

Flora and Vegetation in Different Physiognomies of a *Mussununga* in Southeastern Brazil

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ABSTRACT

Mussununga is an understudied ecosystem within the Atlantic Forest domain, in sandy spodosol lowlands from Bahia to Espírito Santo. Its physiognomy varies from grassland to forest, with a transitional savannic area. We evaluated the life-form spectra differences between the grassland and savanna *Mussunungas* and its relationship with the depth of a soil impermeable layer (ortstein). The study area is located in the municipality of Linhares, Espírito Santo State. Ten plots were settled in each physiognomy. The floristic and vegetation spectra (accordingly to Raunkiaer) were compared using the G-test. A total of 35 species into three life-forms were found: Phanerophytes, hemicyptophytes and cryptophytes. The floristic spectra were similar in both physiognomies, with a greater richness of phanerophytes. However, the vegetation spectra of the two areas were different. Phanerophytes dominated in the savannas (where ortstein is deeper), while the shallower ortstein of the grasslands favored hemicyptophytes.

Keywords: biological spectra, flooding areas, life-forms, plant-soil relationship, tropical forests.

1. INTRODUCTION

The distribution of plant species is related to environmental variables of ecosystems that limit or favor plant establishment. Little is known about this subject in many tropical environments and the comprehension of this relationship is important to understand the ecosystem functionality (Ribeiro et al., 2009; Paula et al., 2015; König et al., 2019). The Atlantic Forest is the most biodiverse Brazilian biome (BFG, 2018) and some of its ecosystem types are still poorly studied, like the *Mussunungas* (Saporetto-Júnior et al., 2012).

Mussununga is a kind of ecosystem into the Atlantic Forest domain, occurring in lowlands from southern Bahia to northern Espírito Santo State. The *Mussununga* physiognomy varies from grasslands to woodlands with sparse, low-statured trees contrasting with the surrounding matrix with dense Ombrophylous forest (Saporetto-Júnior et al., 2012).

Soils are very important in determining the different Atlantic Forest phytophysiognomies (Magnago et al., 2012; Costa et al., 2016). In the lowlands of the Atlantic Forest of the Southeastern to Northeastern Brazilian coastal plains, the vegetation varies from *restingas*, *tabuleiro* forest, swamps and *Mussunungas*, depending on soil features (Peixoto et al., 2008).

Meira-Neto et al. (2005) reported that the Bahia *Mussunungas* are floristically similar to the *restingas*, where the dominant soil types, respectively the Spodosols and the Entisols, are both sandy and shallow (Oliveira et al., 2010). However, Meira-Neto et al. (2005) pointed out that the presence of an impermeable layer (ortstein) in the spodosols is the main edaphic feature determining floristic differences between the *Mussunungas* and the *restingas*. According to these authors, this impermeable layer restricts root penetration and water percolation, resulting some seasonally flooded sites.

Soil can also print variation in the *Mussununga* physiognomies, which varies from forest to grassland (Peixoto et al., 2008; Saporetto-Júnior et al., 2012; Gastauer et al., 2017). The functionality of the *Mussunungas* in Bahia was well studied by Saporetto-Júnior et al. (2012). These authors identified different physiognomies with diverse functional group composition determined mainly by the depth of ortstein and soil granulometry features. These authors reported a dominance of therophytes and chamaephytes in grasslands and open savannas,

and phanerophytes in the savannas or forest-like *Mussunungas*. In addition, Meira-Neto et al. (2005) found a higher richness of phanerophytes in Caravelas (Bahia) followed by chamaephytes and hemicryptophytes. Otherwise, in another Bahia *Mussununga* (Mucuri) the richness of hemicryptophytes was higher due to anthropogenic disturbances, mainly fire and grazing. Heringer et al. (2019) also mentioned changes in the *Mussununga* vegetation due to anthropogenic impact.

