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Floristic and phytogeographic pattern of native field in southeastern Brazil

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ABSTRACT

The waterlogging of soils creates selective environments for plant species. The frequency and duration of flooding influence the responses to ecological processes, determining the structure and floristic composition of vegetation formations. We investigated the relationship between floristic composition and environmental heterogeneity of native field, one physiognomic type found interspersed with semideciduous forest in the plains in the northern part of the state of Espírito Santo, Brazil, which is characterized by varying degrees of waterlogging. Our results indicate that the differentiation of physiognomic types of native field is related to the frequency and duration of waterlogging to which each is subjected, resulting in a somewhat shared flora, dominated by phanerophytes. Flooding was also found to account for differences between the areas analyzed in terms of the soil pH, which ranged from strongly acid to extremely acid. The geographic proximity between the native field studied and areas of *muçununga* (or mussununga, a coastal forest ecosystem associated with the Atlantic Forest) did not increase the floristic similarity between the two.

Key words: Atlantic Forest, groundwater depth, muçununga, Vale Nature Reserve, soil

Introduction

The status of the water table is one of the most influential factors affecting the diversity, structural complexity and dynamics of vegetation formations (Scarano *et al.* 1997). The duration and periodicity of flooding, for example, determine several ecological processes, such as the productivity, distribution, demography and reproductive biology of plant populations (Junk *et al.* 1989; Megonigal *et al.* 1997). Ecological models (Odum 1979) suggest that, for a given vegetation formation, long periods of flooding decrease productivity, whereas periodic flooding can increase productivity (Megonigal *et al.* 1997).

The waterlogging of soils creates highly selective environments for plant species by reducing or eliminating soil oxygenation (Lieberman *et al.* 1985; Joly 1991). Such stressful environments come to be dominated by a few species with large populations and high biomasses, typically displaying low diversity in comparison with vegetation formations established in well-drained soils (Teixeira & Assis 2009; Scarano 2006). The presence of well-drained sites can increase the local diversity of the flora of floodplain vegetation formations (Menezes *et al.* 2010) by allowing the establishment of species that are less tolerant to water saturation, which prevail in the neighboring vegetation formations (Scarano 2002; Rocha *et al.* 2005; Teixeira *et al.* 2008). Therefore, floristic and structural differences can be observed between different sites within the same vegetation formation, because of different drainage conditions (Loures *et al.* 2007; Teixeira *et al.* 2008) and of influence from the neighboring vegetation (Ivanauskas *et al.* 1997; Teixeira & Assis 2009).

Although the relationship between the structure of vegetation formations and local environmental variations has been investigated, especially in forest formations (e.g. Joly & Crawford 1982; Oliveira Filho *et al.* 1990; Felfili 1995; Souza & Martins 2005; Damasceno Junior *et al.* 2005), little is known about the plant ecology of the wetlands of the Atlantic Forest Biome in southeastern Brazil (Scarano *et al.* 2005), and even less is known about species distribution in relation to the environmental characteristics of such wetlands on a small spatial scale (Teixeira & Assis 2009).

This study analyzed the floristic composition of native fields, a physiognomy found within the so-called *tabuleiro* forests (coastal lowland forests on Tertiary deposits) in the northern part of the state of Espírito Santo, Brazil (Veloso *et al.* 1991). Native fields occur interspersed with a forest type known as *muçununga* (or mussununga, a coastal forest ecosystem associated with the Atlantic Forest), as described by Peixoto *et al.* (2008). Physiognomically, the muçununga differs from the native field, because the former is composed of tree species of up to 30 m in height, whereas the latter is composed of graminoids and shrubs.

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The few studies performed in native fields have focused on their flora, physiognomy and origin (Heinsdijk *et al.* 1965; Veloso & Góes-Filho 1982; Peixoto 1982; Peixoto & Gentry 1990; Araujo *et al.* 2008). Native fields can be categorized into four types, considering the physiognomy and frequency of the species: dense graminoid, graminoid, closed shrubland and open shrubland. The first three refer to native fields on Tertiary soils and the last refers to native fields on Quaternary soils, which, in fact, constitute a vegetation formation known as *restinga* (coastal woodland) on Pleistocene soils (Suguio *&* Dominguez 1982).

Assuming the premise that the duration and periodicity of flooding are responsible for differences in diversity, richness and structure among vegetation formations within the same phytogeographic unit, we investigated the relation between the floristic composition and the environmental heterogeneity of two native fields in the Vale Natural Reserve (municipality of Linhares, Espírito Santo). Our hypothesis is that the floristic composition differs between these native fields, even at a small spatial scale (a few hundred meters of distance from one field to another), and that such difference is related to the different levels of soil waterlogging found in each vegetation formation. Additionally, another hypothesis is that the flora of the areas of muçununga is the main source of propagules to the native fields, due to their proximity.

