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Climate change impacts on the biogeography and population status of *Sclerocarya birrea* (A. Rich.) Hochst.: Implications for sustainable conservation

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ABSTRACT

Major climatic changes have continuously influenced the evolutionary dynamics of plant populations throughout Earth's history. Although extensive literature exists on paleobotany and paleoclimatology, these data have been only marginally integrated to reconstruct the historical dynamics of plant species. This study combines paleoclimatic and paleobotanical evidence to reconstruct the biogeographic history and assess the current population status of *Sclerocarya birrea* (A. Rich.) Hochst., commonly known as the afplum tree. *Sclerocarya birrea* is an endemic African tree species valued for its edible fruits and oil-rich seeds. The study covers the period from the Tertiary to the Quaternary and aims to investigate the processes of population emergence, extinction, recolonization, and distribution in response to climatic fluctuations. The literature review focused on the Sahara and its surrounding regions, sub-Saharan Africa, and the Kenya–Tanzania region. Vegetation history was reconstructed using paleoclimatic sequences and paleobotanical record. The findings indicate that successive climatic fluctuations during the Tertiary and Quaternary largely shaped the present-day biogeography of *Sclerocarya birrea* populations. Furthermore, the ongoing aridification that has characterized the Holocene poses an increasing threat to the persistence of the species. Based on these findings, region-specific strategies are proposed to ensure the sustainable conservation of the genetic resources of *Sclerocarya birrea* across the different study areas.

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INTRODUCTION

Since the end of the Cretaceous (145–66 Ma), the African continent has experienced major climatic fluctuations that have profoundly influenced the evolution, distribution, and population dynamics of plant species (White, 1986; Mologni, 2021). These environmental changes have consistently shaped the evolutionary trajectories of vegetation. Consequently, the long-term conservation of plant species depends largely on the resilience of their populations to environmental change. Developing effective long-term conservation strategies therefore requires a comprehensive understanding of the climatic processes that have influenced the history and persistence of plant populations. To investigate these processes, *Sclerocarya birrea* (A. Rich.) Hochst., commonly known as the African plum tree, was selected as a model species. This endemic African plum tree valued for its edible fruits and oil-rich seeds (Hall *et al.*, 2002). According to Faye *et al.* (2011) and Bationo-Kando *et al.* (2016), its fruits provide significant economic opportunities for local communities.

The family Anacardiaceae, to which *S. birrea* belongs, is believed to have originated during the Cretaceous period of the Mesozoic Era, approximately 100 million years ago (Müller, 1981). According to Belfadel (2009) and Abed (2014), the family originated in tropical and subtropical regions. Surprisingly, however, *S. birrea* is absent from the Mediterranean regions of North Africa and the Sahara. Today, the species is primarily associated with savanna and steppe ecosystems (Arbonnier, 2012), with a distribution extending across the Sudanian–Sahelian zone, East Africa, and southern Africa. Nevertheless, isolated populations have been reported on several mountain massifs within the Sahara Desert and on the highlands of East Africa (Quezel, 1954; Fabregues and Lebrun, 1976; Chenoune, 2005).

To date, no study has provided a comprehensive explanation for this fragmented distribution pattern. This raises the following question : How have past climatic fluctuations shaped the biogeographic history and current population status of *Sclerocarya birrea*? The overall objective of this study is to reconstruct the evolutionary history of *S. birrea* populations in response to climatic fluctuations from the Cretaceous to the present. Specifically, the study aims to: (i) assess the effects of climate change on the geographic distribution of the species; and (ii) analyze the influence of climatic changes on the current status of its populations. To achieve these objectives, paleobotanical and paleoclimatic evidence was synthesized using published studies covering the entire distribution range of the species.

