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Research article

The historical origins of palaeotropical intercontinental disjunctions in the pantropical flowering plant family Annonaceae

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ABSTRACT

Geographic isolation of sister taxa in the African and Asian tropics (palaeotropical intercontinental disjunction; PID) is a major biogeographic pattern explained by four competing hypotheses: rafting on the Indian tectonic plate ('Gondwanan vicariance hypothesis'); migration facilitated by a northern mid-latitude corridor of frost-free climates during the Eocene ('boreotropical migration hypothesis'); overland dispersal across Arabia associated with the Miocene Climatic Optimum; and transoceanic dispersal. The explanatory challenges posed by PIDs are addressed here using the pantropical flowering plant family Annonaceae as a study system. Molecular dating and ancestral area reconstructions were undertaken using plastid DNA sequence data (ca. 6 kb) derived from an extensive taxon sampling, incorporating ca. 75% of all genera, with phylogenetically informed sampling of species within genera that are distributed across the African and Asian tropics. Statistical dispersal-vicariance analysis and likelihood reconstructions indicated 12 intercontinental dispersal events between Africa and Asia. All but one of these dispersals were from Africa to Asia. Between 10 and 12 vicariance events were inferred, ranging from the late Palaeocene to the late Miocene, with mean divergence times of seven events in the Miocene. Although migration through the Eocene boreotropics has previously been highlighted as the predominant process underlying intercontinental disjunctions in Annonaceae, our results indicate that post-boreotropical processes have also had a major impact on shaping PIDs. Palaeogeographic reconstructions and the fossil record from the Arabian Peninsula support the plausibility of a hypothesized window of overland dispersal opportunity for lowland tropical forest taxa prior to climate deterioration commencing in the late Middle Miocene, providing an alternative to transoceanic dispersal. The patterns observed underscore the hypothesis that intercontinental floristic exchange, facilitated by both the Eocene boreotropics and the erosion of oceanic and climatic biogeographic barriers between Africa and Asia in the Miocene, had a substantial impact on the assembly of palaeotropical forest floras.

Introduction

The African and Asian tropics, collectively referred to as the Old World tropics or Palaeotropics, comprise about 50% of the world's tropical rain forests (Morley, 2000) and harbour some of the hottest biodiversity hotspots on the planet (Myers et al., 2000). Tropical forest biomes in Africa and Asia are separated by vast expanses of ocean and climatically unsuitable terrain. Associated with this geographical gap in the distribution of tropical forests is the major

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biogeographic pattern of palaeotropical intercontinental disjunction (PID) of tropical forest taxa, i.e. geographical isolation of sister taxa in the African and Asian tropics.

The close floristic relationship between the African and Asian tropics, with numerous disjunct palaeotropical vascular plant taxa, has long been recognized (e.g. Brenan, 1978; Thorne, 1972). Thorne (1972) identified hundreds of genera (e.g. *Canarium*, *Claoxylon*, *Mansonia*, *Nepenthes*, *Syzygium*, *Wrightia*) and several flowering plant families (e.g. Ancistrocladaceae, Dipterocarpaceae, Pandaceae, and Pandanaceae) which show discontinuous ranges between the African (Africa and Madagascar) and the Indian, Malesian or Australasian-Pacific tropics. Molecular phylogenetic analyses have shown that some traditionally recognized taxa showing presumed PIDs are para- or polyphyletic (e.g. Saunders et al., 2011; Sirichamorn et al., 2012; Wang et al., 2012), but many other PIDs at the infrageneric and deeper levels have been shown to represent reciprocally monophyletic groups on either continent. These intercontinental tropical disjunctions are of considerable biogeographic interest as they pose an explanatory challenge, and may provide insights into the formation and erosion of biogeographic barriers and assembly of tropical floras in the past (Givnish and Renner, 2004; Milne, 2006; Thorne, 2004). Four major competing hypotheses on the origin of PIDs can be differentiated (Fig. 1).

The 'Gondwanan vicariance' or 'Indian raft' hypothesis (Fig. 1A)

Distributional disjunction between tropical Africa and Asia has been explained by the sequential break-up of the Gondwanan supercontinent, rafting of biota on the Indian plate, and facilitation of biotic exchange between India and Southeast Asia by convergence and collision of the Indian and Eurasian plates (Conti et al., 2002; McKenna, 1973; Morley, 1998, 2000, 2003; Raven and Axelrod, 1974). Gondwana began to fragment in the Middle Jurassic, with India separating from Madagascar in the Late Cretaceous, 90–85 Ma, and drifting north-eastwards: the centre of the Indian craton moved ca. 6000 km from ca. 30°S in the Late Cretaceous to its current position, 23.5°N (Ali and Aitchison, 2008). The exact timing and mode of collision of India with continental Asia are disputed. Geodynamic models by van Hinsbergen et al. (2012) indicate a collision of an extended microcontinental fragment and continental Asia at approximately 50 Ma, followed by 'hard' continent to continent collision ca. 25 Ma, whereas previous models have indicated collision of India and continental Asia at ca. 35 Ma (Ali and Aitchison, 2008). Dispersal and establishment of floristic elements of Indian origin in Southeast Asia during the middle Eocene, 50–39 Ma, has been hypothesized based on palynological data (Morley, 2003).

