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REVIEW

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The puzzling ecology of African Marantaceae forests

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Abstract

Marantaceae forests are tropical rainforests characterized by a continuous understory layer of perennial giant herbs and a near absence of tree regeneration. Although widespread in West-Central Africa, Marantaceae forests have rarely been considered in the international literature. Yet, they pose key challenges and opportunities for theoretical ecology that transcend the borders of the continent. Specifically, we ask in this review whether open Marantaceae forests and dense closed-canopy forests can be considered as one of the few documented examples of alternative stable states in tropical forests. First, we introduce the different ecological factors that have been posited to drive Marantaceae forests (climate, soil, historical and recent anthropogenic pressures, herbivores) and develop the different hypotheses that have been suggested to explain how Marantaceae forests establish in relation with other vegetation types (understory invasion, early succession after disturbance, and intermediate successional stage). Then, we review the underlying ecological mechanisms that can explain the stability of Marantaceae forests in the long term (tree recruitment inhibition, promotion of and resilience to fire, adaptive reproduction, maintenance by megaherbivores). Although some uncertainties remain and call for further empirical and theoretical research, we found converging evidence that Marantaceae forests are associated with an ecological succession that has been deflected or arrested. If verified, Marantaceae forests may provide a useful model to understand critical transitions in forest ecosystems, which is of particular relevance to achieve sustainable forest management and mitigate global climate change.

KEYWORDS

Congo Basin, disturbance, multiple stable state, open-canopy forest, tropical rainforest dynamics

Giant herbs from the Zingiberales are an important component of African forests and often occur in such abundance as to form a distinguishable forest type with a reduced tree canopy, commonly known as 'Marantaceae forests' (Figure 1; De Foresta, 1990; Maisels, 1996). Marantaceae forests are widespread in West-Central Africa, from Ivory Coast to the Democratic Republic of Congo (Figure 2). They usually occur as relatively small patches but may exceed thousands of km² in Central Africa (Rollet, 1964; Letouzey, 1985; De Foresta, 1990; Maley, 1990; Doumenge, 1992; Gillet, 2013).

Besides being widely distributed, Marantaceae forests have far-reaching implications for ecosystem goods and services. The use of giant herbs by humans is ubiquitous in central African material culture. Various Marantaceae species provide major forest products used by households and make important contributions to the financial needs of the poorest people (Koto-te-Nyiwa Ngbolua et al., 2016; Sah et al., 2021). Indeed, the leaves of giant herbs are traditionally used for packing food, as medicine, as trading items, to build the houses of indigenous people and sometimes as food (Dhetchuvi and Diafouka, 1993;

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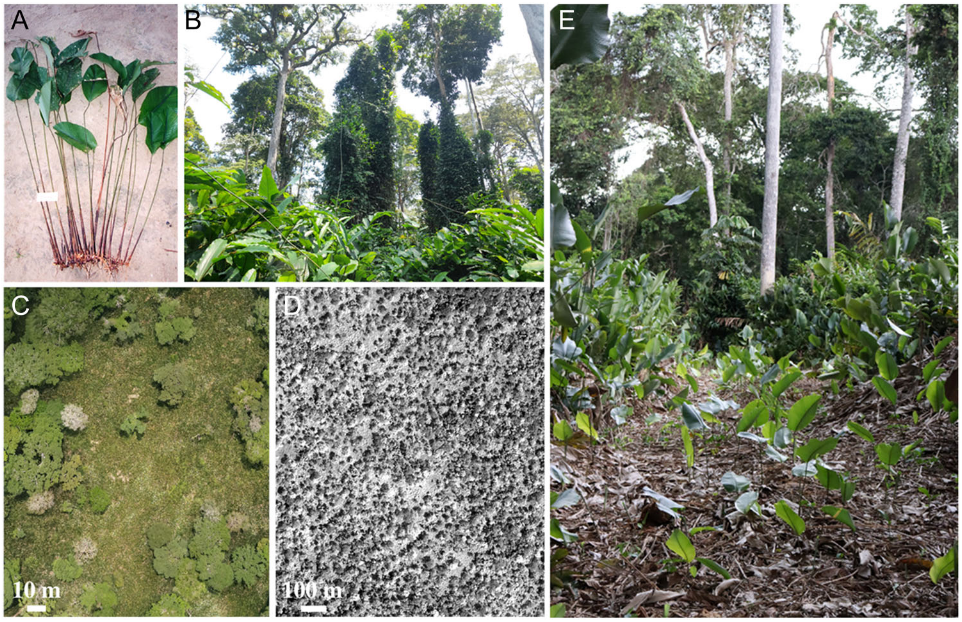

FIGURE 1 (A) Photograph of the whole-plant structure of a *Megaphrynium macrostachyum* individual excavated in the Central African Republic. The label in the photo is approximately 10 cm across. Used from Brncic (2003); (B) Photo of an open Marantaceae forest from the Northern Republic of Congo viewed from the ground. The understory is dominated by *M. macrostachyum*, *Aframomum* spp. and *Haumania liebrechtsiana*. *Haumania liebrechtsiana* is a vine form climbing along the trunk of large trees in the background; (C) Drone image of an open Marantaceae forest photographed in 2022 in the Northern Republic of Congo; (D) Landscape structure of an open Marantaceae forest revealed by a Pléiades image acquired in 2022 in the Northern Republic of Congo; (E) Emergence of a monotypic stand of *Megaphrynium macrostachyum* on a skid trail in the Northern Republic of Congo.

