Restinga forests of the Brazilian coast: richness and abundance of tree species on different soils

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ABSTRACT

The aim of this study was to determine changes in composition, abundance and richness of species along a forest gradient with varying soils and flood regimes. The forests are located on the left bank of the lower Jucu River, in Jacarenema Natural Municipal Park, Espírito Santo. A survey of shrub/tree species was done in 80 plots, 5x25 m, equally distributed among the forests studied. We included in the sampling all individuals with ≥3.2 cm diameter at breast height (1.30 m). Soil samples were collected from the surface layer (0-10 cm) in each plot for chemical and physical analysis. The results indicate that a significant pedological gradient occurs, which is influenced by varying seasonal groundwater levels. Restinga forest formations showed significant differences in species richness, except for Non-flooded Forest and Non-flooded Forest Transition. The Canonical Correlation Analysis (CCA) showed that some species are distributed along the gradient under the combined influence of drainage, nutrient concentration and physical characteristics of the soil. Regarding the variables tested, flooding seems to be a more limiting factor for the establishment of plant species in Restinga forests than basic soil fertility attributes.

Key words: Vegetation, Flooded Forests, Coastal ecosystem, Sandy Soils, Quaternary deposits, Marine influence, Riparian forests.

INTRODUCTION

Marine regressions and transgressions following sea level changes during the Quaternary period allowed the formation of beach ridges, dunes and interdunes along the Brazilain coast (Martin et al. 1997). These depositional features were formed during the Late Pleistocene and Holocene epochs, forming extensive sandy coastal plains, with major deposition of mature quartz sands and local contributions of fluvial sands, especially near large river estuaries (Pereira 2003). On these sandy coastal plains we find the Restinga ecosystem (Araujo et al. 1998) occupying nearly 80% of the Brazilian coastal fringe, or about 7110 km (Suguio and Tessler 1984). This ecosystem is associated with the Atlantic Rain Forest biome (Coutinho 2006).

The topographical differences among the beach ridges, dunes and interdunes in the Restinga are associated with different groundwater levels,

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Figure 1 - Location of Jacarenema Natural Municipal Park, Vila Velha/ES with the the studied areas highlighted.

resulting in varying pedological conditions, which can, among other factors, lead to the heterogeneity of vegetation types in the Brazilian Restinga.

According to ter Braak and Prentice (1988), biotic communities show greater development in the narrow confines of their optimum, varying with the existence of physical gradients. Among the abiotic factors, physical, chemical and soil drainage characteristics have been widely cited as important factors for the distribution of plant species in communities of tropical environments (Lathwell and Grove 1986, Oliveira-Filho et al. 1994, Clark et al. 1999, Budke et al. 2007, Ferreira-Junior et al. 2007). Thus, the various interactions between abiotic factors and their responses in species composition result in high environmental heterogeneity, determining the existence of a mosaic of habitats (Machado et al. 2008, Petty and Douglas 2010).

Soil physical, chemical and hydrological conditions also impose variations in species richness of a given area (Sollins 1998), acting on species selection in such a way that local richness varies depending on the degree of influence of environmental variables (Oliveira-Filho et al. 1994, Ivanauskas and Rodrigues 2000, Budke et al. 2007). However,our knowledge on the relationship between vegetation characteristics and soil factors is patchy, and further studies focusing on indicator species (Jacomine 2004) will be important for a better understanding of Restinga ecosystems, since none of them have been carried out in Brazil.

Thus, we aimed to determine the relationship between vegetation variables, such as composition, abundance and species richness, and soil attributes along a forest gradient in a Restinga.

MATERIALS AND METHODS

STUDY AREA

The study area is located in Barra do Jucu, Espírito Santo State, Brazil. The Jacarenema Natural Municipal Park (PNMJ) has an area of 307 hectares (IPEMA 2005), and is located near coordinates 20°26'25"S and 40°18'45"W (Figure 1). The climate is classified as Aw tropical by Köppen, with hot, wet summers and cold, dry winters.

The forest sites are located on the left bank of the Jucu River, forming an environmental gradient ranging from interdune (River Jucu site) to the innermost dune facing the continent. The varying topographic condition creates different levels of flooding, caused by seasonal floods of the Jucu River, with an accompanying soil gradient (Table I). The terminology for classifying Restinga vegetation types (physiognomies) was based on Pereira (2003), as follows: Well-drained Forest, Transitional Forest, Floodplain Forest and Inundated Forest (Figure 2).
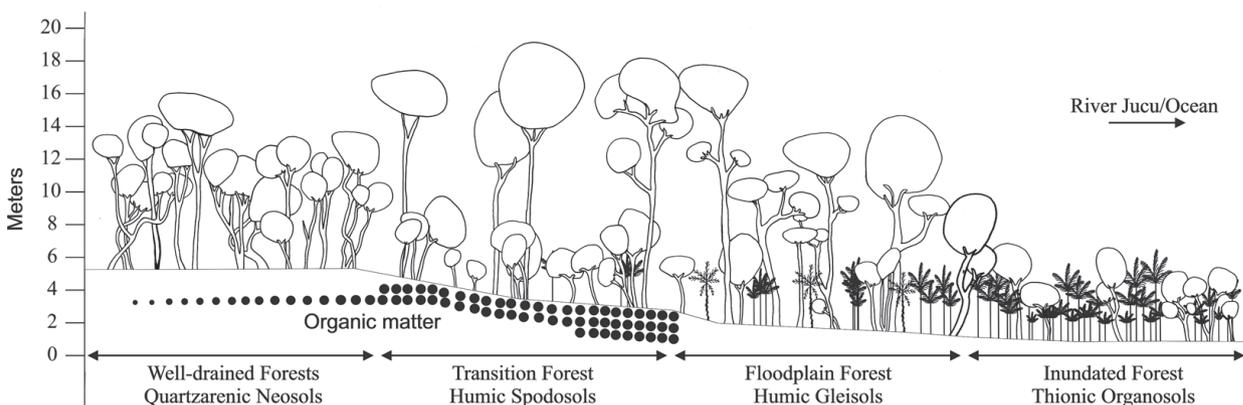

