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Phelps, Leanne N., Chevalier, Manuel, Shanahan, Timothy M. et al. (10 more authors) (2020) Asymmetric response of forest and grassy biomes to climate variability across the African Humid Period:influenced by anthropogenic disturbance? Ecography. pp. 1118-1142. ISSN 0906-7590

https://doi.org/10.1111/ecog.04990

ECOGRAPHY

Research

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

Leanne N. Phelps, Manuel Chevalier, Timothy M. Shanahan, Julie C. Aleman, Colin Courtney-Mustaphi, Christopher Albert Kiahtipes, Oliver Broennimann, Rob Marchant, John Shekeine, Lynne J. Quick, Basil A. S. Davis, Antoine Guisan and Katie Manning

L. N. Phelps (https://orcid.org/0000-0002-7385-3907) ✉ (leannenphelps@gmail.com), M. Chevalier (https://orcid.org/0000-0002-8183-9881), O. Broennimann, B. A. S. Davis, J. Shekeine and A. Guisan, Inst. of Earth Surface Dynamics, Univ. of Lausanne, Lausanne, Switzerland. OB and AG also at: Dept of Ecology and Evolution, Univ. of Lausanne, Lausanne, Switzerland. – T. M. Shanahan, Dept of Geoscience, Univ. of Texas at Austin, Austin, TX, USA. – J. C. Aleman (https://orcid.org/0000-0003-0835-7015), Dépt de Géographie, Univ. de Montréal, Montréal, QC, Canada. – C. Courtney-Mustaphi (https://orcid.org/0000-0002-4439-2590), Geoecology, Dept of Environmental Sciences, Univ. of Basel, Basel, Switzerland. – C. A. Kiahtipes (https://orcid.org/0000-0002-8758-4605), Inst. for the Advanced Study of Culture and the Environment, Univ. of South Florida – Tampa, Tampa, FL, USA. – R. Marchant (https://orcid.org/0000-0001-5013-4056), York Inst. for Tropical Ecosystems, Dept of Environment and Geography, Univ. of York, Heslington, York, North Yorkshire, UK. – L. J. Quick (https://orcid.org/0000-0002-6735-7106), African Centre for Coastal Palaeoscience, Nelson Mandela Univ., Port Elizabeth, Eastern Cape, South Africa. – K. Manning, Geography Dept, King's College London, London, UK.

Ecography
43: 1118–1142, 2020
doi: 10.1111/ecog.04990

Subject Editor: Tim Bonebrake
Editor-in-Chief: Miguel Araújo
Accepted 27 March 2020