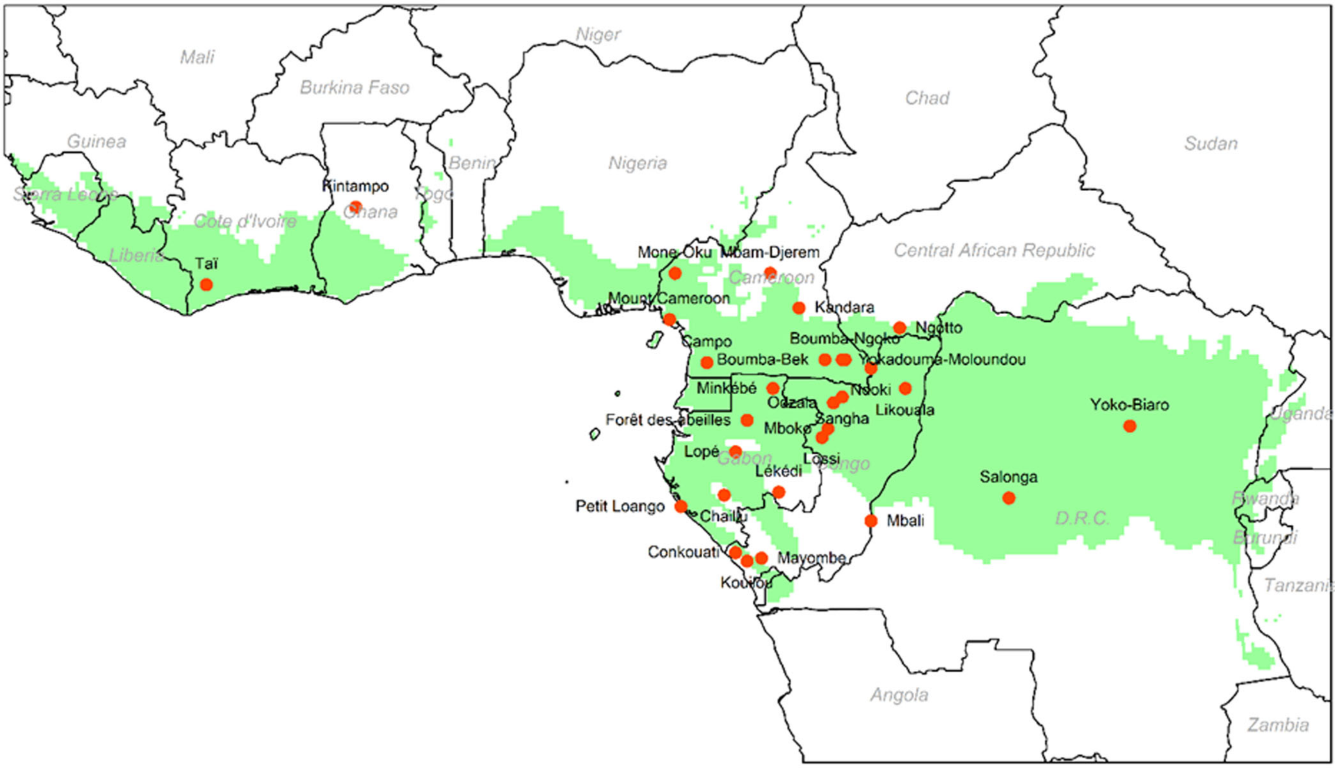

FIGURE 2 Marantaceae forest sites cited in the literature (red points; references provided in Appendix S1) within the West-Central African rainforest matrix (green area).

Hattori, 2006). The leaves are widely traded inside national borders (Koto-te-Nyiwa Ngbolua et al., 2016) but they are also used to pack cassava products, which are then marketed to Europe and North America (Tabuna, 1999). However, at the ecosystem scale, due to their lower tree density and floristic diversity, Marantaceae forests are likely to provide fewer timber products and less diversified non-timber forest products (e.g., nuts, berries, seeds, medicinal plants) than dense mixed forests. The low tree density of Marantaceae forests also means a lower level of carbon sequestration. As illustrated in this review paper, Marantaceae forests are also unique in that they provide a valuable framework for understanding how exogenous forcings in conjunction with ecological feedback can lead to alternative forest types coexisting over the long term (dense mixed-species forests versus Marantaceae forests; Tovar et al., 2014).

Marantaceae forests can exhibit a wide variety of structures and compositions. Here, we use a broad definition covering any lowland tropical rainforest characterized by a dense and continuous understory layer of perennial giant herbs belonging to the Zingiberales (Figure 1). These giant perennial herbs, usually with rhizomatous root systems and densely branched (Figure 1A), may reach a density of more than 10 stems/m^2 (Brugière et al., 2000; Kouka, 2004). They are described as giant because they can reach up to 5 m high (White and Abernethy, 1996), and even more for species with a vine growth habit, which can form 'climber towers' densely draping scattered emergent trees (Figure 1B). They belong to the Marantaceae, Zingiberaceae, and Costaceae (Zingeribales) and, to a lesser extent, to the Commelinaceae (Commelinales) (Table 1). The composition and relative abundance of these giant herb communities vary across biogeographic regions and more locally along a canopy openness gradient. For example, in the Northern Republic of Congo, Marantaceae species such as *Haumania danckelmaniana*, *Sarcophrynium schweinfurthianum*, or *Ataenidia conferta* are associated with a continuous tree canopy cover whereas *Megaphrynium macrostachyum* or *Haumania liebrechtsiana* are characteristic of open to very open forest canopies (Gillet, 2013).

When abundant, these giant herbs result in a significant tree regeneration deficit favoring an open-canopy cover (which can be as low as 20%; Rollet, 1964; White et al., 1995; Lejoly, 1996; Figure 1D) with few medium to large sized trees (>20–30 m high; Hecketsweiler et al., 1991; Figure 1C). Marantaceae forests thus often display a relatively low basal area (only 10 m^2/ha in some cases; White, 1992; Fay, 1997; Brncic, 2003; Gillet, 2013), floristic diversity (Letouzey, 1968; Kouka, 2002; Kimpouni, 2017), and number of timber species (CTFT, 1972; Gillet, 2013). Tree species occurring in Marantaceae forests seemingly belong to the same regional species pool as that of surrounding forests but with a higher

TABLE 1 Main giant herb taxa composing 'Marantaceae forests' (adapted from Gillet, 2013).

