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

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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

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 endemicity 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 Afromontane 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 hotpots (Mittermeier *et al.*, 2011), was estimated to have the highest concentration of endemic plants (number of endemics per 100 km^2) 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 (McClean *et al.*, 2005; Blach-Overgaard *et al.*, 2015; Stévart *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).

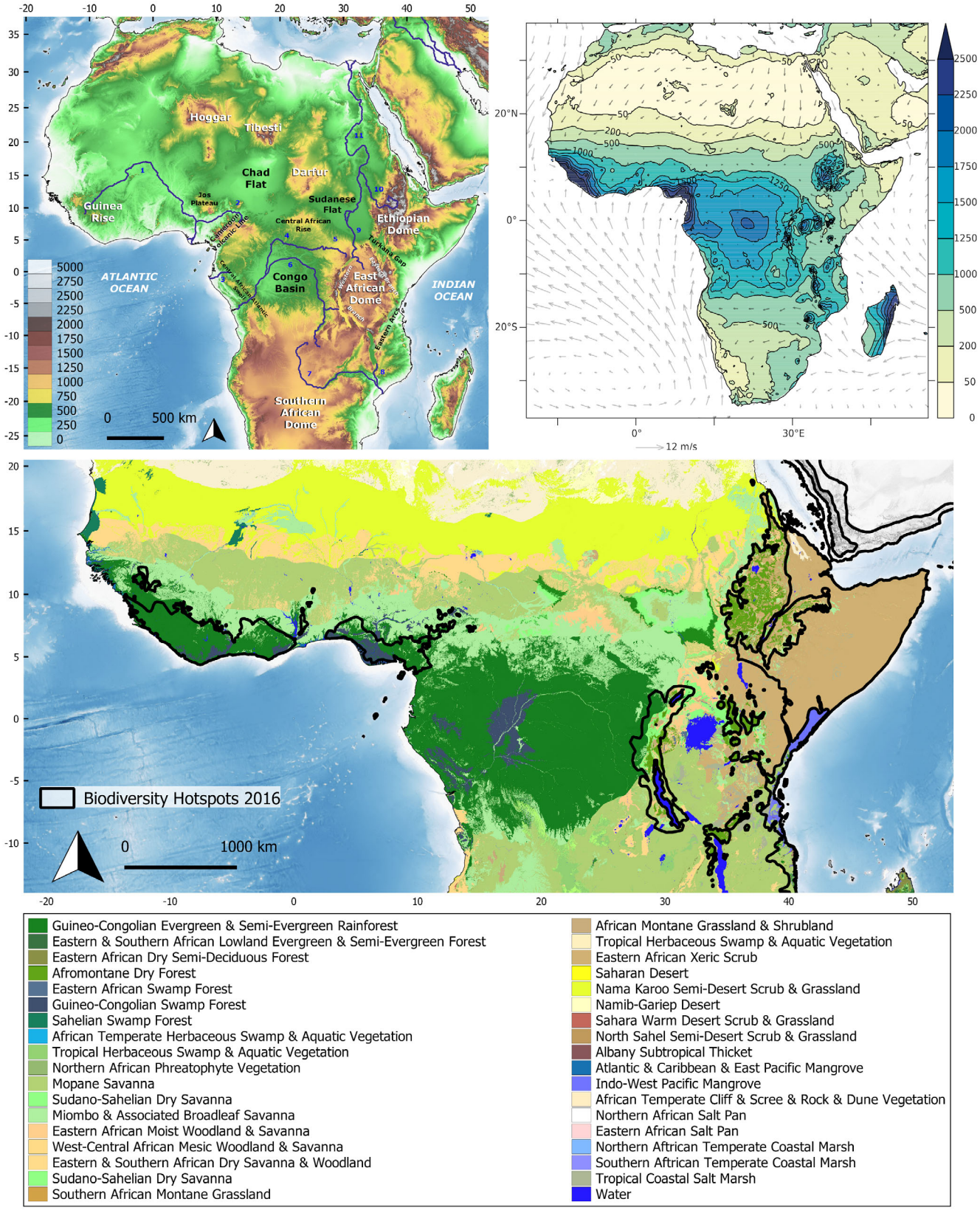
To date, around 90 dated molecular phylogenies have been published documenting the diversification of tropical African animals and plants (see online Supporting Information, Appendix S1). Most clades diversified *within* tropical Africa and this will be the focus of our review. Biogeographic analyses 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 fieldwork 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 geodiversity 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



