1 **Running head:** Million-year climate effect on diversity

2 **Title:** Multimillion-year climatic effects on palm species diversity in Africa

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1 **ABSTRACT**

2 Past climatic changes have caused extinction, speciation and range dynamics, but assessing the
3 influence of past multimillion-year climatic imprints on present-day biodiversity patterns
4 remains challenging. We analyzed a new continental-scale dataset to examine the importance
5 of paleoclimatic effects on current gradients in African palm richness patterns. Using climate
6 reconstructions from the late Miocene (~ 10 mya), the Pliocene (~ 3 mya) and the Last Glacial
7 Maximum (0.021 mya), we found that African palm diversity patterns exhibit pronounced
8 historical legacies related to long-term climate change. Notably, pre-Pleistocene
9 paleoprecipitation variables differentially affected current diversity patterns of palms grouped
10 by contrasting habitat requirements. Accounting for present-day environment, rainforest palms
11 exhibit greater species richness in localities where Pliocene precipitation was relatively high,
12 whereas open-habitat palms show higher species richness in areas of relatively low
13 precipitation during the Miocene Epoch. Our results demonstrate that diversity-climate
14 relationships among African palm species include multimillion-year lagged dynamics, i.e.,
15 with historical legacies persisting across much longer time periods than commonly recognized.

16

17 **Keywords:** Arecaceae, historical legacies, non-equilibrium dynamics, macroecology, Palmae,
18 paleoclimate, past climate change, refugia, species richness, Neogene, tropics.

1 INTRODUCTION

2 Over geological time, climatic changes such as global cooling or warming events and resultant
 3 changes in precipitation regimes have coincided with major biological shifts throughout the
 4 world (Zachos et al. 2001). Areas that experience a stable climate over long periods of time
 5 may facilitate the origination and persistence of species (Fjelds and Lovett 1997, Carnaval et
 6 al. 2009). Areas having unstable climates on the other hand may selectively favor the survival
 7 of taxa with specific ecological adaptations (Svenning 2003). Paleoclimatic conditions may
 8 influence present-day biodiversity patterns through their effects on speciation, extinction, and
 9 dispersal (Dynesius and Jansson 2000, Ricklefs 2004, Hewitt 2004, Svenning and Skov 2007,
 10 Kissling et al. 2012a). However, the relative contributions of contemporary vs. historical
 11 factors in determining present-day species diversity patterns remain highly controversial
 12 (Ricklefs 2004). Few studies have used advanced paleoclimatic simulations to explicitly test
 13 for historical legacies in contemporary biodiversity patterns. Most studies have focused on the
 14 last 2.6 million years' (the Quaternary) glacial-interglacial climatic fluctuations. These cycles
 15 have caused obvious range changes and extinctions (Dynesius and Jansson 2000) and thus have
 16 strongly influenced current species distributions and species richness patterns (Svenning and
 17 Skov 2007, Arajo et al. 2008, Sandel et al. 2011, Kissling et al. 2012b, Rakotoarinivo et al.
 18 2013). Nevertheless, pronounced climatic changes have also occurred in the more distant past,
 19 e.g., during the Pliocene (5.3–2.6 million years ago, Haywood and Valdes 2004) and the
 20 Miocene (23.0–5.3 mya, Pound et al. 2011) Epochs that preceded the Quaternary. To our
 21 knowledge, the effects of these pre-Quaternary climatic changes on present-day biodiversity
 22 patterns have not been quantified in an analytical, spatially explicit framework.

23 Strong paleoclimatic changes have affected not only temperate and arctic regions (e.g.,
 24 Hewitt 2004), but also tropical areas such as Africa (Morley 2000, Plana 2004). During the
 25 Neogene Period, significant climatic change began in Africa causing a shift towards more arid
 26 conditions over the last 10–20 million years (Senut et al. 2009). This shift towards arid

conditions during the middle to late Miocene reversed course in the early Pliocene during which time Africa began to experience warmer and more humid conditions (Morley 2000, Plana 2004). Temperatures dropped during the late Pliocene when several abrupt and pronounced shifts towards drier and cooler conditions occurred in Africa (deMenocal 1995, Morley 2000, Plana 2004). Glacial-interglacial cycles during the subsequent Quaternary period also affected African climate, manifesting as alternating cold/dry glacial and warm/wet interglacial periods (Hamilton and Taylor 1991, Plana 2004). These climatic oscillations resulted in the expansion of rainforest ecosystems during warm/wet climates and open habitats such as savanna and grasslands during the cold/dry phases (Maley 1996, Morley 2000, Plana 2004, Jacobs 2004, Bobe 2006, Bonnefille 2010). During the driest periods, many rainforest taxa likely persisted in refugia, but with the potential to re-expand during later wetter periods (Mayr and O'Hara 1986).

The specific effects of past climate regimes on the present-day biodiversity of African ecosystems remain highly uncertain. Effects of deep-time climatic conditions on different groups of organisms in Africa have been inferred from paleobotanical data (e.g., Morley 2000, Bonnefille 2010) and dated molecular phylogenies (Davies et al. 2002, Couvreur et al. 2008, Voelker et al. 2010, Holstein and Renner 2011, Tolley et al. 2011). According to some interpretations, paleoclimatic variation may even provide a more consistent explanation for present-day species endemism patterns in Africa than modern climate (Fjeldså and Lovett 1997, Linder 2001). Recent reports furthermore suggest that the relatively low levels of diversity observed in a number of organism groups in Africa relative to that of other tropical regions partly may be due to Neogene climate change (Morley 2000, Parmentier et al. 2007, Kissling et al. 2012b). Direct analyses of spatially-explicit paleoclimatic reconstructions and broad-scale species distribution patterns have not yet verified the role of paleoclimate in shaping current species diversity patterns in Africa.

