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Research

Asymmetric response of forest and grassy biomes to climate variability across the African Humid Period: influenced by anthropogenic disturbance?

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A comprehensive understanding of the relationship between land cover, climate change and disturbance dynamics is needed to inform scenarios of vegetation change on the African continent. Although significant advances have been made, large uncertainties exist in projections of future biodiversity and ecosystem change for the world's largest tropical landmass. To better illustrate the effects of climate–disturbance–ecosystem interactions on continental-scale vegetation change, we apply a novel statistical multivariate envelope approach to subfossil pollen data and climate model outputs (TraCE-21ka). We target paleoenvironmental records across continental Africa, from the African Humid Period (AHP: ca 14 700–5500 yr BP) – an interval of spatially and temporally variable hydroclimatic conditions – until recent times, to improve our understanding of overarching vegetation trends and to compare changes between forest and grassy biomes (savanna and grassland). Our results suggest that although climate variability was the dominant driver of change, forest and grassy biomes responded asymmetrically: 1) the climatic envelope of grassy biomes expanded, or persisted in increasingly diverse climatic conditions, during the second half of the AHP whilst that of forest did not; 2) forest retreat occurred much more slowly during the mid to late Holocene compared to the early AHP forest expansion; and 3) as forest and grassy biomes diverged during the second half of the AHP, their ecological relationship (envelope overlap) fundamentally changed. Based on these asymmetries and associated changes in human land use, we propose and discuss three hypotheses about the influence of anthropogenic disturbance on continental-scale vegetation change.

Keywords: African humid period, climate–disturbance–ecosystem interactions, disturbance dynamics, land use and land cover change, paleoecological reconstruction, vegetation change



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Introduction

Variability during the African Humid Period (AHP)

The AHP was an interval of exceptionally wetter conditions over much of tropical Africa (Kutzbach and Otto-Bliesner 1982, Street-Perrott and Perrott 1990, deMenocal et al. 2000, Gasse 2000, Lézine et al. 2011), characterized by continental-scale changes in the patterns and spatial extents of vegetation, aquatic ecosystems, and an expanded footprint of human occupation (deMenocal et al. 2000, Renssen et al. 2006, Lézine et al. 2011, Manning and Timpson 2014, Tierney et al. 2017). The AHP is thought to be primarily driven by the response of the west African summer monsoon to orbital forcing (Haug et al. 2001, Fleitmann et al. 2003) through a modulation of the Saharan heat low (Chauvin et al. 2010) and land-sea temperature contrasts (Gasse 2000, Lézine et al. 2011). Summer insolation peaked ca 11 000–9000 BP (Holocene Thermal Maximum: HTM), then decreased from ca 10 000 BP to the present day (Fig. 1). However, uncertainty remains over the drivers, timing and abruptness of change during the AHP, resulting in discrepancies between observed data and predicted conditions.

Models frequently underestimate the amplitude and extent of the northern monsoon (Braconnot et al. 2012, Perez-Sanz et al. 2014, Claussen et al. 2017), and many paleoclimate proxy records find that vegetation responded non-linearly to insolation change, with a locally abrupt and spatially asynchronous termination of the AHP (Claussen et al. 1999, deMenocal et al. 2000, Shanahan et al. 2015). While some climatic events in southern Africa are contemporaneous with those that characterise the AHP, the AHP wet period has never been recorded in any southern Africa records (Chase et al. 2019, Scott et al. 2012, Chevalier and Chase 2015, Burrough and Thomas 2013). Due to these complexities and the influence of different weather systems in different geographical areas (Schefuß et al. 2005), the hydroclimatic response of the African rainbelt in and out of the AHP was variable between regions (Table 1).

In this study, we focus on continental-scale vegetation changes during the termination of the AHP, ca 5500–3500 BP, and during an earlier, short-lived dry event that we define as the ‘Green Sahara pause’ after Tierney et al. (2017). The Green Sahara Pause was a pronounced dry interval ca 8000–7000 BP (although some records date as early as 8400 BP; Shanahan et al. 2008), associated with prolonged desiccation

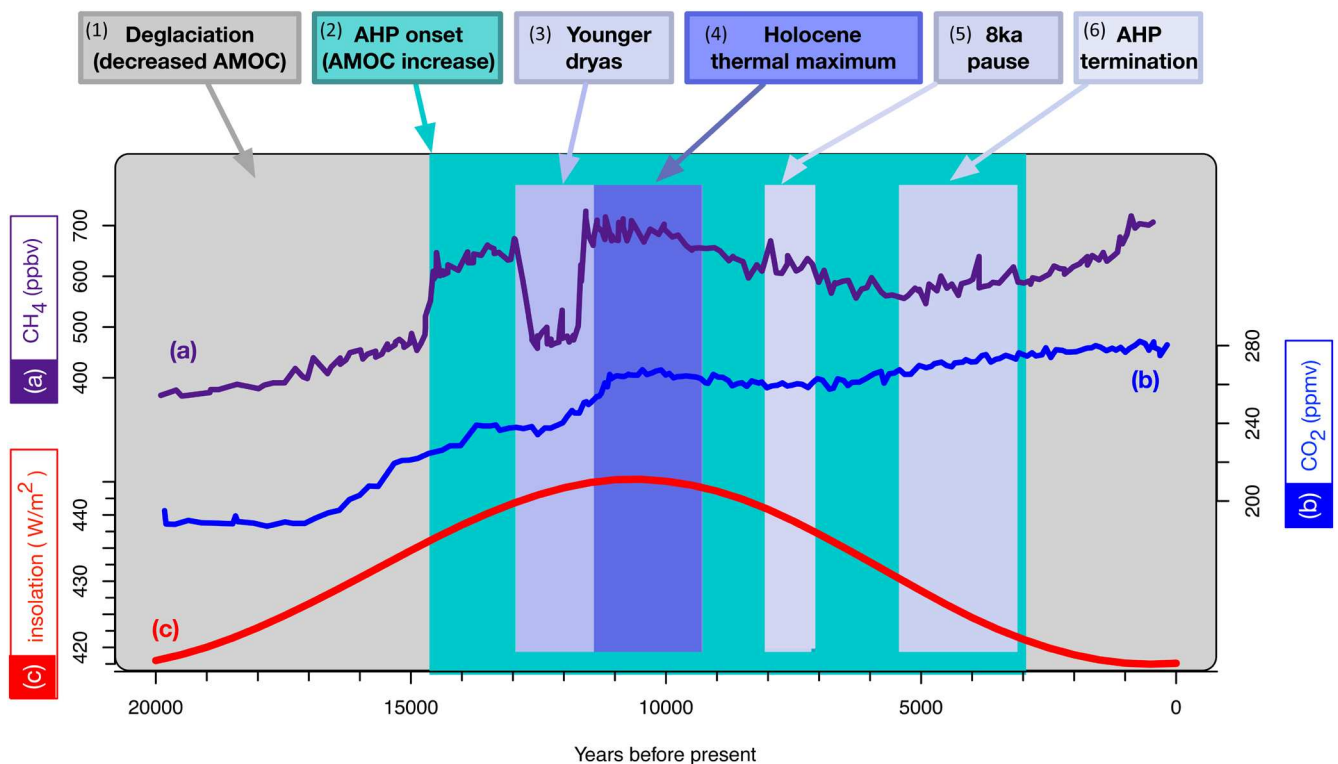


Figure 1. Major climatic events indicated over records of (a) atmospheric methane concentrations (EPICA community members 2006), (b) atmospheric carbon dioxide concentrations (Monnin 2006), (c) June–August insolation at 6°N (Laskar et al. 2004). Key climatic events include: (1) a period of pre-AHP increasing insolation and reduced precipitation due to the combined effects of cold global temperatures, deglaciation meltwater on the Atlantic meridional overturning circulation (AMOC) and the presence of polar ice caps, (2) the onset of the AHP at the beginning of the Bølling-Allerød period, associated with increasing AMOC ca 14 700 BP, (3) the Younger Dryas ca 12 700–11 500 BP, (4) peak insolation levels during the Holocene climatic optimum (HTM), (5) the 8 ka Green Sahara Pause and (6) the time-transgressive termination of the AHP.

Table 1. Summary of regional context during the African Humid Period (references provided in the Supplementary material).

Northern Africa: lake status databases indicate enhanced annual precipitation-evaporation during the AHP (Jolly et al. 1998b, Lézine et al. 2011), and vegetation records show that the Sahara was vegetated with species from modern tropical forests and wooded grasslands, which arrived at various rates and increased biodiversity, forming land cover compositions with no modern analogue (Jolly et al. 1998a, Hély et al. 2009, Lézine 2009, Watrin et al. 2009, Amaral et al. 2013). Geological and archaeological records indicate that the Sahara-Sahel boundary reached as far as 23–31°N (Kuper and Kröpelin 2006, Tierney et al. 2017), and that the AHP had significant impacts on the radiocarbon footprint of human activity (Manning and Timpson 2014). Due to diverse mechanisms and feedbacks in the arid and sub-arid belt, ecosystem change during the termination of the AHP was likely variable across the Sahara (Renssen et al. 2006, Liu et al. 2007), although spatial differences are difficult to interpret due to a paucity of continuous, reliable vegetation records (Hoelzmann et al. 2004, Lézine 2009, albeit see Kröpelin et al. 2008).

Eastern Africa: broadly synchronous and abrupt transitions into and out of the AHP were observed across eastern Africa (Tierney and deMenocal 2013), implying a common driver of vegetation change (Tierney et al. 2008, Tierney et al. 2011, Tierney and deMenocal 2013). The termination of the AHP occurred ca 5000–3000 BP (Msaky et al. 2005), as elsewhere in western and central Africa, with a relatively abrupt shift towards arid conditions ca 4500–3500 BP (Hamilton 1982, Vincens 1986, Bonnefille and Chalié 2000, Wooller et al. 2000, 2003, Kiage and Liu 2006, Marchant et al. 2018). This period was characterized by reduced rainfall, strengthened precipitation seasonality, and increased abundances of drought-adapted taxa (e.g. *Podocarpus*; Bonnefille and Chalié 2000, Thompson et al. 2002, Kiage and Liu 2006), with high altitude changes becoming apparent from ca 4500 BP (Hamilton 1982, Vincens 1986) and aridification events centering around 4000 BP (Jolly et al. 1997, Gasse 2000, Marchant and Hooghiemstra 2004, Kiage and Liu 2006).

Western Africa: evidence exists for both abrupt (Salzmann and Hoelzmann 2005) and gradual (Salzmann et al. 2002, Lézine 2009) vegetation change during the AHP in northern tropical Africa; this likely occurred in a time-transgressive manner, e.g. as a result of differing ecological communities and edaphic conditions, or nonlinear response of vegetation to precipitation thresholds (Marchant and Hooghiemstra 2004, Liu et al. 2007, Waller et al. 2007, Vincens et al. 2010, Lebamba et al. 2016), whereby the northernmost and driest geographic areas of west Africa were first affected by the termination of the AHP (Salzmann and Hoelzmann 2005, Waller et al. 2007, Vincens et al. 2010, Amaral et al. 2013, Bremond et al. 2017). During the termination of the AHP, aridification often occurred in two stages and at varying speeds, punctuated by a short-term increase in precipitation. Aridification from ca 5000 BP was frequently associated with increasing appearances of *Elaeis guineensis* (Waller et al. 2007, Vincens et al. 2010, Shanahan et al. 2015).

Central African forests: few records from the central and west African forest zone capture the entirety of the AHP, but where present, records show forest expansion ca 15 000 BP, followed by an accelerated expansion after the Younger Dryas (Maley and Brenac 1998, Miller and Gosling 2014, Lézine et al. 2019). Forest reached its maxima ca 10 000 BP, with Guineo-Congolian taxa appearing in records as far north as 10°N (Salzmann et al. 2002). Regional records indicate that the termination of the AHP unfolded in a stepwise fashion, demonstrating savanna encroachment and culminating in a dramatic reduction of forest by ca 4000 BP (Vincens et al. 2010); this was also associated with the disappearance of forest taxa from pollen records outside the modern forest boundary (Salzmann et al. 2002, Salzmann and Hoelzmann 2005). A later phase of forest perturbation appears clearest in Atlantic Central African records ca 2500 BP (Ngomanda et al. 2009a, b, Lebamba et al. 2016), signaled by greater representation of light-demanding forest taxa, and savanna to a limited extent (Elenga et al. 1996, Vincens et al. 1999). In contrast, records from the interior of the forest zone demonstrated limited disturbance (Brncic et al. 2007).

Southern Africa: while many records exhibit change during AHP onset or termination, no site exhibits both. This indicates that the AHP did not extend into southern Africa, but that there was a strong connection to changes observed elsewhere in Africa. For example, rainfall decreased ca 4500 BP in Namibia, followed by more apparent drying from ca 3800 BP (Scott et al. 1991, Dupont et al. 2008, Chase et al. 2009, 2010). An abrupt drying also began in Angola ca 3700 BP, associated with an increase in Cyperaceae and grasses, suggesting a strong increase in savanna patches, light-loving trees (e.g. *Alchornea*, *Elaeis guineensis*) and fire-associated taxa (Dupont et al. 2008). These synchronies with the drivers of Northern Hemisphere climate change reflect a strong correlation to coastal upwelling in the southeast Atlantic (Farmer et al. 2005, Chase et al. 2019). Records from southwestern Africa also reflect a wetter early-to-mid-Holocene compared to present (Scott et al. 1991, Dupont et al. 2008, Chase et al. 2019), but fail to document any strong increase in rainfall contemporaneous with the onset of the AHP. In the eastern tropical and subtropical regions, rainfall variability appears to be more sensitive to local summer insolation and global temperatures (Holmgren et al. 1999, 2003, Schefuß et al. 2011, Chevalier and Chase 2015, Cordova et al. 2017). Records from Zambia and Malawi suggest little to no change during the Holocene (Konecky et al. 2011, Burrough and Willis 2015, Haberyan 2018). Variability in the winter-rainfall and year-round zones to the South (cf. Chase and Meadows 2007) respond to changes in several regional climate drivers, e.g. strength and position of the southern Westerlies, temperature of the Agulhas Current, and strength of the summer rain-bearing systems (Chase et al. 2013, 2015a, b, 2017, Quick et al. 2016, 2018, Chase and Quick 2018, Faith et al. 2018).

across much of tropical Africa. Evidence for drying occurs in paleo-records from the Sahara (~19–23°N: Tierney et al. 2017), Sahel (~15°N in Niedermeyer et al. 2010), eastern and western Africa (Gasse and Van Campo 1994, Shanahan et al. 2008, Tierney et al. 2008), and numerous lake level records from the tropics and subtropics (Gasse 2000). The beginning of this interval is roughly coeval with the north Atlantic 8.2 ka cooling event, but is thought to have lasted much longer in Africa (ca 1000 yr: Shanahan et al. 2008, Tierney et al. 2017) relative to other continents, and corresponded with a decrease in plant richness and abundance (Hély and Lézine 2014).

Evidence suggests that AHP termination occurred in a time-transgressive manner, whereby humid conditions ended earliest and most abruptly in northeastern Africa, ca 5500 BP, and later and more gradually in west and central Africa, ca 3000 BP (Schefuß et al. 2005, Shanahan et al. 2015, Tierney et al. 2017, Garcin et al. 2018). A review of data from eastern and central Africa demonstrates that numerous sites shifted to drier, more pronounced seasonality, particularly after 4000 BP (Marchant and Hooghiemstra 2004). Even if the AHP did not reach southern Africa, contemporaneous yet heterogeneous changes in rainfall trends and patterns have been

Table 2. Summary of vegetation–environment interactions (references provided in the Supplementary material).

Vegetation–climate feedbacks and nonlinear changes in rainfall: vegetation feedbacks (Foley et al. 1998, Richardson et al. 2013) likely had significant and sudden impacts on mid-Holocene monsoon change, particularly during the termination of the AHP. It is widely acknowledged that vegetation responds to transitional climatic intervals in complex and varied ways, often exhibiting non-linear or individualist behaviors (Watrin et al. 2009, Tierney et al. 2010, Vincens et al. 2010, Lézine et al. 2013, Platts et al. 2013), capable of affecting climate change in return (e.g. changes in albedo, surface roughness, leaf area index, fractional vegetation coverage, soil moisture: Kutzbach et al. 1996, Claussen 1997, Galopolski et al. 1998, Claussen et al. 1999, deMenocal et al. 2000). The mechanics of this relationship are debated for the AHP: some research suggests that vegetation–climate feedbacks are a primary driver of instability and nonlinear changes in the AHP rainbelt (Braconnot et al. 1999, Claussen et al. 1999, deMenocal et al. 2000, Renssen et al. 2003, 2006), while other research suggests that this instability reflects a nonlinear response of vegetation to climate change, i.e. a non-linear response to precipitation thresholds in the face of strong climate variability (Liu et al. 2007).

Hydrological dynamics: hydrological dynamics affect the vegetation–climate relationship, and likely had significant effects on climate and vegetation change during the AHP, e.g. via climate feedbacks from open water surfaces and variable recharge and discharge rates of aquifers (Hoelzmann et al. 1998, Mulitza et al. 2008, Stager et al. 2011, Krinner et al. 2012, Shanahan et al. 2012, Lézine et al. 2011, Armitage et al. 2015). Hydrological dynamics may be responsible for asynchronous rates of aridification (e.g. Bodélé Basin [Armitage et al. 2015] vs Lake Yoa [Eggermont et al. 2008, Kröpelin et al. 2008, Francus et al. 2013]). In addition, the rapid aridification of large open water surfaces, e.g. Lake Chad's Bodélé Basin, are thought to exert strong control over biogeochemical cycling and to act as a climatic 'tipping element' (Hoelzmann et al. 1998, Rosenfeld et al. 2001, Bristow et al. 2009, Washington et al. 2009, Krinner et al. 2012). However the timing of these transitions are debated (Lézine et al. 2011, Krinner et al. 2012, Armitage et al. 2015), making it difficult to determine their effects on vegetation change.

Disturbance dynamics: vegetation–climate relationships during the AHP are complicated by natural and anthropogenic disturbance dynamics (e.g. herbivory, fire, land clearance, atmospheric CO₂, niche construction), which are capable of producing non-linear responses to climate change. For example, elephant herbivory is capable of modifying African savannas (Valeix et al. 2011), and anthropogenic land cover change is capable of affecting forest composition (Finch et al. 2017), aboveground carbon stocks (Pellikka et al. 2018), and ecohydrological feedbacks (Muchura et al. 2014). A number of studies have pointed to the role of dynamic instabilities as a mechanism behind non-linear vegetation change during the AHP (Brovkin et al. 1998, Scheffer et al. 2001, Renssen et al. 2006, Shanahan et al. 2015, Wright 2017), but the roles of different types of disturbance are unclear.

reconstructed across the subcontinent (Scott et al. 2012, Chevalier and Chase 2015, Quick et al. 2018, Chase et al. 2019).

The drivers of vegetation change during the AHP are numerous and difficult to disentangle (Table 2), and non-analogue vegetation assemblages make temporal comparison challenging (Watrin et al. 2009). Many drivers of forest and grassy biome distribution have been proposed, including climate (McCarthy et al. 2001, Good and Caylor 2011), human land use (Greve et al. 2011, Lehmann and Parr 2016), herbivory (Goheen et al. 2010, Odadi et al. 2011, Hempson et al. 2015), changing fire regimes (Bowman et al. 2009, Hempson et al. 2018), soils (Furley et al. 1992), varying atmospheric CO₂ (Ehleringer et al. 1997, Bond and Midgley 2012, Buitenwerf et al. 2012, Scheiter et al. 2012), and interactions between drivers (Smit and Prins 2015, Archibald and Hempson 2016). This complexity makes the spatially and temporally dynamic patterns of forest-savanna vegetation mosaics difficult to predict (House et al. 2003, Sankaran et al. 2008, Murphy and Bowman 2012). Thus, understanding the effects of climate–disturbance–ecosystem interactions is critical for informing future ecosystem change under different climate and land use scenarios (Sala et al. 2000, Bond 2008, Lehmann and Parr 2016).