Subsequent to the separation of Africa, Madagascar and India, and prior to the collision of India and Asia, some biotic exchange was likely between these areas due to dispersal. Palynological data suggest that dispersal between Africa and Madagascar occurred frequently until the mid-Maastrichtian, ca. 68 Ma (Morley and Dick, 2003). Prior to collision, India may have made a glancing contact with Sumatra, potentially facilitating biotic exchange with Southeast Asia in the late Palaeocene from ca. 57 Ma onwards (Ali and Aitchison, 2008).

The 'Gondwanan vicariance' hypothesis has been advanced for a variety of tropical vascular plant taxa based on macrofossil evidence (Bande, 1992; Bande and Prakash, 1986; Srivastava and Mehrotra, 2013), palynological data (Dutta et al., 2011; Morley, 1998, 2000), fossil resin chemistry (Dutta et al., 2011) and molecular divergence time estimates or phylogenetic relationships (Conti et al., 2002; Dayanandan et al., 1999; Ducousso et al., 2004; Rutschmann et al., 2004).

The 'boreotropical migration' hypothesis (Fig. 1B)

Micro- and macrofossil evidence from numerous localities including the early Eocene London Clay (Collinson, 1983; Reid and Chandler, 1933) and the middle Eocene Clarno Formation in north-central Oregon (Manchester, 1994) indicates the presence of an extensive frost-free and humid climate belt in the northern mid-latitudes, the boreotropics (Wolfe, 1975), during a warm phase peaking in the Late Palaeocene-Early Eocene thermal maximum, ca. 52 Ma (Zachos et al., 2001). The boreotropics harboured closed tropical aspect rain forests comprising various plant lineages which have been characterized as megathermal, i.e. frost-intolerant and restricted to tropical climates (Morley, 2000; van Steenis, 1962). Climate deterioration in the late Eocene, and a drastic temperature drop at the Eocene-Oligocene boundary, ca. 34 Ma, resulted in expansion of vegetation adapted to drier and colder climates in large parts of Eurasia and Northern America, disrupting the northern megathermal forest belt (Collinson, 1992; Wolfe, 1992). It has been hypothesized that the boreotropics facilitated intercontinental exchange of tropical biota in the Palaeocene and Eocene, not only across northern mid-latitudes, facilitated by land bridges that connected Laurasian fragments (Brikiatis, 2014), but also between the northern mid-latitude and equatorial megathermal forests (Davis et al., 2002; Morley, 2000, 2003, 2007). In the late Eocene and Oligocene, when the boreotropics were disrupted and climates suitable for megathermal vegetation receded to equatorial regions, boreotropical taxa were driven to extinction or retreated towards the equator, forming isolated megathermal forest pockets in southern North America and Europe, and finding refuge in megathermal forests of Southeast Asia (Kubitzki and Krutsch, 1996; Mai, 1995; Morley, 2000, 2003, 2007).

Based on fossil evidence and temporally congruent molecular divergence time estimates, several authors have suggested that the boreotropics and its disruption in the late Eocene-early Oligocene played an important role in shaping current tropical disjunction patterns in several vascular plant lineages by vicariance, i.e. geographic isolation of previously connected populations (e.g. Baker and Couvreur, 2013; Chanderbali et al., 2001; Couvreur et al., 2011a; Davis et al., 2002; Erkens et al., 2009; Muellner et al., 2006; Renner et al., 2001; Richardson et al., 2004).

The 'Miocene geodispersal' hypothesis (Fig. 1C)

Micro- and macrofossil evidence indicates that megathermal elements almost completely disappeared from the northern mid-latitudes after the end of the Eocene cooling event (Morley, 2000, 2007). There is evidence for the persistence of pockets of rainforest and monsoonal forests in Europe and North America, but these were separated from each other and palaeoequatorial rainforests and monsoonal forests in Africa, America and Asia by vast stretches of climatically unsuitable terrain and marine gaps (Morley, 2007). Some studies, however, have suggested that dispersal from Africa to Asia via Arabia may have been feasible for tropical forest taxa during the early to middle Miocene, ca. 23–12 Ma (Cruaud et al., 2011; van Welzen et al., 2014; Zhou et al., 2012). Land connections formed between Africa and Southwest Asia due to the collision of the Afro-Arabian plate with the Iranian and Anatolian plates during this time (Popov et al., 2004; Rögl, 1998), coinciding with a warming phase peaking in the Middle Miocene Climatic Optimum (MMCO), 17–15 Ma (Zachos et al., 2001). Extensive biotic exchange between Asia and Afro-Arabia, i.e. range expansion of independent clades (geodispersal *sensu* Lieberman, 2000), particularly well documented for fossil mammal faunas including primates, has been linked to the formation of these land bridges (Bernor et al., 1987; Kappelman et al., 2003). During the MMCO pockets of subtropical