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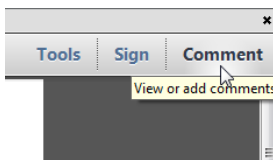
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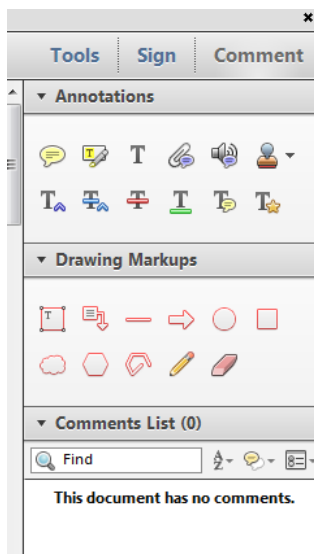
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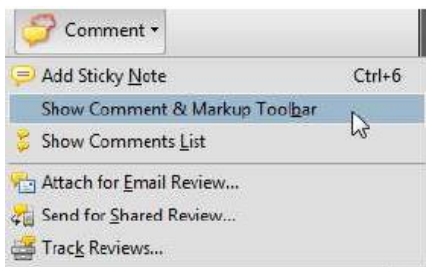


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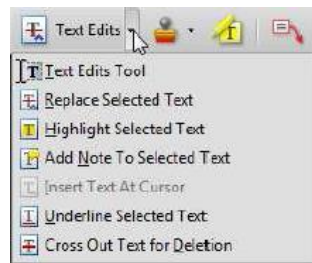
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REVIEW

Co-evolution assists geographic dispersal: the case of Madagascar

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Interspecific associations may limit the dispersal of individual species, but may also facilitate it when entire co-evolved systems expand their geographic ranges. We tested the recent proposal that episodic land bridges linked Africa and Madagascar at three stages during the Cenozoic by comparing divergence estimates of Madagascar's angiosperm taxa with their dispersal mechanisms. Plants that rely on gravity for seed dispersal indicate at least two episodes of land connection between Africa and Madagascar, in the Early Palaeocene and Early Oligocene. Seed dispersal by strepsirrhine primates possibly evolved in the Palaeocene, with the divergence of at least one endemic Malagasy angiosperm genus, *Burasaia* (Menispermaceae). This genus may have facilitated the lemur colonization of Madagascar. Frugivory, nectarivory and gummivory probably generalized in the Oligocene, with the co-evolution of modern lemurs and at least 10 new Malagasy angiosperm families. In the Late Miocene, more angiosperms were probably brought from Africa by birds via a discontinuous land connection, and radiated on Madagascar in diffuse association with birds (asities) and dwarf nocturnal lemurs (cheirogaleids). During the same connective episode, Madagascar was probably colonized by hippopotamuses, which both followed and re-seeded a variety of plants, forming the grassy *Uapaca* 'tapia' forest and ericoid 'savoka' thicket.

ADDITIONAL KEYWORDS: anachronism – biomes – climax vegetation – grassland – niche construction – land bridges – pollination – seed dispersal.

INTRODUCTION

Historically, biomes were defined as vegetation types that form the main features of the landscape: e.g. forest biomes, grassland biomes. Although they were defined botanically, biomes also included the fauna of these habitats. The biome concept was largely developed alongside the climax hypothesis: the idea that, given enough time under particular climatic conditions, the

same (climax) formations would become established, regardless of edaphic conditions (Clements, 1917; Clements & Shelford, 1939; Meeker & Merkel, 1984; Olson *et al.*, 2001; Mucina, 2019). Consequently, biomes are associated with bioclimatic zones, although some appear to be sub-climax and are influenced by other factors. For instance, grassland biomes are associated with a variety of climates and maintained by recurrent fire and large herbivores (McNaughton, 1984; Belsky, 1986; Paige & Whitham, 1987; Bond, 1994; Bond *et al.*, 2008).

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Although the original biome concept essentially ignored evolutionary processes, more recent interpretations are strongly aware of the importance of organismal interactions and co-evolution in the construction of distinct biotic formations (Carmona *et al.*, 2015; Agrawal & Zhang, 2021). Interspecific co-evolution, or reciprocal evolution, is more frequent than generally assumed; a species does not drive the extinction of another population by exploiting it (particularly for food) without risking its own extinction (Roughgarden, 1983). This interdependence may result in the co-evolution of associated lineages, as was first documented in butterflies and the plants on which their caterpillars feed (Ehrlich & Raven, 1964; Mitter & Brooks, 1983). In its early stages, co-evolution often involves chemical or mechanical defences against exploitation. Remarkably, such defences (toxicity, spines, thick seed coats) do not deter co-evolved consumers, and may even attract them by acting as interspecific signals (Ehrlich & Raven, 1964). There are many ways exploitative associations may become more benign over time, and therefore more resilient against extinction. Herbivores often keep their food alive by feeding only on some plant parts. In the most spectacular cases, co-evolution may yield reciprocal benefits (Futuyma & Slatkin, 1983). For instance, butterflies may increase the reproductive rates of the plants they parasitize as caterpillars by pollinating them in exchange for nectar when they reach the imago stage (Feinsinger, 1983); and many plants produce edible fruits adapted in terms of size, shape, colour and scent for the animals that disperse their seeds (zoochory syndromes) (Feinsinger, 1983; Janzen, 1983; Tiffney, 1986; Sussman, 1991; Mack, 2000; Sussman *et al.*, 2013; Génin & Rambeloarivony, 2018; Valenta *et al.*, 2018).

Indeed, habitats are dynamic biotic constructions, made up of co-evolved organisms (Lewontin, 1983; Varela *et al.*, 1991; Laland & Boorgert, 2008; Odling-Smee *et al.*, 2013). Such interdependence among organisms may limit the dispersal of species, but may also facilitate it when entire co-evolved systems expand their geographic ranges, and generalize interspecific relationships as pre-existing associations are joined by new species (Génin & Rambeloarivony, 2018; Watson, 2020). This generalization forms stable systems of diffuse co-evolution, identified as biomes.

Islands offer particularly good conditions for testing such hypotheses, although they also share characteristics that make them different from continents, codified as the Island Rule (Whittaker & Fernández-Palacios, 2007). Some of these characteristics are explained by climatic factors, as in the case of small islands that tend to be wetter and show less extreme climatic variations than continents, while others are explained by differences in phylogenetic harmony (higher on continental islands due to recurrent connections with

the mainland) and ecological structuration (more interspecific associations exist on older oceanic islands owing to long isolation). Among islands, Madagascar is exceptional because it exhibits characteristics of both a continental island (many affinities with the African mainland; high levels of biodiversity; a terrestrial fauna that includes dwarf and giant forms; the presence of frogs and freshwater fish) and an oceanic island (many continental taxa missing; high levels of endemism; idiosyncratic systems of pollination and seed dispersal; woodiness; the presence of near-flightless birds) (Masters *et al.*, 2021).

A recent study attributed the 'hybrid' nature of Madagascar's biota to a history of alternating periods of insularity and episodic connections to Africa driven by regional uplifts (Masters *et al.*, 2021, *In press*). Limited periods of land connection (< 5 Myr) yielded continental phases, reflected in the chorology of the Malagasy vegetation by phylogenetic harmonization of island and mainland floras. These periods of uplift were linked to global events involving major tectonic movements, climate change and extinction, followed by active radiation in the Palaeocene, Oligocene and Pliocene, and creating synchronous divergence patterns among the phylogenies of plants and animals [e.g. angiosperms (Buerki *et al.*, 2013); insects (Jordal, 2021); vertebrates (Poux *et al.*, 2005; Crottini *et al.*, 2012)]. Such synchrony may also be explained by the expansion of co-evolved systems, which facilitated both the colonization of the island by new taxa and their long-term survival (Masters *et al.*, *In press*). However, plant and animal phylogenies also suggest that radiation continued well into the much longer oceanic phases, associated with increased ecological structuring and the evolution of endemic biomes exhibiting original physiognomies.

Co-evolution may also explain the much-debated origin of Madagascar's grasslands. A striking characteristic of the island's endemic vegetation is its virtual restriction to forest and thicket, while a vast, cosmopolitan and impoverished secondary grassland covers the interior highlands (Humbert, 1927, 1955; Perrier de la Bâthie, 1936; Paulian, 1961; Humbert & Cours Darne, 1965; Bosser, 1969; Carlquist, 1974). This distribution suggests original woodiness in Madagascar (Carlquist, 1974), a view also based on the concept of climax (Humbert, 1927, 1959; Perrier de la Bâthie, 1936; Lowry *et al.*, 1997) (Fig. 1). Indeed, remnants of forest mapped by Humbert on the highlands indicate that much of this area was covered by woody vegetation until recently.

