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The Amazonian Savannas of French Guiana: Cultural and Social Importance, Biodiversity, and Conservation Challenges

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Abstract

The Amazonian savannas of French Guiana are rare and of high ecological and cultural value but are also highly threatened. They are socioecological systems that have been coconstructed by humans and nature and today form mosaic landscapes along the country's coast. From pre-Columbian raised fields through colonial and Créole uses to contemporary uses, they have been largely shaped and modified by human activities. They are currently threatened by changes in fire regimes, agricultural practices, invasive species, and infrastructure development. Less than 3% are protected, despite their importance for several endangered animal and plant species. A shift is required in the way we think about their conservation to create a new strategy that would be completely different from existing French environmental protection tools and adapted to the complexity of these landscapes.

Keywords

archeology, biodiversity, conservation, French Guiana, savanna, socioecological systems

Introduction

Tropical savannas cover between 15 and 24.6 million km² in South America, Africa, and Asia (Silva & Bates, 2002). A large part of the world's population lives and works in these ecosystems, with key economic uses being the production of both crops and livestock (Sankaran et al., 2005; Scholes & Archer, 1997), and increasingly commercial tree plantations, often with the objective of "reforesting" open areas (Fernandes et al., 2016). Indeed, savanna ecosystems are often targeted for use as, compared with forests, they are considered to be both more easily modified and less "valuable" in their unmodified state. Unsustainable use of these ecosystems has caused them to become increasingly degraded, leading to significant losses of biodiversity and ecosystem services (Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014; Strassburg et al., 2017; Vieira, Ribeiro, & Resende, 2017).

In South America, the largest complexes of tropical savannas are the Cerrado in Brazil, Bolivia, and

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Indeed, studies have already shown that heterogeneity exists in the flora and fauna in different Amazonian savannas, at smaller and larger scales (Barbosa, Campos, Pinto, & Fearnside, 2007; Carvalho & Mustin, 2017; Mustin et al., 2017; Silva & Bates, 2002), and consequently, knowledge and conservation priorities from other Amazonian savannas cannot be simply applied to French Guiana. The "Amazon" savannas of French Guiana in fact fall within the Guiana Shield, a region that is distinct from the Amazon Basin because its rivers flow directly into the Atlantic (Hammond, 2005), and furthermore, French Guiana as a whole represents a center of plant endemism in South America (Prance, 1996). Given all this, it is therefore of particular concern that the Amazonian savannas of French Guiana have not been mentioned in the main reviews of the South American tropical savannas and are absent from the maps in these and other key references (see Figure 1 in Adeney, Christensen, Vicentini, & Cohn-Haft, 2016; Barbosa et al., 2007; Marchant, 2010; Werneck, 2011). Therefore, the objective of this review is to remedy this gap. We provide a description of the Amazonian savannas of French Guiana, including their distribution, history, cultural importance, human use, biodiversity, and conservation challenges. We conclude by discussing the future of these habitats and the ways in which socially just and equitable solutions may be put in place to conserve these unique habitats.

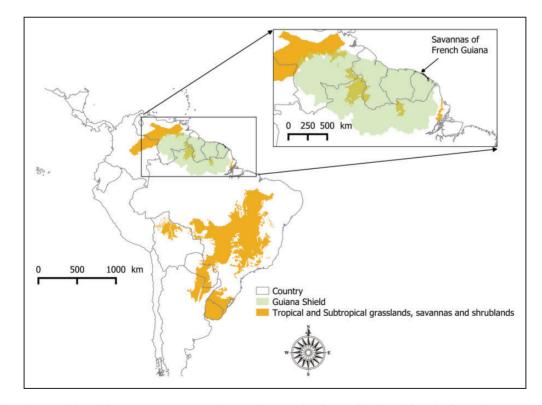


Figure 1. Distribution of South American savannas with inset showing the Guiana Shield and French Guiana's savannas. Adapted from The Nature Conservancy (2008, 2009) terrestrial and freshwater ecoregions accessible at http://maps.tnc.org/. Based on the vegetation map of French Guiana from the ONF Guyane from 2015 (ONF, 2017). The delimitation of the Guiana Shield is based on the fusion of entities 315, 311, 310, and 308 (Amazonas Guiana Shield, Guianas, Essequibo, and Orinoco Guiana Shield) of the freshwater ecoregions (Abell et al., 2008).

The Amazonian Savannas of French Guiana

General Presentation

French Guiana is a French overseas department and thus part of Europe, despite being located in South America. Ninety-seven percent of its territory is covered by one of the least impacted tropical forests in the world, attracting global scientific interest (de Pracontal & Entraygues, 2009; Gond et al., 2011). In contrast, French Guiana's Amazonian savannas, characterized by a complex mosaic of seasonally flooded and terra firme savannas, with varying amounts of woody vegetation (Buzancais, 2018; de Granville, 1986; de Pracontal & Entraygues, 2009; Léotard, 2012; Léotard & Stier, 2013; Stier & de Pracontal, 2015), have received far less research attention, in common with open ecosystems elsewhere in South America and across the world. Although these savannas cover just 251 km² or $\sim 0.3\%$ of French Guiana (Office National des Forêts [ONF], 2017) and thus are some of the rarest environments of the territory, almost 16% of the plants present in the country can be found there (Léotard, 2012; Stier & de Pracontal, 2015). The savannas are part of a mosaic coastal landscape, where waterfront mangroves extend along the Atlantic shore mudflats, replaced further inland by freshwater marshes, seasonally flooded savannas with forest patches, and finally terra firme tropical forest (Figure 2) (de Granville, 1986; Gond et al., 2011; Iriarte et al., 2012; ONF, 2010; Rostain, 2010). The savannas themselves occur on the coastal plain of the Guianas, which stretches for 1,600 km between the Orinoco Delta and the mouth of the Amazon, but which is extremely narrow in French Guiana (5 to 40 km wide—8% of the territory of the department) compared with neighboring countries (up to 180 km wide in western Suriname and eastern Guyana), which could explain the small area covered by the savannas in French Guiana (Figure 2) (de Granville, 1986; Rostain, 2010). Within the coastal plain, narrow and elongated sandy beach ridges called "cheniers" run parallel to the shore. The cheniers are generally tens of meters wide and sometimes over 20 kilometers in length (Rostain, 2010). Despite its small area, the coastal plain also supports 95% of the department's human population (ONF, 2010), with the largest cities and infrastructure concentrations (de Granville, 1986; ONF, 2010;

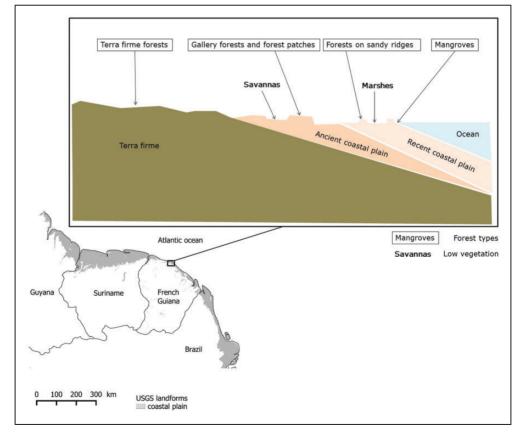


Figure 2. Coastal plain of the Guiana Shield and cross section of the coastal area of French Guiana. Adapted from de Granville (1986) and Rostain (2010). Area covered by the coastal plain was extracted from the USGS maps available at https://www.usgs.gov/. USGS = United States Geological Survey.

