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Grassland, woodland, and forest are three key vegetation types that co-occur across the central highlands of Madagascar, where the woodland has historically been considered as degraded forest. Here, we use grass functional traits to inform our understanding of the biogeography of Malagasy vegetation and the differentiation of vegetation types in the region. We sampled grass community composition at 56 sites across the central highlands of Madagascar spanning grassland, woodland, and forest. We selected seven functional traits known to correlate with different aspects of life history collated via *GrassBase* (habit, culm type, physiology, leaf consistency, plant height, leaf width, and leaf length) for the 71 constituent species. Via analyses of the beta diversity, rank abundance, functional dispersion, functional group richness, and community phylogenetic structure of grassland communities, we differentiate these vegetation types using plant functional traits. Grassland and woodland are highly similar in grass species composition and dominated by the same species (*Loudetia simplex*, *Trachypogon spicatus,* and *Schizachyrium sanguineum*). In contrast, forest grass species composition significantly differs from both grassland and woodland. Consistent with these species composition patterns, the vegetation types can be distinguished based on physiology, culm type, and leaf consistency. Forests harbor primarily C_3 grasses, which are almost invariably laterally spreading with herbaceous leaves. In contrast, both grassland and woodland species are predominantly tall, caespitose C_4 grasses with coriaceous leaves. Forest grasses are phylogenetically clustered and less diverse than the grassland and woodland communities. Further, we sampled bark thickness of the common woody species occurring in the woodland and forest of the region and found that the relative bark thickness of the woodland tree species was significantly greater than that of forest species from the same genus. We found that the functional traits and architecture of grasses diverge strongly between forest and the grassland-woodland mosaic. We conclude that the woodlands, primarily dominated by *Uapaca bojeri* Baill., are a form of savanna and not forest as has been previously suggested.

Keywords: functional traits, species diversity, grassland, Poaceae, woodland, forest, savanna, *Uapaca bojeri*

INTRODUCTION

Forest and savanna are vegetation types that can co-occur within landscapes and found in areas with similar climate and soils (Bond, 2005; Bond and Parr, 2010; Charles-Dominique et al., 2015). While savanna and forest can appear superficially similar in terms of the density and number of trees, the functional traits of the trees of each vegetation type differ (Ratnam et al., 2011; Griffith et al., 2017). Savanna and tropical grasslands are open canopy environments with variable tree cover and a continuous grassy ground layer (Bond et al., 2003a; Bond, 2008; Lehmann et al., 2009; Bond and Parr, 2010; Edwards et al., 2010). Defining the functional nature of a vegetation type is often linked to a broader issue of vegetation classifications based on structural associations and even climatic definitions (Schimper and Fisher, 1903; Whittaker, 1975; Scholes and Hall, 1996; Woodward et al., 2004), and often almost entirely based on the woody components of vegetation. The Food and Agriculture Organization of the United Nations (FAO) defines forest as land spanning more than 0.5 ha with more than 10% tree canopy cover and trees higher than 5 m (or having the potential to reach a height of 5 m; FAO, 2006). Alternatively, the United Framework Convention on Climate Change (UNFCCC) defines thresholds of 0.5–1.0 ha forested land, 10–30% tree canopy cover, and 2–5 m tree height. While savannas are defined as mixed tree–grass systems with a discontinuous tree canopy in a continuous grass layer (Scholes and Archer, 1997; House et al., 2003), the notion of the limits of tropical grassy vegetation types as being defined by dominance of C_4 grasses in the ground layer is more recent (Bond, 2008). House and Hall (2001) described savannas as a continuum between tropical forests and grasslands and use the term to include all plant communities from treeless grasslands to closed canopy woodlands. In other literature, grasslands encompass non-woody and woody grasslands (savannas, woodlands, shrublands, and tundra) together (White et al., 2000) because they are defined as terrestrial ecosystems dominated by herbaceous and shrub vegetation, maintained by fire, grazing, drought, and/or freezing temperatures.

Persistent confusion around the delineation of vegetation types often centers on the limited ecological information in structural definitions (Ratnam et al., 2011; Parr et al., 2014; Lehmann and Parr, 2016). While structural definitions offer precision, they are inadequate when the functional responses of forest and savanna plant species to processes such as fire, herbivory, and drought differ (Lehmann et al., 2011). Several studies have shown functional trait differences between trees of forests and savannas in South America (Hoffmann et al., 2003, 2005, 2012), Australia (Lawes et al., 2013) and Africa (Charles-Dominique et al., 2015), all demonstrating that savanna trees have morphological and physiological traits which make them adapted to the frequent fires that characterize savannas in high rainfall regions (Ratnam et al., 2011; Charles-Dominique et al., 2015). Hoffmann et al. (2003, 2012) showed that bark thickness is a key trait to attain fire-resistance threshold and savanna species have thicker bark than forest species, thereby reducing the risk of stem death during fire.

However, the composition and traits of the grassy ground layer are often neglected yet responsible for the physiognomic structure of vegetation (Bond, 2008), promoting either fire, or herbivory due to grass productivity and architecture (Knapp et al., 1998; Sage and Monson, 1998; Archibald and Hempson, 2016). On the other hand, C_4 grasses are considered absent from forest understorey, which can be dominated by herbaceous life forms (Ratnam et al., 2011). However, some C_4 grasses are known from forest understories [e.g., *Setaria palmifolia* (J. Koenig) Stapf, *Microstegium nudum* (Trin.) A. Camus, and *Digitaria radicosa* (J. Presl) Miq. (Clayton, 1970)]. There are numerous areas of the world where C_3 grasses either dominate or co-dominate with C_4 grasses and these are still considered savanna [e.g., Neotropical savannas (Cabido et al., 1997; Bremond et al., 2012), and tropical savannas in Africa and Australia (Lattanzi, 2010)]. Overall, the focus of studies examining the functional traits of vegetation in distinguishing forest and savanna has been woody rather than grass species (Hoffmann et al., 2003, 2005, 2012; Ratnam et al., 2011; Lawes et al., 2013; Charles-Dominique et al., 2015). While photosynthetic pathway is no doubt of high relevance, this focus also belies important functional variation among grasses of the same photosynthetic pathway (Forrestel et al., 2015; Simpson et al., 2016).