The palm family (Arecaceae) is a keystone plant group for tropical and subtropical

climate regions and exhibits pronounced regional differences in its diversity pattern (Dransfield et al. 2008, Kissling et al. 2012b, Couvreur and Baker 2013). Of the palm family's 2400+ species only 65 species occur naturally in Africa exhibiting relatively low diversity levels in Africa compared to other tropical and subtropical regions. Moreover, a relatively high proportion of African palm species occupy open habitats (Dransfield et al. 2008). Moore (1973) attributed low levels of species richness among continental African palms to extinctions caused by late Quaternary climate shifts. However, recently presented fossil evidence suggests that many palm extinctions in Africa instead date back to paleoclimatic changes during the Paleogene and Neogene Periods (Pan et al. 2006). Pre-Quaternary historical drivers of low levels of palm diversity in Africa have also been suggested from a new global analysis of the palm family (Kissling et al. 2012b), but the relative timing and/or efficacy of these pre-Quaternary mechanisms remain unexplored. As an analogue, phylogenetic studies of non-palm African rainforest trees also point to the importance of Neogene dynamics for their current diversity (Plana et al. 2004, Couvreur et al. 2011a). Hence, there is a clear need to test for pre-Quaternary climate effects on geographic diversity patterns of palms and other taxa in Africa.

Here, we use recently published paleoclimatic reconstructions for the late Miocene (Pound et al. 2011), the late Pliocene (Haywood and Valdes 2004), and the Last Glacial Maximum (LGM) in the Late Pleistocene (Braconnot et al. 2007). While accounting for contemporary climatic and non-climatic environmental drivers, these data are used to test for paleoclimatic legacies in present-day palm diversity patterns in Africa. These legacies potentially span 10^4 – 10^5 years (climate shifts since the LGM, c. 21,000 years ago) or 10^6 – 10^7 (multimillion) years (climate shifts since c. 3 million years ago (late Pliocene) or c. 9 million years ago (late Miocene)). We mapped continent-scale geographic species richness patterns using a comprehensive new database of palm locality records and advanced species distribution modeling. We divided African palms into two ecologically distinct groups (rainforest and open-habitat species) according to their differing habitat and climate affinities. As rainforest

species are by definition sensitive to drought, we expected greater modern-day species richness in areas that experienced relatively more humid climatic conditions in the past. In contrast, we expected open-habitat species to be more diverse in areas characterized by relatively dry past climates due to their ability to withstand drought. We specifically tested whether (1) paleoclimatic changes since the Miocene, Pliocene and Late Pleistocene Epochs contribute to explaining current palm species diversity patterns across continental Africa, and (2) the diversity of rainforest palms exceeds that expected from current climate in areas having relatively wet paleoclimatic conditions, and vice versa for open-habitat palms. Our results reveal clear evidence of pre-Quaternary paleoclimatic legacies in African palm species richness patterns, demonstrating that climate mechanisms may influence diversity patterns in tropical and subtropical regions via multimillion-year lagged dynamics.

METHODS

Palm distributions and diversity

We estimated continent-scale palm species richness (Fig. 1a–c) by combining a comprehensive geographical database of palm locality records with advanced ecoinformatic tools (see Appendix A). We selected the 2138 entries that were unique at a spatial resolution of 10×10 km from a total of 5500 occurrence records, all quality-checked for geographical location and taxonomy (see Appendix A for details). The occurrence records included 1 to 294 occurrences per species (mean $\pm$ SD = 34.5 ± 46.9 , median = 16, Appendix A, Table A1) and represent 62 (95%) of the 65 native African palm species. Three native palm species which are currently officially recognized (Govaerts et al. 2013) were excluded as these are doubtful species for Africa (J. Dransfield, pers. obs.) without any collections available. In addition, we excluded introduced species such as the cultivated date palm *Phoenix dactylifera* whose distribution is primarily determined by humans. We employed species distribution modeling in an ensemble approach to predict the geographic range of each species by combining advanced machine-

learning techniques such as Maxent (Phillips et al. 2006) and generalized boosting models with simple bioclimatic envelope modeling (the latter two implemented in the R package ‘Biomod’ version 1.1-5, Thuiller et al. 2009). The distributions of species with ≥ 5 unique records were modeled at 10×10 km resolution using either 5 or 11 principal components (depending on sample size – see Appendix A for details) derived from a Principal Component Analysis of climatic and non-climatic [habitat and human impact] predictors (for details see Appendix A). The principal components were combined with an equal number of spatial filters (*sensu* Blach-Overgaard et al. 2010). Spatial filters are eigenvectors derived from a Principal Coordinate Analysis of a truncated pairwise distance matrix based on the geographic locations of all grid cells (for details see Appendix A). These were included to take into account spatial constraints such as dispersal limitations and thus to prevent potential over-predictions of species distributions (cf. De Marco et al. 2008, Blach-Overgaard et al. 2010). The individual species distribution models were summed to estimate species richness at a resolution of 100×100 km (Figs. 1a–c). Detailed description of model evaluation and selection is given in Appendix A (also see Appendix A, Tables A2–A3). The richness estimates were computed by summing the predicted presences of all modeled species with the observed presences of more sparsely distributed species (sample sizes of < 5 records). Total palm species richness ($n = 62$) was divided into rainforest ($n = 43$) and open-habitat ($n = 16$) species to further assess potentially divergent richness drivers of these ecologically different groups. These two groups include rainforest palms found only in dense and humid tropical rainforests and open-habitat palms which tolerate drier, more exposed habitats (e.g., savanna woodlands and deserts), and do not occur in dense forests. The species *Elaeis guineensis*, *Jubaeopsis caffra* and *Phoenix reclinata* are not restricted to rainforests or open habitats and were therefore excluded from these habitat categories (see Appendix A, Table A1 for details).