Material and methods

Study sites

The Vale Natural Reserve is located in the Doce river watershed, in the northern part of Espírito Santo (19°06' to 19°18'S; 39°45' to 40°19'W), and occupies approximately 22,000 hectares (Fig. 1). According to the Köppen classification system (Köppen 1946), the climate of the region is type Awi (tropical wet-dry isothermal), with rainy summers and dry winters. Jesus *et al.* (2010) analyzed 26 years of data from the meteorological station within the reserve and reported a mean annual rainfall of 1202 mm, noting that June, July and August were the driest months. The mean annual temperature is 23.3°C, the monthly mean ranging from 14.8°C to 34.2°C. The mean annual relative air humidity has ranged from 82.1% to 84.7% the monthly means ranging from 80.6% to 86.6%

The native fields within the Vale Natural Reserve occur on sandy, nutrient-poor soils. The first layer of the soil does not exceed a depth of 60 cm, at which there is aggregation of fine roots; in this aspect, the native fields resemble muçununga forests (Garay 2003). The water table frequently lies below that depth. These soils are under an intense podzolization process, which is accentuated by hydromorphism

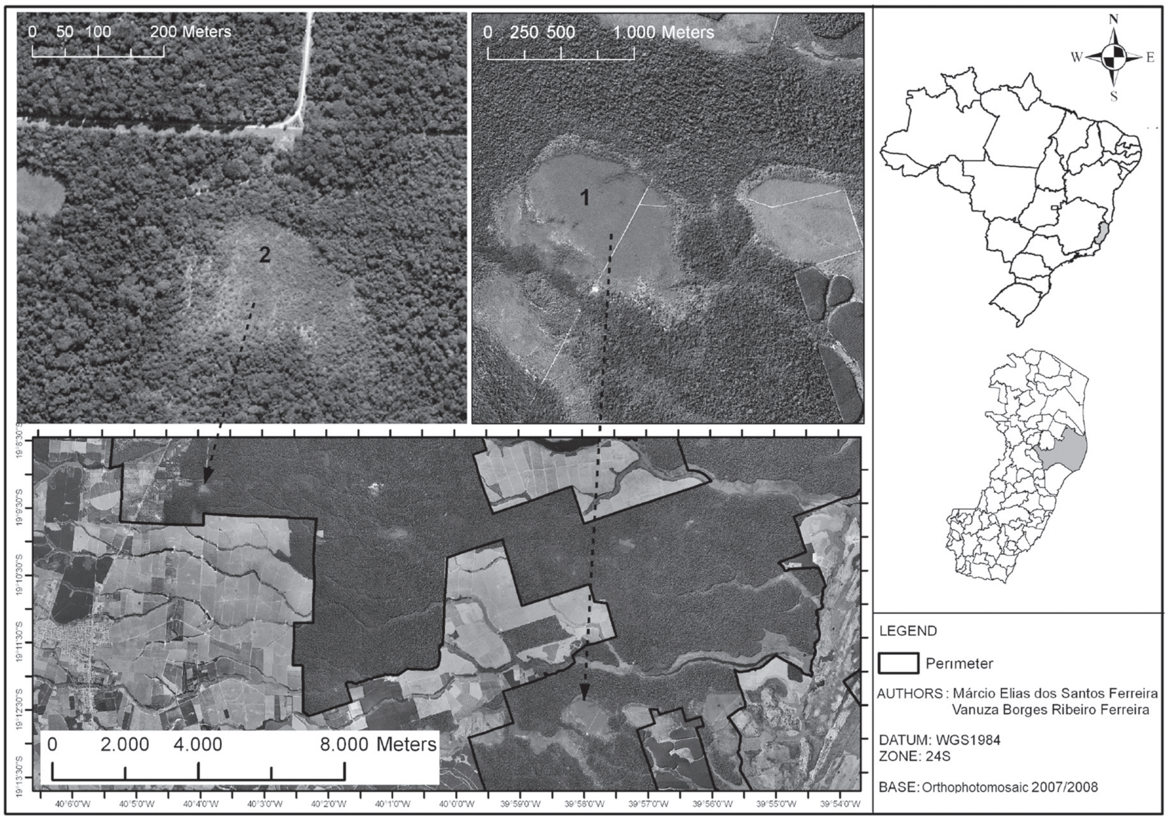

Figure 1. Map of Vale Nature Reserve detailing the native field studied in the state of Espírito Santo, Brazil.
1) Gávea site; 2) Roxinho site.

(Jesus & Rolim 2005). According to Santos *et al.* (2004), native fields occur on Spodosols, derived mainly from sand and quartzite, formed under high humidity, in tropical and subtropical climates. This soil type occurs in plain, slightly undulated relief; in areas of natural springs and depressions; under different vegetation types (Embrapa 1999). In the native fields studied, water availability is affected by the fact that the level of the water table varies considerably, according to the rainfall regime, between periods of flooding and water restriction.