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(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 planations 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#.Xvu69lVKiUk (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 Karroo 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_2 partial pressure, pCO_2) 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

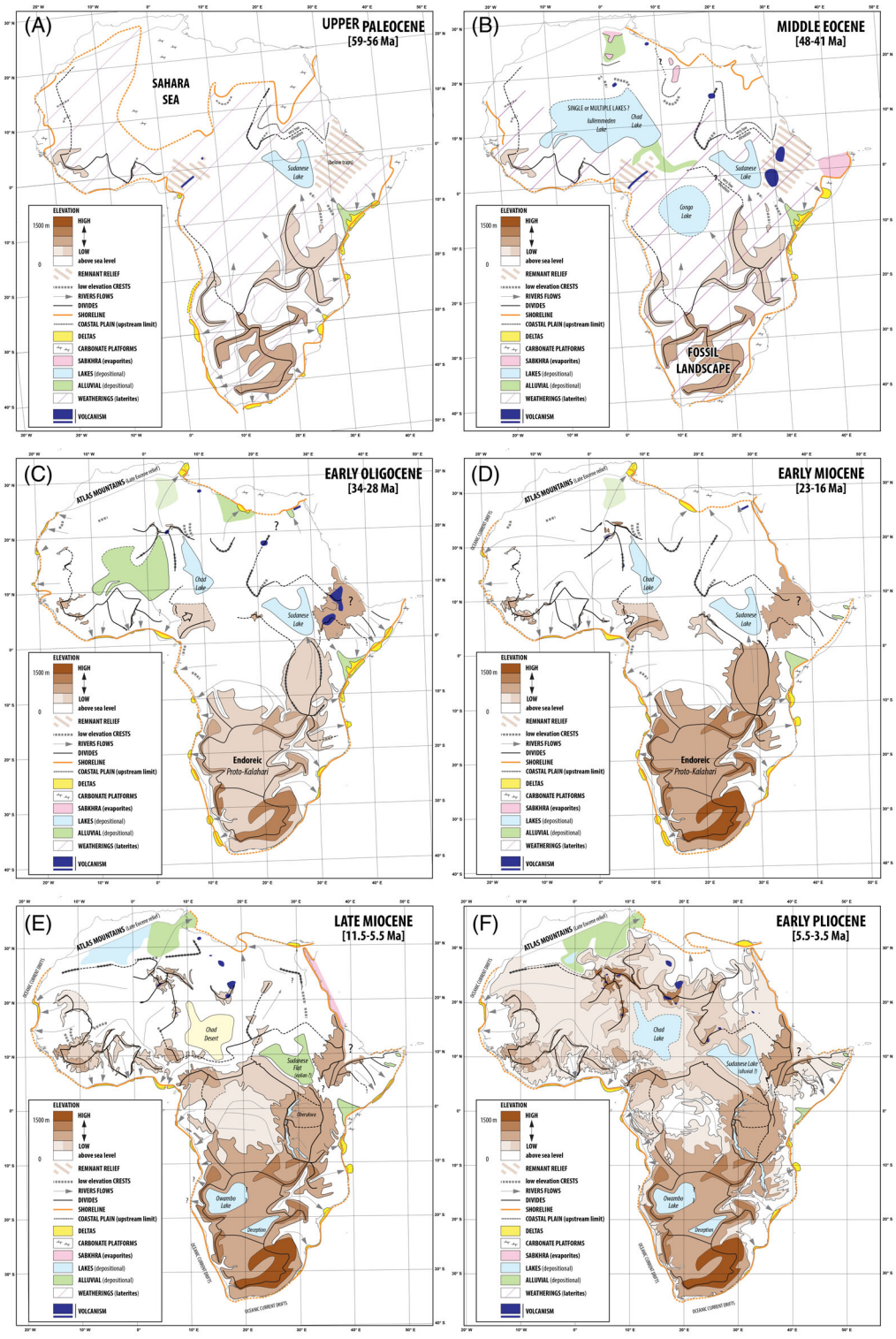

Fig 2. Geological evolution of Africa during the Cenozoic. The maps depict the geological setting for six periods of the Cenozoic: (A) Late Paleocene (59–56 Ma), (B) Middle Eocene (48–41 Ma), (C) Early Oligocene (34–28 Ma), (D) Early Miocene (23–16 Ma), (E) Late Miocene (11.5–5.5 Ma) and (F) Early Pliocene (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) (Courtillot & 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-Cheboldaeff (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_2 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, &

