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Grass survey of the Itremo Massif records endemic central highland grasses

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ABSTRACT

Despite the substantial area covered by grasslands in Madagascar (65%), the taxonomy of the grasses (Poaceae), which represent the main plant component of these vegetation types, is still understudied. Inventories and detailed specimen identification work from 12 localities in the Itremo Massif Protected Area allowed us to compile a list of grasses present in the area. In total, members of eight subfamilies, 56 genera, and 99 species have been recorded from the Itremo Massif. Grasslands cover 75% of the Itremo Massif Protected Area and are dominated by Panicoideae (65%) and by C₄ plants. The genera Eragrostis and Panicum, with nine and eight species respectively, are the best represented genera in Itremo. Eragrostis betsileensis and Tristachya betsileensis are the two species known to be local endemics. Twenty species are endemic to the central highlands, and a further 14 species are restricted to Madagascar. Five ecological groups of grasses were identified in the Itremo Massif: shade species in gallery forests, open wet area species, fire grasses, anthropogenic disturbance associated grasses and rock-dwelling grasses. Grasslands of the Itremo Massif are likely to be at least partly natural as shown by their richness in terms of endemic and native grass species. Conservation of such grasslands is thus an important issue, not only for grasses but for all species that inhabit these open canopy habitats.

RÉSUMÉ

Malgré la superficie importante occupée par les formations herbeuses de Madagascar (65%), la taxonomie des graminées (Poaceae) dominant ces écosystèmes reste mal connue. Les inventaires effectués dans 12 localités de l'Aire Protégée (AP) du Massif d'Itremo et les travaux d'identification nous ont permis de dresser une liste des espèces de Poaceae de la région. Au total, la liste établie est composée de huit sous-familles, 56 genres et 99 espèces dont la sous-famille des Panicoideae (65 %) et des espèces à photosynthèse en $\rm C_4$ sont les taxons dominants. Les genres $\rm \it Eragrostis$ et $\rm \it Panicum$, avec respectivement neuf et huit

espèces, sont les mieux représentés. Eragrostis betsileensis et Tristachya betsileensis sont les seules espèces localement endémiques, tandis que 20 espèces sont endémiques des hautes terres du centre, et 14 sont endémiques de Madagascar. Cinq groupements de Poaceae qui correspondent à des milieux différents ont été identifiés au sein de l'AP: les espèces ombrophiles des forêts galeries, les espèces de milieux humides ouverts, les espèces associées au feu, les espèces rupicoles et les espèces anthropiques. Les formations herbeuses de l'Itremo seraient au moins en partie d'origine naturelle et ancienne, comme le suggère leur richesse en espèces endémiques et indigènes, et méritent donc d'être conservées, non seulement pour les Poaceae mais pour toutes les autres espèces qui y cohabitent.

INTRODUCTION

Grasses are members of the plant family Poaceae, and are primarily known for their critical role in food provision. Cultivated rice Oryza sativa L., maize Zea mays L., and sugar cane Saccharum officinarum L. are all members of this family. In 2015, 1.104 billion tonnes of these cereals were produced for human consumption (FAO 2015). The second critical role of grasses is their cornerstone function in many of the world's ecosystems. Grasslands as defined by the FAO cover about 26% of the land on Earth (FAOSTAT 2000), and 65% of Madagascar (Moat and Smith 2007). Open canopy vegetation types with a grassy understory have a history of being undervalued compared to closed canopy forest, even when they are known to represent ancient ecosystems (Bond and Parr 2010, Parr et al. 2014, Bond 2016). Many grassy biomes have only recently been recognised as natural and valuable ecosystems (e.g., Bond et al. 2008, Vorontsova et al. 2016). Multiple authors documenting the vegetation of Madagascar (e.g., Koechlin et al. 1974) have traditionally assumed that Malagasy grasslands are degraded formations resulting from the destruction of climax forests.

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Despite their critical role in the landscape, Malagasy grasses have been poorly studied taxonomically, causing a significant species knowledge gap not only in the flora of Madagascar but also in that of the world (Bond et al. 2008). The only comprehensive taxonomic reference published to date is that by Bosser (1969) in his book Graminées des pâturages et des cultures à Madagascar, which is limited to the central highlands and accounts for approximately half of the island's grass species diversity. Recent progress has been made in documenting Madagascar's bamboos, but much remains to be done (Dransfield 1998, 2000, 2003). Accurate grass identification requires careful microscope observation of the reproductive organs, in addition to high quality collection of reference specimens. The superficial similarity of unrelated taxa, the complexity and small size of the flowering structures, and the frequently incomplete specimens can make the identification process challenging, and this has previously discouraged collecting activity. In the national herbarium of the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo (TAN), the majority of grass collections identified to species level are relatively old, largely collected between 1960 and 1970 by the French botanists Jean Bosser and Philippe Morat. This study is part of an ongoing project seeking to document grasses and grasslands of Madagascar, working towards a taxonomic revision of all Poaceae of Madagascar (Vorontsova et al. 2013, Vorontsova and Rakotoarisoa 2014), carried out by the Royal Botanic Gardens Kew and the Kew Madagascar Conservation Centre (KMCC).

This study evaluates the grass diversity in the Itremo Massif Protected Area. We establish a list of species, present an identification key, and survey ecological preferences of the species, building a knowledge platform to study the origin of grasslands in this area.

STUDY SITE

The Itremo Massif Protected Area (PA), managed jointly by the local community and KMCC, was chosen to study the grasses of the Malagasy central highlands. The Itremo Massif PA covers an area of 24 788 ha dominated by grassy biomes (70% of the land area). The choice was justified by an increasing knowledge base of Itremo's flora following ongoing study by the KMCC (Kew Madagascar Conservation Centre 2012). The Itremo Massif PA has been established as a protected area in 2015 (established by decree n° 2015-713 of the Ministry of Environment, Ecology, Sea and Forests), and is located in the southern part of the central highlands. The Itremo Massif is 117 km west of Ambositra, Ambatofinandrahana district, Amoron'i Mania Region, ex-Province of Fianarantsoa, between E046°38'10" and E046°14'35" longitude, and S20° 35' 40" and S20° 35' 36" latitude (Figure 1).