1 **Paleoclimate and present-day environment**

2 To detect the influence of paleoclimatic conditions on the geographic variation of African palm
 3 species richness, we constructed six paleoclimatic predictor variables (for details see Appendix
 4 A, Table A4). These were derived from coupled ocean-atmosphere general circulation models
 5 representing: i) the late Miocene (11.61–7.25 mya, Pound et al. 2011), ii) the late Pliocene
 6 (3.29–2.97 mya, Haywood and Valdes 2004), and iii) the Last Glacial Maximum (LGM,
 7 21,000 years before present, Braconnot et al. 2007) of the Late Pleistocene. The paleoclimatic
 8 variables were calculated as the deviation of past annual mean temperature or precipitation
 9 from its present-day value (past minus contemporary climate, see Appendix A, Table A4). The
 10 principal reason for using the deviations rather than actual values of past precipitation and
 11 temperature is because present-day climatic effects covary with paleoclimatic variables
 12 (Appendix A, Table A5) and would cause multicollinearity issues in the regression analyses.
 13 Representing paleoclimate by anomalies is conservative, as only patterns related to deviations
 14 from current climate relationships will be ascribed to paleoclimate even if paleoclimate may
 15 well contribute to such current climate-richness relationships (cf. Ricklefs 2004). The resulting
 16 six paleoclimatic variables (Fig. 1d–i) represented precipitation and temperature anomalies for
 17 the Miocene (MIO_{PREC}, MIO_{TEMP}), the Pliocene (PLIO_{PREC}, PLIO_{TEMP}), and the LGM
 18 (LGM_{PREC}, LGM_{TEMP}). We interpreted the LGM climate anomalies as representative of glacial-
 19 interglacial climate cycles that occurred throughout the Quaternary (Jansson 2003, Kissling et
 20 al. 2012b).

21 We used ten predictor variables to represent the present-day environment. These
 22 included five climatic or climate-related variables, three variables related to habitat
 23 heterogeneity, and two variables related to human impact (see Appendix A, Table A4 for
 24 sources and details). Contemporary climate variables consisted of annual precipitation (PREC),
 25 mean annual temperature (MAT), actual evapotranspiration (AET), potential
 26 evapotranspiration (PET) and the normalized difference vegetation index (NDVI) as an

indicator of net primary productivity. This latter variable was included as a climate variable because climate is the main determinant of primary productivity levels at coarse spatial grains (e.g., Wang et al. 2003). Habitat heterogeneity variables included topographic range (TOPO), soil heterogeneity (SOIL) and heterogeneity in vegetation type (VEG). The TOPO variable was calculated as the difference between maximum and minimum elevation within each grid cell. The SOIL and VEG variables were calculated for each grid cell as the number of soil classes or vegetation types, respectively. Human impact variables included the human influence index (HII) and the historical human population density (HPH) computed as the average human population density per square km for the years 0 Anno Domini (AD), 500 AD, 1000 AD and 1500 AD. All predictor variables were projected to the Lambert Azimuthal Equal Area projection and mean values were extracted at the resolution of the richness data (see Appendix A, Table A4). All GIS operations were conducted in ArcGIS 9.3 (ESRI, Redlands, CA, USA).

Statistical analyses

Our statistical analysis of the dataset initially explored relationships among variables by calculating bivariate correlations between the response variables and potential predictors. Significance was assessed after adjusting for spatial autocorrelation using Dutilleul's method to estimate the corrected number of degrees of freedom (Dutilleul et al. 1993). We subsequently developed minimum adequate multivariate predictor regression models for each of the three response variables (total species richness, rainforest species richness, and open-habitat species richness). We initially included all predictor variables in ordinary least square (OLS) multiple regression models and subsequently applied a stepwise, backward model selection based on the Akaike Information Criterion (AIC) to select the most parsimonious multivariate models by minimizing AIC (Burnham and Anderson 2002). In a second step, we then fitted simultaneous autoregressive (SAR) models if the OLS model residuals exhibited spatial autocorrelation (SAC). We used the SAR error model due to its superior performance relative to other SAR

models (Kissling and Carl 2008). The SAR error model supplements OLS regression with a spatial weights matrix (W) that accounts for SAC in model residuals. Spatial weights matrices were defined by successively fitting SAR models with k -nearest neighbors of each site, starting with $k = 2$ until the operation had fully accounted for the observed levels of SAC. Residual SAC was examined in all models (OLS and SAR) using the “morand.mc” function in R and the four nearest neighbors of each site. Permutation tests were used to assess the significance of the Moran’s I ($n = 1000$ permutations). We report two pseudo- R^2 values for the SAR models computed as the squared Pearson’s correlation coefficients for predicted versus observed values (Kissling and Carl 2008). The R^2_{pred} represented the explained variance excluding space (i.e., W) and the $R^2_{\text{pred+space}}$ represented explained variance of space (W) along with the predictor variables.

All response variables were transformed to $\log_{10}$ values to enhance the dataset’s adherence to assumptions of normality. Predictor variables were similarly subjected to $\log_{10}$, square root or cubic-term transformations as needed (Appendix B, Table B1). Multicollinearity among predictor variables was assessed by computing pairwise Pearson’s correlation coefficients (r). These analyses showed that the NDVI and AET predictor variables were strongly correlated ($r > 0.7$), both with each other and with other predictor variables (PREC, PET; Appendix B, Tables B2–B4). Hence, further regression analysis did not include the NDVI and AET variables. Quadratic and cubic versions of predictor variables were used to capture non-linear relationships with the observed species richness. These terms were retained if they improved the AIC of single-predictor models by $\geq 5\%$. To reduce collinearity, predictors with non-linear effects were centered (subtracting the sample mean from all predictor values) before polynomial computation. All statistical analyses were computed in R (R Development Core Team 2012). For the spatial analyses we used the packages ‘spdep’ version 0.5-37 and ‘modtest’ version 1.2.

RESULTS

The highest overall levels of palm species richness and the highest levels of rainforest palm species richness occur along the Atlantic coast in the western part of the Guineo-Congolian floristic region (Fig. 1a,b) and exhibit a strong latitudinal gradient (Appendix C, Fig. C1a,b). In contrast, open-habitat palms exhibit the highest degree of species richness in eastern and western Africa (Fig. 1c) and show a less pronounced latitudinal gradient (Appendix C, Fig. C1c).

