

Ecography

**ECOG-04990**

Phelps, L. N., Chevalier, M., Shanahan, T. M., Aleman, J. C., Courtney-Mustaphi, C., Kiahtipes, C. A., Broennimann, O., Marchant, R., Shekeine, J., Quick, L. J., Davis, B. A. S., Guisan, A. and Manning, K. 2020. Asymmetric response of forest and grassy biomes to climate variability across the African Humid Period: influenced by anthropogenic disturbance? – Ecography doi: 10.1111/ecog.04990

**Supplementary material**

1 **SUPPLEMENTARY MATERIALS :** "Asymmetric response of Forest and Grassy biomes to climate variability  
2 across the African Humid Period: influenced by anthropogenic disturbance?"  
3  
4

5 **Vegetation groups for the 'indirect' method**

6 For supplementary analysis using the indirect method, five mutually exclusive taxa groups were assigned.  
7 Each group is primarily re  
8 presentative of one biome, but may also be found in other biomes: (a) F: forest, (b) FS: savanna, but may  
9 also occur in forest, (c) FSst: steppe, but may also occur in forest and savanna, (d) FSstD: desert, but may  
10 also occur in forest, savanna, and steppe, (e) FSstDx: xeric, but may also occur in all other groups.  
11 Information about vegetation groups and which taxa were included (*PFT\_conflict* = 0 or 0.5;  
12 *indirect\_status* = "analyzed") or excluded (*PFT\_conflict* = 1; *indirect\_status* = "not analyzed") from indirect  
13 analyses is detailed in Appendix 9 (Phelps et al., 2019a). For example, African Acacia without species  
14 identification was excluded from indirect analyses because conflict between PFT assignments  
15 ("PFT\_conflict" = 1) made it impossible to assign Acacia to a mutually exclusive vegetation group;  
16 oppositely, Uapaca without species identification could be attributed to one mutually exclusive vegetation  
17 group ("F\_S"), and was therefore included.

18  
19 In order to calculate the relative vegetation percentages of each group, the same analyses were  
20 performed on each sample, as in the direct method, by calculating the proportion of the pollen sum that  
21 belongs to each vegetation group. As with the direct method, the pollen sum only includes taxa utilized in  
22 our analyses, i.e., those taxa that were selected for the vegetation groups. These relative vegetation  
23 percentages were then linearly interpolated on a yearly basis between samples, and separated into 100-  
24 year time intervals. After separation, a mean vegetation percentage was assigned to each core in a given  
25 time interval.

26  
27 During climatic envelope quantification, the indirect method requires extra steps to isolate the results into  
28 individual vegetation groups, e.g., in order to isolate 'st' from 'FSst' or 'x' from 'FSstDx'. This was done by  
29 taking the difference between the scores of the original groups: for example, to isolate steppe, we  
30 calculated the following, then reassigned all negative values to zero:  
31  $st = FSst - FS - F$

32  
33 **The climatic envelopes of desert and xeric taxa**

34 Due to conflicting results between analyses, caution should be taken when interpreting trends from xeric  
35 and desert climatic envelopes. This conflict is not surprising, because the appearance of extensive desert  
36 biomes is likely to be highest when fossil pollen data are least likely to preserve. For all analyses of desert  
37 vegetation, one consistent increase in extent and density was observed, coinciding with the Younger Dryas  
38 (Fig. A5a). The climatic envelope trends observed for xeric-dominated landscapes (Fig. A5) are likely to be  
39 affected by increasing average abundances of forest pollen (Fig. A7), which in turn, could reflect increasing  
40 atmospheric CO<sub>2</sub> levels (Fig. 1; e.g. Norby et al., 2005; Keenan et al., 2013; Prentice & Harrison, 2009; Jolly  
41 & Haxeltine, 1997). Despite these cautions, it should be noted that both the extent and density of the xeric  
42 envelope spiked anomalously across analyses c. 9000 BP (Fig. A5d). Indirect methods show that the  
43 climatic extent and density of savanna peaked at the same time, just after 9000 BP (Fig. A5d).

44  
45 **Methodological limitations**

46 In this study we utilize two different methodological approaches (direct, indirect). To supplement our  
47 analyses using TracE-21ka information, we also test the robustness of our model with auxiliary

exploration of the model using present-day WorldClim data, whereby the same climate data is used to define and calibrate the climate space for each time interval (Fick et al., 2017; for input variables, see Table A4). We do this because each presents benefits and drawbacks, and by analyzing all of these, we can focus on the most robust results across all types of analysis. The direct methodological approach, for example, relies on much fewer taxa than the indirect method: this is a potential drawback because the results may be less representative of an entire vegetation biome, whereas the indirect method is more likely to reflect the entire biome through considering higher numbers of taxa. In contrast, the direct method may be more accurately sensitive to and representative of changes in climatic drivers, whereas the indirect method may lack sensitivity and introduce confounding ecological factors because of its reliance on the ‘difference’ between many different types of taxa with different pollen dispersal habits: this is likely reflected in the contrasting results observed for the forest envelope, between direct and indirect methods c. 4500 BP (Fig. A5). In addition, a suite of different issues are associated with each set of climate information: modern-day WorldClim data clearly fails to capture past changes in the climate gradient and may consequently amplify or underestimate climatically insignificant changes in geographic space; however, it is more likely to reflect fine-scale climatic changes, for example, those that result from altitudinal differences. While modeled climate information is expected to more accurately represent past climates, it is also prone to inaccuracies: for example, the TrACe-21ka simulation, as well as the latest PMIP3/CMIP5 models, are unable to accurately simulate the magnitude of the observed precipitation anomalies during the AHP, causing the northern extent of the mid-Holocene African monsoon to be underestimated (Harrison et al., 2014, 2015; Perez-Sanz et al., 2014; Shanahan et al., 2015). For this reason, gridded precipitation variables contain some NA values, for which it was necessary to exclude associated occurrence records.

Additional limitations include the effects of pollen transport on subfossil pollen records, although this is likely to be limited somewhat because occurrence records are weighted by relative pollen percentages. In addition, the biomization schemes utilized in this study are not adequately representative of the highly endemic taxa of southern Africa. Generally speaking, our findings should not be used to interpret change at fine spatial scales, due to the coarse resolution of our study and the uncertainties associated with the utilized climate information (see Fig. A8 for average radiocarbon date uncertainties). Because our interpolations are climatically resolved, individual sites may show divergent trends from the climatic ‘norm’. This is especially pertinent for areas of rapid change, e.g. mountains, for which coarse resolution of some analyses are not representative.

Two limitations to the use of pollen-based records for biogeographical analyses include spatial and temporal aggregation. Subfossil pollen records are an incomplete subset of true historical vegetation biodiversity (e.g. Blarquez et al., 2014; Birks et al., 2016), with a study site containing only a nested spatial aggregation of pollen transported across multiple scales (e.g. Solomon & Silkworth, 1986; Mustaphi et al., 2017). For these analyses, it is therefore important to acknowledge that finer-scale geographic features on the African continent remain aggregated into the resolution of available pollen records, such as wetlands, riverine forests, kopjes, and cliff faces, which cannot be filtered out of the datasets. But the contribution of these features to biodiversity patterns, biogeographical expansion, and contraction, and long-term resilience of African ecosystems is well established.

### Future applications

Future applications of our methodology include data-model comparisons, e.g., to evaluate differences between climate models, to produce reconstructions of plant biodiversity (albeit the relationship between pollen-assemblage richness and floristic richness is not straightforward: e.g. Birks et al., 2016; Goring et

95       *al., 2013; Blarquez et al., 2014), to produce continental-scale reconstructions of leaf area index through*  
96       *comparisons between fossil indicators (pollen data, phytoliths, and carbon isotopes; Aleman et al., 2012),*  
97       *and to make comparison with phytolith-based reconstructions of grassland (e.g., tall or short grasses*  
98       *discriminated by phytolith index as in Alexandre et al., 1997). In addition, chronologies may be improved*  
99       *in the future by incorporating uncertainty intervals, i.e., through the use Bayesian methods (i.e., BACON:*  
100      *Blaauw & Christen, 2011), which permit analyses of the timing of key events (Parnell et al., 2008): e.g.,*  
101      *precise differences in the timing of climate, vegetation and land use changes could be clarified during*  
102      *critical time periods, such as the termination of the AHP. In addition, large-scale analyses provide a*  
103      *general trend by which to compare findings at individual sites.*

---

106  
107      **APPENDICES (captions)**

108      Appendices are available at <https://doi.pangaea.de/10.1594/PANGAEA.905309> (Phelps et al., 2019a).

111      **Appendix 1:** a list of collated **sites** from the APD, EPD, and other publications (csv file).

112      **Appendix 2:** a list of collated **entities** from the APD, EPD, and other publications (csv file).

113      **Appendix 3:** a list of **citations** for each entity in appendix 2, whether analyzed or not (csv file).

114      **Appendix 4:** a **harmonized taxa list** with original taxa names and numbers (csv file).

115      **Appendix 5:** a list of collated **samples** from the APD, EPD, and other publications (csv file).

116      **Appendix 6:** a list of **counts** from the APD, EPD, ACER, and other publications (csv file).

117      **Appendix 7:** a list of **radiocarbon (<sup>14</sup>C) dates** from the APD, EPD, ACER, and other publications (csv file).

118      **Appendix 8:** a list of **CLAM outputs** calculated (Blaauw, 2010) from the list of radiocarbon dates (csv file).

119      **Appendix 9:** a **harmonized biomization scheme** for “direct” and “indirect” methods (csv file).

120      **For use of these datasets, associated publications (see appendix 3) and databases should be cited.**

121      (1) *African Pollen Database* (APD: Vincens et al., 2007: <http://fpd.sedoo.fr/fpd/bibli.do>)

122      (2) *European Pollen Database* (EPD: Fyfe et al., 2009: <http://www.europeanpollendatabase.net/getdata/>)

123      (3) *ACER Pollen and Charcoal Database* (Sánchez Goñi et al., 2017)

126      Information was also added to these appendices in association with the following publications (note:  
127      information was extracted from publications and/or contributed by authors): Brenac, 1988; Burrough &  
128      Willis, 2015; Chase et al., 2015b; Cheddadi et al., 2015, 2016, 2017; Cordova et al., 2017; Giresse et al.,  
129      1994; Lim et al., 2016; Maley, 1991; Maley & Brenac, 1998; Metwally et al., 2014; Quick et al., 2016, 2018;  
130      Valsecchi et al., 2013; Waller et al., 2007. The harmonized biomization scheme (Appendix 9), is based on  
131      six primary publications: Jolly et al., 1998b; Elenga et al., 2000; Vincens et al., 2006; Vincens et al., 2007;  
132      Lebamba et al., 2009; Lézine et al., 2009, with reference to the African Plant Database (version 3.4.0).

## SUPPLEMENTARY TABLES

**Table A1:** Summary of taxa associated with direct analyses of forest and grassy biome vegetation groups, harmonized from African biomization schemes (see Appendix 9 in Phelps et al., 2019a for more detail).

FOREST			
GROUP	FAMILY	GENUS	SPECIES
Angiosperms	Acanthaceae	Acanthus	
Angiosperms	Acanthaceae	Anisotes	
Angiosperms	Acanthaceae	Brachystephanus	
Angiosperms	Acanthaceae	Hygrophila	
Angiosperms	Acanthaceae	Mimulopsis	
Angiosperms	Achariaceae	Scottellia	klaineana
Angiosperms	Alismataceae	Limnophyton	
Angiosperms	Amaranthaceae	Alternanthera	
Angiosperms	Amaranthaceae	Sericostachys	scandens
Angiosperms	Anacardiaceae	Antrocaryon	
Angiosperms	Anacardiaceae	Pseudospondias	microcarpa
Angiosperms	Anacardiaceae	Pseudospondias	
Angiosperms	Anacardiaceae	Sorindeia	juglandifolia
Angiosperms	Anacardiaceae	Sorindeia	madagascariensis
Angiosperms	Anacardiaceae	Sorindeia	
Angiosperms	Anacardiaceae	Trichoscypha	arborea
Angiosperms	Anacardiaceae	Trichoscypha	
Angiosperms	Annonaceae	Cleistopholis	patens
Angiosperms	Aphloiaceae	Aphloia	theiformis
Angiosperms	Apocynaceae	Alstonia	boonei
Angiosperms	Apocynaceae	Alstonia	congensis
Angiosperms	Apocynaceae	Alstonia	
Angiosperms	Apocynaceae	Funtumia	
Angiosperms	Apocynaceae	Isonema	smeathmannii
Angiosperms	Apocynaceae	Pleiocarpa	
Angiosperms	Apocynaceae	Rauvolfia	vomitoria
Angiosperms	Apocynaceae	Rauvolfia	
Angiosperms	Apocynaceae	Tabernaemontana	
Angiosperms	Apocynaceae	Tacazzea	apiculata
Angiosperms	Aquifoliaceae	Ilex	mitis
Angiosperms	Araliaceae	Polyscias	fulva
Angiosperms	Araliaceae	Polyscias	
Angiosperms	Araliaceae	Schefflera	abyssinica
Angiosperms	Araliaceae	Schefflera	barteri
Angiosperms	Araliaceae	Schefflera	myriantha
Angiosperms	Araliaceae	Schefflera	volkensii
Angiosperms	Araliaceae	Schefflera	
Angiosperms	Arecaceae	Calamus	deerratus
Angiosperms	Arecaceae	Cocos	nucifera
Angiosperms	Arecaceae	Eremospatha	
Angiosperms	Arecaceae	Laccosperma	secundiflorum
Angiosperms	Arecaceae	Laccosperma	
Angiosperms	Arecaceae	Phoenix	reclinata
Angiosperms	Arecaceae	Podococcus	barteri
Angiosperms	Arecaceae	Raphia	
Angiosperms	Arecaceae	Sclerosperma	
Angiosperms	Asparagaceae	Dracaena	afromontana
Angiosperms	Asparagaceae	Dracaena	steudneri
Angiosperms	Balsaminaceae	Impatiens	
Angiosperms	Betulaceae	Alnus	
Angiosperms	Betulaceae	Betula	
Angiosperms	Betulaceae	Carpinus	betulus
Angiosperms	Betulaceae	Carpinus	orientalis
Angiosperms	Betulaceae	Carpinus	
Angiosperms	Burseraceae	Canarium	
Angiosperms	Burseraceae	Dacryodes	
Angiosperms	Burseraceae	Santiria	trimera
Angiosperms	Caryophyllaceae	Drymaria	cordata
Angiosperms	Celastraceae	Salacia	senegalensis
Angiosperms	Chrysobalanaceae	Marันthes	
Angiosperms	Clusiaceae	Garcinia	gnethoides
Angiosperms	Clusiaceae	Garcinia	volkensii
Angiosperms	Clusiaceae	Pentadesma	butyracea
Angiosperms	Clusiaceae	Symphonia	globulifera
Angiosperms	Compositae	Brachylaena	
Angiosperms	Compositae	Crassocephalum	montuosum
Angiosperms	Compositae	Tarchonanthus	camphoratus
Angiosperms	Connaraceae	Cnestis	
Angiosperms	Cornaceae	Alangium	chinense
Angiosperms	Cornaceae	Cornus	volkensii
Angiosperms	Dilleniaceae	Tetracerá	alnifolia
Angiosperms	Eriocaulaceae		
Angiosperms	Euphorbiaceae	Alchornea	cordifolia
Angiosperms	Euphorbiaceae	Alchornea	
Angiosperms	Euphorbiaceae	Anthostema	senegalense
Angiosperms	Euphorbiaceae	Anthostema	
Angiosperms	Euphorbiaceae	Erythrococca	africana
Angiosperms	Euphorbiaceae	Klaineanthus	gaboniae
Angiosperms	Euphorbiaceae	Macaranga	capensis
Angiosperms	Euphorbiaceae	Macaranga	kilimandscharica
Angiosperms	Euphorbiaceae	Macaranga	monandra
Angiosperms	Euphorbiaceae	Macaranga	