The Itremo Massif PA is surrounded by three villages and two rivers: Itremo village in the east, Amborompotsy and Mangataboahangy villages in the west, Mania river in the north and Matsiatra river in the south. The landscape is dominated by plains interspersed with rocky outcrops. These are composed of micaschistes (at lower elevation; ca. 500 m), quartzite (from 700 to 1500 m), dolomitic marbles (from 900 to 1000 m) and marbles at the summit (> 1500 m; Birkinshaw et al. 2008). Itremo Massif has a subhumid bioclimate, characterized by dry and rainy seasons, an annual average temperature of 19.5°C and an annual average rainfall of 1416 mm, with December, January and February being the wettest months of the year (Cornet 1974; Birkinshaw et al. 2008).

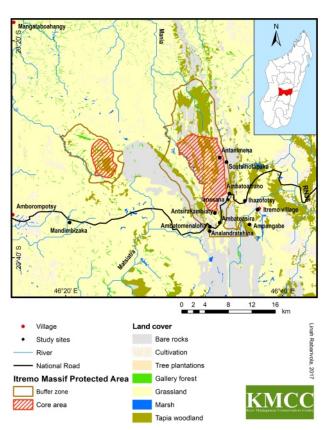


Figure 1. Vegetation map of the Itremo Massif Protected Area. (Map by Linah Rabarivola and the Kew Madagascar Conservation Centre. Study sites are marked with black circles; the checklist also includes older herbarium specimens collected throughout the area with no specific location data)

The Itremo Massif PA is home to 549 known species of plants in 278 genera and 99 families, with 77% of species endemic to Madagascar, and 30 local endemics (Kew Madagascar Conservation Centre 2012). The vegetation of Itremo Massif is composed of gallery forests, tapia forests, grasslands, swamps, and rock outcrops, as well as secondary vegetation types (Birkinshaw et al. 2008, Kew Madagascar Conservation Centre 2012).

METHODS

A field inventory of the grasses was carried out in all habitats of Itremo during repeated visits by the first author in March 2013, February 2014, and June 2014. Local sites surveyed include Ambatoatrano, Ambatoasira, Ambatomenaloha, Ampangabe, Analandratehina, Antanimena, Antsirakambiaty, Ianasana, Ihazafotsy, Itremo village, Mandimbizaka, Soatsihotapaka (Figure 1). Every fertile grass suspected of being a distinct species was collected to make herbarium vouchers distributed to Tsimbazaza (TAN), Kew (K) and Paris (P) herbaria (abbreviations fide Thiers 2015). Habitat metadata, photographs, and silica gel samples were collected, and data were recorded in a BRAHMS (2015) database. Images of all the genera are available online at https://goo.gl/ugyCtJ. Previous collections of grasses in Itremo made by M. S. Vorontsova and by KMCC were added to the dataset as well as all Itremo Poaceae specimens held at K and P herbaria. Occurrence records were used to compile a list of species characteristic of each habitat type.

Reliable species-level identification of the grasses requires dissection of the spikelet, as the spikelet contains almost all characters distinguishing genera and species. Spikelet structure was recorded, including the composition of glumes, florets, lemmas,

paleas, the number of veins and the placement of indumentum, and the size of all spikelet parts. Full drawings of the spikelet dissections were made for at least one member of each genus (example presented in Figure 2). Identification was carried out by reference to existing herbarium collections, and using keys in Bosser (1969), Clayton (1970), Clayton et al. (1974), Clayton and Renvoize (1982), Vorontsova et al. (2013) and Kellogg (2015). The keys were modified and adapted to create an identification key to Poaceae species of Itremo (Supplementary material). Species distribution data are from the World Checklist of Selected Plant Families (2017) and from taxonomic work by the authors. Data on the photosynthetic system is from Osborne et al. (2014) and Kellogg (2015).

RESULTS

POACEAE DIVERSITY. The grasses are a species-rich family represented in the Itremo Massif PA by 56 genera and 99 species (Table S1). These can be identified using the keys provided in the Supplementary Material. Grasses are the most diverse plant family in the Itremo Massif PA. Within the Poaceae these species belong predominantly to the tropical PACMAD clade (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae, 92%), with some also belonging to the temperate BEP clade (Bambusoideae, Ehrhartoideae, and Pooideae, 8%). They belong to eight subfamilies and 14 tribes within the Poaceae according to the classification by Kellogg (2015). With 64 species, the common tropical mesic environment group Panicoideae is the best represented subfamily, followed by the tropical arid subfamily Chloridoideae with 20 species. The temperate Pooideae and the bamboos (Bambusoideae) are represented by just five and three species, respectively. Aristidoideae, Arundinoideae and Micrairoideae are represented by two species each. The rice relatives Ehrhartoideae are represented in the Itremo Massif PA by only one native species, Leersia hexandra. The genera Eragrostis and Panicum sensu lato are the most diverse with nine and eight species respectively. Common tropical grass genera of Africa including Andropogon, Brachiaria (note these have not been moved to the genus Urochloa due to their diverse phylogenetic placements not currently fully resolved), Oplismenus, Setaria, Sporobolus, Digitaria and Hyparrhenia are moderately diverse and represented

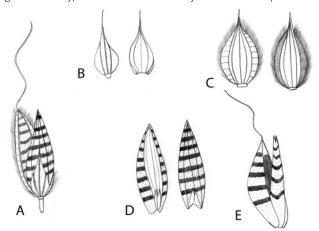


Figure 2. Spikelet dissection of *Alloteropsis semialata*, illustrating dissection work carried out in order to identify grasses through their spikelet structure. (A: spikelet (9 mm long including awn); B: lower glume, dorsal and ventral views (4.5 mm long); C: upper glume, dorsal and ventral views (6 mm long); D: lower floret, ventral and dorsal views (5 mm long); E: upper floret, the upper lemma with awn shown on the left hand side, the immature grain inside (9 mm long including awn). Drawing by Nanjarisoa Olinirina Prisca from *Nanjarisoa 23*, Ampangabe, collection made on 26 March 2013)

by three to five species each. The remaining 47 genera are represented by a single species each. Species with the C_4 photosynthetic system predominate with 68 species, suggesting a flora adapted to open and seasonally dry habitats.