Family	Genus	Species	Habit
Commelinaceae	*Palisota*	*ambigua* C.B.Clarke *hirsuta* K.Schum. ex C.B.Clarke *schweinfurthii* C.B.Clarke	Herb with branched erect stems
Costaceae	*Costus*	*lucanusianus* J.Braun & K.Schum.	Herb with unbranched erect stems
Marantaceae	*Ataenidia*	*conferta* (Benth.) Milne-Redh.	Rosulate herb (when sterile), branched (when fertile)
Marantaceae	*Halopegia*	*azurea* K.Schum.	Rosulate herb
Marantaceae	*Megaphrynium*	*macrostachyum* (Benth.) Milne-Redh.	Rosulate herb
Marantaceae	*Sarcophrynium*	*brachystachyum* K.Schum. *schweinfurthianum* (Kuntze) Milne-Redh.	Herb with unbranched erect stems
Marantaceae	*Haumania*	*danckelmaniana* (J.Braun & K.Schum.) Milne-Redh. *liebrechtsiana* (De Wild. & T.Durand) J.Léonard	Vine
Marantaceae	*Hypselodelphys*	*violacea* (Ridl.) Milne-Redh.	Herb with "bamboo-like" shoots or vine
Marantaceae	*Trachyphrynium*	*braunianum* Baker	Herb with "bamboo-like" shoots
Marantaceae	*Marantochloa*	*purpurea* (Ridl.) Milne-Redh.	Ramose erect herb
Zingiberaceae	*Aframomum*	*angustifolium* K.Schum. *giganteum* K.Schum. *subsericeum* K.Schum. *thonneri* De Wild.	Herb with unbranched erect stems
Zingiberaceae	*Renealmia*	*cincinnata* Baker *macrocolea* K.Schum.	Herb with unbranched erect stems

proportion of light demanding and deciduous trees and a lower proportion of shrub species (Letouzey, 1985; Gillet, 2013).

Little research has focused on the ecology of Marantaceae forests and the conditions of their establishment and maintenance. Yet, the origin of Marantaceae forests has long puzzled foresters and forest ecologists. For instance, in one of the first mentions of Marantaceae forests in the literature, Aubréville (1932) noticed that 'under the sparse and low layer of the old growth forest, there is a low shrubby and herbaceous thicket where Marantaceae plants are exuberant, as if the usual understory of these forests had been cut or burnt and the floor had thus been invaded by the large herbaceous monocots' (translated from French by the authors). Even more intriguing is that the few available studies suggest that Marantaceae forests are extremely stable over time (Brncic, 2003; Gillet, 2013; Tovar et al., 2014; Cuni-Sanchez et al., 2016), some of them possibly dating back over two millennia (Brncic, 2003; Gillet, 2013). This raises questions about the ecological mechanisms responsible for the potential stability of Marantaceae forests.

This long-term persistence has motivated the assumption that Marantaceae forests could be an alternative stable state, i.e., a vegetation community arising from a succession that has been deflected or arrested, to dense mixed-species forests in the Congo Basin (Tovar-Ingar, 2015). Since its introduction into ecology (Lewontin, 1969), 'alternative stable state' or 'alternative stable equilibrium' has become an influential concept (Soto and Puettmann, 2020). It has evoked a lot of attention by both theoreticians and empiricists and stimulated a large body of research activities. Alternative stable states occur when ecosystems shift discontinuously from one stable state to another as environmental parameters cross a critical ecological threshold, sometimes referred to as 'tipping point' (Suding et al., 2004). Such ecosystems are then subject to catastrophic reorganization either in response to changing environmental conditions or to severe disturbance. Alternative stable state dynamics found a particular resonance in lake ecosystems, but the theory has also been documented in a variety of other ecosystems such as rivers, oceans, and woodlands (Didham et al., 2005; Scheffer, 2020). For instance, a fire-forest feedback where the post-disturbance vegetation may generate positive feedbacks with fire to perpetuate compositional changes can lead to the existence of alternative stable states (Petraitis and Latham, 1999).

While giant herbs of the order Zingiberales are present in all tropical forests, they never reach, to our knowledge, such a high density and impact on forest structure, as found in African Marantaceae forests. However, there are several other examples of tropical forests dominated by non-tree life forms including lianas, bamboos, palms, and grasses that have also been posited to be able to arrest succession in a similar way (see several examples in Soto and Puettmann, 2020). For instance, in French Guiana and Panama, positive feedbacks between liana infestation and tree fall gaps may lead to an alternative successional pathway, whereby lianas maintain the system in a low-canopy state for many years (Schnitzer et al., 2000; Tymen et al., 2016). In Uganda, plants from the Acanthaceae family invade disturbed forests and suppress tree regeneration through positive interactions with elephants (Lawes and Chapman, 2006). In Bolivia, tropical dry forests co-exist with a less densely wooded formation whose understory is highly invaded by pyrophilic alien grasses, which would be maintained by fire and selective logging (Veldman et al., 2009). Finally, in the Chilean Andes, selective logging leads the understory to be dominated by dense thickets of native bamboos in the genus *Chusquea* (Poaceae), which has been shown to arrest succession by preventing regeneration of *Nothofagus* (Fagaceae) forests (Soto et al., 2019). These few examples illustrate that if arrested forest succession or alternative forest states are often associated with disturbances that trigger a dominance of non-tree life forms, the main ecological mechanisms, or the nature of the disturbance in play, may differ among systems.

The regional importance of Marantaceae forests is reflected in a large body of gray literature (e.g., reports, unpublished studies, dissertations) but, despite representing a fascinating model for ecological research, this peculiar forest type has so far been overlooked in international academic publications (e.g., a Web of Science search using 'marantaceae forest*' returns only fourteen published articles as of May 2023). In this paper, we synthesize the existing body of knowledge on the origin and maintenance of African Marantaceae forests. We conducted a bibliographic survey by applying the keywords 'marantaceae forest', 'giant herbs', 'open-canopy forest' and 'sparse forests' in Web of Science and Google Scholar (both in English and French). We included all types of studies (from purely descriptive to experimental). Gray literature was also included as it was found to supply valuable information, often not published elsewhere. The documentation was reviewed until December 2022. We kept close to one hundred references as a basis for this review. First, we review the different ideas that have been brought forward to explain how Marantaceae forests establish. Second, we discuss progress and limitations in our current understanding of the ecological mechanisms that might explain the stability of Marantaceae forests over ecologically relevant timescales. We finally conclude with the most promising research avenues in the dual context of climate and land-use change.