GRASSY BIOMES			
GROUP	FAMILY	GENUS	SPECIES
Angiosperms	Acanthaceae	Duosperma	
Angiosperms	Acanthaceae	Dyschoriste	
Angiosperms	Acanthaceae	Justicia	odora
Angiosperms	Amaranthaceae	Aerva	
Angiosperms	Amaranthaceae	Digera	muricata
Angiosperms	Amaranthaceae	Suaeda	
Angiosperms	Amaranthaceae	Volkensteinia	prostrata
Angiosperms	Amaryllidaceae	Haemanthus	
Angiosperms	Araceae	Lemna	
Angiosperms	Arecaceae	Borassus	aethiopum
Angiosperms	Arecaceae	Borassus	
Angiosperms	Arecaceae	Borassus/Hyphaene	
Angiosperms	Arecaceae	Hyphaene	
Angiosperms	Boraginaceae	Trichodesma	
Angiosperms	Burseraceae	Commiphora	edulis
Angiosperms	Cannabaceae	Lobelia	
Angiosperms	Capparaceae	Capparis	decidua
Angiosperms	Caryophyllaceae	Gymnocarpos	sclerocephalus
Angiosperms	Caryophyllaceae	Polycarpon	prostratum
Angiosperms	Cleomaceae	Cleome	brachycarpa
Angiosperms	Commelinaceae	Commelina	ramulosa
Angiosperms	Compositae	Ambrosia	maritima
Angiosperms	Compositae	Ambrosia	
Angiosperms	Compositae	Baccharoides	schimperi
Angiosperms	Compositae	Centaurea	perrottetii
Angiosperms	Compositae	Dendrosenecio	
Angiosperms	Convolvulaceae	Hildebrandtia	obcordata
Angiosperms	Euphorbiaceae	Jatropha	
Angiosperms	Lamiaceae	Plectranthus	otostegoides
Angiosperms	Leguminosae	Bauhinia	reticulata
Angiosperms	Leguminosae	Canavalia	
Angiosperms	Leguminosae	Delonix	
Angiosperms	Leguminosae	Senna	italica
Angiosperms	Leguminosae	Stylosanthes	fruticosa
Angiosperms	Leguminosae	Vatovaea	pseudolablab
Angiosperms	Malpighiaceae	Caucanthus	
Angiosperms	Malvaceae	Corchorus	fascicularis
Angiosperms	Malvaceae	Hermannia	
Angiosperms	Malvaceae	Waltheria	
Angiosperms	Menispermaceae	Cocculus	hirsutus
Angiosperms	Moraceae	Dorstenia	foetida
Angiosperms	Nyctaginaceae	Boerhavia	
Angiosperms	Ranunculaceae	Ranunculus	
Angiosperms	Rubiaceae	Coptosperma	graveolens
Angiosperms	Rubiaceae	Ixora	brachypoda
Angiosperms	Rubiaceae	Kohautia	
Angiosperms	Rubiaceae	Spermacoce	radiata
Angiosperms	Salicaceae	Salix	mucronata
Angiosperms	Salvoraceae	Azima	tetraantha
Angiosperms	Zygophylaceae	Balanites	rotundifolia
Pteridophytes	Anemiaceae	Mohria	

Families in forest & grassy biomes  
Genera in forest & grassy biomes

Angiosperms	Euphorbiaceae	Mallotus	oppositifolius
Angiosperms	Euphorbiaceae	Neoboutonia	macrocalyx
Angiosperms	Euphorbiaceae	Plagiostyles	africana
Angiosperms	Euphorbiaceae	Tetrorchidium	
Angiosperms	Euphorbiaceae	Tragia	
Angiosperms	Fagaceae	Quercus	ilex
Angiosperms	Fagaceae	Quercus	pubescens
Angiosperms	Fagaceae	Quercus	suber
Angiosperms	Haloragaceae	Laurembergia	tetrandra
Angiosperms	Hamamelidaceae	Trichocladus	ellipticus
Angiosperms	Humiriaceae	Sacoglottis	gabonensis
Angiosperms	Hydrocharitaceae		
Angiosperms	Hypericaceae	Harungana	
Angiosperms	Hypericaceae	Psorospermum	febrifugum
Angiosperms	Icacinaeae	Apodytes	dimidiata
Angiosperms	Icacinaeae	Iodes	
Angiosperms	Icacinaeae	Raphiostylis	
Angiosperms	Irvingiaceae	Irvingia	gabonensis
Angiosperms	Juglandaceae	Juglans	
Angiosperms	Leguminosae	Afzelia	
Angiosperms	Leguminosae	Anthonotha	



**Table A2:** Percentage contribution of climate variables to explained variance of PCA axes one and two.

WorldClim variables	ax.1_contrib	ax.2_contrib
bio1	0.015678333	21.67937813
bio2	6.273577383	0.052872283
bio3	8.886625302	0.280426103
bio4	9.347332799	0.496209282
bio5	5.000603065	9.790094978
bio6	5.445561038	10.24599369
bio7	9.996478378	0.100872017
bio8	0.000160318	13.39192697
bio9	0.003280972	7.905767391
bio10	3.479396849	12.60849887
bio11	3.881416974	13.79083845
bio12	9.907884346	0.065742712
bio13	8.190119767	0.139521506
bio14	4.300227524	0.474610198
bio15	0.459456342	7.361487902
bio16	8.228270658	0.024132168
bio17	5.093120706	0.461404224
bio18	7.551494712	0.997945858
bio19	3.939314533	0.132277268

TraCE variables	ax.1_contrib	ax.2_contrib
precipmean	13.82160166	0.570566528
precipseasonality	14.44596071	4.582608332
tempdiurn	13.385928	0.110587872
tempiso	10.33313016	0.254751042
tempmax	8.086501187	21.38339502
tempmean	0.826799127	48.49138883
tempmin	6.852182512	23.96531794
temprange	16.2071891	0.289979916
tempseasonality	16.04070754	0.351404521

**Table A3:** TraCE-21ka variable correlations: highly correlated variables are shaded in orange ( $> |0.7|$ ). Variable names are indicated below.

TraCE-21ka (pooled)	precipmean	precipseasor	tempdiurn	tempiso	tempmax	tempmean	tempmin	temprange	tempseasonality
precipmean	1								
precipseasonality	-0.825	1							
tempdiurn	-0.652	0.772	1						
tempiso	0.734	-0.645	-0.46	1					
tempmax	-0.588	0.769	0.793	-0.322	1				
tempmean	0.127	0.075	-0.146	0.196	0.462	1			
tempmin	0.371	-0.353	-0.697	0.372	-0.116	0.782	1		
temprange	-0.832	0.834	0.751	-0.751	0.544	-0.265	-0.584	1	
tempseasonality	-0.828	0.83	0.739	-0.75	0.53	-0.27	-0.581	0.998	1

(1) mean temperature (tempmean)  
(2) diurnal temperature (tempdiurn)  
(3) isothermality (tempiso)  
(4) temperature seasonality (tempseasonality)  
(5) maximum temperature (tempmax)  
(6) minimum temperature (tempmin)  
(7) temperature range (temprange)  
(8) mean precipitation (precipmean)  
(9) precipitation seasonality (precipseasonality)

148

149

150

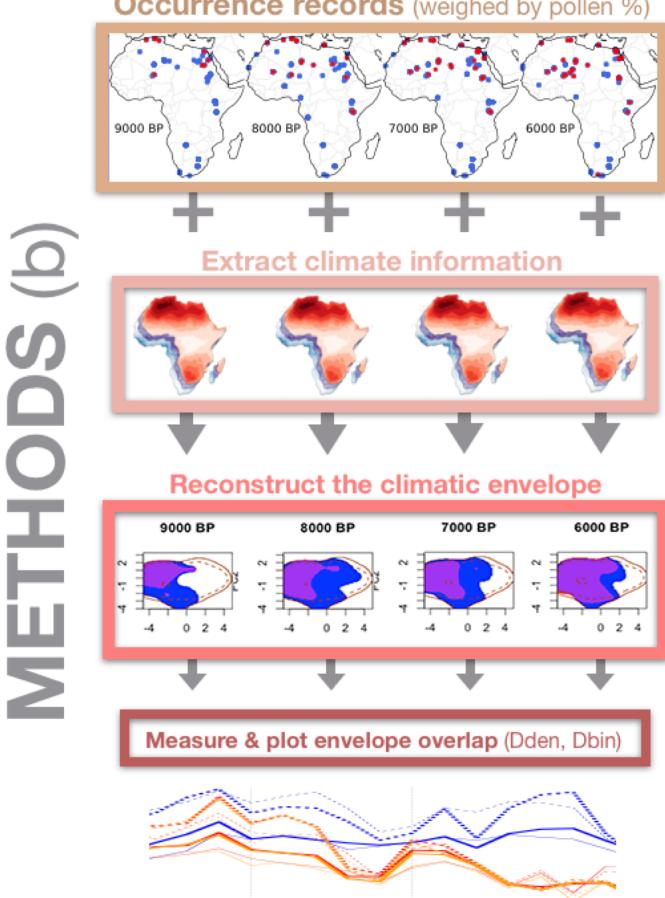
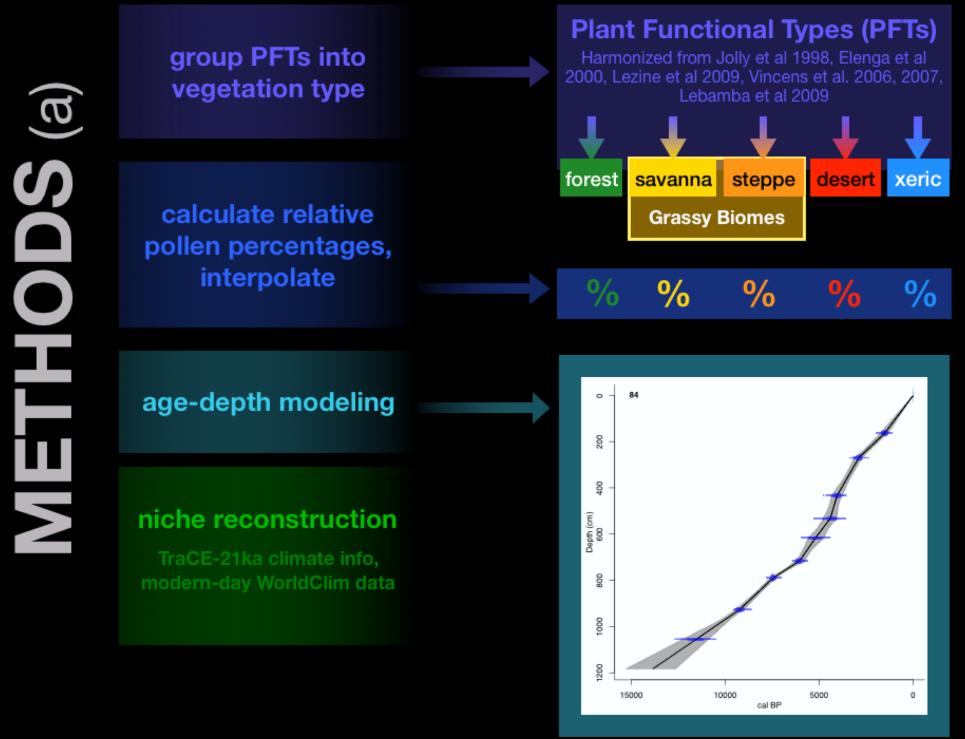
**Table A4:** WorldClim (version 2: Fick et al. 2017) variable correlations: highly correlated variables are shaded in orange ( $> |0.7|$ ). Variable names are indicated below.

WorldClim	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio1	1																		
bio2	0.023	1																	
bio3	0.142	-0.504	1																
bio4	-0.154	0.594	-0.919	1															
bio5	0.647	0.575	-0.56	0.608	1														
bio6	0.692	-0.594	0.708	-0.746	-0.044	1													
bio7	-0.088	0.809	-0.883	0.941	0.681	-0.762	1												
bio8	0.756	0.12	0.136	-0.144	0.442	0.482	-0.067	1											
bio9	0.559	-0.178	-0.005	0.024	0.483	0.449	-0.016	0.075	1										
bio10	0.754	0.388	-0.483	0.523	0.966	0.118	0.54	0.519	0.548	1									
bio11	0.795	-0.357	0.657	-0.717	0.093	0.949	-0.636	0.598	0.41	0.218	1								
bio12	-0.015	-0.63	0.744	-0.773	-0.577	0.549	-0.777	-0.064	0.024	-0.505	0.471	1							
bio13	0.083	-0.52	0.657	-0.775	-0.474	0.556	-0.715	0.013	0.033	-0.42	0.543	0.918	1						
bio14	-0.06	-0.436	0.544	-0.375	-0.366	0.323	-0.474	-0.062	0.288	0.19	0.558	0.317	1						
bio15	0.465	0.291	-0.088	-0.057	0.344	0.174	0.095	0.555	0.073	0.333	0.342	-0.252	-0.006	-0.407	1				
bio16	0.042	-0.52	0.645	-0.762	-0.497	0.521	-0.704	-0.016	0.008	-0.448	0.506	0.935	0.989	0.333	-0.05	1			
bio17	-0.058	-0.492	0.594	-0.422	-0.401	0.366	-0.529	-0.07	0.051	-0.316	0.221	0.62	0.367	0.983	-0.437	0.381	1		
bio18	-0.148	-0.576	0.672	-0.668	-0.662	0.377	-0.706	-0.036	-0.192	-0.579	0.294	0.82	0.704	0.521	-0.249	0.722	0.571	1	
bio19	0.083	-0.419	0.436	-0.409	-0.219	0.43	-0.457	-0.067	0.214	-0.167	0.329	0.627	0.554	0.416	-0.236	0.566	0.454	0.278	