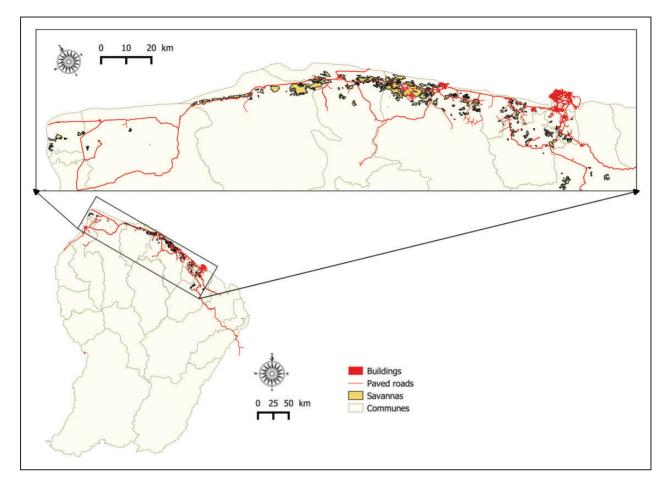


Figure 3. Location of savannas in French Guiana, with inset showing the human influence through the road network and built-up areas. Based on the vegetation map of French Guiana from the Office National des Forêts (ONF Guyane) from 2015 (ONF, 2017), with location of the road network and built-up areas, based on data from the Institut National de l'Information Géographique et Forestière (2018).

Stier & de Pracontal, 2015), making the savannas easily accessible (Figure 3).

Origin and Maintenance

Vegetation cover in the Amazon has not been stable over geological timescales, and successive expansion and retraction of forests has occurred four times over the past 60,000 years, with savannas expanding during dry and cold periods, and tropical forest expanding in warm and humid interglacial periods, like those of the present (Prance, 1996). It is likely that during the Pleistocene, connections existed between savanna blocks north and south of the Amazon, though how these connections were shaped and where they occurred is unclear. Evidence from, for example, distributional ranges of savanna species and patterns of morphological differentiation between populations strengthens the hypothesis that current savanna patches are relicts of a past, more extensive savanna stretching from the Venezuelan Llanos to the Brazilian Cerrado (Barbosa et al., 2007; Prance, 1996; Silva & Bates, 2002; Werneck, 2011). In French Guiana, the coastal savannas were probably once connected to more inland inselbergs (called "*rock savannas*", the same term used for any rocky outcrop in French Guianan Créole), which currently act as refuges for a xeric flora, as do savannas and the forest canopy (de Granville, 1982). More recently, the coastal savannas were also certainly submerged by the ocean about 6,000) years ago (de Granville, 1982).

However, the Amazonian savannas in their current formation, including those of French Guiana, are very much biocultural in nature, having been formed and being in part maintained by a combination of climatic, paleoclimatic, and edaphic factors, but also having been managed and intensively transformed by humans during pre-Columbian and Colonial times, and continuing to be transformed to the present day via herbivore activity, fire, and other human influences (de Granville, 1982, 1986; Marchant, 2010). This is also true for French Guiana's current landscapes and habitats found in coastal savannas, as they have been partially generated by paleoclimatic and edaphic conditions, but also managed and intensively transformed by humans during pre-Columbian and Colonial times, and continue to be transformed to the present day. They are considered to be dynamic ecotones controlled by interactions between climatic and edaphic processes on one hand and disturbance processes on the other, among which fire is just one factor. These processes are categorized into (Beckage, Platt, & Gross, 2009) (a) the niche partitioning *model*, where edaphic conditions (such as access to soil water) favor grasses or trees and (b) the disturbance *model*, where the persistence of savannas is due to any recurrent mechanism that negatively-but noncatastrophically-affects trees. This mechanism is sensitive to long-term variations in disturbance regimes (e.g., frequency of recurring fires). Fire frequency enters into the second model, and if there is no interaction with a partitioning model, the ecosystem will have many stable states (Staver, Archibald, & Levin, 2011): forests without fire on one hand, and many other possible stable states with fire on the other (due to positive and negative tradeoffs between fire, grasses, forest, and savanna trees that will not be described here (Beckage et al., 2009; Hoffman, 2000)).

Before the end-Pleistocene megafaunal extinctions, which were especially massive in South America (Svenning & Faurby, 2017), megafauna were important in savanna functioning in South America (Doughty, Faurby, & Svenning, 2016). Currently, herbivores are a less important factor in the maintenance of savannas in South America compared with comparable African habitats. More broadly in South America, savanna patches may persist in the forest because of environmental conditions such as flooding or poor soils (Barbosa et al., 2007; Prance, 1996; Werneck, 2011); however, in French Guiana, savannas can occur on a wide variety of soils, the composition of which does not explain the savanna habitat type, with the exception of white sands, where highly characteristic short grass savannas, known as campinas are found (Le Fol, 2012; Léotard, 2012; Léotard & Stier, 2013; Stier, 2012; Stier & de Pracontal, 2015). In savannas where the soils are similar to those of adjacent forests, the savannas are maintained by historical and ongoing human interventions, including historical and contemporary fires, pre-Columbian raised fields, colonial polders, and extensive farming systems, as well as recent uses (Prance, 1996; Rostain, 2010). However, the historical and contemporary role of fire regimes remains a subject of wide and unresolved debate which has just begun to be studied (Girault & Silland, 2015; Palisse, 2013; Procopio, 2014; Stier & de Pracontal, 2015).

Cultural Importance and Human Use

Pre-Columbian Raised Fields

Acceptance of the notion that Amazonian landscapes (including savannas) are of a biocultural nature is very recent, coming mainly from the accumulation of data about the impact of pre-Columbian human occupation. Indeed, there is evidence that the first 500 years of the last millennium (1000-1500 AD) were marked by agricultural expansion, with many seasonally flooded tropical savannas of South and Central America transformed into agricultural landscapes through the construction of raised fields (Iriarte et al., 2012; McKey et al., 2014; Rostain, 1991, 2010). These raised fields provided better drainage, soil aeration, and moisture retention; facilitated weeding and harvesting; and likely had increased fertility, thanks to careful management of organic matter, at least over the short term (Iriarte et al., 2012; McKey et al., 2014; Renard et al., 2012; Rostain, 2010). Findings in raised fields in the Congo Basin that are used today confirm these advantages (Comptour, Caillon, Rodrigues, & Mc Key, 2018); they also show that raised fields can have functions beyond agriculture, although this has not been proven for pre-Columbian raised fields.