Origin of Marantaceae forests

Role of current climate and soil

The current climate appears of little influence in determining the occurrence of Marantaceae forests as their widespread distribution across the tropical forest region of Central Africa suggests that they are to a certain extent climatically ubiquitous (Figure 2). However, as discussed below, climate history, such as the decline of the strong African monsoon in the Late Holocene rainforest crisis, might have played a significant role in shaping the current distribution of Marantaceae forests.

Marantaceae forests always occur on terra-firma soils, except a peculiar form of flooded forests with an understory of *Trachyphrynium braunianum* (Gillet, 2013). Early observations suggested that local differences in Marantaceae forest composition might be due to soil variation (Gibert, 1984). Fay (1997) suggested that *Megaphrynium macrostachyum* might prefer sandy soils and Gillet (2013) observed that open Marantaceae forests tend to occur on yellow ferralitic soils in a logging concession from the Northern Republic of Congo. In more detailed studies and experiments, Brncic (2003) found that sensitivity to soil conditions actually depends on the giant herb species involved. *Megaphrynium macrostachyum* showed little preference for specific soil types and primarily responded to disturbance (closely associated with canopy openness and soil charcoal abundance). Species that persisted in their smaller, understory form were more associated with soil factors. For example, *Aframomum thonneri, P. brachythyrsa*, and *S. schweinfurthianum* were more abundant on yellowish-brown, sandy soils with lower pH and available water content and *A. conferta* mainly occurred on reddish-brown, clayey soils of high pH and high gravel content. *Haumania danckelmaniana* was most likely to occur in reddish-brown soils without gravel. This suggests that the species able to become large and dominant may be less constrained by abiotic factors. This is consistent with observations by Maisels (1996) and Brugière et al. (2000), who found no evidence for a role of substrate or microtopography on the presence or density of giant herbs.

Main hypotheses underpinning the development of Marantaceae forests

There is no consensus about how Marantaceae forests establish in interaction with closed-canopy forests, but the various suggestions can be summarized as three main hypotheses that are linked to disturbances at different spatial and temporal scales (Figure 3). First, the 'understory invasion' hypothesis proposes that giant herbs can invade closed-canopy forests via gradual takeover of natural individual tree fall gaps, without intense disturbance. Second, the 'early succession after disturbance' hypothesis states that Marantaceae forests develop directly after an intense and large-scale forest disturbance, such as fire, cyclone, or logging, resulting in an abrupt ecosystem shift. Third, the 'intermediate successional stage' hypothesis suggests that giant herbs promote forest encroachment into savannas at the forest–savanna ecotone and thus constitute an indicator of the historical presence of savannas.

At the smallest scale, the 'understory invasion' hypothesis was originally based on the interpretation of a single-date aerial photograph over the Northern Republic of Congo. Rollet

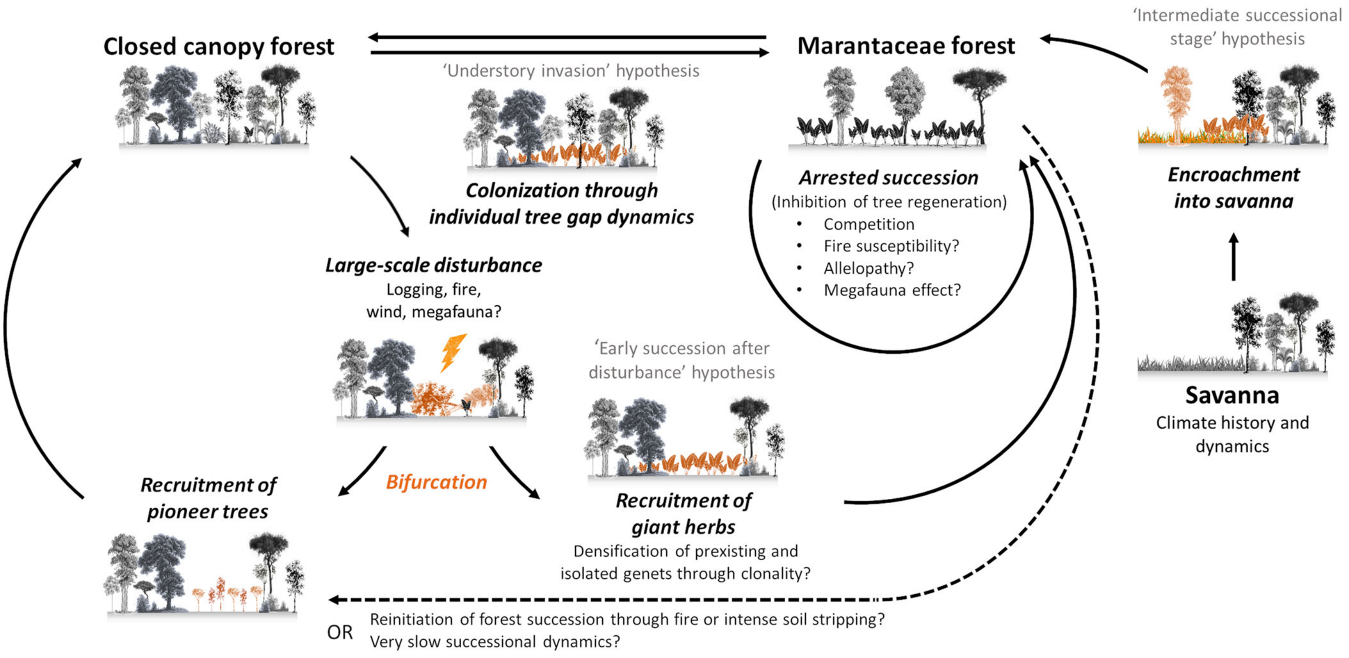

FIGURE 3 Summary of the ecological mechanisms that could be behind the local co-existence of Marantaceae forests and dense mixed-species forests in West-Central Africa. Arrows show the possible evolution of the system in different states. The three main hypotheses underlying the origin of Marantaceae forests are illustrated in the figure: (1) the 'understory invasion' hypothesis, where giant herbs gradually invade closed-canopy forests through natural tree fall gaps, (2) the 'early succession after disturbance' hypothesis, where giant herbs quickly invade the gaps after intense forest disturbances, and (3) 'the 'intermediate successional stage' hypothesis, where giant herbs participate in the encroachment of savannas by forests and return slowly to a dense forest state.

