Nonlinear detection of paleoclimate-variability transitions possibly related to human evolution

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Potential paleoclimatic driving mechanisms acting on human evolution present an open problem of cross-disciplinary scientific interest. The analysis of paleoclimate archives encoding the environmental variability in East Africa during the past 5 Ma has triggered an ongoing debate about possible candidate processes and evolutionary mechanisms. In this work, we apply a nonlinear statistical technique, recurrence network analysis, to three distinct marine records of terrigenous dust flux. Our method enables us to identify three epochs with transitions between qualitatively different types of environmental variability in North and East Africa during the (*i*) Middle Pliocene (3.35–3.15 Ma B.P.), (*ii*) Early Pleistocene (2.25–1.6 Ma B.P.), and (*iii*) Middle Pleistocene (1.1–0.7 Ma B.P.). A deeper examination of these transition periods reveals potential climatic drivers, including (*i*) large-scale changes in ocean currents due to a spatial shift of the Indonesian throughflow in combination with an intensification of Northern Hemisphere glaciation, (*ii*) a global reorganization of the atmospheric Walker circulation induced in the tropical Pacific and Indian Ocean, and (*iii*) shifts in the dominating temporal variability pattern of glacial activity during the Middle Pleistocene, respectively. A reexamination of the available fossil record demonstrates statistically significant coincidences between the detected transition periods and major steps in hominin evolution. This result suggests that the observed shifts between more regular and more erratic environmental variability may have acted as a trigger for rapid change in the development of humankind in Africa.

African climate | Plio-Pleistocene | climate-driven evolution | dynamical transitions | nonlinear time series analysis

Recent comparisons of terrestrial and marine paleoclimate archives have resulted in an intense debate concerning global vs. regional forcing of East Africa's climate and its relationship to human evolution during the past 5 Ma (1–4). The gradual long-term retreat of equatorial rain forests and the emergence of drier environments in East Africa (2, 5, 6) were interrupted by distinct epochs of increased humidity indicated by paleo-lake levels in different basins of the East African Rift System (EARS) displaying synchronous highs at about 2.7–2.5, 1.9–1.7, and 1.1–0.9 Ma B.P. (7). Notably, these epochs coincide well with certain global-scale climate transitions like the final closure of the Panama isthmus (8–10), intensification of the atmospheric Walker circulation (11), and the shift from a predominance of obliquity-driven glacial variability (41 ka period) to glacial-interglacial cycles with a 100 ka period (12, 13). Further reconstructions revealed additional relevant lake periods at 4.7–4.3, 4.0–3.9, 3.4–3.3, and 3.2–2.95 Ma B.P. (3). Previous findings suggest that the dominating summer aridity in the East African climate was controlled mainly by orbitally driven changes in the local irradiation driving regional monsoon activity via changes of sea-surface temperatures (SSTs) (5, 14–18) rather than by high-latitude glacial dynamics. In addition, tectonic activity and the resulting complex topography of East Africa could have triggered particularly variable climate conditions during the Plio-Pleistocene (18, 19).

As early as Darwin (20), scholars have speculated on if and how climate change shaped human evolution (4). On the basis of the present-day knowledge of the Plio-Pleistocene African climate, three general hypotheses concerning mechanisms of climate-induced mammalian evolutionary processes are currently discussed (18): (*i*) The *turnover pulse hypothesis* postulates progressive habitat changes (21, 22) due to abrupt climate shifts (1, 2) enforcing the adaptation of existing and the evolution of new species. (*ii*) The *variability selection hypothesis* proposes an increasing instability of environmental conditions as a driver for the simultaneous emergence of species (23, 24). (*iii*) Finally, the *pulsed climate variability hypothesis* promotes spikes of more variable climate conditions unrelated to high-latitude glacial cycles as a key driver of evolutionary selection (3, 6, 7, 25). With the currently available paleoclimate and paleoanthropological records, it has not been possible to provide clear evidence for one of these hypotheses by means of traditional (linear) statistical analysis.