SEARCH STRATEGY

The literature review covered the period from the Tertiary to the Quaternary (Table 1). For the bibliographic search, databases such as Science Direct and the Google Scholar search engine were consulted. The search keywords included several combinations of the following terms : “Sahara,” “Southern Africa,” “East Africa,” “Kenya,” “Tanzania,” “West Africa,” “Central Africa,” “Tertiary,” “Quaternary,” “Holocene,” “Pleistocene,” “Miocene,” “Pliocene,” “paleoclimate,” “equatorial zone,” “wildebeest, “paleobotany,” “vegetation,” “Anacardiaceae,” “*Sclerocarya birrea*,” “tropical species,” “mountain massifs,” “highlands,” “origin,” “drought,” “Namib Desert,” and “genetic diversity.” More than 327 documents were examined, but only 33 were used to explain the biogeography of the populations. The selected articles were those that made it possible to reconstruct paleoclimatic sequences and seed dispersal, and to analyze the current status of the populations. To identify the periods that were favorable to the emergence of the African marula tree, two approaches were used: (i) the reconstruction of paleoclimatic sequences from the Paleocene to the Holocene based on findings from paleobotanical studies; and (ii) to characterize the vegetation of the early Holocene, that is, before the last aridification of the Sahara, the vegetation of the mountain massifs was compared with that of the current natural distribution areas of the African marula tree.

Table 1. Different epochs of the tertiary and quaternary geological periods

Periods	Epochs	Duration (Ma)
Quaternary	Holocene	0.012-present
	Pleistocene	2.6-0,012
Tertiary	Pliocene	5.3-2.6
	Miocene	23-5.3
	Oligocene	33.9-23
	Eocene	55.8-33.9
	Paleocene	65.5-55.8

RESULTS

Impact of climatic variations on the biogeography of populations

The Sahara

As a prelude, Table 2 presents the paleoclimatic sequences of the Sahara reconstructed from paleobotanical data. Analysis of this table shows that, since the Paleocene, the Sahara has undergone a succession of major humid, dry, and arid periods that varied according to geographical location. However, according to Maley (2010), when the dominant climatic phase was humid, it was interrupted by several decades of aridity, and vice versa. In the southern Sahara, Millot (1964) reported that the presence of the Meliaceae and Burseraceae families in sedimentary deposits indicates that, from the Paleocene to the Eocene, the region experienced an equatorial climate. At the beginning of the Oligocene, the climate became tropical of the Sudanian type (Maley, 2010). According to Louvet (1971), the dominant woody vegetation during this period consisted of species belonging to the Meliaceae, Sapotaceae, and Fabaceae families. This vegetation was similar to that currently found in the savannas of humid tropical regions. According to Boureau *et al.* (1983), the climate became progressively drier during the Miocene. This is evidenced by the abundance of species belonging to the Fabaceae, Zygophyllaceae, Combretaceae, Bombacaceae, Malvaceae, and Anacardiaceae families. According to Hall *et al.* (2002), most species within these families currently form plant communities associated with *Sclerocarya birrea*. During the Pliocene, the abundance of Miocene plant families in the lower sedimentary layers, together with the scarcity of plant remains in the upper layers, indicates that the climate had become desertic (Maley, 1980). In this regard, Médail and Quézel (2018) reported that several *Acacia* species survived only in mountain massifs and along wadis. During the Pleistocene, the occurrence in the sediments of savanna plant families similar to those of the Miocene indicates that the climate once again became tropical humid to semi-arid. The gradual reappearance of plant families characteristic of arid environments in Holocene sediments, around 6000 BC, marks the beginning of the aridification process that led to the present-day desert.

In the central and northern Sahara, Maley (1996) reported the presence of the Arecaceae and Meliaceae families in Paleocene and Eocene sediments. Schuster *et al.* (2006) inferred that the climate during this period was humid tropical. During the Miocene, from approximately 11 Ma onwards, paleobotanical evidence revealed the presence of Fabaceae, dominated by the *Acacia* group. Based on the current natural distribution of acacias, Zhang *et al.* (2014) concluded that the climate was semi-arid. During the Pliocene, the presence of plant families characteristic of arid environments in the middle sedimentary layers and the scarcity of plant remains in the upper layers indicate that desertification had become established (Kroepelin, 2006). During the Pleistocene, these two regions once again experienced tropical semi-arid to subtropical climatic conditions before the recent desertification that began during the Holocene. It should be noted that, during the various unfavorable climatic periods experienced by the Sahara, some plant species survived only in mountain massifs and along wadis.