The extent of this apparently intensive form of human intervention is suggested by widespread vestiges of raised fields, which run over 600 km along the coast of the Guianas, from the Berbice River in Guyana to Cayenne in French Guiana, with at least 30 km² of savannas in French Guiana alone still bearing vestiges of raised fields (McKev et al., 2014: Rostain, 2012: Rostain & McKey, 2015). These earthworks were built by people of the Arauquinoid cultural tradition during their eastward migration from the Orinoco region along the coast of the Guianas between 650 and 1650 AD (Rostain, 1991, 2010). They pushed the initially flat homogeneous landscapes into an alternative, topographically heterogeneous state, maintained by positive feedback loops driven by soil engineers (Iriarte et al., 2010; McKey et al., 2010, 2014; Renard, 2010; Rostain, 2010). Naturally occurring earth-mound landscapes, such as those found in the surales of the Orinoco Llanos of Colombia and Venezuela (Zangerlé et al., 2016) and the sartenejales and campos termiteros of the Llanos de Mojos of Bolivia (McKey et al., 2014), are however seemingly absent or very uncommon in the seasonally flooded coastal savannas of French Guiana. This absence could be explained by the limited size of the French Guianan savannas, their more recent formation and their distance from other similar environments: There has not been enough time and space to permit the evolution of adaptations to seasonal flooding, including the capacity of soil engineers such as earthworms and termites to build large, high mounds, or to permit colonization by engineers that already possess such adaptations. However, the earth-moving capacities of the generalist soil engineers present in French Guianan savannas do allow them, under a certain range of environmental conditions, to maintain abandoned pre-Columbian raised fields (McKey et al., 2014). While earth mounds of natural origin and raised fields have sometimes been confused, the very regular orientation (often in square-grid patterns) of the Guianan mounds indicates they are all of anthropogenic origin (McKey et al., 2014; Renard, 2010; Rostain, 2010). Nevertheless, confusion is likely to continue because, regardless of their origin, many mounds today bear the marks of both humans and soil animals. Thus, French Guianan raised fields have been reengineered by soil animals (McKey et al., 2010; Renard et al., 2013), and termite mounds in Bolivian flooded savannas appear to have been converted into raised fields by pre-Columbian farmers (McKey, Renard, & Comptour, 2017).

The raised fields along the coast of the Guianas, and especially those of French Guiana, are unique because the majority are round, distinguishing them from most other South American examples, but see Rodrigues, Lombardo, and Veit (2018), which are elongated (Rostain, 2010). The raised fields in French Guiana can be classified into three main types: (a) small round fields (1-1.5 m in diameter), (b) larger, round, or square medium-sized fields (5 m in diameter), and (c) elongated fields (1 m high, 1–5 m wide, and 30–50 m long) (Iriarte et al., 2010; Rostain, 2010). The different types were arranged following a complex and highly organized system that permitted drainage or water retention, depending on slope and flood level (Rostain, 2008, 2010). Analysis of phytoliths and starch grains has shown that maize was the main crop cultivated in these fields, as well as manioc and squash (Iriarte et al., 2010; McKey et al., 2010; Rostain, 2010). As some of these sites seem to have been occupied continuously over centuries, this land use appears to have been sustainable, for sometimes quite large populations (Iriarte et al., 2010; Rostain, 2010). This is in accordance with the fact that raised-field agriculture today is often associated with relatively dense populations. In the Guianan coastal savannas, as elsewhere (McKey et al., 2014), raised-field agriculture was certainly only one component of complex subsistence systems including numerous activities in rich coastal biotopes, making long-term sedentarism possible (Rostain, 2010). This is confirmed by raised-field landscapes in the Congo Basin, where fishing and trading play a great role, and not all the raised-field areas are currently used (Comptour et al., 2018). This may also mean that previous estimates of population density made based on

the areal extent of raised-field vestiges may be biased (Comptour et al., 2018). Following the European conquest, epidemics and pandemics were rapid and widespread throughout the Americas and according to some estimates may have resulted in the loss of 80% to 95% of the agricultural population across the neotropics (Denevan, 1992, 2001; Koch, Brierley, Maslin, & Lewis, 2019). The labor-intensive raised-field systems must have faced particular stress, leading to their abandonment (Iriarte et al., 2012; Rostain, 2010). However, it is also possible that, independent of the European conquest, changes in other activities may have diminished the relative efficiency and advantages of raised fields, contributing to the decline of their use and construction (Comptour et al., 2018). The extent to which vestiges of raised fields have survived since their abandonment has depended upon various factors including the actions of soil engineers, erosion driven by centuries of heavy rainfall and favored by burning, modern agricultural activities, and construction of current earthworks, such as roads, that modify the local hydrography and accelerate the process of return to a flat topography (McKey et al., 2010; Rostain, 2008; Rostain & McKey, 2015).

Colonial and Créole Uses

Over the past 500 years, French Guiana's savannas have been marked by actions of European colonists and their slaves, and later by Créole societies (Rostain, 2012). All these groups used savannas very differently than their Amerindian predecessors.

From the 18th century onward, European colonists on the coast of the Guianas used African slave labor to build immense polders in Suriname and Guyana; however, only small areas in the lowlands of French Guiana were modified in this way. These polders were practically the opposite of the raised-field technique: Instead of building mounds above water level, polders are large areas drained by canals (Rostain, 2010). In 1769, slaves began to build polders east of Cayenne; the last ones near Mana (in northwestern French Guiana) were used for rice cultivation in the 1980s and abandoned at the beginning of the new Millennium (Rostain, 2010) but are still dedicated to agricultural use in land planning documents. However, in general at this time, colonist farmers largely shunned savannas and turned to the *terra firme* forest, lured by the apparent lushness of the vegetation. Soon learning that forest soils were not as fertile as they seemed, they adopted slash-and-burn agriculture (Rostain, 2010). In 1764, during the Kourou expedition (L'Expédition de Kourou), colonists were given cattle, and savannas then began to be used as pastures. By the 18th century, the savannas were being burned to favor the growth of grasses (Le Roux, 1995), and livestock production increased until the end of the century, reaching 15,000 head. Indeed, high fire frequency in the coastal savannas of French Guiana is a post-Columbian phenomenon. Charcoal analyses reveal low levels of burning during periods when savannas were used for pre-Columbian raised-field agriculture and a sharp increase in fires following colonization (Iriarte et al., 2012). In coastal French Guiana, fires were introduced by colonial farmers to improve the quality of the pasture, and Créole farmers have continued this practice to the present day (Palisse, 2013). At the beginning of the 19th century, exotic species such as the African grasses Panicum maximum and Brachiaria mutica were introduced to improve the pastures (Huguenin, 2008). Later, the technique of using raised planting beds (usually less than 15–20 centimeters high, much smaller than wetland raised fields) on well-drained land spread along the coast and the remains of these mounds and their associated canals are widespread (Rostain, 2012).

Créole society appeared in French Guiana during the slavery period, continued after the abolition of slavery in 1848, and has since occupied the savannas of the central coast of French Guiana. Prior to the abolition of slavery, poor settlers with a few slaves and freed people of color owned small farms (Mam-Lam-Fouck, 2002), and between Kourou and Sinnamary, a small group of people arriving from Acadia-then part of New France in northeastern North America (today part of Canada and United States)—began to develop a society based on peasantry at the margins of plantation society (Cherubini, 2008). After slavery's abolition in 1848, former slaves also shifted to peasantry and attempted to become landowners. However, while some were able to buy parcels of land, many used land without having a title to it (Jolivet, 1982). Peasantry in French Guiana took the form of *petite habitation*, characterized by small-scale farming combining different activities in savannas, forests, and around the house (Jolivet, 1993). This form of peasantry was based on individualism and self-sufficiency (Jolivet, 1993; Mintz, 1983) and was hence opposed to the slave system of labor (Barthélémy, 1997). Small and loosely scattered habitations were built on cheniers or in forest islands within savannas. During this period, savannas were specifically used for several activities: agriculture adapted to the habitat, cattle raising, hunting and fishing, and the harvesting of wild plants (Jolivet, 1982; Palisse, 2014; Rostain, 2012).