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

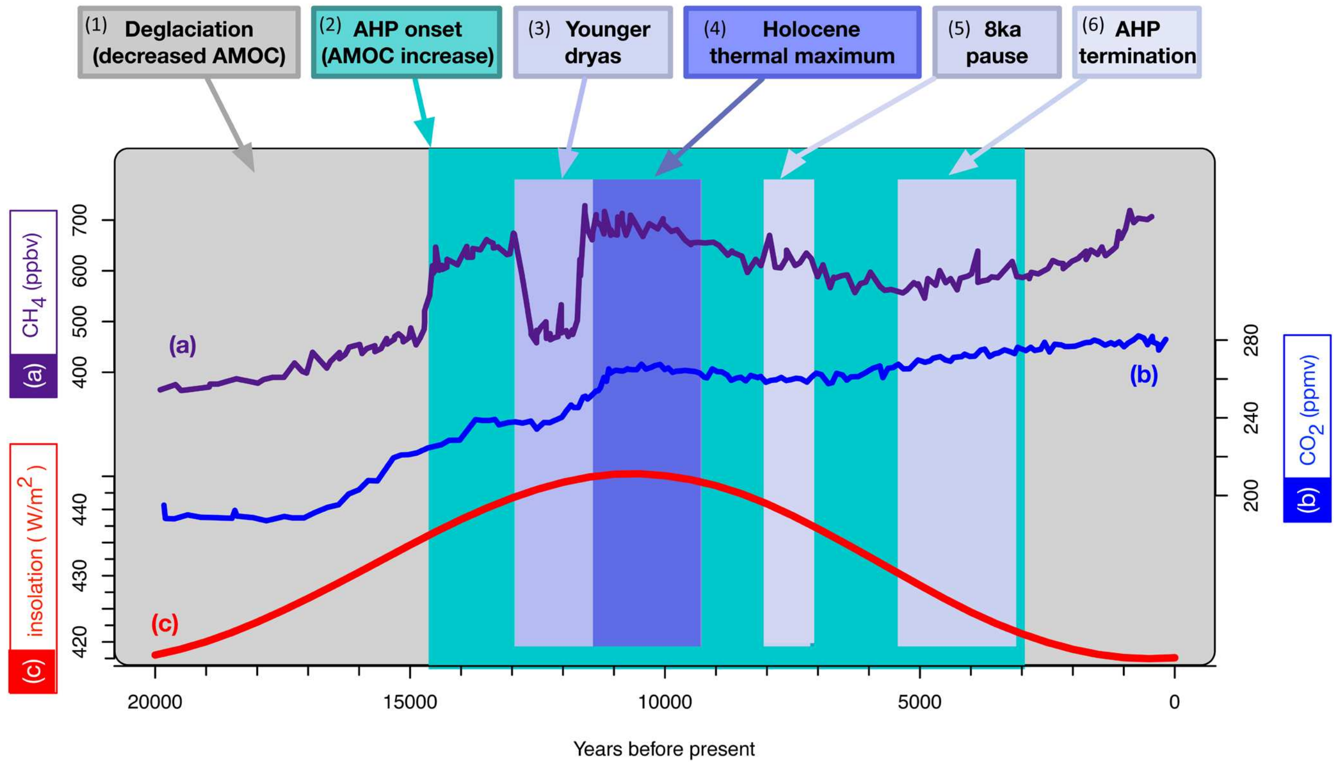

Figure 1. Major climatic events indicated over records of (a) atmospheric methane concentrations (EPICA community members 2006), (b) atmospheric carbon dioxide concentrations (Monnin 2006), (c) June–August insolation at 6°N (Laskar et al. 2004). Key climatic events include: (1) a period of pre-AHP increasing 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 heterogenous 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 CO_2, 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 CO_2 (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 CO_2 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 (Sànchez 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 ± 50) at 2.5 × 2.5° 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