Figure 2 - Schematic profile perpendicular to the River Jucu in Jacarenema Natural Municipal Park, Vila Velha, Brazil.

TABLE I
Soil classes and groundwater fluctuation in the four forests of Jacarenema Natural Municipal Park, Vila Velha,
Brazil. INF=Inundated Forest; FPF=Floodplain Forest; TRF=Transitional Forest; WDF=Well-drained Forest.
TH=Thiomorphic Histosols; MG=Melanic Gleysols; HS=Humic Spodosols; QN= Quartzarenic Neossols.

Vegetation type	Soil classes	Classes of soil drainage	Fluctuation of groundwater (m)		
			Max	Min	Annual Average
INF	TH	Very poorly drained	0.60	-0.05	0.25
FPF	MG	Poorly drained	0.15	-0.30	-0.06
TRF	HS	Moderately drained	-0.90	-1.60	-1.23
WDF	QN	Excessively drained	-3.70	-5.00	-4.22

VEGETATION DATA

The floristic composition of shrub and tree species was determined in 80 plots (Mueller-Dombois and Ellenberg 1974), 5x25 m (125 m^2), totaling one hectare of sample area. The plots were equally distributed in the four forest formations, i.e., 20 plots for each forest type, with a minimum spacing of 2 m apart. We aimed to represent the core areas of each forest when allocating the plots in the phytocoenoses. The plots were arranged in each physiognomy parallel to the Jucu River bank. We recorded shrub and tree species with diameter at breast height (1.30 m) ≥ 2 cm.

The palms *Bactris setosa* and *Bactris vulgaris* have a caespitose growth habit, forming clumps. The former species occurs in wetlands in large populations (Reis 2006), rendering the separation of each individual virtually impossible. Thus, for this study each stipe was considered to be an individual.

The plant material was determined by consulting the CVRD Herbarium (Vale do Rio Doce), the VIES Herbarium (Universidade Federal do Espírito Santo) and the MBML Herbarium (Museu de Biologia Prof. Mello Leitão). Consultations were also made of specific literature and material was sent to specialists. Fertile specimens were deposited in the collection of the VIES Herbarium (Universidade Federal do Espírito Santo). The species were classified in their respective families according to Angiosperm Phylogeny Group II (APG II 2003).

SOIL SAMPLE

Soil samples were collected for chemical and physical analysis taking three replicates of surface soil (0-10 cm) in each sample unit, for a total of 40 samples. The samples were air-dried and sieved with a 2 mm diameter mesh. These samples were analyzed in the Soil Analysis Laboratory, Department of Soils, Universidade Federal de Viçosa. The soil and drainage classes of each physiognomy were classified according to the Brazilian System of Soil Classification (EMBRAPA 2006).

DATA ANALYSIS

Differences in species richness and chemical and physical soil attributes between the four forests were tested by the analysis of variance (one way ANOVA). Subsequently, we used the Tukey test to determine significant differences between areas. In addition, we employed the Pearson linear correlation "r" to check the ratio of species increase with variations in fertility (Mg, P, K, Ca), acidity, aluminum content and soil drainage. Shapiro-Wilk (W) tested all the data distribution for normality. To test the use of variance (ANOVA), in addition to the normality test we tested the homoscedasticity of Levene.

To investigate the differences in the species richness of each physiognomy a rarefaction curve was employed (Colwell and Coddington 1994, Magurran 2004), and adjustments were made using the Mao Tau index with standard deviations

at 95% confidence. This analysis was performed in the EstimateS 8.0 program, employing 100 randomizations to generate curves (Colwell 2006).

To analyze correlations between the environmental gradients (soil and drainage) and vegetation we used the Canonical Correspondence Analysis (CCA) (ter Braak 1987). For this analysis, we grouped vegetation data at every two plots. We used only species that had values greater than or equal to five individuals sampled. These data were correlated with eight chemical variables of soil: pH in H20, available phosphorus (P), exchangeable Calcium (Ca), Aluminum (Al), Sodium (Na), Magnesium (Mg), Potassium (K) and Organic Matter (MO). The soil physical attributes used for the CCA were the amounts of coarse sand, fine sand, silt and clay. The species were also correlated with drainage classes for each vegetation type. The program PC-ORD for Windows version 4.14 generated analyses and the ordered CCA axes (McCune and Mefford 1999). To check the significance level of the results given by the main axis of the canonical ordering, we employed the Monte Carlo permutation (ter Braak 1988, 1994).

