



**HAL**  
open science

## **Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna**

Thomas L P Couvreur, Gilles Dauby, Anne Blach-Overgaard, Vincent Deblauwe, Steven Dessein, Vincent Droissart, Oliver J Hardy, David J Harris, Steven B Janssens, Alexandra C Ley, et al.

### ► To cite this version:

Thomas L P Couvreur, Gilles Dauby, Anne Blach-Overgaard, Vincent Deblauwe, Steven Dessein, et al.. Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna. *Biological Reviews*, 2021, 96 (1), pp.16-51. <10.1111/brv.12644>. <insu-02940669>

**HAL Id: insu-02940669**

**<https://insu.hal.science/insu-02940669v1>**

Submitted on 16 Sep 2020















**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY-NC 4.0 - Attribution - Non-commercial use - International License

# Tectonics, climate and the diversification of the tropical African terrestrial flora and fauna

Thomas L.P. Couvreur<sup>1†\*</sup> , Gilles Dauby<sup>2,3</sup> , Anne Blach-Overgaard<sup>4,5</sup> , Vincent Deblauwe<sup>6,7</sup> , Steven Desein<sup>8</sup> , Vincent Droissart<sup>2,9,10,11</sup> , Oliver J. Hardy<sup>3</sup> , David J. Harris<sup>12</sup> , Steven B. Janssens<sup>8</sup> , Alexandra C. Ley<sup>13</sup>, Barbara A. Mackinder<sup>12</sup> , Bonaventure Sonké<sup>9</sup> , Marc S.M. Sosef<sup>8</sup> , Tariq Stévant<sup>10,11</sup>, Jens-Christian Svenning<sup>4,5</sup> , Jan J. Wieringa<sup>14</sup> , Adama Faye<sup>15</sup> , Alain D. Missoup<sup>16</sup> , Krystal A. Tolley<sup>17,18</sup> , Violaine Nicolas<sup>19</sup> , Stéphan Ntie<sup>20</sup> , Frédéric Fluteau<sup>21</sup> , Cécile Robin<sup>22</sup>, François Guillocheau<sup>22</sup>, Doris Barboni<sup>23</sup>  and Pierre Sepulchre<sup>24†</sup> 

<sup>1</sup>IRD, DIADE, University of Montpellier, Montpellier, France

<sup>2</sup>AMAP Lab, IRD, CIRAD, CNRS, INRA, University of Montpellier, Montpellier, France

<sup>3</sup>Laboratoire d'évolution Biologique et Ecologie, Faculté des Sciences, Université Libre de Bruxelles, CP160/12, Avenue F.D. Roosevelt 50, Brussels, 1050, Belgium

<sup>4</sup>Section for Ecoinformatics & Biodiversity, Department of Biology, Aarhus University, Ny Munkegade 114, Aarhus C, DK-8000, Denmark

<sup>5</sup>Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Ny Munkegade 114, Aarhus C, DK-8000, Denmark

<sup>6</sup>Center for Tropical Research (CTR), Institute of the Environment and Sustainability, University of California, Los Angeles (UCLA), Los Angeles, CA, 90095, U.S.A.

<sup>7</sup>International Institute of Tropical Agriculture (IITA), Yaoundé, Cameroon

<sup>8</sup>Meise Botanic Garden, Nieuwelaan 38, Meise, 1860, Belgium

<sup>9</sup>Laboratoire de Botanique Systématique et d'Écologie, École Normale Supérieure, Université de Yaoundé I, PO Box 047, Yaoundé, Cameroon

<sup>10</sup>Herbarium et Bibliothèque de Botanique Africaine, Université Libre de Bruxelles, Boulevard du Triomphe, Brussels, B-1050, Belgium

<sup>11</sup>Africa & Madagascar Department, Missouri Botanical Garden, St. Louis, MO, U.S.A.

<sup>12</sup>Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, U.K.

<sup>13</sup>Institut für Geobotanik und Botanischer Garten, University Halle-Wittenberg, Neuwerk 21, Halle, 06108, Germany

<sup>14</sup>Naturalis Biodiversity Center, Darwinweg 2, Leiden, 2333 CR, The Netherlands

<sup>15</sup>Laboratoire National de Recherches sur les Productions Végétales (LNRPV), Institut Sénégalais de Recherches Agricoles (ISRA), Route des Hydrocarbures, Bel Air BP 1386- CP18524, Dakar, Senegal

<sup>16</sup>Zoology Unit, Laboratory of Biology and Physiology of Animal Organisms, Faculty of Science, University of Douala, PO Box 24157, Douala, Cameroon

<sup>17</sup>South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont, Cape Town, 7735, South Africa

<sup>18</sup>School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits, 2050, South Africa

<sup>19</sup>Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, CP51, 57 rue Cuvier, Paris, 75005, France

<sup>20</sup>Département de Biologie, Faculté des Sciences, Université des Sciences et Techniques de Masuku, Franceville, BP 941, Gabon

<sup>21</sup>Institut de Physique du Globe de Paris, CNRS, Université de Paris, Paris, F-75005, France

<sup>22</sup>CNRS, Géosciences Rennes, UMR6118, University of Rennes, Rennes, 35042, France

<sup>23</sup>CEREGE, Aix-Marseille University, CNRS, IRD, Collège de France, INRA, Technopole Arbois Méditerranée, BP80, Aix-en-Provence cedex4, 13545, France

<sup>24</sup>Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSIL, CEA-CNRS-UVSQ, Université Paris-Saclay, Gif-sur-Yvette, F-91191, France

\* Address for correspondence (Tel: +00 593 (0)9 86 19 44 55; E-mail: thomas.couvreur@ird.fr)

† Authors contributed equally.

## ABSTRACT

Tropical Africa is home to an astonishing biodiversity occurring in a variety of ecosystems. Past climatic change and geological events have impacted the evolution and diversification of this biodiversity. During the last two decades, around 90 dated molecular phylogenies of different clades across animals and plants have been published leading to an increased understanding of the diversification and speciation processes generating tropical African biodiversity. In parallel, extended geological and palaeoclimatic records together with detailed numerical simulations have refined our understanding of past geological and climatic changes in Africa. To date, these important advances have not been reviewed within a common framework. Here, we critically review and synthesize African climate, tectonics and terrestrial biodiversity evolution throughout the Cenozoic to the mid-Pleistocene, drawing on recent advances in Earth and life sciences. We first review six major geo-climatic periods defining tropical African biodiversity diversification by synthesizing 89 dated molecular phylogeny studies. Two major geo-climatic factors impacting the diversification of the sub-Saharan biota are highlighted. First, Africa underwent numerous climatic fluctuations at ancient and more recent timescales, with tectonic, greenhouse gas, and orbital forcing stimulating diversification. Second, increased aridification since the Late Eocene led to important extinction events, but also provided unique diversification opportunities shaping the current tropical African biodiversity landscape. We then review diversification studies of tropical terrestrial animal and plant clades and discuss three major models of speciation: (i) geographic speciation *via* vicariance (allopatry); (ii) ecological speciation impacted by climate and geological changes, and (iii) genomic speciation *via* genome duplication. Geographic speciation has been the most widely documented to date and is a common speciation model across tropical Africa. We conclude with four important challenges faced by tropical African biodiversity research: (i) to increase knowledge by gathering basic and fundamental biodiversity information; (ii) to improve modelling of African geophysical evolution throughout the Cenozoic *via* better constraints and downscaling approaches; (iii) to increase the precision of phylogenetic reconstruction and molecular dating of tropical African clades by using next generation sequencing approaches together with better fossil calibrations; (iv) finally, as done here, to integrate data better from Earth and life sciences by focusing on the interdisciplinary study of the evolution of tropical African biodiversity in a wider geodiversity context.

*Key words:* tropical Africa, dated molecular phylogenies, palaeoclimate models, speciation models, fossils, African geology, Cenozoic

## CONTENTS

I. Introduction	3
II. The physical context	3
III. Six major ‘geo-climatic’ periods impacting tropical african biodiversity	6
(1) Mass extinction? The Cretaceous–Paleogene boundary (~66 Ma)	8
(2) Extreme conditions: the Paleocene–Eocene climatic optimum (66–51 Ma)	8
(a) <i>A pan-African rain forest?</i>	10
(b) <i>The golden age of mangroves</i>	11
(3) ‘Descent into the icehouse’: Eocene–Oligocene transition (34.1–33.6 Ma)	11
(4) Renewed warm climates: early Miocene to the middle Miocene climatic optimum (~17–14.7 Ma)	12
(5) The middle Miocene climate transition (15–13 Ma)	13
(6) The end of equable climates: from the late Miocene to the mid-Pleistocene (11–1.5 Ma)	14
IV. Major speciation models of tropical african biodiversity	16
(1) The geographic model	17
(a) <i>Pleistocene lowland forest refugia mechanism</i>	17
(b) <i>Fragmentation–refugia mechanism</i>	19
(c) <i>Montane refugia mechanism</i>	20
(d) <i>Riverine barrier mechanism</i>	21
(2) The ecological model	22
(a) <i>Ecotone speciation mechanism</i>	22
(b) <i>Montane gradient speciation mechanism</i>	23
(c) <i>Peripatric speciation mechanism</i>	23
(d) <i>Vanishing refugia mechanism</i>	23
(e) <i>Adaptive radiation</i>	24
(3) The genomic model: polyploidization	24
V. Conclusions	25
VI. Acknowledgements	26

VII. References .....	26
VIII. Supporting information .....	36

## I. INTRODUCTION

The African continent is a land of biological contrasts (Linder, 2001). Africa hosts the largest desert in the world, the Sahara, together with some of the most endemic-rich (e.g. Cape Flora; Linder, 2003) and species-rich (e.g. African rain forests; Linder *et al.*, 2012) ecosystems worldwide. In this review, we focus on tropical Africa, loosely defined as the region below the Sahara and excluding southern (austral) Africa and Madagascar (Fig. 1). A central focus is the tropical rain forests as they contain the highest levels of species diversity and endemism for both plants (Linder *et al.*, 2012; Droissart *et al.*, 2018) and animals (Jenkins, Pimm, & Joppa, 2013) across the continent. Tropical rain forests are distributed from West Africa into the Congo Basin, Guineo-Congolia, and in smaller patches along the East African coast and Eastern Arc Mountains (Tanzania–Kenya). African rain forests are, however, overall less species rich than tropical rain forests in other tropical regions such as the Neotropics (Richards, 1973; reviewed in Couvreur, 2015).

Besides tropical rain forest, numerous other biomes have been identified but their limits and characteristics depend on the biota studied, the data and the approach used (White, 1983; Linder, 2001; Klerk *et al.*, 2002; Linder *et al.*, 2005, 2012; Lévêque *et al.*, 2007; Droissart *et al.*, 2018). East Africa is particularly diverse with substantially more bioregions identified than in West or Central Africa, reflecting higher topographic and climatic diversity (Linder, 2017; Droissart *et al.*, 2018). Remarkably, bioregions defined using different groups (e.g. plants, animals) show broad general congruence (Linder *et al.*, 2012). Finally, using a slightly different concept to that of a biome (which is solely based on species composition), Linder (2014) identified six different groups of clades or ‘floras’ for Africa, which shared similar geographical distributions, extra-African geographical affinities, diversification histories, and maximum ages.

Africa contains eight of the now 36 recognized global biodiversity hotspots (Fig. 1B; Mittermeier *et al.*, 2011). Additional hotspots defined in terms of species richness have been identified in the coastal regions of Cameroon, Gabon, the Republic of Congo, and Mozambique (Küper *et al.*, 2004; Sosef *et al.*, 2017). Noteworthy are the East Afro-montane hotspots which contain the second highest total number of endemic vertebrate genera on Earth (Mittermeier *et al.*, 2011). The Eastern Arc Mountain hotspot, as originally defined but now comprising two separate hotspots (Mittermeier *et al.*, 2011), was estimated to have the highest concentration of endemic plants (number of endemics per 100 km<sup>2</sup>) of all hotspots (Myers *et al.*, 2000). Overall, African biodiversity is vulnerable with a high risk of extinction by the end of this century for both plants (McClellan *et al.*, 2005; Blach-Overgaard *et al.*, 2015; Stévant

*et al.*, 2019) and animals (Thuiller *et al.*, 2006; Tolley *et al.*, 2016), and Africa is expected to host more than half of global population growth by 2050 (Gerland *et al.*, 2014).

Understanding the evolutionary history of regions and how clades originated and diversified are important facets of biodiversity conservation (Erwin, 1991). Indeed, molecular dating and subsequent biogeographic and diversification analyses of reconstructed phylogenetic trees have become routine in many studies on the evolution of biodiversity (Sauquet, 2013; Morlon, 2014; Sanmartín & Meseguer, 2016; Silvestro *et al.*, 2018). However, as for all methods, these approaches have potential limits (e.g. Carruthers & Scotland, 2020; Louca & Pennell, 2020) which are important to keep in mind when interpreting their outcome. The latest review on the evolution of tropical African flora and fauna, mainly focused on the tropical rain forest biome, is now 15 years old (Plana, 2004), and concluded that “The small number of species-level phylogenies for African rainforest plants hinders a more incisive and detailed study into the historical assembly of these continental forests” (p. 1585).

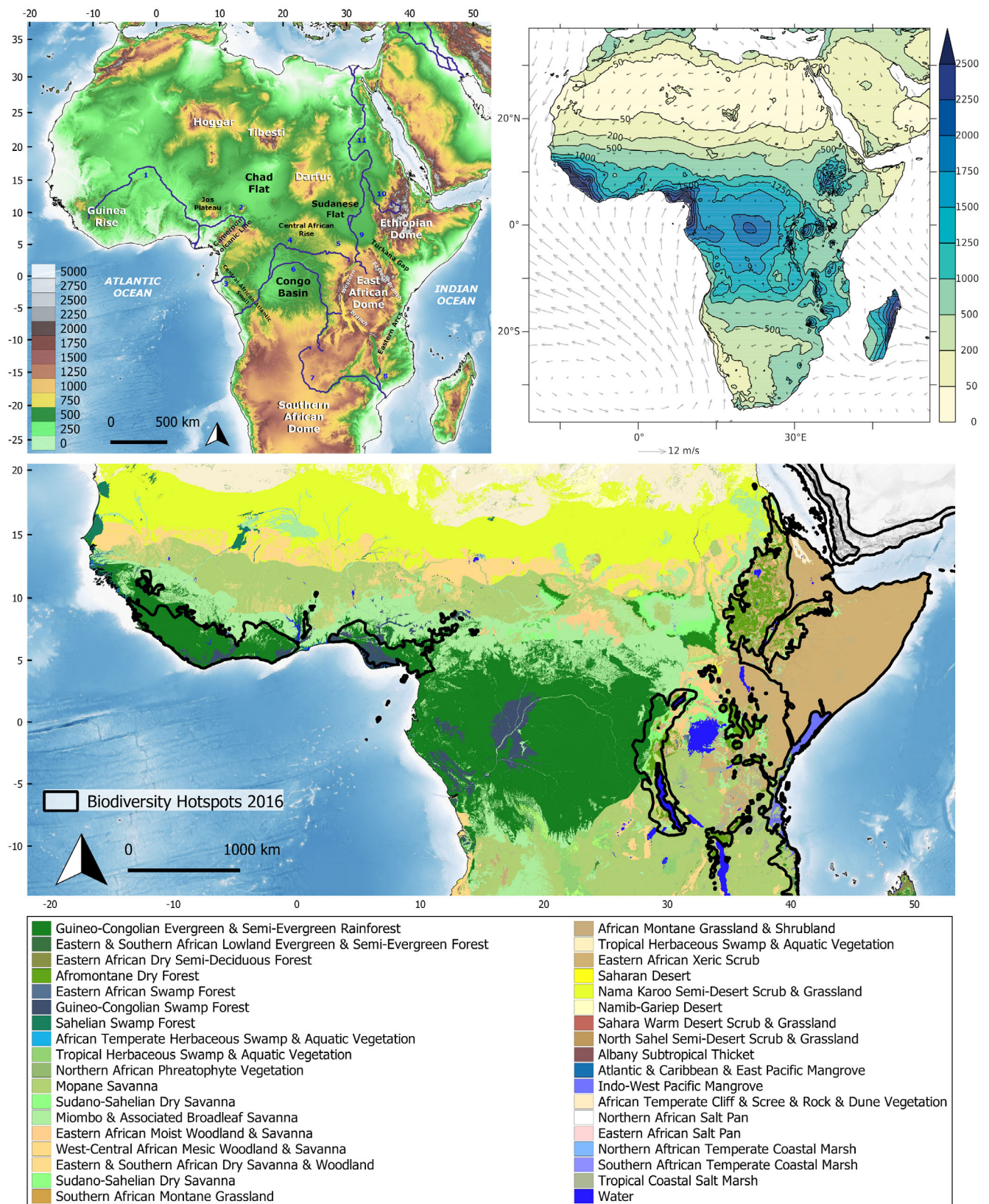
To date, around 90 dated molecular phylogenies have been published documenting the diversification of tropical African animals and plants (see online Supporting Information, Appendix S1). Most clades diversified *within* tropical Africa and this will be the focus of our review. Biogeographic analyses of pantropical plant clades tend to support the idea that Africa has been an important source of tropical diversity (the ‘out of Africa’ hypothesis), with numerous major tropical families inferred to have originated in Africa (e.g. Muellner *et al.*, 2006; Zhou *et al.*, 2012; Couvreur, 2015). In animals, the origin of major groups is less clear with studies disagreeing on the geographical origin of groups such as Mammalia (Springer *et al.*, 2011; O’Leary *et al.*, 2013).

In parallel, knowledge of the geophysical settings of Africa has improved. Information from both modelling and field-work has improved our understanding of the topographic history of the continent, and numerical climate simulations have begun to clarify how these changes influenced the climate of Africa. This new wealth of information provides a unique opportunity to improve our understanding of the diversification of tropical African biodiversity.

Here, we first review African biodiversity and climate events throughout the Cenozoic and link these to diversification processes in tropical African terrestrial plant and animal clades. Finally, using dated molecular phylogenetic and diversification studies, we synthesize the different speciation models and mechanisms proposed for tropical Africa.

## II. THE PHYSICAL CONTEXT

Climatically, tropical Africa is bounded by three regions receiving less than 200 mm of precipitation per year



(Figure legend continues on next page)

(Fig. 1B): the Sahara Desert to the north; the Kalahari and Namib deserts to the south; and the Ogaden desert in the Horn of Africa to the northeast. The rainfall regime in tropical Africa also varies longitudinally, with the western African monsoon region and the western Congo Basin being far wetter (Fig. 1B; >2000 mm/year) than the margin of the continent east of the East African and Ethiopian Domes. Rainfall over the Congo Basin is considered to follow a bimodal regime, with the rainiest seasons (precipitation ~200 mm/month) occurring during so-called ‘transition seasons’, from March to May and September to November. During these two seasons, convective activity is at its peak and as a result, the Congo Basin climate has considerable influence over atmospheric dynamics at the planetary scale (Washington *et al.*, 2013). The transition seasons are separated by two dry seasons from June to August and December to February. While the western and southern regions of the Congo Basin exhibit this precipitation regime, the dry season is less pronounced to the east of the Basin, along the western flank of the East African Dome. Further north and south of the Congo Basin, the bimodal rainfall regime subsides, and a single rainy season occurs.

Rainfall patterns in the East African Dome region also display a bimodal distribution, although less pronounced than in the Congo Basin. Precipitation is highest over the topographical highs, enhanced by orographic lift and the convergence of the Atlantic and Indian air masses. To the east, surface winds over coastal areas are controlled by the Asian monsoon circulation over the Indian Ocean. The dry season occurs during boreal summer, when moisture from the Indian Ocean is transported north-eastward toward the Indian continent. Conversely, during boreal winter wet air masses blowing from the tropical Indian Ocean enter coastal East Africa and trigger rainfalls. To the north, the region of the Horn of Africa is arid and marked by repeated events of severe inland droughts (Viste, Korecha, & Sorteberg, 2013), and even hyper-arid with deserts near the coast (Somali–Chelbi deserts). Conversely, the Ethiopian highlands (i.e. Ethiopian Dome) capture moisture from multiple sources (Viste & Sorteberg, 2013) and are characterized by high rates of orographic precipitation.

Finally, the climate of western tropical Africa is characterized by a monsoonal regime, the so-called West African monsoon. Thermal contrasts between sea-surface temperatures in the Gulf of Guinea and the surface temperature in the Sahelian region drive the seasonal reversal of surface winds,

bringing moisture inland. West African monsoon progression inland is characterized by a ‘jump’ between a first regime of high rainfall along the Guinean coast in May to July and a second period of less-intense precipitation over the Sahel from July to September (Im & Eltahir, 2018). During boreal winter, the Sahelian region is dry, with the tropospheric dynamics driven by north-easterlies channelled by the topographic features at the border of the Chad Basin, namely Hoggar, Tibesti and Darfur reliefs.

The modern topography of Africa (Fig. 1A; Guillocheau *et al.*, 2018) is characterized by a set of heterogeneously elevated plateaus that strongly influence temperature and rainfall patterns at the continental scale. The largest, the southern African (or Kalahari) Plateau, extends from 1500 to 2000 km longitudinally, and 2500 km latitudinally, with an elevation ranging between 1000 and 1500 m. In contrast to other major tropical regions such as South America and Southeast Asia, Africa is defined by passive rather than active continental margins (Goudie, 2005). The distribution of elevation in Africa is bimodal, an ancient feature probably inherited from the upper Palaeozoic (Doucouré & de Wit, 2003), with one peak around 300–400 m above sea level (asl) in central and west Africa and one ranging from 900 to 1100 m asl in southern and East Africa (Guillocheau *et al.*, 2018). The highest elevations correspond to the Kalahari Plateau, and the East African and Ethiopian Domes, but also to the Cameroon Highlands, Darfur, Tibesti, Hoggar and the Guinea Rise (Fig. 1A). The lowest elevations correspond to the Sahara and the Congo Basin (Fig. 1A).

Overall, the present-day topography of Central Africa is mostly a post-Eocene product of so-called very long (1000–2000 km) wavelength deformations that result from mantle dynamics. The study of planation surfaces (i.e. large-scale mainly flat surfaces) recording these deformations shows that the growth of the Cameroon Dome and East African Dome initiated 34 million years ago (Ma), the Angola mountains at 15–12 Ma, and that the low-elevation Congo Basin was uplifted between 10 and 3 Ma (Guillocheau *et al.*, 2018). However, understanding of the precise timing of topographic changes in Africa remains limited at the regional scale.

The relief in the East African Dome (East African Plateau, Fig. 1A) results both from large-scale doming [deformation of the crust due to mantle dynamics (plume, convection cell) and characterized by a long horizontal wavelength (500–1000 km) and some uplift of the Earth’s surface

**Fig 1.** The modern geophysical, climatic and vegetation setting of tropical Africa. (A) Topography of tropical Africa, modified from Guillocheau *et al.* (2018). Topographic and bathymetric data taken from the GEBCO 2020 Grid (doi: 10.5285/a29c5465-b138-234de053-6c86abc040b9). Scale on bottom left is altitude in meters. Numbers refer to major rivers: 1, Niger; 2, Benue; 3, Ogooué; 4, Ubangi; 5, Uele; 6, Congo; 7, Zambezi; 8, Shire; 9, White Nile; 10, Blue Nile; 11, Nile. (B) Summed annual rainfall amount (colour-shading, in millimetres) and averaged surface wind velocity (vectors, in m/s); rainfall data retrieved from the 1961–1990 climatology from the Climate Research Unit data set, wind velocities are averages from the 1989–2010 ERA-Interim reanalyses [data from New *et al.* (2002) and Dee *et al.* (2011)]. (C) Major vegetation types across Tropical Africa following Sayre *et al.* (2013). Major divisions are shown according to Sayre *et al.* (2013). Delimitation of biodiversity hotspots taken from <https://zenodo.org/record/3261807#.Xvu69IVKiUk> (doi: 10.5281/zenodo.3261807).

(0.1–2 km)] and from rifting [stretching and thinning of the lithosphere leading to the formation of a single or several central linear depressions bounded by normal faulting and, in the case of a single depression, by rift-flank uplifts] propagation within the East African Rift System (EARS) during the Late Miocene and the Pliocene (Macgregor, 2015). The EARS is divided into two major branches: the eastern branch, running from northern Ethiopia to northern Tanzania, and the western branch from Uganda to central Mozambique (Fig. 1A). Active rifting started during the Oligocene (30–24 Ma) along the northern East branch (Afar and Ethiopian plateau) progressing southwards raising the East African plateau (Chorowicz, 2005; but see Roberts *et al.*, 2012). Rifting in the western branch remains controversial (Roberts *et al.*, 2012) and is suggested to have initiated either during the middle Late Miocene, around 12 Ma (Chorowicz, 2005) or synchronously with the East branch around 25 Ma (Roberts *et al.*, 2012). Nevertheless, the Middle Miocene was an important period of tectonic activity and major uplift phases of the rift shoulders (Chorowicz, 2005; Ring, Albrecht, & Schrenk, 2018). Dynamic topography modelling suggests that the Kenyan dome uplifted from 500 m to 1000 m asl between 15 and 10 Ma (Wichura *et al.*, 2015).

Finally, the Eastern Arc Mountains consist of a series of 13 isolated fault-bounded mountain blocks that stretch from southern Kenya to eastern Tanzania (Burgess *et al.*, 2007) independent from the EARS (Fig. 1A). Geologically, these reliefs belong to the Mozambique Orogenic Belt, a major suture zone along which eastern and western Gondwana collided to form the Gondwana continent (Muhongo & Lenoir, 1994; Johnson *et al.*, 2003). The Eastern Arc Mountains were mainly formed by block faulting, which results from tensional forces in the Earth's crust causing large bodies of rock to uprise. The origin of this geological relief is possibly the result of thickening of the continental crust (due to magmatic underplating) *ca.* 640 Ma that subsequently exhumed in response to the continental collision that led to the formation of Gondwana at *ca.* 550 Ma (Muhongo, Kröner, & Nemchin, 2001; Johnson *et al.*, 2003). Faulting was suggested to have occurred between 290 and 180 Ma during the Karoo period (Griffiths, 1993; Newmark, 2002). Since then, the Eastern Arc Mountains have gone through repeated cycles of erosion and uplifting, with the latest uplift suggested to have occurred during the last 7 million years (Myr) coinciding with the development of the EARS (Griffiths, 1993; Newmark, 2002). Thus the Eastern Arc Mountains are geologically very old (>100 Ma), with their modern topography the result of more recent activity occurring in the region.

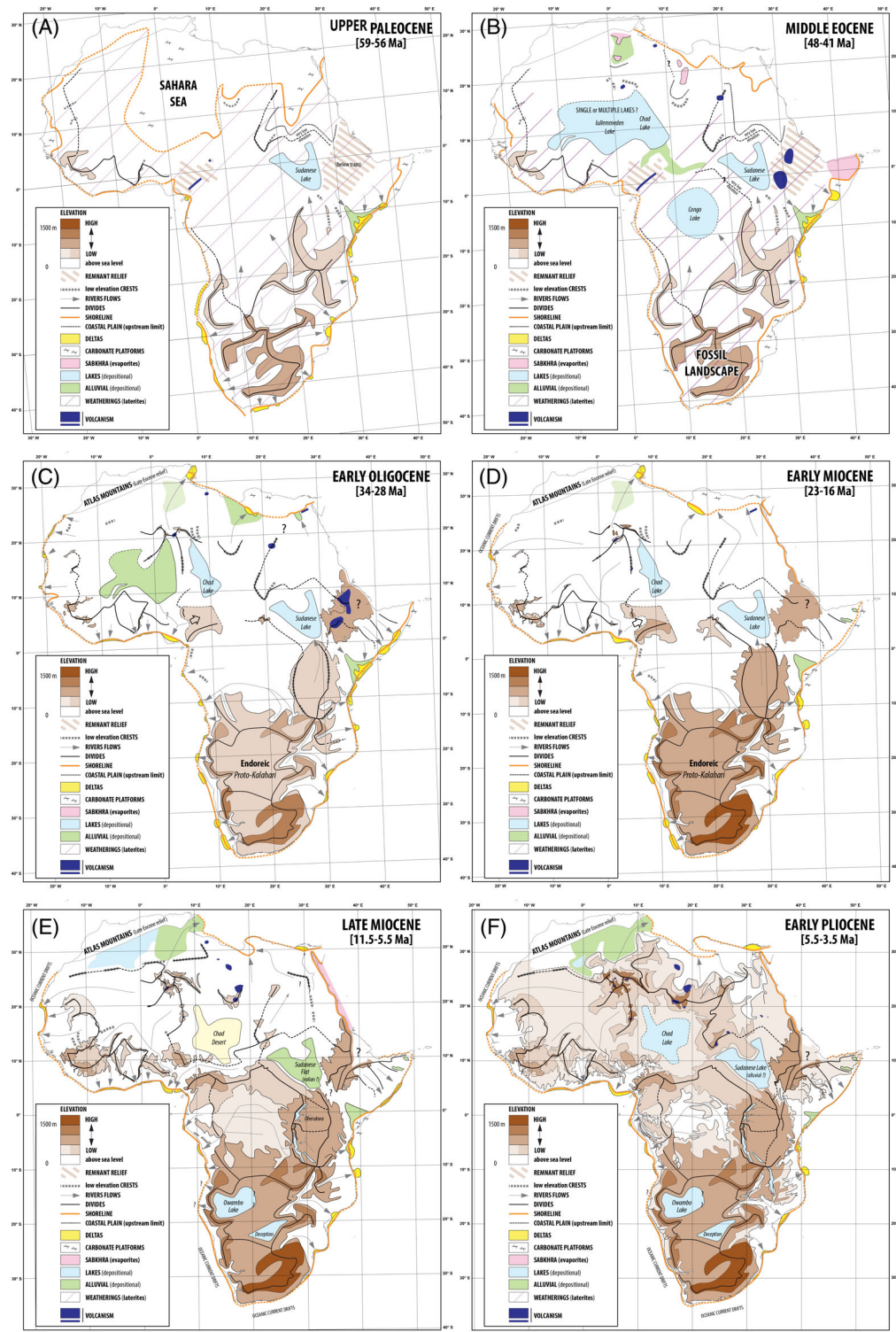
Understanding how these topographic changes altered the environment and biota during the Neogene is still challenging, as it requires (i) a rare combination of fine topographic reconstruction in space and time with climate simulations, and (ii) deciphering signals from larger climate changes induced by variations in atmospheric carbon dioxide concentration (CO<sub>2</sub> partial pressure, *p*CO<sub>2</sub>) and/or insolation.

### III. SIX MAJOR 'GEO-CLIMATIC' PERIODS IMPACTING TROPICAL AFRICAN BIODIVERSITY

Understanding climate change in tropical Africa requires the consideration of multiple drivers, including greenhouse gas-induced global cooling/warming, oceanic upwellings, continental drift, tectonic uplift, rifting, and insolation variations. Knowledge of African climatic evolution over the Cenozoic is incomplete because of (i) under-sampling compared to other continents, (ii) the relative rarity of fossilization in humid environments that was prevalent through the Cenozoic and, (iii) the weak sedimentation rates that affect most of the continent with the exception of East Africa.

The opening of the Equatorial Atlantic Ocean during the Albian (*ca.* 100 Ma) isolated the African continent from other landmasses which lasted until the closure of the east-Tethys seaway during the Middle Miocene Climatic Transition at *ca.* 14 Ma [see Hamon *et al.* (2013) for a review]. This ~84–65 Myr isolation contributed to the radiation of the Afrotheria, a unique group of mammals found only in Africa (Meredith *et al.*, 2011; O'Leary *et al.*, 2013). It was suggested as an important reason for the absence or low diversity of several major tropical plant clades in Africa compared with other tropical regions (e.g. Chloranthaceae, Elaeocarpaceae, Lauraceae, Winteraceae; Morley, 2000). Long-distance dispersal from Africa to other regions has been inferred for at least one plant family before the Cenozoic (Baker & Couvreur, 2013). Nevertheless, Late Cretaceous land connections between Gondwana landmasses might still have been possible. Such land connections have been suggested to explain distribution patterns within the Gondwanan salt-intolerant frogs Microhylidae and Natatanura which diverged during the Late Cretaceous (Van Bocxlaer *et al.*, 2006). The African continent has drifted northward by ~15° and rotated counter clockwise since the Early Cenozoic (Figs 2, 3A). This drift and the latitudinal palaeo-position of the African continent were likely crucial in determining the location of moisture advection and convection, and associated palaeo-temperature and rainfall patterns, as well as oceanic currents (Walker, 1990). Yet, among the numerous detailed accounts of the African fossil record for plants and animals throughout the Cenozoic, few have considered the influence of this drift and palaeo-position on biodiversity (Morley, 2000; Murray, 2000; Werdelin & Sanders, 2010; Gardner & Rage, 2016).