(1964) observed that, overall, what he called 'sparse forests with Marantaceae' ('*forêts clairsemées à Marantacées*') tend to take over closed-canopy forests without apparent anthropogenic influence. Rollet (1964) then proposed that Marantaceae forests result from a process of invasion due to the aggressive nature of giant herbs. Rollet's idea was later supported by De Foresta (1990) who suggested that an understory layer of the climbing *Haumania liebrechtsiana* could become established and self-perpetuating ('auto-succession'; Willie, 2012), such that it inhibits further tree establishment. As closed-canopy forest trees then naturally die, they are not replaced due to the suppressive effect of giant herbs on tree recruitment once they expand in the light gap created by the tree-fall (Figure 3). Brugière et al. (2000) even put forward that Marantaceae forests may be colonizing both savanna and closed-canopy forests given its apparent success in the Northern Republic of Congo.

The 'early succession after disturbance' hypothesis states that Marantaceae forests develop after large-scale disturbances, either recent or historical (Gillet, 2013; Tovar et al., 2014). Canopy opening is indeed expected to stimulate colonization and growth of light-demanding and fast-growing giant herbs (Figure 3). On a recent timescale, dry years with widespread fires, current logging, agricultural activities, or large forest gaps due to extreme storms are expected to promote Marantaceae forest expansion (Bertault, 1992; Favier et al., 2004; Mbayu et al., 2016). More specifically, by felling trees and creating roads, logging activities open the tree canopy and disturb the surface soil horizon, favoring giant herb colonization (Figure 1E). For example, both White et al. (1995) and Gillet (2013) found that the density of giant herbs was more than twice as high in logged than in unlogged places in Gabon and Northern Republic of Congo, respectively, only a few years after logging operations. Similarly, in a survey of fallow fields in Kisangani, in the north central part of the Democratic Republic of Congo, Bebwa (1990) showed that, two years after the forest was logged, the biomass of giant herb species was seven times higher than that of woody species. However, giant herbaceous cover appears to be lower on the main logging trails than in treefall gaps and undisturbed places because their rhizomes are mostly destroyed by intense soil stripping, resulting in a higher tree recruitment (Gillet, 2013). On the contrary, superficial soil stripping tends to stimulate rhizome activity and giant herb colonization (Gillet, 2013). Also, fires that can penetrate the dense forests, especially in very dry years, can lead to the death of 25 to 50% of the adult trees depending on the initial openness of the canopy, and favor the invasion of giant herbs (Dupuy et al., 1997). Finally, many Marantaceae forests co-occur with high densities of charcoal and archaeological artifacts (e.g. pottery shards, polished stone tools), some of which date back to 1000–2500 years ago (Brncic, 2003, Oslisly et al., 2013; Mbayu et al., 2016). This suggests that Marantaceae forests bear witness to ancient disturbances such as slash-and-burn agriculture or large-scale fires fostered by ancient dry climatic conditions (Brncic, 2003; Gillet and Doucet, 2013). The decline of the strong African monsoon in the Late Holocene might have played a significant role in shaping the current distribution of Marantaceae forests, either directly by shrinking lowland forest massifs or indirectly by accelerating the settlement of human populations including Bantu people in the forest zone (Gillet and Doucet, 2013; Oslisly et al., 2013; Garcin et al., 2018; but see Clist et al., 2021 for a contrary view). For instance, Marantaceae forests on Mount Cameroon, a volcano in Cameroon, were interpreted as a signature of forest opening that occurred during a dry period several thousand years ago (Letouzey, 1985; Maley and Brenac, 1998).

Finally, the 'intermediate successional stage' hypothesis involves natural processes of colonization of savannas where climate is more favorable to the spread of forests (Figure 3). In certain regions, giant herbs start to establish at the same time as or after the first pioneer trees such as *Aucoumea klaineana* (Burseraceae), *Lophira alata* (Ochnaceae), *Sacoglottis gabonensis* (Humiriaceae) and sometimes *Musanga cecropioides* (Urticaceae) (Massimba, 1987; De Foresta, 1990; Dhetchuvi and Diafouka, 1993; White et al., 1995; Brugière et al., 2000; White, 2001; Peyrot, 2008; Kamgang et al., 2018). This idea emerged from the observation that Marantaceae forests form a wide buffer strip between savannas and dense forests (e.g., 20 km wide in Lopé National Park, Gabon; White and Abernethy, 1996). According to this hypothesis, Marantaceae forests would be a transient successional stage from savannas to mature dense forests whose dynamics are difficult to perceive since the time needed to go from a Marantaceae forest to a mixed dense forest is supposedly very long (Massimba, 1987; De Foresta, 1990; White, 2001). Using long-term permanent tree surveys, Cuni-Sanchez et al. (2016) showed that Marantaceae forests did not change substantially in structure or diversity over a 20-year period. According to Nasi (1997), it would even take centuries for Marantaceae forests to turn into mature closed-canopy forests.

It is likely that all these hypotheses could be true for different types of Marantaceae forests in different regions. Critical questions for understanding the dynamics of Marantaceae forest include understanding whether Marantaceae forest generated from larger disturbances persist longer than Marantaceae forests generated from smaller disturbances, and how climate might influence the direction and speed of succession.

Ecological mechanisms explaining the stability of Marantaceae forests

Once established, Marantaceae forests may persist from tens to thousands of years (Brncic, 2003; Gillet, 2013; Tovar et al., 2014; Cuni-Sanchez et al., 2016), such that it could be considered an alternative stable state to closed-canopy forests (Tovar-Ingar, 2015; Figure 3). Here we present a detailed analysis of the ecological processes that may explain the long-term persistence of Marantaceae forests. Among potential mechanisms, giant herbs might: (1) inhibit tree recruitment; (2) increase forest susceptibility to fires;

(3) rapidly recolonize disturbed areas via vegetative reproduction; or (4) attract megaherbivores that maintain forest opening and thus giant herb recruitment.