To verify the relationships between species and environmental variables expressed by each forest type, we used the Indicator Species Analysis (Dufrêne and Legendre 1997) and the calculations were processed by PC-ORD for Windows version 4.14 (McCune and Mefford 1999). According to Machado et al. (2008), this method combines information on the abundance of a species in a certain group of sampling units, revealing information about the confidence of occurrence of this species in the same habitat. The results are expressed by the observed indicator value (OIV), in which the significance of data is given by the permutation test of Monte Carlo. Thus, only one species is considered an indicator of habitat when it has the highest OIV, and the, Monte Carlo test is significant at p ≤ 0.05 (Machado et al. 2008).

RESULTS

PHYSICAL ENVIRONMENT

The chemical and physical soil variables showed significant differences among soil classes in the four forest types (Table II). However, the major changes were observed between the Humus-alluvial Spodosols (Transition Forest) compared to Melanic Gleysols (Inundated Forest) and Thiomorphic Histosols. The Quartzarenic Neossols were very close to Spodosols in terms of physical and chemical characteristics.

Soil drainage classes varied significantly between all formations (ANOVA, P <0.001), reinforcing the importance of flooding in the sedimentary environment. The pH values were lower for the formations with greater influence of groundwater, following the highest values of exchangeable Al in these formations. Following the same pattern, the soil drainage gradient showed increasing concentrations of organic matter, sodium, potassium, magnesium, silt and clay as the soil becomes more subject to flooding. The variables with the highest values in Well-drained Forests were pH and coarse sand. However, all soils studied are dystrophic, with a very low fertility status.

The soils of Floodplain Forests and Inundated Forest showed higher levels of nutrients, with higher percentages of silt and clay; they were less leached than the sandier soils of the Well-drained uplands. Organic matter in these formations also exhibited significantly higher values when compared to the Well-drained Forest. This condition depends on the hydromorphic environment, since soil reduction and low oxygen condition slows downs organic matter decomposition.

RICHNESS ANALYSIS

In four forest types of PNMJ, 3804 individuals were sampled and 132 species identified. The Transition Forest had the greatest richness, with 82 species, followed by Well-drained Forest (74), Floodplain Forest (47) and Inundated Forest (29).

TABLE II

Chemical and physical soil variables (0-10) in four forest types analyzed in Jacarenema Natural Municipal Park, Vila Velha, Brazil. p = significance level. INF=Inundated Forest; FPF=Floodplain Forest; TRF=Transitional Forest; WDF=Well-drainedForest. Each line shows the value of the soil variable in each forest type. Similar letters denote values that could not be differentiated by the Tukey test (p ≤0.05).

| Soil variables	INF	FPF	TRF	WDF	p
pH in H_2O	4.73 ± 0.23a	4.35 ± 0.26b	3.78 ± 0.12c	4.06 ± 0.24d	**
P (mg/dm^3)	2.45 ± 0.57a	5.11 ± 2.07b	9.44 ± 3.09c	9.37 ± 2.40c	**
K (mg/dm^3)	16.00 ± 5.88a	22.70 ± 6.24a	55.80 ± 16.17b	74.30 ± 32.56c	***
Na (mg/dm^3)	6.89 ± 5.42a	8.69 ± 4.68a	60.90 ± 12.76b	209.99 ± 81.8c	**
Ca (cmolc/dm^3)	1.38 ± 0.57a	1.13 ± 0.36a	1.26 ± 0.51a	2.59 ± 0.85c	***
Mg (cmolc/dm^3)	0.34 ± 0.09a	0.52 ± 0.23a	0.96 ± 0.46b	2.72 ± 0.85c	***
Al (cmolc/dm^3)	0.19 ± 0.17a	0.87 ± 0.64b	3.00 ± 1.00c	1.91 ± 0.77d	***
MO (dag/Kg^{-1})	2.39 ± 0.52a	5.07 ± 2.81a	35.07 ± 12.12b	48.31 ± 8.01c	***
Coarse sand (%)	90.00 ± 1.03a	88.00 ± 2.34a	42.50 ± 13.68b	24.20 ± 15.59c	**
Fine sand (%)	4.90 ± 0.72a	5.10 ± 1.17a	17.20 ± 12.75b	5.50 ± 4.52a	**
Silt (%)	1.00 ± 0.79a	0.60 ± 0.68a	6.90 ± 2.17b	16.70 ± 3.92c	***
Clay (%)	4.10 ± 1.07a	6.30 ± 2.60a	33.40 ± 9.01b	53.60 ± 15.67c	***

**p < 0.01; ***p < 0.001.
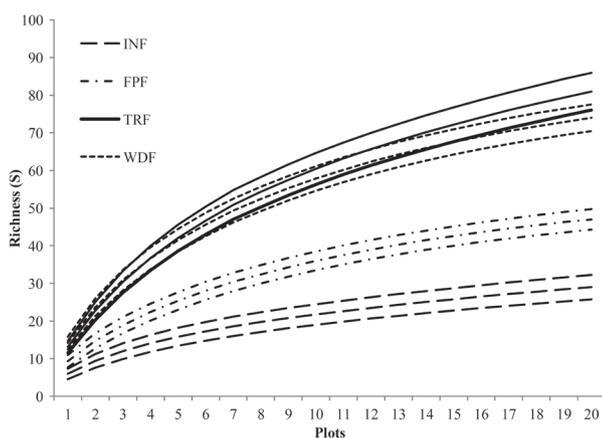
Figure 3 - Mao Tao rarefaction curves for the four forest formations in Jacarenema Natural Municipal Park, Vila Velha/ES. INF=Inundated Forest; FPF=Floodplain Forest; TRF=Transitional Forest; WDF=Well-drained Forest.