Disturbance and grassy biomes

Used here, the term 'disturbance' (no value judgement inferred) refers to changes in environmental conditions that affect ecosystems, e.g. composition, structure and function. Examples of disturbance dynamics include changes in herbivory patterns (Hempson et al. 2015) and fire regimes

(Bond et al. 2005, Archibald et al. 2013, Archibald and Hempson 2016, Oliveras and Malhi 2016), niche construction processes (O'Brien and Laland 2012), and changing atmospheric CO₂ concentration (Bond and Midgley 2012). Because the long-term influence of disturbance at continental-scale is poorly understood, substantial uncertainties exist in future projections of biodiversity and ecosystem change (Niang et al. 2014, Midgley and Bond 2015), especially for African grassy biomes (savanna and grasslands), which are exceptionally extensive (White et al. 2000) and disproportionately affected by disturbance dynamics (Bond 2005). The role of human land use in past vegetation change is especially difficult to discern, given the many confounding drivers of climate and vegetation change, which are both spatially and temporally variable.

Anthropogenic changes in fire regimes, whether via hunting-gathering or agriculture, have been found to increase or maintain open woodland and savanna biomes (Bird et al. 2008, Burrough and Willis 2015, Roos et al. 2018) and can have significant impacts on vegetation change (Eriksen and Watson 2009, Rucina et al. 2009). There is little doubt that anthropogenic changes to fire regimes shape African vegetation cover today (Bowman et al. 2009, Kull and Laris 2009), but the extent and timing of these impacts in the past are less clear. The radiocarbon footprint of human activity was affected by climatic change on a broad scale during the Holocene (Manning and Timpson 2014), but there is considerable debate over the extent to which anthropogenic disturbance affected environmental change: for example, the human contribution to west-central African forest decline ca 2500 BP (Clist et al. 2018, Garcin et al. 2018), and whether the expansion of pastoralism prematurely advanced

(Wright 2017) or delayed (Brierley et al. 2018) the termination of the AHP.

Archaeological summary

From the last glacial period until the HTM, there is evidence for diverse hunting-gathering populations across the African continent (Phillipson 2005). Evidence for increasing occupation by hunter-gatherers in northern Africa began during the early Holocene (Kuper and Kröpelin 2006, Manning and Timpson 2014), followed by pastoralist societies from ca 7500 BP (Di Lernia 2006, Dunne et al. 2012). Changes in central Saharan land use strategies are evidenced during the early-mid Holocene ca 8900–7400 BP, with evidence of increased sedentism, corralling of Barbary sheep, and storage of wild cereals (Cancellieri and di Lernia 2014). However, by 7000 BP, there was a distinct shift in Saharan land use strategies as domestic animals were widely adopted and residential mobility may have increased (Tafuri et al. 2006). Radiocarbon date densities further reflect major demographic change in north Africa, including a large increase after 11 000 BP, a temporary decline ca 7600–6700 BP, and a second major decline ca 6300–5200 BP (Manning and Timpson 2014). From ca 5000 BP, animal production spread southwards into sub-Saharan Africa, occurring in mosaics or multiple events that often preceded cultivation in the east and resulted in complex interactions between pastoralists and hunter-gatherers (Marshall and Hildebrand 2002, Crowther et al. 2018). Genetic data points to population expansion of Bantu-speaking agropastoralists out of west Africa from ca 5000 to 4000 BP (Coelho et al. 2009, Gignoux et al. 2011, Skoglund et al. 2017), tending to follow savanna corridors southward and eastward over the following millennia (Grollemund et al. 2015). Expansion is thought to have occurred in two phases, both associated with central African forest decline. The first phase is thought to have facilitated early settlement in the forest periphery ca 4000 BP, and the second phase, ca 3000–2500 BP, is thought to have facilitated extensive and rapid expansion into the core of the central African forest block, associated with cereal cultivation, metallurgy and increasing appearance of oil palm *Elaeis guineensis* in east Africa (de Maret 2013, Oslisly et al. 2013, Bostoen et al. 2015). Furthermore, quantification of the Holocene animal production niche demonstrates anthropogenic niche construction processes at a continental scale, with the most significant expansion events occurring ca 6500 BP and 4500 BP (Phelps et al. 2020).

Research aims

We present the first African vegetation reconstructions, from the last glacial period to modern times, using a statistical multivariate envelope approach on synthesized subfossil pollen records and simulated climate information. Our reconstructions reflect the effects of climate-disturbance-ecosystem interactions at the continental scale, however, we do not aim to determine causality between these factors. Instead, we aim to 1) provide a quantitative summary of broadscale vegetation

change during the AHP; a period of high spatial and temporal variability; 2) to describe asymmetries between changes in forest and grassy biomes; and 3) to provide results-based hypotheses about the continental-scale role of anthropogenic disturbance on the observed asymmetries, which require testing in future studies. While this research does not focus on the localized impacts of human land use, it does discuss the broader role that anthropogenic disturbance could have played in the observed vegetation trends.

Material and methods

1) Compile pollen datasets and generate a harmonized pollen taxa list

The datasets compiled for this study comprise an updated set of pollen records, extracted from the African Pollen Database (APD: Vincens et al. 2007; online APD paradox database <<http://fpd.sedoo.fr/fpd/bibli.do>>), the European Pollen Database (Fyfe et al. 2009), the ACER pollen and charcoal database (Sánchez Goñi et al. 2017), and additional recent publications (Appendices: <<https://doi.pangaea.de/10.1594/PANGAEA.905309>> [Phelps et al. 2019a]). These datasets represent 349 distinct pollen records and 11 259 pollen samples since 20 000 BP (Supplementary material Fig. A2). Using these records, we generated a harmonized pollen taxa list from 5010 different taxa names (Appendix 4, using The Plant List 2013, ver. 1.1), resulting in 2217 consolidated names across all data sources.

2) Generate chronologies for each sediment core

We updated all the site chronologies that were either uncalibrated, or calibrated with old calibration curves (8: Phelps et al. 2019a) using linear age-depth modeling (clam: Blaauw 2010) of calibrated radiocarbon dates (INTcal13 for Northern Hemisphere sites: Reimer et al. 2013; SHcal13 for Southern Hemisphere: Hogg et al. 2013).

3) Sort pollen taxa into vegetation groups using a harmonized PFT assignment

Because different regions contain different floras, plant taxa are typically grouped based on their ‘functional convergence’, or ability to grow in similar environments, i.e. Plant functional type (PFT: Prentice et al. 1992, Steffen 1996), so that inter-regional comparisons can be made (i.e. using biomization schemes: Prentice et al. 1996, Prentice and Webb 1998). A number of pollen-based biome reconstructions exist for select regions and time intervals on the African continent (Jolly et al. 1998, Elenga et al. 2000, Vincens et al. 2006, Lebamba et al. 2009, Lézine et al. 2009). However, PFT assignments often vary between schemes (Dallmeyer et al. 2019). In order to make use of these reconstructions, we therefore systematized African PFT assignments under a unified pollen taxa list (Appendix 9: Phelps et al. 2019a).

Using the systematized list of PFTs, we then sorted pollen taxa into mutually exclusive vegetation groups: forest (F), grassy biomes (S.st: 'savanna' and 'steppe' categories were pooled), xeric (x), and desert (D). A complete taxa list is provided for forest and grassy biomes (Supplementary material Table A1). To ensure that our vegetation reconstructions accurately reflect our vegetation groups, we excluded any conflicting taxa from our analyses, i.e. those classified under more than one vegetation group, such as African *Acacia* and *Uapaca* without species identifications that occur in both forest and savanna biomes. Although previous research demonstrates that plant species are likely to maintain their ancestral ecological traits (i.e. biome stasis: Crisp et al. 2009), excluding these taxa allowed us to filter out pollen that represents multiple vegetation groups or taxa that could change biomes through time, producing robust vegetation groups. In this sense, one can use modern-day biomization schemes to understand long-term change.

The aforementioned vegetation groups comprised our primary methodological approach (the 'direct' method). Since this classification relies on sensitive, yet few, indicator taxa, we also conducted supplementary analyses (the 'indirect' method) using a deductive approach. In the indirect method, classification relied on calculating the difference between broader vegetation groups, while maximizing the number of taxa used, and permitted comparison between savanna and steppe separately. For further detail on the indirect method, see Supplementary material. Hereafter, the term 'steppe' explicitly refers to the group of taxa defined by PFT assignments for Africa (Appendix 9; for geographic distributions see Supplementary material Movie S4), and is representative of grasslands.

4) Calculate relative pollen percentages (occurrence records) for each vegetation group

To enable comparability between all the samples, we calculated relative group percentages for each sample using exclusively the taxa belonging to one of the four groups (forest, grassy biomes, desert, xeric). We excluded pollen presences lower than 0.5% prior to rescaling. Ultimately, we define non-null values for each group as geolocated occurrence records. Using the generated chronological information for each sediment core, we linearly interpolated relative vegetation percentages between samples at 100-yr resolution. Note, however, that our results and discussion focus on millennial-scale trends due to chronological uncertainties.

5) Obtain paleoclimate information and define the background climate space

We obtained nine paleoclimate variables for Africa from the TraCE-21ka simulation (Liu et al. 2009) of the Community Climate System Model (CCSM3) – a global coupled atmosphere-ocean-sea-ice-land general circulation model. Projections were obtained from 20 000 to 100 BP,

using 100-year averages centered on each century (e.g. 900 BP \pm 50) at $2.5 \times 2.5^\circ$ spatial resolution (Fordham et al. 2017). We then performed a principal component analysis (PCA), thus providing a bi-dimensional climate space with which to compare climatic conditions and realized climatic envelopes. The first two PCA axes explain 84.1% of variance (PC1 = 62.8%, PC2 = 21.3%: Fig. 2) and summarize the main African temperature and precipitation gradients (mean, seasonality and range: Supplementary material Fig. A3 [top], Table A2, A3); this provides the background climate space of our study, within which we plotted, measured and compared vegetation envelopes.

6) Quantify temporal changes in the climatic envelope using niche dynamic metrics

Niche dynamic metrics are traditionally used to quantify and compare climatic niches, i.e. the set of climatic conditions, or envelope, where a species occurs and maintains populations. The realized climatic niche is traditionally inferred from field observations (Holt 2009) and represents the portion of the fundamental niche that is occupied at a given time. We quantified climatic envelope dynamics from our occurrence records using a modified set of methods from Phelps et al. (2020; see also Broennimann et al. 2012, Petitpierre et al. 2012, Maiorano et al. 2013, Guisan et al. 2014; R Core Team; 'ecospat' package in R), whereby we pooled together the niches of indicator taxa to form a mutually exclusive climatic envelope for each vegetation group. We applied these methods continent-wide to reconstruct and quantify changes in African vegetation climatic envelopes at 100-yr intervals, beginning at 20 000 BP. These methods are suitable for our purposes because they are equipped to deal with incomplete sampling coverage in geographic space, which is a significant limitation of paleo-records on the African continent. They also allow analysis of temporal patterns of ecological change, i.e. changes in climatic envelope breadth for vegetation groups that include a variety of distinct vegetation biomes. This approach is suitable for reconstructing vegetation envelopes in non-analogous climatic conditions because vegetation envelopes are allowed to overlap, rather than assigning one biome per grid cell as in traditional approaches.

We calculated and plotted the density of occurrence records for each vegetation group along the two primary PCA axes (Fig. 2; see PCA-env in Broennimann et al. 2012). Each occurrence was weighted by the rounded percentage of the vegetation group being reconstructed. For example, if forest comprised 40.4% of the pollen sum for site one and 80.8% at site two, then we duplicated occurrence records 40 and 81 times, respectively. To quantify changes in the climatic envelope through time, we then used two overlap metrics to determine the breadth of our multidimensional vegetation envelopes. First, we used a density-based metric (a niche overlap metric [Broennimann et al. 2012] based on Schoener's D [Warren et al. 2008], implemented as in Phelps et al. [2020]) to measure the breadth of each

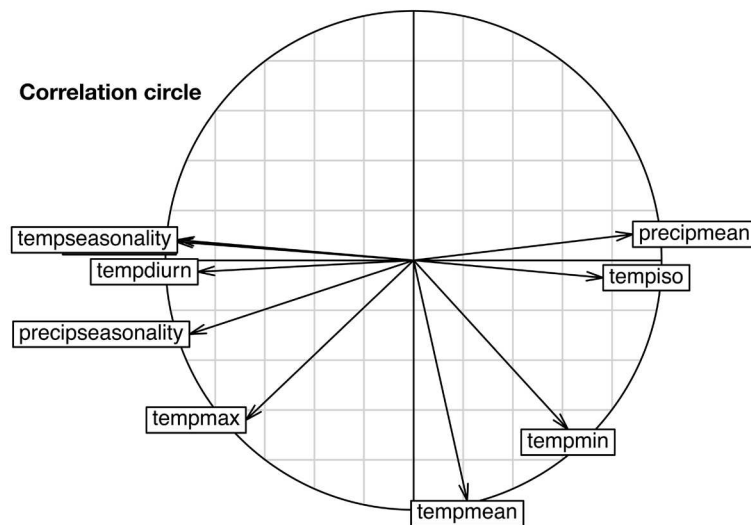
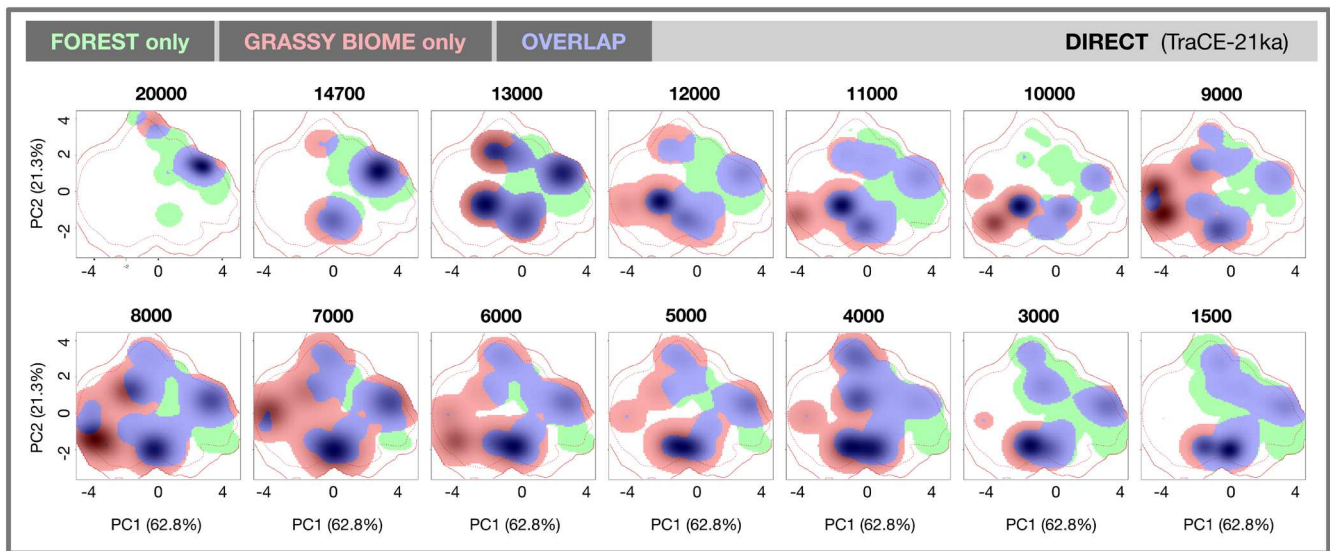


Figure 2. Climatic envelope overlap between forest and grassy biomes, mapped in climate space using TraCE-21ka climate information and the direct methodological approach ('ecospat' package in R, R Core Team; for additional methodology: Broennimann et al. 2012). Green areas represent climatic spaces where only forest taxa occurred; red areas represent climatic spaces where only savanna or steppe taxa occurred (grassy biomes); and blue/purple areas represent climatic spaces where forest and grassy biomes overlapped in their climatic distribution. The solid red outline indicates the extent of the pooled climatic space across the entire study period. Darker areas represent higher densities of overlap. For visualizations of more time intervals, see Supplementary material Fig. A4 and Movies 8a–b; for climate variable contribution to PCA axes, see Table A2.

vegetation envelope, according to the climatic density of occurrence records (Dden). Second, we used a binarized metric (Dbin), independent of climate density, to measure the climatic extent of the vegetation envelope (Guisan et al. 2014). Third, we used both of these metrics to measure overlap between forest and grassy biome climatic envelopes at each time interval (Fig. 3, Supplementary material Fig. A5). Climatic envelopes reflect the effects of climate–disturbance–ecosystem interactions on a continental scale, as these are based on the climatic density and extent of any given taxa.

7) Map vegetation reconstructions

We reconstructed and projected each climatic vegetation envelope into geographic space using modern WorldClim information, then rescaled its occurrence density from 0 to 1 based on the maximum occurrence density of its vegetation group across 20 000 yr, to permit visual comparison between vegetation groups. This results in continuous maps of climatic suitability for each vegetation group (Fig. 4, Supplementary material Fig. A6a–d). We also generated multivariate environmental similarity surfaces (MESS) for each time interval

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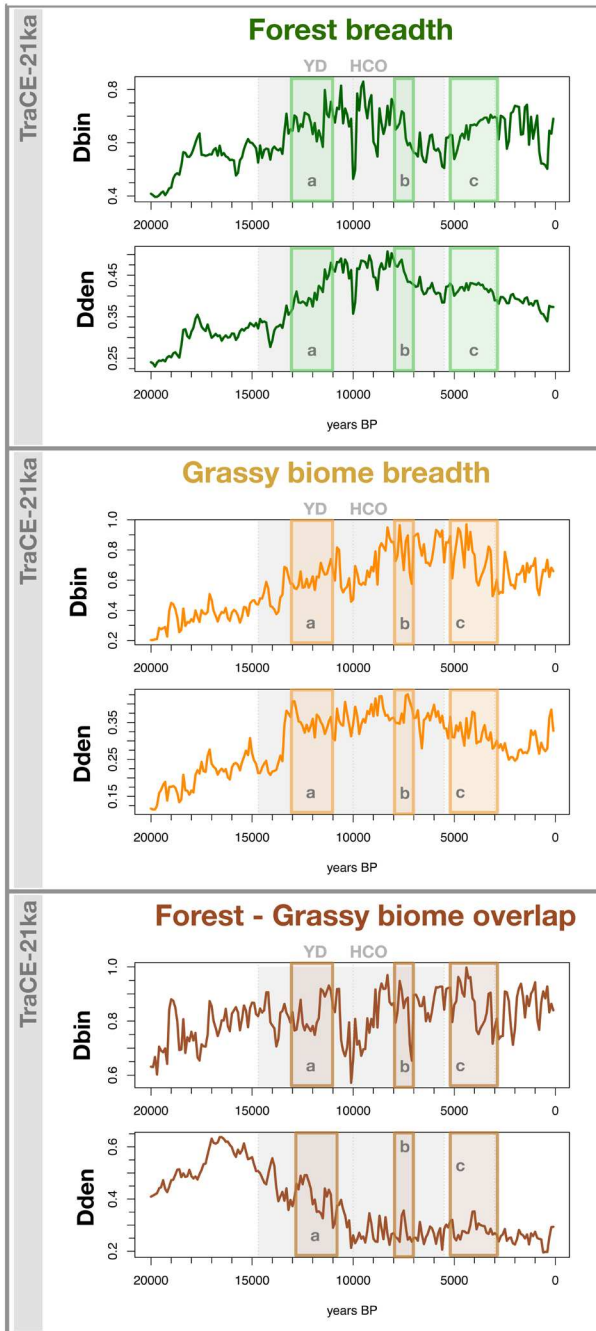


Figure 3. Schoener's D envelope overlap (Dden) and binarized D (Dbin) values plotted from the last glacial period until recent times, using the direct methodological approach and TraCE-21ka climate information. 'Forest breadth': D values represent the proportion of the entire African climate space occupied by forest taxa; 'Grassy biome breadth': D values represent the portion occupied by grassy biome taxa; 'Forest-Grassy biome overlap': D values represent the climatic overlap between the forest and grassy biome envelopes. Rectangle (a) represents the Younger Dryas, (b) the Green Sahara Pause and (c) the termination of the AHP, including the first phase of central African forest decline. For further analysis, see Supplementary material Fig. A5.