In a provocative paper, Bond *et al.* (2008) observed that the surprising diversity of endemic grasses in Madagascar suggests the evolution of true grasslands, perhaps as old as the Late Miocene, when C₄ grasslands spread in East Africa at latitudes and altitudes

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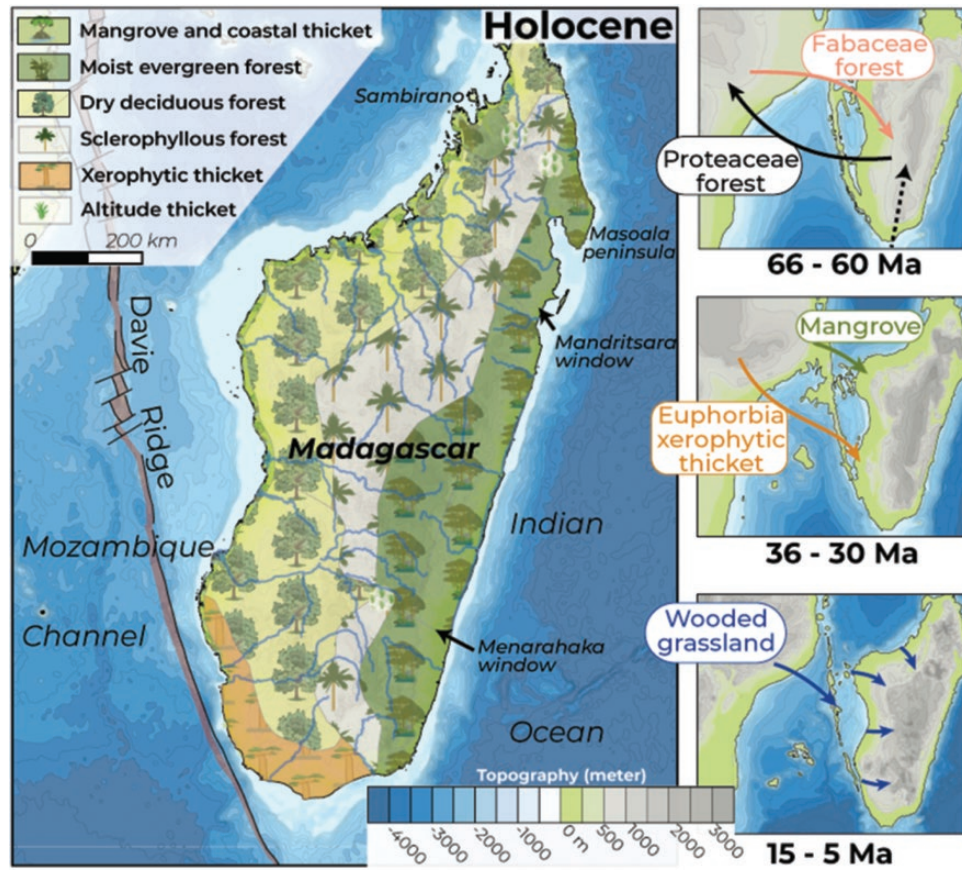


Figure 1. Left: main physiognomic vegetation types of Madagascar corresponding to the bioclimatic zones formed by the topography comprising three central highlands separated by deep valleys (Mandritsara and Menarahaka windows). The north-western monsoons bring seasonal moisture to the north-west (Sambirano region), while eastern trade winds bring year-round rains to the east coast. The complex history of colonization of the island is summarized on the right-hand maps, showing a Late Cretaceous connection with Antarctica (*c.* 90 Mya, dotted arrow) and three Cenozoic connections with Africa.

similar to those of Madagascar (see also Vorontsova *et al.*, 2016). However, few of the vertebrate species they listed are found exclusively in grassland and throughout their life cycles (e.g. Madagascar partridge *Margaroperdix madagarensis*). In fact, these species may originally have been associated with woody *Erica* thicket (similar to modern heathland and fynbos and known locally as ‘savoka’) rather than true grassland, as testified by charcoal and pollen deposits (Humbert, 1927, 1959; Burney, 1997; Gasse, 1998; Burney *et al.*, 2004; Virah-Sawmy *et al.*, 2009). Alternatively, a minor grassland biome may have been constructed by extinct giant tortoises and hippopotamuses, perhaps aided by extinct browsers (elephant birds and the large, widespread, semi-terrestrial lemur *Archaeolemur*) (Bond *et al.*, 2008; Godfrey & Crowley, 2016).

More recently, Joseph & Seymour (2020) have proposed a return to the classical view of secondary grassland, suggesting that no co-evolution between herbivores and grasses occurred. This is indicated particularly by the catastrophic response of Malagasy

ecosystems to the introduction of fire and cattle, in stark contrast to the situation on the African mainland (Humbert, 1927).

We reconstructed the Cenozoic evolution of forest and grassland on Madagascar to investigate the relative influences of climate change (climax hypothesis) and habitat construction (co-evolution hypothesis). Focussing on seed dispersal by animals and the construction of grassland by large herbivores, we derived six hypotheses from the proposal of episodic land bridges and the role of zoochory in the colonization of Madagascar (Masters *et al.*, 2021): (1) zoochory facilitates island colonization and tends to become diffuse over time, involving more plant species and more dispersers; (2) conversely, Malagasy plants that are not capable of long-distance seed dispersal are indicators of ancient land connections; (3) co-evolution also occurred *in situ*, as revealed by unique systems of pollination and seed dispersal, a common characteristic of islands. We then applied the principles of co-evolution and niche construction

to the origin of Malagasy grasslands: (4) islands are often dominated by woody vegetation, i.e. insular woodiness, an effect of moderate climatic conditions observed on small islands; (5) applied to a large island, this phenomenon is explained by archaism, i.e. Madagascar may have become isolated before the spread of herbaceous plants; (6) alternatively, a true grassland biome evolved in the Late Miocene, but the large herbivores that maintained it are now extinct.

MATERIAL AND METHODS

PHYSIOGNOMIC RECONSTRUCTION

Our palaeo-environmental reconstruction was based on a previously published hypothesis of episodic land connections between eastern Africa and Madagascar (Masters *et al.*, 2021, In press) using data collected by the Passive Margins Exploration Laboratories (PAMELA) research programme and the PLACA4D freeware, an interactive tool for palinspastic reconstruction in 4D (Matias *et al.*, 2005; Pelleau *et al.*, 2015). The PAMELA programme conducted sedimentary, tectonic, volcanic, kinematic and palaeo-environmental studies of Mozambique and Madagascar covering the period from the opening of the Mozambique Channel to the present day. It involved eight oceanographic cruises between 2014 and 2017 (224 days at sea) and three onshore geological surveys in 2017–2018 (50 land days). The compilation of the PAMELA results presents a far more complex and dynamic picture of the channel's bathymetric and topographic evolution than was previously envisioned. The data indicate three intermittent periods of subaerial land connection (Early Palaeocene, Late Eocene and Late Miocene) (Masters *et al.*, 2021, In press) associated with global tectonic and kinematic events (Moulin *et al.*, 2010; Leroux *et al.*, 2018) leading to uplift (Delaunay, 2018; Ponte *et al.*, 2019), volcanism (Courgeon *et al.*, 2017) and periodic emersion of the Davie Ridge. Connectivity was probably enhanced by sea level lows, which we did not try to reconstruct; hence, the Davie Ridge emergences figured here are minimal estimates.

Following the vegetation classification of Moat & Smith (2007), we first reconstructed the physiognomy of the vegetation, beginning with Humbert's climax reconstruction (republished by Paulian, 1961). Contrary to the assumption that Madagascar's current topography existed as early as the Cretaceous-Palaeocene boundary (Ohba *et al.*, 2016), we followed the proposal of Delaunay (2018) and Masters *et al.* (2021) that Madagascar's highlands were uplifted in three phases, contributing to the emergence of the land bridges. Indeed, the complex bioclimatic zonation of Madagascar today is in large part a result

of its dome-shaped topography. The rains brought by the eastern trade winds are captured by the central highlands, creating a contrast between the moist eastern and north-western regions and the dry south-west (Fig. 1). Because this topography also creates a pattern of parallel transverse river systems that influence the distribution of plant and animal species (Wilmé *et al.*, 2006), we included the palaeo-river systems reconstructed by Delaunay (2018) on the basis of his palaeo-topographic reconstruction.

CHOROLOGICAL RECONSTRUCTION

We limited our chorological reconstruction of the vegetation to those angiosperm families for which information is available, as indicators of three major vegetation types (forest, thicket and wooded grassland) (Masters *et al.*, 2021) (Fig. 1). We identified zones of endemism (Wilmé *et al.*, 2012), which possibly served as refugia for relict species, particularly in mountainous areas. Isolated populations of *Dilobeia thouarsii* (Proteaceae) in a small region of the central-west that was mountainous in the Palaeocene indicate such a refugium (<http://legacy.tropicos.org/Project/Madagascar>). The extreme north and the north-east have Oligocene xerophytic relicts indicating a drier climate prior to the Late Miocene northern uplift. The Ankarafantsika (north-west) and Menabe forests (west), as well as the extreme south-west spiny thickets, are regions of endemism that probably remained wooded during a period of forest regression in the Late Miocene. We applied a method of reconstruction based on the principle of anachronism, which occurs when one partner of a co-evolved association survives the extinction of another, sometimes becoming rare [see Bond & Silander (2007), Midgley & Iling (2009), Godfrey & Crowley (2016) and Albert-Daviau *et al.* (2020) for instances of anachronism in Madagascar]. If hippopotamuses colonized the island in the Late Miocene following river courses (Masters *et al.*, 2021), we would expect to find a greater variety of grasses (Poaceae, Cyperaceae and Juncaceae) in the western catchment basin. Finally, we consulted Madagascar's limited fossil record, which attests to the presence of forest on the central highlands (eight important lemur subfossil sites) and hippopotamuses in the Pleistocene (Mittermeier *et al.*, 2010; Godfrey & Crowley, 2016).