Although there is an unequivocal correlation of terrestrial and marine paleoclimate records, to date, marine sediments (Fig. 1) provide the only archive that allows the study of the Plio-Pleistocene African climate on all relevant time scales. However, earlier analyses of terrigenous dust flux records using traditional time series analysis techniques to detect important transitions in the African climate yielded contradictory results with respect to the signature and timing of these events (1, 2, 17). Difficulties like these are to be expected when applying linear methods to the highly nonlinear climate system underlying paleoclimate proxy records. Linear techniques of time series analysis by definition are limited to the study of linear dynamics. To circumvent this problem and explore the vast remainder of nonlinear phenomena, here we present results on the basis of a nonlinear method of time series analysis, recurrence network (RN) analysis (see *SI Text*). RN analysis enables us to reliably detect qualitative changes within observational time series, which are largely indiscernible for linear methods of data analysis (26–28). This instrument leads to an improved detection of a particular flavor of Plio-Pleistocene African climate change and its potential influence on the habitats of early humans. On the basis of concepts of dynamical systems and graph theory, RN analysis is particularly efficient in applications where the number of observations is limited and the data points are unevenly spaced, which is common for paleoclimate proxy records such as time series of dust accumulation rates (29).

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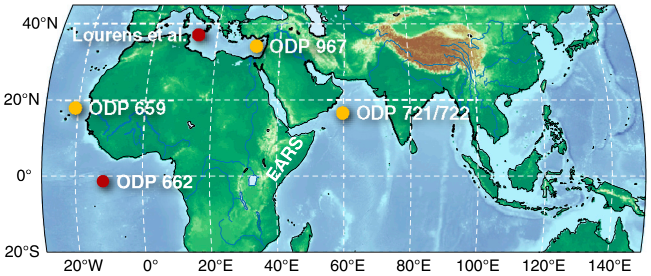

Fig. 1. Map displaying the locations of the marine sediment cores analyzed in this study (orange): ODP 659 (East Atlantic) (34), 721/722 (Arabian Sea) (1, 2), and 967 (Eastern Mediterranean Sea) (66). In addition, locations of additional complementary records of Plio-Pleistocene climate evolution (red) in the Atlantic [ODP site 662 (61)] and the Mediterranean [composite sequence of marine sediments at the Sicilian and Calabrian coast (69)] as well as the EARS are shown.

Specifically, RN analysis is sensitive to general changes in the dynamics rather than those in the amplitudes of the entire record (e.g., trends in mean or variance) or modes with a certain periodicity. Therefore it is well suited for detecting tipping points or, more generally, bifurcations in the behavior of nonlinear complex systems like Earth's climate (28–30).

Results

For detecting significant shifts in the dynamics of Plio-Pleistocene African climate as reflected by terrigenous dust flux (see *Materials and Methods*), we rely on two established measures of complex network theory: transitivity and average path length (31). It has been theoretically and empirically shown in several studies that, when calculated for RNs of selected time series segments (see *SI Text*), transitivity reflects the regularity of the dynamics within this segment or time window (28, 30, 32). Noisy or chaotic dynamics gives rise to low values, whereas (almost) periodic or laminar behavior induces high values of transitivity. We therefore refer to it as a climate regularity (CR) index in the following. Along the same lines, extreme values of the average path length indicate an abrupt dynamical change (ADC) between different dynamical regimes within the considered time window (28, 30, 32) (see *SI Text*). It is a crucial feature of our approach that CR and ADC do not reflect changes in long-term trends but are, in contrast, sensitive to the regularity of short-term fluctuations (CR) and general abrupt changes in this short-term dynamics (ADC). Both measures are hence responsive to different nonlinear aspects of the time series data and do not necessarily show transitions at the same epochs (27, 29, 30). If they do so, however, this double-evidence points at a particularly relevant feature in the data.