Of the various native field formations that occur in the Vale Natural Reserve, two were selected because of the physiognomic differences between them. These two sites, known locally as Gávea and Roxinho, have not been subjected to significant disturbance related to human activity for at least fifty years. Both sites are circular and are surrounded by muçununga forest (Fig. 1), showing a transition zone that is characterized by a gradual increase in the number of woody individuals and a decrease in the abundance of graminoid life forms.

The Gávea native field (19°12'S; 39°57'W) occupies 85 ha. It is almost completely covered by the dominant grasses and sedges, with few patches of bare soil. A thin sheet of water (≤ 10 cm) can be observed covering the soil during the rainy season.

The Roxinho native field (19°09'S; 40°03'W) occupies 4.75 ha. Within this site, shrubs are noticeably more abundant than in the Gávea native field. Grasses and sedges are interspersed with patches of bare soil. Although the soil is flooded in the rainy season, sheets of water cover the soil only occasionally, when the rainfall is above average.

Floristic survey and vegetation analysis

Surveys were performed between April 2010 and September 2011. The botanical material was preserved according to Mori *et al.* (1989) and deposited in the Herbarium of the Federal University of Espírito Santo in Vitória, Brazil (code, VIES), with duplicates in the Herbarium of the Vale Natural Reserve in Linhares, Brazil (code, CVRD). Species were identified in the field, whenever possible, or by consulting the literature and specialists at CVRD. The botanical families were listed alphabetically according to the Angiosperm Phylogeny Group III guidelines (APG III 2009).

The species were classified by life form, following the Raunkiaer system, as adapted by Mueller-Dombois & Ellenberg (1974), considering mainly the position of the buds on the plant. The proportional distributions of species by life form in the different vegetation formations were compared by the chi-square test (Zar 1996).

For the floristic comparison with other vegetation formations on sandy soils in Espírito Santo and in the neighboring state of Bahia, we consulted 18 floristic lists from studies conducted in native fields, areas of muçununga and areas of *restinga* (Tab. 1). We built a presence/absence matrix for the multivariate analyses, using the unweighted pair group method with arithmetic mean (Chatfield & Collins 1983) and the Jaccard similarity index (Kent & Coker 1992), calculated with the Multivariate Statistics Package MVSP, version 3.1 (Kovach Computing Services, Pentraeth, Wales). We verified botanical synonyms and considered only taxa identified to the species level.

Table 1. List of works used for analysis of floristic similarity of vegetation on sandy soils in the Espírito Santo and Bahia.

Locations		Physiognomy	References
A	Ceolin - Linhares/ES	native grasslands	Araújo *et al.* 2008
B	Macanaíba - Linhares/ES	native grasslands	Araújo *et al.* 2008
C	Parajú e Barra Seca - Linhares/ES	native grasslands	Araújo *et al.* 2008
D	Gávea - Linhares/ES	native grasslands	Our data
E	Roxinho- Linhares/ES	native grasslands	Our data
F	Mucurí/BA	Muçununga	Meira Neto 2005
G	Caravelas/BA	Muçununga	Meira Neto 2005
H	Linhares/ES	Muçununga	Simonelli 2008
I	Caravelas/BA	Muçununga	Saporetti Jr. 2009
J	Caravelas/BA	Muçununga	Saporetti Jr. 2009
K	Caravelas/BA	Muçununga	Saporetti Jr. 2009
L	Caravelas/BA	Muçununga	Saporetti 2009
M	Caravelas/BA	Muçununga	Saporetti 2009
N	Caravelas/BA	Muçununga	Saporetti 2009
O	Setiba/ES	Restinga	Assis *et al.* 2004
P	Regência/ES	Restinga	Colodete & Pereira 2007
Q	Fazenda São Jorge/ES	Restinga	Pereira & Assis 2004
R	Fazenda São Jorge/ES	Restinga	Pereira *et al.* 2004
S	Maraú/BA	Restinga	Souza 2008
T	Salvador/BA	Restinga	Britto *et al.* 1993

Collection and analysis of environmental variables

To evaluate the variation in the water table, we installed observation wells, randomly distributed throughout the two study sites (five wells per site). In brief, we perforated the soil with an auger and inserted perforated PVC tubes (40 mm in diameter and 1 m in length) into the soil. The PVC tubes were wrapped in nylon mesh to facilitate water percolation and prevent sand from entering. At the bottom of each well, we placed a thin layer of gravel, which acted as a filter. To keep rainwater out, we sealed the top of the tube with a plug.