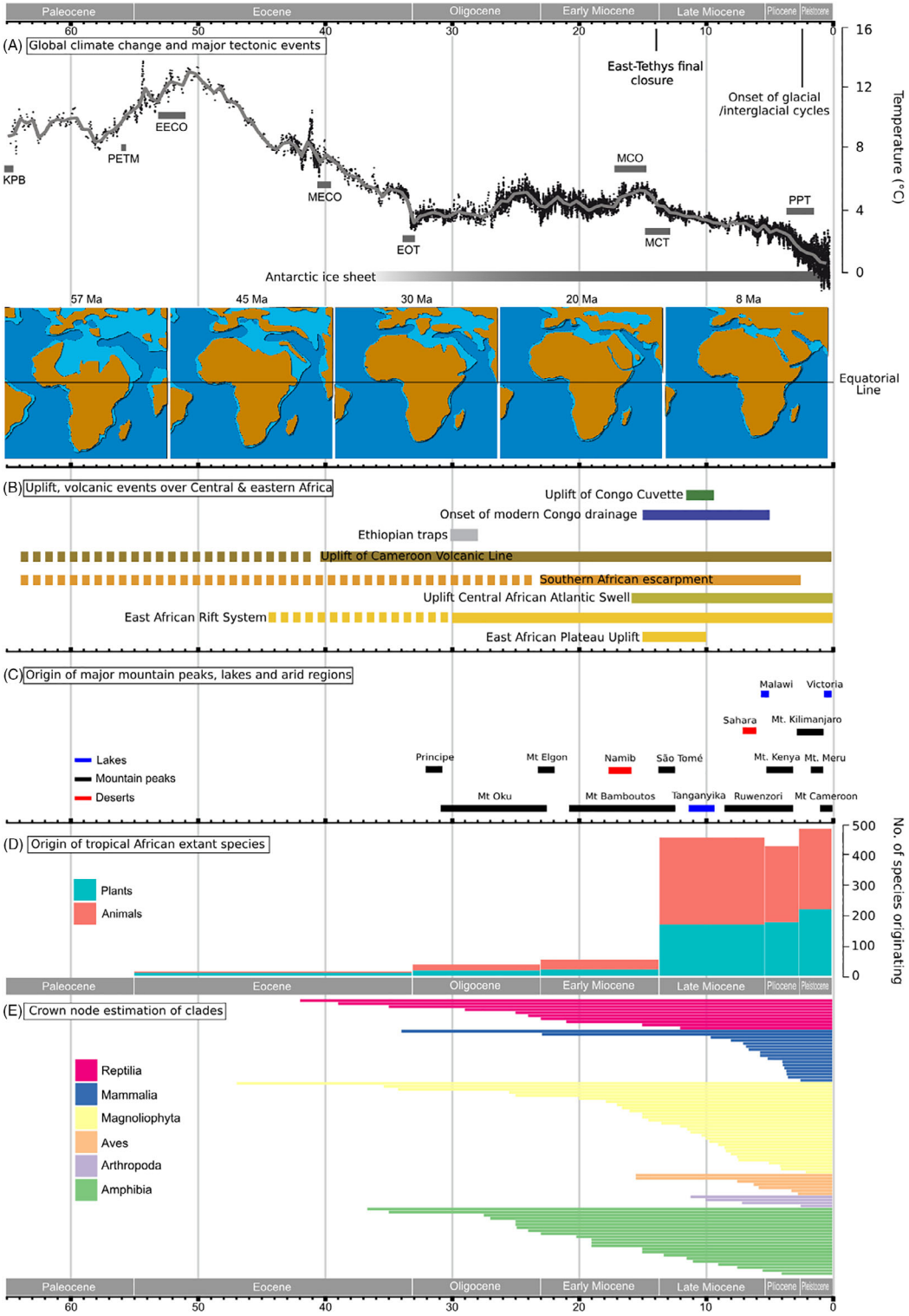

Fig 3. Geo-climate evolution and biological diversification of tropical African biodiversity. (A) Global temperature change during the Cenozoic (Hansen *et al.*, 2008) and major climate and tectonic events across Africa. KPB, Cretaceous–Paleogene Boundary; PETM, Paleocene–Eocene Thermal Maximum; EECO, 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; Pokorny *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-Cheboldaeff, 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 endemicity 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; Jongsma *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 lamniform 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 pCO_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 pCO_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 ∼70-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 KPB (Morley, 2000; Pan *et al.*, 2006), for example with the mangrove palm *Nypa* 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.*, 2016*b*) and the legume tribe Podalyrieae (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.*, 2010*b*; Bouchenak-Khelladi, Muasya, & Linder, 2014a), although it does not correlate with the well-studied origin of C_4 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.2*a*). 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 pCO_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 pCO_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 pCO_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_4 carbon fixation in grasses, or C_4 grasses, in Africa, a dominant component of present-day African savannas which evolved independently in numerous Poaceae (Bobe, 2006; Ségalen, Lee-Thorp, & Cerling, 2007; Bouchenak-Khelladi *et al.*, 2009, 2014*b*; 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; Pokorny *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 pCO_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_4 photosynthesis is complex and decoupled from the earliest evolutionary origins of C_4 grasses during the EOT (Bouchenak-Khelladi *et al.*, 2014*b*). The transition to C_4 grass-dominated biomes has been discontinuous and spatially heterogeneous, with at least two phases of C_4 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_4 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_4-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_2 decrease in this process (Polissar *et al.*, 2019).

In animals, the evolutionary shift to C_4-grazing amongst large mammalian herbivores seems to have been immediate for some lineages like the proboscideans (elephants), which started to include C_4 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_4-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 (subfamilly 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.*, 2010*a*).

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_4 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_3 to C_4 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 (Larrasoaña *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_4-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_4 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.2*a*). 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 complied 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.*, 2011*b*). 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 Coffeeae (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 Zambezian 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 *et al.* (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 *et al.* (2008); Tolley *et al.* (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 *et al.* (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 *et al.* (2010); Tolley *et al.* (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 *et al.* (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 *et al.* (2009); Cox *et al.* (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 *et al.* (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 *et al.* (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 *et al.* (2015); Donkpegan *et al.* (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, & Siegismund, 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.2*a*), 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).