BIOME EVOLUTION AND CO-EVOLUTION IN MADAGASCAR

EARLY ANGIOSPERM CO-EVOLUTION WITH ANIMALS

Krassilov (2012) proposed that angiosperms evolved during an arid period in the Early Cretaceous (Early

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Aptian, ~120 Mya), possibly around the Tethys Sea, as herbaceous, semi-aquatic *Ranunculus* (buttercup)-like plants. Krassilov referred to this evolutionary process as ‘neoteny’ (implying in fact paedomorphosis, or the retention of juvenile characteristics in adults); the model he described was a combination of accelerated growth in sporophytes that became herbaceous, and truncated development forming progenetic gametophytes reduced to reproductive organs, possibly as an effect of nematode or insect infestations leading to the formation of galls (Feinsinger, 1983; Krassilov, 2012). In this view, the first flowers were condensed inflorescences, possibly pollinated by the parasites they contained, although reconstructions have been complicated by high levels of homoplasy, as early angiosperms co-occurred with a wide variety of angiosperm-like plants. Early angiosperm evolution is likely to have involved diffuse co-evolution regarding pollination and herbivory by insects, and vertebrate seed dispersal (Regal, 1977). In the Late Cretaceous, angiosperms formed mangroves around the Tethys Sea, probably under the influence of wetter conditions that drove peramorphosis [i.e. prolonged ontogeny resulting in woodiness or lignification (Krassilov, 2012)], which may have offered protection against herbivores. Arboreal mammals, including primate ancestors and relatives, may thus have originated in mangroves as well as the first dry forests dominated by early angiosperms similar to extant *Cercidiphyllum* (katsura trees).

Endo-zoochory potentially evolved as a by-product of defence against seed predation, possibly also through heterochrony (Janzen, 1983; Tiffney, 1986; Mack, 2000). Woody fruits have a soft stage before the pulp becomes lignified, and fleshy fruits may thus be paedomorphic (Tiffney, 1986; Mack, 2000). Watson (2020) proposed a scenario for the evolution of fleshy fruits involving small Cretaceous mammals that may have included early primates. Ancestral mistletoes likely evolved as root parasites that were transferred to the treetops by small arboreal mammals (Watson, 2020). Extending this scenario, the first fleshy fruits would have been produced by hemiparasitic plants and creepers (epiphytes, lianas and vines), explaining the rapid spread of ancient primate relatives (plesiadapiforms) that apparently consumed a variety of plant parts, including bark and seeds. Again, reconstructions are complicated by homoplasy, notably by the subsequent evolution of fleshy pseudo-fruits in many older groups of plants including gymnosperms (yellowwood family Podocarpaceae) and even ‘pre-gymnosperms’ (*Ginkgo*), in the Early Palaeocene (Tiffney, 1986; Mack, 2000).

THE FIRST COLONIZATION OF MADAGASCAR BY ANGIOSPERMS

Several ancient biogeographic patterns suggest a Late Cretaceous (100–90 Mya) land connection between Antarctica and Madagascar, which enabled a number of animals to colonize the island: iguanid lizards, ratites [the aepyorniforms or elephant birds known from subfossils (Monnier, 1913)], the ancestors of the Malagasy boas (Noonan & Chippendale, 2006) and even dinosaurs (Krause *et al.*, 1997), although details of such a connection are unknown. At that time, Antarctica had temperate ‘rainforests’ dominated by tree ferns (*Cyathea*) and gymnosperms (araucarias and Podocarpaceae) (Klages *et al.*, 2020). A connection with Antarctica may explain the presence in Madagascar of some Cretaceous angiosperm families such as the Proteaceae (*Dilobeia* and *Malagasia* with Australian affinities), Winteraceae (the endemic ancient *Takhtajania*) (Callmander *et al.*, 2011; Buerki *et al.*, 2013) and the Hernandiaceae [*Hazomalania*, although Michalak *et al.* (2010) suggested that this genus only diverged in the Early Palaeocene]. The evolution of the Hernandiaceae is particularly interesting because the family includes genera that produce seeds dispersed by gravity and wind (e.g. propeller-like samaroid seeds of *Gyrocarpus* and *Illigera*), which require land connections, as well as genera that have fleshy fruits that were dispersed by birds to oceanic islands (*Hernandia*) (Michalak *et al.*, 2010). The Malagasy endemic *Hazomalania* (sister to *Illigera*) has slightly fleshy fruits not known to be consumed by animals (Capuron, 1966), implying that seed dispersal evolved first as a by-product of seed predation. Indeed, seed-eating birds like parrots probably evolved in the southern hemisphere, which appears to have lacked fleshy fruits in the Late Cretaceous.

EARLY PALAEOGENE SEED DISPERSAL BY LEMURS

The idea that the first vertebrates to engage in seed dispersal were seed predators gains support from Madagascar’s oldest and strangest primate, the aye-aye (*Daubentonia*), a major seed-eater that diverged from the other lemur lineages at least 10 Mya before their radiation. The long delay between the evolution of the daubentoniids and the other six or seven families has led to the proposal that they colonized Madagascar from Africa earlier than the common ancestor of the other lemurs (Montagnon, 2013). A continuous land bridge probably linked the two landmasses in the earliest Palaeocene (Fig. 2), when the flora of Madagascar was dominated by plants producing hard seeds often protected by woody pods, such as the bean family (Fabaceae) and the mahogany family (Meliaceae). In the Eocene and Oligocene, both



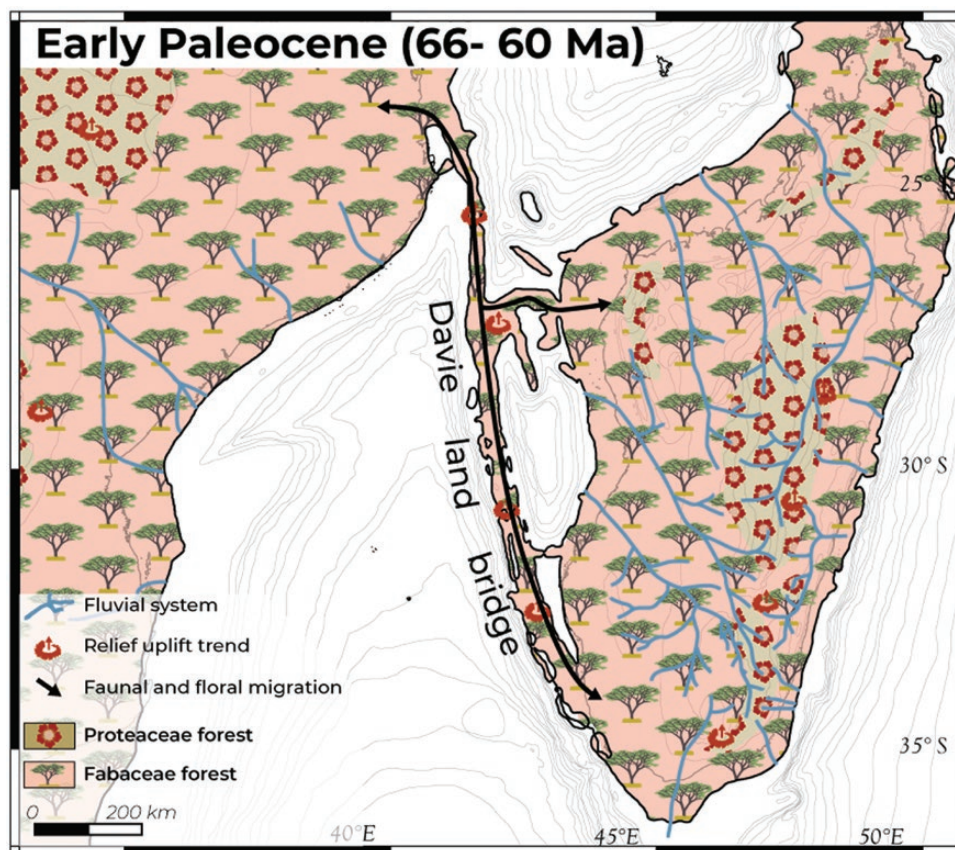


Figure 2. Reconstruction of the Palaeocene vegetation of Madagascar and East Africa suggesting that a continuous land connection led to an exchange between the two landmasses at a time when both Africa and Madagascar were located at higher latitudes than today. During an initial cold period, Malagasy Cretaceous woodland including Proteaceae that probably originated in Antarctica first colonized Africa, while Madagascar was colonized by aye-aye (*Daubentonia* spp.) ancestors, a lineage of seed-eating lemurs. During a subsequent warmer period, African woodlands dominated by Fabaceae and Meliaceae colonized the lowlands of Madagascar, probably bringing the frugivorous ancestors of all the other lemurs. Proteaceae woodland survived in altitude refugia, as suggested by the modern distribution of the family.

families evolved forms that produced fleshy fruits (e.g. *Brenierea* in the Fabaceae and *Malleastrum* in the Meliaceae), suggesting again that seed dispersal by animals evolved convergently as a by-product of defence against seed predation (Janzen, 1983; Tiffney, 1986; Mack, 2000).