POACEAE BIOGEOGRAPHIC AFFINITIES. The ecological preferences and distribution ranges of the 99 species of Poaceae in the Itremo Massif PA are presented in Table S1 and Figure 3. Two of the species (2%) are narrow endemics only known from the Itremo Massif PA: Eragrostis betsileensis and Tristachya betsileensis (Figure 4). Despite the comparatively low local endemicity, 22 of the species recorded (22.2%) are restricted to the central highlands and a further 12 (12.1%) are endemic to Madagascar. Overall, 36 of the grass species (36.4%) are endemic to the island. The majority of the species (59 species, 59.6%) are thought to be native to Madagascar and also occur in other parts of the world, predominantly in tropical Africa. Only four species have been recorded as likely introduced, a figure which is highly uncertain due to poor records of species origins. The native versus introduced status of Madagascar's grasses is largely unknown and challenging to establish. We have tentatively assigned native status to the majority of African grasses following notes by Bosser (1969), long term taxonomic work by the last author, the authors' personal impression of similarity to African ecosystems, and limited data indicating significant genetic diversity within Malagasy Aristida (Besnard et al. 2014, Hackel et al. 2017).

POACEAE HABITAT PREFERENCES. The greatest diversity of grasses was recorded in fallow fields (41 species, 41.4%) and roadsides (37 species, 37.4%). Both of these habitats are rich in C₄ grasses, particularly from the subfamily Chloridoideae, which are adapted to arid conditions. The characteristic species of fallow fields and roadsides are those commonly observed in disturbed areas all over Madagascar: *Chloris pycnothrix, Cynodon dactylon, Eragrostis tenuifolia* and *Cenchrus polystachios* (Table 1). Environmental heterogeneity was noted as particularly high in the disturbed areas, likely indicating increased species turnover with

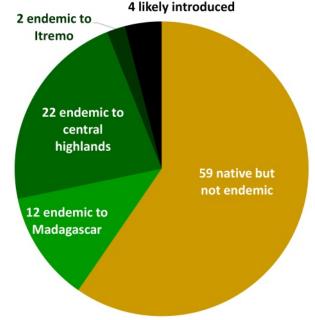


Figure 3. Distribution ranges and likely native/introduced status of the 99 grass species recorded in Itremo.



Figure 4. *Tristachya betsileensis*, locally endemic to Itremo. (Spikelets 12 mm long; live plant scanned using an Epson 10000XL scanner)

dispersal occurring along the road and associated with movement of zebu. The natural habitat with the greatest species diversity was the tapia forest (37 species) and the majority of its grasses were the same as those found in the grassland (34 species). Five species endemic to the highlands were reported in tapia and grasslands, these two habitats sharing a similar continuous grassy understory: *Andropogon ibityensis*, *A. itremoensis*, *Panicum cinctum*, *P. ibityense*, and *P. perrieri*. The highest endemicity was observed on the rocky outcrops. Almost all rocky outcrop grasses sampled are endemic to the central highlands. The Itremo endemic *Tristachya betsileensis* is restricted to these outcrops (Fig-

ure 4). One $\rm C_3$ species (*Styppeiochloa hitchcockii*) highly tolerant of desiccation and able to recover rapidly was also reported in this habitat. The grass flora of gallery forests and marshes, swamps and streamsides (group I: high moisture habitats protected from fire) is clearly distinct from tapia, grassland, rocky outcrops, and disturbed places (group II: dry and sunny habitats with regular fire). Habitats associated with high moisture and no fire are home to a notably diverse Poaceae flora with 33 species recorded in the gallery forests and 32 species in open wet habitats. These are also home to the greatest diversity of subfamilies: Bambusoideae (bamboos) and Ehrhartoideae (rice relatives) have only been recorded in the high moisture and no fire habitats. Species judged to be characteristic of each habitat and their environmental correlates are presented in Table 1.

DISCUSSION

POACEAE DIVERSITY. The Itremo floristic data summary compiled by the Missouri Botanical Garden in 2008 listed 27 species of Poaceae (Birkinshaw et al. 2008). This study has increased threefold the number of grasses recorded, now reaching 99 species. Twenty of these species (including the three endemic bamboos) do not appear in the standard reference book of Madagascar grasses by Bosser (1969). The sharp increase in the number of recorded species has been achieved by our first ever targeted Poaceae survey of this area, which redressed a longterm bias against botanical collecting in similar grassland areas, previously assumed to be botanically depauperate (e.g., Lowry et al. 1997). Specialist skills of spikelet structure observation, working with Poaceae taxonomic reference literature, as well as the use of international herbaria have also made this possible, since some of the species were not represented or not correctly named at TAN. We demonstrate that specialist studies of grasses can reveal previously undocumented diversity. This study presents the first reference list of Itremo Poaceae species and their habitats, to be used in the management of the PA as well as for future diversity and ecosystem research. The subfamily and genus identification keys written during this study are the first for the Itremo Massif PA. We hope that with these keys, other botanists will be able to identify grasses from Itremo and other parts of the highlands.

The new total of 99 Poaceae species in Itremo PA is significantly higher than previous regional grass studies published for Madagascar. This likely reflects a lack of deliberate effort to record the grasses by Lewis et al. (1996) who listed only 18 species in Andringitra National Park, and Gautier (1997) who listed 42 species in the Manongarivo Reserve. The Poaceae specialist Morat (1973) lis-

Table 1. Poaceae species judged to be characteristic of Itremo's habitats.