Across Madagascar, a mosaic of grassland covers 65 % of the island and in the central region, it is interspersed with subhumid forest, along with extensive areas of woodland (Moat and Smith, 2007). In this region, woodlands are dominated almost solely by *Uapaca bojeri* Baill. (commonly called Tapia) in association with a few other woody species that belong to families endemic to Madagascar, especially Sarcolaenaceae (*Leptolaena pauciflora* Baker, *Sarcolaena oblongifolia* F. Gérard, *Schizolaena microphylla* H. Perrier) and Asteropeiaceae (*Asteropeia densiflora* Baker, *A. labatii* G.E. Schatz, Lowry & A.-E. Wolf). Malagasy grasslands and savannas have long been considered as anthropogenically derived, the result of forest degradation via clearing, and altered fire and grazing regimes over the last 2,000 years (Perrier de la Bâthie, 1921; Humbert, 1927; Koechlin et al., 1974; Lowry et al., 1997). As such, woodlands of the central highlands have been historically and persistently classified as degraded forests (Koechlin et al., 1974; White, 1983; Faramalala, 1995) and managed as such through suppression of fire (Kull, 2002). Recent studies however support early origins of these extensive grasslands with their numerous endemic grass, forb, and animal species that evolved locally millions of years before human colonization (Bond et al., 2008; Vorontsova et al., 2016; Hackel et al., 2018), which occurred only a few 1,000 years before present (Pierron et al., 2017). Grassland, woodland and forest co-occur in the central highlands of Madagascar with changes in vegetation types occurring over small scales, often just meters where there are no discernible differences in climate and soils. These mosaics offer an opportunity to study the functional and compositional characteristics of the ground layer among these vegetation types to identify the disturbance regimes each is adapted to. Within Poaceae are a broad suite of architectural and morphological functional traits commonly assessed in woody plants, but little explored in grasses. In this study, we examine the composition and functional traits of grass communities

among these three vegetation types to quantify differences in community composition and grass functional traits. This allows us to test whether any differences map to vegetation types, in a region where woodlands have long been considered degraded forests but where limits between woodland and grassland appear idiosyncratic. We then assess the phylogenetic structure of each vegetation type as an indicator of its evolutionary history. Finally, as an independent test of vegetation type differences, i.e., savanna vs. forest, we compare the relative bark thickness of woody species, including closely related species of *Uapaca* that characterize woodland and forest, to determine whether functional traits known to differ between forest and savanna can corroborate findings of the grass communities. We hypothesize that grassland and woodland harbor a high phylogenetic diversity of grass species which have evolved for a long period before human arrival. We predict a functional similarity between grassland and woodland grass community, where light availability and fire regimes are similar. In contrast, forest vegetation, characterized by a low-light environment in the ground layer, will select for a different grasses community with another set of functional traits.

MATERIALS AND METHODS

Study Sites

The grass flora was sampled at 56 sites distributed across the central ecoregion of Madagascar, which measures 192,141 km^2 (Humbert, 1955) (**Figure 1** and **Supplementary Table 1**). From North to South, Ibity, Ambatofinandrahana, Itremo, Ambalavao, Andringitra, Isalo, and Ihorombe were the study locations. Rajeriarison and Faramalala (1999) categorized the climate of these regions as subhumid with a mean annual rainfall ranging from 1,000 to 1,500 mm and 5–7 months of dry season. The elevation ranges from 800 to 1,800 meters and soils are primarily ferrallitic, on sandstone and basement gneiss (Moat and Smith, 2007). Fire regime in the sites is every one to 3 years (Alvarado et al., 2018). In our study, we are going to use "grassland" for treeless vegetation, consisting of continuous C$_4$ grass layer, and "woodland" for woody grasslands. Forest is defined as closed-canopy vegetation, with no C$_4$ grass layer. We selected sites considered as undisturbed by the absence of invasive species and overgrazing. Each site was in an area of uniform vegetation that was a minimum of 60 m wide. We sampled 24 sites of grassland, 20 sites of tapia (*Uapaca bojeri*) dominated woodland with herbaceous layer and 12 sites of gallery forest.

Data Collection

Grass Species Composition

Based on the sampling method described by Vorontsova et al. (2016), we collected data on grass species composition at 56 sites; data from 17 sites from Vorontsova et al. (2016) that met the above criteria were also included. The method focuses on grass species composition and frequency and consists of four transects. First, all grass species within a center circle plot of one meter diameter were documented. Then, from the center point, four 25-m transects, each following a random direction (based on a compass bearing), were laid out. Along each transect, the same

circular plot of one-meter diameter was sampled at five-meter intervals, representing grass species composition over 16.5 m^2 for a single site (see **Supplementary Table 1**).

Grass Functional Traits

Across these 56 sites, 71 grass species were recorded, and for each species, seven functional traits were collated: (1) habit (annual, perennial); (2) culm type (prostrate, decumbent, ascendant, erect); (3) leaf consistency (herbaceous, coriaceous); (4) culm height; (5) leaf width; (6) leaf length, and (7) photosynthetic pathway. These traits were derived from *GrassBase*, a global database of 11,369 standardized grass species descriptions compiled from taxonomic literature (Clayton et al., 2006). These data were supplemented from literature (Bosser, 1969; Van Oudtshoorn, 2002) and by data gathering from multiple herbarium specimens held at the herbarium of the Parc Botanique et Zoologique de Tsimbazaza and the Royal Botanic Gardens, Kew, UK. Photosynthetic pathway data were obtained from the checklist of Osborne et al. (2014); for species with an undetermined pathway, it was inferred from their position in known C$_3$ or C$_4$ lineages (Hackel et al., 2018).

The choice of these seven traits was based on their role related to light acquisition and flammability. The annual or perennial habit of the species was recorded. In *GrassBase,* perennials are described as possessing one or more of the following: rhizome or rootstock; a compact mass of dead basal sheaths remaining from previous year's growth; dormant buds in the basal leaf axils for the following year's growth. Annual grass species are commonly considered more abundant than perennials in disturbed habitats, even those with frequent fire (Grime, 1977; Pitelka, 1977). Culm type was categorized into four types: prostrate (lying flat), decumbent (lying along the ground, but with culm apex upright), ascendant (growing upward after an initial horizontal segment) and erect (fully upright) (Beentje, 2010). A prostrate culm type is expected to aid light interception in shaded environments by minimizing self-shading within the plant via lateral spreading (Falster and Westoby, 2003). Erect life forms tend to be species with intravaginal buds [buds between leaf sheaths, not breaking through them to form stolons and rhizomes as in extravaginal buds (Brejda et al., 1989)], that can increase protection of buds from fire, but also confine the architecture of a grass by preventing lateral spreading as by definition these grass species cannot root at the node (Linder et al., 2018), and are therefore generally associated with environments characterized by frequent fire and high light. Depending on the toughness of the leaf blade, we recorded leaf consistency which was categorized into two groups: coriaceous [leathery, tough (Beentje, 2010)], or herbaceous [with the texture of herb, soft and pliable (Beentje, 2010)] leaves.