Mussunungas of Espírito Santo State (ES) are not well studied as those in Bahia. Ferreira et al. (2014) reported that they exhibit low floristic similarity. The *Mussunungas* found in ES also present different phytophysiognomies into two major groups: *Mussununga* forests and *Mussununga* grasslands (Peixoto et al., 2008). Araújo et al. (2008) classified the grassland *Mussunungas* of ES in four types: Graminoid, dense graminoid, closed scrub, and open scrub. According to these authors, this variation seems to be related to the seasonality of flooding events. In ES the grassland *Mussununga* is known locally as *campo nativo* or simply *nativo* (Araújo et al., 2008). Ferreira et al. (2014), also studying ES *Mussunungas*, reported that the frequency and duration of flooding conditioned floristic differences between grassland and shrubby-grassland *Mussunungas*. These authors found similar floristic spectra in these two phytophysiognomies, with a higher richness of phanerophytes, followed by hemicryptophytes. However, they did not assess the abundance or dominance of the life-forms in order to compare the vegetation spectra. A floristic spectrum is built with a species list, where every species has the same weight. For ecological investigations, assessing the vegetation response is better than merely the flora data. In this case, the species have to be weighted by their abundance and/or dominance to build the vegetation's spectrum (Martins & Batalha, 2011).

Despite the high biological importance of the ES *Mussunungas* (Peixoto et al., 2008), little is known about its soil-vegetation relationship, highlighting the importance of new studies to understand the functionality of this ecosystem. According to Martins & Batalha (2011), studies of life-forms portray the similarities and peculiarities of environments, which are relevant for the understanding of the ecosystems' structure and function.

Ferreira et al. (2014) studied the flora and floristic spectra in ES *Mussunungas*. However, they did not evaluate the vegetation spectra. The study of Araújo et al.

(2008) includes both flora and vegetation, but does not address the functionality aspect (life-forms) associated with the environmental characteristics of the different physiognomies. Despite these previous studies have provided important information about ES *Mussunugas*, the present study presents, for the first time, aspects of the vegetation (physiognomy), including the species functionality, and their relationship with environment features. As such, this study aimed to assess the effect of the ortstein depth on the flora and vegetation patterns of savannic and grassland *Mussunungas* of ES, taking into account the occurring species, their life-forms and the respective proportions with which they occur in the communities.

2. MATERIAL AND METHODS

2.1. Study area

The studied site is known as Ceolin (Araújo et al., 2008), at 19°9'8.98" S – 19°9'17.69" S; 40°3'49.91" W – 40°3'59.54" W, at Vale Natural Reserve (VNR), a private nature reserve with 22,000 ha in the municipality

of Linhares, Espírito Santo State, Brazil (Figure 1). The altitude in the VNR ranges from 28 to 65 m, and the climate is tropical wet, with annual precipitation of 1,093 mm and a dry season from May to September (Kierulff et al., 2015).

VNR is characterized by the following vegetation formations: High or dense ombrophyllous forests, *Mussunungas*, marshlands, marsh forests, riparian forests and *nativo* grasslands that appear as enclaves in the forest areas, occupying approximately 6% of the total reserve area (Araújo et al., 2008). This study was performed at two continuous sampling sites with different *Mussununga* physiognomies: A savanna and a grassland. The savanna is a transition between the *Mussununga* forest and the *Mussununga* grassland, herein denominated savannic *Mussununga*. In this phytophysiology there is an herbaceous layer mixed with shrubs and small trees widely spaced. The trees can reach 10 m in height, but do not form a continuous canopy, similarly to the “open scrub” described by Araújo et al. (2008). The grassland is located in the central portion of the studied area (Figure 1). This phytophysiology