('ecospat' package in R, see Elith 2010), as an indication of sampling coverage (Fig. 4, Supplementary material Fig. A6a–d): blue areas indicate well-sampled climatic spaces, whereas red areas indicate poorly-sampled climatic spaces.

Results

We provide the first continental-scale African vegetation reconstructions from the last glacial period until recent times, and detail three non-linear responses between forest and grassy biomes to insolation change. Our results improve the understanding of broadscale vegetation trends during the AHP and lead us to propose three hypotheses about the potential role of anthropogenic disturbance.

Sampling coverage

Multivariate environmental similarity surface (MESS) analyses demonstrate that our sampling coverage is relatively comprehensive in sub-Saharan Africa throughout the study interval (blue spaces in Fig. 4), especially for east Africa. Coverage is relatively poor in northern Africa, albeit to varying degrees through time, and in parts of central and southwestern Africa (red spaces: Fig. 4, Supplementary material Movies S7a–d). Vegetation patterns reconstructed in red areas thus have higher uncertainties, requiring further sampling to improve reconstructions. For example, the section of persistent reduced vegetation cover in the middle of the central African forest block is an artefact caused by limited sampling of the climate affecting the region (Fig. 4).

Forest and grassy biome response to northern hemisphere summer insolation

Our vegetation envelope reconstructions demonstrate that the climatic density of forest and grassy biomes were closely linked to changes in northern hemisphere summer insolation on a continental scale (Fig. 3 Dden; Fig. 1). From the end of the last glacial period until the HTM, forest and grassy biomes expanded into northern Africa (Fig. 3, Supplementary material Fig. A5, Movies S1, S2), with grassy biomes reaching beyond forest into higher latitudes, especially after the Younger Dryas. The climatic density of forest and grassy biomes peaked during the early Holocene, then contracted after the HTM as northern hemisphere summer insolation decreased (Fig. 3: Dden). Although plotted envelope metrics do not provide a clear indication of hydrological changes at different latitudes, mapped forest reconstructions clearly reflect the time-transgressive nature of forest expansion and contraction (Supplementary material Movies S1–S6). These observed trends are in accordance with existing research on the African continent and reflect findings from numerous studies, e.g. that during the AHP, changes in vegetation distribution reflect wetter conditions in the Sahara (Supplementary material Movies S1, S2).

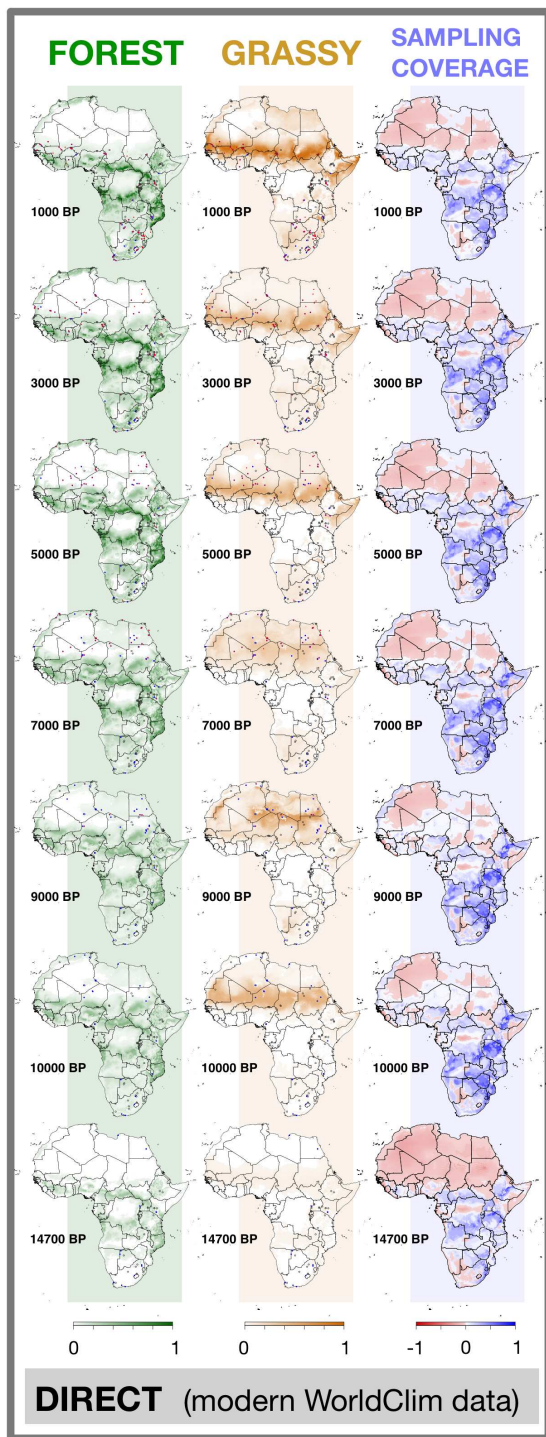


Figure 4. The climatic envelope of forest projected into geographic space (left); the climatic envelope of grassy biomes (savanna and steppe) projected into geographic space (center); sampling coverage, determined using multivariate environmental similarity surface (MESS) analysis (right). For all maps, the direct methodology and repeated modern-day WorldClim data were utilized (for further time intervals see Supplementary material Movies and Fig. A6). For MESS analyses (–1 to 1), negative (red) values indicate a dissimilar sample area to the overall climate space, i.e. poor sampling coverage, and positive values (blue) indicate climate similarity, i.e. good sampling coverage.

Non-linear vegetation responses to climate change

By comparing temporal changes in forest and grassy biomes, we observed three novel, non-linear vegetation responses to insolation change.

1) Trends in the climatic extent of forest and grassy biomes diverged significantly after the HTM as grassy biomes expanded

While the climatic extent (Dbin) of forest remained closely linked to insolation until the termination of the AHP, the climatic extent of grassy biomes increased significantly after the HTM, leading into the first phase of central African forest decline, ca 4000 BP (Fig. 3, Supplementary material Fig. A5).

2) A strong hysteresis was observed in the rate of forest response to climate change between the beginning and end of the African Humid Period

Forest envelope expansion occurred significantly faster leading up to the HTM than the rate of contraction afterwards. This hysteresis was associated with increasing atmospheric CO₂ concentrations (Fig. 1) and relative abundance of forest pollen (Supplementary material Fig. A7). Given changes in sampling through time (Supplementary material Fig. A2), this finding requires closer investigation, yet comparison between envelopes (Dbin: no hysteresis; Dden: hysteresis) strongly suggests that sampling bias is not responsible for this observed non-linear response, nor for the observed differences between forest and grassy biome trends, as these were reconstructed using the same methodology.

3) As forest and grassy biomes diverged after the HTM, their relationship (envelope overlap) fundamentally changed

As insolation increased from the end of the last glacial period until the HTM, the overlapping climatic density of forest and grassy biome envelopes decreased significantly (Fig. 3). Rather than reconverging as insolation decreased after the HTM, the overlapping climatic density between them remained low and relatively stable until recent times (Dden: 0.2–0.36; Fig. 3). This post-HTM stasis was further associated with high but variable overlap between the extent of forest and grassy biomes (Dbin; 0.65–1), as well as differences in their geographic distribution (Fig. 4, Supplementary material Movies S1, S2). In other words, forest and grassy biomes continued to occupy similar climates, but their climatic densities became more distinct from one another.

At ca 4500–4000 BP, nearing the first phase of the Bantu expansion and central African forest decline, indirect methods indicate that the climatic extent (Dbin) and density (Dden) of forest contracted substantially and anomalously (Supplementary material Fig. A5c). In contrast, direct methods show that the forest envelope expanded ca 5000–4000 BP, coinciding with a recorded precipitation increase from leaf wax records (Fig. 3, Supplementary material Fig. A5; Shanahan et al. 2015). Here, our results are likely recording two separate but complementary findings: first, when few indicator taxa are considered (direct analyses), the increasing precipitation signal is apparent; second, when a larger

number of taxa are analyzed (indirect analyses), a large decline in forest taxa is apparent. These concurrent changes between forest and grassy biomes suggest that a temporary instability or tipping point may have been reached ca 4500–4000 BP, characteristic of disturbance-driven alternative stable states (Hirota et al. 2011). In this sense, forest decline appears to have been driven by additional factors besides climate change, closely associated with or caused by the expansion of grassy biomes into forested areas (Supplementary material Fig. A5; indirect; Fig. 3: Dbin).

After AHP termination, the climatic density (Dden) of forest decreased from ca 3000 BP until modern times (Fig. 3, Supplementary material Fig. A5); the average relative percent of forest stabilized (Supplementary material Fig. A7); and a clear southward contraction of forest was observed in the Sahel during the second phase of central African forest decline (ca 3000–2000 BP; Supplementary material Movies S1a–d, Fig. 3c, Supplementary material Fig. A5c). In contrast to forest, the climatic density and extent of grassy biomes increased after AHP termination (Fig. 3, Supplementary material Fig. A5) and the average relative percentage of grassy biomes peaked (Supplementary material Fig. A7). From ca 4000 to 1500 BP, savanna in particular expanded and shifted southward, becoming noticeably patchier in its geographic distribution (Supplementary material Fig. A5, Movie S3). These post-AHP patterns suggest that taxa from grassy biomes continued to encroach on forested areas, especially due to the simultaneous increase in climatic overlap between forest and grassy biome extent (Dbin), the expansion of the grassy biome envelope, and the contraction of the forest envelope (Fig. 3).

Disturbance-driven hypotheses

By modeling the climatic vegetation envelope, we inherently reconstruct temporal changes that result from climate–disturbance–ecosystem interactions. Although we cannot conclusively determine the causality of vegetation change, we employ complementary methods that reveal clues about potential drivers of change and allow us to form hypotheses. The three observed non-linear vegetation responses to insolation change raise questions about the role of disturbance in vegetation changes observed after the HTM, especially by way of savanna expansion and the formation of alternative stable states. To this end, we form three disturbance-driven hypotheses that are interlinked, but require explicit testing: 1) increasing human population levels, the development of pyrotechnologies, and land clearance associated with the spread of cultivation and Bantu expansion contributed to the expansion of grassy biomes during and after the termination of the AHP. 2) The spread and development of African animal production into sub-Saharan Africa preferentially benefited grassy biome development over forest and may have influenced the first phase of (peripheral) central African forest decline, typically assumed to be driven solely by climate change. 3) Increasing anthropogenic landscape disturbance and carbon dioxide concentrations interacted to cause the

formation of alternative stable states detectable at continental scale, especially during and after the termination of the African Humid Period.

Supporting details for these hypotheses are discussed below.

Discussion

We reconstructed continental-scale vegetation trends in Africa by synthesizing paleo-records and analyzing temporal changes in the climatic envelopes of select vegetation groups, namely forest and grassy biomes. By measuring the climatic breadth of these mutually exclusive, taxa-based groups, our approach is suitable for reconstructing broadscale vegetation trends, while maintaining the integrity of vegetation and climatic conditions for individual occurrence records. Using this approach, we provide a novel perspective from which to understand the combined effects of climate–disturbance–ecosystem interactions on forest and grassy biome change since the end of the last glacial period. Given that the rate and amplitude of vegetation change is highly variable across paleo-records, our reconstructions are useful for understanding continental-scale trends during the onset and termination of the AHP.

We observed three non-linear vegetation responses to climate change between the beginning and end of the AHP, suggesting Holocene disturbance as a potential driver that requires investigation. However, nonlinear changes can also result from or interact with vegetation–climate feedbacks, nonlinear changes in rainfall and hydrological dynamics (Table 2). Potential sources of disturbance include anthropogenic land use change, e.g. the expansion of agriculture (Neumann et al. 2012a, Kahlheber et al. 2014, Russell et al. 2014, Stevens et al. 2014, Burgarella et al. 2018) and the animal production niche (Marshall and Hildebrand 2002, Phelps et al. 2020); the development of metal production (Chirikure 2018); fire management (Phillipson 2005, Butz 2009, Killick 2016); and natural disturbance, e.g. the effects of increasing atmospheric carbon dioxide (Fig. 1) on tree recruitment (Bond and Midgley 2012) and changes in grazing and browsing patterns of wild herbivores (Valeix et al. 2011). To this end, we propose and discuss three vegetation–disturbance hypotheses, focusing on the role of anthropogenic land use and the establishment of alternative stable states.

Hypothesis (1): increasing anthropogenic disturbance associated with the spread of agriculture, the development of pyrotechnologies and the Bantu expansion led to land clearances, which provided grassy biomes with an increased advantage after the AHP.

The termination of the AHP was a period of rapid agricultural expansion along the Sahara-Sahel border and into west Africa. Domesticated pearl millet *Pennisetum glaucum* first appeared ca 5500 BP in northern Mali (Manning et al. 2011) and spread rapidly into the Sahelo-Sudanian belt, intensifying around 4000 BP (Neumann et al. 1996, Klee et al. 2000, D'Andrea et al. 2001, Zach and Klee 2003, Ozainne et al. 2009). The spread of agriculture and associated increase in social

complexity into west Africa was driven by a broad scale migration of populations from the north, moving in response to the increasing aridification of the Sahara. Recent genomic analysis of other West African cultivars furthermore indicates the Niger basin as a major cradle of African agriculture (Meyer et al. 2016, Scarcelli et al. 2019). This southward spread of population also brought with it a new suite of pyrotechnologies (Killick 2016), including large scale ceramic production throughout the Sahelian region (Jordan et al. 2016), and by ca 3500 BP, the emergence of centralized urban settlements (Bedaux et al. 2005) and early metal production (Chirikure 2018). These changes occurred around the first phase of west-central African forest decline, ca 4000 BP, which is often attributed to climate change alone (Bostoen et al. 2015). However, patterns of change in climatic vegetation envelopes suggest that forest contraction ca 4000 BP occurred during a period of increased precipitation (Shanahan et al. 2015; direct methods: Fig. 3), as grassy biomes encroached (indirect methods: Supplementary material Fig. A5). Furthermore, these changes were preceded, ca 5000 BP, by evidence for early Bantu expansion (Coelho et al. 2009, Gignoux et al. 2011, Henn et al. 2011) – which progressively spread south and east out of west-central Africa and tended to follow savanna corridors (Grollemund et al. 2015) – and the spread of pastoralism into east Africa (Marshall and Hildebrand 2002).

Whereas the first phase of central African forest decline is thought to have facilitated early Bantu settlement in the forest periphery, the second phase ca 3000–2500 BP, is thought to have facilitated extensive and rapid expansion of Bantu-speech communities with cereal cultivation and metallurgy into the core of the central African forest block (Bostoen et al. 2015). Whether this migration could have caused or contributed to the second phase of forest decline is hotly debated (Bayon et al. 2012, Neumann et al. 2012b, Clist et al. 2018, Garcin et al. 2018). While our results reflect forest decline during this second phase, the decline was much less pronounced and anomalous than the first (Fig. 3, Supplementary material Fig. A5), with forest appearing to fall back in line with a linear response to insolation change. Oppositely, grassy biomes demonstrated a highly non-linear response to insolation change, expanding from ca 3000 BP until recent times (Fig. 3) as forest continued to contract (albeit potentially buffered by increasing atmospheric CO₂ [Fig. 1]) and Bantu-speaking communities spread into eastern and southern Africa (Grollemund et al. 2015). Although the causal relationship between land use and land cover change is not tested here, the observed expansion of grassy biomes corresponds with increasing human disturbance, and therefore requires consideration as a possible cause of vegetation change.

Hypothesis (2): the expansion of the African animal production niche preferentially benefitted grassy biome development after the HTM.

Compared with the expansion of the animal production niche (Phelps et al. 2020), our results circumstantially

suggest that from the Green Sahara Pause until recent times, animal production may have played a role in preferentially benefitting grassy biome development. The climatic niche of animal production expanded significantly after the Green Sahara Pause (Phelps et al. 2020). This was coincident with a non-linear (heightened) response of grassy biomes to insolation forcing (Fig. 3) and a period of declining radiocarbon date densities in North African archaeological records (Manning and Timpson 2014). Furthermore, simultaneous changes in the extent and overlap (Dbin) between forest and grassy biomes suggest that grassy biomes, especially savanna, encroached on forests after the HTM, and that a new ecological relationship was established between them (Fig. 2, 3). It is known that savanna expansion can result from disturbance dynamics, including changing fire regimes and grazing patterns, (see ‘Gulliver effect’: Bond and Van Wilgen 1996, Bond et al. 2005, ‘pyromes’: Archibald et al. 2013). Therefore, these coincident changes suggest that modifications to land use strategies, e.g. the introduction and subsequent expansion of mobile pastoralist strategies (Marshall and Hildebrand 2002, Smith 1992), could have driven a heightened extent of grassy biomes and the divergence between forest and grassy biomes (Fig. 3). This would be consistent with previous findings that pastoralism provided an adaptive strategy during this period of high susceptibility to population collapse, and that traditional pastoral strategies may have provided a competitive advantage to savanna grass species (Brierley et al. 2018). Other forms of early to mid Holocene land use change also require investigation, including changes in hunting-gathering fire and grazing regimes (Phillipson 2005) and the management of wild flora and fauna (Cancellieri and di Lernia 2014).

As discussed above, the first phase of central African forest decline is typically attributed to climate change, however, the direct or indirect effects of expanding animal production on vegetation change are poorly understood. The extent of grassy biomes was heightened for millennia before the first phase of central African forest decline, ca 8000–4500 BP, potentially putting pressure on continued savanna expansion during the termination of the AHP. Similar changes are apparent between the distributions of grassy biomes (Supplementary material Movies S1–S3) and animal production (Phelps et al. 2020), as both became increasingly concentrated in the Sahel. This was followed by a significant expansion of the animal production niche into sub-Saharan Africa ca 5000–4500 BP (Phelps et al. 2020), peak grassy biome extent and an increase in the climatic density of grassy biomes (Fig. 3), concurrent with the aforementioned evidence for early Bantu expansion (Grollemund et al. 2015) and the spread of pastoralism into east Africa (Marshall and Hildebrand 2002).

Hypothesis (3): interactions between anthropogenic disturbance and increasing atmospheric CO₂ interacted to form alternative stable states, especially during and after the termination of the AHP.

Savanna expansion has the capacity to drive significant ecological change, especially by perpetuating alternative

stable states or ‘hysteresis’ (McNaughton 1984, D’Antonio and Vitousek 1992, Scheiter et al. 2012, Hempson et al. 2015, 2019). Oppositely, increasing atmospheric CO₂ concentrations are known to increase tree recruitment (Bond and Midgley 2000, Kgope et al. 2010, Scheiter et al. 2012). In modern studies, it is well established that opposing forces such as these can lead to conflictual ecological relationships between forest and grassy biomes, i.e. alternative stable states influenced by disturbance dynamics (e.g. changes in fire, herbivory, atmospheric CO₂), hydroclimatic interactions and soils (Bond et al. 2003, Hirota et al. 2011, Staver et al. 2011a, b, Favier et al. 2012, Dantas et al. 2016, Hempson et al. 2019). The long-term ecological manifestation of alternative stable states is much less clear, however (Moncrieff et al. 2014).