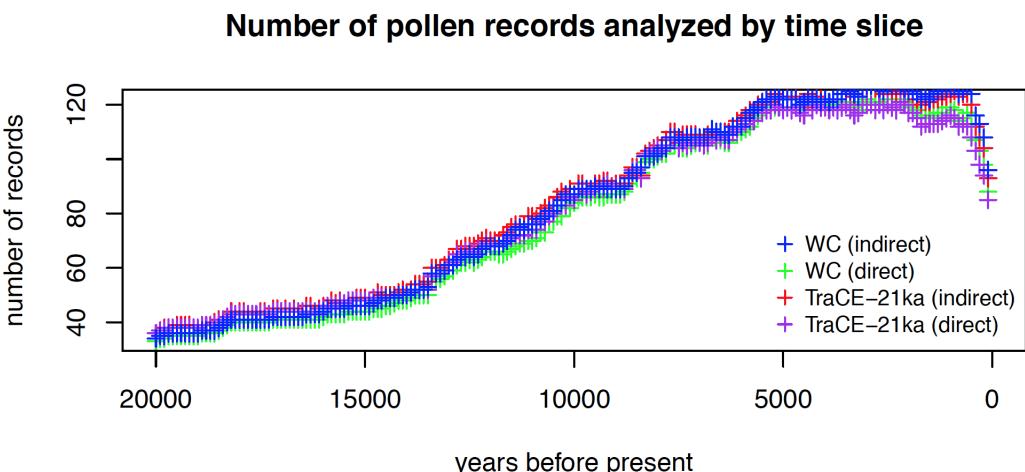
(bio1) Annual Mean Temperature  
(bio2) Mean Diurnal Range  
(bio3) Isothermality  
(bio4) Temperature Seasonality  
(bio5) Max temperature of Warmest Month  
(bio6) Min Temperature of Coldest Month  
(bio7) Temperature Annual Range  
(bio8) Mean Temperature of Wettest Quarter  
(bio9) Mean Temperature of Driest Quarter  
(bio10) Mean Temperature of Wettest Quarter  
(bio11) Mean Temperature of Coldest Quarter  
(bio12) Annual Precipitation  
(bio13) Precipitation of Wettest Month  
(bio14) Precipitation of Driest Month  
(bio15) Precipitation Seasonality  
(bio16) Precipitation of Wettest Quarter  
(bio17) Precipitation of Driest Quarter  
(bio18) Precipitation of Warmest Quarter  
(bio19) Precipitation of Coldest Quarter

151

## SUPPLEMENTARY FIGURES

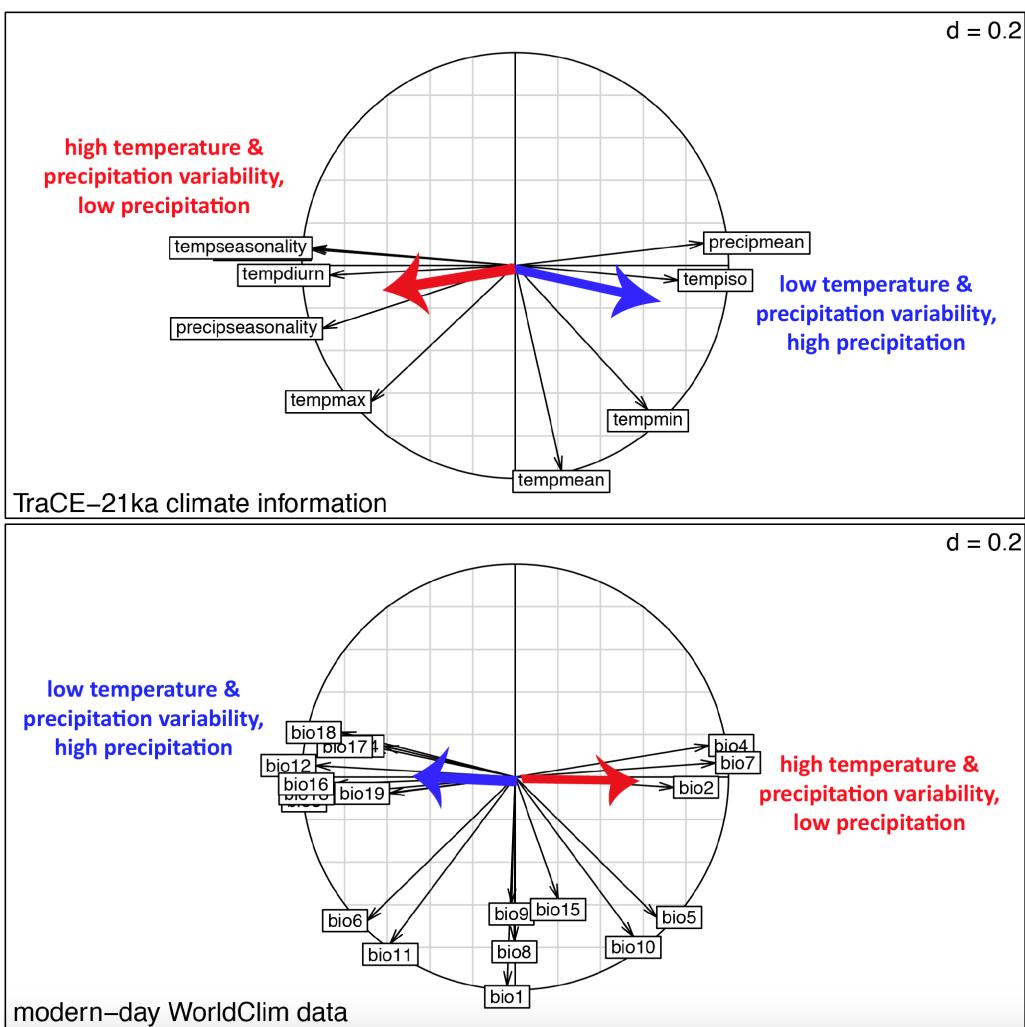


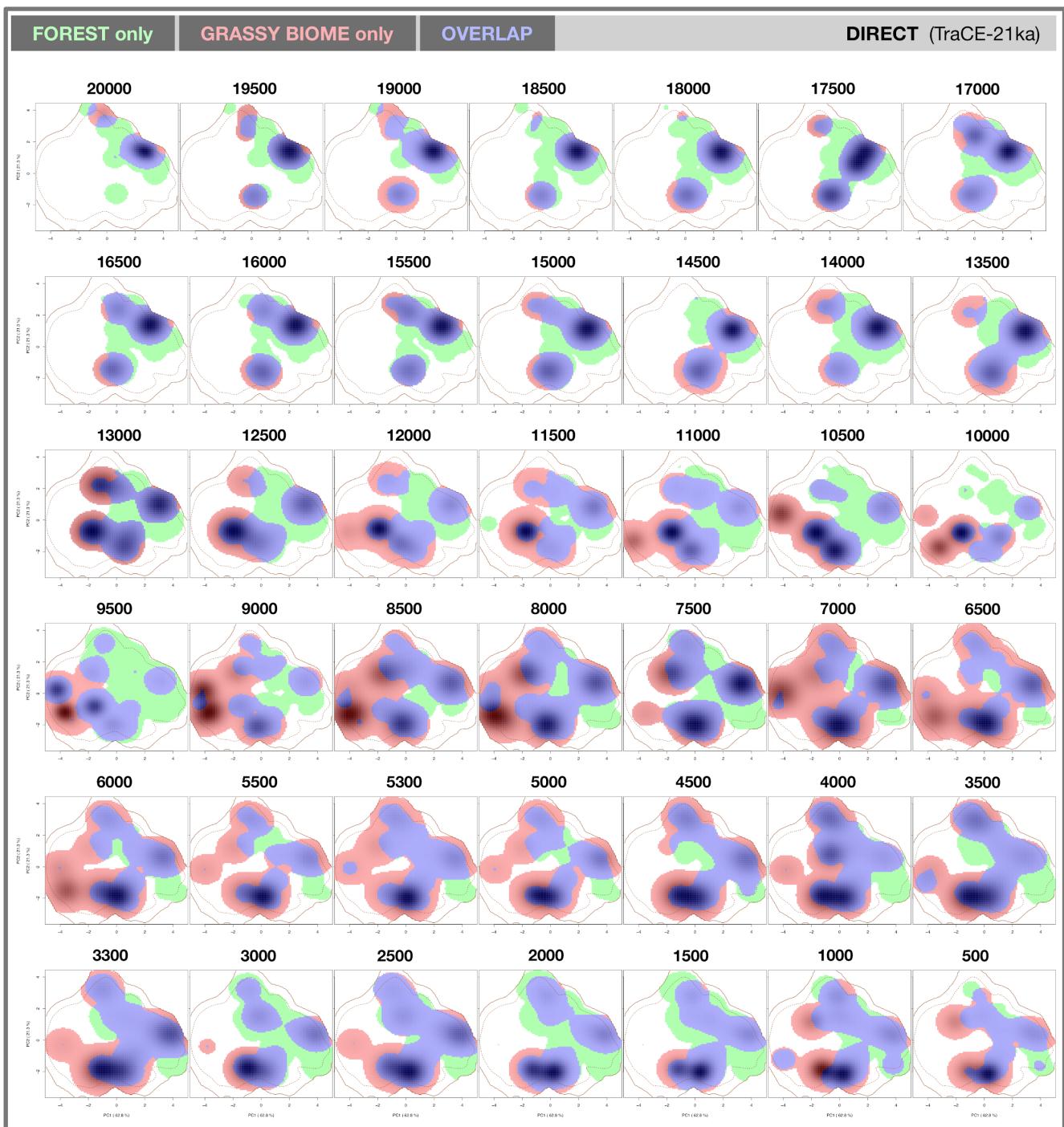
**Figure A1:**  
Flowcharts of the methodological process used to analyze subfossil pollen records in this study: flowchart (a) describes the grouping of vegetation from plant functional types, the calculation of relative percentages for each group, and age depth modeling. Flowchart (b) describes the process used to quantify temporal changes in vegetation envelopes.



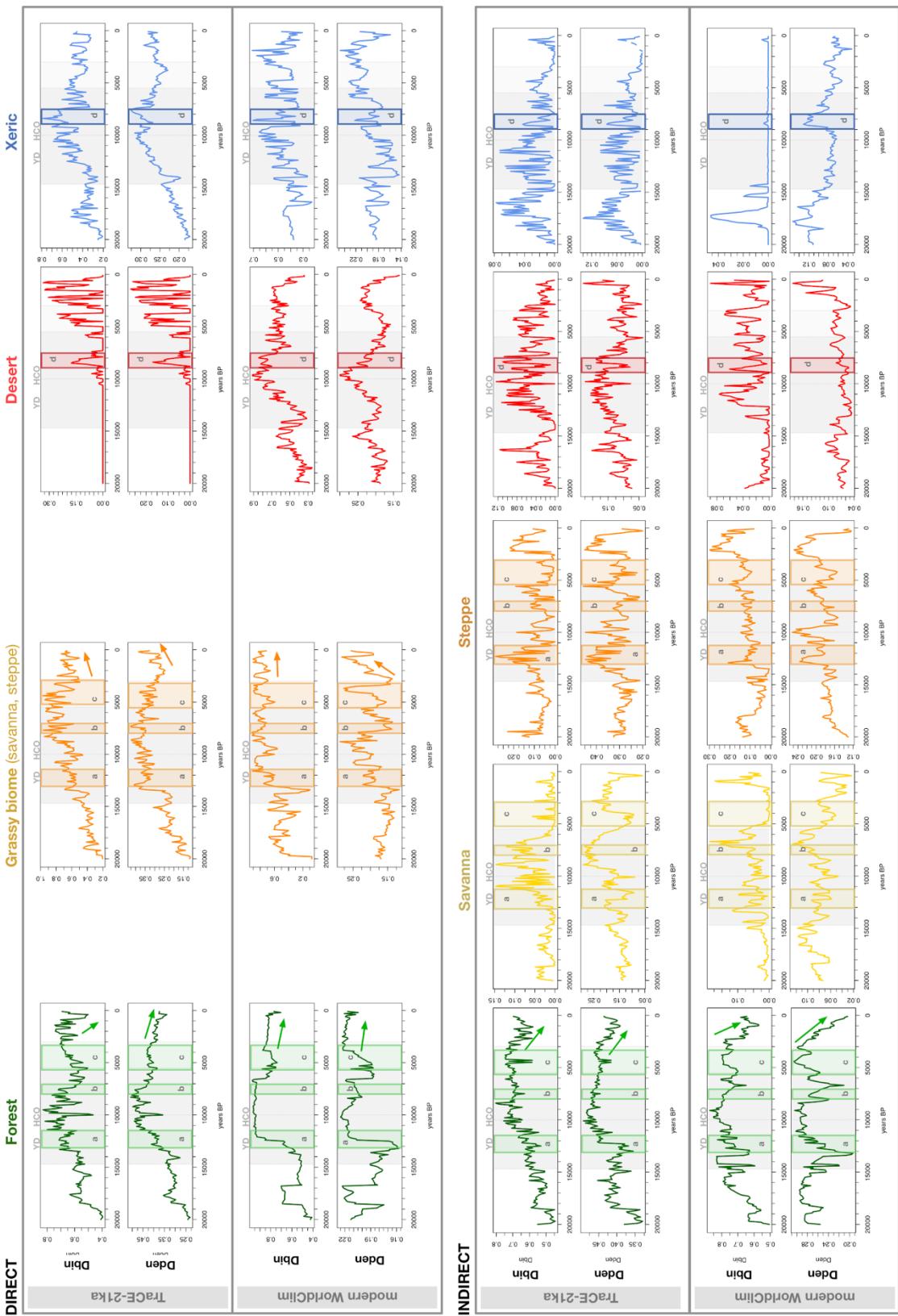
**Figure A2:** The number of pollen records utilized for each time interval using direct and indirect methods, TraCE-21ka climate information, and Modern-day WorldClim data (WC).

153

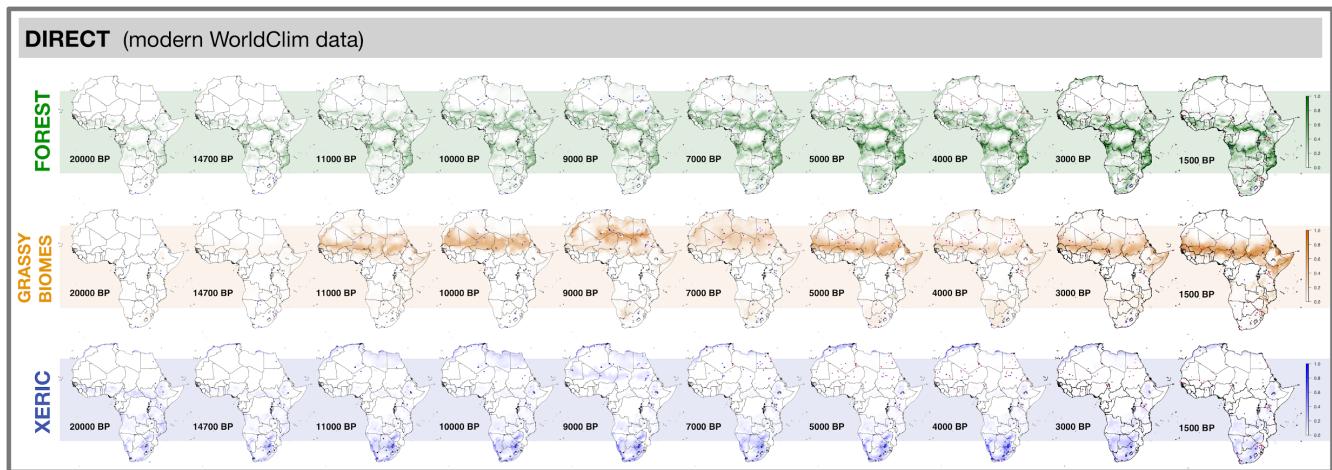




**Figure A4:** Climatic envelope overlap between forest and grassy biomes mapped in climate space using the direct methodological approach (a); envelope overlap between forest and savanna using the indirect methodological approach (b); and envelope overlap between forest and steppe using the indirect methodological approach (c). All analyses were performed with TraCE-21ka climate information using the ECOSPAT package in R ('ecospat' package in R; for further methodological information, see Broennimann et al., 2012). Numbers indicate years before present (BP). For visualizations of more time intervals, see Movie S8a; for savanna and overlapping area with forest, see Movie S8b.