Minimum adequate regression models revealed significant contributions from paleoclimatic variables in describing variation of palm species richness patterns across Africa (Table 1; also cf. Appendix B, Tables B5, B6). Pliocene or Miocene precipitation anomalies ranked among the four most important predictor variables in each model (Table 1). For all palm species and for rainforest palms, the strongest paleoclimatic effect was a positive effect of the Pliocene precipitation anomaly (Fig. 2b,d), ranking second only to contemporary precipitation for the rainforest palm species and third to contemporary precipitation and temperature for all palm species (Fig. 2a,c). Contemporary precipitation and temperature were the strongest drivers of species richness of open-habitat palms (Table 1) in combination with a negative influence of the Miocene precipitation anomaly (Fig. 2e,f). Insignificant correlation coefficients indicated that Quaternary glacial–interglacial climate oscillations did not contribute to explain variation in current palm species richness patterns across Africa (Table 1). Human influence (HII, HPH), topographic range (TOPO), soil heterogeneity (SOIL), and heterogeneity in vegetation types (VEG) all exerted only weak to moderate influences on palm species richness patterns (Table 1).

DISCUSSION

Our results show that paleoclimatic changes on a multimillion-year time scale still constrain present-day patterns of palm species richness across Africa. Among the paleoclimatic factors

tested, the Pliocene precipitation anomaly showed the highest (positive) effect for all palms and for rainforest palms, whereas the Miocene precipitation anomaly exerted a negative effect on open-habitat palms. Interestingly, more recent Quaternary climatic changes as well as current habitat heterogeneity and human impact did not explain variation in palm species richness patterns across Africa, or only had weak effects. Our findings demonstrate that deep-time climate change complements current climate as drivers of species richness at continental scales and further highlights that including pre-Quaternary paleoclimatic information into spatially explicit analyses of large-scale biodiversity patterns is important for providing a more complete understanding of their drivers.

Our results show that current species richness in African rainforest palms is particularly high in areas that experienced elevated precipitation during the late Pliocene (~ 3 mya), as seen from the relatively large positive correlation coefficient associated with the late Pliocene precipitation anomaly (Fig. 1e, 2d). These conditions might have promoted high palm species richness in areas such as the Guineo-Congolian floristic region that have persisted to the present-day despite a drying climate. This result supports rainforest refugia interpretations (e.g., the Cameroon-Gabon refugia, Maley 1991, Hamilton and Taylor 1991, Blach-Overgaard et al. 2010), but suggests that they operate on longer time scales (i.e., pre-Pleistocene) than commonly recognized. Many rainforest clades (including palms) diversified and achieved relatively high degrees of species richness already during the Cenozoic (Wing et al. 1993, Couvreur et al. 2011b), possibly due to high diversification rates in constantly warm and wet climatic conditions (e.g., Svenning et al. 2008). Accordingly, the lower diversity of palms in Africa has been linked to severe extinctions caused by Neogene drying on this continent (Kissling et al. 2012a), albeit alternative explanations also are possible (Baker and Couvreur 2013a). The Pliocene effects detected by our analysis suggest that Quaternary range changes and extinctions have not totally decreased the high species richness that probably was built up in areas experiencing relatively high precipitation during the Pliocene. We suggest that the

distribution and intensity of Pliocene precipitation via dispersal limitation (Blach-Overgaard et al. 2010) and perhaps delayed extinctions supplement current environmental factors (especially current precipitation and temperature, see Table 1) in determining the present-day palm species richness patterns across African rainforests.

Open-habitat palms are more resistant to drought than rainforest palms (Tuley 1995). In contrast to the Pliocene precipitation effect on rainforest palm species richness we found that the Miocene precipitation anomaly was the strongest predictor of open-habitat palm species richness among the paleoclimatic variables. The Miocene precipitation effect was negative (Fig. 2f) indicating that areas having a more arid climate during the late Miocene (relative to modern conditions) today harbor greater species richness among open-habitat palms than expected purely from modern environmental conditions. This finding may reflect the vegetation history of arid ecosystems in Africa because open habitats became more widespread in Africa during the Miocene Epoch (Jacobs 2004, Bobe 2006, Senut et al. 2009). The temporal establishment and expansion of open habitats varied spatially for different regions of Africa, but possibly began with the first appearance of these habitats in East Africa during the late Miocene (Bonnefille 2010). Vegetation reconstructions from the late Miocene, middle Pliocene and LGM (late Pleistocene) consistently estimate that open habitat vegetation was present in eastern Africa during these periods (Harrison and Prentice 2003, Salzmann et al. 2008, Pound et al. 2011). Such conditions likely favored diversification in palm lineages that are adapted to arid environments (Dransfield 1988). Supporting this interpretation, Eastern Africa hosts the highest degree of species richness of open-habitat palms in Africa, with divergence times (11.1–11.5 mya node age, Baker and Couvreur 2013b) of some open-habitat palm genera (*Hyphaene*, *Borassus* and *Medemia*) that are concurrent with the temporal expansion of these open habitats in Africa.

Early studies have suggested that continental African palm diversity patterns partially reflect historical legacies, but with a focus on Quaternary glacial-interglacial climatic

oscillations as the potential driver (Moore 1973, Dransfield 1988). Our results suggest that longer-term pre-Quaternary climate mechanisms also play a significant role and that previous interpretations of diversity patterns that invoked only Quaternary paleoclimate require refinement. This is supported by an additional statistical analysis of the current data set (Appendix B, Table B7) which shows that the relative importance of current environment (e.g., precipitation, habitat heterogeneity, and human impact) and Quaternary climate change (represented as LGM anomalies) would be over-estimated if deeper-time (Pliocene and Miocene) climate shifts had not been represented in the modeling. Dated molecular phylogenies further show the pre-Quaternary origin of most palm clades (Baker and Couvreur 2013b) and many other African plant clades and therefore support the potential importance of deeper-time historical events for current African biodiversity patterns (e.g., Plana et al. 2004, Couvreur et al. 2011a). These findings are also consistent with the fossil record of African palms, which indicates that regional palm extirpations have occurred during the Miocene, Pliocene, and/or Pleistocene Epochs (Pan et al. 2006); such regional extirpations could conceivably still affect current diversity levels.