In this section, we review the climatic, geological and fossil history of Africa during the Cenozoic by focusing on six defining periods suggested to have impacted the diversification of tropical African biodiversity above the species level. We synthesize the latest data from Earth sciences – namely from geological fieldwork, palaeoclimate and palaeovegetation modelling – and life sciences (mainly dated molecular phylogenies). We do not review how these changes affected the evolution of hominoids which is covered elsewhere (e.g. Joordens *et al.*, 2019). Finally, we do not review in detail



**Fig 2.** Geological evolution of Africa during the Cenozoic. The maps depict the geological setting for six periods of the Cenozoic: (A) Late Paleocene (59–56 Ma), (B) Middle Eocene (48–41 Ma), (C) Early Oligocene (34–28 Ma), (D) Early Miocene (23–16 Ma), (E) Late Miocene (11.5–5.5 Ma) and (F) Early Pliocene (5.5–3.5 Ma). These maps characterize the palaeotopography and the palaeohydrography (drainage divides, catchment areas and paths of the main rivers) of Africa. They also include data such as shorelines, deltas, depositional alluvial plains and lakes. Reconstruction of the palaeotopography was based on the restoration of the stepped planation surfaces constituting the plateaus (Guillocheau *et al.*, 2018). These planation surfaces, mainly pediments and pediplains associated with weathering processes of laterite type, result from uplifts sometimes enhanced by climate (precipitation) changes. See Guillocheau *et al.* (2018) for details. The highest surfaces are the oldest (from Late Cretaceous to Middle Eocene) and the lowest are the youngest (Pliocene).

climate evolution during the Pleistocene (Trauth, Larrasoana, & Mudelsee, 2009; see Hoag & Svenning, 2017).

### (1) Mass extinction? The Cretaceous–Paleogene boundary (~66 Ma)

Although global climate exhibited a long-term cooling trend at the end of the Cretaceous (i.e. the late Maastrichtian), deposits of black shales in Egypt indicate a hot and humid climate in northern Africa at that time (Fathy *et al.*, 2018). However, both marine and continental records indicate a highly perturbed climate system in the 100000 years preceding the Cretaceous–Paleogene boundary (KPB) (Barnet *et al.*, 2018; Huber *et al.*, 2018). The KPB is marked by the last recorded mass extinction, triggered by global-scale environmental perturbations driven by both the massive volcanic eruptions of the Deccan Traps (India) (Courillot & Fluteau, 2014; Schoene *et al.*, 2015; Zhang *et al.*, 2018) and the Chicxulub bolide impact (Schulte *et al.*, 2010).

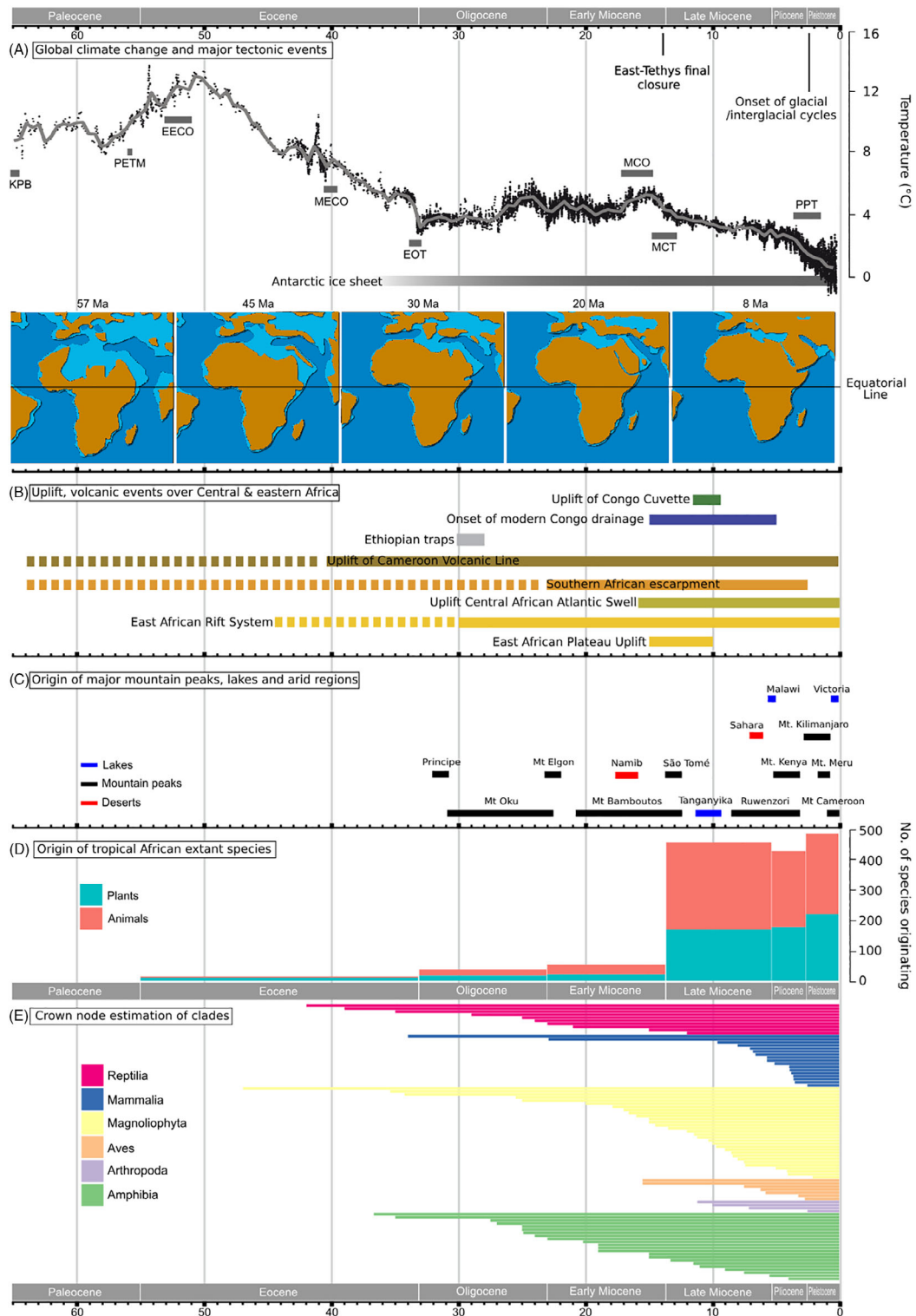
Our understanding of how these climatic fluctuations of variable length altered tropical African biodiversity remains limited because of the near absence of studied KPB fossils (Nichols & Johnson, 2008; Schulte *et al.*, 2010; Spicer & Collinson, 2014; Vajda & Bercovici, 2014). This is mirrored by few dated molecular phylogenies stretching back to the KPB (e.g. Koenen *et al.*, 2020). Based on these few data, extinction events are inferred at the KPB across the tropical African flora and fauna (Coetzee, 1993; Morley, 2000; Pan *et al.*, 2006; Schulte *et al.*, 2010). However, there is mounting evidence that the KPB did not lead to a large-scale taxonomic disruption in plants globally in contrast to marine biodiversity (McElwain & Punyasena, 2007; Cascales-Miñana & Cleal, 2014; Silvestro *et al.*, 2015). To a certain extent, this is also visible for the western African palm fossil record where most fossil genera span the boundary, going extinct during the Paleocene rather than at the KPB (Morley, 2000; Pan *et al.*, 2006). The study of west to central African palaeofloras by Salard-Chebaldaff (1990) also documents a continuous transition in fossil taxa throughout the boundary, with many forms common to the Late Cretaceous and Early Cenozoic. Globally, diversification analyses of vascular plant fossils suggested little extinction rate variation across the KPB (Cascales-Miñana & Cleal, 2014; Silvestro *et al.*, 2015). Dated molecular phylogenies also inferred little or no diversification rate changes across the KPB for several key pantropical lineages which originated during the Cretaceous (e.g. Arecaceae; Couvreur, Forest, & Baker, 2011a), although these should be interpreted with caution given the few data points available during that time period. Rather the KPB initiated an increase in speciation leading to a rapid increase in generic diversity (Cascales-Miñana & Cleal, 2014). Overall, the KPB also provided more ecological opportunities for increased global diversification of major animal groups such as mammals (Meredith *et al.*, 2011), frogs (Feng *et al.*, 2017; Portik *et al.*, 2019), birds (Feduccia, 2014; Jarvis *et al.*, 2014) and certain plant groups such as Leguminosae (or Fabaceae), one of the most dominant plant families in

African biomes (Koenen *et al.*, 2020). Thus, the meteorite impact and the Deccan volcanism could have led to short-lived ecosystem traumas and extinction, with plant and animal clades quickly recovering (Spicer & Collinson, 2014), especially in tropical ecosystems (Johnson & Ellis, 2002). Overall, the KPB was the start of a second large-scale flowering plant and animal diversification burst (O’Leary *et al.*, 2013; Silvestro *et al.*, 2015; Feng *et al.*, 2017; Koenen *et al.*, 2020), which initiated the diversification of tropical African biota (Linder, 2014).

### (2) Extreme conditions: the Paleocene–Eocene climatic optimum (66–51 Ma)

The Paleocene and Eocene were the warmest intervals of the Cenozoic, dominated by ‘greenhouse’ climates, characterized by the absence of polar ice caps (Foster *et al.*, 2018). The Paleocene ended with the short-lived Paleocene–Eocene Thermal Maximum (PETM) (*ca.* 56 Ma, Fig. 3A), a ‘hyperthermal’ period characterized by 5–7°C global warming (Turner, 2018). The early Eocene was marked by the longest and warmest interval of the Cenozoic (Zachos, Dickens, & Zeebe, 2008), the Early Eocene Climatic Optimum (EECO; 53–51 Ma, Fig. 3A). A final climatic optimum occurred during the Mid-Eocene Climatic Optimum (MECO; ~40 Ma, Fig. 3A), followed by a cooling trend that culminated with the Eocene–Oligocene transition (EOT; 34.1–33.6 Ma, Fig. 3A). During the Paleocene, Africa had a lower elevation than at present and most of the northern part of the continent was submerged by the large Sahara Sea (Fig. 2A). Exceptions include southern Africa which inherited the Late Cretaceous uplift of the South African Plateau (Flowers & Schoene, 2010) and the Guinea Rise in western Africa (Fig. 1A), a remnant of the early Cretaceous rift shoulders of the Equatorial Atlantic Ocean Rift (J. Ye *et al.*, 2017a). Other reliefs were likely present in Ethiopia and Cameroon, but are quite difficult to map in detail because of active magmatism. Volcanic activity was maintained in the Cameroon Volcanic Line over the last 42 Ma (Marzoli *et al.*, 2000). Continental palaeoclimate data is almost non-existent for the Paleocene–Eocene in Africa, and large uncertainties remain especially regarding precipitation. Results from cores in Tanzania suggest “overall hot and arid conditions punctuated by intense, perhaps seasonal, precipitation events” in East tropical Africa during the PETM (Handley *et al.*, 2012, p. 10), but do not document pre- and post-PETM climate states. Climate models of the early Eocene in Africa simulate temperatures warmer than present-day by 4°C to 18°C, depending on the prescribed pCO<sub>2</sub> and the region considered (Lunt *et al.*, 2012). Precipitation responses in tropical Africa to Eocene conditions are highly variable, ranging from less than 1000 mm/year to more than 3300 mm/year, depending on the model used (Huber & Caballero, 2011; Lunt *et al.*, 2012; Carmichael *et al.*, 2016).

Few fossil sites are recorded for the Paleocene and Eocene for both plants (Bonnefille, 2010; Jacobs, Pan, &



**Fig 3.** Geo-climate evolution and biological diversification of tropical African biodiversity. (A) Global temperature change during the Cenozoic (Hansen *et al.*, 2008) and major climate and tectonic events across Africa. KPB, Cretaceous–Paleogene Boundary; PETM, Paleocene–Eocene Thermal Maximum; EECO, Early Eocene Climatic Optimum; MECO, Mid-Eocene Climatic Optimum; EOT, Eocene–Oligocene transition; MCO, Miocene Climatic Optimum; MCT, Miocene Climate Transition; PPT, Pliocene–Pleistocene Transition. (B) Temporal representation of major uplift and volcanic events in central and eastern Africa (Sepulchre *et al.*, 2006; Guillocheau *et al.*, 2015, 2018). (C) Origin of major mountain peaks, lakes and arid regions in Africa (Marzoli *et al.*, 2000; Gehrke & Linder, 2014; Zhang *et al.*, 2014). (D) Origin of extant species of plants and animals based on time-calibrated molecular phylogenies (see Appendix S1). (E) Crown node mean age estimates of plant and animal genera based on time-calibrated molecular phylogenies (see Appendix S1).

Scotese, 2010) and animals (Mayr, 2009; Werdelin & Sanders, 2010; Gardner & Rage, 2016) across tropical Africa, leading to a poor understanding of vegetation distribution and biodiversity at this time (Mayr, 2009; Jacobs *et al.*, 2010; Gardner & Rage, 2016). Nevertheless, the favourable warm and humid Paleocene–Eocene climate is suggested to have led to an important period of diversification in plants and animals, ultimately defining tropical Africa's current biodiversity (Plana, 2004; Morley, 2007; Tolley, Townsend, & Vences, 2013; Koenen *et al.*, 2020).

#### (a) A pan-African rain forest?

During the Paleocene and Eocene a pan-African rain forest is suggested to have extended continuously from western to East Africa linked to the favourable climatic conditions (Axelrod & Raven, 1978; Coetzee, 1993; Lovett, 1993; Morley, 2000, 2007; Willis & McElwain, 2014). Its existence plays a central role in explaining present-day faunal and floral biogeographic patterns across tropical Africa (Moreau, 1966; Hamilton & Faden, 1974; White, 1979). The repeated fragmentation of this pan-African rain forest into western/central and East or West and Central blocks (Morley, 2000), during drier periods of the Late Oligocene, mid-Miocene and Pliocene, is invoked to explain the origin of major trans-African disjunct distributions (Hamilton & Faden, 1974; Loader *et al.*, 2007; Couvreur *et al.*, 2008; Zimkus, Rödel, & Hillers, 2010; Pokorný *et al.*, 2015).

The existence of a continuous Eocene coast-to-coast rain forest, however, has been called into question (Bonnefille, 2010; Linder, 2017). Fossil evidence suggesting the presence of a humid closed-canopy type vegetation during these times is clearly documented, especially in the west (Salard-Cheboua, 1990; Morley, 2000). Fossil taxa belonging to characteristic rain forest plant families, such as Annonaceae, Arecaceae, Meliaceae and Myristicaceae were recovered from the Paleocene and Eocene (Morley, 2000; Jacobs *et al.*, 2010). These conditions were also suggested to be favourable for animal taxa, with, for example, dated molecular phylogenies documenting the radiation of modern chameleon genera during the Eocene, ancestrally inferred to be arboreal in closed-canopy forests (Tolley *et al.*, 2013). However, there is very little direct fossil evidence for rain forest vegetation in East Africa during the Paleocene and Eocene. This is not surprising given the few fossil sites available in that region (Jacobs & Herendeen, 2004; Jacobs *et al.*, 2010; Linder, 2017). The Middle Eocene Mahenge site from north-central Tanzania in East Africa documents a woodland resembling present-day miombo rather than rain forest vegetation (Jacobs & Herendeen, 2004). However, during the Eocene, Africa was located some 10° south of its present location and Arabia was still connected to the continent (Figs 2B, 3A). Climate simulations of the Eocene suggest a hot climate and a strong hydrological cycle in the tropics, but also show reduced precipitation south of 20°S (Sagoo *et al.*, 2013, see Fig. S1). Thus, it is likely that during the Paleocene–early Eocene the Tanzanian region, including

Mahenge, was too far south (about 15°S) to permit the development of rain forest vegetation. In contrast to Mahenge, the Kaninah Formation, a Middle Eocene fossil site in Yemen located near the palaeo-equator during that time, documents the presence of rain forest-type vegetation, with fossils linked to, for example, Annonaceae (As-Saruri, Whybrow, & Collinson, 1999). Additionally, evidence of rain forests from the Paleocene was found along the Red Sea in Egypt (Boureau *et al.*, 1983). Thus, Paleocene and Eocene rain forest vegetation on the east coast of Africa is not undocumented, but was probably located further north than its current location (Bonnefille, 2010).

Biogeographic studies based on dated molecular phylogenies of clades restricted to rain forests also support the existence of a once-continuous pan-African rain forest during the Cenozoic. If the fragmentation of this pan-African forest was responsible for the observed disjunct patterns between East and West/Central blocks we expect vicariant events to be synchronous with periods of increased African aridity (Loader *et al.*, 2007; Couvreur *et al.*, 2008). In addition, we would expect these events to be temporally concordant between different rain forest clades. Interestingly, independently inferred vicariant events have been dated to around the EOT (~33 Mya) in at least two major plant (Annonaceae; Couvreur *et al.*, 2008) and animal clades (chameleons; Tolley *et al.*, 2013). These were suggested to be the result of the break up of the pan-African forest, leading to the isolation and speciation of lineages in western/central and East Africa. Unfortunately, there are only two studies to date that uncover this pattern for the Eocene, as most extant clades diversified after the Eocene (Fig. 3D, E). Nevertheless, the concordance in the recovered dating of these vicariant events between clades is quite striking, favouring a common response between these groups, rather than relying on random processes such as long-distance dispersal (Linder, 2017).

The history of forest fragmentation between the West (or upper Guinea) and Central (or lower Guinea) Africa, which are separated by the *ca.* 200 km wide drier 'Dahomey gap' corridor located in Benin and Togo (Salzmann & Hoelzmann, 2005), is less clear. Differences in species diversity are less marked between these two forest blocks than between West/Central and East Africa (Linder *et al.*, 2012; Droissart *et al.*, 2018). Even though there are high levels of taxonomic endemism in West Africa (Linder, 2001; Penner *et al.*, 2011), numerous species are common between both regions (Linder *et al.*, 2012; Droissart *et al.*, 2018). In addition, diversity studies in plants or animals still do not agree on where the biogeographic separation lies between West and Central Africa (e.g. Volta and Niger rivers, Dahomey gap or the Cross River region in eastern Nigeria), and this is probably species dependent (Booth, 1958; White, 1979; Nicolas *et al.*, 2010; Penner *et al.*, 2011; Linder *et al.*, 2012; Droissart *et al.*, 2018). This suggests a closer biogeographic link between these regions than between West/Central and East Africa. Numerous phases of savanna expansions are documented for the last 7 Myr (Dupont *et al.*, 2000; Bonnefille, 2010), linking and unlinking west and central

forests, potentially allowing recent floristic and faunistic exchanges. Estimated ages of vicariance, based on dated phylogenies between animal species on either side of West and Central Africa, span the Late Miocene and Plio-Pleistocene (e.g. Nicolas *et al.*, 2006, 2019; Hassanin *et al.*, 2015; Huntley & Voelker, 2016; Gaubert *et al.*, 2018; Jongasma *et al.*, 2018). The late Pliocene–early Pleistocene, between 3 and 2 Ma, appears to concentrate most of these vicariance events across studies. Indeed, this period is marked by a sudden and strong increase in savanna across West Africa (see Section III.6). Finally, more recent forest fragmentation (last 150 Kyr; Dupont *et al.*, 2000) mainly impacted within-species genetic diversity structuring (e.g. Nicolas *et al.*, 2012; Fuchs & Bowie, 2015; Demenou, Doucet, & Hardy, 2018; Huntley *et al.*, 2019; Leaché *et al.*, 2019).

### (b) The golden age of mangroves

The warm Paleocene and Eocene climates were favourable for mangrove vegetation (Morley, 2000). Probably, the most striking geological feature of the Paleocene was the presence of the epicontinental Sahara Sea in northern Africa (Fig. 2A). It was connected to the Tethys Ocean to the north and at its maximum extent reached western Africa in present-day northern Nigeria (Luger, 2003; Guiraud *et al.*, 2005; Ye *et al.*, 2017a). This marine incursion originated during the middle Cretaceous (*ca.* 98 Ma) and disappeared during the middle Eocene (Guiraud *et al.*, 2005). The influence of this incursion on African biodiversity has been little studied, possibly because it is just too old to have had lasting effects on present-day biodiversity (Fig. 3D, E) in contrast to a similar event during the Early Miocene in the Amazon region (the Pebas system; Hoorn *et al.*, 2010). Nevertheless, the presence of marine-like herring fishes in east and west African lakes has been linked to the existence of this palaeo-sea (Wilson, Teugels, & Meyer, 2008). It was also suggested to have provided a passage between northern and western Africa for fossil ostracod taxa (Luger, 2003) and marine fishes such as lamniiform sharks and rays (Murray, 2000). This extended shoreline of the Tethys sea was inferred to be the origin of the mangrove vegetation (Descombes *et al.*, 2018), which became well established during the Paleocene and Eocene across Africa based on palynological data (Morley, 2000). During the Eocene, mangrove taxa represented up to 20% of plant diversity in certain sites around the Benue River catchment (Utescher & Mosbrugger, 2007). The Paleocene and Eocene correspond to a global increase and diversification of mangroves worldwide and models suggest a strong presence of mangrove taxa along most of the African coast at that time (Descombes *et al.*, 2018).

### (3) ‘Descent into the icehouse’: Eocene–Oligocene transition (34.1–33.6 Ma)

Following the MECO, global temperatures decreased gradually, a trend that culminated with abrupt cooling at the EOT (Zachos *et al.*, 2008). During this time, Earth switched

from a greenhouse to an ‘icehouse’ climate state (Thomas, 2008), characterized by a permanent ice sheet over Antarctica (Fig. 3A; Zachos *et al.*, 2008; Thomas, 2008; Inglis *et al.*, 2015). The onset of the Antarctic glaciation is attributed to a decrease in  $p\text{CO}_2$  (Ladant *et al.*, 2014) and/or continental reconfiguration opening the southern seaways (the Drake passage and the Tasman seaway), ultimately modifying ocean heat transport (Lear & Lunt, 2016). How the EOT altered the African climate remains unclear mainly because of uncertainties in  $p\text{CO}_2$  reconstructions during the Eocene and Oligocene (Steinthorsdottir *et al.*, 2016). While a cooling trend has been recorded by ocean proxies, continental indicators have shown contradictory results (Pound & Salzmann, 2017). Numerical simulations suggest that the intensification of the Atlantic meridional overturning circulation associated with the EOT also caused a northward shift of the Inter Tropical Convergence Zone (ITCZ), increasing precipitation over northern Africa (Elsworth *et al.*, 2017). The inception of Antarctic glaciation is also thought to have produced a  $\sim 70\text{-m}$  sea-level drop (Miller *et al.*, 2005). Meanwhile, the growth of the Hoggar swell in northern Africa (Fig. 2B, C) led to the establishment of a modern-like west African drainage geometry (Grimaud *et al.*, 2017). Alluvial deposits in the Niger Basin, as well as along the northern African coast, testify to humid conditions and rivers flowing both towards the Atlantic and Tethys oceans during the early Oligocene (Fig. 2C). The Sahara Sea slowly shrank due to doming, leaving large lakes in huge depressions in western Africa from Mali to Chad (Fig. 2B). In East Africa, the onset of volcanic activity is dated to 45–40 Ma (Roberts *et al.*, 2012; Prave *et al.*, 2016) but reached a peak with the outpouring of important magma *ca.* 31 Ma leading to formation of the Ethiopian traps (Figs 2C, 3B).

As for the rest of the Paleogene, the Oligocene is poor in fossil sites for animals and plants as well as palaeoclimate proxy records (Murray, 2000; Jacobs *et al.*, 2010; Seiffert, 2010; Gardner & Rage, 2016). The Kwa-Kwa palaeoflora core near present-day Douala in Cameroon documents an important turnover of the vegetation at or around the EOT, with numerous taxa disappearing followed by a rapid increase in new, mainly angiosperm taxa (Salard-Cheboldaeff, 1979). Morley (2000, p. 87), based on a compilation of west African palaeoflora data (Salard-Cheboldaeff, 1990), documents a decrease in overall plant diversity immediately after the EOT. This decrease in rain forest palaeodiversity appears to be a tropical-wide phenomenon at the EOT, with similar patterns reported in the Neotropics (Jaramillo, Rueda, & Mora, 2006). Fossil data document considerable extinction in palms, more so than across the KPBB (Morley, 2000; Pan *et al.*, 2006), for example with the mangrove palm *Nyba* disappearing from records across Africa.

Diversification analyses using dated phylogenies also document (mass) extinction around the EOT in several clades, such as climbing palms (Faye *et al.*, 2016b) and the legume tribe Podalyriaceae (Crisp & Cook, 2009). By contrast, other groups did not show signs of mass extinction across the EOT, for example in the mainly African legume tree clade

Detarioideae, although extinction rates were inferred to be generally quite high in this clade between 45 and 15 Ma (de la Estrella *et al.*, 2017). The EOT also marked an important evolutionary turn in grasses (Poaceae), which shifted and subsequently diversified from their ancestrally closed habitats into open ones (Bouchenak-Khelladi *et al.*, 2010b; Bouchenak-Khelladi, Muasya, & Linder, 2014a), although it does not correlate with the well-studied origin of C<sub>4</sub> metabolism in grasses (Edwards *et al.*, 2010).

Overall, rain forests are thought to have retracted significantly during the EOT, breaking up the Eocene pan-African forest that potentially persisted until then (see Section III.2a). In northern Africa, there is fossil evidence for the extinction of tropical taxa and the appearance of savannah- and woodland-associated ones (Boureau *et al.*, 1983). This pan-African fragmentation had an important impact on the distribution of present-day diversity, leading to the first vicariance of once-widespread groups into west/central and east clades and the origin of endemic East African genera (Couvreur *et al.*, 2008; Tolley *et al.*, 2013).

The EOT led to what is known as the ‘Grande Coupure’ for primates, a sudden reduction in their diversity mainly documented in the fossil record of Europe and North America. Interestingly, molecular diversification analyses either failed to find support for a turnover of primate palaeodiversity overall (Springer *et al.*, 2012; Herrera, 2017) or detected moderate support for declining diversification rates at the EOT (Herrera, 2017). In Africa, despite the few fossil sites available, the EOT potentially led to a gradual reduction in primate diversity, linked to a continent-wide contraction of rain forests, although only a few major lineages went extinct (Seiffert, 2007). It also marked the origin of the oldest present-day primates, the Galagidae or bush babies, which started to diversify at 33 Mya just after the EOT (Pozzi, Disotell, & Masters, 2014; Pozzi, 2016).

More favourable conditions after the EOT might have led to a renewed expansion of rain forests, reconnecting the west and east forest blocks (Morley, 2000). Indeed, analyses of palaeosurface formed during the Late Oligocene (29–24 Ma) depict a hot climate with seasonal precipitation in West Africa (Beauvais & Chardon, 2013) and increased humidity (Robert & Chamley, 1987). This is consistent with the northward drift of Africa and the position of the equator south of western Africa, above the present-day Gulf of Guinea. Rain forest-resembling fossil taxa are documented from Ethiopia and Cameroon (Bonnefille, 2010; Jacobs *et al.*, 2010). Although palm diversity never recovered after the EOT, palm fossils remained an important component of the few documented Oligocene palaeofloras (Salard-Cheboldaeff, 1979; Pan *et al.*, 2006). Finally, dated molecular phylogenies support the idea that the post-EOT period marked an important phase of diversification for certain reptile groups such as burrowing snakes (Aparallactinae; Portillo *et al.*, 2018) and chameleons (Tolley *et al.*, 2013) and for major clades in skinks (Scincidae; Medina *et al.*, 2016).

#### (4) Renewed warm climates: early Miocene to the middle Miocene climatic optimum (~17–14.7 Ma)

The Miocene (*ca.* 23–5.3 Ma) is considered one of the most pivotal periods for tropical Africa (Plana, 2004), with several climatic, geological and physiographic changes hypothesized to have led to a complex evolution of African biodiversity (White, 1981; Morley, 2000; Senut, Pickford, & Ségalen, 2009; Bonnefille, 2010). How African vegetation responded to these changes is far from clear, since (i) absolute dating of the fossil record is rare for the early and Middle Miocene of Africa, and (ii) numerous factors, either proximal, like mountain uplift and rifting, giant lakes and palaeodrainage upheavals, or remote, like  $p\text{CO}_2$  variations, closure of tropical seaways (e.g. Hamon *et al.*, 2013; Sepulchre *et al.*, 2014) and orbital cycles, altogether altered the tropical climate of Africa during this period (Linder, 2017).

The global long-term cooling trend initiated after the EECO is less marked in the early Miocene deep-sea record (Fig. 3A), and is obscured by the major interruption of the Middle Miocene Climatic Optimum (MCO; *ca.* 17–14.7 Ma, Fig. 3A). This interval was characterized by global temperatures about 3–8°C higher than the pre-industrial period of the late Holocene, similar to those of the late Oligocene (You *et al.*, 2009; Holbourn *et al.*, 2015), and an increase in  $p\text{CO}_2$  when compared to the Oligocene–Miocene transition (Kürschner, Kvaček, & Dilcher, 2008). Given the lack of constraints on palaeobotanic dates and the absence of direct continental palaeoclimate proxies for the Middle Miocene in Africa, inferring how the *ca.* 2 million-year-long warming of the MCO influenced the fate of tropical African biodiversity remains very challenging.

In western Africa, the fossil record documents the presence of rain forests and the reappearance of mangrove vegetation following its EOT demise (Salard-Cheboldaeff, 1979; Jacobs *et al.*, 2010). In addition, the lack of charred grass cuticles and pollen indicates the absence of widespread open habitats (Morley & Richards, 1993). There is also fossil evidence of early Miocene (*ca.* 19 Ma) rain forest assemblages from Kivu in the East Democratic Republic of the Congo (Jacobs *et al.*, 2010). In addition, unfavourable conditions for dry-adapted plants during the Early Miocene led to the first vicariance events inferred within some elements of the Rand Flora (Pokorny *et al.*, 2015; Mairal, Sanmartín, & Pellissier, 2017), an assemblage of unrelated drought-adapted taxa co-distributed around the subtropical and drier margins of Africa (Sanmartín *et al.*, 2010).

In East Africa, the picture is even less clear, with several fossil sites documenting the presence of rain forest, a mix of rain forest and grassland patches, woodland or grasslands (Andrews & Van Couvering, 1975; Bobe, 2006; Bonnefille, 2010; Jacobs *et al.*, 2010; Wichura *et al.*, 2015; Linder, 2017). This heterogeneity in the East African early Miocene fossil record could either reflect stronger climate variability, or an early role of changing elevations leading to different palaeoenvironmental, geomorphological, and palaeohydrogeological settings. Indeed, although the overall

elevation of the African continent was still lower than present-day (Fig. 2C), the East African surface underwent large-scale doming during the Early to Middle Miocene, and changes in basin configuration were initiated in the western branch (Lake Albert) of the East African Dome during the Early Miocene (17 Ma; Simon *et al.*, 2017; Guillocheau *et al.*, 2018).

The extent of the Early to Middle Miocene rain forests in East Africa remains controversial (Bonnefille, 2010; Fer *et al.*, 2017; Linder, 2017), and the question is open as to whether a pan-African rain forest was once again in place. Climate and vegetation modelling have produced a variety of results, depending on the experimental design (You *et al.*, 2009; Henrot *et al.*, 2010, 2017; Hamon *et al.*, 2012; Goldner, Herold, & Huber, 2014). Henrot *et al.* (2017) showed an increase in temperature and rainfall in East Africa during the MCO, but no clear signal could be extracted amongst the five models tested regarding a continuous rain forest band across tropical Africa. By contrast, other experiments with low topography suggested numerous combinations of rainfall and temperatures which could have allowed the presence of a pan-African rain forest (Fer *et al.*, 2017). However, the above-mentioned models are based on an homogeneous East African Dome ranging from 500 to 800 m asl (Herold *et al.*, 2008) and are likely over-simplifications, since evidence of high elevations (1400 m asl) shortly after the MCO (13.4 Ma) suggests a very rapid uplift in this region during the Middle Miocene (Wichura *et al.*, 2010).

Several Oligocene to early Miocene fossil sites suggest the presence of rain forest in Eastern Africa (Ethiopia, Kenya, and Uganda). Interestingly, these palaeofloras and faunas were shown to have elements linked to West/Central African forests (Andrews & Van Couvering, 1975; Vincens, Tiercelin, & Buchet, 2006; Jacobs *et al.*, 2010; Wichura *et al.*, 2015; Linder, 2017). The presence of a 17-Myr-old whale fossil (Wichura *et al.*, 2015) from the now 600 m high Turkana Basin (northern Kenya, Fig. 1A) attests to an active eastward-directed drainage basin linking the African interior with the Indian Ocean. This, coupled with fossil pollen evidence for closed-canopy vegetation and humid (rainfall >1000 mm/year) conditions (Vincens *et al.*, 2006), suggests a possible role of the Turkana Basin as an important corridor for faunal and floral transcontinental connections (Feibel, 1993).

In addition, the Eastern Arc Mountains, an ancient crystalline mountain chain ranging from East Tanzania to south-east Kenya (Lovett, 1993) could have played a crucial role in connecting west/central and east forests. Indeed, this mountain range has been suggested as climatically stable on a multimillion year scale, probably continuously harbouring forests since the Miocene (Lovett *et al.*, 2005). Dated molecular phylogenies of certain Eastern Arc clades find support for Oligocene–Miocene origins and long-term persistence in these forests (Tolley *et al.*, 2011; Dimitrov, Nogués-Bravo, & Scharff, 2012; Loader *et al.*, 2014; Grebennikov, 2017). This stability has been linked to the proximity of the mountain range to the Indian Ocean, providing significant and

constant moisture through time (Lovett *et al.*, 2005; Finch, Leng, & Marchant, 2009).