Groups	Subgroups	Habitats	Characteristic species
Group I: Damp area	Subgroup 1: Shade species,	,	Brachiaria epacridifolia, Brachypodium madagascariense, Isachne
grasses, require	require significant shade, do		mauritiana, Hickelia madagascariensis, Oldeania itremoensis, Oplismenus
permanent soil moisture	not tolerate strong sunlight		hirtellus, Oplismenus flavicomus, Oplismenus compositus, Saccharum
_			perrieri, Acroceras boivinii, Pseudobromus breviligulatus, Panicum mitopus
	Subgroup 2: Open wet	Marshes and swamps,	Adenochloa hymeniochila, Calamagrostis emirnensis, Ischaemum
	habitat	streamsides	polystachyum, Setaria sphacelata, Trichopteryx dregeana
Group II: Dry area grasses,	Subgroup 3: Anthropogenic	Roadsides, fields	Chloris pycnothrix, Cynodon dactylon, Cenchrus polystachios
require prolonged	grasses (highly tolerant to		
exposure to sunlight	disturbance); i.e., ruderal		
	species, weeds of		
	cultivation and roadside		
-	Subgroup 4: Fire grasses;	Tapia forest, grassland	Andropogon ibityensis, Andropogon itremoensis, Ctenium concinnum,
	tolerant of frequent burning		Digitaria ciliaris, Digitaria pseudodiagonalis, Panicum cinctum, Panicum
	or dependent on it		ibityensis
	Subgroup 5: Rock grasses	Rocky outcrops, schiste, quartzite, marble, basalt	Andropogon ivohibensis, Oldeania ibityensis, Setaria bathiei, Styppeiochloa hitchcockii
		quartzito, marbie, basait	TITLOTICOCKII

ted 43 species in Madagascar's southwestern grasslands (species list adjusted to modern taxonomic concepts), which is close to the 34 species we record in Itremo grassland and 37 in Itremo tapia forest. The overall species richness and subfamily composition of Madagascar's grass flora is remarkably close to that of East Africa (Bond et al. 2008; Vorontsova et al. 2016) and most of Madagascar's endemic grass lineages have arrived from tropical Africa (Hackel et al., 2017), leading to the expectation that regional grass checklists in Madagascar may be similar to those in Africa. Specialist Poaceae checklists in three much larger areas of Tanzania have recorded 123 grass species in the Mkomazi National Park (Vollesen et al. 1999), 200 in the Serengeti Ecosystem (Williams et al. 2016), and 239 in the Selous Game Reserve (Vollesen 1980). This is the first study to present regional grass diversity in Madagascar as comparable to equivalent ecosystems in Tanzania.

POACEAE ENDEMICITY. Poaceae endemicity for Itremo is documented here for the first time: 36 species (36.4%) are endemic to Madagascar, and these are present across all vegetation types except the disturbed roadsides and fallow fields. More than a quarter (28%) of the species found in the grasslands are endemic, 38% of those in the tapia forests are endemic, as well as 30% of those on rocky outcrops. For Madagascar as a whole, 217 of 541 grass species are endemic. This country wide endemicity level of 40% is low compared to Madagascar's other plant families (e.g., Buerki et al. 2013), but Poaceae are unlike other families in their broad distribution ranges and lower levels of endemism across the world (e.g., Sandel et al. 2017). Poaceae endemicity in the Malagasy floristic region is in fact in line with other subtropical islands, or somewhat higher than other subtropical islands (Vorontsova et al. 2016). Hence Poaceae endemicity in Itremo is in line with the expectations for a Malagasy natural grass flora.

POACEAE SPECIES ECOLOGY. Our species inventory has documented a complex flora with a different group of grasses defining each of Itremo's habitats, in accordance with their adaptations and evolutionary niches. There is a broad division between two types of strategies: C₃ often broad-leaved forest grasses and bamboos tend to be restricted to high moisture, often shaded, fire protected gallery forest and riverine environments (Table 1: group I), while generally C₄ frequently erect and caespitose species are found in drier open-canopy regularly burned ecosystems (Table 1: group II). Each of these two habitat types is home to endemic species, but the frequently burned habitats of group II have a particularly large number of species restricted to the highlands: Andropogon ibityensis, Andropogon itremoensis, cinctum, Panicum ibityense, Andropogon ivohibensis, Oldeania ibityensis, Setaria bathiei, and Styppeiochloa hitchcockii. Grasses of the quartz and marble rock outcrops have the most restricted distribution ranges. Tapia forest and grassland have almost the same continuous Poaceae ground layer, although some species preferentially grow in the tapia forest (i.e., Panicum ibityense and P. perrieri).

GRASSLAND ORIGINS AND CONSERVATION. Total Poaceae diversity in Itremo correlates with fire, sharp elevational gradients, strong disturbance, and high exposure to sunlight, as expected for a largely C_4 flora with anatomic and biochemical adaptations that allow limiting photorespiration in exposed environments (Sage et al. 1999; Sage 2004). Sixty-eight species (69%) of

the Itremo Poaceae have a C4 photosynthetic system, including seventeen out of 36 Madagascar endemics (47% of Itremo endemic grasses are C₄). Hackel et al. (2017) have documented 45 C₄ grass lineages endemic to Madagascar, with divergences and crown ages compatible with the Miocene grassland expansion 3-8 million years ago (Edwards et al. 2010, Strömberg 2011). It seems plausible that Itremo's C4 grasses diversified and established the grass-dominated ecosystems as part of the global Miocene grassland expansion. However, it is worth noting here that the model of C₃ versus C₄ photosynthetic types signifying open versus closed canopy vegetation is an oversimplification: the different C4 grass clades have different C4 subtypes which occupy quite different ecophysiological niches (Visser et al. 2012, Christin and Osborne 2014). The history of Madagascar's grasses and grasslands is a complex story which needs to be studied carefully by detailed functional ecology studies for the different ecoregions and habitats, clades, and functional groups.

Malagasy grassland has traditionally been assumed to constitute secondary vegetation resulting from human-driven forest degradation (Perrier de la Bâthie 1921, Humbert 1927, Koechlin et al. 1974). A relatively recent shift in thinking has suggested that considerable parts of Malagasy grasslands could be both natural and ancient (Bond et al. 2008, Willis et al. 2008), likely part of the global C₄ grass biome expansion during the Late Miocene-Pliocene (Strömberg 2011, Hoetzel et al. 2013). The commonly cited figure of 90% forest loss across Madagascar has now been thoroughly discredited (McConnell and Kull 2014) and may be nothing but a bibliographic myth (Lowry et al. 1997). Understanding the difference between old growth grasslands and superficially similar secondary vegetation (severely degraded forests, or derived open woodlands) is a complex task (Veldman 2016) which is outside the scope of this study. It is generally agreed that old growth grasslands frequently differ from secondary vegetation by their greater species diversity, and greater species endemicity (e.g., Parr et al. 2014, Veldman et al. 2015, Veldman 2016). Our results demonstrate a high diversity (34 species) and a significant level of endemicity (13 species, 40%) of Poaceae in grasslands of the Itremo Massif PA. Our results thus lend support to possible natural origins of Itremo grasslands. Experimental studies on vegetation response to fire and disturbance regimes are required for further understanding of the likely history of these systems.