Data Analysis

Environmental Occurrence of Grassland, Woodland, and Forest

The central highlands were delimited following Humbert's (1955) ecoregion map classifying it as "Central ecoregion." The vegetation map developed by Moat and Smith (2007) was used to define the limits of our three vegetation types. Vegetation
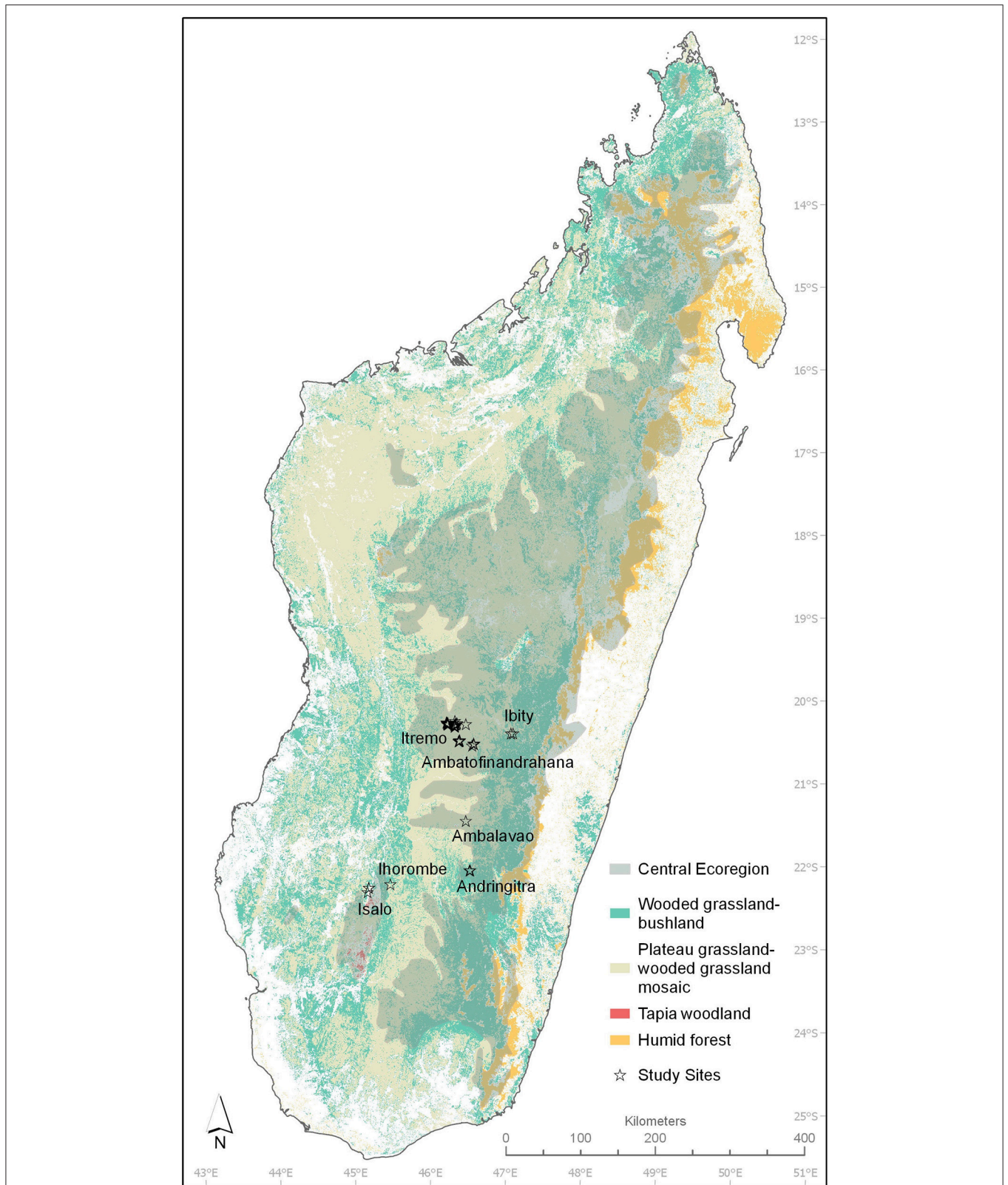
FIGURE 1 | Map of the central ecoregion as per Humbert (1955); grassland ("plateau grassland—wooded grassland mosaic and wooded grassland—bushland," tapia woodland and humid forest distribution as per Moat and Smith (2007) and the study sites location.

units classified as "plateau grassland—wooded grassland mosaic and wooded grassland—bushland," "tapia forest" and "humid forest" in the vegetation map correspond, respectively to our studied vegetation types grassland, woodland, and forest. Any other vegetation units in the vegetation map were omitted from our analysis. The distribution of the three vegetation types across climatic variables (Bio_1: annual mean temperature and Bio_12: annual precipitation) obtained from Worldclim Global Climate Data version 2 (Fick and Hijmans, 2017), within the central ecoregion was plotted (see **Supplementary Figures 1, 2**). The variables were downloaded at 30 s spatial resolution. From these, we have generated datasets per climatic variable for our studied ecoregion. Data for each environmental variable were ordered from lowest to highest and binned in the relevant 1°C and 50-mm intervals, respectively. Due to the very high density of points within each bin, we randomly subsampled our data into 1,000 points, using 1,000 iterations, without replacement. For the subsampled data within each interval, the probability of the presence of each of the three vegetation types was calculated as the mean of all points within the temperature and precipitation interval and the standard errors were calculated for each proportion. The probability was then plotted against Bio_1 and Bio_12 to compare the distribution of grassland, woodland and forest within the region. We fitted our 56 sampled sites within the temperature and precipitation gradient as rugs on each x-axis of the probability plots. For each temperature and precipitation interval, the area of land covered by each vegetation was plotted. From the raw climate data, the area of each vegetation type was obtained by counting the number of points within each interval as each point corresponds to one kilometer square of land.

Grass Species and Trait Composition

We examined the composition of grass communities from three distinct vegetation types as defined by their woody component (or its absence) and its traits: grassland, woodland and forest. All statistical analyses were performed in R 3.0.2 (R Core Team, 2013). We used permutational multivariate analysis of variance (PERMANOVA) using the Bray–Curtis dissimilarity (see **Supplementary Table 2**) and accounted for spatial autocorrelation by including latitude and longitude as predictor variables to assess differences in plant community composition between the three vegetation types, with the R package "vegan" (Oksanen et al., 2016). Grass species and tribes were ranked by frequency per vegetation type with the "BiodiversityR" package (Kindt and Coe, 2005).

To measure species functional diversity in each vegetation type, we computed the functional dispersion index (FDis) which estimates the dispersion of species in a trait space, based on principal coordinate analysis (PCoA) and calculated on a Gower dissimilarity matrix (Gower, 1971; Laliberté and Legendre, 2010) with the "FD" package (Laliberté et al., 2014). We compared the three vegetation types in terms of FDis with an analysis of variance (ANOVA) while accounting for spatial autocorrelation. A functional group richness (FGR) was used to group grass species based on functional traits, using the same package. The resulting dendrogram was plotted against the functional traits.

The number of clusters was identified visually on the resulting dendrogram.

Community phylogenetic structure was assessed per site to test how closely related the average pair of grass individuals were in each vegetation type. We used a Bayesian time-calibrated phylogenetic tree of the 71 species sampled (**Supplementary Figure 3**) extracted from a larger analysis of Malagasy grass species (Hackel et al., 2018). Hackel et al. (2018) did not include *Andropogon trichozygus* Baker, *Hyparrhenia variabilis* Stapf and *Ischaemum polystachyum* J. Presl, which were replaced with the closest available species [*Andropogon huillensis* Rendle, *Hyparrhenia schimperi* (Hochst. ex A. Rich.) and *Ischaemum koleostachys* (Steud.) Hack., respectively]. The species richness (Whittaker, 1972) within each vegetation type was calculated. Phylogenetic relatedness of species within grassland, woodland, and forest was measured via phylogenetic diversity (PD) index (Faith, 1992). The differences in species richness and phylogenetic diversity between vegetation types were assessed with a generalized linear model (GLM) with a Poisson distribution and log link function. The net relatedness index (NRI) and nearest taxon index (NTI) (Webb, 2000; Webb et al., 2002) for each site was calculated with the "picante" package (Kembel et al., 2010). The observed phylogenetic relatedness was compared to the expected pattern using the functions ses.mpd and ses.mntd with the "richness" null model, not taking into account species abundances in each plot, and using 999 randomizations.