Fig. 1 shows the geographical location of the main mountain massifs of the Sahara. According to De Miré and Gillet (1956), observations of the present-day vegetation of these mountain massifs reveal the dominance of tropical species in those located within the Tropic of Cancer. In contrast, Quezel (1954) reported a high proportion of Mediterranean and Saharo-Sindian species in the mountain massifs of the central Sahara, which are situated in the subtropical zone.

Table 2. Paleoclimatic sequences of the Sahara Desert during the Tertiary and Quaternary

Epochs	Southern Sahara	Central Sahara	Northern Sahara
Paleocene	Equatorial	Humid tropical	Humid tropical
Eocene	Equatorial	Humid tropical	Humid tropical
Oligocene	Humid tropical	Humid tropical	Humid tropical
Miocene	Semi-arid tropical	Semi-arid tropical	Semi-arid tropical
Pliocene	Desertic	Desertic	Desertic
Pleistocene	Humid tropical	Semi-arid tropical	Semi-arid tropical
Holocene	Desertic	Desertic	Desertic

Fig. 1. Geographical location of the major mountain massifs of the Sahara (Médail and Quézel, 1965)

Table 3 lists the vegetation types and some tropical woody species recorded on selected mountain massifs of the Sahara. Examination of this table shows the presence of *Sclerocarya birrea* on the mountain massifs of the southern and central Sahara, whereas the species is absent from the mountain massifs of the northern Sahara.

The Sahara continuums

For the African Mediterranean fringe, located in the subtropical zone, Ballais *et al.* (1996) reported the presence in Miocene and Pliocene sediments of several Fabaceae, Zygophyllaceae, and Anacardiaceae families. This type of vegetation is similar to that currently found in the savannas of semi-arid tropical regions. At the end of the Pleistocene, according to Aouraghe and Palevol (2006), climatic conditions became Mediterranean with the occurrence of frost at high elevations. Consequently, considering the current distribution range of savanna species, several populations probably disappeared from the mountain massifs that may have served as refugia. During the Holocene, the climate remained Mediterranean. This is evidenced by the presence of Mediterranean plant species belonging to the Pinaceae (pines) and Fagaceae (oaks) families. For the Sudanian–Sahelian region, Maley (2013) reported that the succession of paleoclimatic sequences followed the same pattern as that of the southern Sahara. However, during the Holocene, climatic conditions became tropical semi-arid. The dominant vegetation consisted of savannas and steppes, characterized by the presence of semi-arid Fabaceae, Zygophyllaceae, Combretaceae, Bombacaceae, Malvaceae, and Anacardiaceae families.

Southern and Southern African regions

In southern Africa, De Ploey (1968) reported that from the Paleocene to the Early Miocene, the climate was arid and, at times, desertic. Under these

conditions, savanna and steppe species could not survive. According to Pickford and Senut (2003), from approximately 17 Ma onward, southwestern Africa also became arid. However, during the Middle Miocene, marked climatic heterogeneity led to the emergence of a wide variety of ecological niches. According to Moreau (1952), this situation accelerated the evolution of the Spondiadeae, the tribe to which *Sclerocarya birrea* belongs. Like the Sudanian–Sahelian region, southern Africa currently harbors numerous populations of the *Sclerocarya birrea* subsp. *caffra*.

Table 3. Vegetation types and selected tropical plant species occurring in the mountain massifs of the Sahara