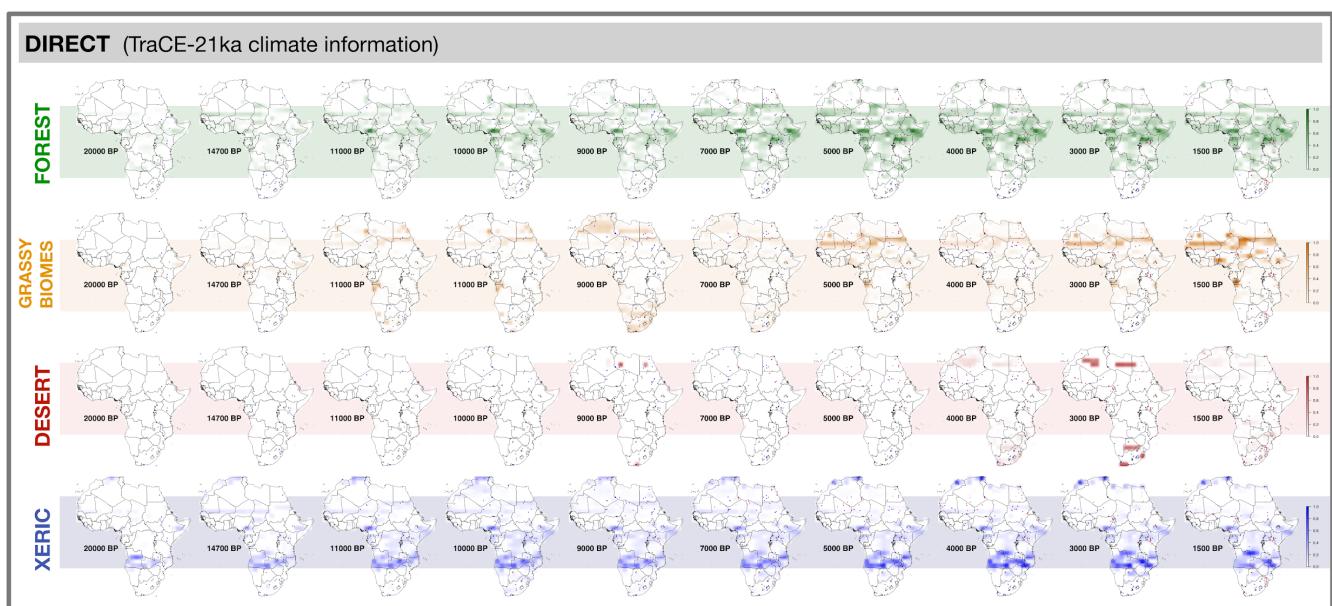
**Figure A5:**  
D-metrics (Dden, Dbin) measure the overlap between vegetation categories and the background African climate space. Values are plotted from the last glacial period until recent times at 100-year intervals, using direct and indirect methods. In addition to TraCE-21ka climate information, WorldClim analyses provide an auxiliary exploration of the model for robustness and enhanced interpretation of results.



**Figure A6a:** Climatic envelopes projected into geographic space using the direct methodology and repeated, modern-day WorldClim information (white background). Note: desert was excluded due to lack of records.

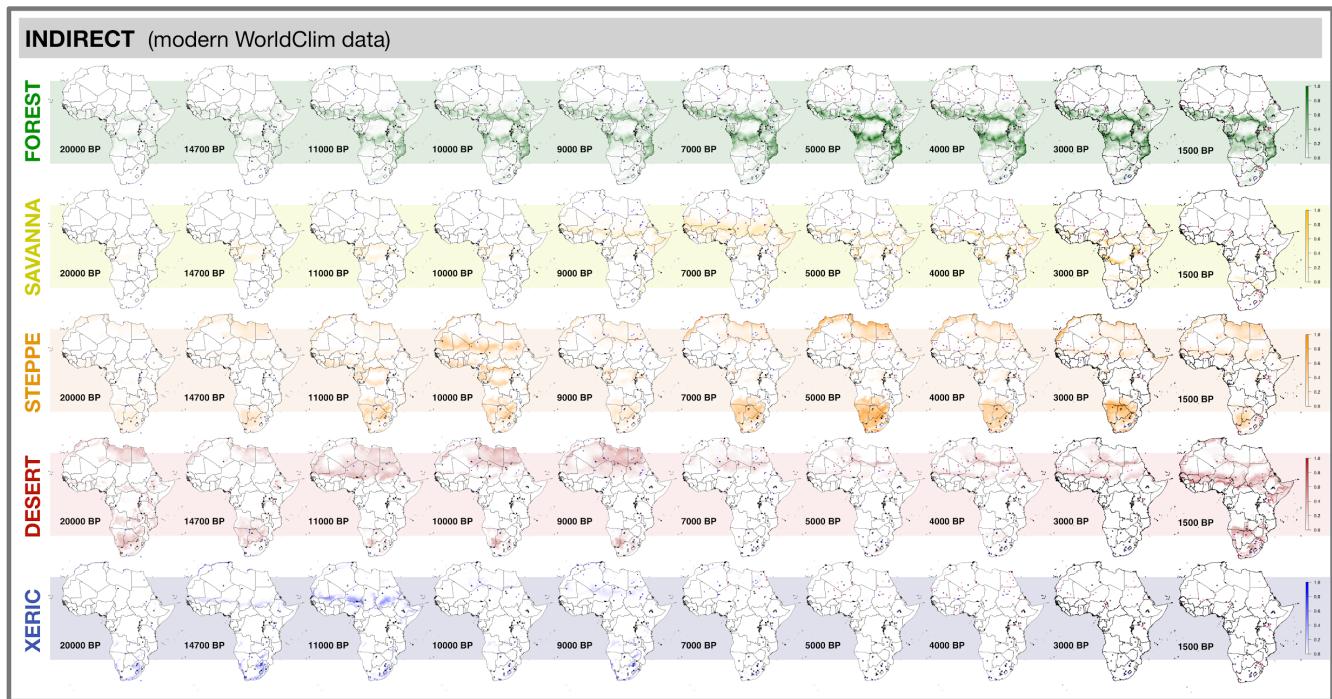
156

157



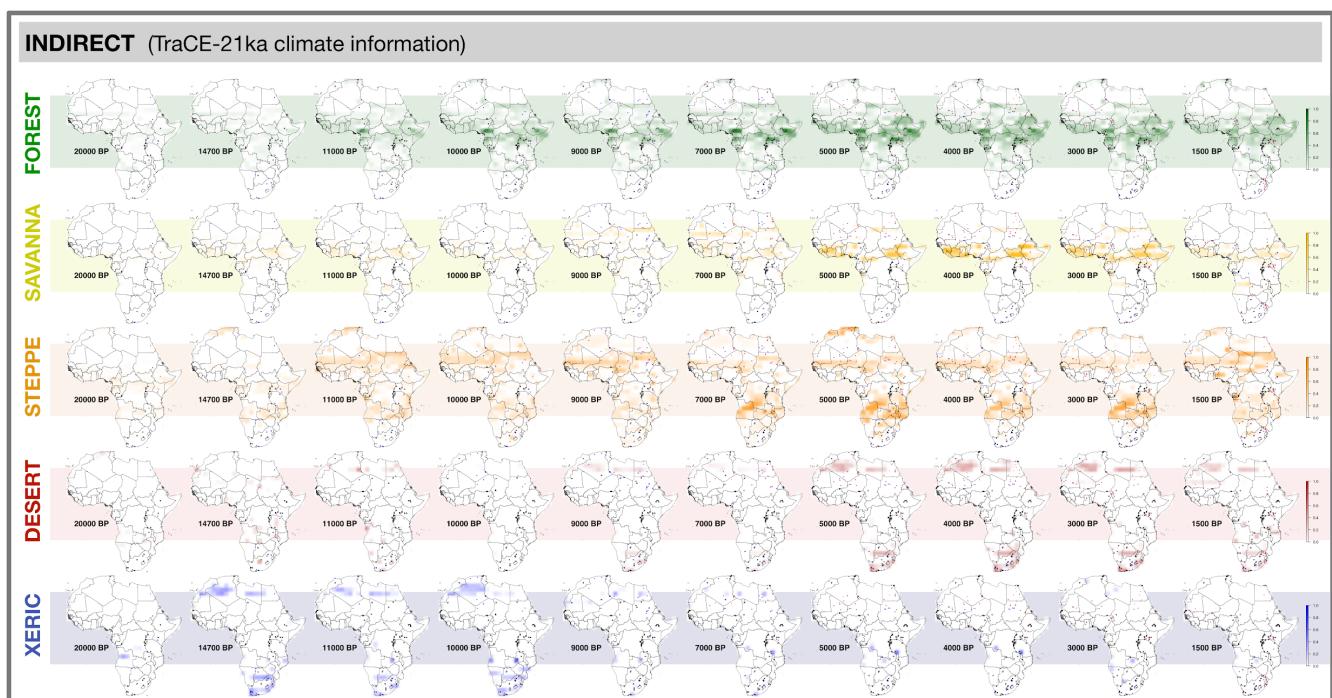
**Figure A6b:** Climatic envelopes projected into geographic space using the direct methodology and TraCE-21ka climate information (white background).

158

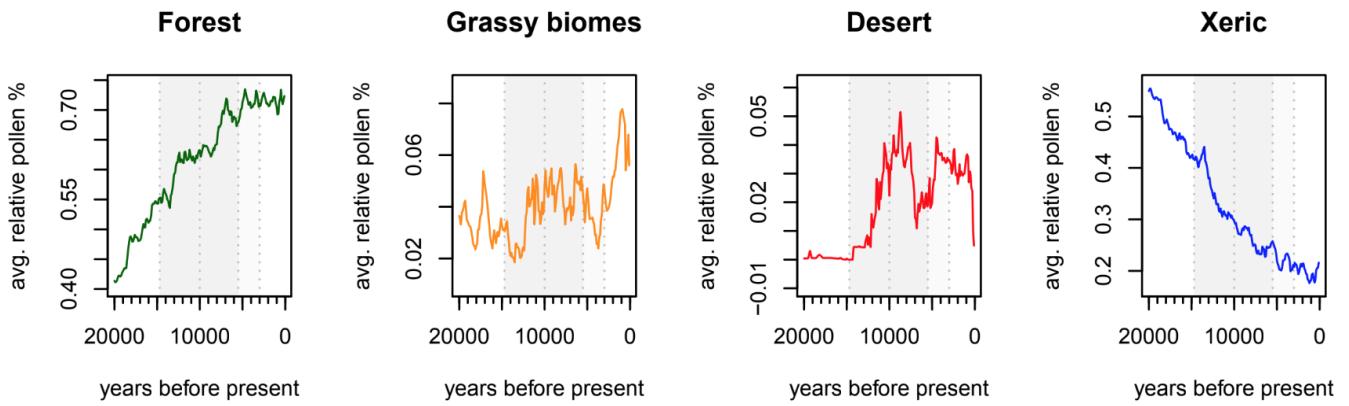


**Figure A6c:** Climatic envelopes projected into geographic space using the indirect methodology and repeated, modern-day WorldClim information (white background).

159



**Figure A6d:** Climatic envelopes projected into geographic space using the indirect methodology and TraCE-21ka climate information (white background).

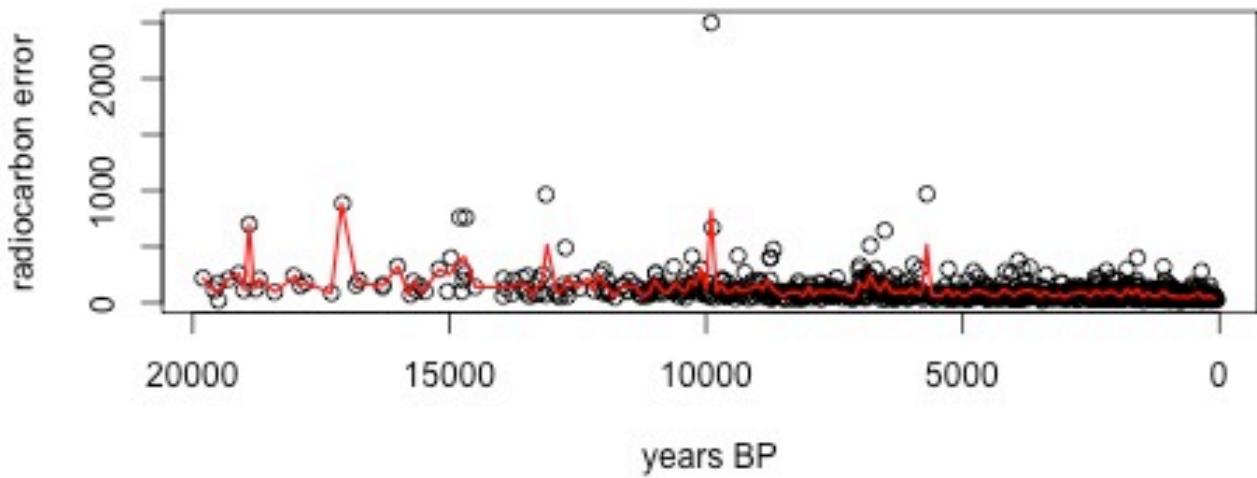


**Figure A7:** The relative pollen abundance for each vegetation type, averaged across all sites for each time interval

160

161

162



**Figure A8:** raw radiocarbon carbon dates plotted from past to present with associated error ranges. Red line indicates average radiocarbon error at 100-year time intervals, always lower than 900 years.

163

164

165

166      **MOVIES (captions)**

167  
168      **Movies files** are accessible at <https://doi.pangaea.de/10.1594/PANGAEA.905979> (Phelps et al., 2019b).  
169      For all mapped movies (Movie S1 - S6), white circles indicate the presence of a pollen record; blue dots  
170      indicate archaeological remains of wild terrestrial ungulates; and red dots indicate the remains of  
171      domestic animals. The distribution of the faunal remains was based on summed probability distributions  
172      of radiocarbon dates at 100-year time intervals (see Phelps et al., 2020 for further methodological  
173      information).

174  
175      **Movie S1a:** The climatic envelope of forest mapped at 100-year intervals, using the direct methodology  
176      with WorldClim data (black background).

177  
178      **Movie S1b:** The climatic envelope of forest mapped at 100-year intervals, using the direct methodology  
179      with WorldClim data (white background).

180  
181      **Movie S1c:** The climatic envelope of forest mapped at 100-year intervals, using the direct methodology  
182      with TraCE-21ka climate information (black background).

183  
184      **Movie S1d:** The climatic envelope of forest taxa mapped at 100-year intervals, using the direct  
185      methodology with TraCE-21ka climate information (white background).

186  
187      **Movie S1e:** The climatic envelope of forest taxa mapped at 100-year intervals, using the indirect  
188      methodology, WorldClim data (black background).

189  
190      **Movie S1f:** The climatic envelope of forest taxa mapped at 100-year intervals, using the indirect  
191      methodology, WorldClim data (white background).