Tree Bark Thickness

The bark thickness and stem circumference of 39 individuals of *Uapaca bojeri* in woodlands, and 27 samples from 16 species in forest (listed in **Supplementary Table 3**) were measured at Isalo National Park and on wood samples from humid forest in the East of Madagascar, available at the forestry department of Antananarivo University, respectively. The tree species from Eastern humid forest are mostly dominant species in our study region (KMCC, 2012). A *t*-test was used to compare bark thickness between *Uapaca bojeri* dominated woodland and forest species, and as bark thickness varies with tree size (Werner and Murphy, 2001; Lawes et al., 2011), measures of bark thickness were transformed into relative bark thickness (the ratio of individual bark thickness to stem diameter; Lawes et al., 2013) prior to analysis.

RESULTS

Distribution of Grassland, Woodland, and Forest Across Temperature and Precipitation

Across the central ecoregion mean annual temperature ranges from 11 to 27°C and mean annual rainfall ranges from 764 to 2,660 mm per year. Here, grassland has a greater than 50% probability of occurrence where mean temperatures range from 16 to 22°C, and a 90% of probability of occurrence where temperature ranges from 11 to 12°C and 22 to 27°C. Grassland
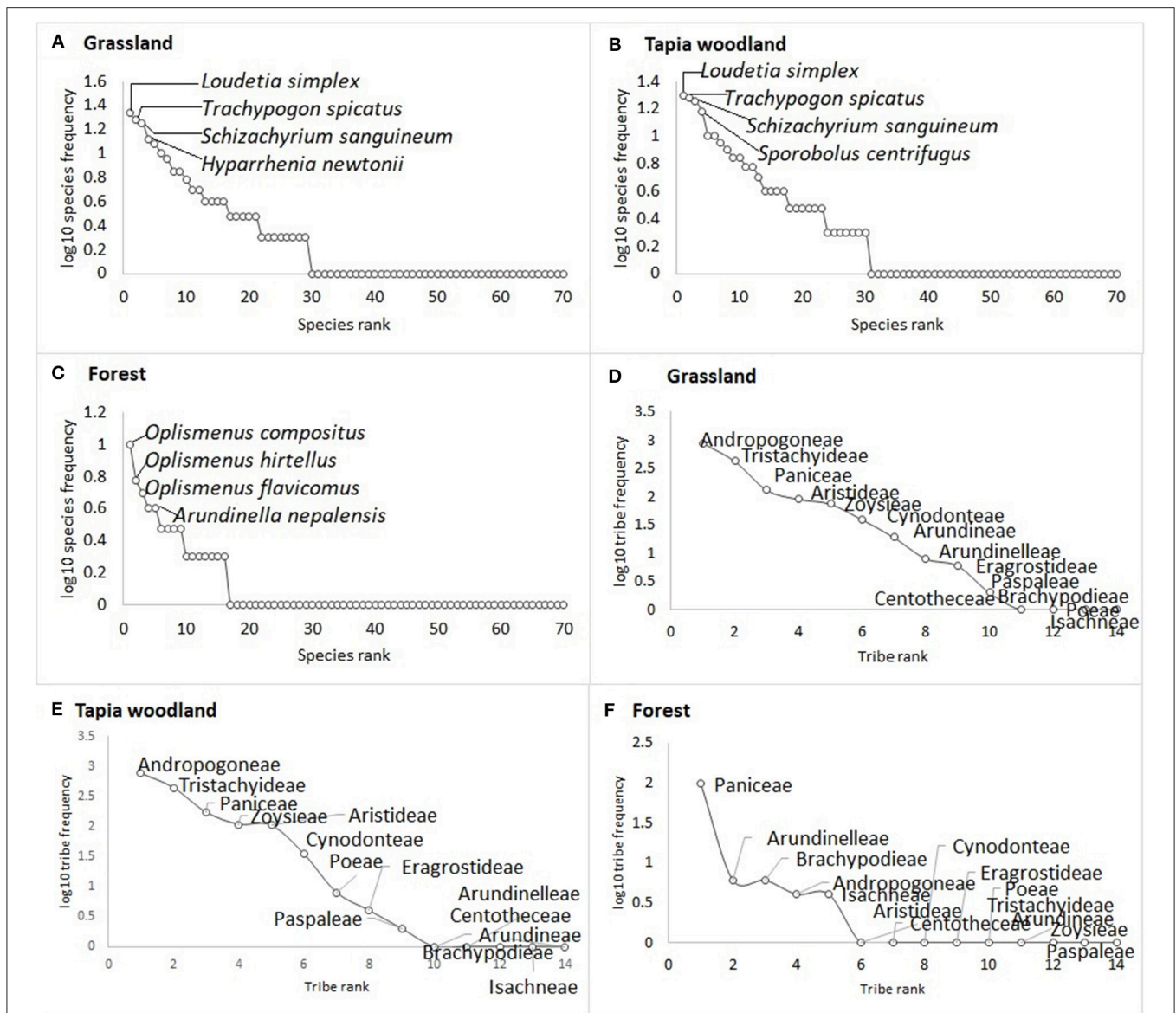
FIGURE 2 | Species rank frequency **(A–C)** and tribe rank frequency **(D–F)** for the 71 grass species sampled within grassland, tapia woodland and forest. The same three species, belonging to the same tribes are the most frequent in grassland and tapia woodland. Forest habitat is dominated by *Oplismenus* species, in the Paniceae tribe.

has a >50% probability of occurrence where rainfall ranges from 764 to 864 mm and from 1,160 to 1,760 mm, and a 90% or greater probability of occurrence where rainfall ranges from 864 to 1,160 mm. The probability of forest occurrence is >50% where temperature ranges from 13 to 15°C and mean rainfall ranges from 1,810 to 2,010 mm and a 90% greater probability of occurrence where rainfall is >2,010 mm.

In total, the sampled woodland covers 4,816 km² which represents only 0.95% of the central highlands total land area (**Supplementary Figures 1B, 2B**). The probability of occurrence of woodland is <5% across the rainfall and temperature gradient, corresponding to the limited land area occupied by this vegetation type. However, the greatest probability of occurrence

is at 23 and 24°C. Our studied sites are primarily located in areas with a medium annual mean temperature (20–23°C). Woodland is only found in very low precipitation areas with a highest probability of occurrence of 25% where rainfall ranges from 760 to 800 mm.