The observed hysteresis in forest response to insolation change reflects existing studies on hydrological dynamics during the AHP: abrupt increases in lakes and wetlands were recorded leading up to the HTM, with maximum values reached ca 9500–7500 BP, followed by a gradual decline of hydrological records during the AHP (Lézine et al. 2011). Vegetation feedbacks from the forest canopy may have slowed this decline of water bodies after the HTM, e.g. through increased transpiration (Lézine et al. 2011) and the formation of stratiform cloud cover (Maley 1996). Also important to consider, is the increased growth of C₃ plants in response to rising atmospheric CO₂ concentrations (Hättenschwiler et al. 1997, Polley et al. 1997, Prentice and Harrison 2009, Bond and Midgley 2012; Fig. 1). For forest, the relative mean abundance of taxa increased consistently from past to present (Supplementary material Fig. A7, Movie S1), potentially supported by increasing CO₂ (Bond and Midgley 2012, Moncrieff et al. 2014; Fig. 1). In this sense it is conceivable that vegetation-CO₂ interactions slowed the decline of forest and affected precipitation levels, especially for C₃ forest canopy, via increased water-use efficiency and evapotranspiration as a result of induced growth stimulation (i.e. increasing ecosystem level photosynthesis and net carbon uptake: Jolly and Haxeltine 1997, Boom et al. 2002, Prentice and Harrison 2009, Keenan et al. 2013). In effect, this could have buffered, i.e. slowed the decline of forest (Bond and Midgley 2012) in the mid-Holocene, contributing to the observed non-linear vegetation response to insolation change.

In contrast to forest, increasing atmospheric CO₂ is disadvantageous for many grassy taxa (those with C₄ photosynthetic pathways: Jolly and Haxeltine 1997, Norby et al. 2005, Keenan et al. 2013, Moncrieff et al. 2014). Despite this, we observed heightened grassy biome extent (D_{bin}) from the Green Sahara Pause until the termination of the AHP, and an expansion of grassy biome extent and density (D_{den}) after the AHP (Fig. 3). This strengthens the idea that heightened grassy biome extent was driven by another form of external disturbance (hypotheses 1/2), which interacted with rising CO₂ concentrations. However, direct consideration of grasses and C₃–C₄ plant composition are required.

Aside from the observed shift in post-HTM overlap between forest and grassy biomes (Fig. 3), the geographic appearance of high abundance savanna patches after the AHP may further indicate stable alternative states (research suggests that spatial organization in patches is a sign of alternative stable states: Gillson 2004, Kéfi et al. 2016). Although disturbance dynamics can have a stabilizing effect on vegetation, they may also result in ‘catastrophic transitions’ or ‘tipping points’, such as sudden deforestation (D’Antonio and Vitousek 1992, Scheffer and Carpenter 2003, Aleman and Staver 2018). In this sense, changes in fire regimes could have interacted with rising CO₂ to stabilize vegetation change (Brierley et al. 2018) and to cause rapid ecological shifts, e.g. during the first phase of central African forest decline. Therefore, the roles that anthropogenic disturbance and atmospheric CO₂ played in the first and second phases of central African forest decline require further consideration and testing.

Our results raise questions about the impacts of changing land use practices on continental-scale vegetation change, e.g. changes in grazing and fire regimes, the spread or intensification of cultivation, and niche construction processes associated with the expanding animal production niche (Phelps et al. 2020). While our methods capture the effects of climate–disturbance–ecosystem interactions at continental-scale and provide insight about the potential causes of vegetation trends, our hypotheses require explicit testing in future studies. Generally speaking, our findings should not be used to interpret change at fine spatio-temporal scales due to the coarse resolution of our study and chronological uncertainties (Supplementary material Fig. A8). Unique combinations of plant functional traits across African savannas result in variable ecosystem response to disturbance (Osborne et al. 2018), and these require targeted research and management strategies that we do not address here. Additional limitations to consider include differing amounts and distributions of pollen records before and after the HTM, which may influence the observed vegetation trends. For further discussion of methodological limitations and future applications, see Supplementary material.

Conclusion

We present the first African vegetation reconstructions, from the last glacial period to modern times, using a statistical multivariate envelope approach on synthesized subfossil pollen records and simulated climate information. Our novel approach quantifies variations in the bioclimatic envelopes of vegetation groups through time, providing insight into the development of forest and grassy biomes during an interval of hydroclimatic variability. Our results clarify broad-scale vegetation trends during the African Humid Period, and are in accordance with previous studies on the AHP. We additionally demonstrate three non-linear vegetation responses to insolation change: first, grassy biome expansion led to a divergence between forest and grassy biome envelopes after

the HTM; second, there was a strong hysteresis in forest response to insolation change between the beginning and end of the AHP; and third, the ecological relationship between forest and grassy biomes fundamentally shifted after the HTM, suggesting the formation of stable alternative states. We pose three hypotheses to explain these non-linear responses: first, increasing human population levels, the development of pyrotechnologies, and land clearance associated with the spread of cultivation and Bantu expansion contributed to vegetation change; second, the spread and development of African animal production into sub-Saharan Africa preferentially benefitted grassy biome development; and third, increasing anthropogenic landscape disturbance and carbon dioxide concentrations interacted to cause the formation of alternative stable states detectable at continental scale. The rate and amplitude of vegetation change is variable across African paleo-records, making it difficult to discern broad-scale trends and to consider different drivers of change at local-to-regional scales. Thus our broad-scale perspective addresses this deficit and investigates the patterns that dominate complex vegetation change during and after the AHP, with implications for modeling vegetation change under future projected climate scenarios.

Data availability statement

The data utilized in this study are available at <<https://doi.pangaea.de/10.1594/PANGAEA.905309>> (Phelps et al. 2019a: relational pollen datasets). For movies referenced in this manuscript, see: <<https://doi.pangaea.de/10.1594/PANGAEA.905979>> (Phelps et al. 2019b). For credit to the primary sources on which our analyses are based, please see the Appendix in this paper.

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Author contributions – AG and KM shared last-authorship.

References

- Aleman, J. C. and Staver, C. A. 2018. Spatial patterns in the global distributions of savanna and forest. – *Global Ecol. Biogeogr.* 27: 792–803.
- Archibald, S. and Hempson, G. P. 2016. Competing consumers: contrasting the patterns and impacts of fire and competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. – *Phil. Trans. R. Soc. B* 371: 20150309.
- Archibald, S. et al. 2013. Defining pyromes and global syndromes of fire regimes. – *Proc. Natl Acad. Sci. USA* 10: 6442–6447.
- Bayon, G. et al. 2012. Intensifying weathering and land use in iron age central Africa. – *Science* 335: 1219–1222.
- Bedaux, R. et al. 2005. Recherches archéologiques à Dia dans le delta intérieur du Niger (Mali): bilan des saisons de fouilles 1998–2003. – *Mededelingen van het Rijksmuseum voor Volkenkunde, Leiden* 33, CNWS Publications, Leiden.
- Bird, R. B. et al. 2008. The “fire stick farming” hypothesis: Australian aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. – *Proc. Natl Acad. Sci. USA* 105: 14796–14801.
- Blaauw, M. 2010. Methods and code for ‘classical’ age-modelling of radiocarbon sequences. – *Quat. Geochronol.* 5: 512–518.
- Bond, W. J. 2005. Large parts of the world are brown or black: a different view on the ‘green world’ hypothesis. – *J. Veg. Sci.* 16: 261–266.
- Bond, W. J. 2008. What limits trees in C4 grassland and savannas. – *Annu. Rev. Ecol. Evol. Syst.* 39: 641–659.
- Bond, W. J. and Van Wilgen, B. W. 1996. Fire and plants. – Chapman and Hall.
- Bond, W. J. and Midgley, G. F. 2000. A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. – *Global Change Biol.* 6: 865–869.
- Bond, W. J. and Midgley, G. F. 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. – *Phil. Trans. R. Soc. B* 367: 601–612.
- Bond, W. J. et al. 2003. The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. – *Global Change Biol.* 9: 973–982.
- Bond, W. J. et al. 2005. The global distribution of ecosystems in a world without fire. – *New Phytol.* 165: 525–538.
- Boom, A. et al. 2002. CO₂- and temperature-controlled altitudinal shifts of C₄- and C₃-dominated grasslands allow reconstruction of palaeoatmospheric pCO₂. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 177: 151–168.
- Bostoen, K. et al. 2015. Middle to late Holocene paleoclimatic change and the early Bantu expansion in the rain forests of western central Africa. – *Curr. Anthropol.* 56: 354–384.
- Bowman, D. M. J. S. et al. 2009. Fire in the earth system. – *Science* 324: 481–484.
- Braconnot, P. et al. 2012. Evaluation of climate models using palaeoclimatic data. – *Nat. Clim. Change* 2: 417–424.
- Brierley, C. et al. 2018. Pastoralism may have delayed the end of the Green Sahara. – *Nat. Commun.* 9: 1–9.
- Broennimann, O. et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. – *Global Ecol. Biogeogr.* 21: 481–497.
- Buitenwerf, R. et al. 2012. Increased tree densities in South African savannas: >50 years of data suggests CO₂ as a driver. – *Global Change Biol.* 18: 675–684.
- Burgarella, C. et al. 2018. A western Sahara centre of domestication inferred from pearl millet genomes. – *Nat. Ecol. Evol.* 2: 1377–1380.

- Burrough, S. L. and Thomas, D. S. G. 2013. Central southern Africa at the time of the African Humid Period: a new analysis of Holocene palaeoenvironmental and palaeoclimate data. – *Quat. Sci. Rev.* 80: 29–46.
- Burrough, S. L. and Willis, K. J. 2015. Ecosystem resilience to late-Holocene climate change in the upper Zambezi Valley. – *Holocene* 25: 1811–1828.
- Butz, R. J. 2009. Traditional fire management: historical fire regimes and land use change in pastoral east Africa. – *Int. J. Wildl. Fire* 18: 442–450.
- Cancellieri, E. and di Lernia, S. 2014. Re-entering the central Sahara at the onset of the Holocene: a territorial approach to Early Acacus hunter-gatherers (SW Libya). – *Quat. Int.* 320: 43–62.
- Chase, B. M. et al. 2019. Orbital controls on Namib Desert hydroclimate over the past 50,000 years. – *Geology* 47: 1–5.
- Chauvin, F. et al. 2010. Intraseasonal variability of the Saharan heat low and its link with midlatitudes. – *J. Clim.* 23: 2544–2561.
- Chevalier, M. and Chase, B. M. 2015. Southeast African records reveal a coherent shift from high- to low-latitude forcing mechanisms along the east African margin across last glacial–interglacial transition. – *Quat. Sci. Rev.* 125: 117–130.
- Chirikure, S. 2018. Precolonial metallurgy and mining across Africa. – In: *Oxford Research Encyclopedia, African History*. Oxford Univ. Press.
- Claussen, M. et al. 1999. Simulation of an abrupt change in Saharan vegetation in the mid-Holocene. – *Geophys. Res. Lett.* 26: 2037–2040.
- Claussen, M. et al. 2017. Theory and modeling of the African Humid Period and the Green Sahara. – In: *Oxford Research Encyclopedia of Climate Science*. Oxford Univ. Press.
- Clist, B. et al. 2018. Did human activity really trigger the late Holocene rainforest crisis in central Africa. – *Proc. Natl Acad. Sci. USA* 115: E4733–E4734.
- Coelho, M. et al. 2009. On the edge of Bantu expansions: mtDNA, Y chromosome and lactase persistence genetic variation in southwestern Angola. – *BMC Evol. Biol.* 9: 80.
- Crisp, M. D. et al. 2009. Phylogenetic biome conservatism on a global scale. – *Nature* 458: 754–756.
- Crowther, A. et al. 2018. Subsistence mosaics, forager–farmer interactions and the transition to food production in eastern Africa. – *Quat. Int.* 489: 101–120.
- D’Andrea, A. C. et al. 2001. Archaeobotanical evidence for pearl millet (*Pennisetum glaucum*) in sub-Saharan west Africa. – *Antiquity* 75: 341–348.
- D’Antonio, C. M. and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. – *Annu. Rev. Ecol. Syst.* 23: 63–87.
- Dallmeyer, A. et al. 2019. Harmonising plant functional type distributions for evaluating earth system models. – *Clim. Past* 15: 335–366.
- Dantas, V. d. L. et al. 2016. Disturbance maintains alternative biomes states. – *Ecol. Lett.* 19: 12–19.
- de Maret, P. 2013. Archaeologies of the Bantu expansion (627–644). – In: Mitchell, P. and Lane, P. (eds), *Oxford handbook of African archaeology*. Oxford Univ. Press, pp. 627–644.
- deMenocal, P. et al. 2000. Abrupt onset and termination of the African humid period: rapid climate responses to gradual insolation forcing. – *Quat. Sci. Rev.* 19: 347–361.
- di Lernia, S. 2006. Building monuments, creating identity: cattle cult as a social response to rapid environmental changes in the Holocene Sahara. – *Quat. Int.* 151: 50–62.
- Dunne, J. et al. 2012. First dairying in the green Saharan Africa in the fifth millennium BC. – *Nature* 486: 390–394.
- Ehleringer, J. R. et al. 1997. C4 photosynthesis, atmospheric CO2 and climate. – *Oecologia* 112: 285–299.
- Elenga, H. et al. 2000. Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP. – *J. Biogeogr.* 27: 621–634.
- EPICA Community Members 2006. One-to-one coupling of glacial climate variability in Greenland and Antarctica. – *Nature* 444: 195–198.
- Eriksen, S. and Watson, H. 2009. The dynamic context of southern African savannas: investigating emerging threats and opportunities to sustainability. – *Environ. Sci. Policy* 12: 5–22.
- Favier, C. et al. 2012. Abrupt shifts in African savanna tree cover along a climatic gradient. – *Global Ecol. Biogeogr.* 21: 787–797.
- Finch, J. et al. 2017. Ecosystem change in the South Pare Mountain bloc, Eastern Arc Mountains of Tanzania. – *Holocene* 27: 796–810.
- Fleitmann, D. et al. 2003. Holocene forcing of the Indian monsoon recorded in a stalagmite from southern Oman. – *Science* 300: 1737–1739.
- Fordham, D. A. et al. 2017. PaleoView: a tool for generating continuous climate projections spanning the last 21 000 years at regional and global scales. – *Ecography* 40: 1348–1358.
- Furley, P. et al. (eds) 1992. *Nature and dynamics of forest-savanna boundaries*. – Chapman and Hall.
- Fyfe, R. M. et al. 2009. The European Pollen Database: past efforts and current activities. – *Veg. Hist. Archaeobot.* 18: 417–424.
- Garcin, Y. et al. 2018. Early anthropogenic impact on western central African rainforests 2,600 y ago. – *Proc. Natl Acad. Sci. USA* 115: 3261–3266.
- Gasse, F. 2000. Hydrological changes in the African tropics since the last glacial maximum. – *Quat. Sci. Rev.* 19: 189–211.
- Gasse, F. and Van Campo, E. 1994. Abrupt post-glacial climate events in west Asia and north Africa monsoon dynamics. – *Earth Planet. Sci. Lett.* 126: 435–456.
- Gignoux, C. R. et al. 2011. Rapid, global demographic expansions after the origins of agriculture. – *Proc. Natl Acad. Sci. USA* 108: 6044–6049.
- Gillson, L. 2004. Evidence of hierarchical patch dynamics in an east African savanna. – *Landscape Ecol.* 19: 883–894.
- Goheen, J. R. et al. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. – *J. Anim. Ecol.* 79: 372–382.
- Good, S. P. and Caylor, K. K. 2011. Climatological determinants of woody cover in Africa. – *Proc. Natl Acad. Sci. USA* 108: 4902–4907.
- Greve, M. et al. 2011. Environmental and anthropogenic determinants of vegetation distribution across Africa. – *Global Ecol. Biogeogr.* 20: 661–674.
- Grollemund, R. et al. 2015. Bantu expansion shows that habitat alters the route and pace of human dispersals. – *Proc. Natl Acad. Sci. USA* 112: 13296–13301.
- Guisan, A. et al. 2014. Unifying niche shift studies: insights from biological invasions. – *Trends Ecol. Evol.* 29: 260–269.
- Haug, G. H. et al. 2001. Southward migration of the intertropical convergence zone through the Holocene. – *Sci. Rep.* 293: 1304–1308.
- Hättenschwiler, S. et al. 1997. Thirty years of in situ tree growth under elevated CO2: a model for future forest responses? – *Global Change Biol.* 3: 463–471.