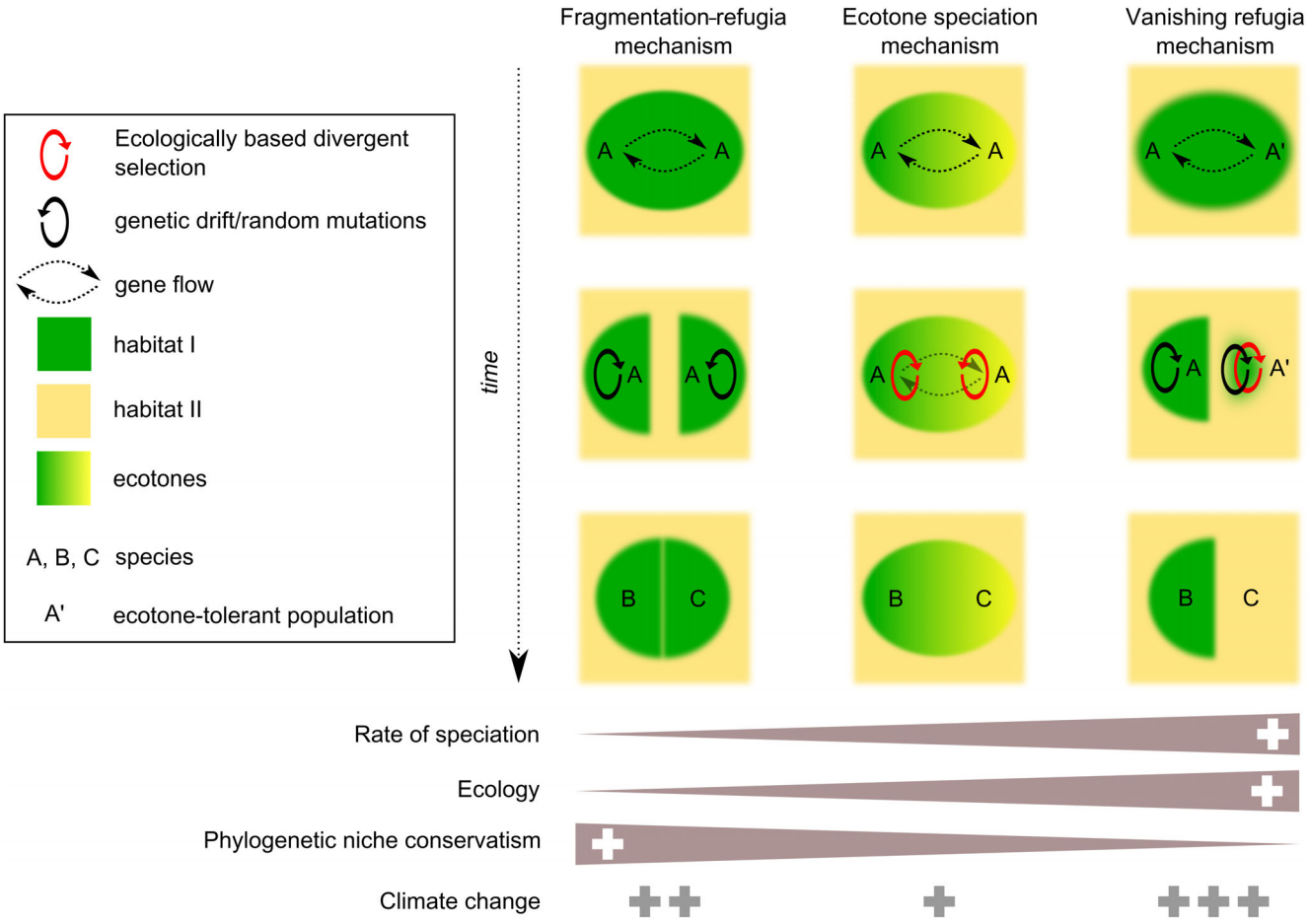

Fig 4. Schematic representations of three selected mechanisms of speciation relevant to tropical Africa. The fragmentation–refugia mechanism is an example of the geographic model, the ecotone speciation mechanism is an example of the ecological model, and the vanishing refugia mechanism has elements 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.*, 2016a; 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; Pokorny *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 endemicity at a global

scale (Fjeldså & Lovett, 1997; Barthlott *et al.*, 2005; Burgess *et al.*, 2007; Antonelli *et al.*, 2018*b*; 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 (Fjeldså *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 (Fjeldså & 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; Fjeldså & 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; Fjeldså & Bowie, 2008; Voelker *et al.*, 2010; Fjeldså, Bowie, & Rahbek, 2012), rodents (Mizerovská *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; Missoup *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 & Gvoždík, 2013; Taylor *et al.*, 2014; Missoup *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 Ogooué 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 Ogooué could explain some species divergences, for example in *Amnirana* (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* (Leaché *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; Mizerovská *et al.*, 2019), reptiles (Leaché & 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_4 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 *Coccinia* (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 *Monodora 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), *Lychnis* (Caryophyllaceae; Gizaw *et al.*, 2016) and giant senecios (Dendrosenecio, Astercaeae; 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; Vamosi *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. eugenioides* 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_4 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.*, 2018*a*), 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; Stévart *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.*, 2018*a*) in the geodiverse region of tropical Africa.

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VII. REFERENCES

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

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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.

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