192  
193      **Movie S1g:** The climatic envelope of forest taxa mapped at 100-year intervals, using the indirect  
194      methodology, TraCE-21ka climate information (black background).

195  
196      **Movie S1h:** The climatic envelope of forest taxa mapped at 100-year intervals, using the indirect  
197      methodology, TraCE-21ka climate information (white background).

---

199  
200      **Movie S2a:** The climatic envelope of grassy biomes (savanna- and steppe-associated taxa) mapped at  
201      100-year intervals, using the direct methodology with WorldClim data (black background).

202  
203      **Movie S2b:** The climatic envelope of grassy biomes (savanna- and steppe-associated taxa) mapped at  
204      100-year intervals, using the direct methodology with WorldClim data (white background).

205  
206      **Movie S2c:** The climatic envelope of grassy biomes (savanna- and steppe-associated taxa) mapped at 100-  
207      year intervals, using the direct methodology with TraCE-21ka climate information (black background).

208  
209      **Movie S2d:** The climatic envelope of grassy biomes (savanna- and steppe-associated taxa) mapped at  
210      100-year intervals, using the direct methodology with TraCE-21ka climate information (white  
211      background).

---

213  
214 **Movie S3a:** The climatic envelope of savanna-associated taxa mapped at 100-year intervals, using the  
215 indirect methodology, WorldClim data (black background).

216  
217 **Movie S3b:** The climatic envelope of savanna-associated taxa mapped at 100-year intervals, using the  
218 indirect methodology, WorldClim data (white background).

219  
220 **Movie S3c:** The climatic envelope of savanna-associated taxa mapped at 100-year intervals, using the  
221 indirect methodology, TraCE-21ka climate information (black background).

222  
223 **Movie S3d:** The climatic envelope of savanna-associated taxa mapped at 100-year intervals, using the  
224 indirect methodology, TraCE-21ka climate information (white background).

---

227  
228 **Movie S4a:** The climatic envelope of steppe-associated taxa mapped at 100-year intervals, using the  
229 indirect methodology, WorldClim data (black background).

230  
231 **Movie S4b:** The climatic envelope of steppe-associated taxa mapped at 100-year intervals, using the  
232 indirect methodology, WorldClim data (white background).

233  
234 **Movie S4c:** The climatic envelope of steppe-associated taxa mapped at 100-year intervals, using the  
235 indirect methodology, TraCE-21ka climate information (black background).

236  
237 **Movie S4d:** The climatic envelope of steppe-associated taxa mapped at 100-year intervals, using the  
238 indirect methodology, TraCE-21ka climate information (white background).

---

240  
241 **Movie S5a:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the  
242 direct methodology with WorldClim data (black background).

243  
244 **Movie S5b:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the  
245 direct methodology with WorldClim data (white background).

246  
247 **Movie S5c:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the direct  
248 methodology with TraCE-21ka climate information (black background).

249  
250 **Movie S5d:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the  
251 direct methodology with TraCE-21ka climate information (white background).

252  
253 **Movie S5e:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the  
254 indirect methodology, WorldClim data (black background).

255  
256 **Movie S5f:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the  
257 indirect methodology, WorldClim data (white background).

258  
259 **Movie S5g:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the  
260 indirect methodology, TraCE-21ka climate information (black background).

260  
261 **Movie S5h:** The climatic envelope of desert-associated taxa mapped at 100-year intervals, using the  
262 indirect methodology, TraCE-21ka climate information (white background).

---

264  
265 **Movie S6a:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the direct  
266 methodology with WorldClim data (black background).

267  
268 **Movie S6b:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the direct  
269 methodology with WorldClim data (white background).

270  
271 **Movie S6c:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the direct  
272 methodology with TraCE-21ka climate information (black background).

273  
274 **Movie S6d:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the direct  
275 methodology with TraCE-21ka climate information (white background).

276  
277 **Movie S6e:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the indirect  
278 methodology, WorldClim data (black background).

279  
280 **Movie S6f:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the indirect  
281 methodology, WorldClim data (white background).

282  
283 **Movie S6g:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the indirect  
284 methodology, TraCE-21ka climate information (black background).

285  
286 **Movie S6h:** The climatic envelope of xeric-associated taxa mapped at 100-year intervals, using the  
287 indirect methodology, TraCE-21ka climate information (white background).

---

288  
289  
290 **Movie S7a:** Multivariate environmental similarity surface (MESS) analyses plotted in geographic space  
291 using the direct methodology with repeated, modern-day WorldClim data. White areas demonstrate  
292 neutrality: i.e., neither similarity nor dissimilarity.

293  
294 **Movie S7b:** Multivariate environmental similarity surface (MESS) analyses plotted in geographic space  
295 using the direct methodology with TraCE-21ka climate information. White areas demonstrate neutrality:  
296 i.e., neither similarity nor dissimilarity.

297  
298 **Movie S7c:** Multivariate environmental similarity surface (MESS) analyses plotted in geographic space  
299 using the indirect methodology with repeated, modern-day WorldClim data. White areas demonstrate  
300 neutrality: i.e., neither similarity nor dissimilarity.

301  
302 **Movie S7d:** Multivariate environmental similarity surface (MESS) analyses plotted in geographic space  
303 using the indirect methodology with TraCE-21ka climate information. White areas demonstrate  
304 neutrality: i.e., neither similarity nor dissimilarity.

---

307 **Movie S8a:** Climatic envelope overlap between forest and grassy biomes (savanna and steppe) plotted in  
308 climate space. Envelopes were generated using the direct methodology and TraCE-21ka climate  
309 information. Red areas indicate the presence of grassy biomes only, whereas purple indicates overlap  
310 between grassy biomes and forest. For reference to the climatic variables used to define the climate  
311 space, see the TraCE-21ka correlation circle in Figure A2.

312 **Movie S8b:** Climatic envelope overlap between forest and savanna only, plotted in climate space.  
313 Envelopes were generated using the indirect methodology and TraCE-21ka climate information. Red areas  
314 indicate the presence of savanna only, whereas purple indicates overlap between savanna and forest. For  
315 reference to the climatic variables used, see the TraCE-21ka correlation circle in Figure A2.  
316

## 321 REFERENCES

- 322 African Plant Database (version 3.4.0). Conservatoire et jardin botaniques de la ville de Genève and South  
323 African national biodiversity institute. Accessible online: <http://www.ville-ge.ch/musinfo/bd/cjb/africa/>
- 324 Aleman, J., Leys, B., Apema, R., Bentaleb, I., Dubois, M., Lamba, B., Lebamba, J., Martin, C., Ngomanda, A.,  
325 Truc, L., Yangakola, J.-M., Favier, C., and Bremond, L. (2012). Reconstructing savanna tree cover  
326 from pollen, phytoliths and stable carbon isotopes. *Journal of Vegetation Science*, 23(1):187–197.
- 327 Aleman, J. C. and Staver, C. A. (2018). Spatial patterns in the global distributions of savanna and forest.  
328 *Global Ecology and Biogeography*, 27(7):792–803.
- 329 Alexandre, A., Meunier, J.-D., Lézine, A.-M., Vincens, A., and Schwartz, D. (1997). Phytoliths: indicators of  
330 grassland dynamics during the late Holocene in intertropical Africa. *Palaeogeography, Palaeoclimatology,*  
331 *Palaeoecology*, 136(1-4):213–229.
- 332 Amaral, P., Vincens, A., Guiot, J., Buchet, G., Deschamps, P., Doumnang, J.-C., and Sylvestre, F. (2013).  
333 Palynological evidence for gradual vegetation and climate changes during the African humid  
334 period termination at 13°N from Mega-Lake Chad sedimentary sequence. *Climate of the Past*, 9:1–  
335 19.
- 336 Archibald, S., Lehmann, C. E., Gómez-Dans, J. L., and Bradstock, R. A. (2013). Defining pyromes and global  
337 syndromes of fire regimes. *PNAS*, 110(16):6442–6447.
- 338 Archibald, S. and Hempson, G. P. (2016). Competing consumers: contrasting the patterns and impacts of  
339 fire and competing consumers: contrasting the patterns and impacts of fire and mammalian  
340 herbivory in Africa. *Philosophical Transactions of the Royal Society B*, 371.
- 341 Armitage, S. J., Bristow, C. S., and Drake, N. A. (2015). West African monsoon dynamics inferred abrupt  
342 fluctuations of Lake Mega-Chad. *PNAS*, 112(28):8543–8548.
- 343 Bateman, M. D., Thomas, D. S., and Singhvi, Ashok, K. (2003). Extending the aridity record of the  
344 southwest Kalahari: current problems and future perspectives. *Quaternary International*,  
345 111(1):37–49.
- 346 Bayon, G., Dennielou, B., Etoubleau, J., Ponevera, E., Toucanne, S., and Vermell, S. (2012). Intensifying  
347 weathering and land use in iron age central Africa. *Science*, 335(6073):1219–1222.
- 348 Bird, R. B., Bird, D., Codding, B., Parker, C., and Jones, J. (2008). The "fire stick farming" hypothesis:  
349 Australian aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *PNAS*,  
350 105(39):14796–14801.

- 353 Birks, H. J. B., Felde, V. A., Bjune, A. E., Grytnes, J.-A., Seppä, H., and Giesecke, T. (2016). Does pollen-  
354 assemblage richness reflect floristic richness? a review of recent developments and future  
355 challenges. *Review of Palaeobotany and Palynology*, 228:1–25.
- 356 Blaauw, M. (2010) Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary*  
357 *Geochronology*, 5(5):512-518.
- 358 Blaauw, M. and Christen, A. (2011). Flexible paleoclimate age-depth models using an autoregressive  
359 gamma process. *Bayesian Analysis*, 6(3):457–474.
- 360 Blarquez, O., Carcaillet, C., Frejaville, T., and Bergeron, Y. (2014). Disentangling the trajectories of alpha,  
361 beta and gamma plant diversity of North American boreal ecoregions since 15,500 years. *Frontiers*  
362 in Ecology and Evolution
- 363 Blümel, W., Eitel, B., and Lang, A. (1998). Dunes in southeastern Namibia: evidence for Holocene  
364 environmental changes in the southwestern Kalahari based on thermoluminescence data.  
365 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 138(1-4):139–149.
- 366 Bond, W., Woodward, F., and Midgley, G. (2005). The global distribution of ecosystems in a world without  
367 fire. *New Phytologist*, 165(2):525–538.
- 368 Bond, W. J. and Parr, C. L. (2010). Beyond the forest edge: Ecology, diversity and conservation of the  
369 grassy biomes. *Biological Conservation*, 143:2395–2404.
- 370 Bonnefille, R. and Chalié, F. (2000). Pollen-inferred precipitation time-series from equatorial mountains,  
371 Africa, the last 40 kyr BP. *Global and Planetary Change*, 26(1-3):25–50.
- 372 Boom, A., Marchant, R., Hooghiemstra, H., and Sinnenhe Damsté, J. (2002). CO<sub>2</sub>- and temperature-  
373 controlled altitudinal shifts of C4- and C3-dominated grasslands allow reconstruction of  
374 palaeoatmospheric pCO<sub>2</sub>. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 177(1-2):151–168.
- 375 Bowman, D. M., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D'Antonio, C. M.,  
376 Defries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A.,  
377 Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., Swetnam, T. W., van der Werf,  
378 G. R., and Pyne, S. J. (2009). Fire in the earth system. *Science*, 324(5926):481–484.
- 379 Braconnot, P., Joussaume, S., Marti, O., and de Noblet, N. (1999). Synergistic feedbacks from ocean and  
380 vegetation on the African monsoon response to mid-Holocene insolation. *Geophysical Research*  
381 Letters, 26(16):2481–2484.
- 382 Braconnot, P., Harrison, S. P., Kageyama, M., Bartlein, P. J., Masson-Delmotte, V., Abe-Ouchi, A., Otto-  
383 Bliesner, B., and Zhao, Y. (2012). Evaluation of climate models using palaeoclimatic data. *Nature*  
384 *Climate Change*, 2:417–424.
- 385 Bremond, L., Favier, C., Ficetola, G., Tossou, M., Akouégninou, A., Gielly, L., Giguet-Covex, C., Oslisly, R.,  
386 and Salzmann, U. (2017). Five thousand years of tropical lake sediment DNA records from Benin.  
387 *Quaternary Science Reviews*, 170:203–211.
- 388 Brenac, P. (1988). Evolution de la végétation et du climat dans l'Ouest-Cameroun entre 25 000 et 11 000  
389 ans BP, volume 25 of *Trav. Sci., Techn.*, pages 91–103. Actes 10e Symposium APLF.
- 390 Brierley, C., Manning, K., and Maslin, M. (2018). Pastoralism may have delayed the end of the green  
391 Sahara. *Nature communications*, 9(4018).
- 392 Bristow, C. S., Drake, N., and Armitage, S. (2009). Deflation in the dustiest place on earth: the Bodélé  
393 depression, Chad. *Geomorphology*, 105(1-2):50–58.
- 394 Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W.,  
395 Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H., and Guisan, A. (2012). Measuring  
396 ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and*  
397 *Biogeography*, 21:481–497.