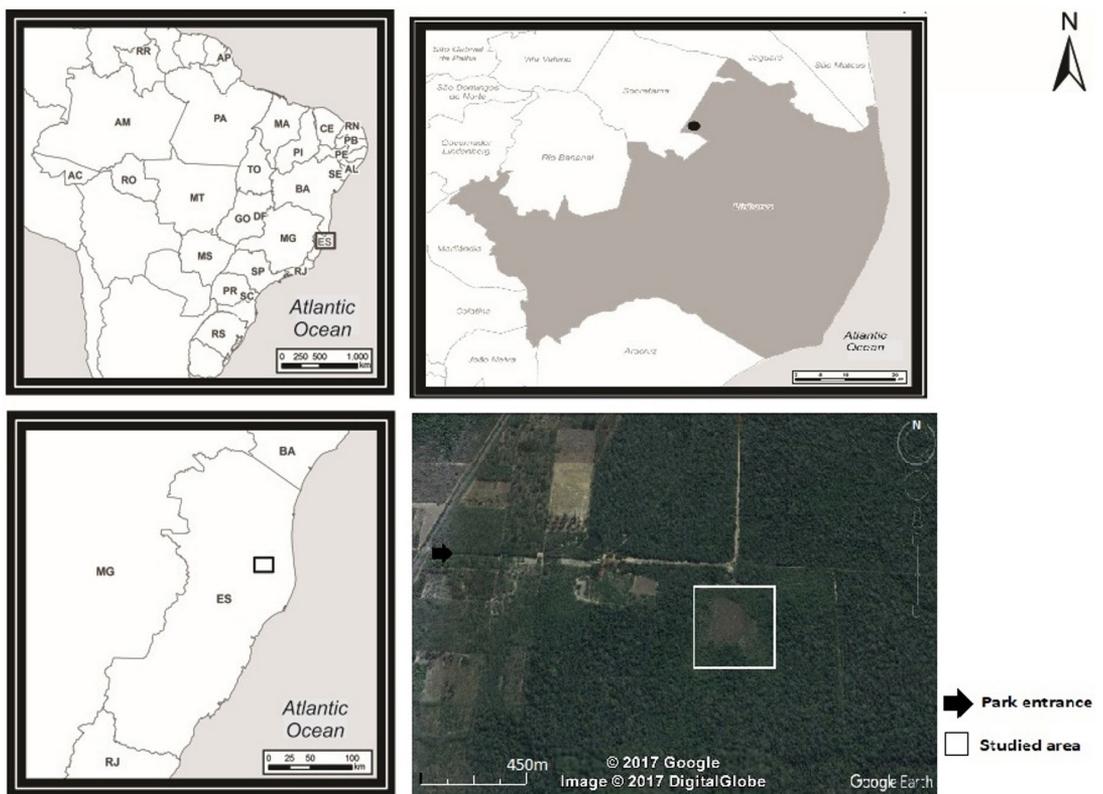


Figure 1. Location of the study area in the Vale's Natural Reserve, Linhares, Espírito Santo State, Brazil.

is dominated mainly by grasses with a more open shrub layer than the savannas, similarly to the “graminoid type” described by Araújo et al. (2008). In these areas, the seasonal rains (from October to March) bring the water table to the soil surface.

The coastal plain forest in the North of ES is associated with sandy oligotrophic soil of the Barreiras Series (Oliveira et al., 2010). Most of the soils of the Espírito Santo *Mussununga* grasslands are characterized as Spodosols (Secretti, 2013). According to this Secretti (2013), these soils are sandy, oligotrophic, with a hard and impermeable layer (ortstein) along the B horizon that inhibits water percolation and favors flooding during the rainy season, similarly to those soils described for Bahia *Mussunungas* (Saporetti-Júnior et al., 2012).

The depth at the beginning of the cemented spodic horizon was measured with a ruler in three representative soil profiles in each phytophysiology, near to the sampling plots. In the grassland areas, the ortstein depth was lower than 0.6 m (0.36-0.59 m), while in the savannic area the ortstein was deeper than 1 m (1.1-1.5 m).

2.2. Sampling design

A transection was established along the two studied physiognomies, at the beginning of the savannic physiognomy (close to the forest border) to the center of the *Mussununga* patch, with grassland *Mussununga*. Ten plots of 10 × 10 m each were systematically delimited (10 m equidistant) along this transection for each kind of physiognomy.

2.3. Floristic and vegetational studies

All vascular species inside the plots were collected, identified, herborized and deposited at the OUPR and CVRD Herbaria. Species identification was done with specialized literature and by comparison with identified Herbarium specimens.

The species cover was visually estimated as the percent cover of the species on the plot (Messias et al., 2011).