These ecosystems need protection to preserve their unique species. Tapia forests and rocky outcrops are already included in the conservation target sites in the Itremo Massif PA, and we suggest grassland could be included in the future. A grassland conservation strategy can only be achieved by first gaining a greater understanding of grassland histories and functional types, something which has not previously been attempted for the central highlands. Moat and Smith (2007) admit their failure to distinguish between the many kinds of open canopy vegetation primarily due to their high seasonality, and a specialist study of these formations is needed. Yet another research gap currently preventing the formation of a grassland conservation strategy is our lack of knowledge of herbaceous non-grass plants found in the grassland understory.

CONCLUDING REMARKS

The first specialised taxonomic inventory of the Itremo Massif Poaceae has revealed this family to be the most diverse of the new protected area, with 99 species in 56 genera and all but four of these believed to be native to the area. Endemicity is low compared to other plant families but in line with the rest of Madagascar's grasses, and high compared to grasses in other parts of the world: 36.4% of the species are endemic to Madagascar, including 22.2% which are restricted to the central highlands, plus two local endemics. As expected, forest grasses intolerant of fire are largely C₃ and form an ecological group distinct from the open canopy grasses which burn regularly and are largely C₄. Significant levels of diversity and endemicity across multiple habitats are comparable to the complex and specialised grass floras of Tanzanian protected areas. The natural habitat with the greatest species diversity is the tapia woodland and the majority of its grasses are the same as those found in the grassland, suggesting ecological similarity between tapia and grassland. More than half of Itremo's grasses are C₄, approximately half of all endemics are also C₄, and these have likely diversified across Madagascar during the global Miocene grassland expansion around 3-8 million years ago. Our data are insufficient for any conclusions on ecosystem identity or origins: nevertheless, this first record of grass diversity and grass endemicity in the grasslands as well as all the other vegetation types is in line with what we would expect to see in natural ecosystems.

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SUPPLEMENTARY MATERIAL

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Table S1. List of Poaceae species recorded in the Itremo Massif Protected Area, their habitats, distribution ranges, and photosynthetic types. (Please note that the native versus introduced status of Madagascar's non-endemic grasses is largely unknown and challenging to establish, and the status presented here is a preliminary one with little data available to support it. In contrast, the endemicity data are presented here with support from herbarium work and a literature review)

Supplementary material 1. Key to the subfamilies of grasses found in the Itremo Massif.

Supplementary material 2. Key to the genera of grasses found in the Itremo Massif.

Table S1. List of Poaceae species recorded in the Itremo Massif Protected Area, their habitats, distribution ranges, and photosynthetic types. Please note that the native versus introduced status of Madagascar's non-endemic grasses is largely unknown and challenging to establish, and the status presented here is a preliminary one with little data available to support it. In contrast, the endemicity data are presented here with support from herbarium work and a literature review.

N	Species	Habitat	Distribution	Photosynthetic type
1	Acroceras boivinii (Mez) A. Camus	Humid forest	Madagascar	C3
2	Adenochloa hymeniochila (Nees) Zuloaga	Gallery forest, rice fields, swamps	Native	C3
3	Agrostis elliotii Hook. ex Scott-Elliot	Degraded Tapia forest	Madagascar	C3
4	Alloteropsis semialata (R.Br.) Hitchc.	Grassland, pine forest	Native	C4
5	Andropogon huillensis Rendle	Seasonally wet places	Native	C4
6	Andropogon ibityensis A.Camus	Tapia forest, rocky outcrops, roadsides	Highlands	C4
7	Andropogon ivohibensis A.Camus	Rocky outcrops	Highlands	C4
8	Andropogon itremoensis Voronts.	Tapia forest, rocky outcrops, roadsides	Highlands	C4
9	Aristida similis Steud.	Tapia forest, grassland, fallow fields and roadsides	Madagascar	C4
10	Aristida tenuissima A.Camus	Open wet places, tapia forest, grassland, fallow fields and roadsides	Highlands	C4
11	Arundinella nepalensis Trin.	Gallery forest, along river	Native	C4
12	Axonopus compressus (Sw.) P.Beauv.	Gallery forest	Likely introduced	C4
13	Bothriochloa bladhii (Retz.) S.T.Blake	Roadsides	Native	C4
14	Brachiaria arrecta (T.Durand & Schinz) Stent	Rice fields	Native	C4
15	Brachiaria bemarivensis A.Camus	Gallery forest, tapia forest	Madagascar	C3
16	Brachiaria epacridifolia (Stapf) A.Camus	Gallery forest	Highlands	C3
17	Brachiaria umbellata (Trin.) Clayton	Fallow fields, roadsides	Native	C4
18	Brachypodium madagascariense A.Camus & H.Perrier	Humid forest	Highlands	C3
19	Calamagrostis emirnensis (Baker) T.Durand & Schinz	Along river, permanent wet places	Madagascar	C3
20	Cenchrus polystachios (L.) Morrone	Roadsides, fallow fields and tapia forest	Native	C4
21	Chloris pycnothrix Trin.	Roadsides and fallow fields	Native	C4
22	Chrysopogon serrulatus Trin.	Roadsides, open grassland, tapia forest	Native	C4
23	Coelachne africana Pilg.	Wet places and swamps	Native	C3
24	Craspedorhachis africana Benth.	Open grassland, wet places	Native	C4
25	Ctenium concinnum Nees	Tapia forest, grassland, rocky outcrops, roadsides	Native	C4