From this perspective, the association between lemurs and plants with fleshy fruits evolved later, possibly during a second wave of dispersal to Madagascar, associated with at least one endemic Malagasy genus thought to have evolved in the Early Palaeocene, *Burasaia* (of the moonseed family Menispermaceae) (Birkinshaw, 2001; Bollen et al., 2004; Atsalis, 2008; Buerki et al., 2013). The Menispermaceae evolved and spread from the Northern Hemisphere in the Early Palaeocene and Eocene, as far as South America (Jud et al., 2018), perhaps assisted by small arboreal mammals. The family mainly comprises lianas and epiphytes, but evolved trees in Madagascar

(Schatz, 2001). We suggest that this later wave of colonization was associated with the spread of the African Fabaceae forest at low altitude, while relicts of the Cretaceous Proteaceae forest remained within higher altitude refugia, possibly also forming the early southern African fynbos (Figs 1, 2).

EOCENE ISOLATION

During the Eocene, the formation of the Antarctic ice cap led to the progressive cooling of the southern hemisphere, while Madagascar and Africa migrated north (Zachos et al., 2001; Couvreur et al., 2021). Contact between Africa and Europe allowed the dispersal of mangroves from the Tethys Sea to the Saharan Sea, possibly bringing haplorhine primates, carnivores and rodents to North Africa along with a variety of angiosperms (Bobe, 2006). Indeed, sub-Saharan Africa remained relatively dry, as indicated by

one of the rare Eocene fossil sites in Africa (Mahenge, Tanzania). The East African landscape was dominated by Fabaceae with narrow leaves (caesalpinoids and the first mimosoids), forming a habitat reconstructed as similar to modern mopane and miombo woodlands (Jacobs & Herendeen, 2004).

OLIGOCENE SUCCULENT *EUPHORBIA* THICKET:
GENERALIZATION OF ZOOCHORY

The Eocene-Oligocene transition was marked by a mass extinction event in the northern hemisphere known as the 'Grande Coupure', when the sister taxon to the living tooth-combed (or lemur-like) primates, the adapiforms, almost died out (Prothero, 1994). These extinctions were again followed by diverse radiations, including the ancestors of many modern primate lineages. In Madagascar, decreased sea levels associated with a new uplift and global cooling caused by the thickening of the southern ice cap (Zachos *et al.*, 2001) led to a second emergence of the Africa-Madagascar land bridge (Masters *et al.*, 2021,

In press). The bridge would have consisted largely of carbonate coral rag, and supported mangrove forests (Fig. 3) which allowed Madagascar to be colonized by a snake family (Lamprophiidae), carnivoran mammals (Eupleridae), rodents (Muridae), and birds such as the ground rollers (Brachypteraciidae), sister to the true rollers (Coraciidae). Several angiosperm families associated with mangroves probably colonized Africa during the Eocene, and Madagascar during the Eocene-Oligocene transition, including families contributing to forest and thicket today, such as Acanthaceae (acanthus family), Arecaceae (palms), Combretaceae (bush-willows and relatives) and bombacoid Malvaceae (the baobab family) (Baum *et al.*, 2004; Couvreur *et al.*, 2021).

Seed-dispersing birds, particularly parrots and pigeons, are likely to have assisted the colonization of Madagascar (and possibly also Africa) by many new angiosperm families. Of the 13 angiosperm families identified as Early Oligocene colonists using molecular dating, ten have species producing fleshy fruits and seeds dispersed by lemurs today (Annonaceae,

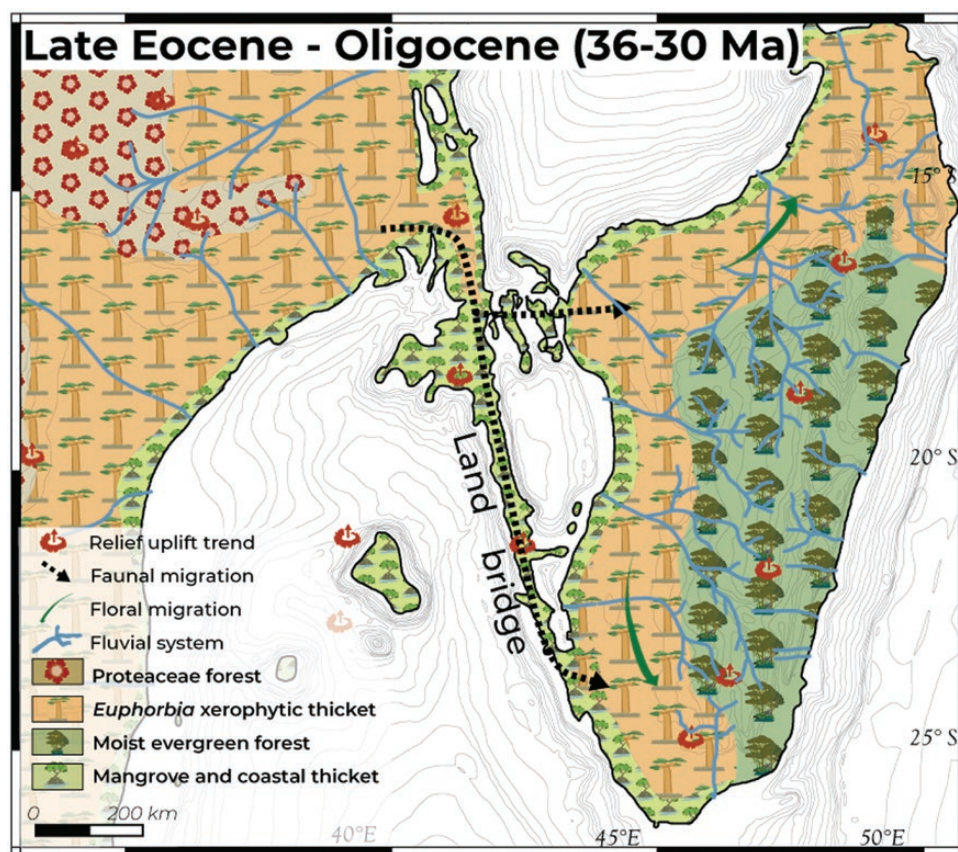


Figure 3. Reconstruction of the Late Eocene-Early Oligocene vegetation of Madagascar at a time of a second land connection with Africa that allowed the colonization of the island by dry *Euphorbia* thicket, rodents and carnivores (grey arrows). Colonizers probably used corridors of mangrove that colonized the Indian Ocean region at that time, probably also bringing a number of other angiosperm families to the island.

Arecaceae, Ericaceae, Euphorbiaceae, Monimiaceae, Myristicaceae, Passifloraceae, Rubiaceae, Rutaceae and Sapindaceae) (Birkinshaw, 2001; Bollen *et al.*, 2004; Buerki *et al.*, 2013; Schwery *et al.*, 2015; Masters *et al.*, 2021) (Table 1 also includes three other genera not considered by Buerki *et al.*, 2013). Other probable Oligocene colonizers, the Didiereaceae, have flowers pollinated by lemurs (in particular *Lepilemur*) and seeds dispersed by parrots. The transition to endo-zoochory is well illustrated by the Malagasy Combretaceae, which have rare species producing non-edible samaroid fruits, and more common species producing green fibrous fleshy fruits (F. Génin, pers. obs.).

SPREAD OF THE XEROPHYTIC THICKET

The Oligocene saw the establishment of the xerophytic thicket dominated by Didiereaceae and Euphorbiaceae, now limited to the south-west (Masters *et al.*, 2021). Xerophytic relicts in the north and the north-east, including coralliform *Euphorbia* trees and two bird species, imply that xerophytic thicket once covered most of Madagascar, with the exception of the east (Masters *et al.*, In press) (Fig. 3). The African analogue of the Malagasy xerophytic thicket, also dominated by succulent Didiereaceae (= Portulacaceae) and Euphorbiaceae, is currently limited to south-east Africa along the coast, on rocky slopes and in steep valleys (Applequist & Wallace, 2003; Cowling *et al.*, 2005).