All forest formations showed significant differences in species richness (Tukey, p <0.01), except Well-drained Forest and Transition Forest, which showed no significant differences (Tukey test, 95% confidence). Corroborating these results, the rarefaction curves showed similar results reported by the Tukey test (Figure 3).

Changes in species richness among Restinga forests had statistically significant negative correlation with magnesium (r=-0.5822, p=0.0001), phosphorus (r=-0.5739, p= 0.0001), potassium (r=-0.6418, p=0.0001), calcium (r=-0.357, p=0.0001), sodium (r=-0.641, p=0.0001) and aluminum (r=-0.441, p=0.0001), while acidity (r=-0.641, p=0.0001) had significant positive correlation with soil drainage (r=0.654, p=0.0001).

VARIATION IN ABUNDANCE AND ANALYSIS
OF INDICATOR SPECIES

For the ordination analysis (CCA) and the analysis of indicator species, 64 species were evaluated from a total of 132 due to the inclusion criteria established in the methodology (Table III). The eigenvalues found in the ordination analysis of chemical and physical variables of soil for the three axes were 0.848, 0.326 and 0.248, for axes 1, 2 and 3, respectively (Table IV). The Pearson correlation was high for all three axes of the CCA (Table IV). Supporting this result, the Monte Carlo permutation

Woody species used in Canonical Correspondence Analysis (CCA) and their abbreviations, for the four forests types studied in Jacarenema Natural Municipal Park, Vila Velha, Brazil. INF=Inundated Forest; FPF=Floodplain Forest; TRF=Transitional Forest; WDF=Well-drained Forest.

Species	Family	Abbreviations	Abundance			
			INF	FPF	TRF	WDF
Alchornea triplinervia (Spreng.) Müll. Arg.	Euphorbiaceae	Alc tri	21	10	0	1
Alibertia myrciifolia Spruce ex K. Schum.	Rubiaceae	Ali myr	1	11	0	0
Andira fraxinifolia Benth.	Fabaceae	And fra	2	2	4	1
Annona acutiflora	Annonaceae	Ann acu	0	0	12	3
Annona acutiflora Mart.	Apocynaceae	Asp par	0	0	2	5
Bactris setosa Mart.	Arecaceae	Bac set	1796	335	26	0
Bactris vulgaris Barb. Rodr.	Arecaceae	Bac vul	0	0	60	2
Brasiliopuntia brasiliensis (Willd.) A. Berger	Cactaceae	Bra bra	0	0	0	12
Buchenavia capitata (Vahl) Eichler	Combretaceae	Buc cap	0	1	1	6
Byrsonima sericea DC.	Malpighiaceae	Byr ser	0	0	5	0
Calophyllum brasiliense Cambess.	Clusiaceae	Cal bra	8	2	1	0
Campomanesia guazumifolia (Cambess.) O. Berg	Myrtaceae	Cam gua	0	0	3	16
Casearia commersoniana Cambess.	Salicaceae	Cas com	0	5	6	2
Cathedra rubricaulis Miers	Olacaceae	Cat rub	0	0	3	3
Chamaecrista ensiformis (Vell.) H.S. Irwin and Barneby	Fabaceae	Cha ens	0	0	13	23
Coccoloba arborescens (Vell.) How	Polygonaceae	Coc arb	0	0	3	5
Cupania emarginata Cambess.	Sapindaceae	Cup ema	0	0	9	16
Cyathea phalerata Mart.	Cyatheaceae	Cya pha	0	30	1	0
Dendropanax selloi Marchand	Araliaceae	Den sel	0	18	5	0
Eugenia bahiensis DC.	Myrtaceae	Eug bah	0	0	4	12
Eugenia excelsa O. Berg	Myrtaceae	Eug exc	0	0	0	5
Eugenia sp. new	Myrtaceae	Eug nov	11	0	0	0
Eugenia rostrata O.Berg	Myrtaceae	Eug ros	0	0	10	55
Eugenia sulcata Spring ex Mart.	Myrtaceae	Eug sul	0	0	0	6
Garcinia brasiliensis Mart.	Clusiaceae	Gar bra	0	0	2	3
Geonoma schottiana Mart.	Arecaceae	Geo sch	32	154	0	0
Gomidesia martiana O. Berg	Myrtaceae	Gom mar	0	0	4	3
Guarea macrophylla Vahl	Meliaceae	Gua mac	0	0	13	3
Guapira opposita (Vell.) Reitz	Nyctaginaceae	Gua opp	0	2	5	0
Henriettea saldanhaei Cogn.	Melastomataceae	Hen sal	0	10	0	0
Hymenaea rubriflora Ducke	Fabaceae	Hym rub	0	0	1	6
Inga laurina Willd.	Fabaceae	Ing lau	5	1	0	1
Jacaranda puberula Cham.	Bignoniaceae	Jac pub	0	3	14	15
Kielmeyera albopunctata Saddi	Clusiaceae	Kie alb	0	0	2	3
Kielmeyera membranacea Casar.	Clusiaceae	Kie mem	0	0	6	3
Manilkara subsericea (Mart.) Dubard	Sapotaceae	Man sub	0	0	4	3
Matayba guianensis Aubl.	Sapindaceae	Mat gui	0	3	10	9
Maytenus obtusifolia Mart.	Celastraceae	May obt	2	1	12	18
Miconia cinnamomifolia (DC.) Naudin	Melastomataceae	Mic cin	4	4	0	0