- Hély, C. and Lézine, A.-M. 2014. Holocene changes in African vegetation: tradeoff between climate and water availability. – *Clim. Past* 10: 681–686.
- Hempson, G. P. et al. 2015. Ecology of grazing lawns in Africa. – *Biol. Rev.* 90: 979–994.
- Hempson, G. P. et al. 2018. Continent-level drivers of African pyrodiversity. – *Ecography* 41: 889–899.
- Hempson, G. P. et al. 2019. Alternate grassy ecosystem states are determined by palatability–flammability trade-offs. – *Trends Ecol. Evol.* 34: 286–290.
- Henn, B. M. et al. 2011. Hunter-gatherer genomic diversity suggests a southern African origin for modern humans. – *Proc. Natl Acad. Sci. USA* 108: 5154–5162.
- Hirota, M. et al. 2011. Global resilience of tropical forest and savanna to critical transitions. – *Science* 334: 232–235.
- Hogg, A. G. et al. 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 years Cal BP. – *Radiocarbon* 55: 1889–1903.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. – *Proc. Natl Acad. Sci. USA* 106: 19659–19665.
- House, J. I. et al. 2003. Conundrums in mixed woody-herbaceous plant systems. – *J. Biogeogr.* 30: 1763–1777.
- Jolly, D. et al. 1998b. Biome reconstruction from pollen and plant macrofossil data for Africa and the Arabian peninsula at 0 and 6000 years. – *J. Biogeogr.* 25: 1007–1027.
- Jolly, D. and Haxeltine, A. 1997. Effect of low glacial atmospheric CO₂ on tropical African montane vegetation. – *Science* 276: 786–788.
- Jolly, D. et al. 1998. Biome reconstruction from pollen and plant macrofossil data for Africa and the Arabian peninsula at 0 and 6000 years. – *J. Biogeogr.* 25: 1007–1027.
- Jordan, P. et al. 2016. Modelling the diffusion of pottery technologies across Afro-Eurasia: emerging insights and future research. – *Antiquity* 90: 590–603.
- Kahlheber, S. et al. 2014. Pearl millet and other plant remains from the Early Iron Age site of Boso-Njafo (inner Congo Basin, Democratic Republic of the Congo). – *Afr. Archaeol. Rev.* 31: 479–512.
- Kéfi, S. et al. 2016. When can positive interactions cause alternative stable states in ecosystems? – *Funct. Ecol.* 30: 88–97.
- Keenan, T. F. et al. 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. – *Nature* 499: 324–327.
- Kgope, B. S. et al. 2010. Growth responses of African savanna trees implicate atmospheric [CO₂] as a driver of past and current changes in savanna tree cover. – *Austral Ecol.* 35: 451–463.
- Killick, D. 2016. A global perspective on the pyrotechnologies of Sub-Saharan Africa. – *Azania Archaeol. Res. Afr.* 51: 62–87.
- Klee, M. et al. 2000. Four thousand years of plant exploitation in the Chad Basin of northeast Nigeria I: the archaeobotany of Kursakata. – *Veg. Hist. Archaeobot.* 9: 223–237.
- Kull, C. A. and Laris, P. 2009. Tropical fire ecology: climate change, land use, and ecosystem dynamics. Cochrane, M. A. (ed.), *Fire ecology and fire politics in Mali and Madagascar*. Springer-Praxis, 171–226.
- Kuper, R. and Kröpelin, S. 2006. Climate-controlled Holocene occupation in the Sahara: motor of Africa's evolution. – *Science* 313: 803–807.
- Kutzbach, J. and Otto-Bliesner, B. 1982. The sensitivity of the African-Asian monsoonal climate to orbital parameter changes for 9000 years B.P. in a low-resolution general circulation model. – *J. Atmos. Sci.* 39: 1177–1188.
- Laskar, J. et al. 2004. A long-term numerical solution for the insolation quantities of the earth. – *Astron. Astrophys.* 428: 261–285.
- Lebamba, J. et al. 2009. Central African biomes and forest succession stages derived from modern pollen data and plant functional types. – *Clim. Past* 5: 403–429.
- Lehmann, C. E. and Parr, C. L. 2016. Tropical grassy biomes: linking ecology, human use and conservation. – *Phil. Trans. R. Soc. B* 371: 20160329.
- Lézine, A.-M. et al. 2009. Are modern pollen data representative of west African vegetation? – *Rev. Palaeobot. Palynol.* 156: 265–276.
- Lézine, A.-M. et al. 2011. Sahara and Sahel vulnerability to climate changes, lessons from Holocene hydrological data. – *Quat. Sci. Rev.* 30: 3001–3012.
- Liu, Z. et al. 2009. Transient simulation of last deglaciation with a new mechanism for Bølling-Allerød warming. – *Science* 325: 310–314.
- Maiorano, L. et al. 2013. Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. – *Global Ecol. Biogeogr.* 22: 302–317.
- Maley, J. 1996. The African rainforest – main characteristics of changes in vegetation and climate from the upper cretaceous to the quaternary. – *Proc. R. Soc. Edinburgh* 104B: 31–73.
- Manning, K. and Timpson, A. 2014. The demographic response to Holocene climate change in the Sahara. – *Quat. Sci. Rev.* 101: 28–35.
- Manning, K. et al. 2011. 4500-year old domesticated pearl millet (*Pennisetum glaucum*) from the Tilemsi Valley, Mali: new insights into an alternative cereal domestication pathway. – *J. Archaeol. Sci.* 38: 312–322.
- Marchant, R. and Hooghiemstra, H. 2004. Rapid environmental change in African and south American tropics around 4000 years before present: a review. – *Earth-Sci. Rev.* 66: 217–260.
- Marshall, F. and Hildebrand, E. 2002. Cattle before crops: the beginnings of food production in Africa. – *J. World Prehist.* 16: 99–143.
- McCarthy, J. J. et al. (eds) 2001. *Climate change 2001: impacts, adaptation and vulnerability*. – In: Contribution of working group II to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.
- McNaughton, S. 1984. Grazing lawns: animals in herds, plant form, and coevolution. – *Am. Nat.* 124: 863–886.
- Meyer, R. S. et al. 2016. Domestication history and geographical adaptation inferred from a SNP map of African rice. – *Nat. Genet.* 48: 1083–1088.
- Midgley, G. F. and Bond, W. J. 2015. Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change. – *Nat. Clim. Change* 5: 823–829.
- Moncrieff, G. R. et al. 2014. Increasing atmospheric CO₂ overrides the historical legacy of multiple stable biome states in Africa. – *New Phytol.* 201: 908–915.
- Monnin, E. 2006. EPICA Dome C high resolution carbon dioxide concentrations. – PANGAEA.
- Murphy, B. P. and Bowman, D. M. 2012. What controls the distribution of tropical forest and savanna? – *Ecol. Lett.* 15: 748–758.
- Neumann, K. et al. 1996. The emergence of plant food production in the west African Sahel: new evidence from northeast Nigeria and northern Burkina Faso. – In: Pwiti, G. and Soper, R. (eds), *Aspects of African archaeology: papers from the 10th congress*

- of the Pan African Association for Prehistory and Related Studies, Harare. Univ. of Zimbabwe Publications, pp. 441–448.
- Neumann, K. et al. 2012a. First farmers in the central African rainforest: a view from southern Cameroon. – *Quat. Int.* 249: 53–62.
- Neumann, K. et al. 2012b. Comment on ‘Intensifying weathering and land use in iron age central Africa’. – *Science* 337: 1040.
- Niang, I. et al. 2014. WGII, chapter 22: Africa. – Fifth Assessment Report, IPCC.
- Niedermeyer, E. M. et al. 2010. Orbital- and millennial-scale changes in the hydrologic cycle and vegetation in the western African Sahel: insights from individual plant wax d and 13c. – *Quat. Sci. Rev.* 29: 2996–3005.
- Norby, R.J. et al. 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. – *Proc. Natl Acad. Sci. USA* 102: 18052–18056.
- O’Brien, M. J. and Laland, K. N. 2012. Genes, culture and agriculture. – *Curr. Anthropol.* 53: 434–470.
- Odadi, W. O. et al. 2011. African wild ungulates compete with or facilitate cattle depending on season. – *Science* 333: 1753–1755.
- Oliveras, I. and Malhi, Y. 2016. Many shades of green: the dynamic tropical forest–savannah transition zones. – *Phil. Trans. R. Soc. B* 371: 1–15.
- Osborne, C. P. et al. 2018. Human impacts in African savannas are mediated by plant functional traits. – *New Phytol.* 220: 10–24.
- Oslisly, R. et al. 2013. Climatic and cultural changes in the west Congo Basin forests over the past 5000 years. – *Phil. Trans. R. Soc. B* 368: 20120304.
- Ozainne, S. et al. 2009. Developing a chronology integrating archaeological and environmental data from different contexts: the Late Holocene sequence of Ounjougou (Mali). – *Radiocarbon* 51: 457–470.
- Perez-Sanz, A. et al. 2014. Evaluation of modern and mid-Holocene seasonal precipitation of the Mediterranean and northern Africa in the cmip5 simulations. – *Clim. Past* 10: 551–568.
- Petitpierre, B. et al. 2012. Climatic niche shifts are rare among terrestrial plant invaders. – *Science* 335: 1344–1348.
- Phelps, L. N. et al. 2019a. Pollen dataset: forest and grassy biomes respond asymmetrically to climate change during the African Humid Period: a result of anthropogenic disturbance? – PANGAEA, Appendices 1–9, <<https://doi.pangaea.de/10.1594/PANGAEA.905309>>.
- Phelps, L. N. et al. 2019b. Time series animations of African vegetation change using pollen records: forest and grassy biomes respond asymmetrically to climate change during the African Humid Period: a result of anthropogenic disturbance? – PANGAEA, Movies S1–S8, <<https://doi.pangaea.de/10.1594/PANGAEA.905979>>.
- Phelps, L. N. et al. 2020. Reconstructing climatic niche breadth of land use for animal production during the African Holocene. – *Global Ecol. Biogeogr.* 29: 127–147.
- Phillipson, D. W. 2005. African archaeology, 3rd ed. Cambridge Univ. Press.
- Polley, H. W. et al. 1997. Viewpoints: atmospheric CO₂, soil water and shrub/grass ratios on rangelands. – *J. Range Manage.* 50: 278–284.
- Prentice, I. C. et al. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. – *J. Biogeogr.* 19: 117–134.
- Prentice, I. C. et al. 1996. Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. – *Clim. Dynamics* 12: 185–194.
- Prentice, I. C. and Webb III, T. 1998. Biome 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological records. – *J. Biogeogr.* 25: 997–1005.
- Prentice, I. and Harrison, S. 2009. Ecosystem effects of CO₂ concentration: evidence from past climates. – *Clim. Past* 5: 297–307.
- Quick, L. J. et al. 2018. A high-resolution record of Holocene climate and vegetation dynamics from the southern cape coast of South Africa: pollen and microcharcoal evidence from Eilandvlei. – *J. Quat. Sci.* 33: 487–500.
- Reimer, P. J. et al. 2013. INTCAL13 and MARINE13 Radiocarbon Age Calibration Curves 0–50,000 years Cal BP. – *Radiocarbon* 55: 1869–1887.
- Renssen, H. et al. 2006. Simulation of the Holocene climate evolution in northern Africa: the termination of the African humid period. – *Quat. Int.* 150: 95–102.
- Roos, C. I. et al. 2018. Indigenous impacts on North American Great Plains fire regimes of the past millennium. – *Proc. Natl Acad. Sci. USA* 115: 8143–8148.
- Rucina, S. M. et al. 2009. Late quaternary vegetation and fire dynamics on mount Kenya. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 283: 1–14.
- Russell, T. et al. 2014. Modelling the spread of farming in the Bantu-speaking regions of Africa: an archaeology-based phylogeography. – *PLoS One* 9: e87854.
- Sala, O. E. et al. 2000. Global biodiversity scenarios for the year 2100. – *Science* 287: 1770–1774.
- Sánchez Goñi, M. F. et al. 2017. The ACER pollen and charcoal database: a global resource to document vegetation and fire response to abrupt climate changes during the last glacial period. – *Earth Syst. Sci. Data* 9: 679–695.
- Sankaran, M. et al. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. – *Global Ecol. Biogeogr.* 17: 236–245.
- Scarcelli, N. et al. 2019. Yam genomics supports west Africa as a major cradle of crop domestication. – *Sci. Adv.* 5: eaaw1947.
- Scheffer, M. and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. – *Trends Ecol. Evol.* 18: 648–656.
- Schefuß, E. et al. 2005. Climatic controls on central African hydrology during the past 20,000 years. – *Nature* 437: 1003–1006.
- Scheiter, S. et al. 2012. Fire and fire-adapted vegetation promoted C₄ expansion in the late Miocene. – *New Phytol.* 195: 653–666.
- Scott, L. et al. 2012. Terrestrial fossil-pollen evidence of climate change during the last 26 thousand years in southern Africa. – *Quat. Sci. Rev.* 32: 100–118.
- Shanahan, T. M. et al. 2008. Abrupt changes in the water balance of tropical West Africa during the late quaternary. – *J. Geophys. Res.* 113: D12108.
- Shanahan, T. M. et al. 2015. The time-transgressive termination of the African humid period. – *Nat. Geosci.* 8: 140–144.
- Skoglund, P. et al. 2017. Reconstructing prehistoric African population structure. – *Cell* 171: 59.e21–71.e21.
- Smit, I. P. and Prins, H. H. 2015. Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African savannas. – *PLoS One* 10: e0137857.
- Smith, A. 1992. Origins and spread of pastoralism in Africa. – *Annu. Rev. Anthropol.* 21: 125–141.
- Staver, C. A. et al. 2011a. Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. – *Ecology* 92: 1063–1072.

- Staver, C. A. et al. 2011b. The global extent and determinants of savanna and forest as alternative biome states. – *Science* 334: 230–232.
- Steffen, W. L. 1996. A periodic table for ecology? A chemist's view of plant functional types. – *J. Veg. Sci.* 7: 425–430.
- Stevens, C. J. et al. 2014. *Archaeology of African plant use*. – Publications of the Inst. of Archaeology, Univ. College London, Walnut Creek, California, Left Coast Press.
- Street-Perrott, F. A. and Perrott, R. A. 1990. Abrupt climate fluctuations in the tropics: the influence of Atlantic ocean circulation. – *Nature* 343: 607–612.
- Tafuri, M. A. et al. 2006. Mobility and kinship in the prehistoric Shara: strontium isotope analysis of Holocene human skeletons from the Acacus Mts. (southwestern Libya). – *J. Anthropol. Archaeol.* 25: 390–402
- The Plant List 2013. Version 1.1. – <www.theplantlist.org/>.
- Thompson, L. G. et al. 2002. Kilimanjaro ice core records: evidence of Holocene climate change in tropical Africa. – *Science* 298: 589–593.
- Tierney, J. E. et al. 2008. Northern hemisphere controls on tropical southeast African climate during the past 60,000 years. – *Science* 322: 252–255.
- Tierney, J. E. et al. 2011. Model, proxy and isotopic perspectives on the East African humid period. – *Earth Planet. Sci. Lett.* 307: 103–112.
- Tierney, J. E. et al. 2017. Rainfall regimes of the Green Sahara. – *Sci. Adv.* 3: e1601503.
- Valeix, M. et al. 2011. Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. – *Biol. Conserv.* 144: 902–912.
- Vincens, A. et al. 2006. Modern pollen-based biome reconstructions in East Africa expanded to southern Tanzania. – *Rev. Palaeobot. Palynol.* 140: 187–212.
- Vincens, A. et al. 2007. African pollen database inventory of tree and shrub pollen types. – *Rev. Palaeobot. Palynol.* 145: 135–141.
- Warren, D. L. et al. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. – *Evolution* 62: 2868–2883.
- Watrin, J. et al. 2009. Plant migration and plant communities at the time of the 'Green Sahara'. – *Comptes Rendus Geosci.* 341: 656–670.
- White, R. P. et al. 2000. *Pilot analysis of global ecosystems: grassland ecosystems*. – World Resources Inst., Washington, D.C.
- Wright, D. K. 2017. Humans as agents in the termination of the African humid period. – *Front. Earth Sci.* 5: 4.
- Zach, B. and Klee, M. 2003. Four thousand years of plant exploitation in the Chad Basin of NE Nigeria II: discussion on the morphology of caryopses of domesticated *Pennisetum* and complete catalogue of the fruits and seeds of Kursakata. – *Veg. Hist. Archaeobot.* 12: 187–204.

Supplementary material (available online as Appendix ecog-04990 at <www.ecogeography.org/appendix/ecog-04990>).

Appendix

Databases:

- EPD: <http://www.europeanpollendatabase.net/getdata/>
- Fyfe, R. M. et al. 2009. The European Pollen Database: past efforts and current activities. – *Veg. Hist. Archaeobot.* 18: 417–424.
- APD: <http://fpd.sedoo.fr/fpd/bibli.do>
- Vincens, A. et al. 2007. African pollen database inventory of tree and shrub pollen types. – *Rev. Paleobot. Palynol.* 145: 135–141.
- ACER: Sánchez Goñi, M. F. et al. 2017. The ACER pollen and charcoal database: a global resource to document vegetation and fire response to abrupt climate changes during the last glacial period. – *Earth Syst. Sci. Data* 9: 679–695.
- Sánchez Goñi, M. F. et al. 2017. The ACER pollen and charcoal database. – PANGAEA. doi: 10.1594/PANGAEA.870867.

Primary sources:

- Agwu, C. 1979. *Vegetations- und klimageschichtliche Untersuchung an marinen Sedimenten vor der westafrikanischen Küste*. – PhD thesis, Univ. of Göttingen, 119 p.
- Agwu, C. O. C. and Beug, H. J. 1982. Palynological studies of marine sediments off the West African coast. – 'Meteor' Forsch. *Ergebn. C* 36: 1–30.
- Andres, W. et al. 1996. Contribution des sédiments de la mare d'Oursi à Berichte SFB 268: 5–15.
- Ballouche, A. 1997. *Dynamique des paysages végétaux sahélo-soudaniens et pratiques agro-pastorales à l'Holocène: exemples du Burkina Faso*. – Monographies-Bulletin de l'Association de Géographes Français, Paris.
- Ballouche, A. et al. 1995. La végétation holocène des montagnes du Sahara Central: une nouvelle conception. – In: Le Thomas, A. and Roche, E. (coords), 2ème symposium de Palynologie africaine. Publications occasionnelles du Centre International pour la Formation et les Echanges Géologiques (CIFEG) 31: 9–17.
- Ballouche, A. and Neumann, K. 1995. A new contribution to the Holocene vegetation history of the West African Sahel: pollen from Oursi, Burkina Faso and charcoal from three sites in northeast Nigeria. – *Veg. Hist. Archaeobot.* 4: 31–39.
- Ballouche, A. and Neumann, K. 1995. La végétation du Sahel Burkinabé à l'Holocène: la mare d' Oursi. – In: Le Thomas, A. and Roche, E. (coords), 2ème symposium de Palynologie africaine. Publications occasionnelles du Centre International pour la Formation et les Echanges Géologiques (CIFEG) 31: 19–25.
- Baruch, U. and Bottema, S. 1991. Palynological evidence for climatic changes in the Levant ca. 17000–9000 BP. – In: Bar Yosef, O. and Valla, F. R. (eds), *The Natufian culture in the Levant. International monograph in prehistory, archaeological series 1*, Ann Arbor, Michigan, USA, pp. 11–20.
- Baxter, A. J. and Meadows, M. E. 1994. Palynological evidence for the impact of colonial settlement within lowland fynbos: a high-resolution study from the Verlorenvlei, southwestern Cape Province, South Africa. – *Hist. Biol.* 9: 61–70.
- Baxter, A. J. 1996. *Late quaternary palaeoenvironments of the Sandveld, Western Cape Province, South Africa*. – PhD thesis, Univ. of Cape Town, South Africa.