The physiognomy of the tall Malagasy xerophytic thicket is primarily the result of true xerophytic adaptations, e.g. underground parts, succulence

including trunks [i.e. pachycauly observed in many families like the emblematic baobabs, *Adansonia* spp. (Bombacoidae: Malvaceae)], deciduous foliage, microphyllly and pseudo-leaves in the form of cladodes or phyllodes (Koechlin *et al.*, 1974). Such adaptations make these plants particularly vulnerable to herbivores, explaining why they often evolve toxicity, resinous exudations or latex, as well as the spines and thorns of the eponymous 'spiny thicket' (Koechlin *et al.*, 1974; Moat & Smith, 2007). This physiognomy has been explained by the activities of extinct browsers such as elephant birds (Aepyornithidae) (Bond & Silander, 2007) and extinct lemurs (Godfrey & Crowley, 2016). Such anachronism was invoked less convincingly by Midgley & Iling (2009), who proposed that the ecto-zoochorous (spiky) seeds of *Uncarina* spp. (Pedaliaceae) were dispersed by elephant birds, although they are effectively dispersed today by ring-tailed lemurs (*Lemur catta*) and sifakas (*Propithecus verreauxi*) (F. Génin, pers. obs.).

Drought associated with increased seasonality is likely to have demanded shorter life histories in both plants and animals. This change in climate led to the spread of new herbaceous plants in the Poaceae (true grasses) and other families such as the Gentianaceae, Malvaceae, Rubiaceae and (papilionoid) Fabaceae (Buerki *et al.*, 2013). Many Malagasy animals have unusual life histories, including hyperfecundity in *Tenrec ecaudatus* which is known to have extraordinarily large litters (up to 31) given its body size (~ 1 kg) (Garbutt, 2007); and the unique case of an annual vertebrate exhibiting a winter diapause, the chameleon *Furcifer labordi* (Karsten *et al.*, 2008). Among lemurs, selection for a short life history led to a

Table 1. Angiosperm genera comprising species producing seeds dispersed by birds and lemurs (Atsalis, 2008; Birkinshaw, 2001; Bollen *et al.*, 2004), and possible dates of first arrival of the families on Madagascar from Africa associated with three proposed continuous (Palaeocene and Oligocene) and discontinuous (Miocene) land connections [from Masters *et al.* (2021) in large part based on Buerki *et al.* (2013)]

Early Palaeocene	Early Oligocene	Late Miocene
Menispermaceae (<i>Burasaia</i> *, <i>Strychnopsis</i> *)	Annonaceae (<i>Monanthes</i> , <i>Polyalthia</i> , <i>Uvaria</i> , <i>Xylopia</i>) Arecaceae (<i>Dyopsis</i>) Burseraceae (<i>Canarium</i> , <i>Commiphora</i>)	Anacardiaceae (<i>Operculicarya</i> *, <i>Poupartia</i> , <i>Sorindeia</i>)
Fabaceae (<i>Brenierea</i> *)	Combretaceae (<i>Combretum</i> , <i>Terminalia</i>)	Brassicaceae-Capparadoideae (all genera)
Meliaceae (<i>Calodectarya</i> *)	Malvaceae-Bombacoidae (<i>Adansonia</i>) Ericaceae (<i>Vaccinium</i>) Euphorbiaceae (<i>Macaranga</i> , <i>Uapaca</i>) Monimiaceae (<i>Tambourissa</i>) Myristicaceae (<i>Brochoneura</i> *) Passifloraceae (<i>Adenia</i>) Rubiaceae (12 genera) Rutaceae (<i>Vepris</i>) Sapindaceae (<i>Plagioscyphus</i> *, <i>Tina</i> *)	Loganiaceae (<i>Strychnos</i>) Loranthaceae (<i>Bakerella</i>) Malvaceae-Tilioidae (<i>Grewia</i>) Salvadoraceae (<i>Salvadora</i> , <i>Azima</i>) Viscaceae (<i>Viscum</i>)

*Endemic genera.

reduction of body size in the Cheirogaleidae (Masters *et al.*, 2014, 2021; Génin & Masters, 2016). Phyletic dwarfing was associated with a dietary shift towards exudativory, i.e. the consumption of gum and nectar (Génin *et al.*, 2010; Andrews *et al.*, 2016), leading to unique plant-animal associations, possibly including other newcomers like the Burseraceae, and with some benefit to the trees [e.g. the cleaning hypothesis of Andrews *et al.* (2016)].

MALAGASY WOODINESS AND SEED DISPERSAL BY DWARF LEMURS

Late Miocene sea level lows and a third uplift associated with the raising of the northern highlands of Madagascar formed a new connection with Africa (Masters *et al.*, 2021) (Fig. 4). This connection was probably discontinuous, however, possibly allowing amphibious animals (hippopotamuses, at least one

crocodile and a frog species) and flying animals (insects, birds and one bat species) to colonize Madagascar. As a result of this limited colonization, the island remained considerably woodier than the continent.

The woodiness of Madagascar is illustrated by plants that probably evolved into trees from herbaceous ancestors, notably among the Asteraceae, Convolvulaceae, Gentianaceae and even Poaceae (bamboos) (Carlquist, 1974; Dransfield, 2003; Strijk *et al.*, 2012; Hackel *et al.*, 2018). Moreover, some trees that originated in African wooded grassland secondarily formed forests on the island: Combretaceae, Euphorbiaceae, mimosoid Fabaceae such as the acacias *Senegalia* and *Albizia*, and the endemic *Alantsilodendron*, sister-genus to *Dicrostachys*, which is also present on Madagascar. Increased woodiness is also testified by seed dispersal systems: Madagascar has curious cases of anemochorous forest trees (Asteraceae) and ecto-zoochorous Poaceae species

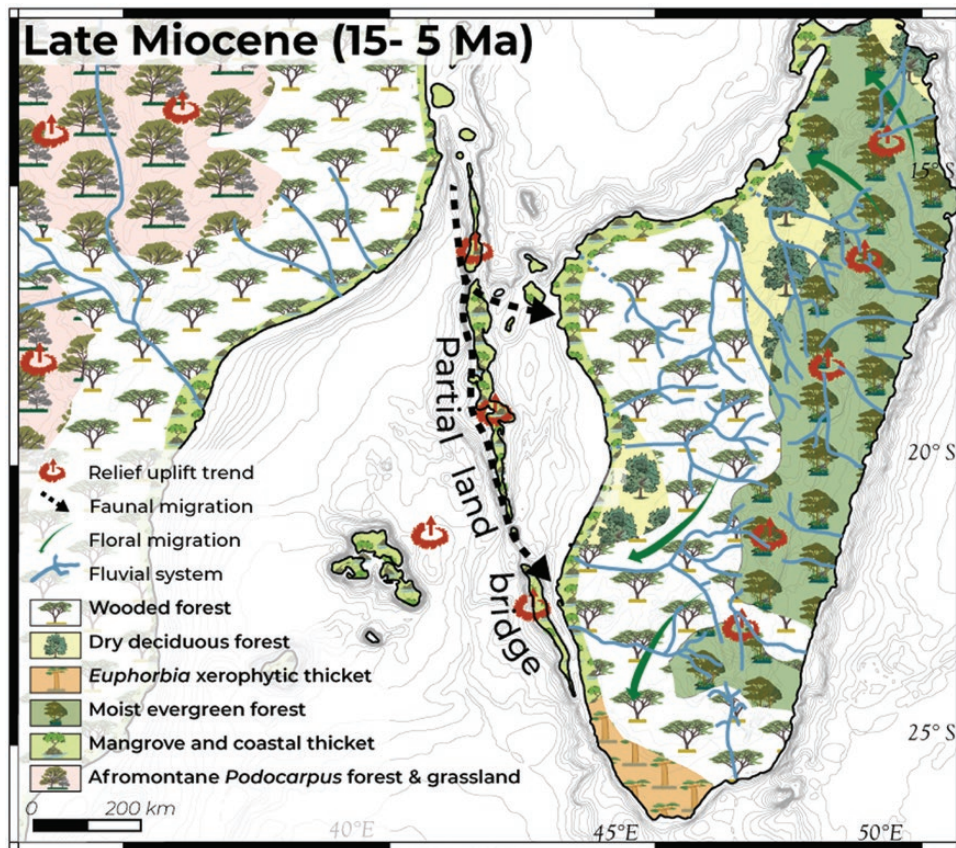


Figure 4. Reconstruction of the Late Miocene vegetation of Madagascar during which a discontinuous land connection with Africa probably established. This event was caused by the northern uplift that also led to a northward expansion of the eastern moist evergreen forest that formed the Sambirano moist sub-region (green arrows), associated with the onset of the north-western monsoons (see Fig. 1). This also represents the time of maximum expansion of wooded grassland brought by extinct hippopotamuses and fragmenting the western dry deciduous forest, and possibly the south-eastern moist evergreen forest separated from the central highlands by the Menarahaka Valley. These fragments of forest correspond to extant sub-domains showed in Figure 1 and are centers of endemism today.

(*Sclerodactylon macrostachyum*, found in *Euphorbia stenoclada* forest on dunes in the south-west, and common in secondary grasslands in dry areas).