Agriculture in the savannas at that time was mostly based on manioc, which is well adapted to local soils, though many other crops such as maize, melon, sugar cane, and coconuts were also cultivated, depending on the soil quality (Palisse, 2014). People usually cultivated at least one plot in the forest, one in the savanna and a small garden around the house, allowing for the diversification of agriculture in different places and helping to safeguard against unpredictable events that could destroy crops (e.g., damage caused by ants or by wild or domestic vertebrates; Palisse, 2014). Savannas were also considered to be excellent for cattle raising, with cattle left free to roam during the day in the mosaic landscape, and the savannas strategically managed, using controlled fires in the middle of the dry season to burn one location, favoring grass growth, before moving to another area as cattle progressively grazed (Palisse, 2013, 2014). Other key reasons to burn savannas were to keep the landscape open and to kill insects, snakes, and other animals considered to be pests (Palisse, 2014). Although flooded savannas were good places to hunt birds and sometimes caimans (Lohier, 1972; Savaria, 1933), hunting in the upland savannas seems to have been more opportunistic, when animals crossed between forest patches or when animals were attracted to the area after fires. However, turtles and armadillos were specifically targeted in these savannas (Palisse, 2014). Fish that ventured into savannas during the high waters of the rainy season and became trapped when water receded could also be easily "harvested." Finally, some edible and medicinal plants were also harvested. The most important in the diet were probably fruits of palm trees including comou (Oenocarpus bacaba) and the famous awara (Astrocaryum vulgare), whose fruits are the basis for a regional dish eaten during Easter (le bouillon d'awara) and were also used to feed pigs. Locals also often mention the edible fruits of prunier savane, also called morossif or poirier savane (Byrsonima crassifolia) and the very rough leaves of Curatella Americana, which were used as scouring pads or sandpaper. These plant species were favored or planted by the savanna inhabitants (Palisse, 2014).

Until the 1960s, the coastal plain was a truly multiuse landscape, in which savannas were only one part of the mosaic. In the 1960s, this system began to come to an end. Three main factors can explain this decline: rural exodus, the expulsion of the inhabitants living in the area where the Guiana Space Centre was established, and the development of new agricultural practices that limited people's access to land.

Contemporary Uses and Changes

In the 1970s, the French government implemented a development plan for Guiana called *Le Plan Vert* and helped farmers to establish in savanna areas. As a result, agricultural practices have changed substantially, with livestock now kept behind fences in defined and private plots that are transformed into more intensive pastures through soil fertilization and plantation of several African pasture grasses, such as *Digitaria swazilandensis*, *Brachiaria decumbens*, *B. mutica* var. Tanner,

B. humidicola ("Kikuvu grass"), and Pennisetum purpureum (Huguenin, 2008). Some are invasive species that could increase threats to vulnerable native taxa (Driscoll et al., 2014). Burning is also now less common as a management strategy as it is excluded from intensive pastures. In the last few years, however, uncontrolled fires seem to have increased in frequency, and firefighters are frequently called (Palisse, 2013). Older farmers blame these increases on the lack of know-how of young people, who do not practice agriculture in the same way, and who do not regularly maintain savannas (Palisse, 2013). This new private land-use system, including land-tenure rights, is in opposition to the past communitarian land use, where people and farm animals were free to go and live wherever they decided (even if the savannas have been state-owned land since the end of 19th century). This new land-use system changes the landscape, the biodiversity it comprises, and the ways of living of Créole and Amerindian Kali'na communities that inhabit savannas, sometimes leading to conflicts. Indeed, Kali'na populations living in or near coastal savannas still use the mosaic landscapes of forest, wetlands, sandy ridges and banks, sea, rivers, and mangroves for a combination of subsistence activities, including fishing, hunting, gathering, and agriculture (Graine, 2017; Palisse, 2014).

The savannas are of cultural importance to both Kali'na and Créole people, who associate them with paths and mobility and-going even further-with freedom (Palisse, 2013). Up until the 1970s, the savannas were the places where they spent a lot of time walking different activities-slash-and-burn between their parcels in the forest, and different places to hunt, to fish, or to gather-and are deeply associated with the combination of activities that characterize their ways of life. For the Créoles, the word savann has a particular meaning. It is often associated with their culture. For example, the *piano-savann* is the Créole drum. The savanna area is recognized as the place where the Créole culture-famous for its dances and culinary specialtiescould fully develop. Créoles and Amerindians wish to preserve savannas and to pass on an intangible cultural heritage made up of knowledge and skills linked with these landscapes (Palisse, 2014). Most of them disagree with modern farmers and their practices. However, they also want to continue hunting, fishing, and gathering and are against the classification of savannas as protected areas in which they could no longer practice these activities (Palisse, 2014). In response, farmers make the case that savannas have always been used and transformed by humans and that they must be used today for sustainable agriculture to avoid the importation of low-quality food into French Guiana (Palisse, 2014).

Urbanization is also contributing to the changing face of French Guianas savannas, with many being crossed by the main road of French Guiana, National Road 1 (Figure 3), which together with other new earthworks modifies the hydrography of the savannas and thus vegetation structure and composition (Rostain, 1991). Villages and cities are also increasingly occupying savanna lands (Figure 3). However, burning, first adopted by European colonists and later maintained by the Créoles, has now become controversial, with some areas now excluded from illegal burning activities, because they are located in protected areas or within the Space Centre zone. These changes in the fire regime are also leading to changes in the savannas, with floristic compositions shifting to alternative stable states. The combination of all the past and current human activities leads to many different configurations from the original "pristine" state of French Guiana's savannas to their

Biodiversity and Environmental Importance

current state (Figure 4).

In common with other Amazonian savannas, and open biomes in eastern South America more generally, the savannas of French Guiana are complex mosaics of different natural habitats. Although a complete habitat typology for all coastal savannas of French Guiana does not yet exist, a study in savannas of the central coast identified 21 different habitats represented in 90 sample points, with floristic composition varying with vegetation height and soil hydromorphism (Léotard, 2012; Léotard & Stier, 2013; Stier, 2012; Stier & de Pracontal, 2015). Additional habitat heterogeneity was created by the earth-moving activities of pre-Columbian inhabitants who may arguably have enhanced biodiversity at the local scale. In terms of their ecological impact, raised fields created heterogeneity in an originally homogeneous, flat, and marshy environment. Combined analyses of phytolith assemblages and of carbon stable isotope profiles in soils show a landscape that was transformed from a relatively homogeneous wetland vegetation with a mixture of C4 and C3 plants (two different photosynthetic cycles) to a heterogeneous vegetation where vestiges of raised fields bear a greater proportion of C4 plants and lower lying intermound areas a greater proportion of C3 plants (Iriarte et al., 2010; McKey et al., 2010, 2014). The mound/intermound heterogeneity appears to be an alternative stable state of the ecosystem, maintained by positive feedbacks driven by soil organisms such as ants, termites, earthworms, and plants, which established on these preexisting mounds, after the raised fields were abandoned (McKey et al., 2010). Largely owing to the mound/