For representative dust flux records from the Atlantic as well as the Indian Ocean [Ocean Drilling Program (ODP) sites 659 and 721/722, Fig. 2*A*], CR reveals surprisingly similar long-term change in short-term fluctuations before about 1.5 Ma B.P. (in contrast to the Mediterranean ODP site 967, Fig. 2*A*), although both sites are strongly geographically separated and, hence, characterized by distinct wind systems and dust sources (1, 17, 33) (Fig. 2*B*). Specifically, the Saharan Air Layer, African Equatorial Jet, and trade winds contribute at ODP site 659 (34), whereas the Shamal winds from the Arabian Peninsula, which are connected to the western branch of the Asian monsoon system, dominate at ODP site 721/722 (35). This overall picture indicates that changes in CR during the Pliocene and early Pleistocene are robust manifestations of long-term variations in the dynamics of large-scale African dust mobilization and transport.

As a particularly striking feature, we identify a pronounced maximum of CR between 3.5 and 3.0 Ma B.P. at both ODP sites 659 and 721/722 signaling a period of exceptionally regular dust flux dynamics. The epochs highlighted by ADC support these findings (Fig. 2*C*). The time interval 3.5–3.0 Ma B.P. is characterized by three distinct and highly significant extrema (two maxima and one minimum) in the ODP site 659 record, indicating shifts between regimes of higher and lower regularity in the variations

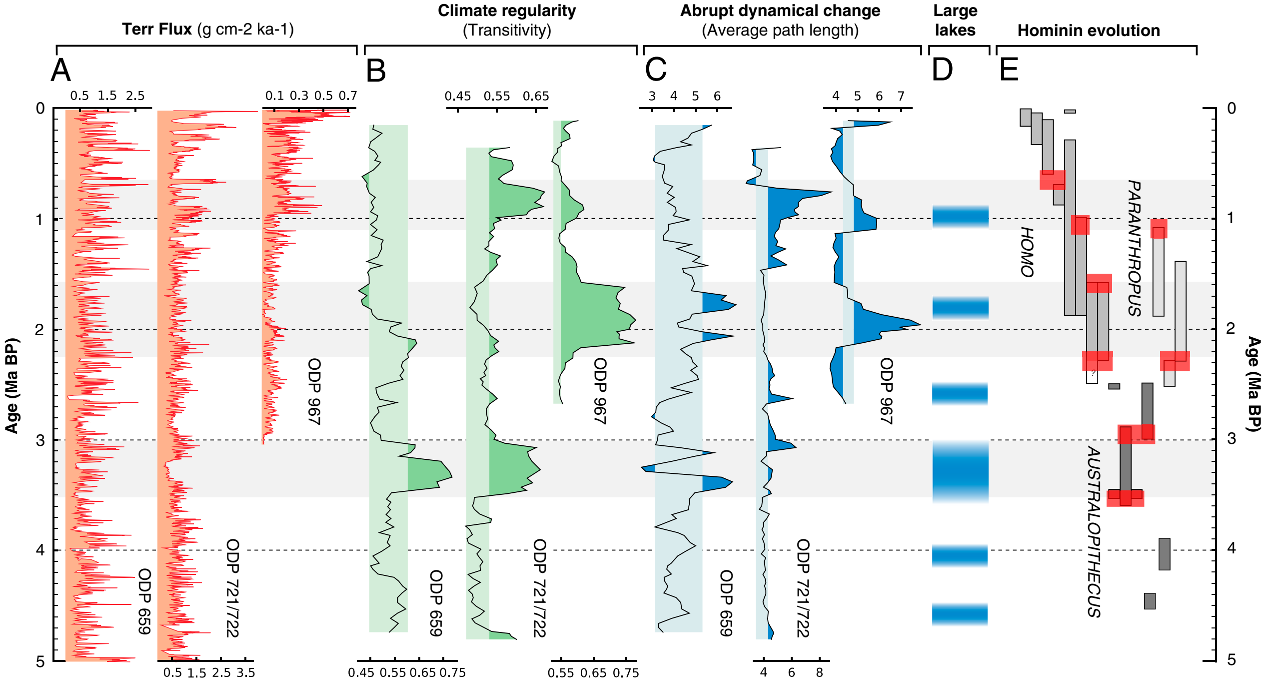

Fig. 2. (*A*) Terrestrial dust flux records from the three considered ODP sites (1, 2, 34, 66). (*B*,*C*) Results of RN analysis of the three dust flux records including 90% confidence bands (vertical shadings) of a stationarity test (*SI Text*). Comparing both measures for all records reveals significant and synchronous large-scale regime shifts in dust flux dynamics (horizontal shadings). (*D*) Time intervals with geological evidence for large lakes in East Africa, comprising collected information from different areas in the EARS (3) and additional results from the Afar basin (65, 70). (*E*) Major known steps of human evolution in East Africa (simplified from ref. 3). Red bars indicate epochs where the possible emergence and/or extinction of known hominin species coincides with detected climate transitions (*SI Text*).