The same phenomenon is evidenced by birds that originated in grassland habitats but colonized forest and thicket in Madagascar (rock thrushes, *Monticola* spp.) and by insects (Paulian, 1961). For instance, Cetoninae are found in open habitats in Africa but in forests on Madagascar; the African grassland genus *Coprini* is replaced by the Malagasy forest *Helictopleurina*. Among butterflies, the Satyrinae (Nymphalidae) tribes Elymniini and Satyrini have speciated extensively on Madagascar [approximately 60 and 40 species, respectively (Krüger, 2007)]. The caterpillars of satyrines feed on grasses, including Poaceae, Cyperaceae (sedges) and Juncaceae (rushes), and inhabit grasslands in Africa and moist evergreen forests in Madagascar (Paulian & Viette, 2003). Another striking example of Madagascar's grassland woodiness is mentioned in the classic co-evolution paper by Ehrlich & Raven (1964): *Parides* (*Atrophaneura*) *antenor*, a Malagasy papilionid, is associated with *Combretum*, which is a genus represented by trees in East African wooded grassland, and by lianas in Malagasy forest.

A discontinuous Late Miocene connection with Africa is also indicated by the presence of zoochorous plants with small fruits that were probably initially dispersed by birds and fruit bats (Génin & Rambeloarivony, 2018). Among the bird taxa that colonized Madagascar at this time, only two lineages, the asities (Philepittinae within Eurylaimidae, related to the insectivorous broadbills) and the sunbirds (Nectariidae), developed strict relationships with plants and became major pollinators and seed dispersers. Interestingly, the asities evolved a frugivorous lineage (*Philepitta*) and a sunbird-like nectarivorous lineage (*Neodrepanis*).

In accordance with Madagascar's tendency to woodiness, the majority of Malagasy zoochorous plants are trees, which dominate the flora (Lowry et al., 1997; Schatz, 2001; Callmander et al., 2011). Many Malagasy plants produce small seeds that were originally dispersed by birds and are now dispersed by lemurs—particularly by the small Cheirogaleidae (mouse and dwarf lemurs). During the Middle to Late Miocene, the cheirogaleids became major pollinators and seed dispersers (Valenta & Lehman, 2016; Génin & Rambeloarivony, 2018) as they experienced a series of dwarfing events that led to very small body size in some species (Masters et al., 2014). Cheirogaleids sometimes pollinate the flowers and disperse the seeds of the same trees (all capparoid Brassicaceae, the cabbage family). Capparoid trees like *Crateva* spp. produce abundant nectar in the night-time, which is consumed by mouse lemurs as well as cathemeral lemurs (*Eulemur* spp.) and moths (F. Génin, pers. obs.) (Table 1).

In African capparoid Brassicaceae and mistletoes (Viscaceae and Loranthaceae), most of the small colourful fruits are dispersed by birds, while small green fruits are dispersed by mouse lemurs in Madagascar (Génin & Rambeloarivony, 2018) [but there are African species with green fruits such as *Viscum anceps*, *Viscum continuum* and *Maerua angolensis*, dispersed by nocturnal bushbabies (*Otolemur* spp.) and fruit bats]. The mouse lemur genus *Microcebus* appears to have co-evolved with many plants that colonized Madagascar in the Late Miocene: fruit plants such as mistletoes, and those in the Anacardiaceae, Brassicaceae, Loganiaceae (*Strychnos*), Malvaceae (*Grewia*, Tilioidae), Salvadoraceae (*Salvadora* and *Azima*), Ebenaceae (*Diospyros*), and the gum trees *Alantsilodendron* and *Terminalia*, and many Anacardiaceae (the mango family) (Andrews et al., 2016; Génin & Rambeloarivony, 2018). The presence of these taxa in Africa at that time is confirmed by the fossil record and by molecular dating (e.g. Bamford, 2011; Grímsson et al., 2018; Maul et al., 2019). Many wood-boring coleopteran larvae responsible for gum exudation probably also colonized Madagascar with the trees they infest. These include longhorn beetles (Cerambycidae), jewel beetles (Buprestidae) and click beetles (Elateridae) infesting trees in the Anacardiaceae, Combretaceae, mimosoid Fabaceae and tilioid Malvaceae (Génin et al., 2010), all possible Late Miocene colonists.

MIocene HIPPOPOTAMUS GRASSY FOREST AND THICKET

Our reconstruction of dry forest refugia suggests that the major river basins of central-west and south-west Madagascar experienced considerable forest regression during the driest period of the Late Miocene, possibly coincident with the spread of hippopotamuses and grasses (Weston & Boissierie, 2010) (Fig. 4). Indeed, grasslands are primarily constructed by large herbivores (McNaughton, 1984; Belsky, 1986; Paige & Whitham, 1987; Bond, 1994; Bond et al., 2008; Zhong et al., 2022). In the early Mid-Miocene (c. 16 Mya), a connection between Eurasia and Africa allowed a rich guild of browsers, grazers and mixed feeders to colonize Africa and radiate in co-evolution with a variety of grasses and trees (Bond, 1994). This was possible because of the large size of the African landmass and its colonization by diverse ancestral taxa capable of seasonal migration. In contrast, Madagascar was only colonized by hippopotamuses, which reduced in body size (Weston & Lister, 2009).

Three extinct hippopotamus species are known from Madagascar. We know little about the largest species, *Hippopotamus laloumena*, which was probably associated with large coastal lakes, wetlands and

10.60

10.65

10.70

10.75

10.80

10.85

10.90

10.95

10.100

10.105


10.110

10.111

10.112

- river mouths, a habitat similar to that of the ancestral colonist (Faure & Guérin, 1990; Masters *et al.*, 2021) (Table 2). Indeed, *H. laloumena* appears to be the least derived Malagasy hippopotamus, most similar to extant *Hippopotamus amphibius*, although it was about a third smaller (Faure *et al.*, 2010). The ancestor of *H. laloumena* may have evolved on the land bridge itself, only reaching Madagascar during the Messinian crisis (c. 6 Mya) during the sea level low stand (Leroux *et al.*, 2018). We speculate that *H. laloumena* formed grassy wetlands inhabited by extinct species such as the Malagasy lapwing (*Vanellus madagascariensis*) (Goodman, 1996), as well as other species that survived but became rare (like the Reunion harrier and many west-coast water birds).
- The two other hippopotamus species are better represented in the subfossil record of Madagascar. They are considerably smaller and apparently more derived, suggesting additional phyletic dwarfing, possibly associated with colonization of the interior regions along river courses during the wet onset of the Pliocene (5 Mya). This period was followed by a long drought during which the ancestral populations are likely to have undergone fragmentation, isolation and shrinkage (3–2 Mya). The rich highland Poaceae flora, which includes most endemic gregarious grass species, suggests the grassy thickets may have formed in response to grazing by *Hippopotamus madagascariensis*. High levels of tooth wear indicate that this species fed on more abrasive food (e.g. sedges) and/or ingested more inorganic material than the other species, leading to the establishment of grassy heathland similar to modern savoka *Erica* thicket on sandy soil. Today, savokas form the pseudo-climax stable stage of degradation of the moist evergreen forest, but they probably expanded to coastal regions in the west and the south during xerophytic periods in the Pleistocene, as is indicated by relicts associated with poor soils and brackish coastal wetlands (Koechlin *et al.*, 1974; Lowry *et al.*, 1997; Gasse, 1998; Willis *et al.*, 2008; Virah-Sawmy *et al.*, 2009; Hackel *et al.*, 2018). Grassy forest, wetlands and savoka thicket formed by *H. madagascariensis* may have been the original habitat of the Betsileo short-tailed rat and the highland streaked tenrec, the extinct aardvark-tenrec (*Plesiorycteropus*) and possibly the extinct endemic crocodile *Voay robustus*. The surprising diversity of endemic ants found in secondary grasslands today is probably also explained by these extinct habitats (Fisher & Robertson, 2002; Buckley, 2013) (Table 2).
- Lower levels of tooth wear in *Hippopotamus lemerlei* (Stuenkel, 1989) suggest that this species inhabited Poaceae-rich dry forest, including dry deciduous forest and evergreen sclerophyllous forest (Table 2). Like the extant pygmy hippopotamus, *Choeropsis* (= *Hexaprotodon*) *liberiensis*, *H. lemerlei* probably fed on forest grasses and fallen fruits, thereby contributing to seed dispersal. This behaviour would have helped to maintain pseudo-climax *Uapaca* ‘tapia’ forest, a stable form of the degraded sclerophyllous forest that dominated parts of the western side of the central highlands (Humbert, 1955; Paulian, 1961; Humbert & Cours Darne, 1965; Koechlin *et al.*, 1974; Lowry *et al.*, 1997; Gasse, 1998). Grassy clearings formed by *H. lemerlei* in western and southern forests around lakes and near rivers were probably the original habitat of the Madagascar sandgrouse (*Pterocles personatus*), as well as extinct species like giant tortoises (*Aldabrachelys* spp.) and elephant birds (aepyornids) (Godfrey & Crowley, 2016).
- Thus, the proposal of a Late Miocene origin of Malagasy hippopotamuses could explain the island’s surprisingly rich grassland flora in terms of co-evolution. Madagascar has 536 Poaceae species, including 271 endemics (Bossler, 1969; Bond *et al.*, 2008; Callmander *et al.*, 2011). Herbaceous Poaceae endemics are mainly found in forests and thickets (52%), coastal wetlands (18%) and at high altitude (10%). Many Malagasy grasses adapted secondarily to forests (e.g. the ‘forest shade clade’), including secondary bamboos (Hackel *et al.*, 2018). Of the ten Poaceae genera considered the main foods of African *H. amphibius* (Kingdon, 1997; Eltringham, 1999; Kingdon & Hoffmann 2013), nine are important components of Malagasy secondary grasslands: *Botriochloa*, *Brachiaria*, *Chloris*, *Cynodon*, *Heteropogon*, *Hyparrhenia*, *Panicum*, *Setaria* and *Sporobolus*. The tenth, *Themeda*, occurs on the island but may have been introduced (Bossler, 1969). Three genera described by Kingdon (1997) as important foods of the pygmy hippopotamus (*Andropogon*, *Imperata* and *Leptaspis*), are also present on Madagascar, suggesting that their spread, too, was facilitated by hippopotamuses. Indeed, the dispersal of small seeds ingested by large herbivores with the foliage of Poaceae, Cyperaceae and Juncaceae has been explained in terms of co-evolution [the ‘foliage is the fruit’ hypothesis (Janzen, 1984)]. Hippopotamuses are unique gut fermenters and their role in seed dispersal is poorly known (van Heukelum, 2010; McCauley *et al.*, 2018).
- Hippopotamuses probably also facilitated the spread of grasslands by stimulating the re-growth of the grass [the ‘grazing lawn’ hypothesis of McNaughton (1984)]. In Africa, hippopotamuses are known to transform their environments drastically by changing the soil chemistry and opening habitats (McCauley *et al.*, 2018), and by inhibiting fire at high densities (Oliver & Laurie, 1974). In striking contrast to their African analogues, Malagasy secondary grasslands are not fire resistant (Bossler, 1969). African grasslands, in part the products of recurrent fire, host a great variety of fire-resistant plants (pyrophytes), including many forbs,