Life-form classification followed the Raunkiaer's original system into the five main classes: Phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes. In this way, epiphytes and lianas were included into the phanerophyte class. Each species was assigned to only one life-form – the one which

the buds were less protected. The floristic spectra represented the richness of species in each life-form. To build the vegetational spectra, the total coverage of individuals in each life-form was considered (Martins & Batalha, 2011).

2.4. Data analysis

A species accumulation curve was built using EstimateS Software to estimate the expected total number of species in the study area using Chao-2, Jackknife-1 and Jackknife-2 estimators, as suggested by Moro et al. (2014).

To test if the biological spectra were different in the two *Mussununga* physiognomies, they were compared pairwise with the Williams G-test.

3. RESULTS

A total of 35 species into 25 families were sampled. The Bromeliaceae and Eriocaulaceae families presented the greatest richness, with three species each. The Dilleniaceae, Myrtaceae, Orchidaceae, Polypodiaceae, Rubiaceae and Sapindaceae presented two species. The other families presented just one species. Even though the Poaceae family presented only one species, *Renvoizea trinii* dominated the sampled area with coverage of 80% (Table 1).

The community richness calculated by Jackknife-1 (40.1), Jackknife-2 (42) and Chao (39.85) indicated that we sampled more than 80% of the estimated species richness.

The savannic *Mussunungas* presented a higher species richness (29), being 18 exclusive from this physiognomy. Eighteen species occurred in both physiognomies and six were exclusive from the grasslands.

Three life-forms were found in the grassland and savannic *Mussunungas*: Phanerophytes, hemicryptophytes and cryptophytes. We did not observe any chamaephytes or therophytes.

The floristic spectra for both phytophysiology of the studied *Mussunungas* were similar ($G = 0.7762$, $p = 0.678$) and presented phanerophytes as the predominant life-form, followed by hemicryptophytes (Figure 2).

On the other hand, there was significant difference ($G = 165.13$, $p < 0.0001$) between the vegetational spectra

Table 1. Checklist, life-form, coverage (C), and voucher (Herbarium acronym+number) of the species, at two sites of a *Mussununga* area in Vale's Natural Reserve, Linhares, Espírito Santo, Brazil.

Family/Species	Life-Form	Physiogy	C (%)	Voucher
Araceae				
<i>Anthurium zeneidae</i> Nadrus	Hem	S	0.23	CVRD11,346
Bignoniaceae				
<i>Tabebuia elliptica</i> (DC.) Sandwith	Phan	G,S	5.45	CVRD8,267
Bromeliaceae				
<i>Tillandsia globosa</i> Wawra	Phan	S	0.78	OUPR26,688
<i>Tillandsia usneoides</i> (L.) L.	Phan	S	0.50	OUPR26,692
<i>Vriesea procera</i> (Mart. ex Schult. & Schult.f.) Wittm.	Phan	S	2.28	OUPR26,689
Burseraceae				
<i>Protium icicariba</i> (DC.) Marchand	Phan	S	13.7	OUPR26,690
Celastraceae				
<i>Monteverdia obtusifolia</i> (Mart.) Biral	Phan	G,S	0.12	OUPR27,397
Chrysobalanaceae				
<i>Hirtella corymbosa</i> Cham. & Schltld.	Phan	G,S	5.38	OUPR26,707
Dilleniaceae				
<i>Davilla flexuosa</i> A.St.-Hil.	Phan	S	0.4	OUPR26,698
<i>Dolioscarpus lancifolius</i> Kubitzki	Phan	G,S	0.10	OUPR26,697
Eriocaulaceae				
<i>Actinocephalus ramosus</i> (Wikstr.) Sano	Hem	G	0.08	OUPR26,704
<i>Leiostrix hirsuta</i> (Wikstr.) Ruhland	Hem	G,S	0.37	OUPR26,696
<i>Leiostrix</i> sp	Hem	G	0.79	OUPR27,396
Fabaceae				
<i>Andira nitida</i> Mart. ex Benth.	Fan	S	2.82	CVRD789
Humiriaceae				
<i>Humiria balsamifera</i> (Aubl.) A.St.-Hil.	Phan	G,S	5.5	OUPR26,695
Iridaceae				
<i>Neomarica sabinei</i> (Lindl.) Chukr	Cry	S	0.3	OUPR26,694
Lauraceae				
<i>Ocotea notata</i> (Nees & Mart.) Mez	Phan	S	4.6	CVRD5,762
Malpighiaceae				
<i>Stigmaphyllon paralias</i> A.Juss.	Phan	S	1.05	OUPR26,691
Melastomataceae				
<i>Pleroma urceolare</i> (Schrank et Mart. ex DC.) Triana	Phan	G	0.2	OUPR26,706
Myrtaceae				
<i>Calypttranthes brasiliensis</i> Spreng.	Phan	G,S	3.28	OUPR26,685
<i>Psidium brownianum</i> Mart. ex DC.	Phan	G,S	0.9	CVRD12,017
Nyctaginaceae				
<i>Guapira pernambucensis</i> (Casar.) Lundell	Phan	G,S	1.55	OUPR26,703
Ochnaceae				
<i>Ouratea cuspidata</i> (A.St.-Hil.) Engl.	Phan	G,S	3.75	CVRD1,551
Orchidaceae				
<i>Epistephium lucidum</i> Cogn.	Cry	G	0.1	OUPR26,702
<i>Vanilla bahiana</i> Hoehne	Phan	S	0.2	CVRD5,366
Poaceae				
<i>Renvoizea trinii</i> (Kunth) Zuloaga & Morrone	Hem	G,S	59.5	OUPR26,686
Polypodiaceae				
<i>Microgramma vacciniifolia</i> (Langsd. & Fisch.) Copel.	Phan	S	0.01	CVRD5,500
<i>Serpocaulon latipes</i> (Langsd. & Fisch.) A.R.Sm.	Hem	S	0.21	OUPR26,699