- Baxter, A. J. and Meadows, M. E. 1999. Evidence for Holocene sea level change at Verlorenvlei, Western Cape, South Africa. – *Quaternary Int.* 56: 65–79.
- Ben Tiba, B. 1987. Recherches pollenanalytiques à Djebel El Ghorra, Tunisie septentrionale: premières approches. – *Agron. Horticult.* 2: 57–60.
- Ben Tiba, B. 1995. Cinq millénaires d'histoire de la végétation à Djebel El Ghorra, Tunisie septentrionale. – In: 2^{ème} symposium de palynologie africaine, CIFE 31: 49–55.
- Ben Tiba, B. and Reille, M. 1982. Recherches pollenanalytiques dans les montagnes de Kroumirie (Tunisie septentrionale): premiers résultats. – *Ecol. Mediterr.* Tome VIII Fascicule 4: 75–86.
- Benslama, M. et al. 2010. Nouvelles contributions l'histoire tardiglaciaire et holocène de la végétation en Algérie: analyses polliniques de deux profils sédimentaires du complexe humide d'El-Kala [Pollen analysis from two littoral marshes (Bourdime and Garaat El-Ouez) in the El-Kala wet complex (North-East Algeria)]. Lateglacial and Holocene history of Algerian vegetation]. – *Comptes Rendus Biol.* 333: 744–754.
- Beuning, K. R. M. 1997. Late-Glacial and Holocene vegetation, climate and hydrology of lakes Albert and Victoria, East Africa. – Unpublished PhD thesis, Univ. of Minnesota, 183 p.
- Beuning, K. R. M. 1999. A re-evaluation of the Late Glacial and early-Holocene vegetation history of the Lake Victoria region. – *Palaeoecol. Africa* 26: 115–136.
- Beuning, K. R. M. et al. 1997. A revised 30,000-year paleoclimatic and paleohydrologic history of Lake Albert, East Africa. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 136: 259–279.
- Bolick, M. R. 1974. A vegetational history of the Mt Meru Lahar, Tanzania. – Unpublished Master thesis, Duke Univ., 96 p.
- Bolick, M. R. 1991. A vegetational history of the Mt. Ujamaa Lahar, Tanzania. – *Palynology* 15: 193–210.
- Bonnefille, R. 1976. Implications of pollen assemblage from the Koobi Fora Formation, East Rudolf, Kenya. – *Nature* 264: 403–407.
- Bonnefille, R. and Hamilton, A. 1986. Quaternary and Late Tertiary history of Ethiopian vegetation. – *Acta Univ. Symb. Bot. Ups.* 26: 48–63.
- Bonnefille, R. and Buchet, G. 1987. Contribution palynologique à l'histoire récente de la forêt de Wenchi (Ethiopie). – *Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier* 17: 143–158.
- Bonnefille, R. and Mohammed, U. 1994. Pollen-inferred climatic fluctuations in Ethiopia during the last 3000 years. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 109: 331–343.
- Bonnefille, R. and Chalié, F. 2000. Pollen-inferred precipitation time-series from equatorial mountains, Africa, the last 40 kyr BP. – *Global Planet. Change* 26: 25–50.
- Bonnefille, R. et al. 1992. Quantitative estimates of full glacial temperatures in equatorial Africa from palynological data. – *Clim. Dyn.* 6: 251–257.
- Bonnefille, R. et al. 1980. Palynologie et interprétation paléoclimatique de trois niveaux Pléistocène Supérieur d'un sondage du lac Abhé (Afar, Territoire de Djibouti). – *Mémoire du Muséum National d'Histoire Naturelle, Série B, Botanique* 27: 149–164.
- Bonnefille, R. and Riollet, G. 1988. Palynologie des sédiments Holocènes de sites archéologiques du Qatar. – In: Inizan, M.-L. (ed.), *Préhistoire à Qatar, Recherche sur les civilisations* 2: 137–145.
- Bonnefille, R. and Riollet, G. 1988. The Kashiru pollen sequence (Burundi) palaeoclimatic implications for the last 40,000 yr B.P. in Tropical Africa. – *Quaternary Res.* 30: 19–35.
- Bonnefille, R. et al. 1991. Nouvelle séquence pollinique d'une tourbière de la crête Zaïre-Nil (Burundi). – *Rev. Palaeobot. Palynol.* 67: 315–330.
- Bonnefille, R. et al. 1995. Glacial/Interglacial record from Intertropical Africa, high resolution pollen and carbon data at Rusaka, Burundi. – *Quaternary Sci. Rev.* 14: 917–936.
- Bonnefille, R. et al. 1986. Palaeoenvironment of Lake Abijata, Ethiopia, during the past 2000 years. – In: Frostick, L. E. et al. (eds), *Sedimentation in the African Rifts*. Geological Society Special Publication 25: 253–265.
- Bonnefille, R. et al. 1982. Organic matter and palynology of DSDP site 367 Pliocene-Pleistocene cores off West Africa. – *Oceanologica Acta* 5: 97–104.
- Botha, G. A. et al. 1992. Palaeosols and palaeoenvironments during the Late Pleistocene Hypothermal in northern Natal. – *South African J. Sci.* 88: 508–512.
- Bousman, C. B. et al. 1988. Palaeoenvironmental implications of late Pleistocene and Holocene valley fills in Blydefontein Basin, Noupoot, C.P., South Africa. – *Palaeoecol. Africa* 19: 43–67.
- Bousman, C. B. and Scott, L. 1994. Climate or overgrazing?: the palynological evidence for vegetation change in eastern Karoo. – *Suid-Afrikaanse Tydskrif vir Wetenskap* 90: 575–578.
- Brenac, P. 1988. Evolution de la végétation et du climat dans l'Ouest Cameroun entre 25000 et 11000 ans BP. – In: Actes Xe Symposium de l'Association des Palynologues de Langue Française, *Trav. Sect. Sci. et Tech. Inst. Français Pondichry*, 25: 91–103.
- Brook, G. A. et al. 1990. Desert paleoenvironmental data from cave speleothems with examples from the Chihuahuan, Somalia-Chalbi, and Kalahari deserts. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 76: 311–329.
- Brook, G. A. et al. 1990. Paleoenvironmental data for Ituri, Zaire, from sediments in Matupi Cave, Mt. Hoyo. – *Virginia Museum Natural History Memoir* 1: 49–70.
- Burney, D. A. et al. 1994. A Holocene pollen record for the Kalahari Desert of Botswana from a U-Series dated speleothem. – *Holocene* 4: 225–232.
- Burney, D. A. 1986. Pre-settlement vegetation changes at Lake Tritrivakely, Madagascar. – *Palaeoecol. Africa* 18: 357–381.
- Burney, D. A. 1987. Late Holocene vegetational change in Central Madagascar. – *Quaternary Res.* 28: 130–143.
- Burney, D. A. 1993. Late Holocene environmental changes in arid southwestern Madagascar. – *Quaternary Res.* 40: 98–106.
- Burrough, S. L. and Willis, K. J. 2015. Ecosystem resilience to late-Holocene climate change in the Upper Zambezi Valley. – *Holocene* 25: 1811–1828.
- Carrion, J. S. et al. 1999. Twentieth century changes in montane vegetation in the eastern Free State, South Africa, derived from palynology of hyrax dung middens. – *J. Quaternary Sci.* 14: 1–16.
- Chase, B. M. et al. 2015. Influence of tropical easterlies in southern Africa's winter rainfall zone during the Holocene. – *Quaternary Sci. Rev.* 107: 138–148.
- Chateaufort, J.-J., Faure, H. and Lézine, A.-M. 1986. Facteurs contrôlant la genèse et la destruction des tourbes tropicales du littoral ouest africain. – *Document du Bureau de Recherches Géologiques et Minières* 110: 77–91.
- Cheddadi, R. et al. 1988. Holocene climatic change in Morocco: a quantitative reconstruction from pollen data. – *Clim. Dyn.* 14: 883–890.
- Cheddadi, R. et al. 2015. History of human impact on Moroccan mountain landscapes. – *Afric. Archaeol. Rev.* 32: 233–248.
- Cheddadi, R. et al. 2016. Environmental changes in the Moroccan western Rif mountains over the last 9,000 years. – *Quaternaire* 27: 15–25.
- Cheddadi, R. et al. 2017. Microrefugia, climate change, and conservation of *Cedrus atlantica* in the Rif Mountains, Morocco. – *Front. Ecol. Evol.* 5: 114.

- Cohen, A. S. et al. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: I. An introduction to the project. – *J. Paleolimnol.* 34: 1–18.
- Cordova, C. E. et al. 2017. Late Pleistocene-Holocene vegetation and climate change in the Middle Kalahari, Lake Ngami, Botswana. – *J. Paleolimnol.* 171: 199–215.
- Coutellier, V. and Stanley, D. J. 1987. Late Quaternary stratigraphy and paleogeography of the eastern Nile Delta, Egypt. – *Mar. Geol.* 77: 257–275.
- Darbyshire, I. et al. 2003. Forest clearance and regrowth in northern Ethiopia during the last 3000 years. – *Holocene* 13: 537–546.
- De Busk, J. H. 1994. Transport and stratigraphy of pollen in Lake Malawi, Africa. – PhD thesis, Duke Univ., 293 pp.
- De Busk, G. H. 1998. A 37,500-year pollen record from Lake Malawi and implications for the biogeography of afro-montane forests. – *J. Biogeogr.* 25: 479–500.
- Delibrias, G. et al. 1982. Les dépôts récents de la vallée du Shati. – In: Petit-Maire, N. (ed.), *Le Shati, Lac Pleistocène du Fezzan (Libye)*, CNRS, Marseille, pp. 86–88.
- Dupont, L. M. 1989. Palynology of the last 680,000 years of ODP Site 658 (off NW-Africa): fluctuations in paleowind systems. – In: Leinen, M. and Sarnthein, M. (eds), *Paleoclimatology and paleometeorology: modern and past patterns of global atmospheric transport*. NATO ASI Series C282, Kluwer Academic Publishers, pp. 779–794.
- Dupont, L. M. 1992. Marine palynology of interglacial-glacial transitions. – In: Kukla, G. and Went, E. (eds), *Start of a Glacial*. NATO, ASI Series I, 3. Springer, Heidelberg, pp. 137–155.
- Dupont, L. M. 1995. Lowland rain forest and afro-montane forest in west equatorial Africa during the Middle and Late Pleistocene. – In: 2nd Symposium on African Palynology, Tervuren (Belgium). Publication Occasionelle CIFE, Orléans, pp. 87–98.
- Dupont, L. M. 1998. Pollen and dinoflagellate cysts of the upper 50 m of site 958. – In: Firth, J. V. (ed.), *Proceedings of Ocean Drilling Program, Scientific Results 159T*, pp. 23–30.
- Dupont, L. M. and Beug, H. J. 1991. Marine palynological studies of NW Africa. – *Palaeoecol. Africa* 22: 135–155.
- Dupont, L. M. et al. 1999. Marine-terrestrial interaction of climate changes in West Equatorial Africa of the last 190,000 years. – *Palaeoecol. Africa* 26: 61–84.
- Dupont, L. M. and Wypytta, U. 2003. Reconstructing pathways of aeolian pollen transport to the marine sediments along the coastline of SW Africa. – *Quaternary Sci. Rev.* 22: 157–174.
- Dupont, L. M. et al. 2000. Vegetation change in equatorial West Africa: time-slices for the last 150 ka. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 155: 95–122.
- Dupont, L. M. et al. 2001. Mid-Pleistocene environmental change in tropical Africa began as early as 1.05 Ma. – *Geology* 29: 195–198.
- Dupont, L. M. et al. 1989. First palynological results from Site 658 at 21°N off Northwest Africa: pollen as climate indicators. – In: Ruddiman, W. et al. (eds), *Proceedings of the Ocean Drilling Program, Scientific Results 108*: 93–111.
- Dupont, L. M. and Agwu, C. O. C. 1992. Latitudinal shifts of forest and savanna in N.W. Africa during the Brunhes chron: further marine palynological results from the site M 16415 (9°N 19°W). – *Veg. Hist. Archaeobot.* 1: 163–175.
- Dupont, L. M. and Weinelt, M. 1996. Vegetation history of the savanna corridor between the Guinean and the Congolian rain forest during the last 150,000 years. – *Veg. Hist. Archaeobot.* 5: 273–292.
- Dupont, L. M. et al. 1998. Land-sea correlation by means of terrestrial and marine palynomorphs from the equatorial East Atlantic: phasing of SE trade winds and the oceanic productivity. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 142: 51–84.
- El Moutaki, S. 1991. La dernière transition glaciaire-interglaciaire dans le canal de Mozambique: analyse palynologique d'une séquence sédimentaire du lagon de Mayotte. – Rapport de DEA, Universités d'Aix-Marseille III, Nancy, Paris VI, Paris VII et Toulouse III.
- El Hamouti, N. et al. 1991. Changements hydroclimatiques abrupts dans le Moyen Atlas marocain depuis le dernier maximum glaciaire. – *Comptes Rendus de l'Académie des Sciences* 313: 259–265.
- El Moutaki, S. et al. 1992. Mayotte (Canal de Mozambique). Evolution de la végétation et du climat au cours de la dernière transition glaciaire-interglaciaire et de l'Holocène. – *Comptes Rendus de l'Académie des Sciences*, Paris 314: 237–244.
- El-Moslimany, A. P. 1983. History of climate and vegetation in the Eastern Mediterranean and the Middle East from the Pleniglacial to the mid-Holocene. – PhD thesis, Univ. of Washington, 229 p.
- Elenga, H. 1992. Végétation et climat du Congo depuis 24 000 ans B.P. Analyse palynologique de séquences sédimentaires du pays Bateke et du littoral. – Thèse de doctorat, Université Aix-Marseille III, 238 p.
- Elenga, H. et al. 1992. Changements climatiques et action anthropique sur le littoral congolais au cours de l'Holocène. – *Bulletin de la Société Géologique de France* 163: 83–90.
- Elenga, H. et al. 1994. Pollen evidence of late Quaternary vegetation and inferred climate changes in Congo. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 109: 345–356.
- Elenga, H. et al. 1996. Diagramme pollinique Holocène du lac Kitina (Congo): mise en évidence de changements paléobotaniques et paléoclimatiques dans le massif forestier du Mayombe. – *Comptes-Rendus de l'Académie des Sciences*, Paris 323, IIa, pp. 403–410.
- Elenga, H. and Vincens, A. 1990. Paléoenvironnements quaternaires récents des plateaux Batéké (Congo): étude palynologique des dépôts de la dépression du bois de Bilanko. – In: Lanfranchi, R. and Schwartz, D. (eds), *Paysages quaternaires de l'Afrique Centrale Atlantique*. Orstom, Paris, pp. 271–282.
- Elenga, H. et al. 1991. Présence d'éléments forestiers montagnards sur les Plateaux Batéké (Congo) au Pléistocène supérieur: nouvelles données palynologiques. – *Palaeoecol. Africa Rotterdam Balkema A.A.* 21: 239–252.
- Elenga, H. et al. 2001. Le marais estuarien de la Songolo (Sud Congo) à l'Holocène moyen et récent. – *Bulletin de la Société Géologique de France* 172: 359–366.
- Eriksson, M. G. et al. 1999. Recent lake level variations in Lake Haubi, central Tanzania, interpreted from pollen and sediment studies. – *J. Paleolimnol.* 22: 457–473.
- Fabing, A. 1995. Contribution à la connaissance des paléoenvironnements holocènes du Sud-Congo: étude par spectrométrie infrarouge de la carotte S2 (marais de la Songolo, Pointe Noire). – Mémoire de Maîtrise de Géographie, Strasbourg Univ., 92 p.
- Fellag, H. 2000. Observations sur la conservation pollinique dans le remplissage de quelques grottes et abris Palolithiques du Sud-Ouest de la France et d'Algérie. – *Revue d'Archéologie* 24: 71–83.
- Finch, J. M. 2005. Late Quaternary palaeoenvironments of the Mfabeni Peatland, northern KwaZulu-Natal. – *Master of Science*, Univ. of KwaZulu-Natal, South Africa, 107 p.
- Foucault, A. and Stanley, D. J. 1989. Late Quaternary palaeoclimatic oscillations in East Africa recorded by heavy minerals in the Nile Delta. – *Nature* 339: 44–46.

- Fredoux, A. 1977. Etude palynologique de quelques sédiments du Quaternaire ivoirien. – *Bulletin de l'Association Française pour l'Etude du Quaternaire* 50: 181–186.
- Fredoux, A. 1978. Pollens et spores d'espèces actuelles et quaternaires de régions périlagunaires de Côte d'Ivoire. – Thèse, Univ. de Montpellier, 106 p.
- Fredoux, A. and Tastet, J. P. 1976. Apport de la palynologie à la connaissance paléogéographique du littoral ivoirien entre 8000 et 12 000 ans BP. – In: 7th African Micropaleontological Colloquium, Ife-Ife, Nigeria, pp. 1–7.
- Gabriel, B. 1977. Zum kologischen Wandel im Neolithikum der stlichen Zentralsahara. – *Berliner Geographische Abhandlungen* 27: 111 p.
- Garcin, Y. et al. 2007. Abrupt resumption of the African Monsoon at the Younger Dryas-Holocene climatic transition. – *Quaternary Sci. Rev.* 690–704.
- Gasse, F. and Van Campo, E. 1998. A 40,000-yr Pollen and Diatom record from Lake Tritrivakely, Madagascar, in the Southern Tropics. – *Quaternary Res.* 49: 299–311.
- Giresse, P. et al. 1994. Late Quaternary palaeoenvironments in the Lake Bormbi Mbo (West Cameroon) deduced from pollen and carbon isotopes of organic matter. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 107: 65–78.
- Guinet, P. and Planque, D. 1969. Résultats de l'analyse pollinique. – In: Camps, G. (ed.), Amekni, Néolithique Ancien du Hoggar. Mémoires du Centre de Recherches anthropologiques préhistoriques et ethnographiques, organisme de coopération scientifique en Algérie, Arts et métiers graphiques, Paris, pp. 186–188.
- Hamilton, A. 1982. Environmental history of East Africa – a study of the Quaternary. – Academic Press, London, 328 p.
- Hamilton, A. 1987. Vegetation and climate of Mt Elgon during the Late Pleistocene and Holocene. – *Palaeoecol. Africa* 18: 283–304.
- Hamilton, A. and Perrott, A. 1978. Date of deglaciation of Mount Elgon. – *Nature* 273: 49.
- Hamilton, A. et al. 1986. Early forest clearance and environmental degradation in south-west Uganda. – *Nature* 320: 164–167.
- Hamilton, A. C. et al. 1989. Neolithic forest clearance at Ahakagyezi, western Uganda. – In: Mahaney, W. G. (ed.), Quaternary and environmental research on East African Mountains. Rotterdam, Balema, pp. 435–463.
- Haynes, C. V. et al. 1989. Holocene palaeoecology of the Eastern Sahara; Selima Oasis. – *Quaternary Sci. Rev.* 8: 109–136.
- Holmes, J. A. et al. 1999. Late Holocene palaeolimnology of Bal Lake, Northern Nigeria, a multidisciplinary study. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 148: 169–185.
- Hooghiemstra, H. et al. 1987. Isopollen maps for 18,000 years B.P. of the atlantic offshore of Northwest Africa: evidence for paleowind circulation. – *Paleoceanography* 2: 561–582.
- Hooghiemstra, H. 1988. Palynological records from northwest African marine sediments: a general outline of the interpretation of the pollen signal. – *Phil. Trans. R. Soc. B* 318: 431–449.
- Hooghiemstra, H. 1988. Changes of major wind belts and vegetation zones in NW Africa 20,000–5000 yr B.P., as deduced from a marine pollen record near Cap Blanc. – *Rev. Palaeobot. Palynol.* 55: 101–140.
- Hooghiemstra, H. 1989. Variations of the NW African trade wind regime during the last 140 000 years: changes in pollen flux evidenced by marine sediment records. – In: Leinen, M. and Sarnthein, M. (eds), Paleoclimatology and paleometeorology: modern and past patterns of global atmospheric transport. Kluwer Academic Publisher, Dordrecht, pp. 733–770.
- Hooghiemstra, H. and Agwu, C. O. C. 1988. Changes in the vegetation and trade winds in equatorial Northwest Africa 140,000–70,000 yr B.P., as deduced from two marine pollen records. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 66: 173–213.
- Hooghiemstra, H. et al. 1992. Vegetational and climatic changes at the northern fringe of the Sahara 250,000–5000 years BP: evidence from 4 marine pollen records located between Portugal and the Canary Islands. – *Rev. Palaeobot. Palynol.* 74: 1–53.
- Irving, S. J. 1998. Late Quaternary Palaeoenvironments at Vankervelsvlei, near Knysna, South Africa. – Unpublished Masters thesis, Univ. of Cape Town, South Africa.
- Jahns, S. 1996. Vegetation history and climate changes in West Equatorial Africa during the Late Pleistocene and Holocene, based on a marine pollen diagram from the Congo fan. – *Veg. Hist. Archaeobot.* 5: 207–213.
- Jahns, S. 1995. A Holocene pollen diagram from El Atrun, northern Sudan. – *Veg. Hist. Archaeobot.* 4: 23–30.
- Jahns, S. et al. 1998. Vegetation and climate history of west equatorial Africa based on a marine pollen record off Liberia (site GIK 16776) covering the last 400,000 years. – *Rev. Palaeobot. Palynol.* 102: 277–288.
- Jolly, D. 1993. Evolution et dynamique des écosystèmes du Burundi. Pollen et Statistique. – Unpublished thesis, Univ. of Aix-Marseille II, 142 p.
- Jolly, D. and Bonnefille, R. 1991. Diagramme pollinique d'un sondage Holocène de la Kuruyange (Burundi, Afrique Centrale). – *Palaeoecol. Africa* 22: 265–274.
- Jolly, D. and Bonnefille, R. 1992. Histoire et dynamique du marécage tropical de Ndurumu (Burundi), données polliniques. – *Rev. Palaeobot. Palynol.* 75: 133–151.
- Jolly, D. et al. 1994. Numerical interpretation of high resolution Holocene pollen record from Burundi. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 109: 357–370.
- Kabonyi Nzabandora, C. 2007. Etude palynologique de la séquence sédimentaire de Musisi-Karashoma II. Synthèse de l'évolution environnementale du Sud Kivu au cours des deux derniers millénaires. – Diplôme d'Etudes Approfondies en Paléontologie Appliquée, publication de l'Unité de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Université Officielle de Bukavu.
- Kadomura, H. and Kiyonaga, J. 1994. Origin of grassfields landscape in the West Cameroon Highlands. – In: Kadomura, H. (ed.), Savannization processes in tropical Africa II. Tokyo Metropolitan Univ., Japan, pp. 47–85.
- Kendall, R. 1969. An ecological history of the Lake Victoria basin. – *Ecol. Monogr.* 39: 121–176.
- Lamb, H. F. and van der Kaars, S. 1995. Vegetational response to Holocene climatic change: pollen and palaeolimnological data from the Middle Atlas, Morocco. 5: 400–408.
- Lamb, H. F. 2001. Multi-proxy records of Holocene climate and vegetation change from Ethiopian crater lakes. – In: Biology and Environment: Proceedings of Royal Irish Academy 101B: 35–46.
- Lamb, H. F. et al. 2003. Vegetation response to rainfall variation and human impact in central Kenya during the past 1100 years. – *Holocene* 13: 285–292.
- Lamb, A. L. et al. 2004. Holocene climate and vegetation change in the Main Ethiopian Rift Valley, inferred from the composition (C/N and $\delta^{13}C$) of lacustrine organic matter. – *Quaternary Sci. Rev.* 23: 881–891.
- Laraque, A. et al. 1998. Origin and function of a closed depression in equatorial humid zones: the Lake Télé in North Congo. – *J. Hydrol.* 207: 236–253.