Finally, the presence of rain forest habitat in East Africa is also suggested by the evolutionary history of forest-restricted lineages that diversified extensively during the Early Miocene, such as chameleons (Matthee, Tilbury, & Townsend, 2004; Tolley *et al.*, 2011). Thus, even though a continuous pan-African forest might not have persisted throughout the entire Early Miocene (Bonnefille, 2010; Linder, 2017), evidence from vegetation and climate models, fossil sites, and dated molecular phylogenies favours the hypothesis of a rain forest band reconnecting east and west forests blocks after the EOT fragmentation (Andrews & Van Couvering, 1975; Morley, 2000; Couvreur *et al.*, 2008).

### (5) The middle Miocene climate transition (15–13 Ma)

Shortly after the MCO, global cooling resumed (Fig. 3A) and the marine isotopic record suggests a phase of important Antarctic ice sheet expansion (Shevenell, Kennett, & Lea, 2008), termed the Middle Miocene Climate Transition (MCT; *ca.* 15–13 Ma; Fig. 3A). Amongst the hypothesized drivers of this cooling are (i) tropical seaway constrictions, in particular Tethys sea closure around 14 Ma (Zhang *et al.*, 2011; Hamon *et al.*, 2013), (ii) a major  $p\text{CO}_2$  decrease between 15 and 14 Ma (Kürschner *et al.*, 2008), and (iii) tectonic uplift at a global scale.

Climate modelling shows that the changing topography of East Africa dramatically influenced climate at the continental scale. Sensitivity experiments to elevation change of the EARS showed that the first-order response to uplift was a precipitation reduction in tropical East Africa (Sepulchre *et al.*, 2006). Altering air mass dynamics also had remote consequences such as the drying of the Congo Basin (Sepulchre, Ramstein, & Schuster, 2009; Prömmel, Cubasch, & Kaspar, 2013; Sommerfeld, Prömmel, & Cubasch, 2016). Another interesting geological development was the uplift of the Central African Atlantic Swell (Fig. 1A), a low mountain range (max. 1200 m asl) stretching from Ngovayang massif (South Cameroon) to the Mayombe massif (South Republic of the Congo), possibly since the Middle Miocene (*ca.* 16 Ma; Guillocheau *et al.*, 2015).

The reconnection of Africa and Eurasia *via* the closure of the Tethys seaway (20–14 Ma) (Hamon *et al.*, 2013) ended the 80 million-year-long isolation of Africa. This led to major faunal interchanges *via* the Arabian plate. Turnover of previous African lineages, that had evolved in isolation within Africa (Springer *et al.*, 1997), with northern migrants are evidenced from the fossil record in East Africa already at the start of the reconnection during the Oligocene–Miocene transition and later during the Miocene–Pliocene transition (Leakey *et al.*, 2011). Several dispersal events between Africa and Asia are also recorded (e.g. Lecompte *et al.*, 2008).

Several authors infer that during the Middle Miocene, overall drier conditions led to the expansion of open habitats such as grasslands and woodlands, providing diversification

opportunities for numerous dry-adapted plant and animal taxa (Retallack, Dugas, & Bestland, 1990; Morley & Richards, 1993; Morley, 2000; Davis *et al.*, 2002; Senut *et al.*, 2009; Jacobs *et al.*, 2010). The Middle Miocene corresponds to the first inferred shifts of forest-adapted species into open and drier habitats followed by subsequent diversification (Davis *et al.*, 2002; Bouchenak-Khelladi *et al.*, 2010a; Armstrong *et al.*, 2014; Veranso-Libalah *et al.*, 2018). This period also marks the presence of C<sub>4</sub> carbon fixation in grasses, or C<sub>4</sub> grasses, in Africa, a dominant component of present-day African savannas which evolved independently in numerous Poaceae (Bohe, 2006; Ségalen, Lee-Thorp, & Cerling, 2007; Bouchenak-Khelladi *et al.*, 2009, 2014b; Edwards *et al.*, 2010; Uno *et al.*, 2011).

Globally, the Middle Miocene marks the retraction of rain forest towards the equator and the expansion of savannas (Morley, 2007). In Africa, the lowland rain forest which may have connected east and west forest blocks during the Early Miocene (see Section III.4) retracted again, as evidenced by semi-arid conditions in the Congo Basin in the Middle Miocene (Senut *et al.*, 2009). In East Africa, rain forests greatly reduced with a marked increase in grassland and gallery forests (Retallack *et al.*, 1990; Morley, 2000; Jacobs *et al.*, 2010). This fragmentation was suggested to have spurred diversification in forest-dwelling animals, such as guenons (tribe Cercopithecini; Guschanski *et al.*, 2013). Numerous independent molecular-dating studies support vicariance within forest-restricted clades around the MCT (15–13 Ma) in plants (Davis *et al.*, 2002; Couvreur *et al.*, 2008; Dimitrov *et al.*, 2012; Pokorný *et al.*, 2015; Tosso *et al.*, 2018; Brée *et al.*, 2020), snakes (Menegon *et al.*, 2014; Greenbaum *et al.*, 2015), amphibians (Loader *et al.*, 2007; Bell *et al.*, 2017), birds (Voelker, Outlaw, & Bowie, 2010) and rodents (Bryja *et al.*, 2017). Once again, these studies strongly support the idea of continental-wide pan-African forest fragmentation (Couvreur *et al.*, 2008) as a main driver of east/west disjunctions rather than random long-distance dispersals.

During the Middle Miocene, the continued uplift of the East African Plateau is contemporaneous with the first radiations of the tropical alpine or Afrotemperate/Afromontane (White, 1981; Linder, 2017) frost-tolerant clades (Galley *et al.*, 2007; Antonelli, 2009; Linder *et al.*, 2013). However, these resulted in lower numbers of species (Cox *et al.*, 2014; Gehrke & Linder, 2014) compared with other tropical Alpine regions like the Andes (Hughes & Eastwood, 2006). The East African Plateau provided an important migration route linking north and south Africa, allowing Cape elements to disperse northwards (Galley *et al.*, 2007), and Eurasian elements to disperse southwards (White, 1981; Gehrke & Linder, 2009; Mairal *et al.*, 2015; Gizaw *et al.*, 2016), favouring longitudinal transcontinental exchanges (Galley *et al.*, 2007). Diversification also occurred in the Cameroon Volcanic Line for certain montane clades such as puddle frogs which find their origins in the mountain range during the Early Miocene (Zimkus & Gvoždík, 2013). Other typical Afromontane clades also started to diverge during this time,

such as the conifer montane-restricted genus *Podocarpus* (Quiroga *et al.*, 2016). Fossil pollen evidence of *Podocarpus* is recorded off the Somali coast as early as 11 Ma (Feakins *et al.*, 2013) however clear presence of this genus in continental Africa dates only to 2.7 Ma from West Africa (Morley, 2011).

### (6) The end of equable climates: from the late Miocene to the mid-Pleistocene (11–1.5 Ma)

The last 11 Myr appear critical in the evolution of tropical African biodiversity, as most extant species or genera have originated during this time interval (Fig. 3D, E). In terms of climate, sea-surface temperature reconstructions depict a global and sustained cooling from 11 Ma to 5.3 Ma, with a steeper decrease in temperatures between *ca.* 7 and 5.4 Ma, the so-called Late Miocene Cooling (LMC), that was very likely driven by a decrease in atmospheric  $p\text{CO}_2$  (Herbert *et al.*, 2016). Between 11 Ma and the end of the LMC (5.4 Ma), high-latitude temperatures dropped by as much as 13°C to reach near-modern values, whereas cooling was less marked in the tropics. The resulting increase in the temperature latitudinal gradient is expected to have reinforced and contracted the Hadley cells (atmosphere circulations around the tropics), thereby expanding arid areas in the subtropics (Herbert *et al.*, 2016). Between 6 Ma and 5.4 Ma, multiple glacial-to-interglacial fluctuations have been inferred from the isotopic record, with a precession-like periodicity (Hodell *et al.*, 2001), likely explaining Late Miocene evidence for partial glacial and ephemeral glaciation in Greenland (Larsen *et al.*, 1994). The LMC also partly overlapped with the Messinian Salinity Crisis (MSC, 5.97–5.33 Ma), during which the Mediterranean turned into deep desiccated basins, with partial or full closure of the Gibraltar Strait (Krijgsman *et al.*, 2018). However the consequences of the MSC on the tropical climate of Africa remain hard to quantify (Murphy *et al.*, 2009).

At the scale of the African continent, the Late Miocene cooling is thought to have triggered a progressive aridification, and overall the Late Miocene palaeovegetation records depict a trend to more open habitats and the rise of grasslands. However, stating that the African biota responded linearly to global climate changes would be an oversimplification, as major proximal factors (e.g. topography, Paratethys retreat) likely altered temperature and precipitation patterns, driving various biota responses during the last 11 Myr. Previous reviews of the Neogene continental and marine palaeobotanical records (Jacobs, 2004; Bonnefille, 2010) show strong heterogeneity of the Miocene ecosystems of tropical Africa. Pollen data also suggest that savannah expansion occurred at *ca.* 10 Ma in East Africa, whereas it would have occurred later in western Africa (8–7 Ma). The northern Chad record shows that between 7.5 and 7 Ma, the vegetation cover of the region was characterized by a “mosaic environment, including closed forest patches, palm groves, and mixed/grassland formations” (Novello *et al.*, 2017, p. 66) whereas a grass-dominated signal appears only during the Pliocene, after 4.5 Ma. The same region has

also provided the earliest firm evidence for a Sahara desert, dated at 7 Ma (Schuster *et al.*, 2006), the onset of which is inferred by climate simulations triggered by the retreat of the Tethys Sea (Zhang *et al.*, 2014). Still, fluctuations among lacustrine, swamp and arid environments in the Chad Basin during the Late Miocene testify to higher-frequency, maybe orbitally paced, climate variations during the Late Miocene in northern Africa (Vignaud *et al.*, 2002). Extensive tropical rain forests were unlikely in north-East Africa any time during the last 12 Ma (Feakins *et al.*, 2013) and Ethiopia was more likely covered by seasonal, deciduous woodland dominated by a diversified Fabaceae family before grassland expansion (Bonnefille, 2010; Feakins *et al.*, 2013). The rise to dominance of C<sub>4</sub> photosynthesis is complex and decoupled from the earliest evolutionary origins of C<sub>4</sub> grasses during the EOT (Bouchenak-Khelladi *et al.*, 2014b). The transition to C<sub>4</sub> grass-dominated biomes has been discontinuous and spatially heterogeneous, with at least two phases of C<sub>4</sub> grass biomass increase (11–9 Ma and 4.3–1.4 Ma; Ségalen *et al.*, 2007; Feakins *et al.*, 2013). A similar trend is seen in the clade Amaranthaceae/Chenopodiaceae, a group of plants characteristic of arid lands and with the largest diversity of C<sub>4</sub> eudicot plants (Kadereit, Ackerly, & Pirie, 2012), where two main peaks are recorded across northern East Africa: Late Miocene 8–6 Ma and Pliocene 5.5–2.5 Ma (Bonnefille, 2010). In addition, C<sub>4</sub>-dominated ecosystems rose abruptly in north-western and East Africa around 10 Ma (Uno *et al.*, 2016). Finally, it has recently been suggested that this transition happened in the absence of any significant aridification signal, rather suggesting a major role for cooling and pCO<sub>2</sub> decrease in this process (Polissar *et al.*, 2019).

In animals, the evolutionary shift to C<sub>4</sub>-grazing amongst large mammalian herbivores seems to have been immediate for some lineages like the proboscideans (elephants), which started to include C<sub>4</sub> plants in their (browsing) diet as early as 9.9 Ma and became grazers at 7 Ma (Uno *et al.*, 2016), and more gradual for others (Ségalen *et al.*, 2007; Uno *et al.*, 2011). In particular, there is a documented rise in herbivorous mammals during the Late Miocene in East Africa (Bobe, 2006) followed by a clear decline in megaherbivores from 7 Ma onwards (Faith, Rowan, & Du, 2019). By contrast, large carnivore species richness declines after 3 Ma possibly linked to the decrease in megaherbivores across East Africa and the expansion of C<sub>4</sub>-dominated ecosystems (Faith *et al.*, 2019). In addition, numerous animal clades are suggested to have progressively diversified during the Late Miocene in relation to more-open ecosystems such as bush crickets (Voje *et al.*, 2009), gazelles (tribe Antilopini; Hassanin *et al.*, 2012), and burrowing snakes (subfamily Aparallactinae; Portillo *et al.*, 2018).

At lower latitudes, offshore marine pollen data from the Niger delta document a possible forested wet phase between 7.5 and 7.0 Ma (Morley, 2000; Bonnefille, 2010). This is in agreement with vegetation simulations of the Turonian period (11.61–7.25 Ma) where rain forests were likely in West, Central and East Africa (Ethiopia and Somalia; Pound *et al.*, 2011).

In the rift system in Kenya, vegetation patterns are biogeographically complex throughout the last 12 Ma, suggesting that palaeobotanical change from wet forest to savanna was not unidirectional (Jacobs *et al.*, 2010). This is likely due to increased topographic complexity linked to ongoing rifting throughout the region during the Late Miocene and the Pliocene.

The transition from the Miocene to the Pliocene depicts a renewal of warm climate at the global scale. Temperatures peaked during the early Pliocene (*ca.* 4 Ma) to reach values globally ~4°C greater than the preindustrial, and 1°C warmer than the following mid-Pliocene warm period (also referred to as the mid-Piacenzian warm period; see Haywood *et al.*, 2013). Numerical simulations suggest this time interval, besides ephemeral cold events [e.g. the Marine Isotope Stage (MIS) M2, 3.31–3.26 Ma; Tan *et al.*, 2017], was characterized by a slowdown of the Hadley circulation that led to increased precipitation over subtropical regions of Africa (Brierley *et al.*, 2009), and a strengthening of the African summer monsoon (Zhang *et al.*, 2016). The early to mid-Pliocene interval was termed the ‘Golden Age’ with tropical rain forests re-expanding and savannas contracting (Morley, 2000). Indeed, several fossil sites from East Africa document the presence of moist-adapted taxa and forest between 5 and 3 Ma (Morley, 2000; Pickford, Senut, & Mourer-Chauviré, 2004; Jacobs *et al.*, 2010; Linder, 2017; Joordens *et al.*, 2019). The East African coastal forests were suggested to extend from southern Africa to the Horn of Africa prior to 3 Ma (Joordens *et al.*, 2019). Once again, this favourable climate possibly allowed west/central and east rain forest blocks to reconnect, either as a continuous forest block (Fer *et al.*, 2017) or *via* moist vegetation corridors linking East and West/Central regions (Joordens *et al.*, 2019). For example, the Turkana gap fossil site in southern Ethiopia dated to 3.4–3.3 Ma documents the presence of evergreen or semi-deciduous forests (Hernández Fernández & Vrba, 2006; Bonnefille, 2010) with the presence of plant (*Antrocaryon*, Anacardiaceae) and animal (*Potadoma*, Pachychilidae) taxa known today only from Central African rain forests (Bonnefille & Letouzey, 1976; Williamson, 1985). Isotopic data on pedogenic carbonates also indicate increased woody plant (tree) cover in the Awash Valley and north Turkana Basin in north East Africa (Cerling *et al.*, 2011). Interestingly, this period might also have led to reversals from open to forested habitats in some Mimosoideae (Fabaceae) clades (Bouchenak-Khelladi *et al.*, 2010a).

Following the mid-Pliocene warm period, the climate gradually cooled during a time interval referred to as the Pliocene–Pleistocene Transition (PPT, 3.6–1.4 Ma; see Fig. 3A). PPT cooling was marked by the intensification of Northern Hemisphere glaciation (iNHG; e.g. Haug *et al.*, 2005). Starting from 2.7 Ma onwards, the Earth system entered full glacial/interglacial cycles with hemispheric glaciations, in contrast to the previous ephemeral ice sheets waxing and waning that characterized the Miocene and the Pliocene. These fluctuations between glacial and interglacial periods had a strong impact on all vegetation types across

Africa during the Pleistocene (Trauth *et al.*, 2009). Interestingly, 2.7 Ma also coincides with a marked shift in both western and eastern African pollen records during which a minimum in tree cover density is reached (Bonnefille, 2010) indicating a hypothetical link between the hemispheric-scale iNHG and vegetation in tropical Africa. Indeed, the iNHG and associated growth of massive ice sheets likely altered atmospheric dynamics through orographic and radiative effects, but did not coincide with any major change in tropical sea surface temperature (SST) patterns (Ravelo *et al.*, 2004). Aridification is inferred from the increased abundance of sub-desertic pollen taxa and C<sub>4</sub> plants (e.g. *Amaranthaceae s.l.*) at the expense of grasses and arboreal taxa in west and east Africa (Feakins *et al.*, 2013; Liddy, Feakins, & Tierney, 2016), and from the increase of terrestrial dust flux off the east, north and west African coasts (Trauth *et al.*, 2009). The numerous palaeoenvironmental records of East Africa [see Maslin *et al.* (2014) for a review] also showed a transition from C<sub>3</sub> to C<sub>4</sub> plants during the Plio-Pleistocene in East Africa, that was attributed to “a gradual progression towards a more variable climate with intensified arid periods” (Maslin *et al.*, 2014, p. 5). Palaeosol data from the Awash valley and the Omo-Turkana Basin depict a transition from woodland/bushland to wooded grasslands during the PPT (Cerling *et al.*, 2011), but the trend to aridification and the increase in variability of the tropical African climate are subject to ongoing debates regarding their pace and driving mechanisms (e.g. stepwise or gradual; deMenocal, 2004; Trauth *et al.*, 2009). The difficulty comes from the hard task of deciphering between (i) the long-term secular trend to more open environments recorded since the Late Miocene and (ii) the orbital-scale vegetation variations recorded in the marine cores or inferred from the cycles of rift lake fluctuations in East Africa (Trauth *et al.*, 2009; Joordens *et al.*, 2011). Indeed, palaeoenvironmental records potentially include (i) threshold effects linked to the ongoing uplifting and rifting in the EARS and (ii) changes in moisture availability and rainfall seasonality driven by the local solar heating, ultimately paced by precession forcing (Larrasoana *et al.*, 2003; Trauth *et al.*, 2009). Interestingly, the analysis of biomarkers retrieved from the eastern Mediterranean Basin for two time slices at 3.05 and 1.75 Ma suggests no significant increase in C<sub>4</sub>-plant cover in the eastern Sahara between those two intervals, while showing large orbital-scale variability within each interval (Rose *et al.*, 2016). The latter authors suggest that the Pleistocene expansion of C<sub>4</sub> vegetation could have been restricted to the East African domain and was not a pan-African vegetation transition. This could be explained by the onset of a modern-like Walker circulation at 1.9–1.6 Ma (Ravelo *et al.*, 2004), that would have changed SST patterns in the tropics and ultimately increased variability and aridity over East Africa, without influencing the eastern Saharan environments.

The major climatic shifts described above have greatly impacted vegetation and herbivore communities. In West Africa, these changes are suggested to have triggered speciation in certain animal clades (e.g. mammals; Nicolas

*et al.*, 2019) and also led to vicariant speciation between West and Central species as discussed above (see Section III.2a). Interestingly, these changes appear to have had little impact on mammal diversification in East Africa, with speciation and extinction rates estimated from the fossil record to have been generally continuous during the Plio-Pleistocene (Bibi & Kiessling, 2015). Nevertheless, about two thirds of the extant African biota for which we compiled age estimates (1482 events) originated during the last 5 million-years (Fig. 3D). How did the secular trends and orbital oscillations combine and influence diversification? On the one hand, the increase in aridification could have led to novel ecological niches which spurred the radiation of dry-adapted clades in animals (e.g. *Mus*; Bryja *et al.*, 2014) and plants [e.g. *Coccinia* (Holstein & Renner, 2011), *Guibourtia* (Tosso *et al.*, 2018), Melastomateae (Veranso-Libalah *et al.*, 2018)]. On the other hand, cycles of forest expansion and contraction during the Plio-Pleistocene could have increased allopatric speciation rates for forest-adapted lineages such as birds (Voelker *et al.*, 2010), frogs (Portik *et al.*, 2019), insects (Hemp *et al.*, 2015), and plants (Couvreur *et al.*, 2011b). Overall, oscillating climates during the last 10 Ma, between relatively stable warm and wet conditions with colder and drier ones appears to have spurred the evolution of the tropical African biota in general, and of hominid evolution in particular (deMenocal, 2004; Joordens *et al.*, 2019).

#### IV. MAJOR SPECIATION MODELS OF TROPICAL AFRICAN BIODIVERSITY

It is within the above-described geodiversity matrix, with dramatic climatic shifts, continental drifting, rifting and mountain uplifts, that the modern tropical African biota evolved. We now review diversification and molecular-dating studies providing insights into the different speciation mechanisms possibly involved across tropical Africa (see Appendix S1, Tables S1 and S2). In most cases, the cited studies do not explicitly test these speciation models but their results are generally concordant with them. Based on our review, we also find that most animal or plant genera show mixed vegetation zonation, with species occupying two or more zones (lowland, 0–700 m; premontane, 701–1500 m; montane, 1501–3000 m; alpine, <3000 m; see Appendix S2, Table S2). Note that several speciation mechanisms might act together within clades with mixed zonation.

Speciation is the process during which new species are formed as a result of reproductive isolation. Although there are numerous speciation models that could apply to tropical fauna and flora (e.g. Hill & Hill, 2001), we here consider three major model types, each of which have nuanced, underlying mechanisms that could apply depending on the clade, temporal scale or environment considered (Table 1, Fig. 4): (i) the geographic model primarily driven by allopatric speciation; (ii) the ecological model primarily driven by ecological speciation (Orr & Smith, 1998; Givnish, 2010);

and (iii) the genomic model primarily driven by genome duplication. For each model, we discuss below the proposed mechanisms linked to spatial and/or temporal factors relating to tropical Africa.

### (1) The geographic model

In the geographic model of speciation, widespread species become geographically disconnected to form isolated populations, with vicariance impeding gene flow resulting in allopatric speciation (Coyne & Orr, 2004). This vicariance can be caused by the appearance of environmental barriers such as novel vegetation types or the formation of, for example, rivers, mountains or arid valleys due to climatic or geological changes. Vicariance can also arise due to biotic factors such as competition, predation or diseases fragmenting an initially widespread population into disconnected areas. Although multiple factors could be involved during allopatric speciation (Gavrilets, 2003), we highlight below mechanisms that could drive the speciation process through random genetic drift and mutation (i.e. in the absence of direct selection). Genetic drift can be accentuated in founder events, but will also occur in large populations (as a result of vicariance) and can lead to different allele frequencies given sufficient generations since disruption of gene flow (Gavrilets, 2003). These allopatric species will remain adapted to their ancestral habitat (Table 1). The geological and climatic history of Africa has provided numerous opportunities for allopatric speciation.

One major mechanism by which the geographic model can lead to speciation is *via* repeated fragmentation and contraction of once-continuous populations into refugia areas [we use the term refugium/refugia rather than refuge, see Keppel *et al.* (2011) for a definition], leading to diversification *via* allopatric speciation (Fig. 4). Several different variants of this mechanism could have led to speciation in tropical Africa, and these are considered in detail below.

#### (a) Pleistocene lowland forest refugia mechanism

One potential explanation for the large number of species in lowland tropical rain forests is the Pleistocene lowland refugia mechanism (Haffer, 2008). Alternation between humid and dry climatic phases during the Pleistocene (2.58–0.01 Ma) is linked to orbitally paced glacial–interglacial Milankovitch cycles resulting in cyclical variation of insolation. These phases have been hypothesized to fragment continuous lowland forest vegetation into refugia in which populations of forest-adapted organisms can persist during adverse climatic periods. Long-term vicariance of these forest patches will promote allopatric speciation between isolated populations. This mechanism was applied to tropical African species based on studies of diversity/endemism patterns and palaeobotanical data (Aubréville, 1975; Diamond & Hamilton, 1980; Mayr & O'Hara, 1986; Hamilton & Taylor, 1992; Sosef, 1994; Maley, 1996; Robbrecht, 1996; Plana, 2004). However, the impact of

Pleistocene climatic fluctuations on rain forest fragmentation across tropical Africa is contested (Cowling *et al.*, 2008; Hardy *et al.*, 2013; Levinsky *et al.*, 2013; Lézine *et al.*, 2019).

Under this mechanism, we expect to find phases of allopatric speciation in lowland rain forests during the Pleistocene (<2.58 Ma) across multiple taxa (Table 1). Indeed, several dated phylogenetic studies across a suite of animal groups have provided support for this. In mammals, Old World fruit bats (megabats, Pteropodidae) show a strong Pleistocene signal of speciation (Nesi *et al.*, 2013; Cunha Almeida, Giannini, & Simmons, 2016). In particular, the forest-restricted tribes Myonycterini (11 species) and Scotonycterini (four species) originated during the last 2.8 Myr, with allopatric speciation linked to rain forest refugia (Nesi *et al.*, 2013; Hassanin *et al.*, 2015). Species of the largely forest-restricted guenons (tribe Cercopithecini), a diverse clade of African primates (63 species), were inferred to have diversified mainly *via* allopatric speciation during the Pleistocene, but also during the Late Miocene (Guschanski *et al.*, 2013). Other examples of allopatric speciation linked to isolation in refugia during the Pleistocene have been reported in mammals (Johnston & Anthony, 2012; Missoup *et al.*, 2012; Bohoussou *et al.*, 2015; Gaubert *et al.*, 2018; Nicolas *et al.*, 2019, 2020) and frogs (Bell *et al.*, 2017). In insects, this mechanism was suggested for the East African Coastal forests of Tanzania and Kenya, where the origin of 25 species of East African flightless grasshoppers (*Parepistaurus*) was dated to the Pleistocene and attributed to allopatric speciation linked to climatic fluctuations (Hemp *et al.*, 2015).

For plants, there is less evidence for this mechanism. Molecular dating of the African genus *Begonia* indicated that around half of the species sampled originated during the Pleistocene, with the other half originating earlier, during the Pliocene/Miocene (Plana *et al.*, 2004). Because *Begonia* species are generally restricted to lowland rain forests and are poor dispersers (Sosef, 1994), this supports, at least in part, a role of Pleistocene cycles in generating plant biodiversity. In the Zingiberales lowland rain forest herbaceous genus *Aframomum*, most speciation events were initially proposed to have taken place during the Pleistocene (Harris *et al.*, 2000), although a revised temporal framework for this genus indicated that only a few species originated during the last 2.5 Myr (Auvrey *et al.*, 2010). A worldwide sampling of the tropical and subtropical montane forest genus *Impatiens* dated part of its diversification to the Pleistocene, although no specific study was undertaken in Africa (Janssens *et al.*, 2009). Most tree species of the genera *Carapa* (Meliaceae) and *Piptostigma* (Annonaceae) originated during the Pleistocene (Koenen *et al.*, 2015; Brée *et al.*, 2020). Within the tribe Coffeaceae (Rubiaceae), which are mainly trees, about half of the species were dated to have originated during the Pleistocene (Kainulainen *et al.*, 2017).

While most studies to date have focused on testing forest refugia, Pleistocene refugia for savanna-restricted clades have been suggested to occur in Sudanian and Zambebian regions, linked to savanna fragmentation (e.g. primates: Dolotovskaya *et al.*, 2017). However, it is unclear whether

Table 1. Main diversification models and mechanisms documented in tropical Africa, with phylogenetic and ecological predictions. Citations refer to studies of African biota.

Model	Mechanism	General phylogenetic predictions	Specific geographic and/or phylogenetic predictions	Geographic locality	Selected references for Africa
Geographic	Pleistocene lowland forest refugia	Sister species have similar ecologies and allopatric/parapatric distributions; high phylogenetic niche conservatism; evidence of past fragmentation or separation	Speciation predominant during the Pleistocene; young species in lowland rain forests; evidence of population contraction/expansion	Lowland rain forests of West, Central and East Africa; savanna	Johnston & Anthony (2012); Bell <i>et al.</i> (2017)
	Fragmentation – refugium (see Fig. 4)		Speciation throughout the Cenozoic	Lowland rain forests of West, Central and East Africa; savannas of West and East Africa	Couvreur <i>et al.</i> (2008); Tolley <i>et al.</i> (2013)
	Riverine barrier		Sister species occur on opposite sides of river; no evidence of population contraction/expansion	Along major river systems of Africa, Congo Basin, East and West African deltas	Voelker <i>et al.</i> (2013)
	Montane refugia		Sister species occur on different mountain blocks (allopatry) and have overlapping altitudinal ranges, speciation is temporally decoupled from mountain orogeny, but congruent with climatic fluctuations	Montane regions, East African Rift, Eastern Arc Mountains, Cameroon Volcanic Line, Guinea rise	Voelker <i>et al.</i> (2010); Tolley <i>et al.</i> (2011)
Ecological	Ecotone speciation (see Fig. 4)	Sister species have different ecologies and sympatric/parapatric (sometimes allopatric) distributions; moderate to low phylogenetic niche conservatism; evidence of ecological selection	Sister species parapatric; numerous transitions between habitats across clades	Vegetation gradients, Congo Basin, West Africa; mountain regions of Africa	Smith <i>et al.</i> (1997)
	Montane gradient speciation		Sister species co-occur on same mountain block and have non-overlapping elevational distributions; speciation concordant with mountain orogeny	Gradient in montane regions, East African Rift, Eastern Arc mountains, Cameroon Volcanic Line, Guinea rise	Voje <i>et al.</i> (2009); Cox <i>et al.</i> (2014)
	Peripatric		Species with restricted distributions sister to more widely distributed species (strong asymmetrical distributions); sister species have different ecologies; genetic signals of founder events	Potentially everywhere, but more likely in dynamic ecosystems, especially high-elevation regions	Lawson <i>et al.</i> (2015)
	Vanishing refugia (see Fig. 4)		Sister species have allopatric/parapatric or disjunct distributions; evidence of habitat fragmentation at time of speciation	Highly dynamic ecosystems, East Africa, savannah–forest ecosystems in Central Africa	Barratt <i>et al.</i> (2018)

(Continues)

Table 1. (Cont.)

Model	Mechanism	General phylogenetic predictions	Specific geographic and/or phylogenetic predictions	Geographic locality	Selected references for Africa
	Rapid adaptive radiation		Key innovation leading to ecological opportunities; numerous species originating in a short period of time; convergent evolution expected, with similar phenotypes originating in geographic isolation, resulting in independent adaptations to similar ecological conditions	Newly formed ecosystems, lakes, savannas, montane regions	Salzburger (2018)
Genomic	Polyploidization	Sister species have different ecologies but not necessarily sympatric/parapatric	Evidence of genome duplication prior to speciation	Potentially everywhere	Evans <i>et al.</i> (2015); Donkpegan <i>et al.</i> (2017)

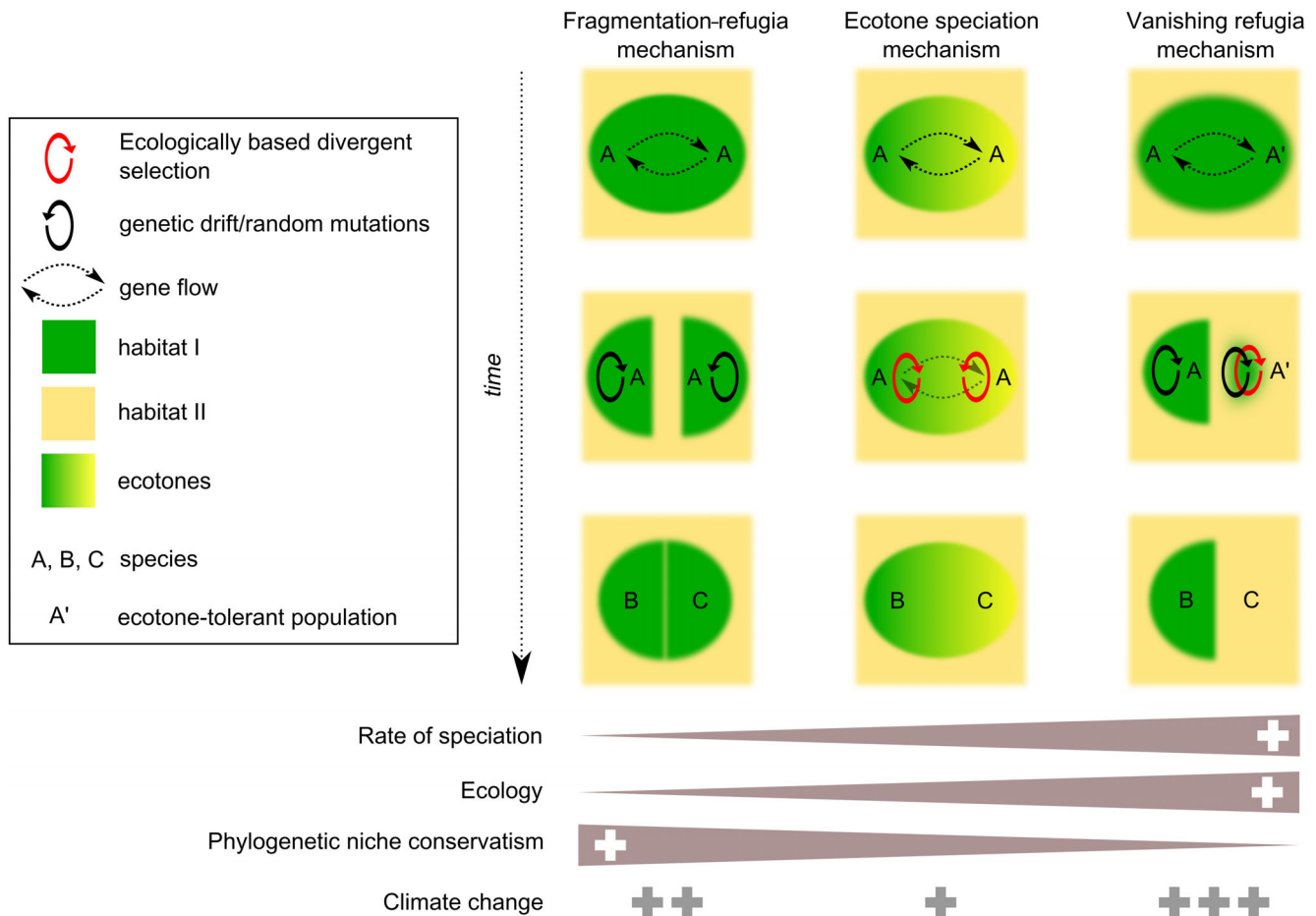
the savanna biome simply shifted in latitude in response to glacial/interglacial fluctuations, rather than becoming fragmented. Nevertheless, intra-specific genetic structuring within savanna species (Lorenzen, Heller, & Siegmund, 2012; Odee *et al.*, 2012; Engelbrecht *et al.*, 2020) linked to Pleistocene climatic fluctuations supports historical fragmentation and expansion cycles of this vegetation type.