Tree recruitment inhibition

Only a few studies have investigated the nature of interactions between giant herbs and tree seedlings (Brugière et al., 2000; Brncic, 2003; Gillet, 2013; Mbangilwa et al., 2019). Among them, Brncic (2003) developed an in-situ experimental design to disentangle the effects of above- and below-ground competition between giant herbs and trees. The results demonstrated that tree germination rate was similar under dense forest canopy and Marantaceae forests but significantly higher when the aerial part of giant herbs was removed (Figure 4). Using measurements of photosynthetically active radiation, Brncic (2003) showed that light availability below *M. macrostachyum* was of similar magnitude to that found below closed-canopy forest (1–2% of full sun). This result suggests that the canopy of giant herbs might limit tree seed germination to a similar extent as a closed-tree canopy. Moreover, Brncic (2003) showed that seedling survival rate was significantly higher under closed-canopy forests than in presence of giant herbs, or only their root system (Figure 4). However, whether this is due to below-ground competition or allelopathic effects (through the production of one or more biochemicals) remains an open question (Brugière et al., 2000; Brncic, 2003; Gillet, 2013). If allelopathic effects exist, they are likely to be species-specific (Brncic, 2003). Thus, the above-ground and below-ground parts of giant herbs prevent tree seed germination and seedling survival, respectively, contributing to the very low tree regeneration observed in Marantaceae forests. For instance, a recent study reported that the density of woody seedlings in Marantaceae forests of the Northern Democratic Republic of Congo was four times lower than in monodominant *Gilbertiodendron dewevrei* (Fabaceae) forests and six times lower than in mixed forests (Mbangilwa et al., 2019). In the Southern Republic of Congo, Massimba (1987) even estimated that young trees <2 m tall were 100 times less abundant in Marantaceae forests (300 trees/ha) than in dense forests (30,000 trees/ha).

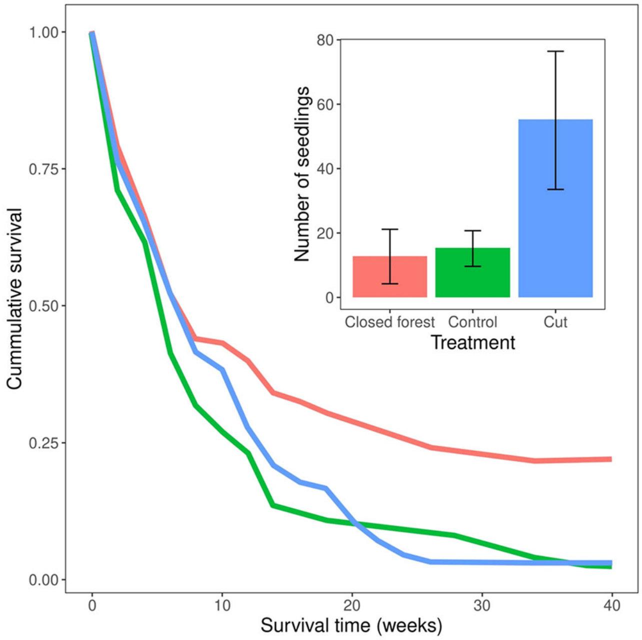

FIGURE 4 Results from an in-situ experiment where tree seed germination and seedling survival were monitored during 40 weeks in three forest types in Central African Republic (adapted from Brncic, 2003). The upper right panel illustrates the total number of seedlings that originated from natural seed rain and the soil seed bank in patches of Marantaceae forests dominated by *Megaphrynium macrostachyum* (referred to as "control" in green), in patches of Marantaceae forests where the aboveground part of giant herbs was regularly cut ("cut" in blue) and in a normal forest understory without giant herbs ("closed forest" in red). The main panel illustrates the cumulative tree seedling survival in the same three treatments during the studied period.

Tree species regeneration might also be weaker in large open Marantaceae forests simply because of the low number of reproductive trees, resulting in a smaller tree seed input than in dense forests. Moreover, the opening of the canopy would be unfavorable to many arboreal animals including small primates and large frugivore birds. Therefore, the scarcity of seed dispersers would possibly aggravate the depletion of tree seedling germination and establishment. However, the number of tree seeds on the ground have been found not to vary along a gradient of giant herb abundance and to be uncorrelated with the number of tree seedlings (Brugière et al., 2000), possibly because of the action of other seed dispersers such as gorillas and elephants. This suggests that the decrease in the number of trees in Marantaceae forests does not arise from a lack of seed potential but rather from the inhibitory action of giant herbs on their germination, but this hypothesis still needs to be further investigated.

Effect of fire

Several authors have suggested that fire events may be a major cause of giant herb expansion and maintenance (Gibert, 1984; Tovar et al., 2014; Mbayu et al., 2016). Tovar et al. (2014) compared fossil charcoal records with phytolith records in sediment cores spanning the last 2500 years in different forest types in Central Africa. They found that, unlike areas currently covered by other forest types, Marantaceae forests were associated with a high frequency of fires (most likely anthropogenic), which created large gaps in which giant herbs may have thrived. Furthermore, the large amount of dry giant herb leaves in Marantaceae forests may be conducive for fire spread while their underground rhizomes might be well protected, allowing for a much faster regrowth than for most trees after the passage of fire (Verhegghen et al., 2016). Major fire events (e.g., following extreme El Niño events) may thus be an important determinant of the persistence of Marantaceae forests. In late January–early February 2016, extensive areas of Marantaceae forests dominated by *M. macrostachyum* and *H. liebrechtsiana* burned in the Northern Republic of Congo. The burned area was estimated to cover ca. 40,000 ha according to the MODIS Burned Area dataset and most of the fires (83%) occurred in Marantaceae forests (Verhegghen et al., 2016; Figure 5). However, the effect of fires on Marantaceae forests remains controversial as it may also reinitiate the successional dynamics and favor dense forest resilience through post-fire recruitment of pioneer trees (Lejoly, 1996). Hence, the effect of fire on the dynamics of Marantaceae forests is still unclear due to a lack of monitoring over a sufficiently long period and the absence of dedicated fire experiments (e.g., combining burnt and unburnt plots) as conducted in African forest–savanna mosaics (Cardoso et al., 2018, 2021).