The water table depth was measured with a ruler, considering the distance from the surface of the soil to the waterline. These measurements were performed once a month for twelve months (October 2010 to September 2011). When there was no water at the pre-established depth of 1 m, we recorded the value as > 1 m.

For soil sampling, we traced 10 lines within each study site. The lines were 50 m in length, at least 20 m apart and at least 20 m from the border of the vegetation. From under each line, we collected composite soil samples at a depth of 20 cm. Each composite soil sample consisted of sub-samples collected at three points, 5 m apart, with 10 m between each composite soil sample collection zone. We collected 30 composite soil samples from each study site. The samples were air-dried, crumbled and sifted with a 2-mm mesh sieve to obtain fine soil. To describe the texture of the soil of each study site, we mixed samples to create a single sample per site, in which we analyzed the sand, silt and clay contents. The chemical and physical analyses of the soil were performed at the Laboratory of Agronomic Soil Analyses of the Federal University of Espírito Santo Northern Espírito Santo University Center, according to the procedures established by the Brazilian Agency for Agricultural Research (Embrapa 1997).

Data analysis

To test whether the mean water table depth varied between the environments, we performed repeated measures ANOVA. For the soil chemical variables, we calculated the means per study site and compared them by ANOVA, at 5% probability, followed by Tukey's test (Zar 1996).

Results and discussion

Floristic analysis

At the Gávea site, we recorded 36 species within 36 genera and 21 families, compared with 43 species within 42 genera and 27 families at the Roxinho site (Tab. 2). The only pteridophyte species, *Polypodium latipes* Langsd. & Fisch, was found at the Roxinho site. *Guapira* was the only genus represented by more than one species at the two study sites. At the family level, the similarity between the two sites was 59%. We recorded 20 and 24 species that were exclusive to the Gávea and Roxinho sites, respectively. The two sites had 17 species in common, corresponding to 39.5% of the species recorded at the Roxinho site and 47% of those recorded at the Gávea site. The high proportion of species exclusive to each site, that is, the variation in species composition at a small spatial scale (within a few hundred meters) reflects the selectivity of these sites, due to edaphic influences (Teixeira & Assis 2009). The native field at the Gávea site is subjected to stronger environmental stressors (longer and more intense periods of seasonal flooding) than is that at the Roxinho site. Those stressors restrict the establishment of species at the Gávea site, as reported by Scarano (1998), who studied the dispersal, germination and establishment of plants subjected to different flooding regimes and the consequences of the oxygen deficit imposed by flooded soils. Studies performed in areas of *restinga* showed that floodplain vegetation formations display a lower richness of plant species than upland vegetation formations (Almeida Jr. *et al.* 2009, Guedes *et al.* 2006, Menezes *et al.* 2010). Therefore, variations in the frequency and intensity of soil waterlogging can be considered determinants of the structural and floristic characteristics of the vegetation. Such variations might also result in altered behavior for certain populations (Rodrigues & Shepherd 2000; Menezes *et al.* 2010).

At the two study sites, we observed that many families were represented by a small number of species, a high proportion of the families being represented by only one or two species. In the Gávea native field, the families with the highest richness were Melastomataceae, with four species; Apocynaceae and Eriocaulaceae, with three each; and Asteraceae, Dilleniaceae, Humiriaceae, Lauraceae, Myrtaceae, Orchidaceae and Rubiaceae, with two each. The remaining families, accounting for 28% of the richness, were represented by only one species. In the Roxinho native field, the families with the highest richness were Eriocaulaceae, Myrtaceae, Orchidaceae and Rubiaceae, with three species each; and Asteraceae, Bignoniaceae, Dilleniaceae, Fabaceae, Humiriaceae, Melastomataceae and Nyctaginaceae, with two each. Another 15 families (55.5%) were represented by a single species. Studies performed in areas of *restinga* also showed that the proportion of families represented by more than one species was low (Pereira & Araujo 2000; Scherer *et al.* 2005; Amaral *et al.* 2008). Most families found in the native fields studied here are shared with the non-forested areas of muçununga in the south of Bahia (Meira Neto *et al.* 2005; Saporetti Jr. 2009; Sarcinelli 2010).

Life forms

Regarding the biological spectrum of the two sites, there was no significant difference in the distribution of the number of species per life form (df=6; $\chi^{2=12.592;}$ *p*>0.01). Phanerophytes constituted the most common life form

Table 2. Families and species sampled in two communities of native field in the north of the Espírito Santo. Lifeforms. CAM-chamaephytes; EPI-Epiphyte, FAN-phanerophytes; HEM-hemicryptophytes; LIA- creeper; TER-therophyte.