N	Species	Habitat	Distribution	Photosynthetic type
26	Cymbopogon caesius (Hook. & Arn.) Stapf	Tapia forest, grassland, fallow fields and roadsides	Native	C4
27	Cynodon dactylon (L.) Pers.	Roadsides and dry fallow fields	Native	C4
28	Cyrtococcum deltoideum (Hack) A.Camus	Wet places, shade	Madagascar	C3
29	Digitaria ciliaris (Retz.) Koeler	Grassland, rocky outcrops	Native	C4
30	Digitaria longiflora (Retz.) Pers.	Wet places, tapia forest, fallow fields and roadsides	Native	C4
31	Digitaria pseudodiagonalis Chiov.	Tapia forest, grassland, rocky outcrops, fallow fields	Native	C4
32	Eleusine indica (L.) Gaertn.	Grassland, roadsides and fallow fields	Native	C4
33	Elionurus tristis Hack.	Dry fallow fields	Madagascar	C4
34	Eulalia villosa (Spreng.) Nees	Swamp, grassland, fallow fields	Native	C4
35	Eragrostis amabilis (L.) Wight & Arn.	Roadsides and fallow fields	Native	C4
36	Eragrostis aspera (Jacq.) Nees	Dry fallow fields	Native	C4
37	Eragrostis atrovirens (Desf.) Trin. ex Steud.	Gallery forest, tapia forest, roadsides and dry fallow fields	Native	C4
38	Eragrostis betsileensis A.Camus	Near stagnant water	Itremo	C4
39	Eragrostis capensis (Thunb.) Trin.	Streamside, tapia forest, roadsides, fallow fields	Native	C4
40	Eragrostis hildebrandtii Jedwabn.	Roadsides	Madagascar	C4
41	Eragrostis japonica (Thunb.) Trin.	Dry fallow fields	Native	C4
42	Eragrostis lateritica Bosser	Tapia forest, roadsides	Highlands	C4
43	Eragrostis tenuifolia L.	Roadsides and fallow fields	Native	C4
44	Eriochloa fatmensis (Hochst. & Steud.) Clayton	Roadsides	Native	C4
45	Festuca camusiana StYves	Tapia forest	Highlands	C3
46	Heteropogon contortus (L.) P.Beauv. ex Roem. & Schult.	Tapia forest, open area, fallow fields	Native	C4
47	Heteropogon melanocarpus (Elliott) Benth.	Streamside	Native	C4
48	Hickelia madagascariensis A.Camus	Gallery forest	Highlands	C3
49	Hyparrhenia newtonii (Hack.) Stapf	Tapia forest, grassland, roadsides	Native	C4
50	Hyparrhenia rufa (Nees) Stapf	Wet places, tapia forest, grassland, roadsides, fallow fields	Native	C4
51	Hyparrhenia schimperi (Hochst.ex A.Rich) Anderson ex Stapf	Streamside, tapia forest, grassland, roadsides, fallow fields	Native	C4
52	Imperata cylindrica (L.) Raeusch.	Wet places, grassland, open area	Native	C4
53	Isachne mauritiana Kunth	Humid forest	Native	C3
54	Ischaemum polystachyum J.Presl	Along the stream, swamp	Native	C4
55	Ischaemum rugosum Salisb.	Rice fields	Likely introduced	C4

N	Species	Habitat	Distribution	Photosynthetic type
56	Leersia hexandra Sw.	Rice fields, swamp	Native	C3
57	Loudetia simplex (Nees) C.E.Hubb.	Edge of forest, wet places, tapia forest, grassland, rocky outcrops, fallow fields, roadsides	Native	C4
58	Melinis minutiflora P. Beauv.	Edge of forest, tapia forest, grassland, rocky outcrops, roadsides, fallow fields	Native	C4
59	Melinis repens (Willd.) Zizka	Tapia forest, open area, roadsides, fallow fields	Native	C4
60	Microchloa kunthii Desv.	Wet places, tapia forest, roadsides	Native	C4
61	Oldeania ibityensis (A.Camus) D.Z.Li, Y.X.Zhang & Haev.	Rocky outcrops	Highlands	C3
62	Oldeania sp. nov.	Along river	Highlands	C3
63	Oplismenus burmanii (Retz.) P.Beauv.	Fallow fields, undergrowth	Native	C3
64	Oplismenus compositus (L.) P.Beauv.	Humid forest	Native	C3
65	Oplismenus flavicomus Mez	Humid forest	Madagascar	C3
66	Oplismenus hirtellus (L.) P.Beauv.	Humid forest	Native	C3
67	Panicum ambositrense A.Camus	Edge of gallery forest	Highlands	C3
68	Panicum brevifolium L.	Streamside	Native	C3
69	Panicum cinctum Hack.	Wet places, grassland	Highlands	C4
70	Panicum ibityense A.Camus	Forest, tapia forest, rocky outcrops	Highlands	C3
71	Panicum luridum Hack. ex Scott-Elliot	Wet places, grassland	Highlands	C4
72	Panicum mitopus K.Schum.	Gallery forest	Native	C3
73	Panicum perrieri A.Camus	Forest, tapia forest, fallow fields	Highlands	C3
74	Panicum subhystrix A.Camus	Wet places, around the rock, shady place, fallow fields	Highlands	C3
75	Paspalum scrobiculatum L.	Wet places, tapia forest, grassland, roadsides, fallow fields	Likely introduced	C4
76	Perotis patens Gand.	Roadsides, fallow fields	Native	C4
77	Phragmites mauritianus Kunth	Streamside	Native	C3
78	Pseudobromus breviligulatus Stapf ex A.Camus	Humid forest	Madagascar	C3
79	Sacciolepis indica (L.) Chase	Gallery forest, wet places, rice fields	Native	C3
80	Sacciolepis viguieri A.Camus	Tapia forest	Madagascar	C3
81	Saccharum hildebrandtii (Hack.) Clayton	Edge of the gallery forest, near the stream	Highlands	C4
82	Saccharum perrieri (A.Camus) Clayton	Humid forest, near the stream	Highlands	C4
83	Schizachyrium brevifolium (Sw.) Buse	Tapia forest, fallow fields	Native	C4
84	Schizachyrium sanguineum (Retz.) Alston	Edge of gallery forest, tapia forest, grassland, rocky outcrop, roadsides	Native	C4