TABLE III (continuation)

Miconia pusilliflora (DC) Naud	Melastomataceae	Mic pus	0	0	6	0
Micropholis venulosa (Mart. and Eichler) Pierre	Sapotaceae	Mic ven	0	1	1	11
Myrcia brasiliensis Kiaersk.	Myrtaceae	Myr bra	0	5	3	0
Myrcia racemosa Barb. Rodr.	Myrtaceae	Myr rac	3	2	0	0
Nectandra oppositifolia Nees	Lauraceae	Nec opp	0	33	0	0
Nectandra psammophila Nees and Mart.	Lauraceae	Nec psa	0	1	8	1
Ocotea lobbii (Meisn.) Rohwer	Lauraceae	Oco lob	0	0	2	15
Ocotea notata (Nees) Mez	Lauraceae	Oco not	0	1	10	13
Pera glabrata Baill.	Peraceae	Per gla	0	5	9	6
Pouteria caimito (Ruiz and Pav.) Radlk.	Sapotaceae	Pou cai	0	0	18	14
Pouteria coelomatica Rizzini	Sapotaceae	Pou coe	0	0	0	15
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	Pro hep	0	19	95	50
Protium icicariba (DC.) Marchand	Burseraceae	Pro ici	0	0	6	1
Pseudobombax grandiflorum (Cav.) A. Robyns	Malvaceae	Pse bom	2	1	4	4
Psidium cattleyanum Sabine	Myrtaceae	Psi cat	0	0	0	15
Qualea cryptantha (Spreng.) Warm.	Vochysiaceae	Qua cry	27	12	0	0
Rauvolfia mattfeldiana Markgr.	Apocynaceae	Rau mat	0	0	5	8
Rhodostemonodaphne capixabensis Baitello and Coe-Teixeira	Lauraceae	Rho cap	0	10	13	0
Sapium glandulatum (Vell.) Pax	Euphorbiaceae	Sap gla	19	6	0	0
Sloanea guianensis (Aubl.) Benth.	Elaeocarpaceae	Slo gui	0	11	4	0
Symphonia globulifera L. f.	Clusiaceae	Sym glo	11	91	15	0
Tapirira guianensis Aubl.	Anacardiaceae	Tap gui	10	16	21	8
Thyrsodium spruceanum Benth.	Anacardiaceae	Thy spr	0	0	9	0
Trichilia casaretti C. DC.	Meliaceae	Tri cas	0	0	3	4
Zollernia glabra (Spreng.) Yakovlev	Fabaceae	Zol gla	0	0	4	16
Total			**1954**	**806**	**477**	**421**

test indicated that the abundance of species varied significantly depending on the environmental variables. The eigenvalue higher than 0.5 in the first axis for the CCA is considered high (ter Braak 1995), indicating the existence of a long gradient with high species turnover in the direction of the gradient of soil and flooding.

The soil chemical variables with higher correlation on the first axis were organic matter, phosphorus, acidity, sodium, magnesium, potassium and aluminum (Table IV). The soil physical variables with the highest correlation were drainage, sand, clay and silt. Fine sand showed low correlation values, but it has influenced the separation of species and plots in the Humic Gleisols.

The proposed ordinances with chemical and physical data clearly separated plots according to their respective soils (Figure 4). Quartzarenic Neosols concentrated in the upper left quadrant, whereas Humic Spodosols were concentrated in the lower quadrant. Humic Gleisols are concentrated in the lower quadrants both to the left and right. Thionic Organosols are concentrated in the right upper quadrant, associated with Humic Gleisols.

These results show the existence of a gradient from right to left in the representation of the CCA, i.e., following Thionic Organosols from topographically lower areas (interdune), with higher organic matter content, exchangeable magnesium, sodium and potassium. Humic Gleisols are also in the interdune,

TABLE IV
Results of the Canonical Correspondence Analysis (CCA) with 64 species in
Jacarenema Natural Municipal Park, Vila Velha, Brazil.