Palaeoclimatic reconstructions, such as those used in our study, usually have larger uncertainties than present-day environmental variables (Haywood et al. 2009, Pound et al. 2011). The high statistical importance of paleoclimate variables in our analyses relative to current environment is therefore notable. Nevertheless, paleoclimate models can have severe deficiencies in simulating past climate patterns, especially as relates to uncertainties in precipitation rates (Randall et al. 2007). Moreover, paleoclimatic simulations may differ depending on which global circulation models and simulation settings are used (Salzmann et al. 2008, Haywood et al. 2009, Pound et al. 2011). Simulated paleoclimates may also show higher uncertainties in some regions relative to others (e.g., Haywood et al. 2009). As paleoclimate modeling likely will experience substantial improvement over the coming decades, the estimated relative importance of paleoclimate might even increase. Nevertheless,

to our knowledge the paleoclimatic reconstructions used in our study provide the best estimates that are currently available at this spatial and temporal resolution.

The detection of long-term (3–10 mya) paleoclimatic legacies in the geographic palm species richness patterns across Africa adds to a growing body of evidence that links historical climate to present-day biodiversity patterns. Our results suggest that paleoclimate changes do not only constrain diversity at higher latitudes where pronounced glacial–interglacial climatic cycles have imposed strong environmental filtering and strong non-equilibrium dynamics (Svenning and Skov 2007, Araújo et al. 2008, Sandel et al. 2011), but also in tropical regions (Fjeldså and Lovett 1997, Linder 2001, Carnaval et al. 2009, Rakotoarinivo et al. 2013) and even on multimillion-year time scales (Kissling et al. 2012a). Future climate change may result in severe range contractions or regional extirpations and we suggest that these may lead to long-term restrictions on biodiversity. West-Central Africa, an area having the highest present-day palm species richness, is expected to be at elevated risk for potential future drought events (Sheffield and Wood 2008). An increasing frequency and/or duration of drought events is likely to affect rainforest biodiversity in Africa, but may diminish open-habitat palm diversity as well (e.g., Blach-Overgaard et al. 2009). Although open-habitat palms are more tolerant of drought, they still depend on relatively high water availability in the soil (Tuley 1995). Together with deforestation and intensification of human land use in many parts of Africa, the effects of future climate change on palm diversity in Africa may thus be long-lasting, even exceeding centennial and millennial time scales.

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DESCRIPTION OF ECOLOGICAL ARCHIVES MATERIAL

APPENDIX A: Detailed description of methods for obtaining palm species distribution and richness patterns.

APPENDIX B: Additional data processing and statistical analyses of palm species richness patterns.

APPENDIX C: Latitudinal species richness patterns of African palms.

LITERATURE CITED

- Araújo M. B., D. Nogués-Bravo, J. A. F. Diniz-Filho, A. M. Haywood, P. J. Valdes and C. Rahbek. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography* 31:8-15.
- Baker W. J. and T. L. P. Couvreur. 2013a. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. II. Diversification history and origin of regional assemblages. *Journal of Biogeography* 40:286-298.
- Baker W. J. and T. L. P. Couvreur. 2013b. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography* 40:274-285.
- Blach-Overgaard A., J.-C. Svenning and H. Balslev. 2009. Climate change sensitivity of the African ivory nut palm, *Hyphaene petersiana* Klotzsch ex Mart. (Arecaceae) - a keystone species in SE Africa. *IOP Conference Series: Earth and Environmental Science* 8:012014.
- Blach-Overgaard A., J.-C. Svenning, J. Dransfield, M. Greve and H. Balslev. 2010. Determinants of palm species distribution across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* 33:380-391.
- Bohe R. 2006. The evolution of arid ecosystems in eastern Africa. *Journal of Arid Environments* 66:564-584.
- Bonnefille R. 2010. Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change* 72:390-411.
- Braconnot P., B. Otto-Bliesner, S. Harrison, S. Joussaume, J.-Y. Peterchmitt, A. Abe-Ouchi, M. Crucifix, E. Driesschaert, T. Fichefet, C. D. Hewitt, M. Kageyama, A. Kitoh, A. Laîné, M.-F. Loutre, O. Marti, U. Merkel, G. Ramstein, P. Valdes, S. L. Weber, Y. Yu and Y. Zhao. 2007. Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum - Part 1: experiments and large-scale features. *Climate of the Past* 3:261-277.

- 1 Burnham K. P. and D. R. Anderson 2002. Model selection and multimodel inference: a
2 practical information-theoretic approach. Springer-Verlag, New York, USA.
- 3 Carnaval A. C., M. J. Hickerson, C. F. B. Haddad, M. T. Rodrigues and C. Moritz. 2009.
4 Stability predicts genetic diversity in the Brazilian Atlantic Forest hotspot. *Science* 323:785-
5 789.
- 6 Couvreur T. L. P., L. W. Chatrou, M. S. M. Sosef and J. E. Richardson. 2008. Molecular
7 phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees.
8 *BMC Biology* 6:54.
- 9 Couvreur T. L. P., H. Porter-Morgan, J. J. Wieringa and L. W. Chatrou. 2011a. Little
10 ecological divergence associated with speciation in two African rain forest tree genera.
11 *BMC Evolutionary Biology* 11:296.
- 12 Couvreur T. L. P., F. Forest and W. J. Baker. 2011b. Origin and global diversification patterns
13 of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC*
14 *Biology* 9:44.
- 15 Couvreur T. L. P. and W. J. Baker. 2013. Tropical rain forest evolution: palms as a model
16 group. *BMC Biology* 11:48.
- 17 Davis C. C., C. D. Bell, P. W. Fritsch and S. Mathews. 2002. Phylogeny of *Acridocarpus*-
18 *Brachylophon* (Malpighiaceae): implications for Tertiary tropical floras and Afroasian
19 biogeography. *Evolution* 56:2395-2405.
- 20 De Marco P., J. A. F. Diniz-Filho and L. M. Bini. 2008. Spatial analysis improves species
21 distribution modelling during range expansion. *Biology Letters* 4:577-580.
- 22 deMenocal P. B. 1995. Plio-Pleistocene African climate. *Science* 270:53-59.
- 23 Dransfield J. 1988. The palms of Africa and their relationships. Pages 95-103 *in* P. Goldblatt
24 and P.P. Lowry, editors. *Modern systematic studies in African botany*. Missouri Botanical
25 Garden Press, St. Louise, USA.