- 398 Broennimann, O., Mráz, P., Petitpierre, B., Guisan, A., and Müller-Schärer, H. (2014). Contrasting spatio-  
399 temporal climatic niche dynamics during the eastern and western invasions of spotted knapweed  
400 in north America. *Journal of Biogeography*, 41(6):1126–1136.
- 401 Broennimann, O., Di Cola, V., Petitpierre, B., Breiner, F., Scherrer, D., D'Amen, M., Randin, C., Engler, R.,  
402 Hordijk, W., Mod, H., Pottier, J., Di Febbraro, M., Pellissier, L., Pio, D., Mateo, R. G., Dubuis, A.,  
403 Maiorano, L., Psomas, A., Ndiribe, C., Salamin, N., Zimmermann, N., and Guisan, A. (2018).  
404 *ecospat: spatial ecology miscellaneous methods. R package version 3.0.*
- 405 Brovkin, V., Claussen, M., Petoukhov, V., and Ganopolski, A. (1998). On the stability of the atmosphere-  
406 vegetation system in the Sahara/Sahel region. *JGR Atmospheres*, 103(D24):31613–31624.
- 407 Brncic, T. M., Willis, K. J., Harris, D. J., and Washington, R. (2007). Culture or climate? the relative  
408 influences of past processes on the composition of the lowland Congo rainforest. *Philosophical  
409 Transactions of the Royal Society B*, 362(1478):229–242.
- 410 Burrough, S.L. and Thomas, (2013).Central southern Africa at the time of the African Humid Period: a new  
411 analysis of Holocene palaeoenvironmental and palaeoclimate data. *Quaternary Science Reviews*,  
412 80(15): 29-46.
- 413 Burrough, S. L. and Willis, K. J. (2015). Ecosystem resilience to late-Holocene climate change in the upper  
414 Zambezi Valley. *The Holocene*, 25(11):1811–1828.
- 415 Chase, B. M. and Meadows, M. E. (2007). Late quaternary dynamics of southern Africa's winter rainfall  
416 zone. *Earth-Science Reviews*, 84(3-4):103–138.
- 417 Chase, B. M., Meadows, M. E., Scott, L., Thomas, D. S. G., Marais, E., Sealy, J. and Reimer, P.J. (2009) A  
418 record of rapid Holocene climate change preserved in hyrax middens from southwestern Africa.  
419 *Geology*, 37(8):703-706.
- 420 Chase, B. M., Meadows, M. E., Carr, A. S. and Reimer, P. J. (2010) Evidence for progressive Holocene  
421 aridification in southern Africa recorded in Namibian hyrax middens: Implications for African  
422 Monsoon dynamics and the ``African Humid Period''. *Quaternary Research*, 74(1):36-45.
- 423 Chase, B. M., Boom, A., Carr, A. S., Meadows, M. E., and Reimer, P. J. (2013). Holocene climate change in  
424 southernmost South Africa: rock hyrax middens record shifts in the southern westerlies.  
425 *Quaternary Science Reviews*, 82:199–205.
- 426 Chase, B. M., Boom, A., Carr, A. S., Carré, M., Chevalier, M., Meadows, M. E., Pedro, J. B., Stager, J. C., and  
427 Reimer, P. J. (2015a). Evolving southwest African response to abrupt deglacial north Atlantic  
428 climate change events. *Quaternary Science Reviews*, 121:132–136.
- 429 Chase, B. M., Lim, S., Chevalier, M., Boom, A., Carr, A. S., Meadows, M. E., and Reimer, P. J. (2015b).  
430 Influence of tropical easterlies in southern Africa's winter rainfall zone during the Holocene.  
431 *Quaternary Science Reviews*, 107:138–148.
- 432 Chase, B. M., Chevalier, M., Boom, A., and Carr, A. S. (2017). The dynamic relationship between  
433 temperate and tropical circulation systems across South Africa since the last glacial maximum.  
434 *Quaternary Science Reviews*, 174:54–62.
- 435 Chase, B. M. and Quick, L. J. (2018). Influence of Agulhas forcing of Holocene climate change in South  
436 Africa's Southern Cape. *Quaternary Research*, 90(2):303–309.
- 437 Cheddadi, R., Nourelbait, M., Bouaissa, O., Tabel, J., Rhoujjati, A., López-Sáez, J., Alba-Sánchez, F., Khater,  
438 C., Ballouche, A., Dezileau, L., and Lamb, H. (2015). A history of human impact on Moroccan  
439 mountain landscapes. *African Archaeological Review*, 32(2):233–248.
- 440 Cheddadi, R., Bouaissa, O., Rhoujjati, A., and Dezileau, L. (2016). Environmental changes in the Moroccan  
441 western Rif Mountains over the last 9,000 years. *Quaternaire*, 27(1):15–25.
- 442 Cheddadi, R., Henrot, A., François, L., Boyer, F., Bush, M., Carré, M., Coissac, E., De Oliveira, P., Ficetola, F.,  
443 Hambuckers, A., Huang, K., Lézine, A.-M., Nourelbait, M., Rhoujjati, A., Taberlet, P., Sarmiento, F.,  
Abel-Schaad, D., Alba-Sánchez, F., and Zheng, Z. (2017). Microrefugia, climate change, and

- 445 conservation of *Cedrus atlantica* in the Rif Mountains, Morocco. *Frontiers in Ecology and*  
446 *Evolution*, 5(114):1–15.
- 447 Chevalier, M. and Chase, B. M. (2015). Southeast African records reveal a coherent shift from high- to  
448 low-latitude forcing mechanisms along the East African margin across last glacial–interglacial  
449 transition. *Quaternary Science Reviews*, 125:117–130.
- 450 Chevalier, M., Brewer, S., and Chase, B. M. (2017). Qualitative assessment of pmip3 rainfall simulations  
451 across the eastern African monsoon domains during the mid-Holocene and the last glacial  
452 maximum. *Quaternary Science Reviews*, 156:107–120.
- 453 Claussen, M. (1997). Modeling bio-geophysical feedback in the African and Indian monsoon region.  
454 *Climate Dynamics*, 13(4):247–257.
- 455 Claussen, M., Kubatzki, C., Brovkin, V., Ganopolski, A., Hoelzmann, P., and Pachur, H.-J. (1999). Simulation  
456 of an abrupt change in Saharan vegetation in the mid-Holocene. *Geophysical Research Letters*,  
457 26(14):2037–2040.
- 458 Clist, B., Bostoen, K., de Maret, P., Eggert, M. K., Höhn, A., Mindzié, C. M., Neumann, K., and  
459 Seidensticker, D. (2018). Did human activity really trigger the late Holocene rainforest crisis in  
460 central Africa. *PNAS*, 115(21):E4733–E4734.
- 461 Cordova, C. E., Scott, L., Chase, B. M., and Chevalier, M. (2017). Late Pleistocene-Holocene vegetation and  
462 climate change in the middle Kalahari, Lake Ngami, Botswana. *Quaternary Science Reviews*,  
463 171:199–215.
- 464 Courtney Mustaphi, C. J., Gajewski, K., Marchant, R., and Rosqvist, G. (2017). A late Holocene pollen  
465 record from proglacial oblong tarn, mount Kenya. *PLOS ONE*, 12(9):e0184925.
- 466 Crisp, M. D., Arroyo, M. T., Book, L. G., Gandolfo, M. A., Jordan, G. J., McGlone, M. S., Weston, P. H.,  
467 Westoby, M., Wilf, P., and Linder, H. P. (2009). Phylogenetic biome conservatism on a global scale.  
468 *Nature*, 458:754–756.
- 469 Dallmeyer, A., Claussen, M., and Brovkin, V. (2019). Harmonising plant functional type distributions for  
470 evaluating earth system models. *Climate of the Past*, 15:335–366.
- 471 Dantas, V. d. L., Hirota, M., Oliveira, R. S., and Pausas, J. G. (2016). Disturbance maintains alternative  
472 biomes states. *Ecology Letters*, 19(1):12–19.
- 473 D'Antonio, C. M. and Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle,  
474 and global change. *Annual Review of Ecology and Systematics*, 23:63–87.
- 475 deMenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., and Yarusinsky, M. (2000).  
476 Abrupt onset and termination of the African humid period:: rapid climate responses to gradual  
477 insolation forcing. *Quaternary Science Reviews*, 19(1-5):347–361.
- 478 Du Toit, J. and Cumming, D. (1999). Functional significance of ungulate diversity in African savannas and  
479 the ecological implications of the spread of pastoralism. *Biodiversity Conservation*, 8(12):1643–  
480 1661.
- 481 Dupont, L., Behling, H., and Kim, J.-H. (2008). Thirty thousand years of vegetation development and  
482 climate change in Angola (ocean drilling program site 1078). *Climate of the Past*, 4(2):107–124.
- 483 Eggermont, H., Verschuren, D., Fagot, M., Rumes, B., Van Bocxlaer, B., and Kröpelin, S. (2008). Aquatic  
484 community response in a groundwater-fed desert lake to Holocene desiccation of the Sahara.  
485 *Quaternary Science Reviews*, 27(25-26):2411–2425.
- 486 Elenga, H., Schwartz, D., Vincens, A., Bertiaux, J., Denamur, C., Martin, L., Wirrmann, D., and Serrant, M.  
487 (1996). Diagramme pollinique holocène du lac Kitina (Congo): mise en évidence de changements  
488 paléobotaniques et paléoclimatiques dans le massif forestier du Mayombe, volume 323 of *Série 2.*  
489 *Sciences de la Terre et des Planètes*, pages 403–410. *Comptes Rendus de l'Academie des Sciences*.
- 490 Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., Andrieu, V., Bottema, S., Buchet, G.,  
491 De Beaulieu, J.-L., Hamilton, A.C., Maley, J., Marchant, R., Perez-Obiol, R., Reille, M., Riollet, G.,

- 492 Scott, L., Straka, H., Taylor, D., Van Campo, E., Vincens, A., Laarif, F. and Jonson, H. (2000) Pollen-  
493 based biome reconstruction for southern Europe and Africa 18,000 yr BP. *Journal of*  
494 *Biogeography*, 27(3):621-634.
- 495 Elith, J., Kearney, M., and Phillips, S. (2010). The art of modelling range-shifting species. *Methods in*  
496 *Ecology and Evolution*, 1(4):330–342.
- 497 Eriksen, S. and Watson, H. (2009). The dynamic context of southern African savannas: investigating  
498 emerging threats and opportunities to sustainability. *Environmental Science Policy*, 12(1):5–22.
- 499 Faith, J. T., Chase, B. M., and Avery, D. M. (2018). Late quaternary micromammals and the precipitation  
500 history of the southern cape, South Africa. *Quaternary Research*, pages 1–13.
- 501 Farmer, E., deMenocal, P., and Marchitto, T. (2005). Holocene and deglacial ocean temperature variability  
502 in the Benguela upwelling region: implications for low-latitude atmospheric circulation.  
503 *Palaeoceanography*, 20.
- 504 Favier, C., Aleman, J., Bremond, L., Dubois, M. A., Freycon, V., and Yangakola, J.-M. (2012). Abrupt shifts  
505 in African savanna tree cover along a climatic gradient. *Global Ecology and Biogeography*,  
506 21(8):787–797.
- 507 Finch, J., Marchant, R., and Courtney Mustaphi, C. J. (2017). Ecosystem change in the south pare  
508 mountain bloc, eastern arc mountains of Tanzania. *The Holocene*, 27(6):796–810.
- 509 Fleitmann, D., Burns, S. J., Mudelsee, M., Neff, U., Kramers, J., Mangini, A., and Matter, A. (2003).  
510 Holocene forcing of the Indian monsoon recorded in a stalagmite from southern Oman. *Science*,  
511 300(5626):1737–1739.
- 512 Foley, J. A., Levis, S., Prentice, I. C., Pollard, D., and Thompson, S. L. (1998). Coupling dynamic models of  
513 climate and vegetation. *Global Change Biology*, 4(5):561–579.
- 514 Francus, P., von Suchodoletz, H., Dietze, M., Donner, R. V., Vouchard, F., Roy, A.-J., Fagot, M., Verschuren,  
515 D., and Kröpelin, S. (2013). Varved sediments of Lake Yoa (Ounianga Kebir, Chad) reveal  
516 progressive drying of the Sahara during the last 6100 years. *Sedimentology*, 60(4):911–934.
- 517 Fyfe, R. M., de Beaulieu, J.-L., Binney, H., Bradshaw, R. H., Brewer, S., Le Flao, A., Finsinger, W., Gaillard,  
518 M.-J., Giesecke, T., Gil-Romera, G., Grimm, E. C., Huntley, B., Kunes, P., Kühl, N., Leydet, M., Lotter,  
519 A. F., Tarasov, P. E., and Tonkov, S. (2009). The european pollen database: past efforts and current  
520 activities. *Vegetation History and Archaeobotany*, 18(5):417–424.
- 521 Ganopolski, A., Kubatzki, C., Claussen, M., Brovkin, V., and Petoukhov, V. (1998). The influence of  
522 vegetation-atmosphere-ocean interaction on climate during the mid-Holocene. *Science*,  
523 280:1916–1919.
- 524 Garcin, Y., Deschamps, P., Ménot, G., de Saulieu, G., Schefuß, E., Sebag, D., Dupont, L. M., Oslisly, R.,  
525 Brademann, B., Mbusnum, K. G., Onana, J.-M., Ako, A. A., Epp, L. S., Tjallingii, R., Strecker, M. R.,  
526 Brauer, A., and Sachse, D. (2018). Early anthropogenic impact on western central African  
527 rainforests 2,600 y ago. *PNAS*, 115(13):3261–3266.
- 528 Gasse, F. (2000). Hydrological changes in the African tropics since the last glacial maximum. *Quaternary*  
529 *Science Reviews*, 19(1-5):189–211.
- 530 Gillson, L. (2004). Evidence of hierarchical patch dynamics in an East African savanna. *Landscape Ecology*,  
531 19(8):883–894.
- 532 Giresse, P., Maley, J., and Brenac, P. (1994). Late quaternary palaeoenvironments in the lake Barombi  
533 Mbo (west Cameroon) deduced from pollen and carbon isotopes of organic matter.  
534 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 107(1-2):65–78.
- 535 Goring, S., Lacourse, T., Pellatt, M. G., and Mathewes, R. W. (2013). Pollen assemblage richness does not  
536 reflect regional plant species richness: a cautionary tale. *Journal of Ecology*, 101(5):1137–1145.
- 537 Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C., and Kueffer, C. (2014). Unifying niche shift  
538 studies: insights from biological invasions. *Trends in Ecology and Evolution*, 29(5):260–269.

- 539 Haberyan, K.A. (2018). A >22,000 yr diatom record from the plateau of Zambia. *Quaternary Research*,  
540 89(1):33–42.
- 541 Hamilton, A. (1982). *Environmental History of East Africa*. Academic Press, New York.
- 542 Harrison, S. P., Bartlein, P., Brewer, S., Prentice, L., Boyd, M., Hessler, I., Holmgren, K., Izumi, K., and Willis,  
543 K. (2014). Climate model benchmarking with glacial and mid-Holocene climates. *Climate  
544 Dynamics*, 43(3–4):671–688.
- 545 Harrison, S. P., Bartlein, P., Izumi, K., Li, G., Annan, J., Hargreaves, J., Braconnot, P., and Kageyama, M.  
546 (2015). Evaluation of cmip5 palaeo-simulations to improve climate projections. *Nature Climate  
547 Change*, 5:735–743.
- 548 Haug, G. H., Hughen, K. A., Sigman, D. M., Peterson, L. C., and Röhl, U. (2001). Southward migration of the  
549 intertropical convergence zone through the Holocene. *Science*, 293(5533):1304–1308.
- 550 Hély, C., Braconnot, P., Watrin, J., and Zheng, W. (2009). Climate and vegetation: simulating the African  
551 humid period. *Comptes Rendus Geoscience*, 341(8–9):671–688.
- 552 Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., Kruger, L. M., Moxley, C.,  
553 Owen-Smith, N., Peel, M. J., Smit, I. P., and Vickers, K. J. (2015). Ecology of grazing lawns in Africa.  
554 *Biological Reviews*, 90(3):979–994.
- 555 Hempson, G. P., Archibald, S., Donaldson, J. E., and Lehmann, C. E. (2019). Alternate grassy ecosystem  
556 states are determined by palatability-flammability trade-offs. *Trends in Ecology and Evolution*, in  
557 press. <https://doi.org/10.1016/j.tree.2019.01.007>
- 558 Hirota, M., Holmgren, M., Van Nes, E. H., and Scheffer, M. (2011). Global resilience of tropical forest and  
559 savanna to critical transitions. *Science*, 334(6053):232–235.
- 560 Hoelzmann, P., Jolly, D., Harrison, S., Laarif, F., Bonnefille, R., and Pachur, H.-J. (1998). Mid-Holocene land-  
561 surface conditions in northern Africa and the Arabian peninsula: a data set for the analysis of  
562 biogeophysical feedbacks in the climate system. *Global Biogeochemical Cycles*, 12(1):35–51.
- 563 Hoelzmann, P., Gasse, F., Dupont, L. M., Salzmann, U., Staubwasser, M., Leuschner, D. C., and Sirocko, F.  
564 (2004). *Past Climate Variability through Europe and Africa*, volume 6 of *Developments in  
565 Paleoenvironmental Research*, chapter Palaeoenvironmental changes in the arid and sub arid belt  
566 (Sahara-Sahel-Arabian Peninsula) from 150 kyr to present. Springer, Dordrecht.
- 567 Holmgren, K., Karlén, W., Lauritzen, S., Lee-Thorp, J., Partridge, T., Piketh, S., Repinski, P., Stevenson, C.,  
568 Svanered, O., and Tyson, P. (1999). A 3000-year high-resolution stalagmite based record of  
569 palaeoclimate for northeastern South Africa. *The Holocene*, 9(3):295–309.
- 570 Holmgren, K., Lee-Thorp, J. A., Cooper, G. R., Lundblad, K., Partridge, T. C., Scott, L., Sithaldeen, R., Talma,  
571 A. S., and Tyson, P. D. (2003). Persistent millennial-scale climatic variability over the past  
572 persistent millennial-scale climatic variability over the past 25,000 years in southern Africa.  
573 *Quaternary Science Reviews*, 22:2311–2326.
- 574 Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary  
575 perspectives. *PNAS*, 106(2):19659–19665.
- 576 Jolly, D. and Haxeltine, A. (1997). Effect of low glacial atmospheric CO<sub>2</sub> on tropical African montane  
577 vegetation. *Science*, 276(5313):786–788.
- 578 Jolly, D., Taylor, D., Marchant, R., Hamilton, A., Bonnefille, R., Buchet, G., and Riollet, G. (1997).  
579 Vegetation dynamics in central Africa since 18,000 yr BP: pollen records from the interlacustrine  
580 highlands of Burundi, Rwanda and western Uganda. *Journal of Biogeography*, 24(4):492–512.
- 581 Jolly, D., Harrison, S., Damnati, B., and Bonnefille, R. (1998a). Simulated climate and biomes of Africa  
582 during the late quaternary: comparison with pollen and lake status data. *Quaternary Science  
583 Reviews*, 17(6–7):629–657.
- 584 Jolly, D., Prentice, I. C., Bonnefille, R., Ballouche, A., Bengo, M., Brenac, P., Buchet, G., Burney, D., Cazet,  
585 J.-P., Cheddadi, R., Edorh, T., Elenga, H., Elmoutaki, S., Guiot, J., Laarif, F., Lamb, H., Lézine, A.-M.,