The Pleistocene was an important period for speciation across tropical Africa for both animal and some herbaceous plant clades (Fig. 3D, E). However, these speciation events generally occurred in clades that were already diversifying (Fig. 3D, E). Thus, it seems unlikely that the Pleistocene lowland forest refugia mechanism was the primary driver of diversity across African rain forests. This mechanism may be more relevant in explaining phylogeographic patterns observed within species rather than diversification at the species level or above (Nicolas *et al.*, 2011; Hardy *et al.*, 2013; Faye *et al.*, 2016a; Portik *et al.*, 2017).

#### (b) Fragmentation–refugia mechanism

The Pleistocene lowland refugia mechanism discussed above was focussed on the Pleistocene (last 2.58 Myr). The fragmentation–refugia mechanism (Fig. 4) extends this across the Cenozoic. Indeed, dated molecular phylogenies demonstrate that speciation events for some extant plant and animal groups in tropical Africa can be dated at least to the Oligocene, although the majority of species-level diversification appears to have taken place from the Late Miocene to Pliocene (Fig. 3D, E) (Plana, 2004; Couvreur *et al.*, 2008; Voelker *et al.*, 2010; Tolley *et al.*, 2013; Koenen *et al.*, 2015; Barlow *et al.*, 2019; Portik *et al.*, 2019; Brée *et al.*, 2020). As reviewed above, Africa is characterized by numerous alternating phases of marked climatic change throughout the Cenozoic. Such climate cycles could lead to a similar pattern to that posited for the Pleistocene of fragmentation of vegetation

types into refugia followed by re-expansion. This repeated habitat fragmentation and contraction could promote allopatric speciation through vicariance, particularly for the Oligocene and Miocene epochs as suggested by numerous dated molecular studies (Fjeldså, 1994; Plana, 2004; Couvreur *et al.*, 2008; Voelker *et al.*, 2010; Branch, Bayliss, & Tolley, 2014; Hughes *et al.*, 2018). It has been invoked to explain major faunistic and floristic disjunctions between Guineo-Congolian and East African rain forest species (see Section III.2a), presumably resulting from climatic shifts from the Oligocene through the Pliocene (Loader *et al.*, 2007; Couvreur *et al.*, 2008). Evidence for this fragmentation mechanism is abundant in rain forest-restricted animal lineages. For example, speciation has been linked to forest fragmentation during the Oligocene and Miocene for at least three genera of chameleons from tropical Africa (Tolley *et al.*, 2013; Branch *et al.*, 2014; Ceccarelli *et al.*, 2014; Hughes *et al.*, 2018). In birds, recurrent forest fragmentation from the Miocene through the Pliocene has been implicated as the main factor impacting diversification (Fjeldså *et al.*, 2007; Njabo, Bowie, & Sorenson, 2008; Voelker *et al.*, 2010). In African woodpeckers, despite the absence of an absolute time frame, the main process of diversification proposed was repeated cycles of fragmentation followed by allopatric speciation (Fuchs, Pons, & Bowie, 2017). Frog lineages also show a strong pre-Pleistocene diversification pattern, especially from the Late Miocene into the Pliocene (Evans *et al.*, 2015; Bittencourt-Silva *et al.*, 2016; Larson *et al.*, 2016; Liedtke *et al.*, 2016; Zimkus *et al.*, 2017; Portik *et al.*, 2019). For example, speciation in clawed frogs started during the Late Miocene, and high diversity in central Africa was linked to persistence of forest refugia that remain today (Evans *et al.*, 2015). Finally, Miocene and Pliocene speciation was suggested to explain diversification of several rodent clades (Demos *et al.*, 2014; Bryja *et al.*, 2017; Nicolas *et al.*, 2020) and within African colobines (Ting, 2008).



**Fig 4.** Schematic representations of three selected mechanisms of speciation relevant to tropical Africa. The fragmentation–refugia mechanism is an example of the geographic model, the ecotone speciation mechanism is an example of the ecological model, and the vanishing refugia mechanism has elements of both model types. The figure provides predictions in relation to rate of speciation, and the roles of ecology, phylogenetic niche conservatism and climate change in the speciation processes (see Table 1 for further details). The time axis is not equivalent between mechanisms.

In plants, Miocene speciation due to lowland rain forest fragmentation was suggested for Annonaceae trees (Couvreur *et al.*, 2008, 2011*b*). Most sister species in this family are allopatric in distribution and show strong ecological similarities (Couvreur *et al.*, 2011*b*) supporting pre-Pleistocene allopatric speciation. Numerous other studies have dated speciation to before the Pleistocene in palms (Faye *et al.*, 2016*a*; Faye *et al.*, 2016*b*), trees (Tosso *et al.*, 2018; Migliore *et al.*, 2019; Monthe *et al.*, 2019; Brée *et al.*, 2020) and herbs (Plana *et al.*, 2004; Auvrey *et al.*, 2010), although to date there have been no attempts to link this to vicariance and allopatric speciation.

Fragmentation as a mechanism for speciation has been suggested for other habitats in tropical Africa that contracted due to climatic shifts. A study of West African lizards showed that ecotone speciation potentially supports a savannah refugia model (Leaché *et al.*, 2014). Vicariance was posited to explain the present-day distribution of the dry Rand Flora elements (Mairal *et al.*, 2015; Pokorný *et al.*, 2015) via the fragmentation of ancestral populations linked with the formation

of the Sahara desert during the Late Miocene (Mairal *et al.*, 2017). Given that tropical Africa has undergone substantial habitat shifts over the Cenozoic, fragmentation of habitats into refugia could apply to a wide range of taxa and circumstances. However, the greatest signal in the existing data appears for allopatric speciation in forest specialists, most likely because of the increasing loss of forest during the Cenozoic (Kissling *et al.*, 2012).

#### (c) Montane refugia mechanism

Tropical mountains harbour exceptional biodiversity (Barthlott *et al.*, 2005, 2007) and have been described as ‘evolutionary arenas’ (Muellner-Riehl, 2019). Mountains are topologically complex regions with high levels of geodiversity which has been shown to correlate with high levels of biodiversity (Antonelli *et al.*, 2018*b*; Rahbek *et al.*, 2019). In tropical Africa, the East African Rift System, the Eastern Arc Mountains and the Cameroon Volcanic Line are exceptional in terms of their species diversity and endemism at a global

scale (Fjelds  & Lovett, 1997; Barthlott *et al.*, 2005; Burgess *et al.*, 2007; Antonelli *et al.*, 2018b; Hoorn, Perrigo, & Antonelli, 2018b; Dagallier *et al.*, 2020). The evolutionary processes leading to high biodiversity in (tropical) mountain regions are complex (see Hoorn, Antonelli, & Perrigo, 2018a) but have recently been summarized under the mountain-geobiodiversity hypothesis (MGH) (Mosbrugger *et al.*, 2018; Muellner-Riehl, 2019). The MGH posits that (i) steep ecological gradients along elevation zones allow adaptation and ecological speciation of species to new environments or immigration of pre-adapted taxa; (ii) climatic fluctuations leading to cycles of disconnection and reconnection of populations could drive allopatric speciation *via* vicariance ('species pumps'); and (iii) there is a lower risk of local extinction under climate change (compared with lowland species) because a change in temperature can be compensated by an elevation shift, requiring limited horizontal displacement (Fjelds  *et al.*, 2007; Mosbrugger *et al.*, 2018). Thus, tropical mountains may be 'cradle' regions where taxa can diversify and/or 'museum' regions allowing taxa to persist over evolutionary time. This has been shown to apply to tropical African mountains, mainly in the east, for both animals and plants (Fjelds  & Lovett, 1997; Dagallier *et al.*, 2020).

In the present context, the montane refugia mechanism refers to speciation of montane taxa by vicariance linked to climatic fluctuations (condition *b* of the MGH; Moritz *et al.*, 2000; Mosbrugger *et al.*, 2018; Rahbek *et al.*, 2019), rather than by ecological speciation and adaptation linked to the evolution of novel habitats appearing during geological events such as mountain orogeny or volcano formation (condition *a* of the MGH; Mosbrugger *et al.*, 2018; Rahbek *et al.*, 2019). The latter condition is referred to herein as the montane gradient speciation mechanism and is discussed in Section IV.2*b*. Under the montane refugia mechanism (see Table 1), we expect speciation or diversification of clades to be congruent with periods of significant climatic fluctuations (Voje *et al.*, 2009; Voelker *et al.*, 2010; Muellner-Riehl *et al.*, 2019).

Numerous studies have provided evidence for this mechanism in tropical African mountains. The exceptional and unique biodiversity of the ancient Eastern Arc Mountains of Tanzania and Kenya (Burgess *et al.*, 2007) was suggested to be driven by long-term persistence of montane forests together with recurrent connections and disconnections between montane isolates since the Oligocene–Miocene (Lovett, 1993; Lovett *et al.*, 2005; Fjelds  & Bowie, 2008; Voelker *et al.*, 2010; Loader *et al.*, 2014). This mechanism was inferred for several clades such as songbirds (Passeriformes) (Bowie *et al.*, 2004; Fjelds  & Bowie, 2008; Voelker *et al.*, 2010; Fjelds , Bowie, & Rahbek, 2012), rodents (Mizerovsk  *et al.*, 2019; Nicolas *et al.*, 2020), forest-restricted chameleons (Tolley *et al.*, 2011; Ceccarelli *et al.*, 2014), brevicipitid frogs (Loader *et al.*, 2014), various insect groups such as Orthoptera (Voje *et al.*, 2009; Hemp *et al.*, 2010) and weevils (Grebennikov, 2017), and plants (Dimitrov *et al.*, 2012). Evidence suggests that most montane sister species in the Eastern Arc Mountains are allopatric but located on different montane areas, refuting *in situ* speciation (Hemp *et al.*, 2010; Voelker *et al.*, 2010; Missoupe *et al.*, 2012; Ceccarelli *et al.*, 2014; Taylor *et al.*, 2014). This mechanism has also been proposed in other mountain

regions of Africa such as the Albertine Rift and Kenyan Highlands (Demos *et al.*, 2014; Hughes *et al.*, 2018), the Cameroon Volcanic Line (Zimkus & Gvozdik, 2013; Taylor *et al.*, 2014; Missoupe *et al.*, 2016) and the inselbergs of northern Mozambique (Branch *et al.*, 2014; Bittencourt-Silva *et al.*, 2016).

#### (d) Riverine barrier mechanism

Wide river systems can limit the distribution of terrestrial animals or zoochorous, balochorous or non-water-dispersed plant species and serve as barriers to gene flow leading to allopatric speciation (Wallace, 1852; Moritz *et al.*, 2000; Plana, 2004; Voelker *et al.*, 2013). Tropical Africa is home to several large rivers systems (Fig. 1A) such as the Niger, Volta and Cross River in West Africa, the Sanaga in Cameroon, the Ogoou  in Gabon, the Congo in the Democratic Republic of Congo (the second longest river in Africa after the Nile), and the Zambezi in East Africa amongst others (Goudie, 2005).

In tropical Africa, the role of river systems in speciation remains ambiguous and few studies have explicitly tested this mechanism above the species level. In vertebrates, river systems appear to be important barriers delimiting the distribution of some extant species but not historically [e.g. Colyn, Gautier-Hion, & Verheyen, 1991; Louette, 1992; Katuala *et al.*, 2008; Nicolas *et al.* (2011) and references therein; Kennis *et al.*, 2011]. Some studies have shown that barriers provided by rivers such as the Congo or Ogoou  could explain some species divergences, for example in *Ammirana* (Ranidae) frogs (Jongsma *et al.*, 2018), between bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*) (Gonder *et al.*, 2011), or certain rodent groups (e.g. *Praomys*; Kennis *et al.*, 2011). The timing of speciation events was not congruent within and among clades (Jongsma *et al.*, 2018), which could be linked with the highly dynamic nature of river basins and substantial changes in their courses during the Cenozoic (Goudie, 2005).

To test whether rivers represent an effective barrier to gene flow in animals, several intra-specific studies of genetic variation within taxa occurring on both sides of major rivers have been carried out (Anthony *et al.*, 2007; Nicolas *et al.*, 2011; Olayemi *et al.*, 2012; Voelker *et al.*, 2013; Jacquet *et al.*, 2014; Bell *et al.*, 2017; Huntley *et al.*, 2019). The results are mixed. In a study of 10 bird species distributed north and south of the Congo River (near Kisangani), Voelker *et al.* (2013) found genetic variation across only four understorey species, providing limited support for the riverine barrier mechanism (see also Huntley & Voelker, 2016). Rivers were not found to be important barriers within certain frog species complexes [*Hyperolius* (Bell *et al.*, 2017); *Chiromantis rufescens* (Leach  *et al.*, 2019)] or in the common pangolin *Manis tricuspis* (Gaubert *et al.*, 2018). By contrast, rivers were shown to be intra-species barriers in several other animal groups including insects (Simard *et al.*, 2009), mammals (Nicolas *et al.*, 2011; Guschanski *et al.*, 2013; Jacquet *et al.*, 2014; Huntley *et al.*, 2019; Mizerovsk  *et al.*, 2019), reptiles (Leach  & Fujita, 2010) and certain bird clades (Huntley *et al.*, 2018, 2019).

For terrestrial plants in tropical Africa, there is no evidence that rivers play a role in diversification. This is possibly because rivers are poor barriers to seed dispersal (Muloko-ntoutoume *et al.*, 2000) as confirmed by recent work on trees (Hardy *et al.*, 2013) and herbs (Ley *et al.*, 2014).

The riverine barrier mechanism has yet to be tested properly above the species level in tropical Africa. Intra-specific studies of animals suggest that rivers might play a role in limiting gene flow, a possible precursor to speciation, depending on the biological traits of that species (e.g. specialists *versus* generalists, water tolerant *versus* water intolerant, dispersal capacity, body size). Moreover, detailed information about African river systems and their history in terms of riverbed position or water level fluctuations remain poorly documented, limiting our understanding of whether rivers played a significant barrier role.

## (2) The ecological model

Ecological speciation is defined as a process by which gene flow between populations is suppressed as a result of ecologically based divergent selection (Orr & Smith, 1998; Rundle & Nosil, 2005; Givnish, 2010). In contrast to the geographical model, ecologically dependent traits (e.g. habitat, pollinators, feeding/mating systems) drive speciation. Ecological speciation can occur in allopatry, parapatry or sympatry (Coyne & Orr, 2004). Although research on ecological speciation in the tropics is relatively scarce (Beheregaray *et al.*, 2015), several studies have been carried out in Africa. Several different mechanisms can lead to speciation under this model, either acting alone or in concert.

### (a) Ecotone speciation mechanism

This mechanism (Fig. 4) postulates that adaptation *via* natural selection to different habitats along ecological gradients (i.e. ecotones) drives phenotypic diversification and ultimately speciation (Smith *et al.*, 1997; Schluter, 1998; Moritz *et al.*, 2000). Parapatric populations occurring along an ecotone progressively adapt to different habitats leading to speciation in the presence of gene flow (Fig. 4). Without physical barriers between these populations, speciation can occur through divergent selection on different ecological traits, if selection is stronger than the homogenizing effects of gene flow (Moritz *et al.*, 2000; Smith, Schneider, & Holder, 2001). Different factors can induce or enhance reproductive isolation (e.g. phenological shift in plants, changes in behaviour in animals). In addition, models have shown that selection gradients of intermediate strength along the ecotone promote speciation (Doebeli & Dieckmann, 2003). In tropical Africa, ecotones are commonly found on the periphery of west/central rain forests that gradually give way to drier habitats such savanna/woodland/gallery forests, or elevational gradients in mountainous regions. Increased aridity in Africa since the Miocene has led to novel arid ecosystems (see Section III.6), and this may have been an important driver of speciation in both animals and

plants (Matthee & Davis, 2001; Davis *et al.*, 2002; Voje *et al.*, 2009). The latter has been linked to the evolution of the C<sub>4</sub> photosynthetic pathway in plants (Bouchenak-Khelladi *et al.*, 2009).

In birds, high levels of recent lineage diversification were identified in forest/savannah ecotones at the periphery of rain forests in the Congo Basin and West Africa, implying that the ecotone speciation mechanism may be relevant (Fjeldså, 1994; Smith *et al.*, 2001). Based on a global phylogenetic analysis, ecological speciation was suggested as the possible mechanism by which the evolution of more-open vegetation could have promoted the origin and diversification of the parrot genus *Poicephalus* from forest-dependent ancestors (Schweizer, Seehausen, & Hertwig, 2011). Speciation linked to ecological gradients was also suggested for some rodents (*Cricetomys*, Nesomyidae; Olayemi *et al.*, 2012) and shrews (Nicolas *et al.*, 2019). Two sister species with very different ecologies in the duiker genus *Cephalopus*, the central African forest-dwelling *C. nigrifrons* and the Sahel savanna species *C. rufilatus*, were found to have diverged during the Pleistocene (Johnston & Anthony, 2012). Another interesting case might be the forest *versus* savanna elephant species, estimated to have diverged during the Pliocene (Rohland *et al.*, 2010; Brandt *et al.*, 2012). In the latter two cases at least, rapid speciation *via* ecological selection to contrasting ecologies might have played a fundamental role.

Detailed population-level studies have provided evidence for the ecotone speciation mechanism in Central and West Africa (Smith *et al.*, 1997). Populations of the little greenbul (*Adropadus virens*) distributed along an ecological gradient in Cameroon showed positive selection for certain morphological traits (Smith *et al.*, 1997, 2001) and local adaptation to different habitats even in the presence of gene flow (Zhen *et al.*, 2017). In another study, genomic evidence for early adaptive diversification to different habitats along a rain forest–savanna ecotone in Cameroon was suggested for the lizard species *Trachylepis affinis* (Freedman *et al.*, 2010). Although these studies do not document species-level diversification *per se*, they do provide evidence of morphological and/or genetic adaptation to different habitats within a species, a prerequisite for this mechanism to operate (Coyne & Orr, 2004, p. 184).

There are examples in plant clades of frequent transitions between closed/forest and open/savanna habitats. Although explicit tests have not been carried out, phylogenetic analyses suggest that these transitions took place by ecological adaptation of ancestral wet-forest species to dry woodland or savanna regions throughout the Miocene. Several transitions between an inferred ancestral forested habitat to a dry forest/savannah ecosystem have been found across a wide range of families and genera such as *Coccimia* (Cucurbitaceae; Holstein & Renner, 2011), *Guibourtia* (Fabaceae; Tosso *et al.*, 2018), *Erythrophleum* (Fabaceae; Duminil *et al.*, 2015), *Acridocarpus* (Malpighiaceae; Davis *et al.*, 2002), African Melastomataceae (Veranso-Libalah *et al.*, 2018), *Entandrophragma* (Meliaceae; Monthe *et al.*, 2019) and *Manilkara* (Sapotaceae; Armstrong *et al.*, 2014).

*(b) Montane gradient speciation mechanism*

Mountains concentrate high topographic complexity and habitat heterogeneity, potentially leading to ecological speciation (Graham *et al.*, 2018). In contrast to the montane refugia mechanism (Section IV.1*c*), in this case biodiversity arises from within-mountain (*in situ*) diversification as populations adapt to the variety of different micro-habitats or along latitudinal/elevational gradients (condition *a* of the MGH; Moritz *et al.*, 2000; Graham *et al.*, 2018; Mosbrugger *et al.*, 2018; Muellner-Riehl, 2019; Rahbek *et al.*, 2019). Mountain or volcano formation provides a wide range of new niches which could also allow, in the latter case rapid, ecologically driven diversification (Muellner-Riehl, 2019; Rahbek *et al.*, 2019).

Evidence for this mechanism in African mountain biota remains poor, with most available studies supporting the montane refugia mechanism (see Section IV.1*c*). One study focusing on the east African montane white-eyes (Zosteropidae) found evidence of niche divergence between species suggesting ecological speciation (Cox *et al.*, 2014), although no clear mechanism was concluded.

*(c) Peripatric speciation mechanism*

Under this mechanism, a small peripheral population becomes isolated and diverges from the source population (Losos & Glor, 2003). The main driver behind peripatric speciation is the geographic isolation of small populations, however this might also be accompanied by shifts into novel habitats, which would involve ecological speciation after physical isolation (Coyne & Orr, 2004). These peripheral isolates originate *via* founder events where either a few individuals disperse to different areas, or the appearance of a geographical barrier isolates (vicariance) a small population from the larger population (Coyne & Orr, 2004). The newly formed species should show signs of severe population contraction (bottleneck) at the time of the divergence. This mechanism has been poorly documented in nature, and appears to be rare (Losos & Glor, 2003). We include it here under the ecological model because the few cases reported in tropical Africa have also involved ecological adaptation of peripheral populations.

An interesting case of peripatric speciation was suggested for the six species of the spiny-throated reed frog (*Hyperolius*) complex distributed in the East Arc Mountains (Lawson *et al.*, 2015). Species with restricted distributions were recovered as sister to more widely distributed species. However, two out of three species pairs showed a difference in ecology: the peripheral species had adapted to rain forest, montane grassland or forest mosaics. This implies a role of ecology during speciation, which is not incompatible with peripatric speciation (Losos & Glor, 2003). Peripatric speciation was proposed as the main speciation mechanism in the rat genus *Otomys* across the Afromontane regions (Taylor *et al.*, 2014).

In plants, there is little evidence for peripatric speciation, although this may be because it has never been explicitly

tested. There are, however, numerous examples of widespread species with sister relationships to range-restricted species. For example, the East African range-restricted *Mondodora hastipetala* (Annonaceae) was inferred to be sister to the widely distributed *M. junodii* (Couvreur *et al.*, 2011*b*) and although not explicitly discussed this could be due to peripatric speciation.

*(d) Vanishing refugia mechanism*

The vanishing refugia mechanism (VRM; Vanzolini & Williams, 1981) is an explicit mechanism (Fig. 4) whereby ecotone speciation (Section IV.2*a*) occurs in concert with peripatric or allopatric speciation (Section IV.2*c*). Under the VRM, a forest gradually contracts and fragments and is replaced by open habitat vegetation with some or all of the forest patches eventually vanishing. Forest-adapted species become trapped in the vanishing forest refugia. These peripatric populations will either go extinct, or adapt to their new conditions through ecological speciation through directional selection. Concurrently, some populations might persist long-term in more stable patches of core forest habitat and remain adapted to that core habitat. Initially, gene flow could occur between the stable core patch and the contracting fragments, but as the fragments become fully isolated, populations undergo allopatric diversification through mutation-order speciation (Nosil & Flaxman, 2011).

The diminishing patches of forest refugia would be surrounded by ecotonal vegetation and embedded in a matrix of novel vegetation. As the forest patch completely disappears, the ecotone habitat initially increases, but eventually gives way to the new habitat. Trapped populations would first be under directional selection for the ecotone, and later for the novel habitat. The distinguishing feature of the VRM from the ecotone speciation mechanism is that gene flow between the core forest patch and the forest fragments has ceased due to vicariance. This provides a clear mechanism for the diversification that is not implicit in the ecotonal mechanism where gene flow still occurs. The VRM requires one of the isolated refugial populations to persist and adapt to the new habitat after which it can expand into the new habitat. The resulting sister species should be genetically, morphologically, functionally and ecologically divergent and are separated by an ecological barrier that prevents subsequent gene flow (Vanzolini & Williams, 1981; Damasceno *et al.*, 2014).

Whether the VRM has influenced the biota of tropical Africa is not known, as it has not been explicitly tested. Testing would require evidence for the timing of habitat shifts, interpreted with respect to the date of diversification through either phylogenetic studies or population-level genetics. The latter approach can also be used to examine whether there has been a population expansion in the newly adapted species, and coalescent methods can be used to examine population-level divergence with absence of gene flow. Validation of the VRM also requires evidence for adaptation to the new habitat, such as differing morphological features that

are linked to functional traits that are optimal for the respective habitats (Vanzolini & Williams, 1981; Damasceno *et al.*, 2014). It is, however, possible that some of the examples of speciation discussed above could have been driven by this mechanism, such as *Coccinia* (Holstein & Renner, 2011), several frog taxa where allopatric sister groups occur in different habitats (Bell *et al.*, 2017), and white-eyes (*Zosterops*) from East Africa where closely related species show niche divergence (Cox *et al.*, 2014). In plants, the VRM was suggested as a potential driver of intra-specific genetic differentiation within the semi-deciduous forest tree species *Erythrophleum suaveolens* (Duminil *et al.*, 2015), although this has not led to full speciation.

### (e) Adaptive radiation

Adaptive radiation is a special case of species diversification where a single ancestor rapidly gives rise to numerous descendant species that are adapted to novel habitats through ecological opportunity [Schluter, 2000; Linder, 2008; Rundell & Price, 2009; but see Gillespie *et al.* (2020) for an in depth discussion]. Although it has some similarities to ecotone speciation, adaptive radiation does not rely on ecological gradients but rather on ecological opportunity, that is the presence of non-exploited resources or habitats. Adaptive radiation requires colonization of, or dispersal to, new habitats or to habitats vacated following extinctions, or the evolution of key innovations allowing rapid exploitation of these new or existing niches (Givnish, 2010; Gillespie *et al.*, 2020).

Besides the classic example of adaptive radiation of cichlid fishes in the East African Great Lakes (Salzburger, Van Bocxlaer, & Cohen, 2014), adaptive radiations have been suggested as a mechanism for diversification in other terrestrial tropical African animal clades. For example, the megabat tribe Epomophorini (Rousettinae) radiated into 12 species during the last 2.5 Myr. These species now occur across a number of different habitats, such as deciduous and montane forests, and savanna woodlands, and are thought to have arisen from an ancestral species inhabiting rain forest (Cunha Almeida *et al.*, 2016). Adaptive radiation has also been reported in the diverse clade of Afrobatrachian frogs (Portik & Blackburn, 2016), especially in the Hyperoliidae family, linked to the origin of sexual dichromatism, suggesting that speciation by sexual selection triggered this radiation (Portik *et al.*, 2019). Although sexual selection is assumed to be decoupled from ecological speciation, and thus considered a non-ecological process (Coyne & Orr, 2004), others have recognized a correlation between habitat type and sexually selected traits (Kraaijeveld, Kraaijeveld-Smit, & Maan, 2011), highlighting the role of sexual selection in adaptive radiations.

Compared to plant clades in southern Africa (Linder, 2003), there are relatively few clear cases of plant adaptive radiations for tropical Africa. Adaptive radiations have however, been suggested for the tropical-alpine flora (e.g. East African Rift; Linder, 2014; Hughes &

Atchison, 2015) resulting from novel habitats created during the uplift of East Africa (Linder, 2017). Adaptive radiations were proposed for genera such as *Alchemilla* (Rosaceae; Gehrke *et al.*, 2008), *Lychmis* (Caryophyllaceae; Gizaw *et al.*, 2016) and giant senecios (Dendrosenecio, Asteraceae; Knox & Palmer, 1995; but see Kandziora, Kadereit, & Gehrke, 2016), although neither of these clades are particularly speciose (Gehrke & Linder, 2014). A final example is the woody genus *Coffea* (Rubiaceae) which was suggested to have radiated in lowland and high-altitude forests of tropical Africa and shows probable convergent evolution in caffeine production (Anthony *et al.*, 2010; Hamon *et al.*, 2017).

### (3) The genomic model: polyploidization

Polyploidization, the duplication of entire genomes either *via* hybridization between different species (allopolyploidy) or within single species (autopolyploidy), is recognized as an important mode of speciation especially in plants (Estep *et al.*, 2014; Vamوسي *et al.*, 2018). Polyploids are suggested to have higher genome plasticity (Leitch & Leitch, 2008) allowing adaptation to different environments in both plants (Leitch & Leitch, 2008; te Beest *et al.*, 2012; Diallo *et al.*, 2016; Han *et al.*, 2020) and animals (Schoenfelder & Fox, 2015). Thus, polyploidization can be a first step in ecological speciation and adaptive radiation (Rundle & Nosil, 2005). To date, few studies have provided indisputable links between polyploidization and ecological speciation in tropical Africa.

Polyploidization appears less common in animals than in plants (Van de Peer, Mizrachi, & Marchal, 2017). The African clawed frogs (*Xenopus*, *Silurana*, Pipidae) provide an unusual case where allopolyploid species have arisen on multiple occasions (Evans *et al.*, 2004, 2015). Over half of the diversity of these frogs is concentrated in Central Africa, and there are several species with high ploidy levels (octoploids and dodecaploids), which has been suggested to have led to selective advantages (Evans *et al.*, 2004, 2015).

Similarly, very few studies report on the impact of polyploidization on speciation in tropical African plants. In the genus *Afzelia* (Leguminosae), which contains four rain forest tetraploids and two dry forest diploid species, there appears to be a strong association between polyploidization and specialization to different habitats (Donkpegan *et al.*, 2017). Diploids and polyploids were also documented in the tree genera *Guibourtia* (Tosso *et al.*, 2018), *Adansonia* (Pettigrew *et al.*, 2012), and *Acacia* (Diallo *et al.*, 2016) but were not linked to biome shifts. Finally, the origin of coffee (*Coffea arabica*, Rubiaceae; allotetraploid) might be the result of recent polyploidization between two wild diploid species: *C. eugenoides* and *C. canephora* (Lashermes *et al.*, 1999). More studies are needed to clarify how polyploidization events have affected the evolution of tropical African biodiversity. In particular it would be interesting to test if polyploidization events in plants and animals enabled successful ecological shifts into novel habitats across Africa (e.g. Han *et al.*, 2020) or occur randomly.