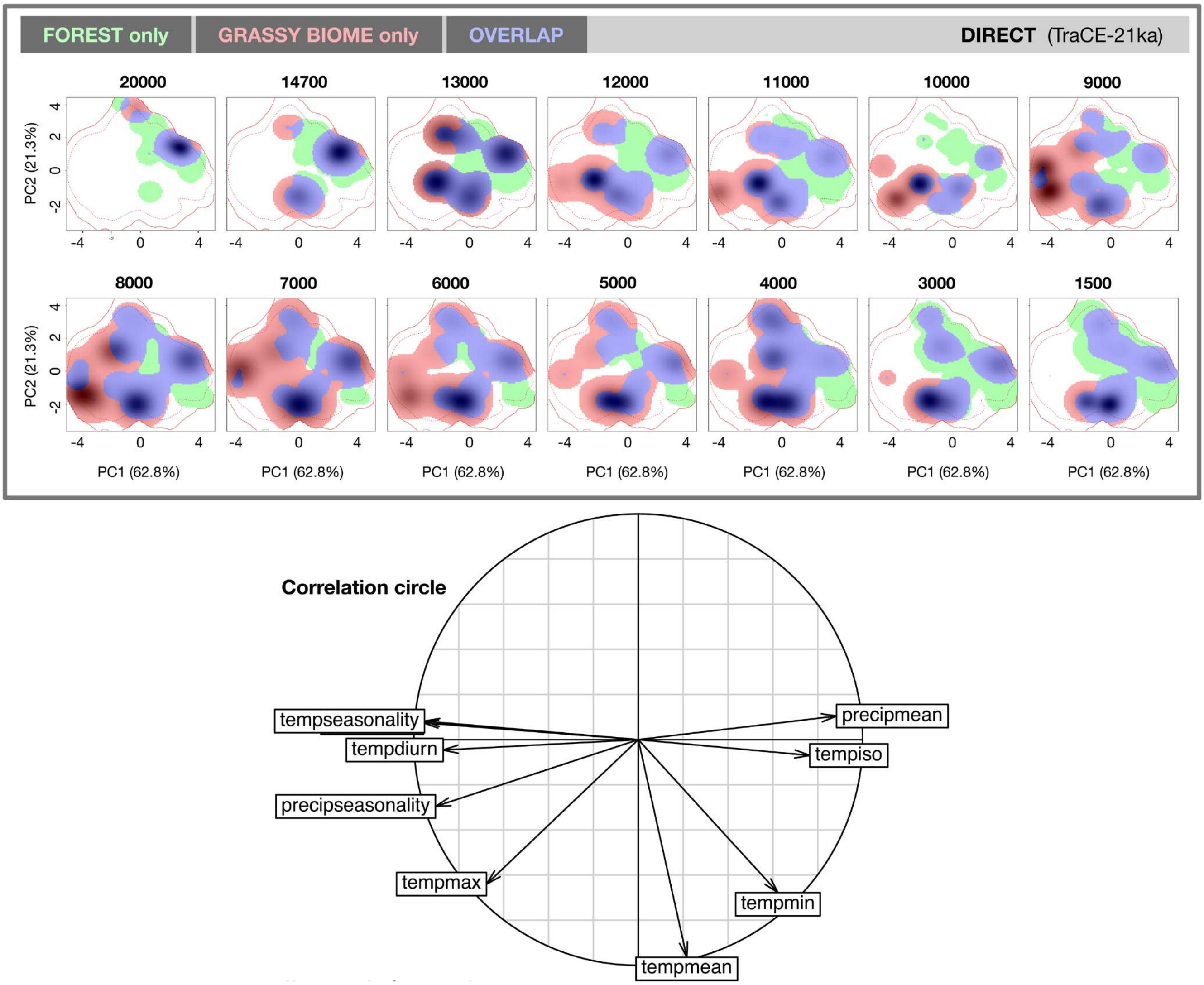

Figure 2. Climatic envelope overlap between forest and grassy biomes, mapped in climate space using TraCE-21ka climate information and the direct methodological approach ('ecospat' package in R, R Core Team; for additional methodology: Broennimann et al. 2012). Green areas represent climatic spaces where 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

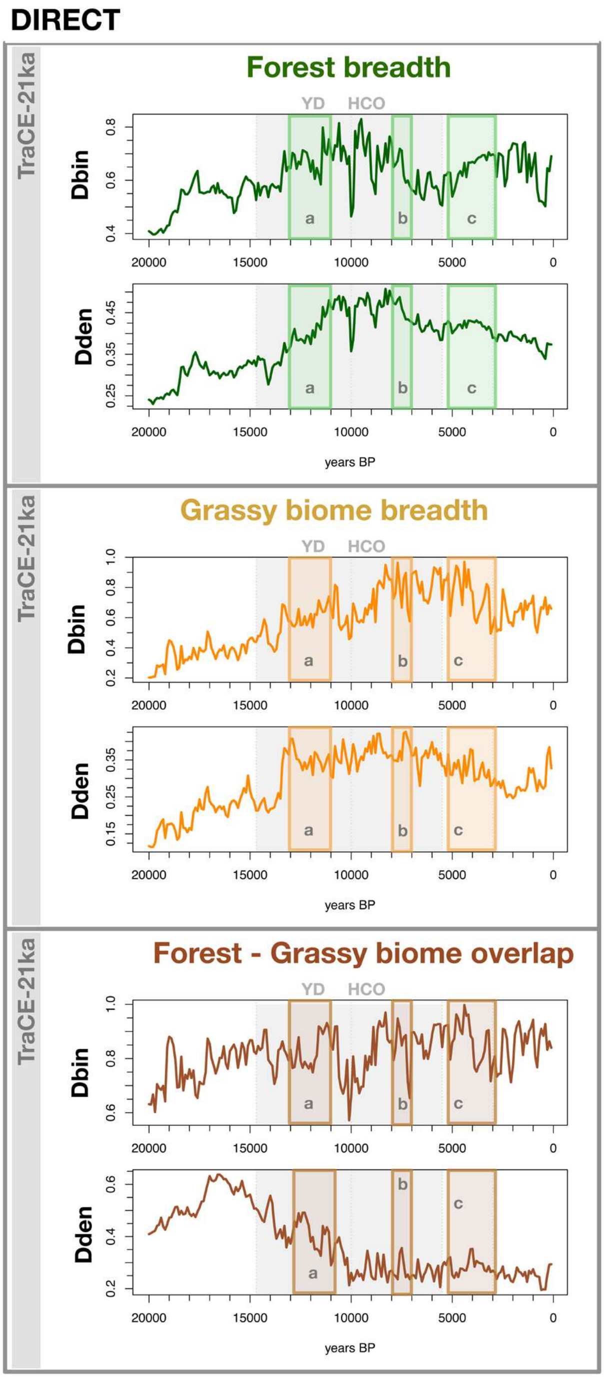

Figure 3. Schoener's D envelope overlap (Dden) and binarized D (Dbin) values plotted from the last glacial period until recent times, using the direct methodological approach and TraCE-21ka climate information. 'Forest breadth': D values represent the proportion of the entire African climate space occupied 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).