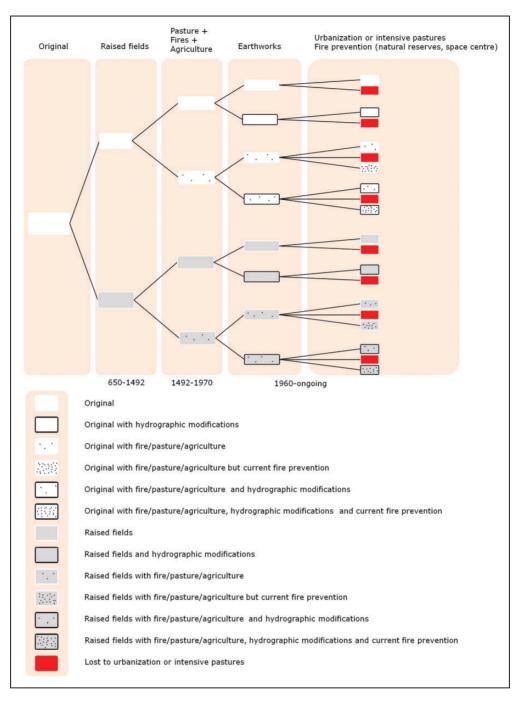


Figure 4. Paths of human-induced modifications in French Guiana's savannas.

intermound heterogeneity, soils of French Guianan coastal savannas bearing ancient raised fields have among the highest densities of soil invertebrates recorded for tropical savannas (Renard et al., 2013), at least some of them also contributing to seed propagation and germination of savanna plant species (Renard, Schatz, & Mc Key, 2010). Moreover, it has been shown in Suriname that 50% of plants currently growing on vestiges of large residential mounds have a recorded practical use for modern Indigenous groups, compared with only 15% in the forest (Rostain, 2010). It is probable that the first inhabitants facilitated the establishment of particular species assemblages on the mounds and that a certain part survived after the site was abandoned. It is possible that this theory is applicable to French Guiana's raised fields and that the plant diversity recorded today reflects remnants from pre-Columbian plantations.

	Total		Found in savannas		Savanna specialists	
	Number of species	Threatened, n (%)	Number of species	Threatened, n (%)	Number of species	Threatened, n (%)
Birds	730	87 (12%)	64	19 (30%)	21	17 (81%)
Terrestrial mammals	197	6 (3%)	55	6 (11%)	2	I (50%)
Reptiles	174	18 (9%)	16	8 (36%)	10	8 (73%)
Amphibians	135	9 (7%)	17	4 (24%)	2	2 (100%)

Table 1. The Number of Species, and the Number and Proportion of Species Threatened (Vulnerable, Endangered, or Critically Endangered) Regionally According to the IUCN Regional Assessment for French Guiana, of Birds, Terrestrial Mammals, Amphibians, and Reptiles in French Guiana, the Savannas of French Guiana, and Those Species That Are Savanna Specialists.

The habitat heterogeneity makes the savannas of French Guiana, much like the larger complexes of savannas found throughout Amazonia (see Carvalho & Mustin, 2017), unique habitats housing a particular flora and fauna, different from those in the forests that surround them (Chaix et al., 2002). Even among the savannas within French Guiana, the flora and fauna vary (Chaix et al., 2002; Hoff & Brisse, 1990). Although we do not know how ancient uses of savannas acted on their original vertebrate fauna, the development of contemporary agriculture and of urbanization and infrastructures is responsible for most of the surface loss and fragmentation of savannas between 2001 and 2015 (ONF, 2010, 2017), potentially putting savannaspecialist species at risk. The recent International Union for Conservation of Nature (IUCN) regional Red List (Union Internationale pour la Conservation de la Nature (UICN) France et al., 2017) enables, for the first time, an analysis of the vertebrates considered endangered at the regional level inhabiting the savannas (Table 1).

Of the 730 bird species of French Guiana (Comité d'Homologation de Guyane, 2018), 64 species are found in the savannas, of which 21 species (33%) are considered to be dependent on savannas to establish at least parts of their life cycles. Although 12% of all French Guianan bird species are considered threatened at the regional level-meaning classified as Vulnerable, Endangered, or Critically Endangered in the IUCN Regional Red List (UICN France et al., 2017)-30% of bird species found in savannas are considered threatened, and 81% of birds strictly dependent on savannas are threatened regionally. None of these species is, however, considered endangered internationally (three are considered Near Threatened and the rest Least Concern) (IUCN, 2019), which suggests that these species are threatened in French Guiana precisely because they are dependent on the savanna habitats, and the savanna habitats are limited in surface and under threat. For example, Colinus cristatus was once common in poor white-sand savannas near Sinnamary; in central coastal French Guiana, however, this openhabitat specialist rapidly declined after 1995, when natural savannas were converted into cultivated lands (C. Bergère *fide* O. Claessens, https://www.faune-guyane.fr/ index.php?m_id = 54&id = 292404). This species is increasing in other parts of its range, and so the fact that it has now vanished from most coastal savannas in French Guiana, with only two records since 1995, seems indicative of ongoing habitat loss and degradation (Groupe d'Étude et de Protection des Oiseaux en Guyane, 2019).

While 55 of the 197 terrestrial mammals of French Guiana are found in savannas, only two are dependent on savannas: the small marsupial Cryptonanus nov sp. (Baglan & Catzeflis, 2014) and Sigmodon alstoni (Voss, 1991), both of which are considered endemic to the Amazonian savannas (Mustin et al.. 2017). Cryptonanus nov sp., strictly dependent on savannas, is listed as "Endangered" regionally (UICN France et al., 2017). While this species has not been evaluated internationally (IUCN, 2019), it has only been described from bones collected from owl pellets in Sinnamary (Baglan & Catzeflis, 2014), though it may also occur in the Savannas of Amapá, in eastern Brazil (Catzeflis, Silva, & de Thoisy, unpublished data). Clearly, the fate of a species endemic to savanna habitats is intimately linked to the fate of the savannas themselves.

Sixteen of the 174 reptiles recorded in French Guiana (9%) are found in savannas, of which 10 species are considered to be dependent on them. Of these 10 species, 8 are endangered regionally (80%). Seventeen of the 135 amphibians recorded in French Guiana (13%) are found in savannas, but just two species, both of which are regionally threatened, are considered dependent on them. Of the regionally threatened amphibians and reptiles found in the savannas that have been evaluated internationally, all are of Least Concern (IUCN, 2019). Like birds, these are species threatened in French Guiana precisely because they are dependent on the savanna habitats and thus are restricted to small, isolated populations in areas suffering increasing anthropogenic threats. The 15 other species are likely to remain

in wet meadows and seem to support a certain degree of anthropization of their habitat.