Grass Diversity and Composition

A total of 71 grass species from 40 genera were recorded and identified using the Poaceae checklist of Itremo Protected Area (Nanjarisoa et al., 2017) and specimens at K, P, and TAN herbaria. We found between 2 and 19 species per plot, with a mean of 8 species. Species richness was higher in woodland and grassland than in forest, with a significant difference between the three

TABLE 1 | Comparison of physical environments, species composition, and traits of dominant grass species and trees in grassland, woodland, and forests.

Habitat type	Grassland	Woodland	Forest
Environmental descriptors and disturbance regime	High-light understorey	Medium-light understorey (15–40% of canopy cover)	Low-light understorey (60–90% of canopy cover)
	Burnt every one to three years	Burnt every one to three years	Very rarely burnt
	Moderately grazed by zebus	Moderately grazed by zebus	Never grazed
Vegetation composition	Herbs	Trees	Trees
	C_4 grasses	Herbs	Herbs
		Mostly C_4 grasses	Mostly C_3 grasses
GRASSES			
Dominant grass species	*Loudetia simplex*	*Loudetia simplex*	*Oplismenus compositus*
	Trachypogon spicatus	*Trachypogon spicatus*	*Oplismenus hirtellus*
	Schizachyrium sanguineum	*Schizachyrium sanguineum*	*Oplismenus flavicomus*
	Hyparrhenia newtonii	*Sporobolus centrifugus*	*Arundinella nepalensis*
	Sporobolus centrifugus	*Aristida tenuissima*	*Acroceras boivinii*
Traits of the dominant grass species	Erect culm	Erect culm	Prostrate culm
	Tufted	Tufted	Creeping
	Intravaginal buds	Intravaginal buds	Extravaginal buds
	Narrow leaves	Narrow leaves	Wide leaves
Seedlings	Underground buds which allow them to survive intense fire	Underground buds which allow them to survive intense fire	Buds above ground, cannot survive fire
TREES			
Dominant trees		*Uapaca bojeri* (Phyllanthaceae)	Apocynaceae
		Sarcolaena oblongifolia (Sarcolaenaceae)	Bignoniaceae
		Schizolaena microphylla (Sarcolaenaceae)	Ebenaceae
		Asteropeia densiflora (Asteropeiaceae)	Euphorbiaceae
Traits of the dominant trees		Short trees	Tall trees
		Thick bark	Thin bark
		Open crowns	Dense crowns
		Can recover from fire	Limited post-fire recovery

habitats (GLM with Poisson distribution, $P < 0.001$). Although there is some spatial autocorrelation, the type of vegetation has a significant effect on species composition according to PERMANOVA ($F = 14.42$, $P = 0.001$). The vegetation type and the spatial location explain 33 and 9% of the variance, respectively. However, when separate pairwise comparisons are made, grassland and woodland do not differ significantly in composition ($F = 1.82$, $P = 0.06$). There are highly significant differences between both the composition of grassland and forest ($F = 19.43$, $P = 0.001$) and woodland and forest ($F = 23.95$, $P = 0.001$).

The same three species that are most common in grassland are also the dominant species in woodland: *Loudetia simplex* (Nees) C.E. Hubb., *Trachypogon spicatus* (L. f.) Kuntze and *Schizachyrium sanguineum* (Retz.) Alston (**Figures 2A,B**). All three are absent from forest, which is most commonly characterized by *Oplismenus compositus* (L.) P. Beauv., *O. hirtellus* (L.) P. Beauv., *O. flavicomus* Mez, and *Arundinella nepalensis* Trin (**Figure 2C**).

Rank-frequency curves per grass tribe also support differences in species composition of grassland and woodland in comparison with forest (**Figures 2D–F**). The two Poaceae tribes Andropogoneae and Tristachyideae dominate grassland and woodland, whereas forest species mostly belong to the tribe Paniceae.

Grass Traits

Beyond the similarities in taxonomic composition, grassland and woodland grass species were also characterized by similar trait communities (**Table 1**). This is evidenced by the functional group richness classification (**Figure 3**) which identified two distinct groups based on the seven functional traits. The two supported clusters demonstrate a close match with vegetation type.

The first cluster of 44 species (called "Non Forest") is primarily composed of species present in grassland and/or woodland (**Figure 3**). Within this group, 89% are C_4, 86% are perennial, 91% are erect and 52.3% have coriaceous leaves. The median values of height, leaf width and leaf length of the species in this group are 100, 0.5, and 30 cm, respectively. The key trait that differentiated this "Non-Forest" from the "Forest" cluster was the architecture of culms (**Figure 3**). Grassland and woodland grass culms are primarily erect, leading to a tufted growth form. Their leaves are narrower but also longer and more coriaceous compared to those in the "forest" group which are wide, herbaceous and flaccid.

Of 19 grass species recorded in forest, 84% cluster in the "Forest" group by traits (**Figure 3**). The three forest grass species [*Arundinella nepalensis, Lasiorrhachis hildebrandtii* (Hack.) Stapf, and *Panicum umbellatum* (Trin.)] which do not cluster in this group are C$_4$ and perennial. Species that also occur in grassland and woodland were assigned to the "forest" cluster (7 of 52 species): *Panicum perrieri* A. Camus, *P. subhystrix* A. Camus, *P. ibitense* A. Camus, *P. spergulifolium* A. Camus, *Festuca camusiana* St.-Yves, *Styppeiochloa hitchcockii* (A. Camus) Cope, and *Trichanthecium brazzavillense* (Franch.) Zuloaga & Morrone. These species are characterized by traits common amongst forest grasses as all species are C$_3$, and all but one have herbaceous leaves that are shorter and wider. The *Panicum* species are often found in the sub-canopy of the grassland and woodland layer.

Species dispersion in functional trait space differed significantly between the three vegetation types according to ANOVA ($P = 0.014$). Grassland communities are significantly less diverse functionally compared to forest communities ($P = 0.009$) and no significant difference was found between grassland and woodland ($P = 0.06$). Functional diversity is similar between forest and woodland ($P = 0.18$).