Table 2. The three grassland biomes of Madagascar probably constructed by three extinct hippopotamuses in distinct habitats, but often forming mosaics leading to sympatry

	Coastal wetlands	Altitude grassy thicket	Forest	
12.55	Endemic Poaceae		Western dry forest and southern thicket	12.60
12.56	<i>Aristida similis</i>	<i>Andropogon</i> spp.†	<i>Aristida ambongensis</i>	12.65
	<i>Digitaria</i> spp.	<i>Agrostis</i> spp.	<i>Camusia perrieri</i> §	12.70
	<i>Leersia perrieri</i>	<i>Anthoxanthum madagascariense</i>	<i>Camusiella vatkeana</i> §	
	 <i>Cymbopogon glanduliferum</i> †	<i>Bracharia</i> spp.	<i>Chloris</i> spp.†	
	<i>Sporobolus</i> spp.†	<i>Digitaria</i> spp.	<i>Cynodon poissonii</i> †	
		<i>Eragrostis lateritica</i> / <i>Eragrostis stolonifera</i>	<i>Daknopholis boivinii</i>	
		<i>Festuca camusiana</i>	<i>Decaryella madagascariensis</i> §	
		<i>Helictotrichon avenoides</i>	<i>Dinebra perrieri</i>	
		<i>Heteropogon betafensis</i> †	<i>Enteropogon sechellensis</i> †	
		<i>Isalus tsalensis</i> § / <i>Isalus humbertii</i> §	<i>Eragrostis</i> spp.	
		<i>Lasiorrhachis viguieri</i> §	<i>Lepturus humbertianus</i>	
		<i>Panicum</i> spp.†	<i>Neostapfella perrieri</i> §	
		<i>Pennisetum pseudotriticoides</i>	<i>Panicum voeltzkowii</i> §	
		<i>Pentastichis perrieri</i>	<i>Sclerodactylon macrostachyum</i>	
		<i>Poa madecasa</i> / <i>Poa ankaratrensis</i>	<i>Thuarea perrieri</i>	
		<i>Rhytachne caespitose</i>	<i>Vigiella madagascariensis</i> §	
		<i>Sacciolepis viguieri</i>	Highland moist evergreen forest	
		<i>Stenotaphrum</i> spp.	<i>Anthraxon antsirabensis</i>	
		<i>Yvesia madagascariensis</i> §	<i>Aristida rufescens</i> / <i>Aristida tenuissima</i>	
			<i>Bracharia antsirabensis</i> / <i>Bracharia epacridifolia</i> †	
			<i>Cyrtococcum deltoideum</i> / <i>Cyrtococcum bosseri</i>	
			<i>Elionurus tristis</i>	
			<i>Isachne muscicola</i>	
			<i>Panicum</i> spp.†	
			<i>Redfieldia hitchcockii</i>	
			<i>Urelythrum humbertionum</i>	
			Lowland eastern moist evergreen forest	
			<i>Aristida similis</i>	
			<i>Bracharia bemariuensis</i> †	
			<i>Digitaria</i> spp.	
			<i>Loudetia madagascariensis</i>	
			<i>Panicum umbellatum</i> †	
			<i>Aepyornis</i> spp.†	
			<i>Archaeolemur</i> spp.†	
	Possible browsers			
				12.110
				12.111
				12.112
				12.105
				12.100
				12.95
				12.90
				12.85
				12.80
				12.75

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Table 2. Continued

	Coastal wetlands	Altitude grassy thicket	Forest
Major grazers	<i>Hippopotamus laloumena</i> [†] <i>Aldabrachelys</i> spp. [†]	<i>Hippopotamus madagascariensis</i> [†]	<i>Hippopotamus lemerlei</i> [†] <i>Aldabrachelys</i> spp. [†]
Associated mammals	Madagascar aardvark tenrec (<i>Plesiorycoteropus</i>) ^{†,*}	Madagascar aardvark tenrec (<i>Plesiorycoteropus</i>) ^{†,*} Betsileo short-tailed rat (<i>Brachyuromys betsileoensis</i>) Highland streaked tenrec (<i>Hemicentetes nigriceps</i>)	Madagascar aardvark tenrec (<i>Plesiorycoteropus</i>) ^{†,*} Betsileo short-tailed rat (<i>Brachyuromys betsileoensis</i>) Highland streaked tenrec (<i>Hemicentetes nigriceps</i>) Madagascar button-quail (<i>Turnix nigricollis</i>) Madagascar partridge (<i>Margaroperdix madagarensis</i>)
Associated birds	Reunion harrier (<i>Circus maillardi</i>) Madagascar lapwing (<i>Vanellus madagascariensis</i>) [†] Madagascar plover (<i>Charadrius thoracicus</i>) Madagascar lark (<i>Mirafra hova</i>) Madagascar wagtail (<i>Motacilla flaviventris</i>) Madagascar cisticola (<i>Cisticola cherina</i>) Madagascar manikin (<i>Lonchura nana</i>)	Slender-billed flufftail (<i>Sarothrura watersi</i>) Madagascar partridge (<i>Margaroperdix madagarensis</i>) Madagascar lark (<i>Mirafra hova</i>) Madagascar cisticola (<i>Cisticola cherina</i>) Grey emutail (<i>Amphispalis seebohmi</i>) Madagascar manikin (<i>Lonchura nana</i>)	Madagascar partridge (<i>Margaroperdix madagarensis</i>) Madagascar sandgrouse (<i>Pterocles personatus</i>) Madagascar lark (<i>Mirafra hova</i>) Madagascar manikin (<i>Lonchura nana</i>)

[†]Extinct since the Holocene.

^{*}In association with termites and ants (Fisher & Robertson, 2002).

[‡]Poaceae endemic genera.

[†]Poaceae genera also consumed by African hippopotamus.

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as well as animals that use deep burrows, mammals capable of rapid running, and terrestrial birds with good flying abilities (e.g. bustards, Otidae), which are absent on Madagascar, which is, by contrast, poor in pyrophytes. For instance, palms like *Bismarkia* and *Borassus*, which often dominate secondary grasslands, are opportunistic pyrophytes.

Hippopotamuses may also have evolved strong associations with coprophagous dung beetles (Scarabaeidae), known to contribute considerable secondary seed dispersal in both forest and grassland habitats (e.g. [Andressen & Feer, 2005](#); [Kunz & Krell, 2011](#)). Madagascar has a rich dung beetle fauna consisting of about 300 species of which 285 are endemic (95%) ([Miraldo *et al.*, 2011](#)). Most are associated with lemurs and are forest dwellers. However, 40 endemic species were found on cattle dung, 20 of which were never found on any other resource ([Rahagalala *et al.*, 2009](#)). We suggest that these species were originally associated with hippopotamuses, a hypothesis largely consistent with the molecular divergence dates compiled by [Miraldo *et al.* \(2011\)](#), which indicate multiple colonizations of the island by scarabaeids, and a much greater age of the species associated with lemurs.