of environmental conditions (30). Similar observations can be made for the ODP site 721/722 data; however, the increased values of ADC are less well pronounced but persist considerably longer (until 2.8 Ma B.P.).

In general, the variations of ADC observed at ODP sites 659 and 721/722 differ remarkably (Fig. 2*C*), although CR traces consistent shifts between more and less regular variability until about 1.5 Ma B.P. By considering the Mediterranean record (ODP site 967), further synchronous events are identified. Specifically, we find an extended, highly significant maximum of CR between about 2.25 and 1.6 Ma B.P. and of ADC between 2.2 and 1.7 Ma B.P. The latter one roughly coincides with the observations made at ODP site 659. Moreover, between about 1.1 and 0.7 Ma B.P., both CR and ADC show significant maxima for ODP site 967 and ODP site 721/722 but not for ODP site 659.

In summary, our analysis identifies three main epochs of interest: 3.5–3.0, 2.25–1.6, and 1.1–0.7 Ma B.P. (Fig. 2). All three are characterized by significant extrema of CR and/or ADC in at least two of the analyzed records. In addition, there are further shorter time periods of considerably increased or decreased CR or ADC observed in different records which are, however, typically less pronounced. Our results do not change significantly if the basic parameters of our analysis method (see *SI Text*) are modified (29).

Discussion

Nonlinear Identification of Critical Transitions in Paleoclimate. Tipping points in the climate system—i.e., values of system parameters at which critical transitions in climate dynamics take place—have gained increasing attention in the course of the ongoing debate on potential impacts of anthropogenic climate change (36–38). Given the large risk (product of impact and likelihood) associated with the activation of certain climate tipping elements (e.g., the Greenland and West Antarctic ice sheets), understanding and anticipating future qualitative changes in climate tipping elements is of major importance and requires a good knowledge of past transitions recorded in paleoclimate data (39). Previous research revealed precursory signatures associated with climate tipping points (39–41). Predominantly, changes in the variance structure of characteristic observables represent a critical slowing down of intrinsic transient responses within the data prior to the instabilities (42–46).

RN analysis is a promising exploratory tool for detecting structural changes in paleoclimate dynamics potentially associated with certain tipping elements in Earth's climate system. It has several advantages above other frequently used techniques for detecting (incipient) bifurcations in time series: (*i*) RN analysis is *not* explicitly based on temporal correlations but on geometric considerations (47). Hence it is more robust with respect to noisy and nonuniformly sampled paleoclimate time series with uncertain timing than methods relying on temporal correlations (42–44, 48) like degenerate fingerprinting (42) and detrended fluctuation analysis (43). (*ii*) As a nonlinear technique, RN analysis is not restricted to detecting only changes in linear statistical properties (i.e., the autocovariance structure) of a time series (42, 44–46). In contrast, it characterizes more general variations in the recorded dynamics, which may become particularly relevant close to bifurcation points. (*iii*) RN analysis has been shown to reliably perform with a comparably small number of data points (29, 32), particularly when contrasting it with linear spectral methods (1, 2) or certain nonlinear stochastic models of climate fluctuations for detecting noisy bifurcations (49, 50).

We emphasize that all existing methods for detecting tipping points from paleoclimate time series (including RN analysis) make use of sliding window techniques. By construction, such methods have a limited temporal resolution of the variations of the statistics of interest. Hence, identified dynamical transitions can be attributed only to epochs rather than distinct points in time. This strategy has the advantage of a higher robustness with respect to uncertainties in the data themselves as well as the associated age models, rendering the results of RN analysis particularly robust and statistically reliable (29).