N	Species	Habitat	Distribution	Photosynthetic type
85	Setaria bathiei A.Camus	Rocky outcrops	Highlands	C4
86	Setaria pumila (Poir.) Roem. & Schult.	Tapia forest, swamp, fallow fields, roadsides, rocky outcrops	Likely introduced	C4
87	Setaria scottii (Hack.) A.Camus	Forest, wet rocky places	Highlands	C4
88	Setaria sphacelata (Schumach.) Stapf & C.E.Hubb. ex Moss	Forest, wet places	Native	C4
89	Sporobolus centrifugus (Trin.) Nees	Tapia forest, grassland, roadsides, fallow fields	Native	C4
90	Sporobolus paniculatus (Trin.) T.Durand & Schinz	Roadsides	Native	C4
91	Sporobolus piliferus (Trin.)Kunth	Tapia forest, rocky outcrops, roadsides, fallow fields	Native	C4
92	Sporobolus pyramidalis P.Beauv.	Tapia forest, grassland, roadsides	Native	C4
93	Stenotaphrum unilaterale Baker	Undergrowth	Highlands	C4
94	Styppeiochloa hitchcockii (A.Camus) Cope	Rocky outcrops	Madagascar	C3
95	Trichanthecium brazzavillense (Franch.) Zuloaga & Morrone	Forest, wet places, grassland	Native	C3
96	Trachypogon spicatus (L.f.) Kuntze	Humid forest, tapia forest, grassland, rocky outcrops, roadsides	Native	C4
97	Trichopteryx dregeana Nees	Forest, swamp, grassland, roadsides	Native	C4
98	Tristachya betsileensis A.Camus	Rocky outcrops	Itremo	C4
99	Urelytrum agropyroides (Hack.) Hack.	Grassland, tapia forest, swamp, rocky outcrop, fallow fields	Native	C4

SUPPLEMENTARY MATERIAL 1. Key to the subfamilies of grasses found in the Itremo Massif.

1. Woody stem, usually developed more than 1m long or climbing,	
dimorphic leaves	MBUSOIDEAE
1'. Herbaceous stem, if the stem is woody and more than 1m long the leaves are not	dimorphic 2
2. Spikelet always with two florets with no rachilla extension	3
2'. Spikelet with one to many florets, rachilla extension present or absent	4
3. Upper floret bisexual, lower floret male or sterile	PANICOIDEAE
3'. Both florets bisexual	CRAIROIDEAE
4. Ligule an entire membrane	5
4'. Ligule a fringe of hairs, with or without membrane	6
5. Lodicules membranous, nerves widely spaced	POOIDEAE
5'. Lodicules fleshy, narrowly spaced	
6. Spikelet with one fertile floret	7
6'. Spikelet with many fertile florets	9
7. Lemma terminated by a 3 awns forming a column in the base	ISTIDOIDEAE
7'. Lemma awnless, or with one awn, or with many awns but not merged in the base	8
8 . Fertile floret subtended by 2 sterile floretsEHRHARTOIDEAE (<i>Le</i>	ersia hexandra)
8'. Fertile floret not subtended by a sterile florets	LORIDOIDEAE
9. Grasses habitually growing along the river, or small grass typically on	
the rock or characteristic of inselberg or rocky outcropARU	JNDINOIDEAE
9'. Grasses generally a small size, not typical of inselbergs	LORIDOIDEAE

SUPPLEMENTARY MATERIAL 2. Key to the genera of grasses found in the Itremo Massif.

1. Grass with woody stem, dimorphic leaves	2
(Hickelia, Oldeania)	
1'. Grass with herbaceous stem, leaves not dimorphic	3
2. Stem climbing	
2'. Stem erect	
3. One-many florets per spikelet	4
3'. Always 2 florets per spikelet, lower floret male or sterile, upper floret	oret bisexual21
4. Spikelet with one bisexual floret	5
(Aristida, Leersia, Sporobolus, Calamagrostis, Agrostis, Microchloa,	Ctenium, Perotis,
Craspedorhachis, Chloris, Cynodon)	
4'. Spikelet with 2 to many bisexuals florets	15
(Phragmites, Styppeiochloa, Eragrostis, Eleusine, Brachypodium, Fe	stuca, Pseudobromus)
5. Lemma with 3 awns	Aristida (2)
5'. Lemma awnless or with one awn	6
6. Lemma coriaceous, glumes absent	Leersia (hexandra)
6'. Lemma membranous, at least 1 glume present	7
7. Inflorescence of several racemes distributed along on a central axis	s Craspedorhachis (africana)
7'. Inflorescence a single raceme, digitate raceme, or a panicle	8
8. Glumes with an oblique awn, inflorescence a solitary raceme	Ctenium (concinnum)
8'. Glumes awnless	9
9. Florets enveloped by glumes, inflorescence a solitary raceme	10
9'. Florets not enveloped by glumes, inflorescence of digitate raceme	s 11
10. Inflorescence a curved raceme, lemma awnless	Microchloa (kunthii)
10'. Inflorescence an erect raceme, lemma awned	Perotis (patens)
11. Inflorescence a digitate raceme	12
11'. Inflorescence a simple raceme or a panicle	13
12. Lemma awned	
12'. Lemma awnless	
13. At least one the glume longer than floret	
13'. Both glumes shorter than or equal to the floret	Sporobolus (4)
14. Lemma awned; inflorescence an open panicle, soft and light	
14'. Lemma awnless, inflorescence a stiff narrow panicle	
15(4'). Grass similar to reeds, more than 1m tall	Phragmites (mauritianus)
15'. Grass not similar to reeds, less than 1 m tall	
16. Typical of inselbergs or rocky outcrop, leaves stiff in basal rosette	
16'. Not occurring on inselbergs or rocky outcrops, leaves soft and po	ositioned on the culm17
17. Inflorescence a simple raceme, pedicel 1-3mm long	hypodium (madagascariense)