Moreover, 762 plant species or subspecies were counted in the savannas of the central coast during a study in 2011 and 2012, showing that despite their small surface, savannas are home to at least 16% of French Guiana's total flora (Léotard, 2012; Stier, 2012; Stier & de Pracontal, 2015). This estimate shows just part of the plant species diversity in savannas, as only the central coast was surveyed. Close to 42% of the flora was made up of rare species that were noted in less than 1% of the 90 sample points. The tendency to have few very common species and many rare species has been confirmed by another study of savannas located further east along the coast (Buzançais, 2018). Numerous species are restricted to savannas and not found elsewhere in the country. Also, 20% of protected plant species of French Guiana have been shown to occur in coastal savannas (Delnatte, 2013).

Conservation Status of the Amazonian Savannas

Across the Neotropics, savannas and other open vegetation types are currently under threat, suffering high clearing rates, largely to make way for large-scale mechanized agriculture and pasture (Carvalho & Mustin, 2017; Carvalho et al., 2019; Françoso et al., 2015; Strassburg et al., 2017). These habitats also tend to be the least protected, with areas under strict protection varying from less than 1% up to 2.2% (Barbosa et al., 2007; Werneck, 2011). The areas that do have protected status still tend to experience high degradation rates across Latin America (Leisher, Touval, Hess, Boucher, & Reymondin, 2013): From 2004 to 2009, 45% of protected areas experienced land and forest degradation, which increased by 250% over this period, and it is particularly worrying that the protected areas in flooded grasslands/savannas experience the highest rates of degradation.

In French Guiana, between 2001 and 2015, the surface area of the savannas was reduced by 7.2%, with most of the loss accounted for by areas transformed for agriculture and a smaller loss due to urbanization. However, most of this loss (5.6%) occurred between 2001 and 2008, and the rate of clearing has slowed in recent years. This is largely because many easily accessible savannas have already been impacted and those that remain are either inside the Space Centre, which is a restricted territory with forbidden access to the public but facing important pressures for infrastructure building, or in protected areas (ONF, 2010, 2017). Only 2.4% of the savannas fall within current protected areas (Figure 5, Table 2). In contrast, 75% of the area of savannas is within Zones Naturelles d'Intérêt Écologique, Faunistique et Floristique (ZNIEFF; natural zones of ecological interest, fauna, and flora) areas: 160 km² in ZNIEFF 1 and 29 km² in ZNIEFF 2, 189 km² in total (Figure 6). ZNIEFFs are a tool of the French State to highlight areas that are of particular ecological interest, owing to the rare or threatened ecosystems or species they host. ZNIEFF status is not a regulatory protection tool but rather a way of showing priority areas. In French Guiana, these areas cover 27% of the territory (Biotope, 2014). ZNIEFF 1 are small in area, particularly sensitive to disturbance and host rare or remarkable species or habitats that characterize national or regional natural heritage. ZNIEFF 2 are large, rich natural units that have been little modified, and harbor important biological potential. They can enclose type 1 areas (Biotope, 2014). ZNIEFF 1 areas, and thus the majority of French Guiana's savannas, are considered to be "natural areas of high patrimonial value" according to the Schéma d'Aménagement Régional that was validated in 2016 by a decree in the Council of State (Collectivité Territoriale de Guyane, 2016). Status as a Schéma d'Aménagement Régional "natural area of high patrimonial value" dictates that the opening of quarries and the establishment of agricultural or industrial activities are not allowed, and regional and local planning stems from this status such that while it does not confer protected area status per se, savannas within ZNIEFF 1 areas are protected from these activities. It is also notable to see that 42.8% of total savanna area falls within the National Centre for Space Studies property (Figure 5, Table 2).

Conservation Issues in the Amazonian Savannas

In general, savannas tend to be under the influence of several human factors (Figure 7), including fire, agricultural practices, invasive species, infrastructure development, urbanization, and poaching (de Pracontal & Entraygues, 2009). In the following paragraphs, the key drivers will be summarized.

Fire

As we have previously highlighted, fire often plays a key role in the maintenance and evolution of savanna ecosystems. However, uncontrolled burning can be a threat to savanna conservation, particularly where the frequency of fires is increasing (Carvalho & Mustin, 2017). The impact of fire regimes on vegetation structure and composition is complex. Several studies have tried to describe floristic impacts and feedbacks between fires and vegetation and to build descriptive models (Adeney et al., 2016; Beckage et al., 2009; Higgins et al., 2007;

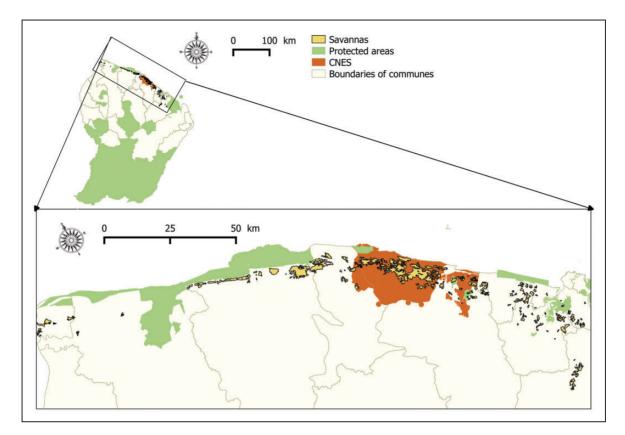


Figure 5. Location of savannas and protected areas. Based on the vegetation map of French Guiana (ONF, 2017). Mapping of the system of protected areas and the CNES based on shapefiles available from www.geoguyane.fr and provided by CNES. CNES = National Centre for Space Studies.

Table 2.	Savannas	and	Protection	Tools	in	French	Guiana.
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	Savanna area (km ²)	Percentage of total savanna area (250.5 km ²) in this category
Protected	6.1	2.4
CNES	107.3	42.8
Other nonprotected	137.1	54.7

Note. CNES = National Centre for Space Studies.

Hoffman, 2000; Roitman, Felfili, & Rezende, 2008; Silva & Batalha, 2010; Stier & de Pracontal, 2015). Study results are often site-dependent, with each site having its specific interaction between savannamaintaining processes. As a result, studies from other countries and regions cannot be applied to French Guiana's savannas.

In French Guiana, it has been shown that the majority (62% of the total surface) of savannas between Cayenne and Organabo burned at least once between 2006 and 2010, with 73% of these burned only in

1 year, 20% burned in 2 years, and 7% burned in 3 years out of the 5 (Stier & de Pracontal, 2015). The savannas east of Cayenne burned less often than those between Cayenne and Iracoubo, a difference that may reflect higher rainfall in the east of French Guiana or different levels of use of the savannas (Stier & de Pracontal, 2015). Here, we used data from the Brazilian National Space Research Institute to quantify the number of days of fire across the savannas of French Guiana, per month, in each year from 2008 to 2017 (Figure 8). There is clear seasonality in the occurrence of fire, with the vast majority taking place in the long dry season from July to December. However, while there does seem to be some tendency toward an increase in fires, at least from 2013 to 2016, there is much interannual variability precluding a clear trend.