Sahara regions	Mountain Massifs	Vegetation types	Selected tropical plant species recorded
Southern Sahara	Adrar des Iforas (De Miré and Gillet, 1956; Sidyenne, 1996)	Tropical (>50%) Saharo-Sindian Mediterranean	Various species of the genus *Acacia*, *Andansonia digitata*, *Anogeissus leocarpus*, *Balanites aegyptiaca*, *Calotropis procera*, *Ziziphus mauritiana*, *Ziziphus mucronata*, *Tamarindus indica*, *Sclerocarya birrea*
	Aïr (De Miré et Gillet, 1956)	Tropical (>56%) Mediterranean Montane Cosmopolitan Saharan	*Acacia seyal*, *Balanites aegyptiaca*, *Calotropis procera*, *Anogeissus leocarpus*,*Tamarindus indica*, *Boscia salicifolia*, *Sclerocarya birrea*
Central Sahara	Tibesti (De Miré *et al.*, 1957)	Tropical (>50%) Saharo-Sindian, Mediterranean	*Acacia seyal*, *Acacia nilotica*, *Acacia raddiana*, *Balanites aegyptiaca*, *Calotropis procera*, *Sclerocarya birrea*
	Hoggar (Quezel, 1954; Chenoune, 2005)	Tropical Saharo-Sindian, Mediterranean (>50%)	*Balanites aegyptiaca*, *Tamarindus indica*, *Calotropis procera*, *Ziziphus mauritiana*, *Sclerocarya birrea*
	Tassili (Quezel, 1954)	Saharo-Sindian	Absent
Northern Sahara	Atlas (Desanges et Riser, 1989)	Mediterranean	Absent

The Kenya–Tanzania region

The paleoclimatic history of this region has been reconstructed mainly from the paleobotanical record of the Rift Valley. Hirsch and Roussel (2009) reported that from the Paleocene to the Miocene, the climate was humid tropical. According to Axelrod and Raven (1978), during this period, the Kenya–Tanzania region was covered by savanna-type vegetation. Subsequently, according to Coppens (2003), about 8 Ma, the uplift of highland relief resulted in a transition to a tropical semi-arid climate. The vegetation rapidly evolved from wooded savanna to steppe. Considering the current distribution range of *Sclerocarya birrea*, this period was likely favorable for the expansion of its populations.

Impact of climate change on the current status of populations

Across the entire distribution range of *Sclerocarya birrea*, the recurrence of severe droughts over the last five decades in the Sahel (Sircoulon, 1984), East Africa (Provost, 2023), and southern Africa (Dudley *et al.*, 2001; Aunthony, 2023) is an indicator of the ongoing aridification that began during the Holocene. This process has affected the current status of the species' populations. However, the extent of its impact varies among regions. In the Sahara, populations confined to mountain massifs are of medium size, similar to those occurring in the Sahelian steppes (De Miré and Gillet, 1956). However, these populations are highly fragmented and geographically isolated from one another (Sidyenne, 1996). In the Sahel, populations are characterized by a discontinuous spatial distribution. According to Diallo *et al.* (2000), most populations occur in an uneven pattern, either as bands along temporary watercourses or as concentric formations on lower glacis. Only a few isolated trees remain on the middle glacis. Such a spatial distribution tends to increase the geographic isolation of populations. Specifically, in the Horn of Africa, Le Gouriellec (2022) reported high tree mortality, including individuals of *Sclerocarya birrea*. In East Africa, particularly in the Kenya–Tanzania region, the climate is becoming increasingly arid (Provost, 2023). This has resulted in high mortality of *Sclerocarya birrea* trees, leading to

a contraction of the species' natural distribution range. Currently, most African plum tree populations are confined to the highlands (Muok *et al.*, 2011). In southern Africa, populations of *Sclerocarya birrea* subsp. *caffra* are similar to those of *S. birrea* subsp. *birrea* in the Sahel. They consist of medium-sized populations with low population density. However, the recurrent droughts that began in the 1980s continue to affect the region and threaten these populations with extinction (Dudley *et al.*, 2001). Moreover, riverbanks, which may serve as potential refugia for *Sclerocarya birrea* under extreme arid conditions, are becoming increasingly dry. For example, Aunthony (2023) reported extensive mortality of trees belonging to various plant species along rivers in the Hwange Reserve, Zimbabwe. A similar situation is observed in the Namib Desert, where permanently dry riverbeds are bordered by tree graveyards composed mainly of *Acacia* species.

DISCUSSION

Based on the paleoclimatic sequences, although the evolutionary history of the Anacardiaceae family dates back to the Cretaceous, that of African plum tree (*Sclerocarya birrea*) populations appears to have begun during the Miocene. In this regard, Hall *et al.* (2002) reported that a species named *Sclerocaryoxylon chiraguii*, described by Biondi (1981) from sedimentary deposits as being closely related to *Sclerocarya birrea*, appeared approximately 15 Ma ago. From this observation, *Sclerocaryoxylon chiraguii* may represent the ancestral lineage that evolved in response to successive environmental changes, giving rise to present-day *Sclerocarya birrea*. The paleoclimatic record indicates that specific periods and regions were favorable either to the expansion or to the extinction of African plum tree populations.