- 1 Dransfield J., N. W. Uhl, C. B. Asmussen, W. J. Baker, M. M. Harley and C. E. Lewis. 2008.
- 2 Genera Palmarum. The evolution and classification of palms. Royal Botanic Gardens, Kew,
- 3 Richmond, UK.
- 4 Dutilleul P., P. Clifford, S. Richardson and D. Hemon. 1993. Modifying the *t* test for assessing
- 5 the correlation between two spatial processes. *Biometrics* 49:305-314.
- 6 Dynesius M. and R. Jansson. 2000. Evolutionary consequences of changes in species'
- 7 geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the*
- 8 *National Academy of Sciences USA* 97:9115-9120.
- 9 Fjeldså J. and J. C. Lovett. 1997. Geographical patterns of old and young species in African
- 10 forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity*
- 11 *and Conservation* 6:325-346.
- 12 Govaerts R., J. Dransfield , S. Zona, D. R. Hodel and A. Henderson. 2013. World Checklist of
- 13 *Arecaceae*. Facilitated by the Royal Botanic Gardens Kew, UK. Available at:
- 14 <http://apps.kew.org/wcsp/>. (Last accessed 8 March 2013).
- 15 Hamilton A. C. and D. Taylor. 1991. History of climate and forests in tropical Africa during
- 16 the last 8 million years. *Climatic Change* 19:65-78.
- 17 Harrison S. P. and C. I. Prentice. 2003. Climate and CO₂ controls on global vegetation
- 18 distribution at the last glacial maximum: analysis based on palaeovegetation data, biome
- 19 modelling and palaeoclimate simulations. *Global Change Biology* 9:983-1004.
- 20 Haywood A. M. and P. J. Valdes. 2004. Modelling Pliocene warmth: contribution of
- 21 atmosphere, oceans and cryosphere. *Earth and Planetary Science Letters* 218:363-377.
- 22 Haywood A. M., M. A. Chandler, P. J. Valdes, U. Salzmann, D. J. Lunt and H. J. Dowsett.
- 23 2009. Comparison of mid-Pliocene climate predictions produced by the HadAM3 and
- 24 GCMAM3 General Circulation Models. *Global and Planetary Change* 66:208-224.
- 25 Hewitt G. M. 2004. Genetic consequences of climatic oscillations in the Quaternary.
- 26 *Philosophical Transactions of the Royal Society of London B* 359:183-195.

- 1 Holstein N. and S. Renner. 2011. A dated phylogeny and collection records reveal repeated
2 biome shifts in the African genus *Coccinia* (Cucurbitaceae). BMC Evolutionary Biology
3 11:28.
- 4 Jacobs B. F. 2004. Palaeobotanical studies from tropical Africa: relevance to the evolution of
5 forest, woodland and savannah biomes. Philosophical Transactions of the Royal Society of
6 London B 359:1573-1583.
- 7 Jansson R. 2003. Global patterns in endemism explained by past climate change. Proceedings
8 of the Royal Society of London B 270:583-590.
- 9 Kissling W. D. and G. Carl. 2008. Spatial autocorrelation and the selection of simultaneous
10 autoregressive models. Global Ecology and Biogeography 17:59-71.
- 11 Kissling W. D., W. L. Eiserhardt, W. J. Baker, F. Borchsenius, T. L. P. Couvreur, H. Balslev
12 and J. C. Svenning. 2012a. Cenozoic imprints on the phylogenetic structure of palm species
13 assemblages worldwide. Proceedings of the National Academy of Sciences USA 109:7379-
14 7384.
- 15 Kissling W. D., W. J. Baker, H. Balslev, A. S. Barfod, F. Borchsenius, J. Dransfield, R.
16 Govaerts and J. C. Svenning. 2012b. Quaternary and pre-Quaternary historical legacies in
17 the global distribution of a major tropical plant lineage. Global Ecology and Biogeography
18 21:909-921.
- 19 Linder H. P. 2001. Plant diversity and endemism in sub-Saharan tropical Africa. Journal of
20 Biogeography 28:169-182.
- 21 Maley J. 1991. The African rain forest vegetation and palaeoenvironments during late
22 Quaternary. Climatic Change 19:79-98.
- 23 Maley J. 1996. The African rain forest - main characteristics of changes in vegetation and
24 climate from the Upper Cretaceous to the Quaternary. Pages 31-37 in I. Alexander, M. D.
25 Swaine, and R. Watling, editors. Essays on the ecology of the Guinea - Congo rain forest.
26 Royal Society of Edinburg Proceedings, Edinburgh.

- 1 Mayr E. and R. J. O'Hara. 1986. The biogeographic evidence supporting the Pleistocene forest
2 refuge hypothesis. *Evolution* 40:55-67.
- 3 Moore H. E. 1973. Palms in the tropical forest ecosystems of Africa and South America. Pages
4 63-88 in B. J. Meggers, E. S. Ayensu, and W. D. Duckworth, editors. *Tropical forest
5 ecosystems in Africa and South America: A comparative review*. Smithsonian Institution
6 Press, Washington, USA.
- 7 Morley R. J. 2000. *Origin and evolution of tropical rain forests*, John Wiley & Sons, Ltd,
8 Chichester, UK.
- 9 Pan A. D., B. F. Jacobs, J. Dransfield and W. J. Baker. 2006. The fossil history of palms
10 (Arecaceae) in Africa and new records from the Late Oligocene (28-27 Mya) of north-
11 western Ethiopia. *Botanical Journal of the Linnean Society* 151:69-81.
- 12 Parmentier I., Y. Malhi, B. Senterre, R. J. Whittaker, A. Alonso, M. P. B. Balinga, A.
13 Bakayoko, F. Bongers, C. Chatelain, J. A. Comiskey, R. Cortay, M. N. D. Kamdem, J. L.
14 Doucet, L. Gautier, W. D. Hawthorne, Y. A. Issembe, F. N. Kouame, L. A. Kouka, M. E.
15 Leal, J. Lejoly, S. L. Lewis, L. Nusbaumer, M. P. E. Parren, K. S. H. Peh, O. L. Phillips, D.
16 Sheil, B. Sonke, M. S. M. Sosef, T. C. H. Sunderland, J. Stropp, H. Ter Steege, M. D.
17 Swaine, M. G. P. Tchouto, B. S. van Gernerden, J. L. C. H. van Valkenburg and H. Woll.
18 2007. The odd man out? Might climate explain the lower tree alpha-diversity of African rain
19 forests relative to Amazonian rain forests? *Journal of Ecology* 95:1058-1071.
- 20 Plana V. 2004. Mechanisms and tempo of evolution in the African Guineo-Congolian
21 rainforest. *Philosophical Transactions of the Royal Society of London B* 359:1585-1594.
- 22 Plana V., A. Gascoigne, L. L. Forrest, D. Harris and R. T. Pennington. 2004. Pleistocene and
23 pre-Pleistocene *Begonia* speciation in Africa. *Molecular Phylogenetics and Evolution*
24 31:449-461.
- 25 Phillips S. J., R. P. Anderson and R. E. Schapire. 2006. Maximum entropy modeling of species
26 geographic distributions. *Ecological Modelling* 190:231-259.