Adaptive reproduction strategy

Giant herbs are adapted to severe disturbance regime through a high rate of clonality, mostly from their rhizomes (Gillet, 2013). Giant herb vegetative reproduction has been thus assumed by some authors to be a great advantage for the rapid colonization of forest gaps and subsequent range expansion (Brugière et al., 2000; Gillet, 2013; Figure 3). Brncic (2003) showed that *M. macrostachyum* has a high leaf production in gaps, coupled with a decrease in the number of fruits produced. She further showed that *M. macrostachyum* seeds poorly germinate under their own canopy, probably as a consequence of intraspecific competition for nutrients or due to the low light availability. This suggests that vegetative reproduction is the prevailing strategy whenever giant herbs are already dominating. However, even if the rhizome growth rate of giant herbs is poorly documented in the literature, it is likely to be lower than 1 m per year (Brncic, 2003), and thus insufficient to rapidly colonize newly cleared areas where giant herbs previously did not occur. We hypothesize that sexual reproduction is the dominant strategy to colonize new areas, e.g., through zoochory, resulting either in isolated 'dwarf' individuals in closed-canopy forests (Brncic, 2003; J.P. and M.R.-M., personal observations in Northern Republic of Congo) or in seeds that may stay dormant for at least seven months in the soil, as shown for *M. macrostachyum* in the Central African Republic (Brncic, 2003). However, despite a high abundance of *Haumania* spp. in a site from the Northern Republic of Congo, Douh et al. (2018) found a low relative frequency of the species in the soil seed bank (0.1%), suggesting that seed dormancy does not constitute a major waiting strategy (state in which populations are maintained under suboptimal conditions; Kudoh et al., 1999). Thus, the most likely waiting stage under closed canopy is in the form of dwarf genet individuals. For instance, some authors consistently showed that *Haumania* spp. remain undeveloped and free-standing in the undergrowth of dense forests, whereas it is often lianescent, forming dense tangles and vine towers in Marantaceae forests (White et al., 1995). Following a canopy opening, genets would then rapidly form a dense herbaceous canopy through accelerated vegetative reproduction, vertical

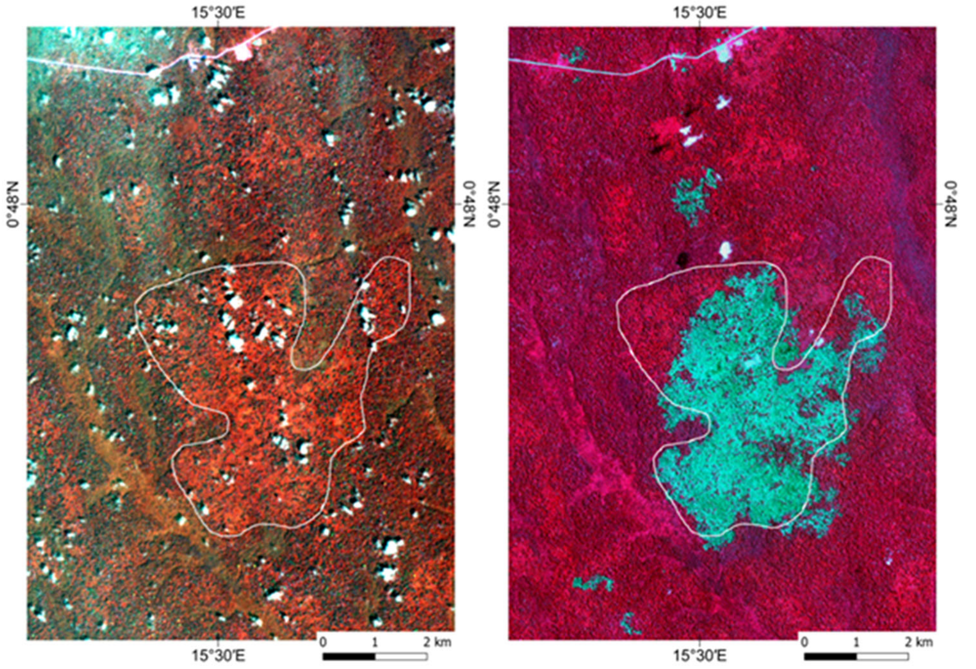

FIGURE 5 Left: open Marantaceae forest delineated in white before a fire (SPOT5 scene acquired on 29-01-2014). Right: after a fire with burnt area appearing in cyan (SPOT7 scene acquired on 04-04-2016). Color composition using the green, red and near infrared bands. This shows that the fire predominantly burned the area of dense Marantaceae forest.

growth, and leaf production, exerting a strong inhibitory effect against tree species. This hypothesis is the opposite of a hypothesis formulated by Kudoh et al. (1999) on the reproductive strategy of a perennial forb native to North America. Interestingly, Ley and Hardy (2016), who genotyped ramets of *H. danckelmaniana* in Eastern Cameroon, reported a predominant outcrossing in an undisturbed and closed-canopy forest and acknowledged that clonality may be much more frequent after disturbance, as observed for woody lianas that also rely on vegetative reproduction to colonize forest gaps faster than tree seedlings after canopy opening (Ledo and Schnitzer, 2014). However, this hypothesis remains to be tested.

Effect of megafauna

Central Africa is characterized by a high diversity and abundance of megafauna, and Marantaceae forests are known to impact several species. Indeed, giant herbs are an important food source for apes and elephants, but also an important nesting area for gorillas (Rogers et al., 1990; Nishihara, 1995; White et al., 1995; van Leeuwe and Gautier-Hion, 1998; Reinartz et al., 2006). They supply food to gorillas and chimpanzees all year round but especially in the dry season, when fruits are scarce (White et al., 1995; Yamagiwa et al., 1995) and they offer resting areas for groups of buffalo (Melletti et al., 2009). However, due to the discontinuous canopy of Marantaceae forests, arboreal primates are half as abundant as in dense forests (Brugière et al., 2000).