Family/Species	FV	Gávea	Roxinho
APOCYNACEAE			
Himatanthus bracteatus (A. DC.) Woodson	FAN	x	
Ditassa nitida E. Fourn.*	LIA	x	
Peplonia asteria (Vell.) Fontella & E.A. Schwarz*	LIA	x	x
ARACEAE			x
Anthurium queirozianum Nadruz sp.nov.ined.	HEM		x
ASTERACEAE			
Chromolaena squalida (DC.) K. & R.	FAN		x
Eupatorium harvardianum Steyerm.	FAN	x	x
Vernonia scorpioides Pers.	CAM	x	x
BIGNONIACEAE			
Tabebuia elliptica (DC.) Sandwith*	FAN	x	x
Bignonia corymbosa (Vent.) L.G. Lohmann	LIA		x
BONNETIACEAE			
Bonnetia stricta (Nees) Nees & Mart.	FAN	x	
BROMELIACEAE			
Vriesea procera Mart. & Schult	CAM	x	x
Tillandsia stricta Solander ex Ker - Gawler	EPI		x
BURSERACEAE			
Protium icicariba var. *talmonii* Daly*	FAN		x
CACTACEAE			
Pereskia aculeata Mill.	LIA		x
CHRYSOBALANACEAE			
Hirtella corymbosa Cham. & Schltdl.	FAN		x
Hirtella sp.	FAN	x	
CLUSIACEAE			
Kielmeyera membranacea Casar.*	FAN		x
CYPERACEAE			
Lagenocarpus rigidus (Kunth) Nees	HEM	x	x
DILLENIACEAE			
Davilla flexuosa A.St.-Hil.*	LIA	x	x
Doliocarpus lancifolius Kubitzki* **	FAN	x	x
ERICACEAE			
Gaylussacia brasiliensis (Spreng.) Meisn.	FAN	x	x
ERIOCAULACEAE			
Leiothrix hirsuta Ruhl.	TER	x	x
Syngonanthus gracilis (Koern) Rubl.	TER	x	
Paepalanthus klotzschianus Koern.*	TER		x
Actinocephalus ramosus (Wikstr.) P.T. Sano	TER	x	x
FABACEAE			
Andira fraxinifolia Benth.	FAN		x
Hymenolobium alagoanum var. *parvifolium* Lima	FAN	x	
Chamaecrista ramosa (Vog.) Irw. et Barn.	CAM		x
GENTIANACEAE			
Chelonanthus purpurascens (Aubl.) Struwe, S. Nilsson & V.A.Albert.	CAM		x
HUMIRIACEAE			
Vantanea bahiaensis Cuatrec.*	FAN	x	x
Humiria balsamifera var. *parvifolia* (Juss.) Cuatr.	FAN	x	x

Continues.

Table 1. Continuation.

Family/Species	FV	Gávea	Roxinho
LAURACEAE			
Ocotea notata (Nees & Mart.) Mez*	FAN		x
Cassytha filiformis L.	LIA	x	
Ocotea lobbii (Meisn.) Rohwer	FAN	x	
MALPIGHIACEAE			
Byrsonima stipulacea (Juss.) Nied.	FAN		x
Byrsonima sericea DC.	FAN	x	
MELASTOMATACEAE			
Tibouchina urceolaris (Schrank & Mart. ex DC.) Cogn.*	FAN	x	x
Pterolepis glomerata Miq.	CAM	x	
Microlicia fulva (Spreng.) Cham.	CAM	x	
Marcetia taxifolia (A.St.-Hil.) DC.	CAM	x	x
MYRTACEAE			
Calyptranthes brasiliensis Spreng.*	FAN	x	x
Psidium macahense O. Berg*			x
Marlierea neuwiediana (O.Berg) Nied.*	FAN	x	x
NYCTAGINACEAE			
Guapira opposita (Vell.) Reitz	FAN		x
Guapira pernambucensis (Casar.) Lundell*	FAN		x
OCHNACEAE			
Ouratea aff. multiflora (Pohl) Engl.*	FAN	x	x
ORCHIDACEAE			
Catasetum discolor (Lindl.) Lindl.			x
Sobralia sessilis Lindl.	HEM		x
Sobralia liliastrum Lindl.	HEM	x	
Epistephium lucidum Cogn.	HEM	x	x
OROBANCHACEAE			
Esterhazya splendida J.C.Mikan	FAN	x	
PERACEAE			
Pera glabrata (Schott) Baill.*	FAN	x	
POACEAE			
Renvoizea trinii (Kunth) Zuloaga & Morrone	HEM	x	x
POLYGALACEAE			
Bredemeyera autranii fo. *obovata* Marques	FAN		
POLYPODIACEAE			
Polypodium latipes Langsd. & Fisch.	GE		x
RUBIACEAE			
Pagamea guianensis Aubl.	FAN	x	x
Emmeorhiza umbellata (Spreng.) Schum.	LIA		x
Rudgea sp.	FAN		x
Palicourea blanchetiana Schled.*	FAN	x	
SAPINDACEAE			
Paullinia riodocensis Somner	FAN		x
XYRIDACEAE			
Xyris ciliata Thunb.	TER	x	

* Species with restricted geographic distribution to Mata Atlantica (Stehmann et al. 2009). ** Specie restricted to the Espirito Santo (Fraga 2010).