CCA	CCA		
Results	**Axis 1**	**Axis 2**	**Axis 3**
Eigenvalues	0.848	0.326	0.248
Total variance explained (%)	21.2	8.1	6.2
Pearson Correlation - spp x Environmetal variables	0.986	0.897	0.878
Monte Carlo test - spp x Environmental variables	**	**	**
Correlations of internal variables:			
Coarse sand	0.906	0.151	0.196
Fine sand	-0.189	0.47	-0.228
Silt	-0.806	-0.44	-0.106
Clay	-0.827	-0.233	-0.129
Drainage	0.958	0.02	-0.254
pH	0.711	-0.426	-0.154
Phosphorus	-0.745	0.169	0.019
Potassium	-0.68	-0.217	-0.014
Sodium	-0.691	-0.456	-0.093
Calcium	-0.45	-0.349	-0.198
Magnesium	-0.679	-0.401	-0.044
Aluminum	-0.634	0.4	0.09
Organic Matter	-0.893	-0.084	-0.141

$**p < 0.01$.

but are located at a topographically higher position compared to the former, so it is relatively less subject to flooding. It showed higher concentrations of phosphorus and aluminum. According to the gradient proposed by the ordination, the Humic Spodosols follow, situated at the dune border, with moderate drainage, intermediate concentration of nutrients and increasing coarse sand content. Quartzarenic Neossols are located on the upper dune with well-drained soils, moderately acid and lowest fertility status.

The results obtained with the CCA ordination suggest that the abundance of species is related to variations in physical and chemical attributes of soils (Figure 5). The test of indicator species using the 64 species analyzed in the CCA revealed that 42 species had a significant indicator value for some of the four types of forest soil studied (Table V). These results consistently demonstrate that edaphic factors control the distribution of species in coastal Restinga forests.

Plants associated with poorly drained soils, with higher percentages of silt and clay, salts and organic matter (Thionic Organosols) are *Bactris setosa*, *Qualea cryptantha*, *Alchornea triplinervia*, *Calophyllum brasiliense*, *Sapium glandulatum*, *Myrcia racemosa*, *Inga laurina* and *Eugenia* sp. This last species was identified as a new species (e.g. M.E.G. Sobral, unpublished data). In our area this species is restricted to the Inundated Forest, showing high abundance values and classified as an indicator species in this environment at Jacarenema Restinga.

On poorly drained, extremely acidic soil, with higher percentages of fine sand and with higher concentrations of phosphorus and aluminum (Humic Gleisols), typical species are *Geonoma schottiana*, *Nectandra oppositifolia*, *Symphonia globulifera*, *Alibertia myrciifolia*, *Cyathea phalerata*, *Henriettea saldanhaei*, *Sloanea guianensis Dendropanax selloi* and *Myrcia brasiliensis*.
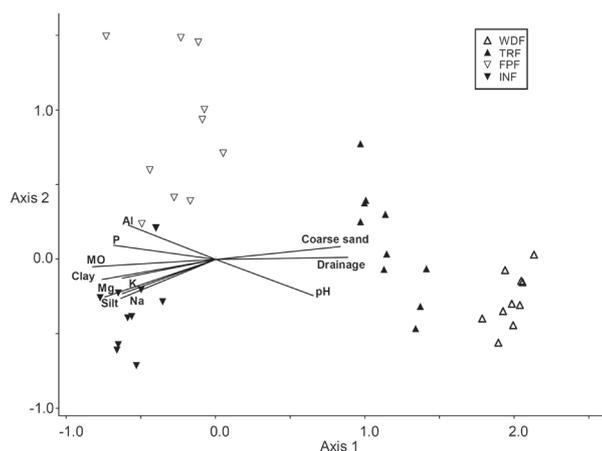
Figure 4 - Canonical Correspondence Analysis (CCA) of the 40 plots sampled and chemical soil features. INF=Inundated Forest; FPF=Floodplain Forest; TRF=Transitional Forest; WDF=Well-drained Forest; pH=acidity in H2O; Na=Sodium; Mg=Magnesium; K=Potassium; P=Phosphorus; Al=Aluminum; MO=Organic matter.

On the sandy border with intermediate characteristics of soil fertility and drainage (Humic Spodosols), typical plants are *Protium heptaphyllum*, *Bactris vulgaris*, *Pouteria caimito*, *Guarea macrophylla*, *Miconia pusilliflora*, *Byrsonima sericea*, *Annona acutiflora*, *Jacaranda puberula*, *Protium icicariba*, *Rhodostemonodaphne capixabensis*, *Nectandra psammophila* and *Guapira opposita*, amongst others.

On the highest dune segment with excessively drained soils, lower soil acidity, lower fertility and higher percentages of sand (Quartzarenic Neossols), the most abundant species were *Eugenia rostrata*, *Ocotea lobbii*, *Campomanesia guazumifolia*, *Pouteria coelomatica*, *Psidium cattleyanum*, *Zollernia glabra*, *Chamaecrista ensiformis* and *Ocotea notata*, amongst others.

DISCUSSION

The overall soil chemical fertility increased from topographically higher areas to the bottom of the landscape, having a positive relationship with increased soil flooding. Thus, this distribution is a typical pedological catena, or soil toposequence (Resende et al.1988, Sobieraj et al. 2002).

Variations in physical and chemical characteristics of surface soils are related to the sedimentary nature associated with different drainage conditions, considering that the most marked changes were related to different levels of flooding to which each forest environment is submitted (Jacomine 2004, EMBRAPA 2006). This condition can be further enhanced by some variation in chemical and physical properties of the soil between the two upland forests since both have the water table far from the surface, so that there is little contribution of groundwater to soil-surface characteristics. However, the levels of phosphorus, aluminum, pH and groundwater height were significantly different between these formations.

It is noteworthy that all forest tracts analyzed are closely related to distinct soils, and therefore significant differences in chemical, physical and morphological properties can be expected. Such differences are only revealed when soils are analyzed in greater depths (Magnago et al. 2010).