## V. CONCLUSIONS

- (1) Tropical Africa has undergone a long and complex evolution, resulting in a spectacular and unique biodiversity (Fig. 3). Modelling past climate, topography and vegetation coupled with the fossil record and dated molecular phylogenies of plants and animals provides a wealth of data allowing us to consider the evolutionary history and diversification processes behind this biodiversity.
- (2) Africa underwent numerous climatic fluctuations at different timescales, linked to tectonic, greenhouse gas, and orbital forcing. One major impact was the fragmentation of African rain forests leading to multiple vicariant speciation events. While the presence of a pan-African rain forest remains subject to debate, there is little doubt from the fossil record, vegetation simulations and dated molecular phylogenies that West/Central and East African rain forests were connected and disconnected several times during the Cenozoic, even after the uplift of the East African rift valley. Evidence for such connections should not only be sought in present-day east Africa but also further north given the northward movement of the African continent during the Cenozoic.
- (3) Compared to other tropical regions, Africa is characterized by significantly increased aridification since the Late Eocene. This led to a number of extinction events generally invoked to explain the lower species diversity across Africa compared to other tropical regions (Kissling *et al.*, 2012; Couvreur, 2015). These events also provided numerous opportunities for speciation and radiation within the newly evolved drier ecosystems (Davis *et al.*, 2002), with the evolution of C<sub>4</sub> plant-dominated ecosystems contributing significantly to the diversification of the African megafauna.
- (4) We discuss three main speciation models (geographic, ecological and genomic) and 10 mechanisms that may apply across tropical Africa (Table 1, Fig. 4). Allopatric speciation *via* vicariance of fragmenting vegetation (rain forests, savannas or montane biota) is likely to be one of the most important mechanisms, linked to the large-scale climate changes during the entire Cenozoic. Overall, these mechanisms are generally implied rather than tested within a phylogenetic and biogeographic framework. This is an important first step, but more detailed studies need to be undertaken to clarify their role in generating biodiversity. In addition, numerous studies underline that several different mechanisms may have led to diversity within the same clade (Tolley *et al.*, 2011; Cox *et al.*, 2014; Bell *et al.*, 2017; Barratt *et al.*, 2018). Thus, like in other tropical regions such as Madagascar (Brown *et al.*, 2014), no single model will be sufficient to explain patterns of diversification and diversity across tropical Africa. These models and mechanisms have similarly been suggested to explain biodiversity in other tropical regions such as the Neotropics (Gentry, 1989; Antonelli *et al.*, 2018a), Madagascar (Vences *et al.*, 2009) and South East Asia (Lohman *et al.*, 2011; Kooyman *et al.*, 2019). It will be interesting to compare the roles of these mechanisms among continents to explain the origin of tropical diversity at global scales.
- (5) We still lack fundamental biodiversity information for tropical African taxa, including accurate taxonomy, ecological studies and estimates of distribution, compared to temperate or other tropical regions. Recent efforts to compile and synthesize currently available data (Klopper *et al.*, 2007; Tolley *et al.*, 2016; Sosef *et al.*, 2017; Stévant *et al.*, 2019) have led to the identification of both well-inventoried regions and important knowledge gaps. Continued efforts to acquire primary data from the field will remain an important challenge across tropical Africa.
- (6) Despite numerous improvements in terms of data and modelling during the last decade, constraining models of the geophysical evolution of the African continent throughout the Cenozoic remains challenging. First, additional field data are required to qualify environmental and topography changes at multimillion year scales. New numerical simulations using Earth System Models, forced by surface conditions, will be required to quantify trends in African climate through time. As computing power increases and geological field and model data improve, more realistic climate simulations will be possible. However, linking these simulated climate changes to biotic evolution requires consideration of the spatial scale. Reconciling the coarse spatial resolution of climate models with biotic phenomena calls for downscaling techniques that currently are only applied to future climate projections. Such a framework will allow us to address questions regarding geologic–climatic–biotic evolution in Africa.
- (7) Next-generation sequencing is providing a massive amount of data leading to larger and more robust phylogenies (Ojeda *et al.*, 2019; Brée *et al.*, 2020; Koenen *et al.*, 2020; Streicher *et al.*, 2020), but has yet to be applied widely to the African biota. Increased sequence data, together with better fossil calibrations, will provide a more precise understanding of the evolution of African biodiversity. In addition, sequence data from different genomic regions (e.g. plastid *versus* nuclear) can lead to different age estimates (e.g. Tosso *et al.*, 2018) which will need to be resolved. Future studies should also perform demographic modelling at intra-specific levels to examine alternative scenarios of population divergences (Portik *et al.*, 2017). Phylogenomic data together with more refined divergence time estimates and additional testing of demographic scenarios will allow a re-evaluation of our understanding of the timing and diversification of tropical African biodiversity.

- (8) Finally, we need to integrate data from Earth and life sciences better, in order to synthesize patterns between major living clades. A huge amount of data has been gathered in recent decades, but this is often only loosely integrated in biogeographic studies. Better interactions between these fields will take us a step closer to ‘a trans disciplinary’ biogeography (Antonelli *et al.*, 2018a) in the geodiverse region of tropical Africa.

## VI. ACKNOWLEDGEMENTS

This synthesis stems from several meetings within the RAINBIO project funded by the French Foundation for Research on Biodiversity (FRB) and the Provence-Alpes-Côte d’Azur (PACA) region through the Centre for Synthesis and Analysis of Biodiversity data (CESAB) program. J.-C.S. considers this work a contribution to his VILLUM Investigator project “Biodiversity Dynamics in a Changing World” funded by VILLUM FONDEN (grant 16549). T.L.P.C. was supported by the Agence Nationale de la Recherche ANR (AFRODYN project; ANR-15-CE02-0002-01). The map in Fig. 1B was created using NOAA Ferret software (<https://ferretop.pmel.noaa.gov/Ferret/>), embedded in iPython notebooks (<https://ipython.org/notebook.html>) using the ferretmagic package ([https://github.com/PBrockmann/ipython\\_ferretmagic](https://github.com/PBrockmann/ipython_ferretmagic)) developed at LSCE; maps in Fig. 2 were compiled by F.G. and C.R. within the framework of ANR project TopoAfrica (ANR-08-BLAN-0247). Finally, we are grateful to three anonymous reviewers and Simon Loader for providing important comments that improved the quality of this review, and Alison Cooper for carefully reading the final version of this manuscript.

## VII. REFERENCES

Asterisks indicate studies that are used only in the online supporting information.

ANDREWS, P. & VAN COUVERING, J. A. (1975). Palaeoenvironments in the east African Miocene. In *Approaches to primate paleobiology* (ed. F. SZALAY), pp. 62–103. Karger, Basel.

ANTHONY, N. M., JOHNSON-BAWE, M., JEFFERY, K., CLIFFORD, S. L., ABERNETHY, K. A., TUTIN, C. E., LAHM, S. A., WHITE, L. J. T., UTLEY, J. F., WICKINGS, E. J. & BRUFORD, M. W. (2007). The role of Pleistocene refugia and rivers in shaping gorilla genetic diversity in Central Africa. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 20432–20436.

ANTHONY, F., DINIZ, L. E. C., COMBES, M.-C. & LASHERMES, P. (2010). Adaptive radiation in *Coffea* subgenus *Coffea* L. (Rubiaceae) in Africa and Madagascar. *Plant Systematics and Evolution* **285**, 51–64.

ANTONELLI, A. (2009). Have giant lobelias evolved several times independently? Life form shifts and historical biogeography of the cosmopolitan and highly diverse subfamily Lobelioideae (Campanulaceae). *BMC Biology* **7**, 82. <https://doi.org/10.1186/1741-7007-7-82>.

ANTONELLI, A., ARIZA, M., ALBERT, J., ANDERMANN, T., AZEVEDO, J., BACON, C., FAURBY, S., GUEDES, T., HOORN, C., LOHMANN, L. G., MATOS-MARAVI, P., RITTER, C. D., SANMARTÍN, I., SILVESTRO, D., TEJEDOR, M., TER STEEGE, H., TUOMISTO, H., WERNECK, F. P., ZIZKA, A. & EDWARDS, S. V. (2018a). Conceptual and empirical advances in Neotropical biodiversity research. *PeerJ* **6**, e5644. <https://doi.org/10.7717/peerj.5644>.

ANTONELLI, A., KISSLING, W. D., FLANTUA, S. G. A., BERMÚDEZ, M. A., MULCH, A., MUELLNER-RIEHL, A. N., KREFT, H., LINDER, H. P., BADGLEY, C., FJELDSÅ, J.,

FRITZ, S. A., RAHBEK, C., HERMAN, F., HOOGHIEMSTRA, H. & HOORN, C. (2018b). Geological and climatic influences on mountain biodiversity. *Nature Geoscience* **11**, 718–725.

ARMSTRONG, K. E., STONE, G. N., NICHOLLS, J. A., VALDERRAMA, E., ANDERBERG, A. A., SMEDMARK, J., GAUTIER, L., NACIRI, Y., MILNE, R. & RICHARDSON, J. E. (2014). Patterns of diversification amongst tropical regions compared: a case study in Sapotaceae. *Frontiers in Genetics* **5** 362. <https://doi.org/10.3389/fgene.2014.00362>.

AS-SARURI, M. L., WHYBROW, P. J. & COLLINSON, M. E. (1999). Geology, fruits, seeds, and vertebrates (? Sirenia) from the Kaninah formation (middle Eocene), Republic of Yemen. In *Fossil Vertebrates of Arabia: With emphasis on the Late Miocene faunas, geology, and palaeoenvironments of the Emirate of Abu Dhabi, United Arab Emirates*, pp. 443–453. Yale University Press, New Haven.

AUBRÉVILLE, A. (1975). Essais sur l’origine et l’histoire des flores tropicales africaines. Application de la théorie des origines polytopiques des angiospermes tropicales. *Adansonia* **15**, 31–56.

AUVREY, G., HARRIS, D. J., RICHARDSON, J. E., NEWMAN, M. F. & SÄRKINEN, T. E. (2010). Phylogeny and dating of *Aframomum* (Zingiberaceae). In *Diversity, Phylogeny, and Evolution in the Monocotyledons* (eds O. SEBERG, G. PETERSON, A. BARFOD and J. I. DAVIS), pp. 287–305. Aarhus University Press, Aarhus.

AXELROD, D. I. & RAVEN, P. H. (1978). Late cretaceous and tertiary vegetation history of Africa. In *Biogeography and Ecology of Southern Africa* (ed. M. J. A. WERGER), pp. 77–130. W. Junk bv Publishers, The Hague.

BAKER, W. J. & COUVREUR, T. L. P. (2013). Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography* **40**, 274–285.

BARLOW, A., WÜSTER, W., KELLY, C. M. R., BRANCH, W. R., PHELPS, T. & TOLLEY, K. A. (2019). Ancient habitat shifts and organismal diversification are decoupled in the African viper genus *Bitis* (Serpentes: Viperidae). *Journal of Biogeography* **46**, 1234–1248.

BARNET, J. S. K., LITTLER, K., KROON, D., LENG, M. J., WESTERHOLD, T., RÖHL, U. & ZACHOS, J. C. (2018). A new high-resolution chronology for the late Maastrichtian warming event: establishing robust temporal links with the onset of Deccan volcanism. *Geology* **46**, 147–150.

BARRATT, C. D., BWONG, B. A., JEHL, R., LIEDTKE, H. C., NAGEL, P., ONSTEIN, R. E., PORTIK, D. M., STREICHER, J. W. & LOADER, S. P. (2018). Vanishing refuge? Testing the forest refuge hypothesis in coastal East Africa using genome-wide sequence data for seven amphibians. *Molecular Ecology* **27**, 4289–4308.

BARTHOLOTT, W., MUTKE, J., RAFIQPOOR, D., KIER, G. & KREFT, H. (2005). Global centers of vascular plant diversity. *Nova Acta Leopoldina* **92**, 61–83.

BARTHOLOTT, W., HOSTERT, A., KIER, G., KÜPER, W., KREFT, H., MUTKE, J., RAFIQPOOR, M. D. & SOMMER, J. H. (2007). Geographic patterns of vascular plant diversity at global scales. *Erdkunde* **61**, 305–315.

BEAUVAIS, A. & CHARDON, D. (2013). Modes, tempo, and spatial variability of Cenozoic cratonic denudation: the west African example. *Geochemistry, Geophysics, Geosystems* **14**, 1590–1608.

TE BEEST, M., LE ROUX, J. J., RICHARDSON, D. M., BRYSTING, A. K., SUDA, J., KUBEŠOVÁ, M. & PYŠEK, P. (2012). The more the better? The role of polyploidy in facilitating plant invasions. *Annals of Botany* **109**, 19–45.

BEHEREGARAY, L. B., COOKE, G. M., CHAO, N. L. & LANDGUTH, E. L. (2015). Ecological speciation in the tropics: insights from comparative genetic studies in Amazonia. *Frontiers in Genetics* **5** 477. <https://doi.org/10.3389/fgene.2014.00477>.

BELL, R. C., PARRA, J. L., BADJEDJE, G., BAREJ, M. F., BLACKBURN, D. C., BURGER, M., CHANNING, A., DEHLING, J. M., GREENBAUM, E., GVOŽDIK, V., KIELGAST, J., KUSAMBA, C., LÖTTERS, S., MCLAUGHLIN, P. J., NAGY, Z. T., RÖDEL, M. O., PORTIK, D. M., STUART, B. L., VANDERWAL, J., ZASSI-BOULOU, A. G. & ZAMUDIO, K. R. (2017). Idiosyncratic responses to climate-driven forest fragmentation and marine incursions in reed frogs from Central Africa and the Gulf of Guinea Islands. *Molecular Ecology* **26**, 5223–5244.

BIBI, F. & KIESSLING, W. (2015). Continuous evolutionary change in Plio-Pleistocene mammals of eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 10623–10628.

BITTENCOURT-SILVA, G. B., CONRADIE, W., SIU-TING, K., TOLLEY, K. A., CHANNING, A., CUNNINGHAM, M., FAROOQ, H. M., MENEGON, M. & LOADER, S. P. (2016). The phylogenetic position and diversity of the enigmatic mongrel frog *Nothophryne* Poynton, 1963 (Amphibia, Anura). *Molecular Phylogenetics and Evolution* **99**, 89–102.

BLACH-OVERGAARD, A., BALSLEV, H., DRANSFIELD, J., NORMAND, S. & SVENNING, J.-C. (2015). Global-change vulnerability of a key plant resource, the African palms. *Scientific Reports* **5**, 12611. <https://doi.org/10.1038/srep12611>.

BOBE, R. (2006). The evolution of arid ecosystems in eastern Africa. *Journal of Arid Environments* **66**, 564–584.

BOHOUSSOU, K. H., CORNETTE, R., AKPATOU, B., COLYN, M., PETERHANS, J. K., KENNIS, J., ŠUMBERA, R., VERHEYEN, E., N’GORAN, E., KATUALA, P. & NICOLAS, V. (2015). The phylogeography of the rodent genus *Malacomys* suggests multiple Afro-tropical Pleistocene lowland forest refugia. *Journal of Biogeography* **42**, 2049–2061.

BONNEFILLE, R. (2010). Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change* **72**, 390–411.

- BONNEFILLE, R. & LETOUZEY, R. (1976). Fruits fossiles d'*Antrocaryon* dans la vallée de L'Omo (Ethiopie). *Adansonia* **16**, 63–82.
- BOOTH, A. H. (1958). The Niger, the Volta and the Dahomey gap as geographic barriers. *Evolution* **12**, 48–62.
- BOUCHENAK-KHELLADI, Y., VERBOOM, G. A., HODKINSON, T. R., SALAMIN, N., FRANCOIS, O., CHONGHAILE, G. N. & SAVOLAINEN, V. (2009). The origins and diversification of C4 grasses and savanna-adapted ungulates. *Global Change Biology* **15**, 2397–2417.
- BOUCHENAK-KHELLADI, Y., MAURIN, O., HURTER, J. & VAN DER BANK, M. (2010a). The evolutionary history and biogeography of Mimosoideae (Leguminosae): an emphasis on African acacias. *Molecular Phylogenetics and Evolution* **57**, 495–508.
- BOUCHENAK-KHELLADI, Y., VERBOOM, G. A., SAVOLAINEN, V. & HODKINSON, T. R. (2010b). Biogeography of the grasses (Poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society* **162**, 543–557.
- BOUCHENAK-KHELLADI, Y., MUASYA, A. M. & LINDER, H. P. (2014a). A revised evolutionary history of Poales: origins and diversification. *Botanical Journal of the Linnean Society* **175**, 4–16.
- BOUCHENAK-KHELLADI, Y., SLINGSBY, J. A., VERBOOM, G. A. & BOND, W. J. (2014b). Diversification of C4 grasses (Poaceae) does not coincide with their ecological dominance. *American Journal of Botany* **101**, 300–307.
- BOUREAU, E., CHEBOLDIAFF-SALARD, M., KOENIGUER, J.-C. & LOUVET, P. (1983). Evolution des flores et de la végétation Tertiaires en Afrique, au nord de l'Equateur. *Bothalia* **14**, 355–367.
- BOWIE, R. C. K., FJELDSÅ, J., HACKETT, S. J. & CROWE, T. M. (2004). Systematics and biogeography of double-collared sunbirds from the eastern Arc Mountains, Tanzania. *The Auk* **121**, 660–681.
- BRANCH, W. R., BAYLISS, J. & TOLLEY, K. A. (2014). Pygmy chameleons of the *Rhampholeon platyceps* complex (Squamata: Chamaeleonidae): description of four new species from isolated 'sky islands' of northern Mozambique. *Zootaxa* **3814**, 1–36.
- BRANDT, A. L., ISHIDA, Y., GEORGIADIS, N. J. & ROCA, A. L. (2012). Forest elephant mitochondrial genomes reveal that elephantid diversification in Africa tracked climate transitions. *Molecular Ecology* **21**, 1175–1189.
- BRÉE, B., HELMSTETTER, A. J., BETHUNE, K., GHOGUE, J.-P., SONKÉ, B. & COUVREUR, T. L. P. (2020). Diversification of African rainforest restricted clades: Piptostigmaeae and Annickiaceae (Annonaceae). *Diversity* **12**, 227. <https://doi.org/10.3390/d12060227>.
- BRIERLEY, C. M., FEDOROV, A. V., LIU, Z., HERBERT, T. D., LAWRENCE, K. T. & LARIVIERE, J. P. (2009). Greatly expanded tropical warm pool and weakened Hadley circulation in the early Pliocene. *Science* **323**, 1714–1718.
- BROWN, J. L., CAMERON, A., YODER, A. D. & VENCES, M. (2014). A necessarily complex model to explain the biogeography of the amphibians and reptiles of Madagascar. *Nature Communications* **5**, 5046. <https://doi.org/10.1038/ncomms6046>.
- BRJJA, J., MIKULA, O., ŠUMBERA, R., MEHERETU, Y., AGHOVÁ, T., LAVRENCHENKO, L. A., MAZOUCH, V., OGUGE, N., MBAU, J. S., WELEGERIMA, K., AMUNDALA, N., COLYN, M., LEIRS, H. & VERHEYEN, E. (2014). Pan-African phylogeny of *Mus* (subgenus *Nannomys*) reveals one of the most successful mammal radiations in Africa. *BMC Evolutionary Biology* **14**, 256. <https://doi.org/10.1186/s12862-014-0256-2>.
- BRJJA, J., ŠUMBERA, R., PETERHANS, K., JULIAN, C., AGHOVÁ, T., BRJJOVÁ, A., MIKULA, O., NICOLAS, V., DENYS, C. & VERHEYEN, E. (2017). Evolutionary history of the thicket rats (genus *Grammomys*) mirrors the evolution of African forests since late Miocene. *Journal of Biogeography* **44**, 182–194.
- BURGESS, N. D., BUTYNSKI, T. M., CORDEIRO, N. J., DOGGART, N. H., FJELDSÅ, J., HOWELL, K. M., KILAHAMA, F. B., LOADER, S. P., LOVETT, J. C., MBILINI, B., MENEGON, M., MOYER, D. C., NASHANDA, E., PERKIN, A., ROVERO, F., STANLEY, W. T. & STUART, S. N. (2007). The biological importance of the eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation* **134**, 209–231.
- \*CARDOSO, D., HARRIS, D. J., WIERINGA, J. J., SO-MATEUS, W. M. B., BATALHA-FILHO, H., TORKE, B. M., PRENNER, G. & DE QUEIROZ, L. P. (2017). A molecular-dated phylogeny and biogeography of the monotypic legume genus *Haplomorpha*, a missing African branch of the otherwise American-Australian Brongniartaceae clade. *Molecular Phylogenetics and Evolution* **107**, 431–442.
- CARMICHAEL, M. J., LUNT, D. J., HUBER, M., HEINEMANN, M., KIEHL, J., LEGRANDE, A., LOPTSON, C. A., ROBERTS, C. D., SAGOO, N., SHIELDS, C., VALDES, P. J., WINGUTH, A., WINGUTH, C. & PANCOST, R. D. (2016). A model-model and data-model comparison for the early Eocene hydrological cycle. *Climate of the Past* **12**, 455–481.
- CARRUTHERS, T. & SCOTLAND, R. W. (2020). Insights from empirical analyses and simulations on using multiple fossil calibrations with relaxed clocks to estimate divergence times. *Molecular Biology and Evolution* **37**, 1508–1529.
- CASCALAS-MINANA, B. & CLEAL, C. J. (2014). The plant fossil record reflects just two great extinction events. *Terra Nova* **26**, 195–200.
- CECCARELLI, F. S., MENEGON, M., TOLLEY, K. A., TILBURY, C. R., GOWER, D. J., LASERNA, M. H., KASAHUN, R., RODRIGUEZ-PIRIETO, A., HAGMANN, R. & LOADER, S. P. (2014). Evolutionary relationships, species delimitation and biogeography of eastern Afrotropical horned chameleons (Chamaeleonidae: *Trioceus*). *Molecular Phylogenetics and Evolution* **80**, 125–136.
- CERLING, T. E., WYNN, J. G., ANDANJE, S. A., BIRD, M. I., KORIR, D. K., LEVIN, N. E., MACE, W., MACHARIA, A. N., QUADE, J. & REMIEN, C. H. (2011). Woody cover and hominin environments in the past 6 million years. *Nature* **476**, 51–56.
- CHOROWICZ, J. (2005). The east African rift system. *Journal of African Earth Sciences* **43**, 379–410.
- COETZEE, J. A. (1993). African flora since the terminal Jurassic. In *Biological Relationships between Africa and South America* (ed. P. GOLDBLATT), pp. 37–61. Yale University Press, New Haven.
- COLYN, M., GAUTIER-HION, A. & VERHEYEN, W. (1991). A re-appraisal of palaeoenvironmental history in Central Africa: evidence for a major fluvial refuge in the Zaire Basin. *Journal of Biogeography* **18**, 403–407.
- COURTILLOT, V. & FLUTEAU, F. (2014). A review of the embedded time scales of flood basalt volcanism with special emphasis on dramatically short magmatic pulses. In *Volcanism, Impacts, and Mass Extinctions: Causes and Effects* (eds G. KELLER and A. C. KERR), pp. 301–317. Geological Society of America, Boulder.
- COUVREUR, T. L. P. (2015). Odd man out: why are there fewer plant species in African rain forests? *Plant Systematics and Evolution* **301**, 1299–1313.
- COUVREUR, T. L. P., CHATROU, L. W., SOSEF, M. S. & RICHARDSON, J. E. (2008). Molecular phylogenetics reveal multiple tertiary vicariance origins of the African rain forest trees. *BMC Biology* **6**, 54.
- COUVREUR, T. L. P., FOREST, F. & BAKER, W. J. (2011a). Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9**, 44. <https://doi.org/10.1186/1741-7007-6-54>.
- COUVREUR, T. L. P., PORTER-MORGAN, H., WIERINGA, J. J. & CHATROU, L. W. (2011b). Little ecological divergence associated with speciation in two African rain forest tree genera. *BMC Evolutionary Biology* **11**, 296. <https://doi.org/10.1186/1471-2148-11-296>.
- COWLING, S. A., COX, P. M., JONES, C. D., MASLIN, M. A., PEROS, M. & SPALL, S. A. (2008). Simulated glacial and interglacial vegetation across Africa: implications for species phylogenies and trans-African migration of plants and animals. *Global Change Biology* **14**, 827–840.
- COX, S. C., PRYS-JONES, R. P., HABEL, J. C., AMAKOBE, B. A. & DAY, J. J. (2014). Niche divergence promotes rapid diversification of east African sky Island white-eyes (Aves: Zosteropidae). *Molecular Ecology* **23**, 4103–4118.
- COYNE, J. A. & ORR, H. A. (2004). *Speciation*. Sinauer, Sunderland.
- CRISP, M. D. & COOK, L. G. (2009). Explosive radiation or cryptic mass extinction? Interpreting signatures in molecular phylogenies. *Evolution* **63**, 2257–2265.
- CUNHA ALMEIDA, F., GIANNINI, N. P. & SIMMONS, N. B. (2016). The evolutionary history of the African fruit bats (Chiroptera: Pteropodidae). *Acta Chiropterologica* **18**, 73–90.
- DAGALLIER, L.-P. M. J., JANSSENS, S. B., DAUBY, G., BLACH-OVERGAARD, A., MACKINDER, B. A., DROISSART, V., SVENNING, J.-C., SOSEF, M. S. M., STÉVART, T., HARRIS, D. J., SONKÉ, B., WIERINGA, J. J., HARDY, O. J. & COUVREUR, T. L. P. (2020). Cradles and museums of generic plant diversity across tropical Africa. *New Phytologist* **225**, 2196–2213.
- DAMASCENO, R., STRANGAS, M. L., CARNAVAL, A. C., RODRIGUES, M. T. & MORITZ, C. (2014). Revisiting the vanishing refuge model of diversification. *Frontiers in Genetics* **5**, 353. <https://www.frontiersin.org/articles/10.3389/fgene.2014.00353/full>.
- \*DAMM, S., DIJKSTRA, K.-D. B. & HADRYIS, H. (2010). Red drifters and dark residents: the phylogeny and ecology of a Plio-Pleistocene dragonfly radiation reflects Africa's changing environment (Odonata, Libellulidae, *Trithemis*). *Molecular Phylogenetics and Evolution* **54**, 870–882.
- DAVIS, C. C., BELL, C. D., FRITSCH, P. W. & MATHEWS, S. (2002). Phylogeny of *Acridocarpus-Brachylophon* (Malpighiaceae): implications for tertiary tropical floras and Afrotropical biogeography. *Evolution* **56**, 2395–2405.
- DEE, D. P., UPPALA, S. M., SIMMONS, A. J., BERRISFORD, P., POLI, P., KOBAYASHI, S., ANDRAE, U., BALMASEDA, M. A., BALSAMO, G., BAUER, P., BECHTOLD, P., BELJAARS, A. C. M., VAN DE BERG, L., BIDLOT, J., BORMANN, N., DELSOL, C., DRAGANI, R., FUENTES, M., GEER, A. J., HAMBERGER, L., HEALY, S. B., HERSBACH, H., HÖLM, E. V., ISAKSEN, I., KÄLLBERG, P., KÖHLER, M., MATRICARDI, M., McNALLY, A. P., MONGE-SANZ, B. M., MORCRETTE, J. J., PARK, B. K., PEUBEY, C., DE ROSNAY, P., TAVOLATO, C., THÉPAUT, J. N. & VITART, F. (2011). The ERA-interim reanalysis: configuration and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society* **137**, 553–597.
- DEMÉNOCAL, P. (2004). African climate change and faunal evolution during the Pliocene–Pleistocene. *Earth and Planetary Science Letters* **220**, 3–24.
- DEMÉNOU, B. B., DOUCET, J.-L. & HARDY, O. J. (2018). History of the fragmentation of the African rain forest in the Dahomey gap: insight from the demographic history of *Terminalia superba*. *Heredity* **120**, 547–561.
- DEMOS, T. C., KERBIS PETERHANS, J. C., AGWANDA, B. & HICKERSON, M. J. (2014). Uncovering cryptic diversity and refugial persistence among small mammal lineages across the eastern Afrotropical biodiversity hotspot. *Molecular Phylogenetics and Evolution* **71**, 41–54.
- DESCOMBES, P., GABORIAU, T., ALBOUY, C., HEINE, C., LEPRIEUR, F. & PELLISSIER, L. (2018). Linking species diversification to palaeo-environmental changes: a process-based modelling approach. *Global Ecology and Biogeography* **27**, 233–244.

- DIALLO, A. M., NIELSEN, L. R., KJER, E. D., PETERSEN, K. K. & REBILD, A. (2016). Polyploidy can confer superiority to west African *Acacia Senegal* (L.) Wild trees. *Frontiers in Plant Science* **7**, 821. <https://www.frontiersin.org/articles/10.3389/fpls.2016.00821/full>.
- DIAMOND, A. W. & HAMILTON, A. C. (1980). The distribution of forest passerine birds and quaternary climatic change in tropical Africa. *Journal of Zoology* **191**, 379–402.
- DIMITROV, D., NOGUÉS-BRAVO, D. & SCHARFF, N. (2012). Why do tropical mountains support exceptionally high biodiversity? The eastern Arc Mountains and the drivers of *Saintpaulia* diversity. *PLoS One* **7**, e48908. <https://doi.org/10.1371/journal.pone.0048908>.
- DOEBELI, M. & DIECKMANN, U. (2003). Speciation along environmental gradients. *Nature* **421**, 259–264.
- DOLOTOVSKAYA, S., TORROBA BORDALLO, J., HAUS, T., NOLL, A., HOFREITER, M., ZINNER, D. & ROOS, C. (2017). Comparing mitogenomic timetrees for two African savannah primate genera (*Chlorocebus* and *Papio*). *Zoological Journal of the Linnean Society* **181**, 471–483.
- DONKPEGAN, A. S. L., DOUCET, J.-L., MIGLIORE, J., DUMINIL, J., DAINOU, K., PIÑEIRO, R., WIERINGA, J. J., CHAMPLUVIER, D. & HARDY, O. J. (2017). Evolution in African tropical trees displaying ploidy-habitat association: the genus *Azelia* (Leguminosae). *Molecular Phylogenetics and Evolution* **107**, 270–281.
- DOUCOURÉ, C. M. & DE WIT, M. J. (2003). Old inherited origin for the present near-bimodal topography of Africa. *Journal of African Earth Sciences* **36**, 371–388.
- DROISSART, V., DAUBY, G., HARDY, O. J., DEBLAUWE, V., HARRIS, D. J., JANSSENS, S., MACKINDER, B. A., BLACH-OVERGAARD, A., SONKÉ, B., SOSEF, M. S. M., STÉVART, T., SVENNING, J.-C., WIERINGA, J. J. & COUVREUR, T. L. P. (2018). Beyond trees: Biogeographical regionalization of tropical Africa. *Journal of Biogeography* **45**, 1153–1167.
- \*DUBEY, S., SALAMIN, N., RUEDI, M., BARRIÈRE, P., COLYN, M. & VOGEL, P. (2008). Biogeographic origin and radiation of the Old World crocidurine shrews (Mammalia: Soricidae) inferred from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* **48**, 953–963.
- \*DUCHEN, P. & RENNER, S. S. (2010). The evolution of *Cayaponia* (Cucurbitaceae): repeated shifts from bat to bee pollination and long-distance dispersal to Africa 2–5 million years ago. *American Journal of Botany* **97**, 1129–1141.
- DUMINIL, J., MONA, S., MARDULYN, P., DOUMENGE, C., WALMACQ, F., DOUCET, J.-L. & HARDY, O. J. (2015). Late Pleistocene molecular dating of past population fragmentation and demographic changes in African rain forest tree species supports the forest refuge hypothesis. *Journal of Biogeography* **42**, 1443–1454.
- DUPONT, L. M., JAHNS, S., MARRET, F. & NING, S. (2000). Vegetation change in equatorial West Africa: time-slices for the last 150 ka. *Palaogeography Palaeoclimatology Palaeoecology* **155**, 95–122.
- EDWARDS, E. J., OSBORNE, C. P., STRÖMBERG, C. A. E. & SMITH, S. A. (2010). The origins of C4 grasslands: integrating evolutionary and ecosystem science. *Science* **328**, 587–591.
- ELSWORTH, G., GALBRAITH, E., HALVERSON, G. & YANG, S. (2017). Enhanced weathering and CO<sub>2</sub> drawdown caused by latest Eocene strengthening of the Atlantic meridional overturning circulation. *Nature Geoscience* **10**, 213–216.
- ENGBRECHT, H. M., BRANCH, W. R., GREENBAUM, E., BURGER, M., CONRADIE, W. & TOLLEY, K. A. (2020). African herald snakes, *Crotaphopeltis*, show population structure for a widespread generalist but deep genetic divergence for forest specialists. *Journal of Zoological Systematics and Evolutionary Research*. <https://doi.org/10.1111/jzs.12361>.
- ERWIN, T. L. (1991). An evolutionary basis for conservation strategies. *Science* **253**, 750–752.
- ESTEP, M. C., MCKAIN, M. R., DIAZ, D. V., ZHONG, J., HODGE, J. G., HODKINSON, T. R., LAYTON, D. J., MALCOMBER, S. T., PASQUET, R. & KELLOGG, E. A. (2014). Allopolyploidy, diversification, and the Miocene grassland expansion. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 15149–15154.
- DE LA ESTRELLA, M., FOREST, F., WIERINGA, J. J., FOUGÈRE-DANEZAN, M. & BRUNEAU, A. (2017). Insights on the evolutionary origin of Detarioideae, a clade of ecologically dominant tropical African trees. *New Phytologist* **214**, 1722–1735.
- EVANS, B. J., KELLEY, D. B., TINSLEY, R. C., MELNICK, D. J. & CANNATELLA, D. C. (2004). A mitochondrial DNA phylogeny of African clawed frogs: phylogeography and implications for polyploid evolution. *Molecular Phylogenetics and Evolution* **33**, 197–213.
- EVANS, B. J., CARTER, T. F., GREENBAUM, E., GVOZDIK, V., KELLEY, D. B., MCLAUGHLIN, P. J., PAUWELS, O. S. G., PORTIK, D. M., STANLEY, E. L., TINSLEY, R. C., TOBIAS, M. L. & BLACKBURN, D. C. (2015). Genetics, morphology, advertisement calls, and historical records distinguish six new polyploid species of African clawed frog (*Xenopus*, Pipidae) from west and Central Africa. *PLoS One* **10**, e0142823.
- FAITH, J. T., ROWAN, J. & DU, A. (2019). Early hominins evolved within non-analog ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 21478–21483.
- FATHY, D., WAGREICH, M., GIER, S., MOHAMED, R. S. A., ZAKI, R. & EL NADY, M. M. (2018). Maastrichtian oil shale deposition on the southern Tethys margin, Egypt: insights into greenhouse climate and paleoceanography. *Palaogeography, Palaeoclimatology, Palaeoecology* **505**, 18–32.
- FAYE, A., DEBLAUWE, V., MARIAC, G., RICHARD, D., SONKÉ, B., VIGOUROUX, Y. & COUVREUR, T. L. P. (2016a). Phylogeography of the genus *Podococcus* (Palmae/Arecaceae) in central African rain forests: climate stability predicts unique genetic diversity. *Molecular Phylogenetics and Evolution* **105**, 126–138.
- FAYE, A., PINTAUD, J.-C., BAKER, W. J., VIGOUROUX, Y., SONKE, B. & COUVREUR, T. L. P. (2016b). Phylogenetics and diversification history of African rattans (Calamoideae, Ancistrophyllinae). *Botanical Journal of the Linnean Society* **182**, 256–271.
- FEAKINS, S. J., LEVIN, N. E., LIDDY, H. M., SIERACKI, A., EGLINTON, T. I. & BONNEVILLE, R. (2013). Northeast African vegetation change over 12 m.y. *Geology* **41**, 295–298.
- FEDUCCIA, A. (2014). Avian extinction at the end of the Cretaceous: assessing the magnitude and subsequent explosive radiation. *Cretaceous Research* **50**, 1–15.
- FEIBEL, C. S. (1993). Freshwater stingrays from the Plio-Pleistocene of the Turkana Basin, Kenya and Ethiopia. *Lethaia* **26**, 359–366.
- FENG, Y.-J., BLACKBURN, D. C., LIANG, D., HILLIS, D. M., WAKE, D. B., CANNATELLA, D. C. & ZHANG, P. (2017). Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Palaeogene boundary. *Proceedings of the National Academy of Sciences of the United States of America* **114**, E5864–E5870.
- FER, I., TIETJEN, B., JELTSCH, F. & TRAUTH, M. H. (2017). Modelling vegetation change during late Cenozoic uplift of the east African plateaus. *Palaogeography, Palaeoclimatology, Palaeoecology* **467**, 120–130.
- FINCH, J., LENG, M. J. & MARCHANT, R. (2009). Late quaternary vegetation dynamics in a biodiversity hotspot, the Uluguru Mountains of Tanzania. *Quaternary Research* **72**, 111–122.
- FJELDSÅ, J. (1994). Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity and Conservation* **3**, 207–226.
- FJELDSÅ, J. & BOWIE, R. C. K. (2008). New perspectives on the origin and diversification of Africa's forest avifauna. *African Journal of Ecology* **46**, 235–247.
- FJELDSÅ, J. & LOVETT, J. C. (1997). Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centers. *Biodiversity and Conservation* **6**, 325–346.
- FJELDSÅ, J., JOHANSSON, U. S., LOKUGALAPPATTI, L. G. S. & BOWIE, R. C. K. (2007). Diversification of African greenbulbs in space and time: linking ecological and historical processes. *Journal of Ornithology* **148**, 359–367.
- FJELDSÅ, J., BOWIE, R. C. K. & RAHBEK, C. (2012). The role of mountain ranges in the diversification of birds. *Annual Review of Ecology, Evolution, and Systematics* **43**, 249–265.
- FLOWERS, R. M. & SCHOENE, B. (2010). (U-Th)/he thermochronometry constraints on unroofing of the eastern Kaapvaal craton and significance for uplift of the southern African plateau. *Geology* **38**, 827–830.
- FOSTER, G. L., HULL, P., LUNT, D. J. & ZACHOS, J. C. (2018). Placing our current 'hyperthermal' in the context of rapid climate change in our geological past. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **376**, 20170086. <https://doi.org/10.1098/rsta.2017.0086>.
- FREEDMAN, A. H., THOMASSEN, H. A., BUERMANN, W. & SMITH, T. B. (2010). Genomic signals of diversification along ecological gradients in a tropical lizard. *Molecular Ecology* **19**, 3773–3788.
- FUCHS, J. & BOWIE, R. C. (2015). Concordant genetic structure in two species of woodpecker distributed across the primary west African biogeographic barriers. *Molecular Phylogenetics and Evolution* **88**, 64–74.
- FUCHS, J., PONS, J.-M. & BOWIE, R. C. K. (2017). Biogeography and diversification dynamics of the African woodpeckers. *Molecular Phylogenetics and Evolution* **108**, 88–100.
- GALLEY, C., BYTEBIER, B., BELLSTEDT, D. U. & LINDER, H. P. (2007). The cape element in the Afrotropical flora: from cape to Cairo? *Proceedings of the Royal Society of London B: Biological Sciences* **274**, 535–543.
- \*GARCÍA-ALOY, S., VITALES, D., ROQUET, C., SANMARTÍN, I., VARGAS, P., MOLERO, J., KAMAU, P., ALDASORO, J. J. & ALARCÓN, M. (2017). North-West Africa as a source and refuge area of plant biodiversity: a case study on *Campanula kreameri* and *Campanula occidentalis*. *Journal of Biogeography* **44**, 2057–2068.
- GARDNER, J. D. & RAGE, J.-C. (2016). The fossil record of lissamphibians from Africa, Madagascar, and the Arabian plate. *Palaebiodiversity and Palaeoenvironments* **96**, 169–220.
- \*GAUBERT, P. & CORDEIRO-ESTRELA, P. (2006). Phylogenetic systematics and tempo of evolution of the Viverrinae (Mammalia, Carnivora, Viverridae) within feliformians: implications for faunal exchanges between Asia and Africa. *Molecular Phylogenetics and Evolution* **41**, 266–278.
- GAUBERT, P., ANTUNES, A., MENG, H., MIAO, L., PEIGNÉ, S., JUSTY, F., NJIROKU, F., DUFOUR, S., DANQUAH, E., ALAHAKOON, J., VERHEYEN, E., STANLEY, W. T., O'BRIEN, S. J., JOHNSON, W. E. & LUO, S.-J. (2018). The complete phylogeny of pangolins: scaling up resources for the molecular tracing of the most trafficked mammals on earth. *Journal of Heredity* **109**, 347–359.
- GAVRILETS, S. (2003). Perspective: models of speciation: what have we learned in 40 years? *Evolution* **57**, 2197–2215.