(accounting for 54% of the species at both sites), followed by chamaephytes (accounting for 13% of the species at the Gávea site and 12% at the Roxinho site) and hemicryptophytes (accounting for 11% of the species at the Gávea site and 14% at the Roxinho site). Epiphytes and geophytes were observed only at the Roxinho site, each accounting for less than 2% of the species (Tab. 2 and Fig. 2).

In general, phanerophytes were sparsely distributed within both sites. However, we observed some species forming "vegetation islands". For example, shrubs of *Humiria balsamifera* var. *parvifolia* had an aggregate distribution with dense populations within the Gávea site, whereas the species occurred in less dense populations or was represented by isolated individuals at the Roxinho site. In contrast, *Pagamea guianensis* and *Tabebuia elliptica* had an aggregate distribution at the Roxinho site. This distribution pattern seems to be common in vegetation formations within *tabuleiro* forests and has been reported for two grassy areas of muçununga in the southern part of Bahia (Meira-Neto *et al.* 2005), where the most common life forms were phanerophytes in one area and hemicryptophytes in the other. Saporetti Jr. (2009) and Sarcinelli (2010) found that the predominant life forms were in graminoid muçununga and graminoid woody muçununga were chamaephytes and phanerophytes, respectively.

The graminoid layer is characteristic of both sites, with dominance of the hemicryptophytes *Lagenocarpus rigidus* and *Renvoizea trinii,* mainly in the dry season, when they become more abundant. According to Walter (1973), the theoretical basis of the classification of vegetation includes the concept that each life form reflects a strategy that was selected by evolutionary pressures and that the composition of a given vegetation formation, in terms of its of life forms, is governed by those strategies. Therefore, a high abundance of hemicryptophyte species indicates the strategy of escaping an unfavorable season, by protecting the buds below the soil (Pessoa *et al.* 2004). At the Gávea site, such species cover the soil almost completely during the rainy season, leaving only small depressions where there is upwelling groundwater. At the Roxinho site, hemicryptophytes also cover most of the soil, although less densely, leaving a higher proportion of bare soil. The dominance of hemicryptophyte species is favored by certain characteristics of the families Cyperaceae and Poaceae, which are typical of fields and savannas (Mantovani & Martins 1993, Batalha & Martins 2002), such as the ability to establish in open formations and to propagate vegetatively, as well as featuring anemochorous pollination and dispersal (Cabral-Freire & Monteiro 1993).

Similarities

Our comparison between the study sites and 18 floristic lists from studies of other vegetation formations that occur on sandy soils, performed with a presence/absence matrix of 767 species, revealed low floristic similarities (Tab. 1 and Fig. 3). The vegetation formations that showed similarities closest to 50% were muçununga forests and muçununga forests on islands (N and M) in the southern part of Bahia, followed by the graminoid areas of muçununga of Mucurí and Caravelas. The *restingas* of the Vale Natural Reserve, Parajú and Barra Seca, were more similar to the Ceolin native field, within the same reserve, and to the shrubland *restingas* of Linhares, forming a subcluster.

Despite the proximity, the muçununga forest of Linhares was not grouped with the *restingas* cited or with the Ceolin native field, but rather with the *restinga* of Setiba, forming an isolated cluster. The muçununga forests of the south of Bahia formed a single cluster. The *restingas* of Maraú and Salvador formed another isolated cluster, indicating floristic particularities for this region, as noted in other studies (Oliveira-Filho & Fontes 2000; Marques *et al.* 2011).