- 586 Maley, J., Mbenza, M., Peyron, O., Reille, M., Reynaud-Farrera, I., Riollet, G., Ritchie, J. C., Roche,  
587 E., Scott, L., Ssemmanda, I., Straka, H., Umer, M., Van Campo, E., Vilimumbalo, S., Vincens, A., and  
588 Waller, M. (1998b). Biome reconstruction from pollen and plant macrofossil data for Africa and  
589 the Arabian peninsula at 0 and 6000 years. *Journal of Biogeography*, 25(6):1007–1027.
- 590 Jousse, H. (2017). *Atlas of mammal distribution through Africa from the LGM (18 ka) to modern times: the zoological record*. Archaeopress Publishing LTD, Oxford, UK.
- 591 Keenan, T. F., Hollinger, D. Y., Bohrer, G., Dragoni, D., Munger, J. W., Schmid, H. P., and Richardson, A. D.  
592 (2013). Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature*, 499:324–327.
- 593 Kéfi, S., Holmgren, M., and Scheffer, M. (2016). When can positive interactions cause alternative stable  
594 states in ecosystems? *Functional Ecology*, 30(1):88–97.
- 595 Kiage, L. M. and Liu, K.-b. (2006). Late quaternary paleoenvironmental changes in East Africa: a review of  
596 multiproxy evidence from palynology, lake sediments, and associated records. *Progress in Physical  
597 Geography: Earth and Environment*, 30(5):633–658.
- 598 Knorr, W. and Schulz, J.-P. (2001). Using satellite data assimilation to infer global soil moisture status and  
599 vegetation feedback to climate (pp. 273–306). In Beniston, M. and Verstraete, M. (Eds.), *Remote  
600 Sensing and climate modeling: Synergies and Limitations*. Dordrecht: Springer.
- 601 Konecky, B. L., Russell, J. M., Johnson, T. C., Brown, E. T., Berke, M. A., Werne, J. P., and Huang, Y. (2011).  
602 Atmospheric circulation patterns during late Pleistocene climate changes at lake Malawi, Africa.  
603 *Earth and Planetary Science Letters*, 312(3-4):318–326.
- 604 Krinner, G., Lézine, A.-M., Braconnot, P., Sepulchre, P., Ramstein, G., Grenier, C., and Gouttevin, I. (2012).  
605 A reassessment of lake and wetland feedbacks on the North African Holocene climate.  
606 *Geophysical Research Letters*, 39(L07701):1–6.
- 607 Kröpelin, S., Verschuren, D., Lézine, A.-M., Eggermont, H., Cocquyt, C., Francus, P., Cazet, J.-P., Fagot, M.,  
608 Rumes, B., Russel, J., Darius, F., Conley, D., Schuster, M., von Suchodoletz, H., and Engstrom, D.  
609 (2008). Climate-driven ecosystem succession in the Sahara: The past 6000 years. *Science*,  
610 320(5877):765–768.
- 611 Kull, C. A. and Laris, P. (2009). Tropical fire ecology: climate change, land use, and ecosystem dynamics,  
612 chapter Fire ecology and fire politics in Mali and Madagascar, pages 171–226. Springer-Praxis,  
613 Heidelberg.
- 614 Kuper, R. and Kröpelin, S. (2006). Climate-controlled Holocene occupation in the Sahara: motor of Africa's  
615 evolution. *Science*, 313(5788):803–7.
- 616 Kutzbach, J., Bonan, G., Foley, J., and Harrison, S. (1996). Vegetation and soil feedbacks on the response  
617 of the African monsoon to orbital forcing in the early to middle Holocene. *Nature*, 384:623–626.
- 618 Lebamba, J., Ngomanda, A., Vincens, A., Jolly, D., Favier, C., Elenga, H., and Bentaleb, I. (2009). Central  
619 African biomes and forest succession stages derived from modern pollen data and plant functional  
620 types. *Climate of the Past*, 5:403–429.
- 621 Lebamba, J., Vincens, A., Lézine, A.-M., Marchant, R., and Buchet, G. (2016). Forest-savannah dynamics on  
622 the Adamawa Plateau (central Cameroon) during the “African humid period” termination: A new  
623 high-resolution pollen record from Lake Tizong. *Review of Palaeobotany and Palynology*, 235:129–  
624 139.
- 625 Lézine, A.-M. (2009). Timing of vegetation changes at the end of the Holocene humid period in desert  
626 areas at the northern edge of the Atlantic and Indian monsoon systems. *Comptes Rendus  
627 Geoscience*, 341(8-9):750–759.
- 628 Lézine, A.-M., Watrin, J., Vincens, A. and Hély, C. (2009). Are modern pollen data representative of west  
629 African vegetation? *Review of Palaeobotany and Palynology*, 156(3-4):265–276.

- 532 Lézine, A.-M., Hély, C., Grenier, C., Braconnot, P., and Krinner, G. (2011). Sahara and Sahel vulnerability to  
533 climate changes, lessons from Holocene hydrological data. *Quaternary Science Reviews*, 30(21-  
534 22):3001–3012.
- 535 Lézine, A.-M., Assi-Kaudjhis, C., Roche, E., and Vincens, Annie Achoundong, G. (2013). Towards an  
536 understanding of West African montane forest response to climate change. *Journal of*  
537 *Biogeography*, 40:183–196.
- 538 Lézine, A.-M., Izumi, K., Kageyama, M., and Achoundong, G. (2019). A 90,000-year record of Afromontane  
539 forest responses to climate change. *Science*, 363(6423):177–181.
- 540 Lim, S., Chase, B. M., Chevalier, M., and Reimer, P. J. (2016). 50,000 years of vegetation and climate  
541 change in the southern Namib Desert, Pella, South Africa. *Palaeogeography, Palaeoclimatology,*  
542 *Palaeoecology*, 451:197–209.
- 543 Liu, Z., Wang, Y., Gallimore, R., Gasse, F., Johnson, T., deMenocal, P., Adkins, J., Notaro, M., Prentice, I.,  
544 Kutzbach, J., Jacob, R., Behling, P., Wang, L., and Ong, E. (2007). Simulating the transient evolution  
545 and abrupt change of northern Africa atmosphere–ocean–terrestrial ecosystem in the Holocene.  
546 *Quaternary Science Reviews*, 26(13-14):1818–1837.
- 547 Maiorano, L., Cheddadi, R., Zimmermann, N. E., Pellissier, L., Petitpierre, B., Pottier, J., Laborde, H., Hurdu,  
548 B. I., Pearman, P. B., Psomas, A., Singarayer, J. S., Broennimann, O., Vittoz, P., Dubuis, A., Edwards,  
549 M. E., Binney, H. A., and Guisan, A. (2013). Building the niche through time: using 13,000 years of  
550 data to predict the effects of climate change on three tree species in Europe. *Global Ecology and*  
551 *Biogeography*, 22(3):302–317.
- 552 Maley, J. (1991). The African rain forest vegetation and palaeoenvironments during late quaternary.  
553 *Climatic Change*, 19(1-2):79–98.
- 554 Maley, J. and Brenac, P. (1998). Vegetation dynamics, palaeoenvironments and climatic changes in the  
555 forests of western Cameroon during the last 28,000 years B.P. *Review of Palaeobotany and*  
556 *Palynology*, 99(2):157–187.
- 557 Manning, K. and Timpson, A. (2014). The demographic response to Holocene climate change in the  
558 Sahara. *Quaternary Science Reviews*, 101:28–35.
- 559 Marchant, R. and Hooghiemstra, H. (2004). Rapid environmental change in African and south American  
560 tropics around 4000 years before present: a review. *Earth-Science Reviews*, 66(3-4):217–260.
- 561 Marchant, R., Richer, S., Boles, O., Capitani, C., Courtney-Mustaphi, C. J., Lane, P., Prendergast, M. E.,  
562 Stump, D., De Cort, G., Kaplan, J. O., Phelps, L., Kay, A., Olago, D., Petek, N., Platts, P. J., Punwong,  
563 P., Widgren, M., Wynne-Jones, S., Ferro-Vázquez, C., Benard, J., Boivin, N., Crowther, A., Cuní-  
564 Sanchez, A., Deere, N. J., Ekblom, A., Farmer, J., Finch, J., Fuller, D., Gaillard-Lemdahl, M.-J.,  
565 Gillson, L., Githumbi, E., Kabora, T., Kariuki, R., Kinyanjui, R., Kyazike, E., Lang, C., Lejju, J.,  
566 Morrison, K. D., Muiruri, V., Mumbi, C., Muthoni, R., Muzuka, A., Ndiema, E., Nzabandora, C. K.,  
567 Onjala, I., Pas Schrijver, A., Rucina, S., Shoemaker, A., Thornton-Barnett, S., van der Plas, G.,  
568 Watson, E. E., Williamson, D., and Wright, D. (2018). Drivers and trajectories of land cover change  
569 in East Africa: human and environmental interactions from 6000 years ago to present. *Earth-*  
570 *Science Reviews*, 178:322–378.
- 571 Mbida, C. M., Van Neer, W., Doutrelepont, H. and Vrydaghs, L. (2000) Evidence for banana cultivation and  
572 animal husbandry during the first millennium BC in the forest of southern Cameroon. *Journal of*  
573 *Archaeological Science*, 27(2):151-162.
- 574 McNaughton, S. (1984). Grazing lawns: animals in herds, plant form, and coevolution. *The American*  
575 *Naturalist*, 124(6):863–886.
- 576 Metwally, A., Scott, L., Neumann, F. H., Bamford, M., and Oberhänsli, H. (2014). Holocene palynology and  
577 palaeoenvironments in the savanna biome at Tswaing Crater, central South Africa.  
578 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 402:125–135.

- 579 Miller, C. S. and Gosling, W. D. (2014). Quaternary forest associations in lowland tropical West Africa.  
580       *Quaternary Science Reviews*, 84:7–25.
- 581 Msaky, E. S., Livingstone, D., and Davis, O. K. (2005). Paleolimnological investigations of anthropogenic  
582       environmental change in Lake Tanganyika: V. palynological evidence for deforestation and  
583       increased erosion. *Journal of Paleolimnology*, 34(1):73–83.
- 584 Muchura, H. M., Chua, M. S., Mworia, J. K., and Gichuki, N. (2014). Role of bryophytes and tree canopy in  
585       mist trapping in Mt. Marsabit Forest. *Journal of Environment and Earth Science*, 4(21):2224–3216.
- 586 Mulitza, S., Prange, M., Stuut, J.-B., Zabel, M., von Dobeneck, T., Itambi, A. C., Nizou, J., Schulz, M., and  
587       Wefer, G. (2008). Sahel megadroughts triggered by glacial slowdowns of Atlantic meridional  
588       overturning. *Paleoceanography and Paleoclimatology*, 23(4):1–11.
- 589 Neumann, K., Bostoen, K., Höhn, A., Kahlheber, S., Ngomanda, A., and Tchiengué, B. (2012). First farmers  
590       in the central African rainforest: a view from southern Cameroon. *Quaternary International*,  
591       249:53–62.
- 592 Ngomanda, A., Jolly, D., Bentaleb, I., Chepstow-Lusty, A., Makaya, M., Maley, J., Fontugne, M., Oslisly, R.,  
593       and Rabenkogo, N. (2007). Lowland rainforest response to hydrological changes during the last  
594       1500 years in Gabon, western equatorial Africa. *Quaternary Research*, 67(3):411–425.
- 595 Ngomanda, A., Chepstow-Lusty, A., Makaya, M., Favier, C., Schevin, P., Maley, J., Fontugne, M., Oslisly, R.,  
596       and Jolly, D. (2009a). Western equatorial African forest-savanna mosaics: a legacy of late Holocene  
597       climatic change? *Climate of the Past*, 5:647–659.
- 598 Ngomanda, A., Neumann, K., Schweizer, A., and Maley, J. (2009b). Seasonality change and the third  
599       millennium BP rainforest crisis in southern Cameroon (central Africa). *Quaternary Research*,  
600       71(3):307–318.
- 601 Nguetsop, V. F., Servant-Vildary, S., and Servant, M. (2004). Late Holocene climatic changes in West  
602       Africa, a high resolution diatom record from equatorial Cameroon. *Quaternary Science Reviews*,  
603       23(5-6):591–609.
- 604 Nogues-Bravo, D. (2009). Predicting the past distribution of species climatic niches. *Global Ecology and  
605       Biogeography*, 18(5):521–531.
- 606 Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H.  
607       R., Moore, D. J., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac,  
608       M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R. (2005). Forest  
609       response to elevated CO<sub>2</sub> is conserved across a broad range of productivity. *PNAS*,  
610       102(50):18052–18056.
- 611 O'Connor, P. and Thomas, D. (1999). The timing and environmental significance of late quaternary linear  
612       dune development in western Zambia. *Quaternary Research*, 52(1):44–55.
- 613 Oliveras, I. and Malhi, Y. (2016). Many shades of green: the dynamic tropical forest-savannah transition  
614       zones. *Philosophical Transactions of the Royal Society B*, 371(1703):1–15.
- 615 Parnell, A.C., Haslett, J., Allen, J.R., Buck, C.E. and Huntley, B., 2008. A flexible approach to assessing  
616       synchronicity of past events using Bayesian reconstructions of sedimentation history. *Quaternary  
617       Science Reviews*, 27(19-20), pp.1872–1885.
- 618 Pearman, P. B., Guisan, A., Broennimann, O., and Randin, C. F. (2008). Niche dynamics in space and time.  
619       *Trends in Ecology and Evolution*, 23(3):149–158.
- 620 Pellikka, P., Heikinheimo, V., Hietanen, J., Schäfer, E., Siljander, M., and Heiskanen, J. (2018). Impact of  
621       land cover change on aboveground carbon stocks in Afromontane landscape in Kenya. *Applied  
622       Geography*, 94:178–189.
- 623 Perez-Sanz, A., Li, G., González-Sampériz, P., and Harrison, S. P. (2014). Evaluation of modern and mid-  
624       Holocene seasonal precipitation of the Mediterranean and northern Africa in the cmip5  
625       simulations. *Climate of the Past*, 10(2):551–568.

- Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C., and Guisan, A. (2012). Climatic niche shifts are rare among terrestrial plant invaders. *Science*, 335(6074):1344–1348.
- Phelps, L. N. and Kaplan, J. O. (2017). Land use for animal production in global change studies: Defining and characterizing a framework. *Global Change Biology*, 23(11).
- Phelps, L. N., Broennimann, O., Manning, K., Timpson, A., Mariethoz, G., Jousse, H., Fordham, Damien, A., Shanahan, T. M., Davis, B. A., and Guisan, A. (2020). Reconstructing climatic niche breadth of land use for animal production during the African Holocene. *Global Ecology and Biogeography*.
- Phelps, L.N., Chevalier, M., Shanahan, T. M., Aleman, J. C., Olivier, B., Courtney-Mustaphi, C., ... Guisan, A. (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., Chevalier, M., Shanahan, T. M., Aleman, J. C., Olivier, B., Courtney-Mustaphi, C., ... Guisan, A. (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>.
- Phillipson, D.W. (2005). African Archaeology. Cambridge University Press, Cambridge.
- Platts, P. J., Gereau, R. E., Burgess, N. D., and Marchant, R. (2013). Spatial heterogeneity of climate change in an Afromontane centre of endemism. *Ecography*, 36(4):518–530.
- Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., and Solomon, A. M. (1992). A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, 19(2):117–134.
- Prentice, C., Guiot, J., Huntley, B., Jolly, D., and Cheddadi, R. (1996). Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. *Climate Dynamics*, 12(3):185–194.
- Prentice, I. C. and Webb III, T. (1998). Biome 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological records. *Journal of Biogeography*, 25(6):997–1005.
- Prentice, I. C. and Harison, S. P. (2009) Ecosystem effects of CO<sub>2</sub> concentration: evidence from past climates. *Climate of the Past*, 5:297–307.
- Quick, L. J., Chase, B. M., Wündsch, M., Kirsten, K. L., Chevalier, M., Mäusbacher, R., Meadows, M. E., and Haberzetti, T. (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. *Journal of Quaternary Science*, 33(5):487–500.
- Quick, L. J., Meadows, M. E., Bateman, M. D., Kirsten, K. L., Mäusbacher, R., Haberzetti, T., and Chase, B. M. (2016). Vegetation and climate dynamics during the last glacial period in the Fynbos afrotemperate forest ecotone, Southern Cape, South Africa. *Quaternary International*, 404(Part B):136–149.
- Renssen, H., Brovkin, V., Fichefet, T., and Goosse, H. (2003). Holocene climate instability during the termination of the African humid period. *Geophysical Research Letters*, 30(4).
- Renssen, H., Brovkin, V., Fichefet, T., and Goosse, H. (2006). Simulation of the Holocene climate evolution in northern Africa: The termination of the African humid period. *Quaternary International*, 150(1):95–102.
- Reynaud-Farrera, I., Maley, J., and Wirrmann, D. (1996). Végétation et climat dans les forêts du Sud-Ouest Cameroun depuis 4770 ans BP: analyse pollinique des sédiments du Lac Ossa, volume 322 of série 2, pages 749–755. *Comptes Rendus de l'Academie des Sciences Paris*.

- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., and Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169:156–173.
- Roos, C. I., Zedeño, M. N., Hollenback, K. L., and Erlick, M. M. (2018). Indigenous impacts on North American Great Plains fire regimes of the past millennium. *PNAS*, 115(32):8143–8148.
- Rosenfeld, D., Rudich, Y., and Lahav, R. (2001). Desert dust suppressing precipitation: a possible desertification feedback loop. *PNAS*, 98(11):5975–5980.
- Rucina, S. M., Muiruri, V. M., Kinyanjui, R. N., McGuiness, K., and Marchant, R. (2009). Late quaternary vegetation and fire dynamics on mount Kenya. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 283(1-2):1–14.
- Salzmann, U. (2000). Are modern savannas degraded forests? A Holocene pollen record from the Sudanian vegetation zone of ne Nigeria. *Vegetation History and Archaeobotany*, 9(1):1–15.
- Salzmann, U., Hoelzmann, P., and Morczinek, I. (2002). Late quaternary climate and vegetation of the Sudanian zone of northeast Nigeria. *Quaternary Research*, 58(1):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. *The Holocene*, 15(2):190–199.
- Sánchez Goñi, M. F., Desprat, S., Daniau, A.-L., Bassinot, F. C., Polanco-Martínez, J. M., Harrison, S. P., Allen, J. R., Anderson, S., Behling, H., Bonnefille, R., Burjachs, F., Carrión, J. S., Cheddadi, R., Clark, J. S., Combourieu-Nebout, N., Courtney Mustaphi, C. J., Debusk, G. H., Dupont, L. M., Finch, J. M., Fletcher, W. J., Giardini, M., González, C., Gosling, W. D., Grigg, L. D., Grimm, E. C., Hayashi, R., Helmens, K., Heusser, L. E., Hill, T., Hope, G., Huntley, B., Igarashi, Y., Irino, T., Jacobs, B., Jiménez-Moreno, G., Kawai, S., Kershaw, A. P., Kumon, F., Lawson, I. T., Ledru, M.-P., Lézine, A.-M., Liew, P. M., Magri, D., Marchant, R., Margari, V., Mayle, F. E., McKenzie, G. M., Moss, P., Müller, S., Müller, U. C., Naughton, F., Newnham, R. M., Oba, T., Pérez-Obiol, R., Pini, R., Ravazzi, C., Roucoux, K. H., Rucina, S. M., Scott, L., Takahara, H., Tzedakis, P. C., Urrego, D. H., van Geel, B., Valencia, B. G., Vandergoes, M. J., Vincens, A., Whitlock, C. L., Willard, D. A., and Yamamoto, M. (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 System Science Data*, 9:679–695.
- Scheffer, M. and Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, 18(12):648–656.
- Schefuß, E., Kuhlmann, H., Mollenhauer, G., Prange, M., and Pätzold, J. (2011). Forcing of wet phases in southeast Africa over the past 17,000 years. *Nature*, 480:509–512.
- Scott, L., Cooremans, B., de Wet, J., and Vogel, J. (1991). Holocene environmental changes in Namibia inferred from pollen analysis of swamp and lake deposits. *The Holocene*, 1(1):8–13.
- Shanahan, T. M., Beck, J. W., Overpeck, J. T., McKay, N. P., Pigati, J. S., Peck, J. A., Scholz, C. A., Heil Jr, C. W., and King, J. (2012). Late quaternary sedimentological and climate changes at lake Bosumtwi Ghana: new constraints from laminae analysis and radiocarbon age modeling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 361-362:49–60.
- Shanahan, T. M., McKay, N. P., Hughen, K. A., Overpeck, J. T., Otto-Bliesner, B., Heil, C. W., King, J., Scholz, C. A., and Peck, J. (2015). The time-transgressive termination of the African humid period. *Nature Geoscience*, 8:140–144.
- Solomon, A. M. and Silkworth, A. B. (1986). Spatial patterns of atmospheric pollen transport in a montane region. *Quaternary Research*, 25(2):150–162.
- Stager, J. C., Ryves, D. B., Chase, B. M., and Pausata, F. S. (2011). Catastrophic drought in the Afro-Asian monsoon region during Heinrich Event 1. *Science*, 331(6022):1299–1302.
- Staver, C. A., Archibald, S., and Levin, S. (2011a). Tree cover in sub-Saharan Africa: rainfall and fire constrain forest and savanna as alternative stable states. *Ecology*, 92(5):1063–1072.

- 318 Staver, C. A., Archibald, S., and Levin, S. A. (2011b). The global extent and determinants of savanna and  
319 forest as alternative biome states. *Science*, 334(6053):230–232.
- 320 Steffen, W. L. (1996). A periodic table for ecology? a chemist's view of plant functional types. *Journal of  
321 Vegetation Science*, 7:425–430.
- 322 Stokes, S., Thomas, D. S., and Shaw, P. A. (1997a). New chronological evidence for the nature and timing  
323 of linear dune development in the southwest Kalahari Desert. *Geomorphology*, 20(1-2):81–93.
- 324 Stokes, S., Thomas, D. S., and Washington, R. (1997b). Multiple episodes of aridity in southern Africa since  
325 the multiple episodes of aridity in southern Africa since the last interglacial period. *Nature*,  
326 388:154–158.
- 327 Telfer, M. and Thomas, D. (2007). Late quaternary linear dune accumulation and chronostratigraphy of  
328 the southwestern Kalahari: implications for aeolian palaeoclimatic reconstructions and predictions  
329 of future dynamics. *Quaternary Science Reviews*, 26(19-21):2617–2630.
- 330 Thompson, L. G., Mosley-Thompson, E., Davis, M. E., Henderson, K. A., Brecher, H. H., Zagorodnov, V. S.,  
331 Mashottta, T. A., Lin, P.-N., Mikhaleko, V. N., Hardy, D. R., and Beer, J. (2002). Kilimanjaro ice core  
332 records: evidence of Holocene climate change in tropical Africa. *Science*, 298(5593):589–593.
- 333 Tierney, J. E., Russell, J. M., Huang, Y., Sinnenhe Damsté, J. S., Hopmans, E. C., and Cohen, A. S. (2008).  
334 Northern hemisphere controls on tropical southeast African climate during the past 60,000 years.  
335 *Science*, 322(5899):252–255.
- 336 Tierney, J. E., Russell, J. M., and Huang, Y. (2010). A molecular perspective on late quaternary climate and  
337 vegetation change in the Lake Tanganyika Basin, East Africa. *Quaternary Science Reviews*, 29(5-  
338 6):787–800.
- 339 Tierney, J. E., Russell, J. M., Sinnenhe Damsté, J. S., Huang, Y., and Verschuren, D. (2011). Late quaternary  
340 behavior of the East African monsoon and the importance of the Congo air boundary. *Quaternary  
341 Science Reviews*, 30(7-8):798–807.
- 342 Tierney, J. E. and deMenocal, P. B. (2013). Abrupt shifts in horn of Africa hydroclimate since the last  
343 glacial maximum. *Science*, 342(6160):843–846.
- 344 Tierney, J. E., Pausata, F. S., and deMenocal, P. B. (2017). Rainfall regimes of the green Sahara. *Science  
345 Advances*, 3(1):e1601503.
- 346 Tingley, R., Vallinoto, M., Sequeira, F., and Kearney, M. R. (2014). Realized niche shift during a global  
347 biological invasion. *PNAS*, 111(28):10233–10238.
- 348 Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming D., and Duncan, P. (2011). Elephant-induced  
349 structural changes in the vegetation and habitat selection by large herbivores in an African  
350 savanna. *Biological conservation*, 144:902–912.
- 351 Valsecchi, V., Chase, B. M., Slingsby, J. A., Carr, A. S., Quick, L. J., Meadows, M. E., Cheddadi, R., and  
352 Reimer, P. J. (2013). A high resolution 15,600-year pollen and microcharcoal record from the  
353 Cederberg Mountains, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 387:6–  
354 16.
- 355 Vincens, A. (1986). Diagramme pollinique d'un sondage Pleistocene supérieur - Holocene du lac Bogoria  
356 (Kenya). *Review of Palaeobotany and Palynology*, 47(1-2):169–179.
- 357 Vincens, A., Schwartz, D., Elenga, H., Reynaud-Farrera, I., Alexandre, A., Bertaux, J., Mariotti, A., Martin,  
358 L., Meunier, J.-D., Nguetsop, F., Servant, M., Servant-Vildary, S., and Wirrmann, D. (1999). Forest  
359 response to climate changes in Atlantic equatorial Africa during the last 4000 years BP and  
360 inheritance on the modern landscapes. *Journal of Biogeography*, 26(4):879–885.
- 361 Vincens, A., Bremond, L., Brewer, S., Buchet, G., and Dussouillez, P. (2006). Modern pollen-based biome  
362 reconstructions in East Africa expanded to southern Tanzania. *Review of Palaeobotany and  
363 Palynology*, 140(3-4):187–212.

- 364 Vincens, A., Lézine, A.-M., Buchet, G., Lewden, D., and Le Thomas, A. (2007). African pollen database  
365 inventory of tree and shrub pollen types. *Review of Palaeobotany and Palynology*, 145(1-2):135–  
366 141.
- 367 Vincens, A., Buchet, G., and Servant, M. (2010). Vegetation response to the "African humid period"  
368 termination in central Cameroon (7°N) - new pollen insight from Lake Mbalang. *Climate of the*  
369 *Past*, 6:281–294.
- 370 Waller, M. P., Street-Perrott, F. A., and Wang, H. (2007). Holocene vegetation history of the Sahel: pollen,  
371 sedimentological and geochemical data from Jikariya Lake, north-eastern Nigeria. *Journal of*  
372 *Biogeography*, 34(9):1575–1590.
- 373 Warren, D. L., Glor, R. E., and Turelli, M. (2008). Environmental niche equivalency versus conservatism:  
374 Quantitative approaches to niche evolution. *Evolution*, 62(11):2868–2883.
- 375 Washington, R., Bouet, C., Cautenet, G., Mackenzie, E., Ashpole, I., Engelstaedter, S., Lizcano, G.,  
376 Henderson, G. M., Schepanski, K., and Tegen, I. (2009). Dust as a tipping element: the Bodélé  
377 depression, Chad. *PNAS*, 106(49):20564–20571.
- 378 Watrin, J., Lézine, A.-M., and Hély, C. (2009). Plant migration and plant communities at the time of the  
379 "Green Sahara". *Comptes Rendus Geoscience*, 341(8-9):656–670.
- 380 Wooller, M., Street-Perrott, F., and Agnew, A. (2000). Late quaternary fires and grassland palaeoecology  
381 of Mount Kenya, East Africa: evidence from charred grass cuticles in lake sediments.  
382 *Palaeogeography, Palaeoclimatology, Palaeoecology*, 164(1-4):207–230.
- 383 Wooller, M., Swain, D., Ficken, K., Agnew, A., Street-Perrott, F., and Eglinton, G. (2003). Late quaternary  
384 vegetation changes around Lake Rutundu, Mount Kenya, East Africa: evidence from grass cuticles,  
385 pollen and stable carbon isotopes. *Journal of Quaternary Science*, 18(1):3–15.
- 386 Wright, D. K. (2017). Humans as agents in the termination of the African humid period. *Frontiers in Earth*  
387 *Science*, 5(4).

388

389

390

391

392

393

394

395

396

397

398

399

400

401

402

403

404

405

406

407

408

409

410