Climatological Interpretation. The three identified transition periods (Fig. 2), which are only partially known from previous studies, can be clearly related to distinct and known climatic mechanisms. Specifically, the interval 1.1–0.7 Ma B.P. corresponds to the Middle Pleistocene transition (MPT) characterized by a change from glacial cycles predominantly related to obliquity variations of Earth's orbit (approximately 41 ka period) to such with an approximately 100 ka periodicity. The timing of this transition and its underlying mechanisms have been extensively studied elsewhere (13, 51). That the MPT is not detected in the record from ODP site 659 by RN analysis does not imply that it did not have any climatic impact in the corresponding dust-source areas in Northwest Africa. It just shows that our technique is not sensitive to the local signature of the transition, if present, e.g., if it manifests itself in some change of trend (1, 2, 17) (see the discussion in *Results*). Alternatively, the locally available data may be insufficient in quality and/or resolution to reveal the subtle type of events RN analysis is focusing on. This reasoning holds for any other known transition that is not detected by our method in any of the considered records. Regarding the transition period in the Early Pleistocene (2.25–1.6 Ma B.P.), the timing well coincides with known large-scale changes in atmospheric circulation associated with an intensification and spatial shift of the Walker circulation (11).

The third identified transition period includes the Middle Pliocene (3.3–3.0 Ma B.P.), the last long period during which global mean temperatures have been consistently higher than present day (52). This epoch is thus considered as an analog for the future climate of the late 21st century if anthropogenic emissions of greenhouse gases continue to rise (53). It was characterized by a strongly reduced meridional temperature gradient due to an intermittent poleward shift of the North Atlantic overturning resulting in a strong warming of the Arctic by oceanic surface currents (54, 55). At the same time, RN analysis reveals an enhanced regularity of African dust flux variations in both the Arabian Sea and Atlantic Ocean. At ODP site 721/722, this observation is predominantly caused by a well-pronounced epoch of relatively weak and approximately constant dust flux between about 3.36 and 3.17 Ma B.P. (Fig. 3*E*). A similar—but shorter—feature is found at ODP site 659 between about 3.25 and 3.19 Ma B.P. (Fig. 3*D*) as well as at ODP sites 661 and 662 in the Eastern Equatorial Atlantic (1, 2). The presence of such very similar features with a clearly different timing suggests the presence of either one common climatological mechanism influencing the Arabian Peninsula *much earlier than* Northwest Africa or two distinct (but eventually interrelated) factors, where the first affected only the Northeast African and/or Arabian dust flux dynamics.

A first important candidate factor is the marine isotope stage (MIS) M2 (56), an unusually cold period (3.32–3.28 Ma B.P.) prior to the Middle Pliocene warm period (57, 58); cf. Fig. 3*A*. This cooling was most likely triggered by a significant reduction of northward heat transport via the North Atlantic Current between 3.33 and 3.283 Ma B.P. (59)—possibly due to intermittent closures and reopenings of the Panamanian Seaway (10)—and led to a strong increase in global ice volume and a global sea-level fall to up to 60 m below present-day values (60). As a consequence, global SST decreased by 2–3 K (59), with a 1–2 K decrease in the tropics (61); see Fig. 3 *C* and *F*. This low-latitude cooling could be related to the reduced dust flux offshore of Northwest Africa but can hardly explain the much earlier signature in the Arabian Sea.

A second possible triggering mechanism is the successive northward displacement of New Guinea, because of which in-