- GEHRKE, B. & LINDER, H. P. (2009). The scramble for Africa: pan-temperate elements on the African high mountains. *Proceedings of the Royal Society of London B: Biological Sciences* **276**, 2657–2665.
- GEHRKE, B. & LINDER, H. P. (2014). Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Botany* **124**, 165–177.
- GEHRKE, B., BRÄUCHLER, C., ROMOLEROUX, K., LUNDBERG, M., HEUBL, G. & ERIKSSON, T. (2008). Molecular phylogenetics of *Alchemilla*, *Aphanes* and *Lachemilla* (Rosaceae) inferred from plastid and nuclear intron and spacer DNA sequences, with comments on generic classification. *Molecular Phylogenetics and Evolution* **47**, 1030–1044.
- GENTRY, A. (1989). Speciation in tropical forests. In *Tropical Forests: Botanical Dynamics, Speciation and Diversity* (eds L. B. HOLM-NIELSEN, I. C. NIELSEN and H. BALSLEV), pp. 113–134. Academic Press, London.
- GERLAND, P., RAFTERY, A. E., ŠEVČÍKOVÁ, H., LI, N., GU, D., SPOORENBERG, T., ALKEMA, L., FOSDICK, B. K., CHUNN, J., LALIC, N., BAY, G., BUETTNER, T., HEILIG, G. K. & WILMOTH, J. (2014). World population stabilization unlikely this century. *Science* **346**, 234–237.
- GILLESPIE, R. G., BENNETT, G. M., DE MEESTER, L., FEDER, J. L., FLEISCHER, R. C., HARMON, L. J., HENDRY, A. P., KNOPE, M. L., MALLET, J., MARTIN, C., PARENT, C. E., PATTON, A. H., PFENNIG, K. S., RUBINOFF, D., SCHLUTER, D., et al. (2020). Comparing adaptive radiations across space, time, and taxa. *Journal of Heredity* **111**, 1–20.
- GIVNISH, T. J. (2010). Ecology of plant speciation. *Taxon* **59**, 1326–1366.
- GIZAW, A., BROCHMANN, C., NEMOMISSA, S., WONDIMU, T., MASAO, C. A., TUSIME, F. M., ABDI, A. A., OKELMAN, B., POPP, M. & DIMITROV, D. (2016). Colonization and diversification in the African 'sky islands': insights from fossil-calibrated molecular dating of *Lychnis* (Caryophyllaceae). *New Phytologist* **211**, 719–734.
- GOLDNER, A., HEROLD, N. & HUBER, M. (2014). The challenge of simulating the warmth of the mid-Miocene climatic Optimum in CESM1. *Climate of the Past* **10**, 523–536.
- GONDER, M. K., LOCATELLI, S., GHOBRIAL, L., MITCHELL, M. W., KUJAWSKI, J. T., LANKESTER, F. J., STEWART, C.-B. & TISHKOFF, S. A. (2011). Evidence from Cameroon reveals differences in the genetic structure and histories of chimpanzee populations. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 4766–4771.
- GOUDIE, A. S. (2005). The drainage of Africa since the Cretaceous. *Geomorphology* **67**, 437–456.
- GRAHAM, C. H., PARRA, M., MORA, A. & HIGUERA, C. (2018). The interplay between geological history and ecology in mountains. In *Mountains, Climate and Biodiversity* (eds C. HOORN, A. PERRIGO and A. ANTONELLI), pp. 231–243. Wiley-Blackwell, John Wiley & Sons, Hoboken.
- GREBENNIKOV, V. V. (2017). Phylogeography and sister group of *Lupangus*, a new genus for three new flightless allopatric forest litter weevils endemic to the eastern Arc Mountains, Tanzania (Coleoptera: Curculionidae, Molytinae). *Fragmenta Entomologica* **49**, 37–55.
- GREENBAUM, E., PORTILLO, F., JACKSON, K. & KUSAMBA, C. (2015). A phylogeny of central African *Boaedon* (Serpentes: Lamprophiidae), with the description of a new cryptic species from the Albertine rift. *African Journal of Herpetology* **64**, 18–38.
- GRIFFITHS, C. J. (1993). The geological evolution of eastern Africa. In *Biogeography and Ecology of the Rain Forest of Eastern Africa* (eds J. C. LOVETT and S. K. WASSER), pp. 9–21. Cambridge University Press, Cambridge.
- GRIMAUD, J.-L., ROUBY, D., CHARDON, D. & BEAUVAIS, A. (2017). Cenozoic sediment budget of West Africa and The Niger delta. *Basin Research* **30**, 169–186.
- GUILLOCHEAU, F., CHELALOU, R., LINOL, B., DAUTEUIL, O., ROBIN, C., MVONDO, F., CALLEG, Y. & COLIN, J.-P. (2015). Cenozoic landscape evolution in and around The Congo Basin: constraints from sediments and planation surfaces. In *Geology and Resource Potential of The Congo Basin* (eds M. J. DE WIT, F. GUILLOCHEAU and M. C. J. DE WIT), pp. 271–313. Springer, Berlin.
- GUILLOCHEAU, F., SIMON, B., BABY, G., BESSIN, P., ROBIN, C. & DAUTEUIL, O. (2018). Planation surfaces as a record of mantle dynamics: the case example of Africa. *Gondwana Research* **53**, 82–98.
- GUIRAUD, R., BOSWORTH, W., THIERRY, J. & DELPLANQUE, A. (2005). Phanerozoic geological evolution of northern and Central Africa: an overview. *Journal of African Earth Sciences* **43**, 83–143.
- GUSCHANSKI, K., KRAUSE, J., SAWYER, S., VALENTE, L. M., BAILEY, S., FINSTERMEIER, K., SABIN, R., GILISSEN, E., SONET, G., NAGY, Z. T., LENGLET, G., MAYER, F. & SAVOLAINEN, V. (2013). Next-generation museum specimens disentangles one of the largest primate radiations. *Systematic Biology* **62**, 539–554.
- HAFFER, J. (2008). Hypotheses to explain the origin of species in Amazonia. *Brazilian Journal of Biology* **68**, 917–947.
- HAMILTON, A. C. & FADEN, R. B. (1974). The history of the vegetation. In *East African Vegetation* (eds E. M. LIND and M. E. S. MORRISON), pp. 188–209. Longman, London.
- HAMILTON, A. C. & TAYLOR, D. (1992). History of climate and forests in tropical Africa during the last 8 million years. In *Tropical Forests and Climate* (ed. N. MYERS), pp. 65–78. Springer, Dordrecht.
- HAMON, N., SEPULCHRE, P., DONNADIEU, Y., HENROT, A.-J., FRANÇOIS, L., JAEGER, J.-J. & RAMSTEIN, G. (2012). Growth of subtropical forests in Miocene Europe: the roles of carbon dioxide and Antarctic ice volume. *Geology* **40**, 567–570.
- HAMON, N., SEPULCHRE, P., LEFEBVRE, V. & RAMSTEIN, G. (2013). The role of eastern Tethys seaway closure in the middle Miocene climatic transition (ca. 14 ma). *Climate of the Past* **9**, 2687–2702.
- HAMON, P., GROVER, C. E., DAVIS, A. P., RAKOTOMALALA, J.-J., RAHARIMALALA, N. E., ALBERT, V. A., SREENATH, H. L., STOFFELN, P., MITCHELL, S. E., COUTURON, E., HAMON, S., DE KOCHKO, A., CROUZILLAT, D., RIGOREAU, M., SUMIRAT, U., AKAFYOU, S. & GUYOT, R. (2017). Genotyping-by-sequencing provides the first well-resolved phylogeny for coffee (*Coffea*) and insights into the evolution of caffeine content in its species: GBS coffee phylogeny and the evolution of caffeine content. *Molecular Phylogenetics and Evolution* **109**, 351–361.
- HAN, T.-S., ZHENG, Q.-J., ONSTEIN, R. E., ROJAS-ANDRÉS, B. M., HAUENSCHILD, F., MUELLNER-RIEHL, A. N. & XING, Y.-W. (2020). Polyploidy promotes species diversification of *Allium* through ecological shifts. *New Phytologist* **225**, 571–583.
- HANDLEY, L., O'HALLORAN, A., PEARSON, P. N., HAWKINS, E., NICHOLAS, C. J., SCHOUTEN, S., McMILLAN, I. K. & PANCOST, R. D. (2012). Changes in the hydrological cycle in tropical East Africa during the Paleocene–Eocene thermal maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **329–330**, 10–21.
- HANSEN, J., SATO, M., KHARECHA, P., BEERLING, D., BERNER, R., MASSON-DELMOTTE, V., PAGANI, M., RAYMO, M., ROYER, D. L. & ZACHOS, J. C. (2008). Target atmospheric CO<sub>2</sub>: where should humanity aim? *The Open Atmospheric Science Journal* **2**, 217–231.
- HARDY, O. J., BORN, C., BUDDÉ, K., DAINOU, K., DAUBY, G., DUMINIL, J., EWÉDJÉ, E.-E. B., GOMEZ, C., HEUERZ, M., KOFFI, G. K., LOWE, J. A., MICHENEAU, C., NDIADÉ-BOUROBOU, D., PIÑEIRO, R. & PONCET, V. (2013). Comparative phylogeography of African rain forest trees: a review of genetic signatures of vegetation history in the Guineo-Congolian region. *Comptes Rendus Geoscience* **345**, 284–296.
- HARRIS, D. J., POULSEN, A. D., FRIMODT-MØLLER, C., PRESTON, J. & CRONK, Q. C. B. (2000). Rapid radiation in *Aframomum* (Zingiberaceae): evidence from nuclear ribosomal DNA internal transcribed spacer (ITS) sequences. *Edinburgh Journal of Botany* **57**, 377–395.
- HASSANIN, A., DELSUC, F., ROPIQUET, A., HAMMER, C., JANSEN VAN VUUREN, B., MATTHEE, C., RUIZ-GARCIA, M., CATZEFELIS, F., ARESKOU, V., NGUYEN, T. T. & COULOUX, A. (2012). Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies* **335**, 32–50.
- HASSANIN, A., KHOUIDER, S., GEMBU, G.-C., GOODMAN, S., KADJO, B., NESI, N., POURRUT, X., NAKOUNÉ, E. & BONILLO, C. (2015). The comparative phylogeography of fruit bats of the tribe Scotonycterini (Chiroptera, Pteropodidae) reveals cryptic species diversity related to African Pleistocene forest refugia. *Comptes Rendus Biologies* **338**, 197–211.
- HAUG, G. H., GANOPOLSKI, A., SIGMAN, D. M., ROSELL-MELE, A., SWANN, G. E. A., TIEDEMANN, R., JACCARD, S. L., BOLLMANN, J., MASLIN, M. A., LENG, M. J. & EGLINTON, G. (2005). North Pacific seasonality and the glaciation of North America 2.7 million years ago. *Nature* **433**, 821–825.
- HAYWOOD, A. M., HILL, D. J., DOLAN, A. M., OTTO-BLESNER, B. L., BRAGG, F., CHAN, W.-L., CHANDLER, M. A., CONTOUX, C., DOWSETT, H. J., JOST, A., KAMAE, Y., LOHMANN, G., LUNT, D. J., ABE-OUCHI, A., PICKERING, S. J., RAMSTEIN, G., ROSENBLUM, N. A., SALZMANN, U., SOHL, L., STEPANEK, C., UEDA, H., YAN, Q. & ZHANG, Z. (2013). Large-scale features of Pliocene climate: results from the Pliocene model Intercomparison project. *Climate of the Past* **9**, 191–209.
- HEMP, C., KEHL, S., HELLER, K.-G., WÄGELE, J. W. & HEMP, A. (2010). A new genus of African *Karniellina* (Orthoptera, Tettigoniidae, Conocephalinae, Conocephalini): integrating morphological, molecular and bioacoustical data. *Systematic Entomology* **35**, 581–595.
- HEMP, C., KEHL, S., SCHULTZ, O., WÄGELE, J. W. & HEMP, A. (2015). Climatic fluctuations and orogenesis as motors for speciation in East Africa: case study on *Parepistaurus* Karsch, 1896 (Orthoptera). *Systematic Entomology* **40**, 17–34.
- HENROT, A.-J., FRANÇOIS, L., FAVRE, E., BUTZIN, M., OUBERDOUS, M. & MUNHOVEN, G. (2010). Effects of CO<sub>2</sub>, continental distribution, topography and vegetation changes on the climate at the middle Miocene: a model study. *Climate of the Past* **6**, 675–694.
- HENROT, A.-J., UTESCHER, T., ERDEI, B., DURY, M., HAMON, N., RAMSTEIN, G., KRAPP, M., HEROLD, N., GOLDNER, A., FAVRE, E., MUNHOVEN, G. & FRANÇOIS, L. (2017). Middle Miocene climate and vegetation models and their validation with proxy data. *Palaeogeography, Palaeoclimatology, Palaeoecology* **467**, 95–119.
- HERBERT, T. D., LAWRENCE, K. T., TZANOVA, A., PETERSON, L. C., CABALLERO-GILL, R. & KELLY, C. S. (2016). Late Miocene global cooling and the rise of modern ecosystems. *Nature Geoscience* **9**, 843–847.
- HERNÁNDEZ FERNÁNDEZ, M. & VRBA, E. S. (2006). Plio-Pleistocene climatic change in the Turkana Basin (East Africa): evidence from large mammal faunas. *Journal of Human Evolution* **50**, 595–626.

- HEROLD, N., SETON, M., MÜLLER, R. D., YOU, Y. & HUBER, M. (2008). Middle Miocene tectonic boundary conditions for use in climate models. *Geochemistry, Geophysics, Geosystems* **9**, 1–10. <https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2008GC002046>.
- HERRERA, J. P. (2017). Primate diversification inferred from phylogenies and fossils. *Evolution* **71**, 2845–2857.
- HILL, J. L. & HILL, R. A. (2001). Why are tropical rain forests so species rich? Classifying, reviewing and evaluating theories. *Progress in Physical Geography* **25**, 326–354.
- HOAG, C. & SVENNING, J.-C. (2017). African environmental change from the Pleistocene to the Anthropocene. *Annual Review of Environment and Resources* **42**, 27–54.
- HODELL, D. A., CURTIS, J. H., SIERRA, F. J. & RAYMO, M. E. (2001). Correlation of late Miocene to early Pliocene sequences between the Mediterranean and North Atlantic. *Paleoceanography* **16**, 164–178.
- HOLBOURN, A., KUHNT, W., KOCHHANN, K. G. D., ANDERSEN, N. & MEIER, K. J. S. (2015). Global perturbation of the carbon cycle at the onset of the Miocene climatic optimum. *Geology* **43**, 123–126.
- HOLSTEIN, N. & RENNER, S. S. (2011). A dated phylogeny and collection records reveal repeated biome shifts in the African genus *Coccinia* (Cucurbitaceae). *BMC Evolutionary Biology* **11**, 28. <https://doi.org/10.1186/1471-2148-11-28>.
- HOORN, C., WESSELENGH, F. P., TER STEEGE, H., BERMUDEZ, M. A., MORA, A., SEVINK, J., SANMARTÍN, I., SANCHEZ-MESEGUER, A., ANDERSON, C. L., FIGUEIREDO, J. P., JARAMILLO, C., RIFF, D., NEGRI, F. R., HOOGHIEMSTRA, H., LUNDBERG, J., STADLER, T., SÄRKINEN, T. & ANTONELLI, A. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution. *Biodiversity Science* **330**, 927–931.
- HOORN, C., ANTONELLI, A. & PERRIGO, A. (eds) (2018a). *Mountains, Climate, and Biodiversity*. Wiley-Blackwell, Hoboken.
- HOORN, C., PERRIGO, A. & ANTONELLI, A. (2018b). Mountains, climate and biodiversity: an introduction. In *Mountains, Climate and Biodiversity*, pp. 1–13. Wiley-Blackwell, Hoboken.
- HUBER, M. & CABALLERO, R. (2011). The early Eocene equable climate problem revisited. *Climate of the Past* **7**, 603–633.
- HUBER, B. T., MACLEOD, K. G., WATKINS, D. K. & COFFIN, M. F. (2018). The rise and fall of the cretaceous hot greenhouse climate. *Global and Planetary Change* **167**, 1–23.
- HUGHES, C. E. & ATCHISON, G. W. (2015). The ubiquity of alpine plant radiations: from the Andes to the Hengduan Mountains. *New Phytologist* **207**, 275–282.
- HUGHES, C. E. & EASTWOOD, R. (2006). Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 10334–10339.
- HUGHES, D. F., TOLLEY, K. A., BEHANGANA, M., LUKWAGO, W., MENEGON, M., DEHLING, J. M., STIPALA, J., TILBURY, C. R., KHAN, A. M. & KUSAMBA, C. (2018). Cryptic diversity in *Rhampholeon boulengeri* (Sauria: Chamaeleonidae), a pygmy chameleon from the Albertine rift biodiversity hotspot. *Molecular Phylogenetics and Evolution* **122**, 125–141.
- HUNTLEY, J. W. & VOELKER, G. (2016). Cryptic diversity in afro-tropical lowland forests: the systematics and biogeography of the avian genus *Bleda*. *Molecular Phylogenetics and Evolution* **99**, 297–308.
- \*HUNTLEY, J. W. & VOELKER, G. (2017). A tale of the nearly tail-less: the effects of Plio-Pleistocene climate change on the diversification of the African avian genus *Sylvietta*. *Zoologica Scripta* **46**, 523–535.
- HUNTLEY, J. W., HARVEY, J. A., PAVIA, M., BOANO, G. & VOELKER, G. (2018). The systematics and biogeography of the bearded Greenbul (Aves: *Crimiger*) reveals the impact of Plio-Pleistocene forest fragmentation on afro-tropical avian diversity. *Zoological Journal of the Linnean Society* **183**, 672–686.
- HUNTLEY, J. W., KEITH, K. D., CASTELLANOS, A. A., MUSHER, L. J. & VOELKER, G. (2019). Underestimated and cryptic diversification patterns across afro-tropical lowland forests. *Journal of Biogeography* **46**, 381–391.
- IM, E.-S. & ELTAHIR, E. A. B. (2018). Simulations of the observed 'jump' in the west African monsoon and its underlying dynamics using the MIT regional climate model. *International Journal of Climatology* **38**, 841–852.
- INGLIS, G. N., FARNSWORTH, A., LUNT, D., FOSTER, G. L., HOLLIS, C. J., PAGANI, M., JARDINE, P. E., PEARSON, P. N., MARKWICK, P., GALSWORTHY, A. M. J., RAYNHAM, L., TAYLOR, K. W. R. & PANCOST, R. D. (2015). Descent toward the icehouse: Eocene Sea surface cooling inferred from GDGT distributions. *Paleoceanography* **30**, 1000–1020.
- JACOBS, B. F. (2004). Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359**, 1573–1583.
- JACOBS, B. F. & HERENDEEN, P. S. (2004). Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania. *Paleogeography, Palaeoclimatology, Palaeoecology* **213**, 115–123.
- JACOBS, B. F., PAN, A. P. & SCOTSESE, C. R. (2010). A review of the Cenozoic vegetation history of Africa. In *Cenozoic Mammals of Africa* (eds L. WERDELIN and J. SANDERS), pp. 57–72. University of California Press, Berkeley.
- JACQUET, F., NICOLAS, V., COLYN, M., KADJO, B., HUTTERER, R., DECHER, J., AKPATO, B., CRUAUD, C. & DENYS, C. (2014). Forest refugia and riverine barriers promote diversification in the west African pygmy shrew (*Crocidura obscurior* complex, Soricomorpha). *Zoologica Scripta* **43**, 131–148.
- JANSENS, S. B., KNOX, E. B., HUYSMANS, S., SMETS, E. F. & MERCKX, V. (2009). Rapid radiation of *Impatiens* (Balsaminaceae) during Pliocene and Pleistocene: result of a global climate change. *Molecular Phylogenetics and Evolution* **52**, 806–824.
- JARAMILLO, C., RUEDA, M. J. & MORA, G. (2006). Cenozoic plant diversity in the Neotropics. *Science* **311**, 1893–1896.
- JARVIS, E. D., MIRARAB, S., ABERER, A. J., LI, B., HOUEDE, P., LI, C., HO, S. Y. W., FAIRCLOTH, B. C., NABHOLZ, B., HOWARD, J. T., SUH, A., WEBER, C. C., DA FONSECA, R. R., LI, J., ZHANG, F., et al. (2014). Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**, 1320–1331.
- JENKINS, C. N., PIMM, S. L. & JOPPA, L. N. (2013). Global patterns of terrestrial vertebrate diversity and conservation. *Proceedings of the National Academy of Sciences of the United States of America* **110**, E2602–E2610.
- JOHNSON, K. R. & ELLIS, B. (2002). A tropical rainforest in Colorado 1.4 million years after the cretaceous-tertiary boundary. *Science* **296**, 2379–2383.
- JOHNSON, S. P., CUTTEN, H. N. C., MUHONGO, S. & DE WAELE, B. (2003). Neoproterozoic magmatism and metamorphism of the western granulites in the central domain of the Mozambique belt, Tanzania: U–Pb shrimp geochronology and PT estimates. *Tectonophysics* **375**, 125–145.
- JOHNSTON, A. R. & ANTHONY, N. M. (2012). A multi-locus species phylogeny of African forest duikers in the subfamily Cephalophinae: evidence for a recent radiation in the Pleistocene. *BMC Evolutionary Biology* **12**, 120. <https://doi.org/10.1186/1471-2148-12-120>.
- JONGSMA, G. F. M., BAREJ, M. F., BARRATT, C. D., BURGER, M., CONRADIE, W., ERNST, R., GREENBAUM, E., HIRSCHFELD, M., LEACHÉ, A. D., PENNER, J., PORTIK, D. M., ZASSI-BOULOU, A.-G., RÖDEL, M.-O. & BLACKBURN, D. C. (2018). Diversity and biogeography of frogs in the genus *Ammirana* (Anura: Ranidae) across sub-Saharan Africa. *Molecular Phylogenetics and Evolution* **120**, 274–285.
- JOORDENS, J. C. A., VONHOF, H. B., FEIBEL, C. S., LOURENS, L. J., DUPONT-NIVET, G., VAN DER LUBBE, J. H. J. L., SIER, M. J., DAVIES, G. R. & KROON, D. (2011). An astronomically-tuned climate framework for hominins in the Turkana Basin. *Earth and Planetary Science Letters* **307**, 1–8.
- JOORDENS, J. C. A., FEIBEL, C. S., VONHOF, H. B., SCHULP, A. S. & KROON, D. (2019). Relevance of the eastern African coastal forest for early hominin biogeography. *Journal of Human Evolution* **131**, 176–202.
- KADEREIT, G., ACKERLY, D. & PIRIE, M. D. (2012). A broader model for C4 photosynthesis evolution in plants inferred from the goosefoot family (Chenopodiaceae s.s.). *Proceedings of the Royal Society B: Biological Sciences* **279**, 3304–3311.
- KAINULAINEN, K., RAZAFIMANDIMBISON, S. G., WIKSTRÖM, N. & BREMER, B. (2017). Island hopping, long-distance dispersal and species radiation in the Western Indian Ocean: historical biogeography of the Coffeaceae alliance (Rubiaceae). *Journal of Biogeography* **44**, 1966–1979.
- KANDZIORA, M., KADEREIT, J. W. & GEHRKE, B. (2016). Frequent colonization and little in situ speciation in Senecio in the tropical alpine-like islands of eastern Africa. *American Journal of Botany* **103**, 1483–1498.
- KATUALA, P. G. B., KENNIS, J., NICOLAS, V., WENDELEN, W., HULSELMANS, J., VERHEYEN, E., HOUTTE, N. V., DIERCKX, T., DUDU, A. M. & LEIRS, H. (2008). The presence of *Praomys*, *Lophuromys*, and *Deomys* species (Muridae, Mammalia) in the forest blocks separated by The Congo River and its tributaries (Kisangani region, Democratic Republic of Congo). *Mammalia* **72**, 223–228.
- KENNIS, J., NICOLAS, V., HULSELMANS, J., KATUALA, P. G. B., WENDELEN, W., VERHEYEN, E., DUDU, A. M. & LEIRS, H. (2011). The impact of The Congo River and its tributaries on the rodent genus *Praomys*: speciation origin or range expansion limit? *Zoological Journal of the Linnean Society* **163**, 983–1002.
- KEPPEL, G., VAN NIEL, K. P., WARDELL-JOHNSON, G. W., YATES, C. J., BYRNE, M., MUCINA, L., SCHUT, A. G. T., HOPPER, S. D. & FRANKLIN, S. E. (2011). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* **21**, 393–404.
- KISSLING, W. D., EISERHARDT, W. L., BAKER, W. J., BORCHSENIUS, F., COUVREUR, T. L. P., BALSLEV, H. & SVENNING, J.-C. (2012). Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 7379–7384.
- KLERK, H. M. D., CROWE, T. M., FJELDSÄ, J. & BURGESS, N. D. (2002). Biogeographical patterns of endemic terrestrial Afrotropical birds. *Diversity and Distributions* **8**, 147–162.
- KLOPPER, R. R., GAUTIER, L., CHATELAIN, C., SMITH, G. F. & SPICHTER, R. (2007). Floristics of the angiosperm Flora of sub-Saharan Africa: an analysis of the African plant checklist and database. *Taxon* **56**, 201–208.
- KNOX, E. B. & PALMER, J. D. (1995). Chloroplast DNA variation and the recent radiation of the giant senecios (Asteraceae) on the tall mountains of eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 10349–10353.