17'. Inflorescence a panicle or subdigitate racemes, pedicel more than 3mm long
18. Glumes acuminate; inflorescence a fragile pendent panicle
18'. Glumes rounded to acute; inflorescence an erect panicle or subdigitate raceme20
19. Glumes weakly acuminate, leaf blades with indistinct transverse nerves
19'. Glumes long-acuminate, leaf blades with clear transverse nerves Festuca (camusiana)
20. Inflorescence of subdigitate racemes, raceme terminated by a fertile spikelet Eleusine (indica)
20'. Inflorescence a panicle
21(3'). Spikelets break up at maturity, glumes remain on the plant
(Arundinella, Tristachya, Trichopteryx, Loudetia)
21'. Entire spikelets detach at maturity
(Cenchrus, Cyrtococcum, Sacciolepis, Eriochloa, Acroceras, Panicum, Trichanthecium,
Oplismenus, Alloteropsis, Brachiaria, Paspalum, Axonopus, Melinis, Digitaria, Stenotaphrum,
Saccharum, Imperata, Eulalia, Trachypogon, Chrysopogon, Bothriochloa, Andropogon,
Schizachyrium, Heteropogon, Ischaemum, Cymbopogon, Hyparrhenia, Urelytrum, Elionurus,
Setaria)
22. Ligule a short membrane
22'. Ligule a line of hairs
23. Lower lemma 5-7-nerved
23'. Lower lemma 3-nerved 24
24. Lobes of upper lemma awned
24'. Lobes of upper lemma awnless
25(21'). Spikelets solitary, all spikelets similar
(Cenchrus, Cyrtococcum, Sacciolepis, Eriochloa, Acroceras, Panicum, Trichanthecium,
Oplismenus, Alloteropsis, Brachiaria, Paspalum, Axonopus, Setaria)
25'. Spikelets paired or in groups of three, spikelets similar or different to one another
(Saccharum, Imperata, Eulalia, Trachypogon, Chrysopogon, Bothriochloa, Andropogon,
Schizachyrium, Heteropogon, Ischaemum, Cymbopogon, Hyparrhenia, Urelytrum, Elionurus)
26. Spikelets subtended by a thick bristles, bristles falling with the spikelet
26'. Spikelets not subtended by a thick bristles or subtended by thick bristles which persist on the
rachis
27. Upper lemma hyaline to coriaceous at maturity, margins inrolled
(Cyrtococcum, Sacciolepis, Eriochloa, Acroceras, Panicum, Trichanthecium, Oplismenus,
Alloteropsis, Brachiaria, Paspalum, Axonopus, Setaria)
27'. Upper lemma cartilaginous or chartaceous, margins thin and flat
(Melinis, Digitaria, Stenotaphrum)
28. Upper floret laterally compressed
28'. Upper floret dorsally compressed
29. Inflorescence an open or contracted panicle
(Sacciolepis, Setaria, Eriochloa, Acroceras, Panicum, Trichanthecium)

29'. Inflorescence a raceme	36
(Oplismenus, Alloteropsis, Brachiaria, Paspalum, Axo	nopus)
30. Inflorescence a contracted panicle	
30'. Inflorescence an open panicle	32
31. Spikelet inflated at the base, no bristles	Sacciolepis (2)
31'. Spikelet not inflated at the base, subtended by one	e to many persistent bristles
32. Spikelet supported by a globular ring	Eriochloa (fatmensis)
32'. Spikelet supported by a stipe or a straight pedicel	33
33. Upper glume and lower lemma compressed in tip,	upper lemma with a crest
	Acroceras (boivinii)
33'. Upper glume and lower lemma not compressed in	
34. Inflorescence axis and leaf sheaths with glandular	hairs Adenochloa (hymeniochila)
34'. Inflorescence axis and leaf sheaths without glands	ılar hairs35
35. Ligule a fringed membrane, upper glumes and low	
35'. Ligule membranous, glumes and lemmas with fev	
36(29'). Glumes and lemmas awned	37
36'. Glumes and lemmas awnless	
37. Spikelets laterally compressed, glumes without broadless.	
37°. Spikelets dorsally compressed, glumes with brow	-
38. Lower glume present	
38'. Lower glume absent	
39 . Spikelets rounded	
39'. Spikelets acute	-
40(27'). Spikelets laterally compressed	` ,
40'. Spikelets dorsally compressed	
41. Inflorescence composed of free digitate or subdigi	
41'. Inflorescence composed of reduced racemes on a	
	Stenotaphrum (unilaterale)
42(25'). Internodes of inflorescence rachis and pedice	
42'. Internodes of inflorescence rachis and pedicel of	, , ,
-	1
43. The two spikelets in a pair are similar	44
(Imperata, Saccharum, Eulalia) 42! The two criticalets in a pair are different	16
43'. The two spikelets in a pair are different	
	on, Schizachyrium, Heieropogon, Ischaemum,
Cymbopogon, Hyparrhenia, Elionurus) 44. Both spikelets in a pair pedicelled	Impovata (ovlindvica)
44'. One of the spikelets in a pair sessile	_ , , ,
45. Inflorescence a panicle, leaves basal	
45'. Inflorescence digitate, leaves present on the culm	
46(43'). Sessile spikelet male or sterile, pedicelled spi	
40(43). Sessife spikelet mate of sterne, pedicented spi	
•••••••••••••••••••••••••••••••••••••••	Truchypogon (spicalus)

46'. Sessile spikelet bisexual, pedicelled spikelet male or sterile and awnle	ess47
47. Inflorescence a panicle with whorled branches, spikelets in groups of	three
	Chrysopogon (serrulatus)
47'. Inflorescence a solitary raceme or a digitate or false panicle, spikelets	
48. Pedicel and rachis internode with a translucent line in the middle	Bothriochloa (bladhii)
48'. Pedicels and rachis without translucent line in the middle	49
49. Raceme solitary	50
(Schizachyrium, Heteropogon, Elionurus)	
49'. Racemes 2-50	52
(Ischaemum, Cymbopogon, Andropogon, Hyparrhenia)	
50. Lower glume of sessile spikelet 2-keeled	
50'. Lower glume of sessile spikelet convex and rounded	51
51. Racemes with prominent awns	
51'. Racemes awnless	Elionurus (tristis)
52. Lower floret of sessile spikelets male, palea present	Ischaemum (2)
52'. Lower floret of sessile spikelets sterile and reduced to lemma only	53
53. Lower glume of sessile spikelets rounded and furrowed	
53'. Lower glume of sessile spikelets 2-keeled	54
54. Racemes retrorse and usually appressed	
54'. Racemes erect	