The great pedological heterogeneity observed between plots allocated on Thionic Organosols and Humic Gleisols probably occurred due to micro-topographic variation of the floodplain, causing a patchy distribution of plants and flooding in the same area. Micro-topographic variation has been reported in other studies of floodplain forests in the Tropics (Ivanauskas et al. 1997, Toniato et al. 1998, Ivanauskas and Rodrigues 2000), and this is typical of the sedimentary floodplains.

The ecotonal character assigned to the Transition Forest is due to the occurrence of species found in flooded areas and in well-drained soils. This transitional floristic composition is matched by intermediate soil characteristics, both in terms of nutrient and groundwater level.

Although species richness in Transition Forest did not show values significantly different from the Well-drained Forest, the absolute result (82 species) agrees with Ashton (1990) and Tilman (1986), who reported that environments with intermediate nutrient availability have greater
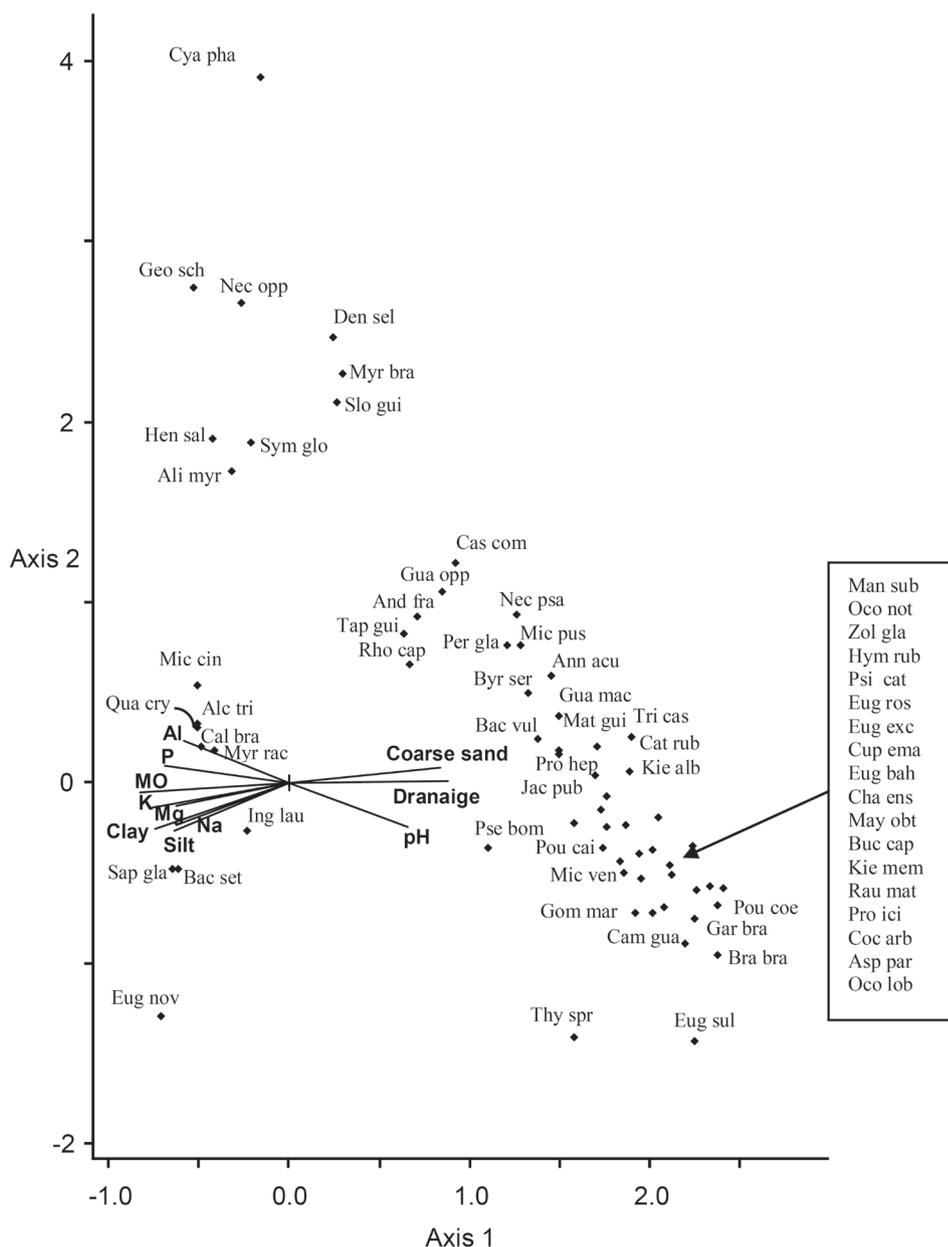
Figure 5 - Canonical Correspondence Analysis of species with the chemical soil features (CCA). Species names are listed in Table IV. pH=acidity in water, Na=sodium, Mg=Magnesium, K=Potassium, P=Phosphorus; Al=Aluminum; MO=Organic matter.

species richness values than those at the extremes of nutrient availability. In our case, differences in soil characteristics and flooding may be not so great as to provide extreme variability in the species richness.

Waterlogging has been considered a determining factor in selecting plant species (Ivanauskas and Rodrigues 2000, Budke et al.