- KOENEN, E. J. M., CLARKSON, J. J., PENNINGTON, T. D. & CHATROU, L. W. (2015). Recently evolved diversity and convergent radiations of rainforest mahoganies (Meliaceae) shed new light on the origins of rainforest hyperdiversity. *New Phytologist* **207**, 327–339.
- KOENEN, E. J. M., OJEDA, D. I., BAKKER, F. T., WIERINGA, J. J., KIDNER, C., HARDY, O. J., PENNINGTON, R. T., HERENDEEN, P. S., BRUNEAU, A. & HUGHES, C. E. (2020). The origin of the legumes is a complex paleopolyploid phylogenomic tangle closely associated with the Cretaceous-Paleogene (K-Pg) mass extinction event. *Systematic Biology* **69**, 1–14. <https://doi.org/10.1093/sysbio/syaa041>.
- KOORMAN, R. M., MORLEY, R. J., CRAYN, D. M., JOYCE, E. M., ROSSETTO, M., SLIK, J. W. F., STRIJK, J. S., SU, T., YAP, J.-Y. S. & WILF, P. (2019). Origins and assembly of Malasian rainforests. *Annual Review of Ecology, Evolution, and Systematics* **50**, 119–143.
- KRAAIJEVELD, K., KRAAIJEVELD-SMIT, F. J. L. & MAAN, M. E. (2011). Sexual selection and speciation: the comparative evidence revisited. *Biological Reviews* **86**, 367–377.
- KRIJGSMAN, W., CAPELLA, W., SIMON, D., HILGEN, F. J., KOUWENHOVEN, T. J., MEIJER, P. T., SIERRA, F. J., TULBURE, M. A., VAN DEN BERG, B. C. J., VAN DER SCHEE, M. & FLECKER, R. (2018). The Gibraltar corridor: Watergate of the Messinian salinity crisis. *Marine Geology* **403**, 238–246.
- KÜPER, W., SOMMER, J. H., LOVETT, J. C., MUTKE, J., LINDER, H. P., BEENTJE, H. J., VAN ROMPAEY, R., CHATELAIN, C., SOSEF, M. & BARTHLOTT, W. (2004). Africa's hotspots of biodiversity redefined. *Annals of the Missouri Botanical Garden* **91**, 525–535.
- KÜRSCHNER, W. M., KVAČEK, Z. & DILCHER, D. L. (2008). The impact of Miocene atmospheric carbon dioxide fluctuations on climate and the evolution of terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 449–453.
- LADANT, J.-B., DONNADIEU, Y., LEFEBVRE, V. & DUMAS, C. (2014). The respective role of atmospheric carbon dioxide and orbital parameters on ice sheet evolution at the Eocene-Oligocene transition. *Paleogeography* **29**, 810–823.
- LARRASOANA, J. C., ROBERTS, A. P., ROHLING, E. J., WINKLHOFFER, M. & WEHAUSEN, R. (2003). Three million years of monsoon variability over the northern Sahara. *Climate Dynamics* **21**, 689–698.
- LARSEN, H. C., SAUNDERS, A. D., CLIFT, P. D., BEGET, J., WEI, W. & SPEZZAFERRI, S. (1994). Seven million years of glaciation in Greenland. *Science* **264**, 952–955.
- LARSON, T. R., CASTRO, D., BEHANGANA, M. & GREENBAUM, E. (2016). Evolutionary history of the river frog genus *Ameletia* (Anura: Pyxicephalidae) reveals extensive diversification in central African highlands. *Molecular Phylogenetics and Evolution* **99**, 168–181.
- LASHERMES, P., COMBES, M.-C., ROBERT, J., TROUSLOT, P., D'HONT, A., ANTHONY, F. & CHARRIER, A. (1999). Molecular characterisation and origin of the *Coffea arabica* L. genome. *Molecular and General Genetics* **261**, 259–266.
- LAWSON, L. P., BATES, J. M., MENEGON, M. & LOADER, S. P. (2015). Divergence at the edges: peripatric isolation in the montane spiny throated reed frog complex. *BMC Evolutionary Biology* **15**, 128.
- LEACHÉ, A. D. & FUJITA, M. K. (2010). Bayesian species delimitation in west African forest geckos (*Hemidactylus fasciatus*). *Proceedings of the Royal Society B: Biological Sciences* **277**, 3071–3077.
- LEACHÉ, A. D., WAGNER, P., LINKER, C. W., BÖHME, W., PAPPENFUSS, T. J., CHONG, R. A., LAVIN, B. R., BAUER, A. M., NIELSEN, S. V., GREENBAUM, E., RÖDEL, M.-O., SCHMITZ, A., LEBRETON, M., INEICH, I., CHIRIO, L., OFORI-BOATENG, C., ENIANG, E. A., BABA EL DIN, S., LEMMON, A. R. & BURBRINK, F. T. (2014). A hybrid phylogenetic-phylogenomic approach for species tree estimation in African *Agama* lizards with applications to biogeography, character evolution, and diversification. *Molecular Phylogenetics and Evolution* **79**, 215–230.
- LEACHÉ, A. D., PORTIK, D. M., RIVERA, D., RÖDEL, M.-O., PENNER, J., GVOZDIK, V., GREENBAUM, E., JONGSMA, G. F. M., OFORI-BOATENG, C., BURGER, M., ENIANG, E. A., BELL, R. C. & FUJITA, M. K. (2019). Exploring rain forest diversification using demographic model testing in the African foam-nest treefrog *Chiromantis rufescens*. *Journal of Biogeography* **46**, 2706–2721.
- LEAKEY, M., GROSSMAN, A., GUTIÉRREZ, M. & FLEAGLE, J. G. (2011). Faunal change in the Turkana Basin during the late Oligocene and Miocene. *Evolutionary Anthropology: Issues, News, and Reviews* **20**, 238–253.
- LEAR, C. H. & LUNT, D. J. (2016). How Antarctica got its ice. *Science* **352**, 34–35.
- LECOMPTÉ, E., APLIN, K., DENIS, C., CATZEFELIS, F., CHADES, M. & CHEVRET, P. (2008). Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. *BMC Evolutionary Biology* **8**, 199. <https://doi.org/10.1186/1471-2148-8-199>.
- LEITCH, A. R. & LEITCH, I. J. (2008). Genomic plasticity and the diversity of Polyploid plants. *Science* **320**, 481–483.
- LÉVÉQUE, C., OBERDORFF, T., PAUGY, D., STIASSNY, M. L. J. & TEDESCO, P. A. (2007). Global diversity of fish (Pisces) in freshwater. In *Freshwater Animal Diversity Assessment. Developments in Hydrobiology* (eds E. V. Ballan, C. LÉVÉQUE, H. SEGERS and K. MARTENS), pp. 545–567. Springer, Dordrecht.
- LEVINSKY, I., ARAÚJO, M. B., NOGUÉS-BRAGO, D., HAYWOOD, A. M., VALDES, P. J. & RAHBEK, C. (2013). Climate envelope models suggest spatio-temporal co-occurrence of refugia of African birds and mammals. *Global Ecology and Biogeography* **22**, 351–363.
- LEY, A. C., DAUBY, G., KÖHLER, J., WYPIOR, C., RÖSER, M. & HARDY, O. J. (2014). Comparative phylogeography of eight herbs and lianas (Marantaceae) in central African rainforests. *Frontiers in Genetics* **5**, 403. <https://doi.org/10.3389/fgene.2014.00403>.
- LÉZINE, A.-M., IZUMI, K., KAGEYAMA, M. & ACHOUNDONG, G. (2019). A 90,000-year record of Afromontane forest responses to climate change. *Science* **363**, 177–181.
- LIDY, H. M., FEAKINS, S. J. & TIERNEY, J. E. (2016). Cooling and drying in Northeast Africa across the Pliocene. *Earth and Planetary Science Letters* **449**, 430–438.
- LIEDTKE, H. C., MÜLLER, H., RÖDEL, M.-O., MENEGON, M., GONWOU, L. N., BAREJ, M. F., GVOZDIK, V., SCHMITZ, A., CHANNING, A., NAGEL, P. & LOADER, S. P. (2016). No ecological opportunity signal on a continental scale? Diversification and life-history evolution of African true toads (Anura: Bufonidae). *Evolution* **70**, 1717–1733.
- LINDER, H. P. (2001). Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography* **28**, 169–182.
- LINDER, H. P. (2003). The radiation of the cape flora, southern Africa. *Biological Reviews* **78**, 597–638.
- LINDER, H. P. (2008). Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **363**, 3097–3105.
- LINDER, H. P. (2014). The evolution of African plant diversity. *Frontiers in Ecology and Evolution* **2**, 38. <https://doi.org/10.3389/fevo.2014.00038>.
- LINDER, H. P. (2017). East African Cenozoic vegetation history. *Evolutionary Anthropology: Issues, News, and Reviews* **26**, 300–312.
- LINDER, H. P., LOVETT, J., MUTKE, J. M., BARTHLOTT, W., JÜRGENS, N., REBELO, T. & KÜPER, W. (2005). A numerical re-evaluation of the sub-Saharan phytochoria of mainland Africa. *Biologische Skrifter* **55**, 229–252.
- LINDER, H. P., DE KLERK, H. M., BORN, J., BURGESS, N. D., FJELDSÅ, J. & RAHBEK, C. (2012). The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography* **39**, 1189–1372.
- LINDER, H. P., ANTONELLI, A., HUMPHREYS, A. M., PIRIE, M. D. & WÜST, R. O. (2013). What determines biogeographical ranges? Historical wanderings and ecological constraints in the danthonioid grasses. *Journal of Biogeography* **40**, 821–834.
- \*LIU, X.-Q., ICKERT-BOND, S. M., CHEN, L.-Q. & WEN, J. (2013). Molecular phylogeny of *Cissus* L. of Vitaceae (the grape family) and evolution of its pantropical intercontinental disjunctions. *Molecular Phylogenetics and Evolution* **66**, 43–53.
- LOADER, S. P., PISANI, D., COTTON, J. A., GOWER, D. J., DAY, J. J. & WILKINSON, M. (2007). Relative time scales reveal multiple origins of parallel disjunct distributions of African caecilian amphibians. *Biology Letters* **3**, 505–508.
- LOADER, S. P., CECCARELLI, F. S., MENEGON, M., HOWELL, K. M., KASSAHUN, R., MENGISTU, A. A., SABER, S. A., GEBRESEBET, F., DE SÁ, R., DAVENPORT, T. R. B., LARSON, J. G., MÜLLER, H., WILKINSON, M. & GOWER, D. J. (2014). Persistence and stability of eastern Afromontane forests: evidence from brevicipitid frogs. *Journal of Biogeography* **41**, 1781–1792.
- LOHMAN, D. J., DE BRUNN, M., PAGE, T., VON RINTELEN, K., HALL, R., NG, P. K. L., SHIH, H.-T., CARVALHO, G. R. & VON RINTELEN, T. (2011). Biogeography of the indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics* **42**, 205–226.
- LORENZEN, E. D., HELLER, R. & SIEGISMUND, H. R. (2012). Comparative phylogeography of African savannah ungulates. *Molecular Ecology* **21**, 3656–3670.
- LOSOS, J. B. & GLOR, R. E. (2003). Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology & Evolution* **18**, 220–227.
- LOUCA, S. & PENNELL, M. W. (2020). Extant timetrees are consistent with a myriad of diversification histories. *Nature* **580**, 502–505.
- LOUETTE, M. (1992). Barriers, contact zones and subspeciation in central equatorial Africa. *Bulletin of the British Ornithologists' Club* **122A**, 209–216.
- LOVETT, J. C. (1993). Eastern arc moist forest flora. In *Biogeography and Ecology of the Rain Forests of Eastern Africa* (eds J. C. Lovett and S. K. Wasser), pp. 33–55. Cambridge University Press, Cambridge.
- LOVETT, J. C., MARCHANT, R., TAPLIN, J. R. D. & KÜPER, W. (2005). The oldest rainforests in Africa: stability or resilience for survival and diversity? In *Phylogeny and Conservation* (eds A. Purvis and J. L. Gittleman), pp. 198–229. Cambridge University Press, Cambridge.
- \*LU, L., WANG, W., CHEN, Z. & WEN, J. (2013). Phylogeny of the non-monophyletic *Cayratia* Jus. (Vitaceae) and implications for character evolution and biogeography. *Molecular Phylogenetics and Evolution* **68**, 502–515.
- LUGER, P. (2003). Paleobiogeography of late early Cretaceous to early Paleocene marine Ostracoda in Arabia and north to equatorial Africa. *Palaogeography, Palaeoclimatology, Palaeoecology* **196**, 319–342.
- LUNT, D. J., DUNKLEY JONES, T., HEINEMANN, M., HUBER, M., LEGRANDE, A., WINGUTH, A., LOPTSON, C., MAROTZKE, J., ROBERTS, C. D., TINDALL, J., VALDES, P. & WINGUTH, C. (2012). A model-data comparison for a multi-model ensemble of early Eocene atmosphere-ocean simulations: EoMIP. *Climate of the Past* **8**, 1717–1736.

- MACGREGOR, D. (2015). History of the development of the east African rift system: a series of interpreted maps through time. *Journal of African Earth Sciences* **101**, 232–252.
- MAIRAL, M., POKORNY, L., ALDASORO, J. J., ALARCON, M. & SANMARTIN, I. (2015). Ancient vicariance and climate-driven extinction explain continental-wide disjunctions in Africa: the case of the Rand Flora genus *Canarina* (Campanulaceae). *Molecular Ecology* **24**, 1335–1354.
- MAIRAL, M., SANMARTIN, I. & PELLISSIER, L. (2017). Lineage-specific climatic niche drives the tempo of vicariance in the Rand Flora. *Journal of Biogeography* **44**, 911–923.
- MALEY, J. (1996). The African Rain forest main characteristics of changes in vegetation and climate from the upper Cretaceous to the Quaternary. In *Essays on the ecology of the Guinea - Congo rain forest* (eds I. ALEXANDER, M. D. SWAINE and R. WATLING), pp. 31–37. Royal Society of Edinburgh Proceedings, Edinburgh.
- MARZOLI, A., PICCIRILLO, E. M., RENNE, P. R., BELLINI, G., IACUMIN, M., NYOBE, J. B. & TONGWA, A. T. (2000). The Cameroon volcanic line revisited: Petrogenesis of continental basaltic magmas from lithospheric and Asthenospheric mantle sources. *Journal of Petrology* **41**, 87–109.
- MASLIN, M. A., BRIERLEY, C. M., MILNER, A. M., SHULTZ, S., TRAUTH, M. H. & WILSON, K. E. (2014). East African climate pulses and early human evolution. *Quaternary Science Reviews* **101**, 1–17.
- MATTHEE, C. A. & DAVIS, S. K. (2001). Molecular insights into the evolution of the family Bovidae: a nuclear DNA perspective. *Molecular Biology and Evolution* **18**, 1220–1230.
- MATTHEE, C. A., TILBURY, C. R. & TOWNSEND, T. (2004). A phylogenetic review of the African leaf chameleons: genus *Rhampholeon* (Chamaeleonidae): the role of vicariance and climate change in speciation. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, 1967–1975.
- \*MAURIN, O., MUASYA, A. M., CATALAN, P., SHONGWE, E. Z., VIRUEL, J., WILKIN, P. & VAN DER BANK, M. (2016). Diversification into novel habitats in the Africa clade of Dioscorea (Dioscoreaceae): erect habit and elephant's foot tubers. *BMC Evolutionary Biology* **16**, 238.
- MAYR, G. (2009). *Paleogene Fossil Birds*. Springer, Berlin.
- MAYR, E. & O'HARA, R. J. (1986). The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution* **40**, 55–67.
- MCCLEAN, C. J., LOVETT, J. C., KÜPER, W., HANNAH, L., SOMMER, J. H., BARTHLOTT, W., TERMANSEN, M., SMITH, G. E., TOKAMINE, S. & TAPLIN, J. R. D. (2005). African plant diversity and climate change. *Annals of the Missouri Botanical Garden* **92**, 139–152.
- MCELWAIN, J. C. & PUNYASENA, S. W. (2007). Mass extinction events and the plant fossil record. *Trends in Ecology & Evolution* **22**, 548–557.
- MEDINA, M. F., BAUER, A. M., BRANCH, W. R., SCHMITZ, A., CONRADIE, W., NAGY, Z. T., HIBBITTS, T. J., ERNST, R., PORTIK, D. M., NIELSEN, S. V., COLSTON, T. J., KUSAMBA, C., BEHANGANA, M., RÖDEL, M.-O. & GREENBAUM, E. (2016). Molecular phylogeny of *Panaspis* and *Afroablepharus* skinks (Squamata: Scincidae) in the savannas of sub-Saharan Africa. *Molecular Phylogenetics and Evolution* **100**, 409–423.
- MENEGON, M., LOADER, S. P., MARSDEN, S. J., BRANCH, W. R., DAVENPORT, T. R. B. & URSENBACHER, S. (2014). The genus *Atheris* (Serpentes: Viperidae) in East Africa: phylogeny and the role of rifting and climate in shaping the current pattern of species diversity. *Molecular Phylogenetics and Evolution* **79**, 12–22.
- \*MERCKX, V., CHATROU, L. W., LEMAIRE, B., SAUGE, M. N., HUYSMANS, S. & SMETS, E. F. (2008). Diversification of myco-heterotrophic angiosperms: evidence from Burmanniaceae. *BMC Evolutionary Biology* **8**, 178.
- \*MERCKX, V., BAKKER, F. T., HUYSMANS, S. & SMETS, E. (2009). Bias and conflict in phylogenetic inference of myco-heterotrophic plants: a case study in Thismiaceae. *Cladistics* **25**, 64–77.
- MEREDITH, R. W., JANEČKA, J. E., GATESY, J., RYDER, O. A., FISHER, C. A., TEELING, E. C., GOODBLA, A., EIZIRIK, E., SIMO, T. L. L., STADLER, T., RABOSKY, D. L., HONEYCUTT, R. L., FLYNN, J. J., INGRAM, C. M., STEINER, C., et al. (2011). Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* **334**, 521–524.
- MIGLIORE, J., KAYMAK, E., MARIAC, C., COUVREUR, T. L. P., LISSAMBOU, B.-J., PIÑEIRO, R. & HARDY, O. J. (2019). Pre-Pleistocene origin of phylogeographical breaks in African rain forest trees: New insights from *Greenwayodendron* (Annonaceae) phylogenomics. *Journal of Biogeography* **46**, 212–223.
- \*MIKULA, O., ŠUMBERA, R., AGHOVÁ, T., MBAU, J. S., KATAKWEBA, A. S., SABUNI, C. A. & BRYJA, J. (2016). Evolutionary history and species diversity of African pouched mice (Rodentia: Nesomyidae: Saccostomus). *Zoologica Scripta* **45**, 595–617.
- MILLER, K. G., KOMINZ, M. A., BROWNING, J. V., WRIGHT, J. D., MOUNTAIN, G. S., KATZ, M. E., SUGARMAN, P. J., CRAMER, B. S., CHRISTIE-BLICK, N. & PEKAR, S. F. (2005). The Phanerozoic record of Global Sea-level change. *Science* **310**, 1293–1298.
- MISSOUP, A. D., NICOLAS, V., WENDELEN, W., KEMING, E., BILONG, C. F. B., COULOUX, A., ATANGA, E., HUTTERER, R. & DENYS, C. (2012). Systematics and diversification of *Praomys* species (Rodentia: Muridae) endemic to the Cameroon volcanic line (west Central Africa). *Zoologica Scripta* **41**, 327–345.
- MISSOUP, A. D., NICOLAS, V., EISEB, S., CHUNG, E. K. & DENYS, C. (2016). Phylogenetic position of the endemic mount Oku rat, *Lamottemys okuensis* (Rodentia: Muridae), based on molecular and morphological data. *Zoological Journal of the Linnean Society* **177**, 209–226.
- MITTERMEIER, R. A., TURNER, W. R., LARSEN, F. W., BROOKS, T. M. & GASCON, C. (2011). Global biodiversity conservation: the critical role of hotspots. In *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas* (eds F. E. ZACHOS and J. C. HABEL), pp. 3–22. Springer, Heidelberg.
- MIZEROVSKÁ, D., NICOLAS, V., DEMOS, T. C., AKAIBE, D., COLYN, M., DENYS, C., KALEME, P. K., KATUALA, P., KENNIS, J., KERBIS PETERHANS, J. C., LAUDISOFF, A., MISSOUP, A. D., ŠUMBERA, R., VERHEYEN, E. & BRYJA, J. (2019). Genetic variation of the most abundant forest-dwelling rodents in Central Africa (*Praomys jacksoni* complex): evidence for Pleistocene refugia in both montane and lowland forests. *Journal of Biogeography* **46**, 1466–1478.
- MONTHE, F. K., MIGLIORE, J., DUMINIL, J., BOUKA, G., DEMENOU, B. B., DOUMENGE, C., BLANC-JOLIVET, C., EKUE, M. R. M. & HARDY, O. J. (2019). Phylogenetic relationships in two African Cedreloideae tree genera (Meliaceae) reveal multiple rain/dry forest transitions. *Perspectives in Plant Ecology, Evolution and Systematics* **37**, 1–10.
- MOREAU, R. E. (1966). *The Bird Faunas of Africa and its Islands*. Academic Press, London.
- MORITZ, C., PATTON, J. L., SCHNEIDER, C. J. & SMITH, T. B. (2000). Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics* **31**, 533–563.
- MORLEY, R. J. (2000). *Origin and Evolution of Tropical Rain Forests*. John Wiley & Sons, New York.
- MORLEY, R. J. (2007). Cretaceous and tertiary climate change and the past distribution of megathermal rainforests. In *Tropical Rainforest Responses to Climatic Changes* (eds M. B. BUSH and J. FLENNLEY), pp. 1–31. Praxis Publishing, Chichester.
- MORLEY, R. J. (2011). Dispersal and paleoecology of tropical podocarps. In *Ecology of the Podocarpaceae in Tropical Forests* (eds B. L. TURNER and L. A. CERNUSAK), pp. 21–41. Smithsonian Institution Scholarly Press, Washington, DC.
- MORLEY, R. J. & RICHARDS, K. (1993). Gramineae cuticle: a key indicator of late Cenozoic climatic change in The Niger Delta. *Review of Palaeobotany and Palynology* **77**, 119–127.
- MORLON, H. (2014). Phylogenetic approaches for studying diversification. *Ecology Letters* **17**, 508–525.
- MOSBRUGGER, V., FAVRE, A., MUELLNER-RIEHL, A. N., PÄCKERT, M. & MULCH, A. (2018). Cenozoic evolution of geo-biodiversity in the Tibeto-Himalayan region. In *Mountains, Climate, and Biodiversity* (eds C. HOORN, A. ANTONELLI and A. PERRIGO), pp. 429–448. Wiley-Blackwell, Hoboken.
- MUELLNER, A. N., SAVOLAINEN, V., SAMUEL, R. & CHASE, M. W. (2006). The mahogany family 'out-of-Africa': divergence time estimation, global biogeographic patterns inferred from plastid rbcL DNA sequences, extant, and fossil distribution of diversity. *Molecular Phylogenetics and Evolution* **40**, 236–250.
- MUELLNER-RIEHL, A. N. (2019). Mountains as evolutionary arenas: patterns, emerging approaches, paradigm shifts, and their implications for plant Phylogeographic research in the Tibeto-Himalayan region. *Frontiers in Plant Science* **10**, 195. <https://doi.org/10.3389/fpls.2019.00195>.
- MUELLNER-RIEHL, A. N., SCHNITZLER, J., KISSLING, W. D., MOSBRUGGER, V., RIJSDIJK, K. F., SEIJMONSBERGEN, A. C., VERSTEEGH, H. & FAVRE, A. (2019). Origins of global mountain plant biodiversity: testing the 'mountain-geobiodiversity hypothesis'. *Journal of Biogeography* **46**, 2826–2838.
- MUHONGO, S. & LENOIR, J.-L. (1994). Pan-African granulite-facies metamorphism in the Mozambique Belt of Tanzania: U-Pb zircon geochronology. *Journal of the Geological Society* **151**, 343–347.
- MUHONGO, S., KRÖNER, A. & NEMCHIN, A. A. (2001). Single zircon evaporation and SHRIMP ages for granulite-facies rocks in the Mozambique Belt of Tanzania. *The Journal of Geology* **109**, 171–189.
- MULOKO-NTOUTOUME, N., PETT, R. J., WHITE, L. & ABERNETHY, K. (2000). Chloroplast DNA variation in a rainforest tree (*Aucoumea klaineana*, Burseraceae) in Gabon. *Molecular Ecology* **9**, 359–363.
- MURPHY, L. N., KIRK-DAVIDOFF, D. B., MAHOWALD, N. & OTTO-BLIESNER, B. L. (2009). A numerical study of the climate response to lowered Mediterranean Sea level during the Messinian salinity crisis. *Palaogeography, Palaeoclimatology, Palaeoecology* **279**, 41–59.
- MURRAY, A. M. (2000). The Palaeozoic, Mesozoic and early Cenozoic fishes of Africa. *Fish and Fisheries* **1**, 111–145.
- MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B. & KENT, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- NESE, N., KADJO, B., POURRUT, X., LEROY, E., PONGOMBO SHONGO, C., CRUAUD, C. & HASSANIN, A. (2013). Molecular systematics and phylogeography of the tribe Myonycterini (Mammalia, Pteropodidae) inferred from mitochondrial and nuclear markers. *Molecular Phylogenetics and Evolution* **66**, 126–137.
- NEW, M., LISTER, D., HULME, M. & MAKIN, I. (2002). A high-resolution data set of surface climate over global land areas. *Climate Research* **21**, 1–25.
- NEWMARK, W. D. (2002). *Conserving Biodiversity in East African Forests: A Study of the Eastern Arc Mountains*. Springer, New York.
- NICHOLS, D. J. & JOHNSON, K. R. (2008). *Plants and the K-T Boundary*. Cambridge University Press, Cambridge.

- NICOLAS, V., QUÉROUIL, S., VERHEYEN, E., VERHEYEN, W., MBOUMBA, J. F., DILLEN, M. & COLYN, M. (2006). Mitochondrial phylogeny of African wood mice, genus *Hylomyscus* (Rodentia, Muridae): implications for their taxonomy and biogeography. *Molecular Phylogenetics and Evolution* **38**, 779–793.
- NICOLAS, V., AKPATOU, B., WENDELEN, W., KERBIS PETERHANS, J., OLAYEMI, A., DECHEUR, J., MISSOUP, A.-D., DENYS, C., BARRIERE, P., CRUAUD, C. & COLYN, M. (2010). Molecular and morphometric variation in two sibling species of the genus *Praomys* (Rodentia: Muridae): implications for biogeography. *Zoological Journal of the Linnean Society* **160**, 397–419.
- NICOLAS, V., MISSOUP, A. D., DENYS, C., PETERHANS, J. K., KATUALA, P., COULLOUX, A. & COLYN, M. (2011). The roles of rivers and Pleistocene refugia in shaping genetic diversity in *Praomys misonnei* in tropical Africa. *Journal of Biogeography* **38**, 191–207.
- NICOLAS, V., MISSOUP, A.-D., COLYN, M., CRUAUD, C., DENYS, C. & JANSEN VAN VUUREN, B. (2012). West-central African Pleistocene lowland forest evolution revealed by the phylogeography of Misonne's soft-furred mouse. *African Zoology* **47**, 100–112.
- NICOLAS, V., JACQUET, F., HUTTERER, R., KONEČNÝ, A., KAN KOUASSI, S., DURNEZ, L., LALIS, A., COLYN, M. & DENYS, C. (2019). Multilocus phylogeny of the *Crocodyra poensis* species complex (Mammalia, Eulipotyphla): influences of the palaeoclimate on its diversification and evolution. *Journal of Biogeography* **46**, 871–883.
- NICOLAS, V., FABRE, P.-H., BRJAJ, J., DENYS, C., VERHEYEN, E., MISSOUP, A.-D., OLAYEMI, A., KATUALA, P., DUDU, A. & COLYN, M. (2020). The phylogeny of the African wood mice (Muridae, *Hylomyscus*) based on complete mitochondrial genomes and five nuclear genes reveals their evolutionary history and undescribed diversity. *Molecular Phylogenetics and Evolution* **144**, 106703. <https://doi.org/10.1016/j.ympev.2019.106703>.
- \*NIE, Z.-L., SUN, H., MANCHESTER, S. R., MENG, Y., LUKE, Q. & WEN, J. (2012). Evolution of the intercontinental disjunctions in six continents in the *Ampelopsis* clade of the grape family (Vitaceae). *BMC Evolutionary Biology* **12**, 17.
- NJABO, K. Y., BOWIE, R. C. K. & SORENSON, M. D. (2008). Phylogeny, biogeography and taxonomy of the African wattle-eyes (Aves: Passeriformes: Platysteiridae). *Molecular Phylogenetics and Evolution* **48**, 136–149.
- NOSIL, P. & FLAXMAN, S. M. (2011). Conditions for mutation-order speciation. *Proceedings of the Royal Society B: Biological Sciences* **278**, 399–407.
- NOVELLO, A., BARBONI, D., SILVESTRE, F., LEBATARD, A.-E., PAILLÈS, C., BOURLÈS, D. L., LIKIUS, A., MACKAYE, H. T., VIGNAUD, P. & BRUNET, M. (2017). Phytoliths indicate significant arboreal cover at Sahelanthropus type locality TM266 in northern Chad and a decrease in later sites. *Journal of Human Evolution* **106**, 66–83.
- OEDE, D. W., TELFORD, A., WILSON, J., GAYE, A. & CAVERS, S. (2012). Plio-Pleistocene history and phylogeography of *Acacia Senegal* in dry woodlands and savannahs of sub-Saharan tropical Africa: evidence of early colonisation and recent range expansion. *Heredity* **109**, 372–382.
- OJEDA, D. I., KOENEN, E., CERVANTES, S., DE LA ESTRELLA, M., BANGUERA-HINESTROZA, E., JANSENS, S. B., MIGLIORE, J., DEMENOU, B. B., BRUNEAU, A., FOREST, F. & HARDY, O. J. (2019). Phylogenomic analyses reveal an exceptionally high number of evolutionary shifts in a florally diverse clade of African legumes. *Molecular Phylogenetics and Evolution* **137**, 156–167.
- OLAYEMI, A., NICOLAS, V., HULSELMAANS, J., MISSOUP, A. D., FICHET-CALVET, E., AMUNDALA, D., DUDU, A., DIERCKX, T., WENDELEN, W., LEIRS, H. & VERHEYEN, E. (2012). Taxonomy of the African giant pouched rats (Nesomyidae: *Cricetomys*): molecular and craniometric evidence support an unexpected high species diversity. *Zoological Journal of the Linnean Society* **165**, 700–719.
- O'LEARY, M. A., BLOCH, J. I., FLYNN, J. J., GAUDIN, T. J., GIALLOMBARDO, A., GIANNINI, N. P., GOLDBERG, S. L., KRAATZ, B. P., LUO, Z.-X., MENG, J., NI, X., NOVACEK, M. J., PERINI, F. A., RANDALL, Z. S., ROUGIER, G. W., SARGIS, E. J., SILCOX, M. T., SIMMONS, N. B., SPAULDING, M., VELAZCO, P. M., WEKSLER, M., WIBLE, J. R. & CIRRNELLO, A. L. (2013). The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* **339**, 662–667.
- ORR, M. R. & SMITH, T. B. (1998). Ecology and speciation. *Trends in Ecology & Evolution* **13**, 502–506.
- PAN, A. D., JACOBS, B. F., DRANSFIELD, J. & BAKER, W. J. (2006). The fossil history of palms (Arecaceae) in Africa and new records from the late Oligocene (28–27 Mya) of North-Western Ethiopia. *Botanical Journal of the Linnean Society* **151**, 69–81.
- PENNER, J., WEGMANN, M., HILLERS, A., SCHMIDT, M. & RÖDEL, M.-O. (2011). A hotspot revisited—a biogeographical analysis of west African amphibians. *Diversity and Distributions* **17**, 1077–1088.
- PETTIGREW, J. D., BELL, K. L., BHAGWANDIN, A., GRINAN, E., JILLANI, N., MEYER, J., WABUYELE, E. & VICKERS, C. E. (2012). Morphology, ploidy and molecular phylogenetics reveal a new diploid species from Africa in the baobab genus *Adansonia* (Malvaceae: Bombacoideae). *Taxon* **61**, 1240–1250.
- PICKFORD, M., SENUT, B. & MOURER-CHAUVIRE, C. (2004). Early Pliocene Tragulidae and peafowls in the Rift Valley, Kenya: evidence for rainforest in East Africa. *Comptes Rendus Palevol* **3**, 179–189.
- PLANA, V. (2004). Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest. *Philosophical Transactions of the Royal Society B-Biological Sciences* **359**, 1585–1594.
- PLANA, V., GASCOIGNE, A., FORREST, L. L., HARRIS, D. & PENNINGTON, R. T. (2004). Pleistocene and pre-Pleistocene Begonia speciation in Africa. *Molecular Phylogenetics and Evolution* **31**, 449–461.
- POKORNY, L., RIINA, R., MAIRAL, M., MESEGUER, A. S., CULSHAW, V., CENDOYA, J., SERRANO, M., CARBAJAL, R., ORTIZ, S., HEUERTZ, M. & SANMARTÍN, I. (2015). Living on the edge: timing of Rand Flora disjunctions congruent with ongoing aridification in Africa. *Frontiers in Genetics* **6**, 154. <https://doi.org/10.3389/fgene.2015.00154>.
- POLISSAR, P. J., ROSE, C., UNO, K. T., PHELPS, S. R. & DEMENOCAL, P. (2019). Synchronous rise of African C4 ecosystems 10 million years ago in the absence of aridification. *Nature Geoscience* **12**, 657–660.
- PORTIK, D. M. & BLACKBURN, D. C. (2016). The evolution of reproductive diversity in Afrobatrachia: a phylogenetic comparative analysis of an extensive radiation of African frogs. *Evolution* **70**, 2017–2032.
- PORTIK, D. M., LEACHÉ, A. D., RIVERA, D., BAREJ, M. F., BURGER, M., HIRSCHFELD, M., RÖDEL, M.-O., BLACKBURN, D. C. & FUJITA, M. K. (2017). Evaluating mechanisms of diversification in a Guineo-Congolian tropical forest frog using demographic model selection. *Molecular Ecology* **26**, 5245–5263.
- PORTIK, D. M., BELL, R. C., BLACKBURN, D. C., BAUER, A. M., BARRATT, C. D., BRANCH, W. R., BURGER, M., CHANNING, A., COLSTON, T. J., CONRADIE, W., DEHLING, J. M., DREWES, R. C., ERNST, R., GREENBAUM, E., GVOZDIK, V., HARVEY, J., HILLERS, A., HIRSCHFELD, M., JONGSMA, G. F. M., KIELGAST, J., KOUETE, M. T., LAWSON, L. P., LEACHÉ, A. D., LOADER, S. P., LÖTTERS, S., MEIJDEN, A. V. D., MENEGON, M., MÜLLER, S., NAGY, Z. T., OFORI-BOATENG, C., OHLER, A., PAFENFUSS, T. J., RÖSSLER, D., SINCSCH, U., RÖDEL, M. O., VEITH, M., VINDUM, J., ZASSI-BOULOU, A. G. & MCGUIRE, J. A. (2019). Sexual dichromatism drives diversification within a major radiation of African amphibians. *Systematic Biology* **68**, 859–875.
- PORTILLO, F., BRANCH, W. R., CONRADIE, W., RÖDEL, M.-O., PENNER, J., BAREJ, M. F., KUSAMBA, C., MUNINGA, W. M., ARISTOTE, M. M., BAUER, A. M., TRAPE, J.-F., NAGY, Z. T., CARLINO, P., PAUWELS, O. S. G., MENEGON, M., BURGER, M., MAZUCH, T., JACKSON, K., HUGHES, D. F., BEHANGANA, M., ZASSI-BOULOU, A. G. & GREENBAUM, E. (2018). Phylogeny and biogeography of the African burrowing snake subfamily Aparallactinae (Squamata: Lamprophiidae). *Molecular Phylogenetics and Evolution* **127**, 288–303.
- POUND, M. J. & SALZMANN, U. (2017). Heterogeneity in global vegetation and terrestrial climate change during the late Eocene to early Oligocene transition. *Scientific Reports* **7**, 43386.
- POUND, M. J., HAYWOOD, A. M., SALZMANN, U., RIDING, J. B., LUNT, D. J. & HUNTER, S. J. (2011). A Tortonian (late Miocene, 11.61–7.25 ma) global vegetation reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **300**, 29–45.
- POZZI, L. (2016). The role of forest expansion and contraction in species diversification among galagos (Primates: Galagidae). *Journal of Biogeography* **43**, 1930–1941.
- POZZI, L., DISOTELL, T. R. & MASTERS, J. C. (2014). A multilocus phylogeny reveals deep lineages within African galagids (Primates: Galagidae). *BMC Evolutionary Biology* **14**, 72. <https://doi.org/10.1186/1471-2148-14-72>.
- PRAVE, A. R., BATES, C. R., DONALDSON, C. H., TOLAND, H., CONDON, D. J., MARK, D. & RAUB, T. D. (2016). Geology and geochronology of the Tana Basin, Ethiopia: LIP volcanism, super eruptions and Eocene–Oligocene environmental change. *Earth and Planetary Science Letters* **443**, 1–8.
- PRÖMMEL, K., CUBASCH, U. & KASPAR, F. (2013). A regional climate model study of the impact of tectonic and orbital forcing on African precipitation and vegetation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **369**, 154–162.
- QUIROGA, M. P., MATHIASSEN, P., IGLESIAS, A., MILL, R. R. & PREMOLI, A. C. (2016). Molecular and fossil evidence disentangle the biogeographical history of *Podocarpus*, a key genus in plant geography. *Journal of Biogeography* **43**, 372–383.
- RAHBEK, C., BORREGAARD, M. K., ANTONELLI, A., COLWELL, R. K., HOLT, B. G., NOGUES-BRAVO, D., RASMUSSEN, C. M. Ø., RICHARDSON, K., ROSING, M. T., WHITTAKER, R. J. & FJELDSÄ, J. (2019). Building mountain biodiversity: geological and evolutionary processes. *Science* **365**, 1114–1119.
- RAVELO, A. C., ANDREASEN, D. H., LYLE, M., LYLE, A. O. & WAR, M. W. (2004). Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature* **429**, 263–267.
- RETALLACK, G. J., DUGAS, D. P. & BESTLAND, E. A. (1990). Fossil soils and grasses of a middle Miocene east-African grassland. *Science* **247**, 1325–1328.
- RICHARDS, P. W. (1973). Africa, the 'odd man out'. In *Tropical Forest Ecosystems of Africa and South America: A Comparative Review* (eds B. J. MEGGERS, E. S. AYENSU and W. D. DUCKWORTH), pp. 21–26. Smithsonian Institution Press, Washington, DC.
- RING, U., ALBRECHT, C. & SCHRENK, F. (2018). The east African rift system: tectonics, climate and biodiversity. In *Mountains, Climate and Biodiversity* (eds M. C. HOORN, A. PERRIGO and A. ANTONELLI), pp. 391–406. Wiley-Blackwell, John Wiley & Sons, Hoboken.