Phan = phanerophyte; Hem = hemicytrophite; Cry = cytrophite; G = Grassland *Mussununga*; S = Savannic *Mussununga*.

Table 1. Continued...

Family/Species	Life-Form	Physiogomy	C (%)	Voucher
Rubiaceae				
<i>Emmeorrhiza umbellata</i> (Spreng.) K.Schum.	Phan	G	0.5	OUPR26,701
<i>Pagamea guianensis</i> Aubl.	Phan	G	5.77	OUPR26,700
Salicaceae				
<i>Casearia selloana</i> Eichler	Phan	S	1.5	OUPR27,398
Sapindaceae				
<i>Matayba discolor</i> (Spreng.) Radlk.	Phan	S	0.2	CVRD1,704
<i>Urvillea rufescens</i> Cambess.	Phan	S	1.0	OUPR26,693
Sapotaceae				
<i>Manilkara triflora</i> (Allemão) Monach.	Phan	S	1.1	CVRD3,075
Smilacaceae				
<i>Smilax rufescens</i> Griseb.	Phan	S	0.1	OUPR26,705

Phan = phanerophyte; Hem = hemicryptophyte; Cry = cryptophyte; G = Grassland *Mussununga*; S = Savannic *Mussununga*.

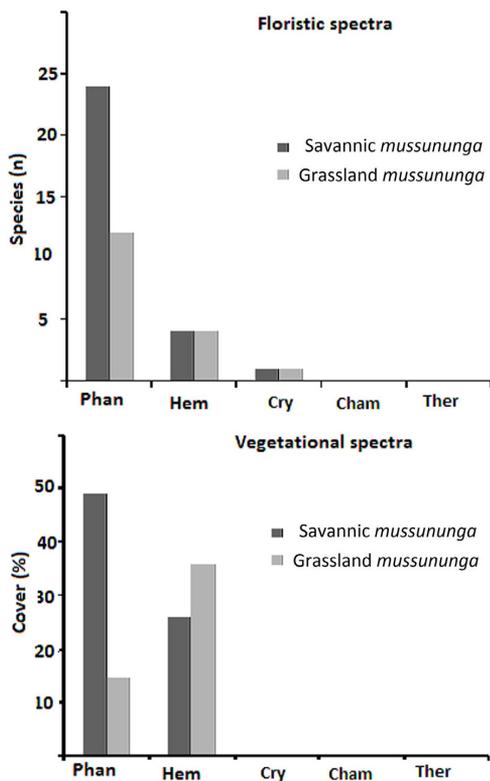


Figure 2. Floristic and vegetational spectra in two *Mussununga* physiognomies at Vale's Natural Reserve, Linhares, Espírito Santo State, Brazil. Phan = phanerophyte; Hem = hemicryptophyte; Cry = cryptophyte; Cham = chamaephyte; Ther = therophyte.