A meta-analysis of available data from 16 savanna sites in French Guiana has shown that the most accessible and most frequently burned savannas are similar to each other in terms of plant species composition, whereas unburned sites that are isolated and difficult to access, or protected savannas presumed not to have burned recently and to have undergone little human-induced

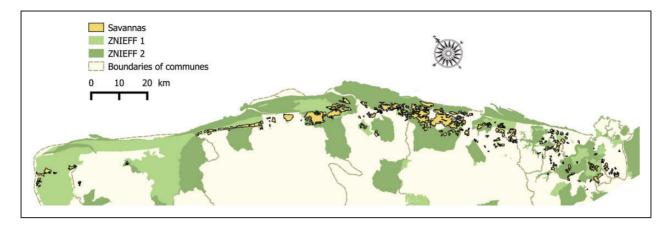


Figure 6. Distribution of savannas and ZNIEFF areas (natural area of ecological, faunistic, and floristic interest) in French Guiana's coastal zone. Based on the vegetation map of French Guiana from the Office National des Forêts (ONF Guyane) from 2015 (ONF, 2017) and the shapefiles available from www.geoguyane.fr.

ZNIEFF = Zones Naturelles d'Intérêt Écologique, Faunistique et Floristique.

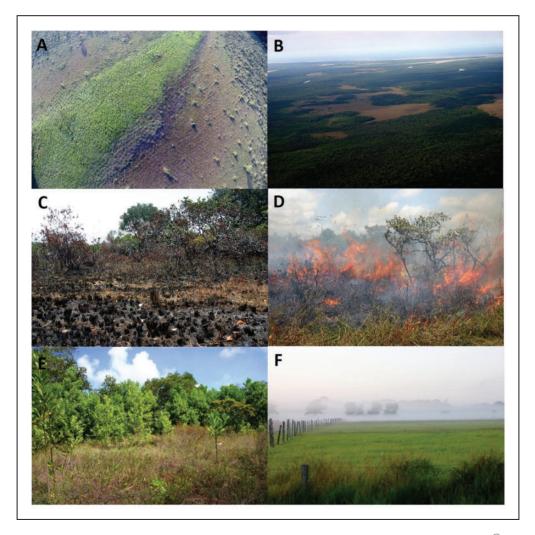


Figure 7. Images of savannas of French Guiana and human influences. If not specified differently, the pictures are [©] A. Stier: (a) savanna mosaic landscape, with vestiges of pre-Columbian-raised fields ([©] Dans les forêts de Guyane); (b) typical habitat transect from the ocean to the interior, with savanna patches; (c) impact of fire on savannas; (d) savanna fire; (e) a savanna invaded by *Acacia mangium*; and (f) savanna transformed into pasture on private agricultural plots ([©] N. de Pracontal).

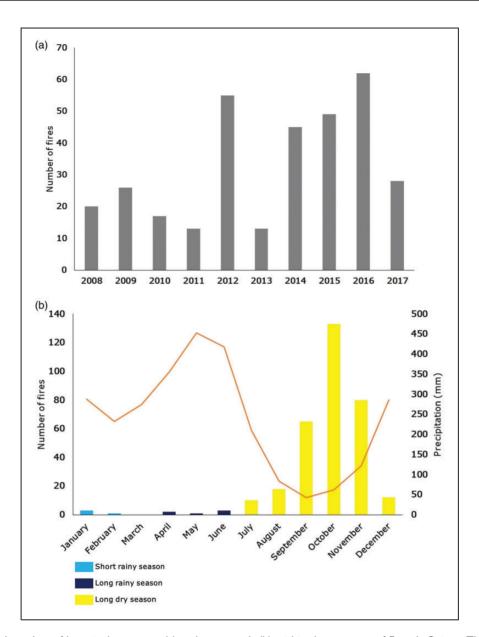


Figure 8. The total number of hot pixels per year (a) and per month (b) within the savannas of French Guiana. The hot pixels were quantified between 2008 and 2017 from shapefiles of the occurrence of burns obtained from the databases of the Instituto Nacional de Pesquisas Espaciais (https://prodwww-queimadas.dgi.inpe.br/bdqueimadas/). Based on these shapefiles and using ArcGIS v10.4.1 (Environmental Systems Research Institute, 2011), the total number of hot pixels was quantified in accordance with the vegetation map of savannas of French Guiana (ONF, 2017). The classification in seasons of the year based on precipitation was based on Vezenegho et al. (2016). In March, classified as part of the "short dry season," there were no hot pixels. Average precipitation per month was adapted from https://fr.climate-data.org/ for Kourou: The data come from climate models made with data from weather stations in the world between 1982 and 2012.

change, tend to have different species compositions not only from the more frequently burned sites but also among themselves (Procopio, 2014). Or rather, the less frequently burned savannas each had a unique species assemblage, whereas frequent burning tended to homogenize the different savanna sites. Floristic monitoring of a site subjected to controlled fire regimes during 2 years, after two decades without burning, showed that the habitats reopened rapidly, with shrub species such as *Clusia nemorosa* that had closed the habitat decreasing, and cover and richness of herbaceous strata increasing, with small annual herbaceous plants typical of short grass savannas appearing (Girault & Silland, 2015).

Burning is officially prohibited, but illegal purposely set fires still occur regularly along French Guiana's coast. This practice leads to different conflicts between the authorities, farmers who try to exclude fires from their plots, farmers and inhabitants who traditionally burn savannas, Amerindians whose opinions are divided about fire in savannas, and managers who still lack evidence concerning the extent to which fire is a necessity for or a threat to biodiversity conservation (Palisse, 2014). One important factor to consider is the capacity of fires to enhance the invasiveness of Acacia mangium, the seeds of which tend to germinate much more after burning (Dezécache, 2013; Stier & de Pracontal, 2015). In conclusion, to make informed conservation or restoration decisions, it will be important to consider the local context at site level when planning for a suitable fire regime that includes the use, or exclusion, of fire for conservation purposes (Stier & de Pracontal, 2015).

Agricultural Practices

Modern agriculture is considered to be one of the main threats to savannas, in French Guiana and elsewhere. Indeed, agricultural activities, during the colonial period but also up to the present day, have erased much of the pre-Columbian legacy of the coastal savannas of the Guianas. Activities such as plowing (e.g., as preparation for planting of exotic pasture grasses) and construction of fish ponds not only erase the raised fields, they also alter drainage patterns, making it more difficult to interpret the hydrological functioning of past landscapes.

Currently, large-scale projects of eucalyptus and pine monocultures and the production of rice and soybeans are increasing in savannas across Latin America, radically transforming the natural habitat into intensive monocultures, where savannas can be considered to be completely lost. In French Guiana, large-scale intensive agricultural projects have been attempted in the past, including cotton or rice production or pine plantations, but all failed or were abandoned, though relicts still exist and are visible along National Road 1 within savanna landscapes.

Traditional cattle-raising activities from the past century—including burning and free animal grazing have also almost vanished from the coastal savannas, and in turn, the types of landscapes these activities created or maintained are vanishing and changing. They are slowly being replaced by a different type of land tenure and activities, where water buffaloes and cows are raised extensively, but in restricted plots, which are plowed and planted with exotic fodder species (Figure 7). This transformation is seen as a loss of savanna areas by some people, though others consider it to be a durable agricultural practice, where a certain type of biodiversity coexists in landscapes that are kept open, with little or no pesticide use, sometimes in organic farms (Palisse, 2014).