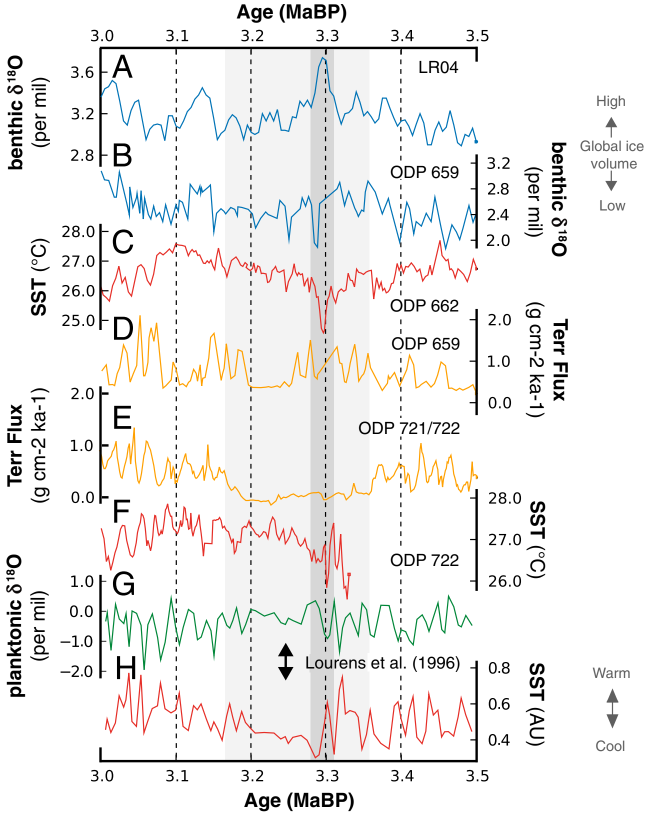

Fig. 3. Comparison of Middle Pliocene (3.5–3.0 Ma B.P.) global ice volume, sea-surface temperature, and dust flux reconstructions: (*A*) $\delta^{18}O$ benthic stack record LR04 (57); (*B*) benthic $\delta^{18}O$ record from ODP site 659; (*C*) alkenone-based SST reconstruction from ODP site 662 (61); (*D*) terrigenous dust flux at ODP site 659 (34); (*E*) terrigenous dust flux at ODP site 721/722 (1, 2); (*F*) alkenone-based SST reconstruction from ODP site 722 (61); (*G*,*H*) planktonic $\delta^{18}O$ and SST reconstruction from ensembles of planktonic foraminifera for a composite sequence from Southern Italy (69). The dark gray vertical bar indicates the MIS M2 (preceding an epoch with cold SST in the Mediterranean Sea and reduced dust flux into the Atlantic Ocean); the light gray bar indicates the interval of reduced dust flux into the Arabian Sea.

stead of warmer Equatorial Pacific water presently only less saline and colder North Pacific water can pass the Indonesian throughflow (62). Recent paleoceanographic reconstructions revealed that, during the Pliocene, subsurface waters in the eastern tropical Indian Ocean freshened and cooled by about 4 K, including a major cooling step between 3.5 and 2.95 Ma B.P. (63). Although SST was much less affected in most parts of the Indian Ocean, the southern coast of the Arabian Peninsula as well as the region around the horn of Africa are known as (wind-driven seasonal) upwelling regions (61, 64), which suggests that cold subsurface waters could have (at least intermittently) reached the ocean surface in this area and, thus, have led to a considerable decrease in the average regional SST. Recent alkenone-based SST reconstructions for ODP site 721/722 (61) actually confirm strong SST variations with partially extremely low values between at least 3.33 (the beginning of the respective record) and 3.28 Ma B.P. (see Fig. 3*F*), which cannot be explained by the known pattern of early glacial activity (57).

In summary, both aforementioned factors would have led to decreasing SSTs and, hence, to lower surface air temperatures and potential changes in the evaporation-precipitation balance. As a consequence, less convective rainfall, but also a shift (and possible weakening) of dominating atmospheric circulation patterns, was likely. Because in the potential source areas of terrigenous dust lower temperatures foster the formation of a closed vegetation cover, erosion and, hence, dust mobilization would have decreased. This interpretation is supported by the existence of large lakes in East Africa between 3.4 and 2.95 Ma B.P. [including the most pronounced lake episode in the Afar region (65) at about 3.33–3.23 Ma B.P.] pointing towards a very humid climate (Fig. 2*D*). Our considerations above are speculative so far and need confirmation from modeling studies and complementary paleoclimate archives.

Climate Variability and Human Evolution. To study the influence of African climate variability on human evolution, we compare the major large-scale transitions in African climate identified above with the currently available fossil record (Fig. 2*E*). Particularly, we observe that transitions in hominin evolution indicated by the appearance and disappearance of hominin species tend to cluster close to the identified climate shifts. These observed coincidences are unlikely to arise by chance even when taking into account dating uncertainties and the inherent incompleteness of the fossil record, as can be shown by using a suitable statistical significance test (*SI Text*).