- 1 Pound M. J., A. M. Haywood, U. Salzmann, J. B. Riding, D. J. Lunt and S. J. Hunter. 2011. A
- 2 Tortonian (Late Miocene, 11.61-7.25 Ma) global vegetation reconstruction.
- 3 *Palaeogeography, Palaeoclimatology, Palaeoecology* 300:29-45.
- 4 R Development Core Team. 2012. R: a language and environment for statistical computing.
- 5 [2.15]. Vienna, Austria.
- 6 Randall, D.A., R.A. Wood, S. Bony, R. Colman, T. Fichefet, J. Fyfe, V. Kattsov, A. Pitman, J.
- 7 Shukla, J. Srinivasan, R.J. Stouffer, A. Sumi and K.E. Taylor, 2007: Climate models and
- 8 their evaluation. In: *Climate change 2007: The physical science basis. Contribution of*
- 9 *Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on*
- 10 *Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt,
- 11 M.Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United
- 12 Kingdom and New York, NY, USA.
- 13 Rakotoarinivo, M., A. Blach-Overgaard, W. J. Baker, J. Dransfield, J. Moat and J.-C.
- 14 Svenning. 2013. Palaeo-precipitation is a major determinant of palm species richness
- 15 patterns across Madagascar: a tropical biodiversity hotspot. *Proceedings of the Royal*
- 16 *Society B* 280: 20123048
- 17 Ricklefs R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology*
- 18 *Letters* 7:1-15.
- 19 Salzmann U., A. M. Haywood, D. J. Lunt, P. J. Valdes and D. J. Hill. 2008. A new global
- 20 biome reconstruction and data-model comparison for the Middle Pliocene. *Global Ecology*
- 21 *and Biogeography* 17:432-447.
- 22 Sandel B., L. Arge, B. Dalsgaard, R. G. Davies, K. J. Gaston, W. J. Sutherland and J.-C.
- 23 Svenning. 2011. The influence of late Quaternary climate-change velocity on species
- 24 endemism. *Science* 334:660-664.
- 25 Senut B., M. Pickford and L. Ségalen. 2009. Neogene desertification of Africa. *Comptes*
- 26 *Rendus Geosciences* 341:591-602.

- 1 Sheffield J. and E. F. Wood. 2008. Projected changes in drought occurrence under future
2 global warming from multi-model, multi-scenario, IPCC AR4 simulations. *Climate*
3 *Dynamics* 31:79-105.
- 4 Svenning J.-C. and F. Skov. 2007. Ice age legacies in the geographical distribution of tree
5 species richness in Europe. *Global Ecology and Biogeography* 16:234-245.
- 6 Svenning J. C. 2003. Deterministic Plio-Pleistocene extinctions in the European cool-temperate
7 tree flora. *Ecology Letters* 6:646-653.
- 8 Svenning J. C., F. Borchsenius, S. Bjorholm and H. Balslev. 2008. High tropical net
9 diversification drives the New World latitudinal gradient in palm (Arecaceae) species
10 richness. *Journal of Biogeography* 35:394-406.
- 11 Tolley K. A., C. R. Tilbury, G. J. Measey, M. Menegon, W. R. Branch and C. A. Matthee.
12 2011. Ancient forest fragmentation or recent radiation? Testing refugial speciation models
13 in chameleons within an African biodiversity hotspot. *Journal of Biogeography* 38:1748-
14 1760.
- 15 Thuiller W., B. Lafourcade, R. Engler and M. B. Araujo. 2009. BIOMOD - a platform for
16 ensemble forecasting of species distributions. *Ecography* 32:369-373.
- 17 Tuley P. 1995. *The palms of Africa*. The Trendrine Press, Zennor, St. Ives, Cornwall, UK.
- 18 Voelker G., R. K. Outlaw and R. C. K. Bowie. 2010. Pliocene forest dynamics as a primary
19 driver of African bird speciation. *Global Ecology and Biogeography* 19:111-121.
- 20 Wang, J., P. M. Rich and K. P. Price. 2003. Temporal responses of NDVI to precipitation and
21 temperature in the central Great Plains, USA. *International Journal of Remote Sensing*. 11:
22 2345-2364.
- 23 Wing, S.L., L.J. Hickey and C. C. Swisher. 1993. Implications of an exceptional fossil flora for
24 Late Cretaceous vegetation. *Nature* 363:342-344.
- 25 Zachos J., M. Pagani, L. Sloan, E. Thomas and K. Billups. 2001. Trends, rhythms, and
26 aberrations in global climate 65 Ma to present. *Science* 292:686-693.

Table 1 Standardized coefficients from minimum adequate ordinary least square (OLS) and spatial autoregressive (SAR) models constructed to explain species richness across all 100 × 100 km grid cells where palms are present for all 62 palm species ($n = 2161$ cells), 43 rainforest species ($n = 999$ cells) and 16 open-habitat species ($n = 1835$ cells). For model selection and details see the *Methods* section. Significant linear effects detected in both OLS and SAR models are indicated by bold text.