Diversity and Phylogenetic Structure

Species richness of grass species is significantly different between the three vegetation types (GLM, $P = 0.001$). Species richness is the highest in woodland with a significant difference compared to grassland (GLM, $P = 0.005$) and forest (GLM, $P < 0.001$; **Figure 4A**). Phylogenetic diversity means are equal to 233.1, 272.3, and 140.1 for grassland, woodland, and forest, respectively. Woodland species are significantly more phylogenetically diverse compared to grassland (GLM, $P < 0.001$) and forest species (GLM, $P < 0.001$; **Figure 4B**). When compared to a null model, forest grass communities exhibit a pattern of phylogenetic clustering but there is a significant difference with grassland, only for NTI (ANOVA, $P = 0.02$). No significant difference is found between grassland and woodland (ANOVA, $P = 0.145$), or woodland and forest (ANOVA, $P = 0.205$) NTI. Woodland communities are only slightly clustered (NRI = 0.28; NTI = 0.20) and grassland communities are slightly over-dispersed phylogenetically (NRI = −0.01; NTI = −0.08; **Figures 4C,D** and **Supplementary Figure 3**).
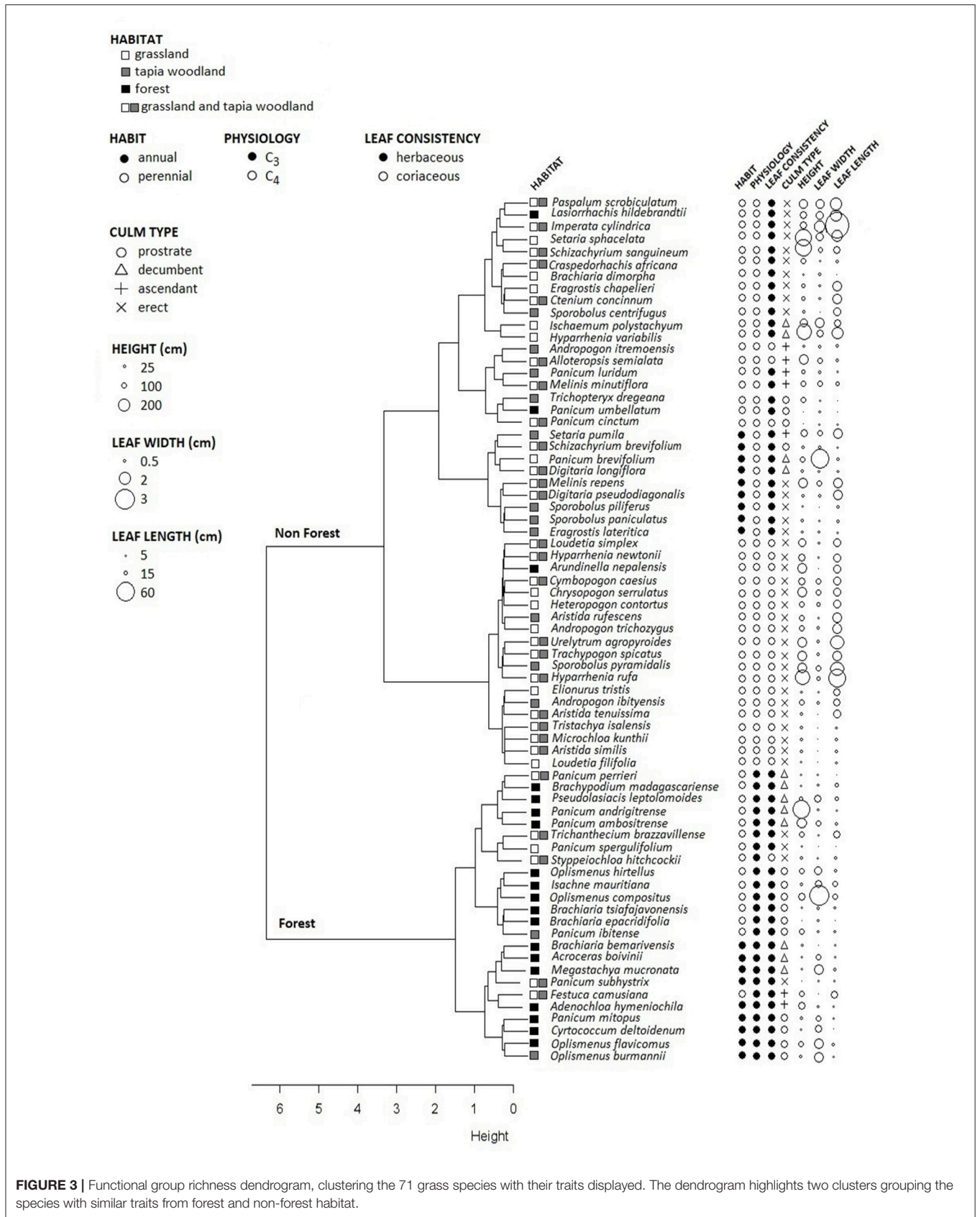
Woodland and Forest Trees Traits

The three vegetation types also differ in terms of woody species composition and traits (**Table 1**). While there are no woody species in grassland, the woodland is dominated by *Uapaca bojeri*, associated with other woody species, especially *Sarcolaena oblongifolia* and *Asteropeia densiflora*. Tapia trees are shorter (8–12 m; Kull, 2002) than humid forest trees. Humid forest canopy height can reach 30–35 m at low to mid-elevations (Moat and Smith, 2007). Moreover, forest trees have wide and dense canopies, creating a low-light understorey. Woodland on the other hand is characterized by a high-light understorey as trees have open crowns which allow light to penetrate.
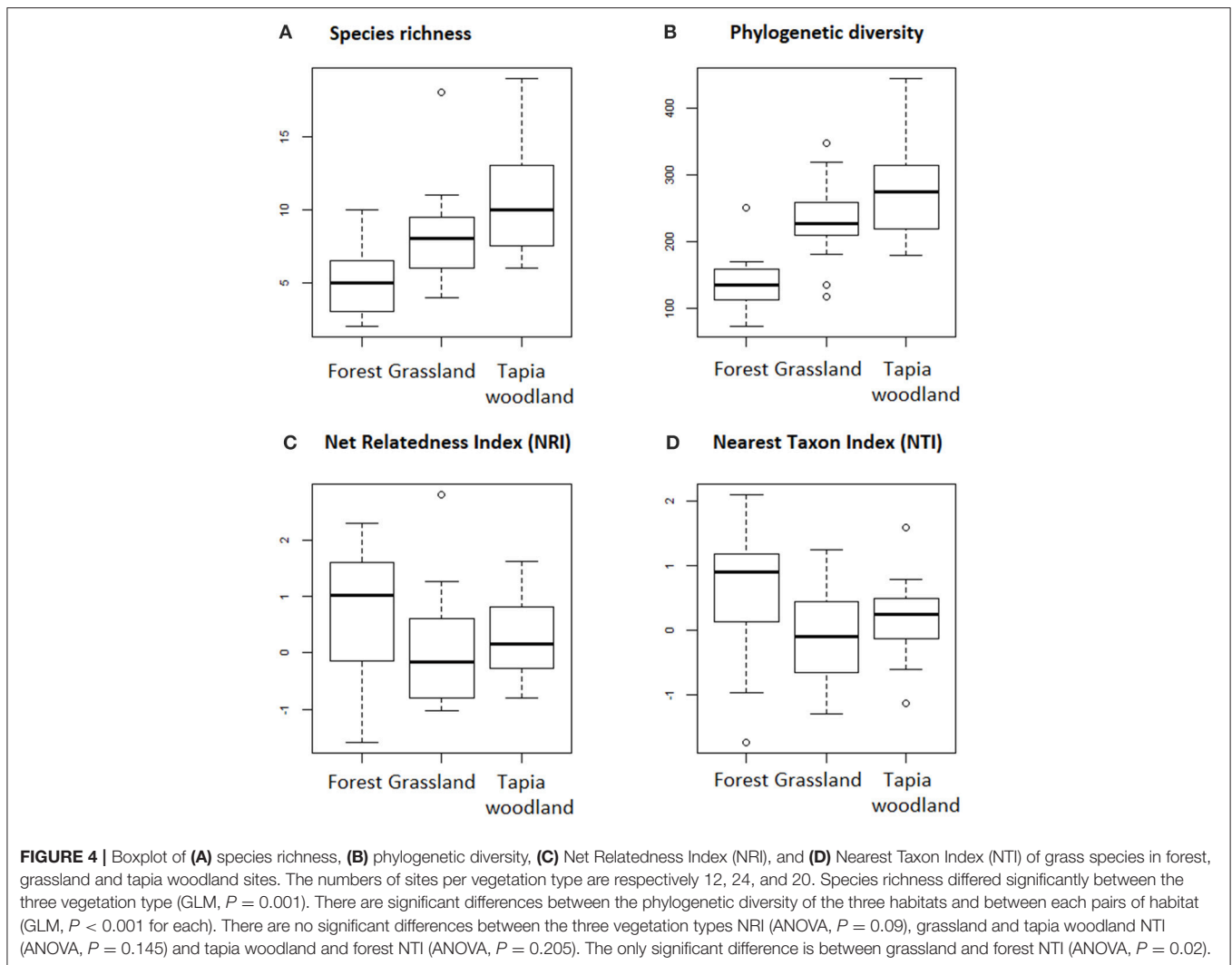
Uapaca bojeri has significantly thicker bark than the forest species ($t = −16.5$, $P < 0.001$; **Figure 5**). Among the forest species, five samples were from the same genus *Uapaca* (two *U. ferruginea* Leandri and three *U. densifolia*). The bark of *U. bojeri* (13.5%) is at least twice thicker that in forest *Uapaca* species (6.15% in *U. ferruginea*; see **Supplementary Table 3**).