The presented results therefore shed some light on the possible interrelationships between long-term climate change and hominin evolution. Specifically, we suggest that shifts between periods of more regular and more erratic environmental variability have been particularly important triggers for the development of humankind in East Africa. On the one hand, epochs of higher regularity could have led to stabilization and gradual increase of a population and, thus, a spread of a species over a larger area. On the other hand, subsequent periods of more irregular climate variability, possibly associated with changes in long-term trends, would have created an additional evolutionary pressure via a fragmentation of habitats and, thus, adaptation and diversification leading to speciation (18).

Supporting and extending Potts' variability selection hypothesis on environmental control of human evolution (23, 24), our point of view strongly suggests that, in addition to the mean climate conditions and the amplitude of variations of environmental parameters, (intermittent) changes in the regularity of climate fluctuations should be considered in future, more refined theories. In line with Potts' hypothesis, this mechanism on orbital time scales would benefit generalists like *Homo*, which are able to cope with strongly varying environmental conditions, but penalize specialists like *Paranthropus* (23). We must, however, keep in mind that the time scales of variations that are possibly relevant for migration of populations are not yet resolved in the available paleoclimate data. The necessity for further testing the extended variability selection hypothesis put forward here against other hypotheses (see the Introduction) calls for future efforts to obtain high-resolution (decadal to centennial scale) data on Plio-Pleistocene African climate history.

Conclusions

The nonlinear technique employed in this study is able to unravel large-scale changes in the temporal variability of African environmental conditions on supermillennial time scales. Comparing our results with findings from linear studies (17) demonstrates that past climate change in Africa includes a significant, previously overlooked nonlinear component. This complementary information supports the conclusions of ref. 17 in that we do not find evidence for sustained and irreversible step-like changes in climate variability that were proposed by refs. 1 and 2.

Our results provide clear evidence for subtle, but significant, transitions in the dynamics of mineral dust transport from the African continent to the adjacent oceans at about 3.35–3.15, 2.25–1.6, and 1.1–0.7 Ma B.P. These transitions unanimously correlate with important global climate transitions, such as changing ocean circulation (after 3.5 Ma B.P.), the intensification of the low-latitude Walker Circulation (*ca.* 1.7 Ma B.P.), and the onset of 100-ka glacial-interglacial cycles during the Middle Pleistocene transition (*ca.* 1.25–0.7 Ma B.P.). The three episodes are characterized by radical changes in the ocean-atmosphere conditions, and hence the timing, magnitude, and style of wet-dry-wet transitions in tropical and subtropical Africa, without doubt influencing the regional climate and environment of early humans.

Indeed, we observe statistically significant coincidences between the detected climate shifts and transitions in human evolution in the geological record. By analogy, this link may be regarded as a warning considering the large risks for future human societies associated with climate tipping elements undergoing potentially irreversible, qualitative transitions due to anthropogenic climate change during the 21st century, even if the time scales involved are very different. To harness the potential of RN analysis and other nonlinear techniques to provide early warning of climate tipping points on these centennial time scales remains a challenge for future research.

Materials and Methods

The terrigenous dust flux records from ODP sites 659 (Atlantic Ocean offshore West Africa) (34), 721/722 (Arabian Sea) (1, 2), and 967 (Eastern Mediterranean Sea) (66) (see Fig. 2) allow reconstruction of North African dust mobilization and transport over the past 5 Ma and, hence, encode temporal changes in both the aridity of the region and the strength and direction of dominant regional atmospheric circulation patterns (17). We chose these records because they are well studied in the literature (1, 2, 17, 34, 66) and are at the same time representatively distributed around North Africa. Terrigenous dust flux has been estimated by using different approaches: from the relative abundance of the noncarbonate fraction and the dry-bulk density for site 659, via linear regression from the magnetic susceptibility (which can be measured much more easily) for site 721/722 (67), to artificially induced magnetic remanescence for site 967 (for more details, see ref. 17).

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