- ROBBRECHT, E. (1996). Geography of African Rubiaceae with reference to glacial rain forest refuges. In *The Biodiversity of African Plants*, pp. 564–581. Springer, New York.
- ROBERT, C. & CHAMLEY, H. (1987). Cenozoic evolution of continental humidity and paleoenvironment, deduced from the kaolinite content of oceanic sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology* **60**, 171–187.
- ROBERTS, E. M., STEVENS, N. J., O'CONNOR, P. M., DIRKS, P. H. G. M., GOTTFRIED, M. D., CLYDE, W. C., ARMSTRONG, R. A., KEMP, A. I. S. & HEMMING, S. (2012). Initiation of the western branch of the east African rift coeval with the eastern branch. *Nature Geoscience* **5**, 289–294.
- ROHLAND, N., REICH, D., MALLICK, S., MEYER, M., GREEN, R. E., GEORGIADIS, N. J., ROCA, A. L. & HOFREITER, M. (2010). Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. *PLoS Biology* **8**, e1000564. <https://doi.org/10.1371/journal.pbio.1000564>.
- ROSE, C., POLISSAR, P. J., TIERNEY, J. E., FILLEY, T. & DEMENOGAL, P. B. (2016). Changes in northeast African hydrology and vegetation associated with Pliocene–Pleistocene sapropel cycles. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 20150243. <https://doi.org/10.1098/rstb.2015.0243>.
- RUNDELL, R. J. & PRICE, T. D. (2009). Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology & Evolution* **24**, 394–399.
- RUNDLE, H. D. & NOSIL, P. (2005). Ecological speciation. *Ecology Letters* **8**, 336–352.
- SAGOO, N., VALDES, P., FLECKER, R. & GREGOIRE, L. J. (2013). The early Eocene equable climate problem: can perturbations of climate model parameters identify possible solutions? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **371**, 20130123. <https://doi.org/10.1098/rsta.2013.0123>.
- \*SAHOO, R. K., LOHMAN, D. J., WAHLBERG, N., MÜLLER, C. J., BRATTSTRÖM, O., COLLINS, S. C., PEGGIE, D., ADUSE-POKU, K. & KODANDARAMAIAH, U. (2018). Evolution of *Hypolimnas* butterflies (Nymphalidae): out-of-Africa origin and *Wolbachia*-mediated introgression. *Molecular Phylogenetics and Evolution* **123**, 50–58.
- SALARD-CHEBOLDAEFF, M. (1979). Palynologie maestrichtienne et tertiaire du Cameroun. Etude qualitative et répartition verticale des principales espèces. *Review of Palaeobotany and Palynology* **28**, 365–388.
- SALARD-CHEBOLDAEFF, M. (1990). Intertropical African palynostratigraphy from cretaceous to late quaternary times. *Journal of African Earth Sciences and the Middle East* **11**, 11N1–24HN6.
- SALZBURGER, W. (2018). Understanding explosive diversification through cichlid fish genomics. *Nature Reviews Genetics* **19**, 705–717.
- SALZBURGER, W., VAN BOCKLAER, B. & COHEN, A. S. (2014). Ecology and evolution of the African Great Lakes and their faunas. *Annual Review of Ecology, Evolution, and Systematics* **45**, 519–545.
- SALZMANN, U. & HOELZMANN, P. (2005). The Dahomey gap: an abrupt climatically induced rain forest fragmentation in West Africa during the late Holocene. *The Holocene* **15**, 190–199.
- SANMARTÍN, I. & MESEGUER, A. S. (2016). Extinction in phylogenetics and biogeography: from timetrees to patterns of biotic assemblage. *Frontiers in Genetics* **7**, 35. <https://doi.org/10.3389/fgene.2016.00035>.
- SANMARTÍN, I., ANDERSON, C. L., ALARCON, M., RONQUIST, F. & ALDASORO, J. J. (2010). Bayesian Island biogeography in a continental setting: the Rand Flora case. *Biology Letters* **6**, 703–707.
- SAUQUET, H. (2013). A practical guide to molecular dating. *Comptes Rendus Palevol* **12**, 355–367.
- SAYRE, R. G., COMER, P., HAK, J., JOSSE, C., BOW, J., WARNER, H., LARWANOU, M., KALBESSA, E., BEKELE, T., KEHL, H., AMENA, R., ANDRIAMASIMANANA, R., BA, T., BENSON, L., BOUCHER, T., et al. (2013). A new map of standardized terrestrial ecosystems of Africa. *African Geographical Review*, **32**(S1), 1–24.
- \*SCHAEFER, H. & RENNER, S. S. (2010). A three-genome phylogeny of *Momordica* (Cucurbitaceae) suggests seven returns from dioecy to monoecy and recent long-distance dispersal to Asia. *Molecular Phylogenetics and Evolution* **54**, 553–560.
- SCHLUTER, D. (1998). Ecological causes of speciation. In *Endless Forms: Species and Speciation*, pp. 3–15. Oxford University Press, Oxford.
- SCHLUTER, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- SCHOENE, B., SAMPERTON, K. M., EDDY, M. P., KELLER, G., ADATTE, T., BOWRING, S. A., KHADRI, S. F. R. & GERTSCH, B. (2015). U–Pb geochronology of the Deccan traps and relation to the end-Cretaceous mass extinction. *Science* **347**, 182–184.
- SCHOENFELDER, K. P. & FOX, D. T. (2015). The expanding implications of polyploidy. *Journal of Cell Biology* **209**, 485–491.
- SCHULTE, P., ALEGRET, L., ARENILLAS, I., ARZ, J. A., BARTON, P. J., BOWN, P. R., BRALOWER, T. J., CHRISTESON, G. L., CLAEYS, P., COCKELL, C. S., COLLINS, G. S., DEUTSCH, A., GOLDIN, T. J., GOTO, K., GRAJALES-NISHIMURA, J. M., GRIEVE, R. A. F., GULICK, S. P. S., JOHNSON, K. R., KIESSLING, W., KOEBERL, C., KRING, D. A., MACLEOD, K. G., MATSUI, T., MELOSH, J., MONTANARI, A., MORGAN, J. V., NEAL, C. R., NICHOLS, D. J., NORRIS, R. D., PIERAZZO, E., RAVIZZA, G., REBOLLEDO-VIEIRA, M., REIMOLD, W. U., ROBIN, E., SALGE, T., SPEIJER, R. P., SWEET, A. R., URRUTIA-FUCUGAUCHI, J., VAJDA, V., WHALEN, M. T. & WILLUMSEN, P. S. (2010). The Chicxulub asteroid impact and mass extinction at the Cretaceous–Paleogene boundary. *Science* **327**, 1214–1218.
- SCHUSTER, M., DURINGER, P., GHENNE, J.-F., VIGNAUD, P., MACKAYE, H. T., LIKIUS, A. & BRUNET, M. (2006). The age of the Sahara Desert. *Science* **311**, 821–821.
- SCHWEIZER, M., SEEHAUSEN, O. & HERTWIG, S. T. (2011). Macroevolutionary patterns in the diversification of parrots: effects of climate change, geological events and key innovations. *Journal of Biogeography* **38**, 2176–2194.
- SÉGALEN, L., LEE-THORP, J. A. & CÉRLING, T. (2007). Timing of C4 grass expansion across sub-Saharan Africa. *Journal of Human Evolution* **53**, 549–559.
- SEIFFERT, E. R. (2007). Evolution and extinction of afro-Arabian Primates near the Eocene–Oligocene boundary. *Folia Primatologica* **78**, 314–327.
- SEIFFERT, E. R. (2010). Chronology of Paleogene mammal localities. In *Cenozoic Mammals of Africa* (eds L. WERDELIN and J. SANDERS), pp. 19–26. University of California Press, Berkeley.
- SENUIT, B., PICKFORD, M. & SÉGALEN, L. (2009). Neogene desertification of Africa. *Comptes Rendus Geoscience* **341**, 591–602.
- SEPULCHRE, P., RAMSTEIN, G., FLUTEAU, F., SCHUSTER, M., TIERCELIN, J. J. & BRUNET, M. (2006). Tectonic uplift and eastern Africa aridification. *Science* **313**, 1419–1423.
- SEPULCHRE, P., RAMSTEIN, G. & SCHUSTER, M. (2009). Modelling the impact of tectonics, surface conditions and sea surface temperatures on Saharan and sub-Saharan climate evolution. *Comptes Rendus Geoscience* **341**, 612–620.
- SEPULCHRE, P., ARSOUZE, T., DONNADIEU, Y., DUTAY, J.-C., JARAMILLO, C., LE BRAS, J., MARTIN, E., MONTES, C. & WAITE, A. J. (2014). Consequences of shoaling of the central American seaway determined from modeling Nd isotopes. *Paleoceanography* **29**, 176–189.
- SHEVENELL, A. E., KENNETT, J. P. & LEA, D. W. (2008). Middle Miocene ice sheet dynamics, deep-sea temperatures, and carbon cycling: a Southern Ocean perspective. *Geochemistry, Geophysics, Geosystems* **9**, Q02006. <https://doi.org/10.1029/2007GC001736>.
- SILVESTRO, D., CASCALES-MINANA, B., BACON, C. D. & ANTONELLI, A. (2015). Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytologist* **207**, 425–436.
- SILVESTRO, D., WARNOCK, R. C. M., GAVRUSHKINA, A. & STADLER, T. (2018). Closing the gap between palaeontological and neontological speciation and extinction rate estimates. *Nature Communications* **9**, 5237. <https://doi.org/10.1038/s41467-018-07622-y>.
- SIMARD, F., AYALA, D., KAMDEM, G. C., POMBI, M., ETOUNA, J., OSE, K., FOTSING, J.-M., FONTENILLE, D., BESANSKY, N. J. & COSTANTINI, C. (2009). Ecological niche partitioning between *Anopheles gambiae* molecular forms in Cameroon: the ecological side of speciation. *BMC Ecology* **9**, 17. <https://doi.org/10.1186/1472-6785-9-17>.
- SIMON, B., GUILLOCHEAU, F., ROBIN, C., DAUTEUIL, O., NALPAS, T., PICKFORD, M., SENUT, B., LAYS, P., BOURGES, P. & BEZ, M. (2017). Deformation and sedimentary evolution of the Lake Albert rift (Uganda, east African rift system). *Marine and Petroleum Geology* **86**, 17–37.
- SMITH, T. B., WAYNE, R. K., GIRMAN, D. J. & BRUFORD, M. W. (1997). A role for ecotones in generating rainforest biodiversity. *Science* **26**, 1855–1857.
- SMITH, T. B., SCHNEIDER, C. J. & HOLDER, K. (2001). Refugial isolation versus ecological gradients. *Genetica* **112–113**, 383–398.
- SOMMERFELD, A., PROMMEL, K. & CUBASCH, U. (2016). The east African rift system and the impact of orographic changes on regional climate and the resulting aridification. *International Journal of Earth Sciences* **105**, 1779–1794.
- SOSEF, M. S. M. (1994). Refuge begonias—taxonomy, phylogeny and historical biogeography of *Begonia* sect. *Loasibegonia* and sect. *Scutobegonia* in relation to glacial rain forest refuges in Africa. *Studies in Begonia V, Wageningen Agricultural University Papers* **94**, 1–306.
- SOSEF, M. S. M., DAUBY, G., BLACH-OVERGAARD, A., VAN DER BURGT, X., CATARINO, L., DAMEN, T., DEBLAUWE, V., DESSEIN, S., DRANSFIELD, J., DROISSART, V., DUARTE, M. C., ENGLEDDOW, H., FADEUR, G., FIGUEIRA, R., GEREAU, R. E., HARDY, O. J., HARRIS, D. J., DE HEIJ, J., JANSSENS, S., KLONBERG, Y., LEY, A. C., MACKINDER, B. A., MEERTS, P., VAN DE POEL, J. L., SONKÉ, B., STÉVART, T., STOFFELEN, P., SVENNING, J. C., SEPULCHRE, P., ZAISS, R., WIERINGA, J. J. & COUVREUR, T. L. P. (2017). Exploring the floristic diversity of tropical Africa. *BMC Biology* **15**, 15. <https://doi.org/10.1186/s12915-017-0356-8>.
- SPICER, R. A. & COLLINSON, M. E. (2014). Plants and floral change at the Cretaceous–Paleogene boundary: three decades. In *Volcanism, Impacts, and Mass Extinctions: Causes and Effects* (eds G. KELLER and A. C. KERR), pp. 117–132. Geological Society of America, Boulder.
- SPRINGER, M. S., CLEVEN, G. C., MADSEN, O., DE JONG, W. W., WADDELL, V. G., AMRINE, H. M. & STANHOPE, M. J. (1997). Endemic African mammals shake the phylogenetic tree. *Nature* **388**, 61–64.
- SPRINGER, M. S., MEREDITH, R. W., JANEČKA, J. E. & MURPHY, W. J. (2011). The historical biogeography of Mammalia. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366**, 2478–2502.
- SPRINGER, M. S., MEREDITH, R. W., GATESY, J., EMERLING, C. A., PARK, J., RABOSKY, D. L., STADLER, T., STEINER, C., RYDER, O. A., JANEČKA, J. E., FISHER, C. A. & MURPHY, W. J. (2012). Macroevolutionary dynamics and historical

- biogeography of primate diversification inferred from a species supermatrix. *PLoS One* 7, e49521. <https://doi.org/10.1371/journal.pone.0049521>.
- STEINTHORSÐOTTIR, M., PORTER, A. S., HOLOHAN, A., KUNZMANN, L., COLLINSON, M. & McELWAIN, J. C. (2016). Fossil plant stomata indicate decreasing atmospheric CO<sub>2</sub> prior to the Eocene-Oligocene boundary. *Climate of the Past* 12, 439–454.
- STÉVART, T., DAUBY, G., LOWRY, P. P., BLACH-OVERGAARD, A., DROISSART, V., HARRIS, D. J., MACKINDER, B. A., SCHATZ, G. E., SONKÉ, B., SOSEF, M. S. M., SVENNING, J.-C., WIERINGA, J. J. & COUVREUR, T. L. P. (2019). A third of the tropical African flora is potentially threatened with extinction. *Science Advances* 5, eaax9444. <https://doi.org/10.1126/sciadv.aax9444>.
- STREICHER, J. W., LOADER, S. P., VARELA-JARAMILLO, A., MONTOYA, P. & DE SÁ, R. O. (2020). Analysis of ultraconserved elements supports African origins of narrow-mouthed frogs. *Molecular Phylogenetics and Evolution* 146, 106771. <https://doi.org/10.1016/j.ympev.2020.106771>.
- TAN, N., RAMSTEIN, G., DUMAS, C., CONTOUX, C., LADANT, J.-B., SEPULCHRE, P., ZHANG, Z. & DE SCHEPPER, S. (2017). Exploring the MIS M2 glaciation occurring during a warm and high atmospheric CO<sub>2</sub> Pliocene background climate. *Earth and Planetary Science Letters* 472, 266–276.
- TAYLOR, P. J., MAREE, S., COTTERILL, F. P. D., MISSOUP, A. D., NICOLAS, V. & DENYS, C. (2014). Molecular and morphological evidence for a Pleistocene radiation of laminate-toothed rats (*Otomys*: Rodentia) across a volcanic archipelago in equatorial Africa. *Biological Journal of the Linnean Society* 113, 320–344.
- THOMAS, E. (2008). Descent into the icehouse. *Geology* 36, 191–192.
- \*THORNHILL, A. H., HO, S. Y. W., KÜLHEIM, C. & CRISP, M. D. (2015). Interpreting the modern distribution of Myrtaceae using a dated molecular phylogeny. *Molecular Phylogenetics and Evolution* 93, 29–43.
- THULLER, W., BROENNIMANN, O., HUGHES, G., ALKEMADE, J. R. M., MIDGLEY, G. F. & CORSI, F. (2006). Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology* 12, 424–440.
- TING, N. (2008). Mitochondrial relationships and divergence dates of the African colobines: evidence of Miocene origins for the living colobus monkeys. *Journal of Human Evolution* 55, 312–325.
- TOLLEY, K. A., TILBURY, C. R., MEASEY, G. J., MENEGON, M., BRANCH, W. R. & MATTHEE, C. A. (2011). Ancient forest fragmentation or recent radiation? Testing refugial speciation models in chameleons within an African biodiversity hotspot. *Journal of Biogeography* 38, 1748–1760.
- TOLLEY, K. A., TOWNSEND, T. M. & VENCES, M. (2013). Large-scale phylogeny of chameleons suggests African origins and Eocene diversification. *Proceedings of the Royal Society B: Biological Sciences* 280, 20130184.
- TOLLEY, K. A., ALEXANDER, G. J., BRANCH, W. R., BOWLES, P. & MARITZ, B. (2016). Conservation status and threats for African reptiles. *Biological Conservation* 204, 63–71.
- \*TOSH, J., DESSEIN, S., BUERKI, S., GROENINGCK, I., MOULY, A., BREMER, B., SMETS, E. F. & DE BLOCK, P. (2013). Evolutionary history of the afro-Madagascan *Ixora* species (Rubiaceae): species diversification and distribution of key morphological traits inferred from dated molecular phylogenetic trees. *Annals of Botany* 112, 1723–1742.
- TOSSE, F., HARDY, O. J., DOUCET, J.-L., DAINOU, K., KAYMAK, E. & MIGLIORE, J. (2018). Evolution in the Amphibio-Atlantic tropical genus *Gaiobertia* (Fabaceae, Detarioideae), combining NGS phylogeny and morphology. *Molecular Phylogenetics and Evolution* 120, 83–93.
- TRAUTH, M. H., LARRASOANA, J. C. & MUELSESE, M. (2009). Trends, rhythms and events in Plio-Pleistocene African climate. *Quaternary Science Reviews* 28, 399–411.
- TURNER, S. K. (2018). Constraints on the onset duration of the Paleocene–Eocene thermal maximum. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 376, 20170082.
- UNO, K. T., CERLING, T. E., HARRIS, J. M., KUNIMATSU, Y., LEAKEY, M. G., NAKATSUKASA, M. & NAKAYA, H. (2011). Late Miocene to Pliocene carbon isotope record of differential diet change among east African herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 108, 6509–6514.
- UNO, K. T., POLISSAR, P. J., JACKSON, K. E. & DEMENOGAL, P. B. (2016). Neogene biomarker record of vegetation change in Eastern Africa. *Proceedings of the National Academy of Sciences of the United States of America* 113, 6355–6363.
- UTESCHER, T. & MOSBRUGGER, V. (2007). Eocene vegetation patterns reconstructed from plant diversity — a global perspective. *Palaogeography, Palaeoclimatology, Palaeoecology* 247, 243–271.
- VAJDA, V. & BERCOVICI, A. (2014). The global vegetation pattern across the Cretaceous–Paleogene mass extinction interval: a template for other extinction events. *Global and Planetary Change* 122, 29–49.
- VAMOSI, J. C., MAGALLÓN, S., MAYROSE, I., OTTO, S. P. & SAUQUET, H. (2018). Macroevolutionary patterns of flowering plant speciation and extinction. *Annual Review of Plant Biology* 69, 685–706.
- VAN BOCKLAER, I., ROELANTS, K., BIJU, S. D., NAGARAJU, J. & BOSSUYT, F. (2006). Late Cretaceous vicariance in Gondwanan amphibians. *PLoS One* 1, e74. <https://doi.org/10.1371/journal.pone.0000074>.
- VAN DE PEER, Y., MIZRACHI, E. & MARCHAL, K. (2017). The evolutionary significance of polyploidy. *Nature Reviews Genetics* 18, 411–424.
- VANZOLINI, P. E. & WILLIAMS, E. (1981). The vanishing refuge: a mechanism for ecogeographic speciation. *Papéis Avulsos de Zoologia* 34, 251–255.
- \*VAN VELZEN, N., WAHLBERG, N., SOSEF, M. S. M. & BAKKER, F. T. (2013). Effects of changing climate on species diversification in tropical forest butterflies of the genus *Cymothoe* (Lepidoptera: Nymphalidae). *Biological Journal of the Linnean Society* 108, 546–564.
- VENCES, M., WOLLENBERG, K. C., VIETTES, D. R. & LEES, D. C. (2009). Madagascar as a model region of species diversification. *Trends in Ecology & Evolution* 24, 456–465.
- VERANSO-LIBALAH, M. C., KADEREIT, G., STONE, R. D. & COUVREUR, T. L. P. (2018). Multiple shifts to open habitats in Melastomataceae (Melastomataceae) congruent with the increase of African Neogene climatic aridity. *Journal of Biogeography* 45, 1420–1431.
- VIGNAUD, P., DURINGER, P., MACKAYE, H. T., LIKIUS, A., BLONDEL, C., BOISSERIE, J.-R., DE BONIS, L., EISENMANN, V., ETIENNE, M.-E., GERAADS, D., GUY, F., LEHMANN, T., LIHOREAU, F., LOPEZ-MARTINEZ, N., MOURER-CHAUVIRÉ, C., OTERO, O., RAGE, J. C., SCHUSTER, M., VIRIOT, L., ZAZZO, A. & BRUNET, M. (2002). Geology and palaeontology of the upper Miocene Toros-Menalla hominid locality, Chad. *Nature* 418, 152–155.
- VINCENS, A., TIERCELIN, J.-J. & BUCHET, G. (2006). New Oligocene–early Miocene microflora from the southwestern Turkana Basin: Palaeoenvironmental implications in the northern Kenya rift. *Palaogeography, Palaeoclimatology, Palaeoecology* 239, 470–486.
- VISTE, E. & SORTEBERG, A. (2013). Moisture transport into the Ethiopian highlands. *International Journal of Climatology* 33, 249–263.
- VISTE, E., KORECHA, D. & SORTEBERG, A. (2013). Recent drought and precipitation tendencies in Ethiopia. *Theoretical and Applied Climatology* 112, 535–551.
- VOELKER, G., OUTLAW, R. K. & BOWIE, R. C. K. (2010). Pliocene forest dynamics as a primary driver of African bird speciation. *Global Ecology and Biogeography* 19, 111–121.
- VOELKER, G., MARKS, B. D., KAHINDO, C., A'GENONGA, U., BAPEAMONI, F., DUFFIE, L. E., HUNTLEY, J. W., MULOTWA, E., ROSENBAUM, S. A. & LIGHT, J. E. (2013). River barriers and cryptic biodiversity in an evolutionary museum. *Ecology and Evolution* 3, 536–545.
- VOJE, K. L., HEMP, C., FLAGSTAD, Ø., SETRE, G.-P. & STENSETH, N. C. (2009). Climatic change as an engine for speciation in flightless Orthoptera species inhabiting African mountains. *Molecular Ecology* 18, 93–108.
- WALKER, N. D. (1990). Links between south African summer rainfall and temperature variability of the Agulhas and Benguela current systems. *Journal of Geophysical Research: Oceans* 95, 3297–3319.
- WALLACE, A. R. (1852). On the monkeys of the Amazon. *Proceedings of the Zoological Society of London* 20, 107–110.
- WASHINGTON, R., JAMES, R., PEARCE, H., POKAM, W. M. & MOUFOUMA-OKIA, W. (2013). Congo Basin rainfall climatology: can we believe the climate models? *Philosophical Transactions of the Royal Society B: Biological Sciences* 368, 20120296.
- \*VAN WELZEN, P. C., STRIJK, J. S., VAN KONIJNENBURG-VAN CITTERT, J. H. A., NUCETE, M. & MERCKX, V. S. F. T. (2014). Dated phylogenies of the sister genera *Macaranga* and *Mallotus* (Euphorbiaceae): congruence in historical biogeographic patterns? *PLoS One* 9, e85713.
- WERDELIN, L. & SANDERS, J. (2010). *Cenozoic Mammals of Africa*. University of California Press, Berkeley.
- WHITE, F. (1979). The Guineo-Congolian region and its relationships to other phytocoria. *Bulletin du Jardin botanique National de Belgique* 49, 11–55.
- WHITE, F. (1981). The history of the Afromontane archipelago and the scientific need for its conservation. *African Journal of Ecology* 19, 33–54.
- WHITE, F. (1983). *The Vegetation of Africa, a Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. UNESCO, Paris.
- WICHURA, H., BOUSQUET, R., OBERHÄNSLI, R., STRECKER, M. R. & TRAUTH, M. H. (2010). Evidence for middle Miocene uplift of the east African plateau. *Geology* 38, 543–546.
- WICHURA, H., JACOBS, L. L., LIN, A., POLCYN, M. J., MANTHI, F. K., WINKLER, D. A., STRECKER, M. R. & CLEMENS, M. (2015). A 17-my-old whale constrains onset of uplift and climate change in East Africa. *Proceedings of the National Academy of Sciences of the United States of America* 112, 3910–3915.
- WILLIAMSON, P. G. (1985). Evidence for an early Plio-Pleistocene rainforest expansion in East Africa. *Nature* 315, 487–489.
- WILLIS, K. J. & McELWAIN, J. (2014). *The Evolution of Plants*, 2nd Edition. Oxford University Press, Oxford.
- WILSON, A. B., TEUGELS, G. G. & MEYER, A. (2008). Marine incursion: the freshwater herring of Lake Tanganyika are the product of a marine invasion into West Africa. *PLoS One* 3, e1979. <https://doi.org/10.1371/journal.pone.0001979>.
- YE, J., CHARDON, D., ROUBY, D., GUILLOCHEAU, F., DALL'ASTA, M., FERRY, J.-N. & BROUCKE, O. (2017a). Paleogeographic and structural evolution of northwestern Africa and its Atlantic margins since the early Mesozoic. *Geosphere* 13, 1254–1284.

- \*YE, Z., ZHEN, Y., ZHOU, Y. & BU, W. (2017b). Out of Africa: biogeography and diversification of the pantropical pond skater genus *Limnogonus* Stål, 1868 (Hemiptera: Gerridae). *Ecology and Evolution* **7**, 793–802.
- YOU, Y., HUBER, M., MÜLLER, R. D., POULSEN, C. J. & RIBBE, J. (2009). Simulation of the middle Miocene climate optimum. *Geophysical Research Letters* **36**, L04702. <https://doi.org/10.1029/2008GL036571>.
- ZACHOS, J. C., DICKENS, G. R. & ZEEBE, R. E. (2008). An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451**, 279–283.
- ZHANG, Z., NISANCIOGLU, K. H., FLATØY, F., BENTSEN, M., BETHKE, I. & WANG, H. (2011). Tropical seaways played a more important role than high latitude seaways in Cenozoic cooling. *Climate of the Past* **7**, 801–813.
- ZHANG, Z., RAMSTEIN, G., SCHUSTER, M., LI, C., CONTOUX, C. & YAN, Q. (2014). Aridification of the Sahara desert caused by Tethys Sea shrinkage during the late Miocene. *Nature* **513**, 401–404.
- ZHANG, R., ZHANG, Z., JIANG, D., YAN, Q., ZHOU, X. & CHENG, Z. (2016). Strengthened African summer monsoon in the mid-Piacenzian. *Advances in Atmospheric Sciences* **33**, 1061–1070.
- ZHANG, L., WANG, C., WIGNALL, P. B., KLUGE, T., WAN, X., WANG, Q. & GAO, Y. (2018). Deccan volcanism caused coupled pCO<sub>2</sub> and terrestrial temperature rises, and pre-impact extinctions in northern China. *Geology* **46**, 271–274.
- ZHEN, Y., HARRIGAN, R. J., RUEGG, K. C., ANDERSON, E. C., NG, T. C., LAO, S., LOHMEYER, K. E. & SMITH, T. B. (2017). Genomic divergence across ecological gradients in the central African rainforest songbird (*Andropadus virens*). *Molecular Ecology* **26**, 4966–4977.
- ZHOU, L., SU, Y. C. F., THOMAS, D. C. & SAUNDERS, R. M. K. (2012). ‘Out-of-Africa’ dispersal of tropical floras during the Miocene climatic optimum: evidence from *Uvaria* (Annonaceae). *Journal of Biogeography* **39**, 322–335.
- ZIMKUS, B. M. & GVOZDIK, V. (2013). Sky Islands of the Cameroon volcanic line: a diversification hot spot for puddle frogs (Phrynobatrachidae: Phrynobatrachus). *Zoologica Scripta* **42**, 591–611.
- ZIMKUS, B. M., RÖDEL, M.-O. & HILLERS, A. (2010). Complex patterns of continental speciation: molecular phylogenetics and biogeography of sub-Saharan puddle frogs (*Phrynobatrachus*). *Molecular Phylogenetics and Evolution* **55**, 883–900.
- ZIMKUS, B. M., LAWSON, L. P., BAREJ, M. F., BARRATT, C. D., CHANNING, A., DASH, K. M., DEHLING, J. M., DU PREEZ, L., GEHRING, P.-S., GREENBAUM, E., GVOZDIK, V., HARVEY, J., KIELGAST, J., KUSAMBA, C., NAGY, Z. T., et al. (2017). Leapfrogging into new territory: how Mascarene ridged frogs diversified across Africa and Madagascar to maintain their ecological niche. *Molecular Phylogenetics and Evolution* **106**, 254–269.
- \*ZIZKA, A., SILVESTRO, D., ANDERMANN, T., AZEVEDO, J., DUARTE RITTER, C., EDLER, D., FAROOQ, H., HERDEAN, A., ARIZA, M. & SCHARN, R. (2019). Coordinate cleaner: standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* **10**, 744–751.

## VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** List of dated molecular phylogeny studies used to generate Fig. 3D,E.

**Fig. S1.** Palaeoclimate during the Eocene across Africa.

**Table S1.** Studies used to estimate the origin of extant species within groups with dated molecular phylogenies.

**Appendix S2.** Assignment of genera to elevation zones as presented in Table S2.

**Table S2.** Studies used to estimate crown and stem nodes for genera or clades, and to estimate vegetation zonation following methodology provided in Appendix S2.

(Received 20 February 2020; revised 7 August 2020; accepted 13 August 2020)