DISCUSSION

The environmental envelopes of the three vegetation types show that grassland and woodland are most likely to co-occur, while forest has a distinct climatic envelope. Forest occurs at temperature ranging from 13 to 15°C and precipitation ranging from 1,810 to 2,660 mm, whereas grassland and woodland occur at temperature ranging from 18 to 25°C and precipitation ranging from 765 to 1,610 mm (**Supplementary Figures 1, 2**). An independent assessment based on herbarium records along environmental variables yielded an extremely similar environmental distribution of the *Uapaca bojeri* dominated woodland (Werkmeister, 2016). Werkmeister (2016) showed that annual temperature and mean annual precipitation are important factors in shaping the woodland's modern distribution, and the overall ranges of the woodland's environmental envelopes (temperature ranging from 15,1 to 25.1°C and precipitation ranging from 731 to 1,576 mm) coincide with our results of its occurrence probability. Our results on grassland and woodland distribution in Madagascar are similar to the distribution of savannas on the African continent where mean annual rainfall and rainfall seasonality are the key environmental correlates (Lehmann et al., 2011). The fire regime of the central highland grasslands has a return time of one to 3 years (Alvarado et al., 2018) which is in line with observations made for the African continent where the climate is similar (Lehmann et al., 2014). The locations sampled in this study span a precipitation gradient from 781 to 1,412 mm, similar to the rainfall of savannas in Africa, and corresponds to geographic regions where the three vegetation types can locally co-occur as a mosaic within the landscape. Further, in this study, we sampled 13% of the grass flora of Madagascar [71 out of 550 species (Vorontsova et al., 2016)] and these are taxonomically representative of the central highlands. Hence, the divergence we found between the diversity and functional traits of grass species in woodland and grassland in comparison to forest (**Figures 2**, **3**) are representative of community composition and biogeographic patterns of these vegetation types across the region. Our analyses identified two distinct functional groups, that of grassland and woodland species vs. forest species defined by differentiation in architecture, physiology, and leaf traits, all of which are related to light interception, fire tolerance and flammability (**Figure 3**). The ground layer of *Uapaca bojeri* dominated woodland is characterized by grasses of the tribes Andropogoneae and Tristachyideae (**Supplementary Figure 3**), the same that characterize central Madagascar grasslands. Studies have shown that the tribe Andropogoneae exhibits a suite of functional traits that are advantageous in regularly burned grasslands (Everson et al., 1988; Morgan and Lunt, 1999; Bond et al., 2003b; Spasojevic et al., 2010; Forrestel et al., 2014; Simpson et al., 2016). The majority of grass species found in woodlands
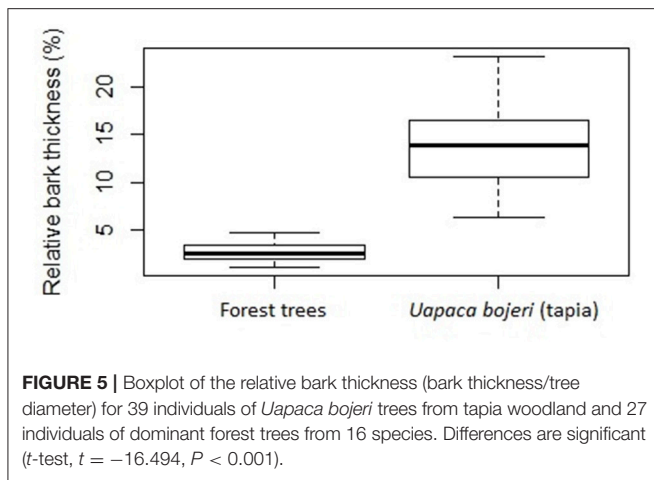
FIGURE 3 | Functional group richness dendrogram, clustering the 71 grass species with their traits displayed. The dendrogram highlights two clusters grouping the species with similar traits from forest and non-forest habitat.

FIGURE 4 | Boxplot of **(A)** species richness, **(B)** phylogenetic diversity, **(C)** Net Relatedness Index (NRI), and **(D)** Nearest Taxon Index (NTI) of grass species in forest, grassland and tapia woodland sites. The numbers of sites per vegetation type are respectively 12, 24, and 20. Species richness differed significantly between the three vegetation type (GLM, $P = 0.001$). There are significant differences between the phylogenetic diversity of the three habitats and between each pairs of habitat (GLM, $P < 0.001$ for each). There are no significant differences between the three vegetation types NRI (ANOVA, $P = 0.09$), grassland and tapia woodland NTI (ANOVA, $P = 0.145$) and tapia woodland and forest NTI (ANOVA, $P = 0.205$). The only significant difference is between grassland and forest NTI (ANOVA, $P = 0.02$).

and grasslands are tall perennial C_4 grasses, with coriaceous leaves, that burn frequently (**Figure 3**).