- Laseski, R. A. 1983. Modern pollen data and Holocene climate change in Eastern Africa. – Unpublished thesis, Brown Univ., 269 p.
- Legesse, D. et al. 2002. Environmental changes in a tropical lake (Lake Abiyata, Ethiopia) during recent centuries. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 187: 233–258.
- Leroy, S. A. G. 1992. Palynological evidence of *Azolla nilotica* Dec. in recent Holocene of the eastern Nile Delta and palaeoenvironment. – *Veg. Hist. Archaeobot.* 1: 43–52.
- Leroy, S. A. G. and Dupont, L. 1994. Development of vegetation and continental aridity in northwestern Africa during the Late Pleistocene: the pollen record of ODP Site 658. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 109: 295–316.
- Lézine, A.-M. 1981. Le Lac Abiyata (Ethiopie) – Palynologie et paléoclimatologie du Quaternaire récent. – Unpublished thesis, Bordeaux Univ., 125 p.
- Lézine, A. M. 1987. Paléoenvironnements végétaux d'Afrique Nord-Tropicale depuis 12 000 B.P.: analyse pollinique de séries sédimentaires continentales (Sénégal-Mauritanie). – Thèse de doctorat, Université Aix-Marseille II, 180 p.
- Lézine, A.-M. 1988. New pollen data from the Sahel, Senegal. – *Rev. Palaeobot. Palynol.* 55: 141–154.
- Lézine, A.-M. 1988. Les variations de la couverture forestière mésophile d'Afrique occidentale au cours de l'Holocène. – *Comptes Rendus de l'Académie des Sciences, Paris* 307: 439–445.
- Lézine, A. M. 1991. West African paleoclimates during the last climatic cycle from Atlantic deep sea pollen record. – *Quaternary Res.* 35: 456–463.
- Lézine, A.-M. 1993. Chemchane, histoire d'une sebkha. – *Sécheresse* 4: 25–30.
- Lézine, A.-M. et al. 1985. Etude palynologique et sédimentologique d'un milieu margine-littoral: la tourbière de Thiaye (Sénégal). – *Sci. Géol. Bull.* 38: 79–89.
- Lézine, A.-M. and Bonnefille, R. 1982. Diagramme pollinique Holocène d'un sondage du Lac Abiyata (Ethiopie, 7°42' Nord). – *Pollen et Spores XXIV*: 463–480.
- Lézine, A.-M., Casanova, J. and Hillaire-Marcel, C. 1990. Across an early Holocene humid phase in Western Sahara: pollen and isotope stratigraphy. – *Geology* 18: 264–267.
- Lézine, A. M. and Casanova, J. 1991. Correlated oceanic and continental records demonstrate past climate and hydrology of North Africa (0–140 ka). – *Geology* 19: 307–310.
- Lézine, A.-M. and Cazet, J.-P. 2005. High resolution pollen record from core KW31, Gulf of Guinea, documents the history of the lowland forests of West Equatorial Africa since 40,000 years. – *Quaternary Res.* 64: 432–443.
- Lézine, A.-M. and Denèfle, M. 1997. Enhanced anticyclonic circulation in the eastern North Atlantic during cold intervals of the last deglaciation inferred from deep-sea pollen records. – *Geology* 25: 119–122.
- Lézine, A.-M., Duplessy, J.-C. and Cazet, J.-P. 2005. West African monsoon variability during the last deglaciation and the Holocene: evidence from fresh water algae, pollen and isotope data from core KW31, Gulf of Guinea. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 219: 225–237.
- Lézine, A.-M. and Hooghiemstra, H. 1990. Land-sea comparisons during the last glacial–interglacial transition: pollen records from West Tropical Africa. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 79: 313–331.
- Lézine, A. M. et al. 1995. Transport pollinique et circulation atmosphérique au large de l'Afrique tropicale occidentale au cours de la dernière déglaciation. – In: *Déserts tropicaux et Changements Globaux. Mémoire spécialisé de la Société Géologique de France en l'honneur de Nicole Petit-Maire. Bulletin de la Société Géologique de France* 166: 247–257.
- Lézine, A. M. et al. 1998. Holocene lakes from Ramlat as-Sab'atayn (Yemen) illustrate the impact of monsoon activity in Southern Arabia. – *Quaternary Res.* 50: 290–299.
- Lézine, A. M. et al. 2002. Mangroves of Oman during the late Holocene: climatic implications and impact on human settlements. – *J. Veg. Hist. Archaeobot.* 11: 221–232.
- Lézine, A. M. et al. 1994. Evidence of atmospheric paleocirculation over the Gulf of Guinea since the Last Glacial Maximum. – *Quaternary Res.* 41: 390–395.
- Lézine, A. M. and Le Thomas, A. 1995. Histoire du massif forestier ivoirien au cours de la dernière déglaciation. – In: *2ème Symposium de Palynologie Africaine, publication occasionnelle CIFEG, Orléans* 31: 73–85.
- Lézine, A. M. et al. 2007. Centennial to millennial-scale variability of the Indian monsoon during the early Holocene from a sediment, pollen and isotope record from the desert of Yemen. – *Palaeogeogr. Palaeoecol. Palaeoclimatol.* 243: 235–249.
- Lézine, A. M. et al. 1995. Pollen analyses off Senegal: evolution of the coastal palaeoenvironment during the last deglaciation. – *J. Quaternary Sci.* 10: 95–105.
- Lézine, A.-M. and Vergnaud-Grazzini, C. 1993. Evidence of forest extension in West Africa since 22,000 BP: a pollen record from the Eastern Tropical Atlantic. – *Quaternary Sci. Rev.* 12: 203–210.
- Lim, S. et al. 2016. 50,000 years of vegetation and climate change in the southern Namib Desert, Pella, South Africa. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 451: 197–209.
- Litt, T. et al. 2012. Holocene climate variability in the Levant from the Dead Sea pollen record. – *Quaternary Sci. Rev.* 49: 95–105.
- Livingstone, D. A. 1962. Age of deglaciation in the Ruwenzori Range, Uganda. – *Nature* 194: 859–860.
- Livingstone, D. A. 1967. Postglacial vegetation of the Ruwenzori Mountains in Equatorial Africa. – *Ecol. Monogr.* 37: 25–52.
- Livingstone, D. A. 1971. A 22,000-year pollen record from the Plateau of Zambia. – *Limnol. Oceanogr.* 16: 349–356.
- Lutze, G. F. et al. 1988. Bericht über die METEOR-Fahrt 6–5 Dakar-Libreville 15.1.-16.2.1988. – *Berichte Reports, Geologisch-Paläontologisches Institut und Museum, Christian-Albrechts-Universität Kiel* 22: 59 p.
- MacPhee, R. D. E. et al. 1985. Early Holocene chronology and environment of Ampasambazimba, a Malagasy subfossil Lemur Site. – *Int. J. Primatol.* 6: 463–489.
- Maley, J. 1981. Etudes palynologiques dans le bassin du Tchad et paléoclimatologie de l'Afrique Nord-Tropicale de 30.000 ans à l'époque actuelle. – *Orstom, Paris, Travaux et Documents* 129: 586 p.
- Maley, J. 1991. The African rain forest vegetation and palaeoenvironments during Late Quaternary. – *Clim. Change* 19: 79–98.
- Maley, J. and Brenac, P. 1998. Vegetation dynamics, palaeoenvironments and climatic change in the forests of western Cameroon during the last 28,000 years BP. – *Rev. Palaeobot. Palynol.* 99: 157–187.
- Maley, J. 2004. Le bassin du Tchad au Quaternaire récent: formations sédimentaires, paléoenvironnements et préhistoire. La question des paléotchads. – In: *Sémah, A.-M. and Renault-Miskovsky, J. (eds), L'évolution de la végétation depuis deux millions d'années. Guides de la Préhistoire Mondiale, Editions Errance*, pp. 179–217.

- Maley, J. et al. 1970. Quelques formations lacustres et fluviales associées à différentes phases du volcanisme au Tibesti (Nord du Tchad). – Cahier ORSTOM, série Géologie II 1: 127–152.
- Marchant, R. et al. 1997. Late Pleistocene and Holocene history at Mubwindi Swamp, Southwest Uganda. – *Quaternary Res.* 47: 316–328.
- Marchant, R. A. and Taylor, D. 1998. Dynamics of montane forest in central Africa during the late Holocene: a pollen-based record from western Uganda. – *Holocene* 8: 375–381.
- Marret, F. 1994. Evolution paléoclimatique et paléohydrologique de l'Atlantique Est-Equatorial et du proche continent au Quaternaire terminal. Contribution palynologique (Kystes des dinoflagellés, pollen et spores). – Thèse de doctorat, Université Bordeaux I, 271 p.
- Marriner, N. et al. 2004. Note on the Vegetation Landscapes of Sidon and Tyre during Antiquity. – *Archaeol. Hist. Lebanon* 19: 85–91.
- Marriner, N. and Morhange, C. 2005. Under the city centre, the ancient harbour. Tyre and Sidon: heritages to preserve. – *J. Cult. Heritage* 6: 183–189.
- Marriner, N. and Morhange, C. 2006. Geoarchaeological evidence for dredging in Tyre's ancient harbour, Levant. – *Quaternary Res.* 65: 164–171.
- Matsumoto, K. and Burney, D. A. 1994. Late Holocene environments at Lake Mitsinjo, northwestern Madagascar. – *Holocene* 4: 16–24.
- McKee, B. A. et al. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: II. Geochronologies and mass sedimentation rates based on ¹⁴C and ²¹⁰Pb data. – *J. Paleolimnol.* 34: 19–29.
- Meadows, M. E. et al. 1994. The Late Holocene vegetation history of lowland fynbos, Verlorenvlei, Southwestern Cape Province, South Africa. – *Hist. Biol.* 9: 47–59.
- Meadows, M. E. et al. 1996. Late Holocene environments at Verlorenvlei, Western Cape Province, South Africa. – *Quaternary Int.* 33: 81–95.
- Meadows, M. E. and Baxter, A. J. 1999. Late Quaternary Palaeoenvironments of the southwestern Cape, South Africa: a regional synthesis. – *Quaternary Int.* 57/58: 193–206.
- Meadows, M. E. and Baxter, A. J. 2001. Holocene vegetation history and palaeoenvironments at Klaarfontein Springs, Western Cape, South Africa. – *Holocene* 11: 699–706.
- Mercuri, A. M. and Grandi, G. T. 2001. Palynological analyses of the Late Pleistocene, Early Holocene and Middle Holocene layers. – In: Garcea, E. A. A. (ed.), *Uan Tabu in the settlement history of the Libyan Sahara. Arid Zone Archaeology, Monographs 2*, ch. 10. Edizioni All'Insegna del Giglio, Firenze, pp. 161–188.
- Mercuri, A. M. et al. 1998. New pollen data from the Uan Muhugiag rockshelter (Libyan Sahara, VII-IV millennia BP). – In: Cremaschi, M. and di Lernia, S. (eds), *Wadi Teshuinat – Palaeoenvironment and prehistory in south-western Fezzan (Libyan Sahara). Survey and excavations in the Tadrart Acacus, Erg Uan Kasa, Messak Settafet and Edeyen of Murzuq, 1990–1995*, Edizioni All'Insegna del Giglio, Firenze, pp. 107–122.
- Mercuri, A. M. 1999. Palynological analysis of the Early Holocene sequence. – In: *The Uan Afuda cave, Hunter-Gatherer societies of Central Sahara. Arid Zone Archaeology, Monographs 1*, ch. 8. Edizioni All'Insegna del Giglio, Firenze, pp. 149–253.
- Metwally, A. A. et al. 2014. Holocene palynology and palaeoenvironments in the Savanna Biome at Tswaing Crater, central South Africa. 402: 125–135.
- Mohammed, M. U. 1992. Paléoenvironnement et paléoclimatologie des derniers millénaires en Ethiopie. Contribution palynologique. – Unpublished thesis, Univ. of Aix-Marseille III, 209 p.
- Mohammed, M. U. and Bonnefille, R. 1992. The recent history of vegetation and climate around Lake Langeno (Ethiopia). – *Palaeoecol. Africa* 22: 275–286.
- Mohammed, M. U. and Bonnefille, R. 1998. A late Glacial/late Holocene pollen record from a highland peat at Tamsaa, Bale Mountains, south Ethiopia. – *Global Planet. Change* 16–17: 121–129.
- Mohammed, U. M. et al. 1995. Pollen and isotopic records in Late Holocene sediments from Lake Turkana, Kenya. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 119: 371–383.
- Morhange, C. et al. 1999. Nouvelle données paléo-environnementales sur le port antique de Sidon. – Proposition de datation, National Museum News Tenth Issue: The Millennium Edition, pp. 42–48.
- Morhange, C. et al. 2000. Etude paléoenvironnementale du port antique de Sidon. – Premiers résultats du programme CEDRE. 1, 2, 91–100.
- Morrison, M. E. S. and Hamilton, A. C. 1974. Vegetation and climate in the uplands of South-Western Uganda during the Later Pleistocene period. II. Forest clearance and other vegetational changes in the Rukiga highlands during the past 8000 years. – *J. Ecol.* 62: 1–31.
- Moscol-Olivera, M. C. 1998. Analyse palynologique d'une séquence sédimentaire Holocène à Musisi-Karashoma (Kivu, R. D. Congo) – influences climatiques et anthropiques sur l'environnement. – Mémoire de DEA, Université de Liege, 51p + annexes.
- Moscol-Olivera, M. C. and Roche, E. 1997. Analyse palynologique d'une séquence sédimentaire Holocène à Musisi-Karashoma (Kivu, R. D. Congo). Influences climatiques et anthropiques sur l'environnement. – *Geo-Eco-Trop* 1–4: 1–26.
- Msaky, E. S. et al. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: V. Palynological evidence for deforestation and increased erosion. – *J. Paleolimnol.* 34: 73–83.
- Nakimera-Ssemmanda, I. 1991. Histoire des végétations et du climat dans le Rift Occidental Ougandais depuis 13 000 ans B. P. – Etude palynologique de séquences sédimentaires des lacs Albert et Edouard. – Mémoire de l'Ecole Pratique des Hautes Etudes, France, 125 p.
- Nakimera, I. 2001. The impact of human activities and climate on the vegetation in the Lake Victoria region and on the Rwenzori Mountain and its neighbourhood. – Unpublished PhD thesis, Makerere Univ., 339 p.
- Ntaganda, C. 1991. Paléoenvironnements et paléoclimats du Quaternaire supérieur au Rwanda par l'analyse palynologique des dépôts superficiels. – Unpublished thesis, Univ. of Liège, 281 p.
- Nyakale, M. 1999. Palynology of late Quaternary deposits from the Central Plateau, South Africa. – Unpublished PhD thesis, University, 115 p.
- Nyakale, M. and Scott, L. 2002. Interpretation of Late Holocene pollen in channel fills in the eastern Free State, South Africa, in terms of local conditions and sediment reworking. – *South Afric. J. Bot.* 68: 1–5.
- Oschadleus, H. D. et al. 1996. Radiometric date for the Port Durnford peat and development of yellow-wood forest along the South African east coast. – *South Afric. J. Sci.* 92: 43–45.