In the Sahara, during the Pliocene arid phase, many populations that had emerged during the Miocene are thought to have disappeared, surviving only in mountain massifs (De Miré and Gillet, 1956; Quezel, 1954), where they continued their evolution. These mountain massifs likely served as the source areas for recolonization during the humid phase of the Pleistocene. With the onset of Holocene aridification, populations progressively declined once again and today persist only within these mountain massifs. These areas therefore constitute climatic refugia in the Sahara Desert, from which recolonization could potentially occur should humid conditions return. The ecological importance of these refugia, which function as natural gene reservoirs, depends on maintaining a high level of genetic diversity to avoid evolutionary dead ends (Leppik, 1956). In this context, based on the findings of Diallo *et al.* (2006) regarding the androdioecious breeding system of the species and considering the fragmented distribution of populations, balanced sex ratios are likely to be critical for long-term population survival. Consequently, germplasm conservation should rely on integrated management strategies aimed at enhancing the genetic diversity of populations through the action of seed dispersers.

Despite repeated extinction and recolonization events, no African plum tree populations have persisted along the African Mediterranean fringe. A plausible explanation is that the species occurred there during the Pliocene, when climatic conditions were tropical. During the Pleistocene, however, the climate became Mediterranean, resulting in population extinction. At that time, the mountain massifs that could have acted as refugia became covered by frost. These new environmental conditions likely caused the complete disappearance of the populations. This finding further highlights the fundamental role of refugia in the recolonization dynamics of natural distribution ranges.

The Sudanian–Sahelian region and the Horn of Africa are the two areas adjacent to the Sahara that currently harbor African plum tree populations. However, their present-day spatial organization into fragmented and increasingly geographically isolated subpopulations (Diallo *et al.*, 2020) suggests that they may be moving toward extinction if Holocene aridification continues to expand over time and space. According to Nanson (2004), such population fragmentation is a major

driver of genetic bottlenecks. Consequently, conservation efforts should include both in situ conservation through the proactive management of refuge habitats along watercourses and *ex situ* conservation through the establishment of botanical gardens and irrigated plantations.

In East Africa, particularly within the Kenya–Tanzania region, the predominance of populations on the highlands is indicative of the continued progression of Holocene aridification. Nevertheless, under conditions of extreme aridity, these highlands may serve as potential climatic refugia, similar to the mountain massifs of the Sahara. Unlike the Saharan massifs, however, these populations already benefit from extensive interpopulation gene flow (Kadu *et al.*, 2006), promoted by the large seasonal migrations of wildebeest, which act as important seed dispersers of *Sclerocarya birrea*. Based on the findings of Hamrick and Godt (1996) and Diallo *et al.* (2007), who demonstrated that genetic diversity is the primary factor determining population persistence in changing environments, African plum tree populations in this region are likely to be maintained over the long term.

In subequatorial Africa, the semi-arid environments of the Miocene were likely favorable for the emergence and expansion of *Sclerocarya birrea* populations. At present, as in East Africa and the Sudanian–Sahelian belt, Holocene aridification continues throughout the region. However, the severe drying of potential refugia located along watercourses represents a major threat to populations of *Sclerocarya birrea* subsp. *caffra*. Under these circumstances, ex situ germplasm conservation through irrigated production plantations and botanical gardens appears to be the most appropriate conservation strategy.

CONCLUSION

At the end of this study, it can be concluded that paleoclimatic fluctuations have shaped the history of African plum tree (*Sclerocarya birrea*) populations through successive phases of emergence, extinction, and recolonization. Consequently, the climatic changes that occurred during the Tertiary and Quaternary played a decisive role in the evolutionary dynamics of the species' populations. The findings of this study provide a scientific basis for developing conservation strategies aimed at preserving *Sclerocarya birrea* populations in the face of the ongoing Holocene aridification, which continues to affect the species' distribution range.

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