	All palms		Rainforest palms		Open-habitat palms	
	OLS	SAR	OLS	SAR	OLS	SAR
PREC	0.667 ^{***}	0.625 ^{***}	0.667 ^{***}	0.532 ^{***}	0.440 ^{***}	0.207 ^{**}
PREC ²	0.014 ^{n.s.}	-0.249 ^{***}	0.132 ^{***}	-0.116 [*]	-0.187 ^{***}	-0.239 ^{***}
PREC ³	-0.229 ^{***}	0.090 [*]	-0.391 ^{***}	-0.032 ^{n.s.}	-0.408 ^{***}	-0.019 ^{n.s.}
MAT	0.190 ^{***}	0.106 [*]	0.140 ^{***}	0.121 [*]	0.152 ^{***}	0.211 ^{***}
MAT ²	-0.225 ^{***}	-0.082 ^{**}	-0.417 ^{***}	-0.315 ^{***}	-0.212 ^{***}	-0.102 ^{**}
MAT ³	-0.147 ^{***}	-0.046 ^{n.s.}	-0.380 ^{***}	-0.223 ^{***}	-0.093 [*]	-0.062 ^{n.s.}
PET	-0.073 ^{***}	0.012 ^{n.s.}	-	-	-0.099 ^{***}	0.004 ^{n.s.}
VEG	0.082 ^{***}	0.053 ^{***}	0.091 ^{***}	0.041 ^{**}	0.179 ^{***}	0.073 ^{***}
SOIL	0.094 ^{***}	0.065 ^{***}	-	-	0.179 ^{***}	0.148 ^{***}
TOPO	0.095 ^{***}	0.078 ^{***}	-0.054 [*]	0.073 ^{***}	-	-
HII	0.041 [*]	0.102 ^{***}	-	-	-	-
HPH	0.130 ^{***}	0.084 ^{***}	0.188 ^{***}	0.087 ^{***}	0.121 ^{***}	0.123 ^{***}
LGM _{PREC}	-	-	-	-	0.166 ^{***}	0.071 ^{n.s.}
LGM _{PREC} ²	-	-	-	-	-	-
LGM _{PREC} ³	-	-	-	-	-	-
LGM _{TEMP}	0.026 ^{n.s.}	0.070 ^{n.s.}	0.042 [*]	0.083 ^{n.s.}	-	-
PLIO _{PREC}	0.138 ^{***}	0.127 ^{***}	0.475 ^{***}	0.259 ^{***}	-0.168 ^{***}	0.002 ^{n.s.}

PLIO _{PREC} ²	0.104 ^{***}	0.002 ^{n.s.}	0.064 [*]	0.056 ^{n.s.}	0.132 ^{***}	0.017 ^{n.s.}
PLIO _{PREC} ³	0.024 ^{n.s.}	0.014 ^{n.s.}	-0.157 ^{***}	0.012 ^{n.s.}	0.059 ^{n.s.}	0.016 ^{n.s.}
PLIO _{TEMP}	0.062 ^{**}	0.029 ^{n.s.}	0.072 ^{**}	0.048 ^{n.s.}	-0.043 ^{n.s.}	-0.006 ^{n.s.}
MIO _{PREC}	-0.237 ^{***}	-0.064 ^{n.s.}	-0.241 ^{***}	-0.084 ^{n.s.}	-0.062[*]	-0.145[*]
MIO _{TEMP}	-0.063 [*]	-0.074 ^{n.s.}	0.076 [*]	0.013 ^{n.s.}	-	-
MIO _{TEMP} ²	-0.018 ^{n.s.}	-0.043 [*]	-	-	-	-
MIO _{TEMP} ³	0.025 ^{n.s.}	0.037 ^{n.s.}	-	-	-	-
R ² _{OLS-adj} [†]	0.708	-	0.699	-	0.392	-
R ² _{PRED} [‡]	-	0.618	-	0.629	-	0.312
R ² _{PRED+SPA}	-	0.923	-	0.917	-	0.818
CE [§]						
AIC	396.9	-1906.5	494.7	-440.9	111.8	-1600.4
Moran's I	0.706 ^{***}	-0.021 ^{n.s.}	0.655 ^{***}	0.021 ^{n.s.}	0.672 ^{***}	0.006 ^{n.s.}
k [¶]	-	5	-	3	-	5

-
- 1 Predictor abbreviations and transformations see Appendix B, Table B1. ‘-’, predictor not
2 selected. The asterisks indicate significance levels: ^{***}, $p < 0.001$; ^{**}, $p < 0.01$; ^{*}, $p < 0.05$; ^{n.s.}, not
3 significant; [†] adjusted explained variance; [‡] variance explained by the predictors alone; [§] variance
4 explained by predictors and space; [¶] number of nearest neighbors used to define the spatial
5 weights matrix (SAR models). Moran's *I* significance levels were determined with permutation
6 tests ($n = 1000$ permutations).

1 **Figure 1** Palm species richness patterns across Africa (a–c) and paleoclimatic predictors used
2 in this study (d–i). Maps show (a) total palm species richness and subsets of (b) rainforest and
3 (c) open-habitat palm species richness (maps are color coded by number of species), along with
4 paleoprecipitation anomalies (in mm/yr) for the (d) Pleistocene (Last Glacial Maximum,
5 LGM), (e) Pliocene, and (f) Miocene, and paleotemperature anomalies (in °C) for the (g)
6 Pleistocene (LGM), (h) Pliocene, and (i) Miocene. All anomalies are relative to current
7 climate. Maps are Lambert Azimuthal Equal Area projections shown at 100×100 km spatial
8 resolution.

9
10 **Figure 2** Partial residual plots showing the effects of the most important contemporary and
11 paleoclimatic climate predictors for species richness among all palms (a,b), rainforest palms
12 (c,d), and open-habitat palms (e,f). Plots illustrate the relationship between variables once all
13 other predictors have been statistically accounted for in a multiple-predictor model (for models
14 see Table 1). The variables include (a) present-day precipitation, (b) Pliocene precipitation
15 anomaly, (c) present-day precipitation (square root transformed), (d) Pliocene precipitation
16 anomaly, (e) present-day precipitation, and (f) Miocene precipitation anomaly. Each dot
17 represents one 100×100 km grid cell.

All palms

Rainforest palms

Open-habitat palms