DISCUSSION

COLONIZATION OF MADAGASCAR BY CO-EVOLVED SYSTEMS

[Masters *et al.* \(2021, In press\)](#) observed that molecular estimates of phylogenetic divergences of endemic Malagasy plants and vertebrates imply three synchronic colonization episodes that correspond to three proposed periods of land connection between the island and the African continent. They questioned the dominant narrative based on trans-oceanic dispersal by rafting (e.g. [Ali & Huber, 2010](#); [Krause, 2010](#); [Krause *et al.*, 2020](#); [Samonds *et al.*, In press](#)), in the light of three axioms: (1) only land bridges can leave hard evidence; invoking rafting scenarios should be reserved for events for which there is no such evidence, and should remain open to falsification; (2) land bridges allow colonization by populations over generations, whereas rafting requires that waifs make the crossing within their reproductive lifetimes, and establish viable populations upon landfall; (3) land bridges provide habitat continuity, whereas rafting requires exceptional habitat flexibility.

We propose that co-evolution provides a means of interrogating the land bridge scenario, explaining both patterns of synchrony and the absence of many African plants and animals from Madagascar (habitat filtering). Exchanges among Africa, Madagascar and other islands were facilitated by diffuse plant-animal associations that included systems of pollination and

seed dispersal, as well as the general construction of landscapes. Some colonization events may have involved entire co-evolved systems as early as the Early Palaeocene, but more can be traced to the Early Oligocene. Others crossed the Mozambique Channel in the Late Miocene, possibly by a discontinuous land bridge, explaining why the only successful animal colonists at that time were volant or amphibious ([Masters *et al.*, 2021, In press](#)). Plant-animal co-evolution may have facilitated air-borne dispersal, for example, mistletoes, capparoid Brassicaceae and several other plants are likely to have been transported to Madagascar by frugivorous birds ([Génin & Rambeloarivony, 2018](#)).

Reasoning *a contrario*, we argue that continuous land connections during the Early Palaeocene and Early Oligocene explain the presence on Madagascar of plants and animals with limited dispersal abilities, which make bad candidates for long-distance rafting or flying. These include trees that produce seeds dispersed by gravity over short distances (e.g. caesalpinoid Fabaceae and Meliaceae), as well as birds not capable of sustained flight (e.g. storks and ibises). Scenarios of colonization by land bridges or rafting are not mutually exclusive. A discontinuous land connection can enhance the likelihood of over-water dispersal by shortening the distances between waypoints, and by providing intermediary habitats to colonists (e.g. crocodiles, hippopotamuses and dugongs).

In this contribution, we suggest that both geodispersal and rafting were involved in the colonization of Madagascar. In our reconstruction, dispersal was facilitated in the Early Oligocene by the spread of mangrove forest seeded by floating propagules ([Wang *et al.*, 2019](#)). Cosmopolitan mangroves would have facilitated the dispersal of forest birds and mammals ([Masters *et al.*, 2021](#)). Spiders [e.g. *Nephilengys* = *Nephila* ([Kuntner & Agnarsson, 2011](#))], birds [ibises, herons, pigeons, kingfishers, batises (sister group to Malagasy endemic Vangidae), paradise flycatchers, wagtails, sunbirds, bulbuls], primates, carnivorans, rodents and hippopotamuses all occupy mangroves today ([Semesi, 1992](#); [Taylor *et al.*, 2003](#); [Kiwango *et al.*, 2015](#); [Ayanlade & Drake, 2016](#); [Gardner, 2016](#); [Robinson *et al.*, 2017](#); [Dawson *et al.*, 2020](#); F. Génin, pers. obs.). Elephants, on the other hand, are not mangrove residents, although they may visit such areas temporarily. African elephants (*Loxodonta*) form large social groups that roam widely across savanna woodlands, with a special preference for mopane vegetation ([Skinner & Chimimba, 2005](#)). Unlike hippopotamuses, they are very competent swimmers; nevertheless, the socio-ecological differences between hippopotamuses and elephants mean that hippopotamuses were able to spread to Madagascar via the Late Miocene land bridge, while

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elephants, to use [Simpson's \(1940\)](#) words, were 'not holders of tickets'.

Crocodyles are also known to be capable of swimming long distances in sea water using islands as stepping stones ([Campbell et al., 2010](#)). Three crocodyliforms have been found on Madagascar, the oldest of which, *Simosuchus clarki*, a diminutive, snub-nosed form was dated around 66 Mya ([Buckley et al., 2000](#)). Its closest known relatives derive from the Late Cretaceous of Libya ([Turner & Sertich, 2012](#)), suggesting a colonization of Madagascar across the first emergence of the Davie Ridge land bridge. At least two other crocodylian lineages probably arrived on Madagascar during periods of discontinuous land connection with Africa, during the Oligocene [*V. robustus*, the extinct horned crocodile ([Hekkala et al., 2021](#))] and the Late Miocene (*Crocodylus niloticus*, the extant Nile crocodile). [Hekkala et al. \(2021\)](#) estimated that the divergence between *Crocodylus* and *Voay* occurred between 32.1 and 18.8 Mya, which could have been commensurate with the presence of the Eocene-Oligocene land bridge. *Crocodylus niloticus* is conspecific with the African Nile crocodile, and may have colonized the island alongside the hippopotamuses.

DOES THE ISLAND RULE APPLY TO MADAGASCAR?

Despite episodes of connection, Africa and Madagascar developed very distinct biotas owing to a combination of different histories and climates. Madagascar is considerably wetter than Africa. Within the same range of latitudes, Africa has a true desert (the Namib) and has little forest, whereas Madagascar is extremely woody and has moist evergreen forest similar in physiognomy to the rainforest of central Africa, but at much higher latitudes (reaching the tropic in the south-eastern littoral forest). The presence of large browsers, grazers and mixed feeders is not sufficient to develop extensive grasslands under equatorial climatic conditions; for instance, the West-Central African rainforest has elephants, forest buffalos and even grassland birds such as lapwings, waxbills and pipits, but all are associated with localized, island-like edaphic grasslands (inselbergs, salty clearings and wetlands).

Our study resolves the controversial origin of Malagasy grasslands ([Humbert, 1927, 1955](#); [Perrier de la Bâthie, 1936](#); [Paulian, 1961](#); [Bossert, 1969](#); [Carlquist, 1974](#); [Burney, 1997](#); [Lowry et al., 1997](#); [Burney et al., 2004](#); [Bond et al., 2008](#); [Willis et al., 2008](#); [Godfrey & Crowley, 2016](#); [Vorontsova et al., 2016](#); [Hackel et al., 2018](#); [Joseph & Seymour, 2020](#); [Salmona et al., 2020](#)). Because Madagascar does not have the moderate climate generally held to explain insular woodiness—in terms of life history—authors have invoked the principle of insular archaism—the dominance of

ancient woody taxa and the rarity of more recently evolved herbaceous plants ([Carlquist, 1974](#); [Whittaker & Fernández-Palacios, 2007](#)). Nevertheless, secondary woodiness appears to apply to Malagasy taxa, such as the Asteraceae, Convolvulaceae, Didiereaceae and Gentianaceae ([Carlquist, 1974](#); [Masters et al., In press](#)), and possibly even the Poaceae [polyphyletic 'bamboos' ([Dransfield, 2003](#); [Hackel et al., 2018](#))]. Our study suggests new interpretations of insular woodiness in general, either as a consequence of phylogenetic disharmony, particularly the absence of large migrating herbivores, or as a by-product of phyletic dwarfing, often observed in insular ungulates that shift from grazing to browsing in woodier habitats ([Lister, 1989, 1996](#); [Weston & Lister, 2009](#)).

We propose that Madagascar evolved three partly extinct, grassy biomes, each associated with a hippopotamus species. *Hippopotamus laloumena* formed large grassy wetlands associated with mangroves, river mouths and coastal lakes; *H. lemerlei* formed grassy forests including formations similar to modern *Uapaca* tapia forest; and *H. madagascariensis* formed mosaics of *Erica* savoka thicket, wetland and grassy forest. This view suggests a new way of approaching the debated issue of the relative roles of climate change and anthropogenic change in the Holocene megafaunal extinction on Madagascar (e.g. [Tofanelli et al., 2022](#)). We propose that many extinct species known from subfossils in Madagascar were parts of co-evolved biomes in which hippopotamuses probably acted as keystone species. This implies that a combination of climatic factors and anthropogenic activity, particularly the introduction of cattle and the use of fire, probably sparked an extinction cascade. Other members of these extinct biomes survived, as revealed by cases of anachronism, particularly in secondary habitats associated with rice cultivation and cattle herding. Future studies should also include information regarding parasites of both plants and animals.

No species is an island, entire unto itself. Emphasis on co-evolution and niche construction provides a powerful tool for the reconstruction of palaeo-environments, based on the cross-validation of information gathered on diverse taxa of plants and animals. Co-evolution is likely to be crucial to successful range expansion and colonization of new areas. Rather than focussing on competition as the most significant interaction among species, exploring organismal interdependence can teach us a great deal about past and future evolution.

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DATA AVAILABILITY

The palaeo-bathymetry files are available on the SEANOE open-data service of Ifremer upon publication.

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