- Palacios-Fest, M. R. et al. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: III. Physical stratigraphy and charcoal analysis 34: 31–49.
- Parkington, J. et al. 2000. Palaeovegetation at the last glacial maximum in the Western Cape, South Africa: wood charcoal and pollen evidence from Elands Bay Cave. – *South Afric. J. Sci.* 96: 543–546.
- Partridge, T. C. et al. 1993. 200,000 year Southern African lacustrine sequence. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 101: 317–337.
- Peglar, S. M. et al. 2001. Terrestrial pollen record of recent land-use changes around nine North African lakes in the CASSARINA Project. – *Aquatic Ecol.* 35: 431–448.
- Pons, A. and Quézel, P. 1958. A propos de l'étude palynologique de quelques sédiments sahariens récents. – *Bull. Liaison Saharienne Alger* 29: 77–80.
- Pons, A. and Quézel, P. 1958. Premières remarques sur l'étude palynologique d'un guano fossile du Hoggar. – *Compte-Rendus de l'Académie des Sciences, Paris* 246: 2290–2292.
- Quézel, P. and Martinez, C. 1962. Premiers résultats de l'analyse palynologique de sédiments recueillis au Sahara méridional à l'occasion de la mission Berliet-Tchad. – *Missions Berliet Ténéré-Tchad, Paris*, pp. 313–327.
- Quick, L. J. et al. 2016. Vegetation and climate dynamics during the last glacial period in the fynbos-afrotemperate forest ecotone, southern Cape, South Africa. – *Quaternary Int.* 404: 136–149.
- Quick, L. J. et al. 2018. A high-resolution record of Holocene climate and vegetation dynamics from the southern Cape coast of South Africa: pollen and microcharcoal evidence from Eilandvlei. – *J. Quaternary Sci.* 33: 487–500.
- Reynaud, I. 1991. Introduction à l'étude des relations Homme-Milieu naturel dans les forêts du Cameroun. Etude palynologique des sédiments du lac Ossa au cours des derniers siècles. – *Mémoire de DEA, Université Montpellier II, France*.
- Reynaud-Farrera, I. 1995. Histoire des paléoenvironnements forestiers du Sud-Cameroun à partir d'analyses palynologiques et statistiques de dépôts Holocènes et actuels. – *Thèse de doctorat, Université Montpellier II*, 198 p.
- Reynaud-Farrera, I. 1996. Late Holocene vegetational changes in South-West Cameroon. – In: Dalfes, H. N. et al. (eds), *Climate change in the third millennium BC climate change and old world collapse. Subseries I 'Global Environmental Change'*, pp. 641–652.
- Reynaud-Farrera, I. et al. 1996. Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4 770 ans BP: analyse pollinique des sédiments du Lac Ossa. – *Comptes Rendus de l'Académie des Sciences, Paris*, 322, IIa, 749–755.
- Ritchie, J. C. 1984. Analyse pollinique de sédiments Holocènes Supérieurs des Hauts Plateaux du Maghreb Oriental. – *Pollen et Spores* 3–4: 489–496.
- Ritchie, J. C. 1987. A Holocene pollen record from Bir Atrun, Northwest Sudan. – *Pollen et Spores* 29: 391–410.
- Ritchie, J. C. 1994. Holocene pollen spectra from Oyo, northwestern Sudan: problems of interpretation in a hyperarid environment. – *Holocene* 4: 9–15.
- Ritchie, J. C. et al. 1985. Sediment and pollen evidence for an early to mid-Holocene humid period in the eastern Sahara. – *Nature* 314: 352–355.
- Ritchie, J. C. and Haynes, C. V. 1987. Holocene vegetation zonation in the eastern Sahara. – *Nature* 330: 645–647.
- Roche, E. and Van Grunderbeek, M. C. 1987. Apports de la palynologie à l'étude du Quaternaire supérieur au Rwanda. – In: *Palynologie et milieux tropicaux, Montpellier, IXe symposium de l'A.P.L.F., Montpellier 1987, Ecole Pratique des Hautes Etudes, Mémoires et Travaux de l'Institut de Montpellier* 17: 111–127.
- Roche, E. 1998. Evolution du paléoenvironnement holocène au Rwanda. Implications climatiques déduites de l'analyse palynologique de séquences sédimentaires. – In: Demarée, G. et al. (eds), *Proceedings of the international conference: 'Tropical climatology, meteorology and hydrology', Brussels 22–24/05/1996*, pp. 108–127.
- Roche, E. and Ntaganda, C. 1999. Analyse palynologique de la séquence sédimentaire Kiguhu II (région des Birunga, Rwanda). Evolution du paléoenvironnement et du paléoclimat dans le domaine afro-montagnard du Rwanda au cours de l'Holocène. – In: *Actes du 4eme Symposium de Palynologie africaine (Sousse, Tunisie) 25–30/04/1999. Geo-Eco-Trop* 22: 71–82.
- Rucina, S. M. et al. 2009. Late Quaternary vegetation and fire dynamics on Mount Kenya. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 283: 1–14.
- Ryner, M. A. et al. 2006. Vegetation changes in Empakaai Crater, northern Tanzania, at 14,800–9300 cal yr BP. – *Rev. Palaeobot. Palynol.* 140: 163–174.
- Ryner, M. A. et al. 2006. Climate change in northern Tanzania during the last 1000 years – implication for human intensive agricultural system. – *Holivar Open Science Meeting, London*. (abstract)
- Salzmann, U. 1999. Zur holozänen vegetations- und klimaentwicklung der westafrikanischen savannen – Paläoökologische untersuchungen in der Sahel- und Sudanzone NO-Nigerias. – *PhD thesis, Univ. of Wuerzburg, Frankfurt*, 144 p.
- Salzmann, U. 2000. Are modern savannas degraded forests? – A Holocene pollen record from the Sudanian vegetation zone of NE Nigeria. – *Veg. Hist. Archaeobot.* 9: 1–15.
- Salzmann, U. et al. 2002. Late Quaternary climate and vegetation of the Sudanian zone of Northeast Nigeria. – *Quaternary Res.* 58: 73–83.
- Salzmann, U. and Hoelzmann, P. 2005. The Dahomey Gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. – *Holocene* 15: 190–199.
- Salzmann, U. and Waller, M. 1998. The Holocene vegetational history of the Nigerian Sahel based on multiple pollen profiles. – *Rev. Palaeobot. Palynol.* 100: 39–72.
- Sanchez Goi, M. F. et al. 2017. The ACER pollen and charcoal database: a global resources to document vegetation and fire response to abrupt climate changes during the last glacial period. – *Earth Syst. Sci. Data* 9: 679–695.
- Schulz, E. 1973. Zur quartären Vegetationsgeschichte der zentralen Sahara unter Berücksichtigung eigener pollenanalytischer Untersuchungen aus dem Tibesti-Gebirge, Staatsexamensarbeit FU Berlin.
- Schulz, E. 1976. Aktueller pollenniederschlag in der zentralen Sahara und interpretationsmöglichkeiten quartärer pollenspektren. – *Palaeoecol. Africa* 9: 8–14.
- Schulz, E. 1980. Zur Vegetation der stlichen zentralen Sahara und zu ihrer Entwicklung im Holozän. – *Wrzburger Geographische Arbeiten* 51: 194.
- Scott, L. 1976. Preliminary palynological results from the Alexandersfontein Basin near Kimberley. – *Ann. South African Museum* 71: 193–199.

- Scott, L. 1982. A 5 000-year old pollen sequence from spring deposits in the Bushveld at the North of the Soutpansberg, South Africa. – *Palaeocol. Africa* 14: 45–55.
- Scott, L. 1982. A Late Quaternary Pollen Record from the Transvaal Bushveld, South Africa. – *Quaternary Res.* 17: 339–370.
- Scott, L. 1983. Late Quaternary palaeoenvironments in the Transvaal on the basis of palynological evidence. – SASQUA International Symposium/Swaziland, 29 August–2 September, pp. 317–327.
- Scott, L. 1986. Pollen analysis and palaeoenvironmental interpretation of Lata Quaternary sediment exposures in the eastern Orange Free State, South Africa. – *Palaeocol. Africa* 17: 113–122.
- Scott, L. 1987. Late Quaternary forest history in Venda, Southern Africa. – *Rev. Palaeobot. Palynol.* 53: 1–10.
- Scott, L. 1987. Pollen analysis of Hyena coprolites and sediments from Equus Cave, Taung, Southern Kalahari (South Africa). – *Quaternary Res.* 28: 144–156.
- Scott, L. 1988. Holocene environmental change at western Orange Free State pans, South Africa, inferred from pollen analysis. – *Palaeocol. Africa* 19: 109–118.
- Scott, L. 1988. The Pretoria Saltpan: a unique source of Quaternary palaeoenvironmental information. – *South Afric. J. Sci.* 84: 560–562.
- Scott, L. 1989. Late Quaternary vegetation history and climatic change in the eastern Orange Free State, South Africa. – *South Afric. J. Bot.* 55: 107–116.
- Scott, L. 1994. Palynology of Late Pleistocene Hyrax middens, Southwestern Cape Province, South Africa: a preliminary report. – *Hist. Biol.* 9: 71–81.
- Scott, L. 1996. Palynology of Hyrax middens: 2000 years of palaeoenvironmental history in Namibia. – *Quaternary Int.* 33: 73–79.
- Scott, L. 1999. Vegetation history and climate in the Savanna biome South Africa since 190,000 ka: a comparison of pollen data from the Tswaing Crater (the Pretoria Saltpan) and Wonderkrater. – *Quaternary Int.* 57/58: 215–223.
- Scott, L. 1999. Palynological analysis of the Pretoria Saltpan (Tswaing Crater) sediments and vegetation history of the Bushveld savanna biome, South Africa. – In: Tswaing – investigations into the origin, age and palaeoenvironment of the Pretoria Saltpan, Partridge, T. C. (ed.), Council for Geoscience, Pretoria, pp. 143–166.
- Scott, L. and Bousman, C. B. 1990. Palynological analysis of hyrax middens from Southern Africa. – *Palaeogeogr. Palaeoclimatol. Palaeocol.* 76: 367–379.
- Scott, L. et al. 2005. Holocene pollen from swamp, cave and hyrax dung deposits at Blydefontein (Kikvorsberge), Karoo, South Africa. – *Quaternary Int.* 129: 49–59.
- Scott, L. and Brink, J. S. 1992. Quaternary palaeoenvironments of pans in Central South Africa: palynological and palaeontological evidence. – *SA Geograaf* 19: 22–34.
- Scott, L. and Cooremans, B. 1990. Late Quaternary pollen from a hot spring in the upper Orange River Basin, South Africa. – *South Afric. J. Sci.* 86: 145–156.
- Scott, L. et al. 1991. Holocene environmental changes in Namibia inferred from pollen analysis of swamp and lake deposits. – *Holocene* 1: 8–13.
- Scott, L. et al. 1992. Preliminary palynological evaluation of the Port Durnford Formation at Port Durnford, Natal, South Africa. – *South Afric. J. Sci.* 88: 470–474.
- Scott, L. and Nyakale, M. 2002. Pollen indications of Holocene palaeoenvironments at Florisbad spring in the central Free State, South Africa. – *Holocene* 12: 497–503.
- Scott, L. and Steenkamp, M. 1996. Environmental history and recent human influence at coastal Lake Teza, KwaZulu-Natal. – *South Afric. J. Sci.* 92: 348–350.
- Scott, L. et al. 1995. Palaeoenvironmental conditions in South Africa at the Pleistocene-Holocene transition. – *Quaternary Sci. Rev.* 14: 937–947.
- Scott, L. and Thacheray, J. F. 1987. Multivariate analysis of late Pleistocene and Holocene pollen spectra from Wonderkrater, Transvaal, South Africa. – *Suid-Afrikaanse Tydskrif vir Wetenskap* 83: 93–98.
- Scott, L. and Vogel, J. C. 1978. Pollen analyses of the thermal spring deposits at Wonderkrater (Transvaal, South Africa). – *Palaeocol. Africa* 10: 155–162.
- Scott, L. and Vogel, J. C. 1983. Late Quaternary Pollen Profile from the Transvaal Highveld, South Africa. – *South Afric. J. Sci.* 79: 266–272.
- Scott, L. and Vogel, J. C. 1992. Short-term changes of climate and vegetation revealed by pollen analysis of hyrax dung in South Africa. – *Rev. Palaeobot. Palynol.* 74: 283–291.
- Scott, L. and Woodborne, S. 2007. Pollen analysis and dating of Quaternary faecal deposits (hyraceum) in the Cederberg, Western Cape, South Africa. – *Rev. Palaeobot. Palynol.* 144: 123–134.
- Shi, N. and Dupont, L. M. 1997. Vegetation and climate history of southwest Africa: a marine palynological record of the last 300,000 years. – *Veg. Hist. Archaeobot.* 6: 117–131.
- Shi, N. et al. 1998. Vegetation and climate changes during the last 21 000 years in S.W. Africa based on a marine pollen record. – *Veg. Hist. Archaeobot.* 7: 127–140.
- Shi, N. et al. 2000. Correlation between vegetation in Southwestern Africa and oceanic upwelling in the past 21,000 years. *Quaternary Research* 54: 72–80.
- Shi, N. et al. 2001. Southeast trade wind variations during the last 135 kyr: evidence from pollen spectra in eastern South Atlantic sediments. – *Earth Planet. Sci. Lett.* 187: 311–321.
- Sowunmi, M. A. 1981. Late Quaternary environmental changes in Nigeria. – *Pollen Spores* 23: 125–148.
- Sowunmi, M. A. 1981. Aspects of Late Quaternary vegetational changes in West Africa. – *J. Biogeogr.* 8: 457–474.
- Sowunmi, M. A. 1981. Nigerian vegetational history from the Late Quaternary to the Present day. – *Palaeocol. Africa* 13: 217–234.
- Sowunmi, M. A. 1987. Palynological studies in the Niger Delta. – In: Alagoa, E. J. et al. (eds), *The early history of the Niger Delta. Sprache und Geschichte in Africa*, SUIGA 8: 29–64.
- Sowunmi, M. A. 1991. Late Quaternary environments in Equatorial Africa: Palynological evidence. – *Palaeocol. Africa* 22: 213–238.
- Ssemmanda, I. et al. 2005. Vegetation history in western Uganda during the last 1200 years: a sediment-based reconstruction from two crater lakes. – *Holocene* 15: 119–132.
- Ssemmanda, I. and Vincens, A. 1993. Végétation et climat dans la Bassin du lac Albert (Ouganda, Zaïre) depuis 13 000 ans B.P.: Apport de la palynologie. – *Comptes Rendus de l'Académie des Sciences, Paris* 316: 2, 561–567.
- Ssemmanda, I. and Vincens, A. 1995. Vegetation and climate of Lake Edward Basin through the last 2000 years. – In: Kohring, R. and Schlüter, T. (eds), *Current geoscientific research in Uganda and Tanzania. Berliner Geowiss. Abh., Berlin A* 175: 91–94.
- Stambouli-Essassi, S. et al. 2007. Evolution de la végétation et du climat dans le Nord-ouest de la Tunisie au cours des 40 derniers millénaires [Evolution of vegetation and climatic changes in

- North-Western Tunisia during the last 40 millennia] 31: 171–214.
- Stanley, D. J. et al. 1988. Heavy minerals and provenance of late Quaternary sands, eastern Nile Delta. – *J. Afric. Earth Sci.* 7: 735–741.
- Taylor, D. M. 1988. The environmental history of the Rukiga Highlands, south-west Uganda, during the last 40 000–50 000 years. – Unpublished PhD thesis, Univ. of Ulster, Coleraine, 247 p.
- Taylor, D. M. 1990. Late Quaternary pollen records from two Ugandan mires: evidence for environmental change in the Rukiga Highlands of southwest Uganda. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 80: 283–300.
- Taylor, D. M. 1992. Pollen evidence from Muchoya Swamp, Rukiga Highlands (Uganda), for abrupt changes in vegetation during the last ca. 21,000 years. – *Bulletin de la Société Géologique de France* 163: 77–82.
- Taylor, D. and Marchant, R. 1995. Human impact in the Interlacustrine region: long-term pollen records from the Rukiga Highlands. *Azania* 29/30: 283–295.
- Taylor, D. and Robertshaw, P. 2000. Sedimentary sequences in western Uganda as records of human environmental impacts. – *Palaeoecol. Africa* 27: 63–76.
- Thinon, M. et al. 1996. Holocene vegetation of the Central Saharan Mountains: the end of a myth. – *Holocene* 6: 457–462.
- Tiercelin, J. J. et al. 1988. 25 000 ans d'histoire hydrologique et sédimentaire du Lac Tanganyika, Rift Est-africain. – *Comptes-Rendus de l'Académie des Sciences, Paris* 307, 2: 1375–1382.
- Tossou, M. G. 2002. Recherche palynologique sur la végétation Holocène du Sud-Bénin (Afrique de l'Ouest). – Thèse de doctorat, Université de Lomé (Togo), 133 p.
- Umer, M. et al. 2007. Late Pleistocene and Holocene vegetation history of Bale Mountains, Ethiopia. – *Quaternary Sci. Rev.* 26: 2229–2246.
- Valsecchi, V. et al. 2013. A high resolution 15,600-year pollen and microcharcoal record from the Cederberg Mountains, South Africa. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 387: 6–16.
- Van Campo, M. et al. 1964. Contribution à l'étude du peuplement végétal quaternaire des montagnes sahariennes: l'Atakor. – *Pollen Spores* 6: 169–194.
- Van Campo, M. et al. 1965. Contribution à l'étude du peuplement végétal quaternaire des montagnes sahariennes. II-Flore contemporaine d'un gisement de mammifères tropicaux dans l'Atakor. – *Pollen Spores* 7: 361–371.
- Van Campo, M. et al. 1966. Nouvelle flore pollinique des alluvions pléistocènes d'un bassin versant Sud du Hoggar. – *Comptes-Rendus de l'Académie des Sciences, Paris* 263: 487–490.
- Van Campo, M. et al. 1967. Contribution à l'étude du peuplement végétal quaternaire des montagnes sahariennes. III-Flore de l'Oued Outoul (Hoggar). – *Pollen Spores* 9: 107–120.
- Vilimbalalo, S. 1995. Palaeoenvironmental and palaeoclimatic evolution of the Southern part of the Kivu Basin, Western branch of the African rift, during the Holocene period. – In: 2nd Symposium on African Palynology, Tervuren (Belgium), Publication Occasionnelle du CIFEG, Orleans, pp. 145–157.
- Vincens, A. 1979. Analyse palynologique du site archéologique FxJj 50. Formation de Koobi Fora, Est Turkana. – *Bulletin de la Société Géologique de France, Paris*, 7, 21, 3, 343–347.
- Vincens, A. 1982. Recherches palynologiques dans la région du Lac Turkana (Kenya). *Palaeoecol. Africa* 14: 85–91.
- Vincens, A. 1982. Palynologie des environnements actuels et Pliocène l'Est du Lac Turkana (Kenya). – Unpublished thesis, Univ. Aix-Marseille II, 244 p.
- Vincens, A. 1986. Diagramme pollinique d'un sondage Pléistocène Supérieur-Holocène du Lac Bogoria (Kenya). – *Rev. Palaeobot. Palynol.* 47: 169–192.
- Vincens, A. 1987. La sédimentation pléistocène supérieur-holocène. 4.1.6. Pollens et spores: indices de l'évolution climatique. – In: Tiercelin, J. J. and Vincens, A. (coords), Le demi-graben de Baringo-Bogoria, Rift Gregory, Kenya. 30 000 ans d'histoire hydrologique et sédimentaire. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine, (Pau, France)* 11: 437–451.
- Vincens, A. 1989. Paléoenvironnements du bassin North-Tanganyika (Zaire, Burundi, Tanzanie) au cours des 13 derniers mille ans: apport de la palynologie. – *Rev. Palaeobot. Palynol.* 61: 69–88.
- Vincens, A. 1989. Early Holocene pollen data from an arid East African region, Lake Turkana (Kenya): botanical and climatic implications. – *Palaeoecol. Africa* 20: 87–98.
- Vincens, A. 1989. Les forêts claires zambéziennes du bassin Sud-Tanganyika. Evolution entre 25 000 et 6000 B.P. – *Comptes-Rendus de l'Académie des Sciences, Paris* 307, 2, 809–814.
- Vincens, A. 1991. Late Quaternary vegetation history of the South-Tanganyika basin. Climatic implications in South Central Africa. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 86: 207–226.
- Vincens, A. 1991. Végétation et climat dans le bassin sud-Tanganyika entre 25 000 et 9000 BP: Nouvelles données palynologiques. – *Palaeoecol. Africa* 22: 253–263.
- Vincens, A. 1993. Nouvelle séquence pollinique du lac Tanganyika: 30,000 ans d'histoire botanique et climatique du Bassin Nord. – *Rev. Palaeobot. Palynol.* 78: 381–394.
- Vincens, A. et al. 2005. A 23,000 yr pollen record from Lake Rukwa (8°S, SW Tanzania): New data on vegetation dynamics and climate in Central Eastern Africa. – *Rev. Palaeobot. Palynol.* 137: 147–162.
- Vincens, A. et al. 1993. Pollen-derived rainfall and temperature estimates from Lake Tanganyika and their implication for late Pleistocene water levels. – *Quaternary Res.* 40: 343–350.
- Vincens, A. et al. 1998. Late Holocene climatic changes in western Equatorial Africa inferred from pollen Lake Sinnda, Southern Congo. – *Quaternary Res.* 50: 34–45.
- Vincens, A. et al. 2003. Pollen-based vegetation changes in southern Tanzania during the last 4200 years: climate change and/or human impact. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 198: 321–334.
- Vincens, A. et al. 2007. Influence of rainfall seasonality African lowland vegetation during Late Quaternary: pollen evidence Lake Masoko, Tanzania. – *J. Biogeogr.* 34: 1274–1288
- Waller, M. and Salzmann, U. 1999. Holocene vegetation changes in the Sahelian zone of NE Nigeria: the detection of anthropogenic activity. – *Palaeoecol. Africa* 26: 85–102.
- Waller, M. P. et al. 2007. Holocene vegetation history of the Sahel: pollen, sedimentological and geochemical data from Jikariya Lake, north-eastern Nigeria. – *J. Biogeogr.* 34: 1575–1590.
- Wolf, F. A. 1967. Fungus spores in East African Lake sediments. – *Bull. Torrey Bot. Club* 94: 31–34.
- Zapata, L. et al. 2013. Holocene environmental change and human impact in NE Morocco: Palaeobotanical evidence from Ifri Oudadane. – *Holocene* 23: 1286–1296.