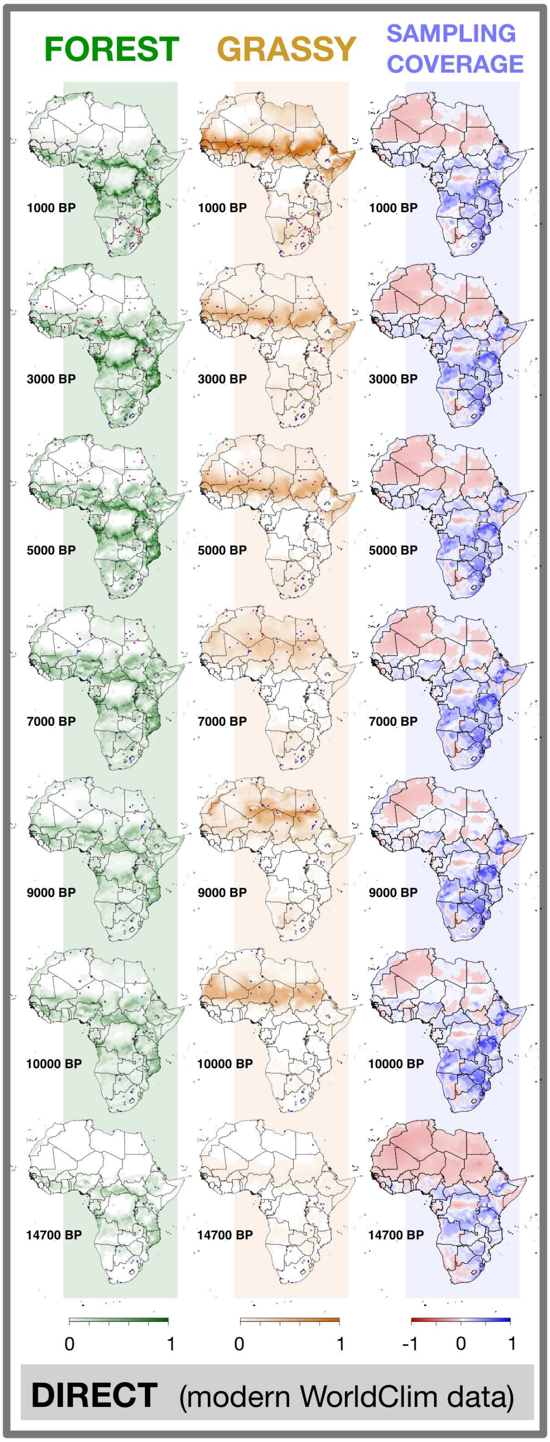

Figure 4. The climatic envelope of forest projected into geographic space (left); the climatic envelope of grassy biomes (savanna and steppe) projected into geographic space (center); sampling coverage, determined using multivariate environmental similarity surface (MESS) analysis (right). For all maps, 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 CO_2 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 benefitted 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 pyrotechologies 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 CO_2 [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 CO_2 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 CO_2 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 CO_2), 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 C_3 plants in response to rising atmospheric CO_2 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 CO_2 (Bond and Midgley 2012, Moncrieff et al. 2014; Fig. 1). In this sense it is conceivable that vegetation-CO_2 interactions slowed the decline of forest and affected precipitation levels, especially for C_3 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 CO_2 is disadvantageous for many grassy taxa (those with C_4 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 (Dbin) from the Green Sahara Pause until the termination of the AHP, and an expansion of grassy biome extent and density (Dden) 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 CO_2 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 CO_2 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 CO_2 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.

Acknowledgements – We thank the following groups and researchers: the Spatial Ecology Group (ECOSPAT) and The Davis Group at UNIL, the Geostatistical Algorithms and Image Analysis lab (GAIA); constructive feedback from researchers, especially AFQUA 2018, SAfA 2018 and IBS 2018 conference attendees, including Norbert Kühl, Caroline Lehmann and David Wright. We also thank the PAGES supported LandCover6k working group to whom this manuscript is a contribution. For their fundamental contributions to the datasets utilized here, we thank and acknowledge the African Pollen Database and European Pollen Database communities, and acknowledge the many contributions from original data contributors; we have cited the associated work accordingly, and acknowledge that future use of our Appendices should follow suit.
Funding – This work was primarily funded by the Faculty of Geoscience and Environment (FGSE) at the Univ. of Lausanne (UNIL) and the Swiss National Science Foundation (P2LAP2_187745). MC was supported through the SNF HORNET project (200021_169598). CCM was supported through the 'Adaptation and Resilience to Climate Change (ARCC)' project under the Sustainability and Resilience – tackling climate and environmental changes programme funded by the Swedish Research Council (Vetenskapsrådet), Sida and Formas (2016-06355). We also acknowledge the Swiss National Science Foundation ACACIA grant (CR10I2_146314).
Author contributions – AG and KM shared last-authorship.

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

Appendix

Databases:

EPD: http://www.europeanpollendatabase.net/getdata/
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