Grass species in forest and woodland showed a pattern of higher dispersion in the functional trait space than in grassland. This indicates a greater environmental heterogeneity in these vegetation types, where species exhibit a wide range of traits to adapt to their habitat (Anderson et al., 2006). Several studies have shown that high light intensity and high temperature environments favor C_4 over C_3 photosynthesis (Ehleringer et al., 1997; Osborne and Sack, 2012), and C_4 grasses dominant in tropical savannas and grasslands (Sage and Monson, 1998; Bond, 2008). C_4 grasses which dominate the woodland generally have coriaceous leaves, linked to traits that retard decomposition (Street et al., 1980) and increase flammability such as high leaf C:N ratios (D'Antonio and Vitousek, 1992; Mouillot and Field, 2005; Bond, 2008; Cardoso et al., 2008). These species are also tall grasses, promoting fire and making the vegetation highly flammable (Fensham et al., 2003; Vigilante et al., 2004; Archibald et al., 2005; Simpson et al., 2016) and are also strong light competitors (Olff and Ritchie, 1998). In

contrast, grass species in the forest understory are essentially C_3 members of the tribe Paniceae (**Supplementary Figure 3**). Forest understories are characterized by high moisture and low light conditions (Hoffmann et al., 2003, 2012), and forest grasses are largely annual, creeping, with wide leaves that enable them to optimize light interception (Milla and Reich, 2007) and minimize self-shading (Falster and Westoby, 2003). Leaf size has been demonstrated to be related to light acquisition. A significant positive relationship between leaf size and specific leaf area has been reported (Ackerly and Reich, 1999); and high specific leaf area has been shown to allow species to optimize light interception in shady conditions (Milla and Reich, 2007). A study from a woodland community in Australia has shown that small-leaved woody species were associated with more light in the understorey (Bragg and Westoby, 2002). In contrast, high-light environments of grassland and woodland are dominated by perennial tufted grasses with erect culms. With an erect architecture, these species can protect their meristematic tissue from fire damage with intravaginal buds protected within basal leaf sheaths or underground, and tillers

FIGURE 5 | Boxplot of the relative bark thickness (bark thickness/tree diameter) for 39 individuals of *Uapaca bojeri* trees from tapia woodland and 27 individuals of dominant forest trees from 16 species. Differences are significant (t-test, $t = -16.494$, $P < 0.001$).

tightly clustered (Linder et al., 2018). Thus, after fire, such species rapidly resprout (Ripley et al., 2015), and proliferate under the disturbance regime that characterizes grassland and woodlands, where humans have limited influence on the fire regimes (Alvarado et al., 2018).

Tapia woodland grass species have higher species richness and phylogenetic diversity compared to grassland and forest species (**Figures 4A,B**). This could be explained by the environmental gradient within the woodland promoted by heterogeneity in tree cover, enabling co-existence of a higher diversity of grass species (Silvertown, 2004) than in grassland or forest. There is an overall greater range of light environments within the woodland. Like grassland, woodland burns frequently, but the forests rarely burn (Ratnam et al., 2011; Charles-Dominique et al., 2015). Our analyses of community phylogenetic structure found evidence of evenness in grassland, slight clustering in woodland and clustering in forest. In forest, ground layer composition must be adapted to light availability (Charles-Dominique et al., 2015), potentially leading to phylogenetically conserved traits at local spatial scales. Here, most grass species found in forest belong to the "Madagascar shade clade" in the tribe Paniceae (Hackel et al., 2018) and share similar physiological and biological traits (creeping C_3 species with herbaceous leaves). In contrast, it has been suggested that competitive exclusion plays a structuring role if co-occurring species are less closely related than expected by chance (Weiher and Keddy, 1995; Webb, 2000). Grassland and woodland grass species are evenly distributed across the phylogeny, and these communities are characterized by competition for resources and regular disturbance (Bond, 2008). No significant difference was found between the phylogenetic distance to the nearest taxon for each taxon in the sample (NTI) between grassland and woodland; and woodland and forest. The inconsistency in the differences of taxa distribution in each vegetation type relative to the whole species pool might be explained by the number of species in our sample. It is important to note that accounting for geographical scale and species abundance are important to draw strong conclusions from phylogenetic community structure (Vamosi et al., 2009). The differences in forest and woodland phylogenetic

structure suggest the species characterizing these environments evolved independently and based on Vorontsova et al. (2016), it appears that both grassland and woodland communities have a long evolutionary history. Hackel et al. (2018) demonstrated that the "Madagascar shade clade" diversified in Madagascar and nearby islands since the Miocene and that endemic C_4 grasses are the result of repeated dispersals to Madagascar mainly since the Late Miocene. It is likely that immigrating C_4 grasses already featured traits similar to those we observed, but further study and comparison with their non-Malagasy relatives is needed.

Our assessment of the grass community composition and their characteristics in grassland, woodland and forest shows that the woodland formation dominated by *Uapaca bojeri* is more likely a type of savanna and has been previously wrongly attributed as forest (Perrier de la Bâthie, 1921; Humbert, 1949; Koechlin et al., 1974; Gade, 1996). Our results support previous studies which distinguished forest and savanna based on tree functional traits and diversity (Ratnam et al., 2011; Dantas et al., 2013; Charles-Dominique et al., 2015). *Uapaca bojeri*, the dominant tree species in woodland does not occur in forest as defined here and our comparative analysis of bark thickness reinforces this conclusion. *Uapaca bojeri* (tapia) has bark at least twice the thickness of nearby forest species. Bark thickness is often presented as a key mechanism for tree survival in frequently burnt ecosystems (Gignoux et al., 1997; Hoffmann et al., 2003; Lawes et al., 2013; Pausas, 2015) where thick bark reduces the probability of stem death and insulates buds buried in stems (Hoffmann et al., 2003; Pausas, 2015). In addition, *Uapaca bojeri* has other traits characteristic of pyrophytic species (**Table 1**), including fire retardant leaves and epicormic resprouting (Kuhnholtz-Lordat, 1938). Our results support Kull's (2002) assertion that *Uapaca bojeri* dominated woodlands are shaped and maintained by fire, suggesting this woodland is a savanna rather than degraded forest. However, comparison of multiple tree traits related to fire resistance, tolerance and recruitment is needed. Previous research has found differences in specific leaf area and leaf:stem allocation patterns in tree species across savanna and forest boundaries (Hoffmann and Franco, 2003) and such trait comparisons along with assessments of conditions of plant recruitment could help further elucidate the functional ecology of these woodlands linked to the functional ecology of the ground layer. These woodlands, with numerous endemic species in both the over- and under-story, are part of the cultural landscape of Madagascar and have therefore undergone changes linked to wood collection and human use (Kull, 2002). Developing effective land management and conservation strategies of the unique and endemic flora of Madagascar requires development of an understanding of the functional characteristics of the species and vegetation types. Our study provides the first assessment of grass species composition and functional traits as being distinct between forest and the mosaic of grassland and *Uapaca bojeri* dominated woodlands, suggesting that functional characteristics of the ground layer can help delimit functionally distinct ecosystems. Further, the grasses of both grassland and woodland are phylogenetically highly diverse, consistent with our hypothesis that the evolutionary

history of these ecosystems is certainly far older that human settlement which occurred only 6,000 years ago on Madagascar such that these woodlands of the central highlands are an ancient feature of these landscapes.

AUTHOR CONTRIBUTIONS

CS, MV, and CL designed research. CS, MV, JH, GB, JW, and CL collected data. CS and JH analyzed data. CS, MV, and CL wrote the paper. JH, GB, SC, JW and VJ contributed to the interpretation and the revision of the work.

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SUPPLEMENTARY MATERIAL

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