Invasive Species

As savannas have a patchy distribution, are surrounded by other types of ecosystems or anthropogenic areas, are sensitive to disturbance, and are easily accessible, they are extremely threatened by the introduction and spread of exotic invasive species, as are "real" islands in general (Delnatte & Meyer, 2011). Of the 490 exotic plant species recorded in French Guiana in 2013, and the 165 naturalized ones, the woody species *Acacia mangium* and *Melaleuca quinquenervia* are considered to be the most problematic because of their distribution and capacity to transform environmental conditions (Delnatte, 2013; Delnatte & Meyer, 2011). Both of these species are fastgrowing and fire-resistant and as such are preadapted to invade savannas (Aguiar, Barbosa, Barbosa, & Mourão, 2014; Delnatte & Meyer, 2011).

The introduction of Acacia mangium was supported by French governmental agencies, first for the Green Plan in the 1970s, and then to reforest mining sites during the 1990s and 2000s (Delnatte & Meyer, 2011; Palisse, 2014). Acacia mangium does not usually spread under the forest canopy but does rapidly invade open areas (Figure 7), with its spread further accelerated by fire, which increases seed germination. Different techniques of control of tree populations and their seed banks have been tested: Eradication and control are possible in restricted areas, even if the eradication of this species from the whole of its current distribution in French Guiana seems now to be impossible (Dezécache, 2013; Stier & de Pracontal, 2015). Indeed, consensus among stakeholders is that savannas need to be kept as open spaces and that Acacia mangium, while useful for some agricultural and reforestation practices, could be easily replaced by native species with similar characteristics if those alternatives were identified, promoted, and made available by the relevant agencies (Palisse, 2014). Technical guidelines for the control of Acacia mangium are now available to all environmental managers (Stier & de Pracontal, 2015).

Melaleuca quinquenervia was first recorded in French Guiana in 1948, but its expansion was favored by the Green Plan in the 1970s for timber and paper industries (Delnatte & Meyer, 2011). It has been far less studied than *Acacia mangium*, and control methods adapted to local conditions are not yet available.

Of the exotic grasses planted in the savanna areas transformed into pastures, *Brachiaria* spp. are among the exotic species that have already successfully invaded savannas around the world (Delnatte & Meyer, 2011) and should thus be under surveillance.

Infrastructure Development and Urbanization

In common with other countries in Latin America and around the world, savannas in French Guiana are also being lost to infrastructure development and urbanization, driven by a combination of population growth, economic liberalization, public land reforms and political, land tenure, and economic shifts (Carvalho & Mustin, 2017; Delnatte, 2013; Marchant, 2010; Mustin et al., 2017; ONF, 2010). Notable projects in French Guiana include the construction and expansion of the Space Centre and the installation of solar panel fields and wind turbines. The earthworks necessary to implement such projects change the local hydrographic conditions and drainage patterns. This might possibly lead to the shift of savannas to forest or other ecosystems, in cases where the natural factors driving maintenance of savannas are suppressed. For example, east of Kourou, construction was undertaken in the 1990s to change the course of National Road 1, and this required the construction of an embankment across a seasonally flooded savanna. This road has had a considerable influence on the hydrological network of the area, creating new checks on the flow of water and sediment, with consequences for the vestiges of pre-Columbian raised fields found in this savanna (Rostain, 2012).

The recent dramatic acceleration of residential construction in French Guiana has also gradually invaded wetlands and savannas. In many cases, flood-prone areas are gradually backfilled with sand taken from adjacent cheniers to gain ground in the marshes and flooded savannas for construction of roads, subdivisions, or residential developments.

The Way Forward

The key first step to better conservation of the savannas of French Guiana, in terms of both biodiversity and ecosystem function, and their archeological and cultural significance, is—as is so often the case—discussions at the political level. Strategic decisions need to be made regarding what kinds of landscapes, human activities, and biodiversity need to be conserved, protected, or sustained. One thing is certain, conservation objectives for the Amazonian savannas of French Guiana should include the preservation of vestiges of pre-Columbian raised fields, for beyond their importance as archeological artifacts and as cultural heritage, they also contribute to ecosystem functioning, preserving ecological functions that enhance local-scale biodiversity and maintain landscapes. However, this is a challenge as the raised fields have never captured the public imagination, or the attention of decision-makers, conservationists, or protected area managers, and as a consequence have never been cited as a conservation priority.

As has been shown here, these socioecological landscapes have been chronically underprotected and are highly threatened by changing agricultural practices and fire regimes and by expansion of infrastructure and urbanization. As a consequence, French Guiana's savannas need new protected areas. A new decree published in September 2019 offers the possibility to protect natural habitats in French Guiana, as was previously only possible for biotopes linked to protected species (France, 2019). This lists the natural habitats, including savannas, which may be the subject of a protection order by the Prefect (the French State's representative in French Guiana). This opens a new possibility of conservation actions for French Guiana's savannas. However, the demarcation and implementation of new protected areas must be done as part of an open, equitable, and participatory process that takes into account not only the diversity of flora and fauna and ecological and environmental processes but also the historical, social, and cultural importance of different savanna areas. This conservation strategy would be completely different from already existing French environmental protection tools and must be designed in a way that allows for decisions to be made, together with local stakeholders, concerning sustainable management practices at the level of each site. This is because each of the different groups of savanna patches, or even individual savanna patches, is maintained through a unique combination of environmental and historical factors that can be quite different even on a scale of just a few kilometers, and because the combinations of people using the savannas,

and therefore the type of human activity, can also vary greatly. Zones of collective use rights (known as "Zones de Droits d'Usage Collectif"), a land-use system that transfers certain management and use rights from the State to autochthonous communities, could be one of the starting points for certain areas, as some have been attributed within savannas. The use of conservation planning tools to guide land-use planning could aid in this process, which will also need to take ecological and archeological issues into account, which in turn can generate time-consuming and costly requests for authorizations, preventive archeological studies, higher expectations by environmental decentralized administrations, higher complexity of projects including these issues, offset solutions, and sometimes, conflicting situations.

Furthermore, to make informed decisions for the conservation of Amazonian savannas, it is also vital that knowledge gaps be filled, particularly in relation to ecological functioning, the response of savannas to environmental changes, and socioenvironmental interactions (Adeney et al., 2016; Carvalho & Mustin, 2017; de Pracontal & Entraygues, 2009; Marchant, 2010). Relationships between soils, hydrography, fire regimes, vegetation structure, and plant and animal communities need to be better understood. Moreover, studies of human interactions with savannas are vital to understand the savanna ecosystems of today and to switch from a narrative of *degradation, disturbance*, or *impact* to a more holistic understanding of how societies have been and are still interwoven with the savannas (Marchant, 2010). This will require a truly transdisciplinary approach with natural and social scientists working together with conservation and development nongovernmental organizations as well as governmental agencies.

Beyond this, at the broader scale, we reiterate the need stated in previous publications for the Amazonian savannas to be recognized as unique and distinct from other, larger savanna areas, to allow for specific policies, agreements, and protections to be designed and implemented at national and international levels (Barbosa et al., 2007; Carvalho & Mustin, 2017; Mustin et al., 2017; Prance, 1996). Local and national authorities must take responsibility for the conservation of these unique socioecological systems, and it is the role of scientists and practitioners to communicate their importance to these decision-makers.

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