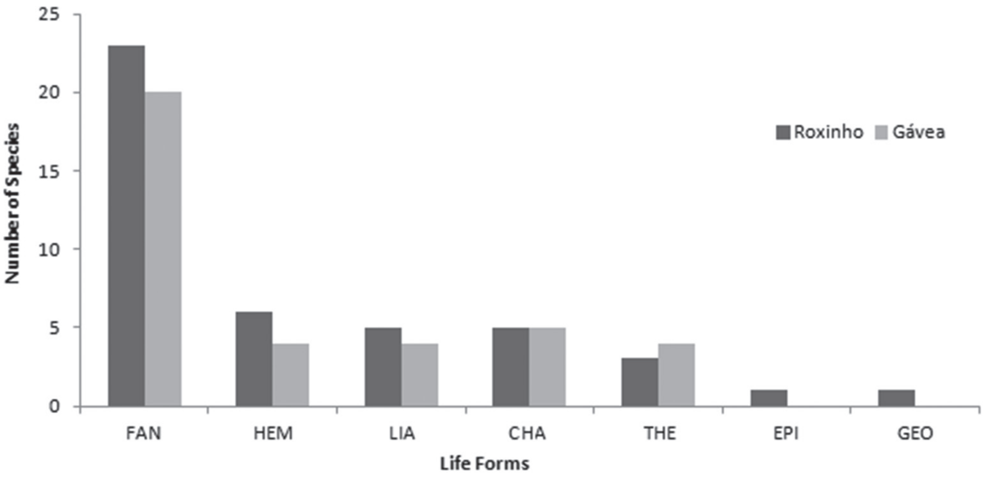

Figure 2. Number of species, by life form, in two formations of native field in the north of the state of Espírito Santo, Brazil.
CHA– chamaephyte; EPI – epiphyte; FAN – phanerophyte; GEO – geophyte; HEM – hemicryptophyte; LIA – liana (creeper); THE – therophyte.

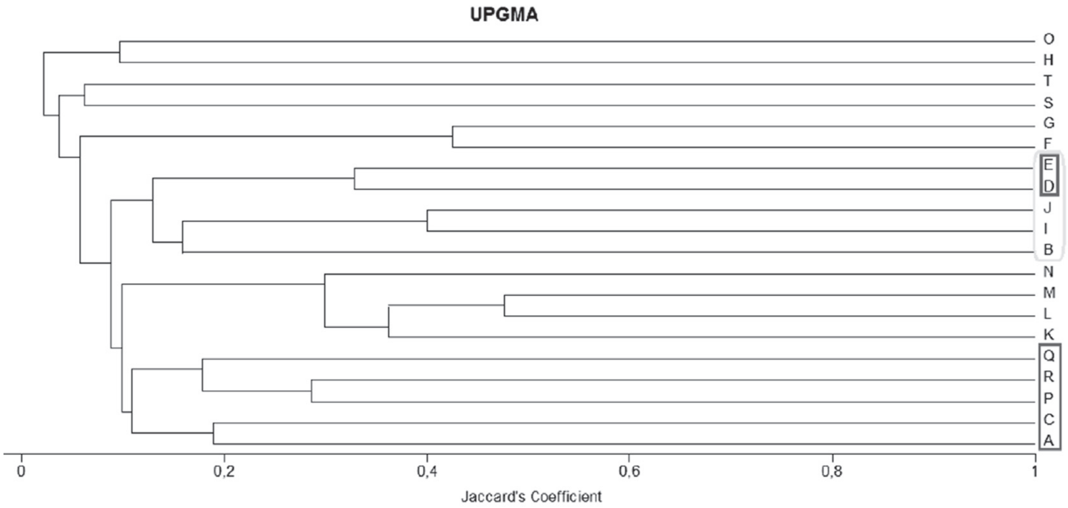

Figure 3. Dendrogram of cluster analysis using the Jaccard similarity index and the unweighted pair group method with arithmetic mean of the floristic data from 20 areas of vegetation on sandy soils in the Brazilian states of Espírito Santo and Bahia.
To identify the areas, see Table 1.

Although muçununga forests are established on Tertiary soils, forming enclaves in the tall *tabuleiro* forest, their soil conditions are similar to those of the *restingas* compared here, where the soils are essentially sandy and well-drained (Simonelli *et al.* 2008). This justifies the position of muçununga forests in the dendrogram, showing higher similarities with *restinga* forests (Meira-Neto *et al.* 2005).

The native fields of the Vale Natural Reserve (with the exception of the dense graminoid native field, which remained isolated) and the graminoid areas of muçununga of the south of Bahia formed another cluster. In contrast, the graminoid areas of muçununga of Caravelas and Mucuri (G and F) formed another cluster, revealing their dissimilarity with the cluster of the vegetation formations here studied. The vegetation formations I and J probably show flooding conditions similar to those of the native fields of the Vale Natural Reserve, favoring the common occurrence of species that tolerate the same type of stress. In this case, the low similarity between the two native fields studied (Jaccard similarity index: 33%) was due to the high proportions of exclusive species found at each site. Our results indicate that this dissimilarity is related to the influence that the nutrient content of the soil, as well as the duration and frequency of soil waterlogging, has on the floristic composition. Differences in the duration of soil waterlogging between vegetation formations usually result in differences in species diversity: species that are dominant in areas subjected to flooding may be rare or absent in drier areas (Gomes *et al.* 2004). Therefore, variations in the frequency and intensity of soil waterlogging can be considered determinants of the structural and floristic characteristics of the vegetation, potentially altering the behavior of certain populations (Silva *et al.* 2007). Flooding defines certain abiotic characteristics, both edaphic and microclimatic, which significantly affect biological processes such as decomposition, germination and recruitment of individuals (Lobo & Joly 2000), thereby defining the spatial distribution of the species within a given vegetation formation.