of the two studied phytophysiognomies (Figure 2). In the grassland *Mussununga*, hemicryptophytes were predominant, followed by phanerophytes and cryptophytes. While in the savannic *Mussununga*, phanerophytes dominated, followed by hemicryptophytes.

4. DISCUSSION

Higher species richness was found in the savanna compared with the grassland, where the environmental conditions are more restrictive. Two severe water stresses occur in *Mussunungas*. First of all, the impermeable cemented soil layer drives waterlogging during the rainy season (Saporetti-Júnior et al., 2012; Ferreira et al., 2014). However, during the dry season, the waterlogging gives place to a severe drought. These environmental constraints in *Mussunungas* are greater in soils with shallower ortstein (Saporetti-Júnior et al., 2012), limiting the flora and functional diversity. In grassland *Mussunungas* a thin water sheet could be seen covering the soil surface during the rainy season, when the intensity and periodicity of flooding is greater (Ferreira et al., 2014). This event may be rare or absent in the savannas (Ferreira et al., 2014). According to Meira-Neto et al. (2005), the ortstein depth determines the drainage regime in *Mussununga*'s spodosol. Some species were typical from the grassland *Mussunungas*, adapted to seasonal flooding like *Pagamea guianensis*. This species was also described by Araújo et al. (2008) as occurring in areas of graminoid *Mussunungas*, where the water table comes to the surface. Other woody species like *Ocotea notata* and *Protium icicariba* were found only in the savannic *Mussununga*. Araújo et al. (2008) reported the occurrence of these species along the transition of grassland to *Mussununga* forests. Other species were found in both physiognomies, showing they were adapted to both conditions, like: *Davilla flexuosa*, *Doliodarpus multiflorus*, *Humiria balsamifera* and *Pagamea guianensis*, as described by Araújo et al.

(2008). However, these authors reported that there is not a floristic pattern able to distinguish the different physiognomies of no-forest ES *Mussunungas*.

In spite of the different *Mussununga* phytophysiognomies, they presented a similar pattern, with higher richness of phanerophytes followed by hemicryptophytes. Other studies also showed similar floristic spectra both in ES (Ferreira et al., 2014) and Bahia *Mussunungas* (Meira-Neto et al., 2005). Although Ferreira et al. (2014) have included chamaephytes as a representative life-form in *Mussunungas*, they used an adapted Raunkiaer System (Martins & Batalha, 2011), in which the height of renewing buds of chamaephytes and phanerophytes is higher than those of the Raunkiaer original method. Thus, many small phanerophytes (by the original Raunkiaer system) would be described as chamaephytes. In addition, by using the original Raunkiaer System, epiphytes and lianas are also considered phanerophytes. Consequently, in this study, four epiphytes (three Bromeliaceae species and a fern) as well as four lianas (*Dolioscarpus elegans*, *Smilax rufescens*, *Urvillea rufescens* and *Vanilla bahiana*) were counted as phanerophytes in the savannic *Mussununga*. However, most phanerophytes are small trees and shrubs from several families common in the forest-like *Mussunungas*, like *Humiria balsamifera*, *Guapira pernambucensis* (Saporetti-Júnior et al., 2012), *Andira nitida* and *Ocotea notata* (Peixoto et al., 2008). Other phanerogamic species are typical from the transitional zone between forest and grassland *Mussunungas* like *Tabebuia elliptica*, *Protium icariba* and *Stigmaphyllon paralias* (Araújo et al., 2008).

