in the past. These ecosystems should therefore be monitored more closely for early warning signs of the impacts of climate change. Tropical forest appeared to have been less affected by climate change before human land use intensified, reflecting the naturally fast post-disturbance recovery in African tropical forests in comparison to most other tropical forests globally (Cole et al., 2014). Widespread intensive human land use, especially burning, in recent millennia is likely to have reduced forest resilience to aridity, a pattern that is consistent with experimental studies of modern tropical forest adaptability to drought stress (Fauset et al., 2012; Réjou-Méchain et al., 2021). Global tropical forests are projected to endure drought over the next century (Huntingford et al., 2013). However, our results suggest that continuing unprecedented human impact could decrease the resilience in African tropical forest. Timely actions to manage anthropogenic influence effectively (e.g., the promotion of sustainable agricultural practices) will help in promoting stability in tropical African forests under projected climatic changes. Any such actions need to take into account the enduring importance of forests for human livelihoods and incentivize the protection of key ecosystem services, such as carbon sequestration (Overpeck & Breshears, 2021).

In addition to ecosystem monitoring and the management of human impacts mentioned above, management targeted at achieving an appropriate amount of biomass burning in landscapes to maximize ecosystem diversity will also contribute to promoting ecosystem resilience, especially in northern African mediterranean-type and tropical savanna ecosystems (Gillson et al., 2019; Humphrey et al., 2021). Such management will benefit from transdisciplinary experimental and palaeoecological studies on long-term plant population and community response to varying frequencies and intensities of burning, in addition to varying timing through the year.

In the present study, we set out to understand the timing and drivers of the pace of vegetation turnover and floristic richness in key African biomes and also to highlight what our results mean for future management in Africa. Although our results agree with existing studies that climate and anthropogenic activities drove broad-scale vegetation change in Africa during the Holocene, we show

that the timing and magnitude of accelerated changes varied among biomes and geographical regions. Given that most African countries encompass one or more of these biomes, our results provide specific information relevant to ecosystem management at national scales. Our results also support evidence of current and projected changes in African biomes indicating that persistent anthropogenic impacts, including burning and climate change, will drive biodiversity changes in Africa (The State of Biodiversity in Africa, 2016). The use of palaeoecological records in tandem with ecological monitoring to detect potential tipping points in ecosystems will assist in achieving desirable outcomes for biodiversity in African biomes. The future of African ecosystems is written in the past. Our study provides insights into the past behaviour of these biodiverse systems as a guide to managing them into an uncertain future.

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AUTHOR CONTRIBUTIONS

M.A.A.: Conceptualization; analysis and writing; S.G.H., S.E.C., S.I. and P.A.A.: Review and editing.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Neotoma Paleocology Database at neotomadb.org, PANGAEA at <https://doi.pangaea.de/10.1594/PANGAEA.925930>, and Global Paleofire Database at <https://www.paleofire.org/>. All datasets used in this synthesis study are already published, and data sources are provided in the main text and Supporting Information Appendix (S1.3). Raw turnover and floristic richness results can also be accessed via Mendeley online data repository (<https://doi.org/10.17632/n23nyb53xn.2>).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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