Water table and soil

In the comparative analyses of the wells installed within the Roxinho site, we found no significant differences in the water table levels. The same was observed for the Gávea site. However, when comparing the two native fields, we observed significant differences in the mean water table depth ($p < 0.001$), the variation in the mean water table depth between months ($p < 0.001$) and the variation in the mean water table depth between the sites over time ($p < 0.001$, interaction between environment and time). During the rainy season, there was upwelling groundwater at the Gávea site, resulting in the formation of a sheet of water of approximately 5 cm in depth covering the soil, whereas there was no such flooding at the Roxinho site, although the water table was close to the surface there as well. During the dry season (July to October), the water table level at both sites was ≥ 1 m below the soil.

The soils of the two sites showed sand contents of 99-100%. According to the Brazilian Agency for Agricultural Research (Embrapa 1999), the soil of the Gávea site is strongly acidic, with a pH of 4.1-4.6, whereas the soil of the Roxinho site is extremely acidic, with a pH < 4.1 (Tab. 3). Although both sites have low-fertility soils, the soil of the Roxinho site showed higher levels of macronutrients and micronutrients and was therefore considered more fertile than that of the Gávea site. The cation exchange capacity was also higher in the soil of the Roxinho site, due to the higher organic matter content (Tab. 3). The aluminum saturation was above 50% at both sites, indicating that their soils can

Table 3. Comparison between the means of the soil chemical variables found in 20 sampling units in two areas of native field in the Reserva Natural Vale, Linhares, ES. The numbers are means ± standard deviation and, in parentheses, the coefficient of variation.

Variables	Gávea	Roxinho	F
pH (H^2O)	4,23 ± 0,14 (3,36)	3,91 ± 0,11 (2,92)	30.81*
P (mg/dm^3)	2,40 ± 0,37 (15,41)	6,65 ± 0,90 (13,59)	189.93*
K (mg/dm^3)	10 ± 0,00 (0,00)	33,33 ± 4,44 (13,33)	275.63*
Na (mg/dm^3)	9,13 ± 1,85 (20,27)	20,33 ± 3,67 (18.04)	74.36*
Ca ($cmolc/dm^3$)	0,12 ± 0,04 (31,34)	0,37 ± 0,13 (34,55)	33.75*
Mg ($cmolc/dm^3$)	0,36 ± 0,08 (23,01)	0,72 ± 0,10 (14,25)	75.46*
Al ($cmolc/dm^3$)	1,05 ± 0,09 (8,52)	1,47 ± 1,16 (10,82)	53.24*
H+Al ($cmolc/dm^3$)	5,38 ± 1,58 (29,32)	18,99 ± 0,34 (16,02)	157.93*
MO (dag/Kg)	5,16 ± 0,88 (16,99)	6,65 ± 0,61 (9,23)	19.19*
Fe (mg/dm^3)	2,5 ± 0,51 (20,22)	3,38 ± 0,80 (23,52)	8.78**
Mn (mg/dm^3)	0,13 ± 0,04 (26,35)	0,48 ± 0,34 (70,58)	10.42**
Zn (mg/dm^3)	0,28 ± 0,10 (36,89)	0,52 ± 0,14 (26,03	19.15*
CTC ($cmolc/dm^3$)	1,59 ± 0,18 (11,32)	2,73 ± 0,36 (13,10)	80.53*
m – saturação por alumínio (%)	66,18 ± 3,85 (5,82)	54,10 ± 2,71 (2,24)	65.61*
v – saturação de bases (%)	10,31 ± 2,16 (20,97)	6,77 ± 2,24 (32,99)	12.96**

* $P < 0,001$, ** $P < 0,01$

be considered Al-saturated—extremely poor soils with high aluminum saturation (Ronquim 2010). There were significant differences between the two sites regarding the soil chemical variables analyzed.

In summary, soil waterlogging was the main abiotic factor, selecting the occurrence of plant species, which resulted in a reduction of the diversity of the native fields. The differences in the frequency and duration of soil waterlogging were responsible for the floristic differences found between the two areas, and acted on the selection of species to such a degree that each area had a group of exclusive species. Despite the low floristic similarity, both areas showed a life form spectrum that supports their classification into the same vegetation formation.

The proximity between the native fields studied and areas of muçununga did not increase the floristic similarity between the two, and the muçununga was not the main source of propagules for the native fields. The floristic similarity between the native fields of the Vale Natural Reserve and the graminoid areas of muçununga in the southern part of Bahia seems to indicate that they are in fact the same type of vegetation formation, despite the distinct designations, and that, in the future, the classification should be standardized to facilitate more robust comparisons.

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