Hemicryptophyte species has shown high species diversity in other ecosystems with sandy, oligotrophic and sharp soils, like the *campos rupestres* (Messias et al., 2011; Costa & Cielo-Filho, 2012; Carmo & Jacobi, 2016; Silveira et al., 2016). Hemicryptophyte are mainly monocots (Le Stradic et al., 2015), which include many desiccation-tolerant (Gaff & Oliver, 2013; Yobi et al., 2017) as well as flooding tolerant species (Colmer & Voesenek, 2009; Yamauchi et al., 2018).

The lack of nutrients in *Mussununga* soils may explain the absence of therophytes. Therophytes need a greater nutrient input to trigger their fast growth since they have a short time to complete their cycle (Schmidt, 2012), being almost absent in dystrophic environments (Mioduski & Moro, 2011). A similar pattern was found in the *Caatinga* (Moro et al., 2016),

where areas with eutrophic soils presented a greater therophyte richness. Meira-Neto et al. (2005) and Saporetti-Júnior et al. (2012) reported some therophytes in Bahia *Mussunungas*. However, the cited Eriocaulaceae and Xyridaceae species are not ephemeral plants and present clonal reproduction by stem buds at the soil level, fitting in the hemicryptophyte description.

The floristic spectrum displays the flora characteristics; that is, the species richness for each life-form, while the vegetational spectrum represents the physiognomy feature. Studies on the distribution of life-forms in tropical environments have evidenced differences in the vegetational spectrum even when there is no difference in floristic spectrum (Batalha & Martins, 2004; Messias et al., 2011).

Saporetti-Júnior et al. (2012) also described a higher dominance of phanerophytes in savannas and forest-like *Mussunungas* in Bahia. In general, higher proportion of phanerophytes are expected in environments with favorable climates, like in the warm, humid tropical rainforests. On the other hand, harsher climates favor life-forms with greater degree of bud protection (Costa et al., 2016). Analyzing the Brazilian Biomes, Costa et al. (2016) reported that in a macroscale view, climate is the most striking factor determining the biological spectra, however, in a regional scale, soil and anthropogenic disturbance also play an important role in defining the spectra. Even though *Mussunungas* can be seen as a marginal physiognomy into the Atlantic Forest domain, the pattern of high richness and dominance of phanerophytes is maintained, unless there is another kind of environmental stress limiting the establishment of this life-form. Meira-Neto et al. (2005) reported a *Mussununga* site (Mucuri, Bahia) with a slight dominance of hemicryptophytes. These authors mentioned that the occurrence of fire and grazing in successive years favored the occurrence of this life-form. Hemicryptophytes are represented mainly by grasses and sedges with a fasciculate root system, exploring the superficial soil layer, and also exhibiting anatomic and physiological adaptations to the seasonal flooding (Visser et al., 2000; Mollard et al., 2008; Hodge et al., 2009; Waring & Maricle, 2012). These abilities explain the high abundance/dominance of hemicryptophytes in grassland *Mussunungas*, since the upper soil layer is richer in organic matter (Nascimento et al., 2013; Barroso et al., 2014), which increases the nutrient levels and water holding capacity during the dry season. In addition, during the rainy season, when the seasonal

flooding occurs, the O₂ concentration in this layer is less limiting (Rich & Watt, 2013).

Saporetto-Júnior et al. (2012), studying a *Mussununga* at Bahia State, found a strong relationship between soil physical characteristics and the abundance of life-forms. The authors reported that the ortstein depth and soil granulometry determine the distribution of functional plant groups. They found that soils with shallower ortstein and coarser granulometry are dominated by therophytes and hemicryptophytes, while phanerophytes dominate in places with deeper ortstein and higher percentage of finer soil particles. Nevertheless, some species described by these authors as therophytes, like *Xyris capensis*, *Actinocephalus ramosus* and *Syngonanthus nitens*, are not annual plants and present clonal reproduction by stem buds at the soil level, fitting in the description of hemicryptophytes. If so, the vegetation spectra are similar in *Mussunungas* of Bahia and ES, with predominance of hemicryptophytes or phanerophytes, depending on the depth of ortstein.