Megafauna has a significant impact on forest structure and composition (Smith et al., 2016). However, only a few studies have explored the specific effect of megafauna on Marantaceae forests. The studied effects mainly concern damages on the vegetation, both on trees and on the herbaceous layer, and seed dispersal. A study in Uganda showed that elephants can inhibit tree regeneration, slowing down or even arresting forest succession in previously disturbed sites (Omeja et al., 2014). Brugière et al. (2000) proposed that the same mechanism may take place in Marantaceae forests with elephants actively maintaining large patches of giant herbs by trampling tree seedlings, debarking or breaking trees. In a Marantaceae forest plot in La Lopé, Gabon, 28% of the trees with a diameter at breast height <10 cm were broken by elephants (White et al., 1995). However, the effects of the damage also depend on the density of elephants, and their preference for Marantaceae forests is not clearly established in the literature. In the Central African Republic, Brncic (2003) showed that only 2% of surveyed plots show signs of gorilla or elephant damage to trees and saplings (broken or bent branches or stems and bark damage from rubbing or feeding). The author also mimicked the effect of megafauna by manually flattening *M. macrostachyum* leaves and found that giant herbs grew back to a full canopy cover within a year thanks to a rapid re-sprouting from rhizomes, limiting the temporal windows in which trees have the opportunity to establish. On the contrary, some authors showed that Marantaceae forests were more attractive than other forest types for elephants as they could find shelter from humans in the dense understory. Barnes et al. (1991) showed that elephants tend to avoid forests with open undergrowth in northeastern Gabon, and Beyers (2008) found that they prefer Marantaceae forests and old secondary forests. However, the latter also found that human presence is the most determining factor of elephant densities, and that further research was needed to understand the link between vegetation types and elephant abundance (Beyers, 2008).

Megafauna (elephants, great apes) are also recognized to be effective dispersers of tree seeds that have not been damaged by mastication or digestion in central Africa (Chapman, 1995; Campos-Arceiz and Blake, 2011; Haurez et al., 2015). Megafauna may thus potentially bring seeds from a large diversity of trees into Marantaceae forests. Nevertheless, giant herbs are also well-dispersed by megafauna. For instance, among the 13 major plant species included in the diet of gorillas in Cameroon, five belong to the genus *Aframomum* and 75% of the feeding sites contain seeds of at least one *Aframomum* species (Calvert, 1985). Seeds of *Aframomum* spp. were also found to be among the most frequently occurring seeds in chimpanzee dung (22–43%, depending on the sample sites) in Uganda (Wrangham et al., 1994). Forest elephants are also known to disperse Marantaceae seeds, which were found in 5.7% of elephant dung in Northern Republic of Congo (Blake, 2002).

To conclude, findings across studies have been inconsistent as to whether large mammals are more abundant in Marantaceae forests than in other forest types, whether they disperse more giant herb than tree seeds and whether their action overall promotes Marantaceae forests at the expense of dense forests. The role of megafauna in maintaining Marantaceae forests is thus far from being precisely known.

CONCLUSIONS

This review illustrates that Marantaceae forests may originate and persist through time thanks to temporally discrete and self-maintaining processes occurring at different spatio-temporal scales. Interestingly, we found that many of the ecological factors that have been put forward to drive other tropical forests dominated by non-tree life forms (e.g., tree fall gaps, anthropogenic activities, herbivores, fire) have also been proposed as drivers of Marantaceae forests. Mounting evidence suggests that Marantaceae forests correspond to an alternative stable state or to a successional stage that has been deflected or arrested in the Congo Basin rainforest (Figure 3), even if this hypothesis remains to be tested empirically and theoretically. If validated, it would confirm that Marantaceae forests constitute one of the few examples of multiple stable states within the forest domain (Soto and Puettmann, 2020), and would thus constitute an ideal study case to understand critical transitions in forest ecosystems (Ghazoul et al., 2015).

Because the available literature suggests that giant herbs are pre-adapted to take advantage of disturbances due to human impact and climate change, we predict that Marantaceae forests will expand at the expense of closed-canopy forests (Gillet, 2013; Tovar et al., 2014). In Central Africa, climate change is expected to result in an increase in drought stress and maximum temperature (Réjou-Méchain et al., 2021), which is likely to cause an increase of large-scale fire events. Furthermore, one third of Central African forests is currently experiencing logging activities (Réjou-Méchain et al., 2021), which, combined with exponential human population growth and the resulting expansion of agricultural lands (Ernst et al., 2013), may also foster the expansion of Marantaceae forests. Given the ecological, economic and cultural consequences of such expansion, monitoring and better understanding the dynamics of Marantaceae forests must become an important component of the research agenda.

We specifically identify three priority research areas where much uncertainty still exists: (1) the variation in species composition, but convergence on similar forest structure. To provide a foundation for understanding long-term dynamics, we must first understand how the ecology of individual species of giant herbs (such as the role of abiotic factors and persistence in the understory in the absence of disturbance) influences the likelihood of Marantaceae forest formation and the dominance of certain species, (2) the spatio-temporal dynamics of Marantaceae forests. Here, many insights might be gained by integrating remote sensing and historical ecology approaches to depict the dynamics of Marantaceae forests at large spatio-temporal scales. This may help to test the importance of the current climate regime in determining whether Marantaceae forests are stable or transitory states, and (3) the ecological mechanisms promoting the stability of Marantaceae forests. Combining experimental and mathematical modeling may help identify the main ecological processes and the conditions under which stability may exist. Hopefully, this review will stimulate further interest in exploring these new research directions and raise interest in the understudied but important Marantaceae forest systems.

AUTHOR CONTRIBUTIONS

Conceptualization: R.P., J.P., and M.R-M; Investigation: R.P., J.P., and M.R-M; writing—original draft: R.P., J.P., and M.R-M. with critical input from C.D. and T.B.; writing—review and editing: All authors.

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SUPPORTING INFORMATION

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

Appendix S1. Marantaceae forest sites cited in the literature.

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