Thus, the physiognomic differences between the studied *Mussununga* are influenced by ortstein depth. These results are corroborated by Secretti (2013), who reported that soil and the impermeable layer are deeper near the forested *Mussununga*, favoring the establishment of taller vegetation in the savannic *Mussununga*. In addition, in the savannic *Mussunungas*, in the rainy season the water table rises but does not reach the land surface (Secretti, 2013). According to this author, in the grassland *Mussununga*, the soil is shallower and the ortstein is more superficial compared to the soils of the forested *Mussununga*, making it substantially more difficult for taller species to grow there. These factors explain the predominance of the hemicryptophytes, such as the grasses, in the grassland *Mussununga*, which according Waring & Maricle (2012) and Yamauchi et al. (2018) are adapted to this condition. Although the species richness of the hemicryptophytes is lower than the phanerophytes, *Renvoizea trinii* (Poaceae) presented a high coverage in these areas, justifying the dominance of hemicryptophytes in the vegetational spectrum. Saporetto-Júnior et al. (2012) observed that a combination of the dry season with flooding episodes is a strong limiting factor that impedes most of the forest species to establish themselves in the *Mussunungas*. According to these authors, the soil is a limiting factor for the phanerophytes. Araújo et al. (2008) also stated that the stretch of transition between the grassland and forested *Mussununga* are easily recognized by the

substitution of the herbaceous species by trees and can be considered distinct in the phytophysiognomies of the *Mussununga*. These authors also comment about the low floristic differentiation among the grassland *Mussunungas* types, and reinforce the idea of the clear difference based on species dominance and vegetation physiognomy.

Silva & Batalha (2008) found similar results in floristic spectra in a hyperseasonal *cerrado* where flooding determined a reduction of species richness and favored the dominance of hemicryptophytes. In *campos rupestres*, where the soil is sandy, shallow and dystrophic, hemicryptophytes also dominate in seasonal flooding areas (Messias et al., 2013; Silveira et al., 2016). Interestingly, many families common in *campos rupestres*, such as Eriocaulaceae, Xyridaceae, Poaceae, Orchidaceae, Cyperaceae and Melastomataceae also occur in *Mussunungas*, which seems to be adapted to these stress conditions.

Soil-vegetation relationship is well described for the *Mussununga* of Bahia (Saporetto-Júnior et al., 2012). Ferreira et al. (2014) also presented a comprehensive study for *Mussunungas* of ES. But these authors only contemplated the floristic spectra, not taking into account the dominance or abundance of the functional groups. Since Ferreira et al. (2014) reported that *Mussunungas* of Bahia and ES exhibit a low floristic similarity, the present study contributes to the comprehension of patterns of biological spectra in *Mussunungas*. Even though this survey was restricted to a small area, more than one-third of the surveyed species had not been listed before in ES *Mussunungas*: *Anthurium zeneidae*, *Tillandsia globosa*, *Actinocephalus ramosus*, *Neomarica sabinei*, *Psidium brownianum*, *Urvillea rufescens*, *Manilkara triflora*, *Smilax rufescens* and *Monteverdia obtusifolia*. These results highlight how diverse is the *Mussununga* flora as well as the importance of focusing on further floristic studies. By analyzing the flora of *Mussunungas* from different sites (Meira-Neto et al., 2005; Saporetto-Júnior et al., 2012; Ferreira et al., 2014) it seems that *Mussunungas* have high species turnover (beta diversity), suggesting the need of future research to elucidate that.

5. CONCLUSION

The environmental constraints resulting from seasonal flooding as well as the physical barriers of the soil influence the vegetational spectra in *Mussunungas*, conditioning phytophysiognomic differences.

Vegetation spectra are similar in *Mussunungas* of Bahia and Espírito Santo, with a predominance of hemicryptophytes or phanerophytes, depending on the ortstein depth. Phanerophytes dominated in the savannas (where ortstein is deeper), while the shallower ortstein of the grasslands favored hemicryptophytes.

The results presented contribute to the knowledge of the flora, physiognomy and functional diversity patterns in *Mussunungas*, as well as in other ecosystems with seasonal flooding.

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