2007), which was confirmed by several studies that showed that species richness in wetland environments is very different from dry-land areas (Sugiyama and Mantovani 1994, Toniato et al. 1998, Romagnolo and Souza 2000, Sztutman and Rodrigues 2002). Several authors also stress that soil acidity and exchangeable aluminum are the

TABLE V

Results of the indicator species analysis in four forests studied based on soil variables and cover value of 64 species in Jacarenema Natural Municipal Park, Vila Velha, Brazil. OIV=Observed indicator value; VIE=expected value indicator; s=standard deviation, p=significance level; INF=Inundated Forest; FPF=Floodplain Forest; TRF=Transitional Forest; WDF=Well-drained Forest.

Species	OIV	VIE			Abundance (%)			
		Average	s	p	INF	FPF	TRF	WDF
Thiomorphic Histosols – INF								
Bactris setosa	83.3	22.1	4.16	***	83	16	1	0
Qualea cryptantha	45	12.6	4.22	***	69	31	0	0
Alchornea triplinervia	39.4	12.7	3.95	***	66	31	0	3
Eugenia sp nov,	35	7.5	3.54	***	100	0	0	0
Sapium glandulatum	30.4	9.7	4.16	**	76	24	0	0
Calophyllum brasiliense	25.5	8.6	3.52	**	73	18	9	0
Inga laurina	17.9	7.4	3.59	*	71	14	0	14
Melanic Gleysols - FPF								
Geonoma schottiana	74.5	15.4	4.86	***	17	83	0	0
Nectandra oppositifolia	65	10.4	4.11	***	0	100	0	0
Symphonia globulifera	62.2	15.5	4.68	***	9	78	13	0
Alibertia myrciifolia	36.7	8.6	3.76	***	8	92	0	0
Cyathea phalerata	29	8.6	4.3	**	0	97	3	0
Henriettea saldanhaei	20	6.7	3.76	**	0	100	0	0
Humic Spodosols – TRF								
Protium heptaphyllum	52.1	21.2	4.36	***	0	12	58	30
Bactris vulgaris	48.4	10.3	4.25	***	0	0	97	3
Pouteria caimito	30.9	13.3	3.98	**	0	0	56	44
Guarea macrophylla	28.4	9.1	3.88	**	0	0	81	19
Miconia pusilliflora	25	6.5	3.37	**	0	0	100	0
Byrsonima sericea	25	6.3	3.46	**	0	0	100	0
Annona acutiflora	24	8.5	3.65	**	0	0	80	20
Jacaranda puberula	21.9	12.9	4.23	*	0	9	44	47
Protium icicariba	21.4	7.1	3.53	**	0	0	86	14
Rhodostemonodaphne capixabensis	19.8	9.7	4.17	*	0	43	57	0
Nectandra psammophila	16	7	3.49	*	0	10	80	10
Quartzarenic Neossols - WDF								
Eugenia rostrata	67.7	13.1	3.99	***	0	0	15	85
Ocotea lobbii	48.5	10.3	3.87	***	0	0	12	88
Campomanesia guazumifolia	46.3	10.5	3.83	***	0	0	16	84
Pouteria coelomatica	45	8.8	3.79	***	0	0	0	100
Psidium cattleyanum	45	8.5	3.58	***	0	0	0	100
Zollernia glabra	44	10.9	3.72	***	0	0	20	80
Chamaecrista ensiformis	31.9	13.7	4.78	**	0	0	36	64
Ocotea notate	29.8	11.6	3.98	**	0	4	42	54
Rauvolfia mattfeldiana	24.6	9.8	3.74	**	0	0	38	62
Cupania emarginata	22.4	11.1	4.27	*	0	0	36	64
Eugenia excelsa	20	6.1	3.32	**	0	0	0	100
Eugenia sulcata	20	6.3	3.27	**	0	0	0	100

TABLE V (continuation)

Eugenia bahiensis	18.7	8.8	4.4	*	0	0	25	75
Buchenavia capitata	18.7	7.5	3.47	*	0	12	12	75
Aspidosperma parvifolium	17.9	7.2	3.25	**	0	0	29	71
Hymenaea rubriflora	17.1	6.5	3.2	*	0	0	14	86
Micropholis venulosa	16.9	7.4	3.69	*	0	8	8	85
Brasilopuntia brasiliensis	15	5.3	3.07	*	0	0	0	100

* p ≤ 0.05; ** p ≤ 0.01; *** p ≤ 0.001.

important limiting factors for the establishment of plant species (Lathwell and Grove 1986, Sollins 1998, Grime 2001).

Exchangeable sodium is commonly high in flooded environments near to the beaches which also, according with (Larcher 2000), turns out to be limiting to plant species. Considering the above mentioned points, the variation in species richness and floristic heterogeneity found among the forests studied here significantly imposes selectivity by the most limiting characteristics in the wetlands when compared to non-flooded forest areas.

The highest levels of organic matter in poorly drained areas also suggest a prominent role in plant distribution in this environment. Even mounds and small vegetation islands on piles of plant debris appear to be favorable microenvironments for the development of certain species over others, in such a way that the organic matter has been correlated with the distribution of vegetation types and abundance of species in different coastal environments subject to flooding (Budke et al. 2007, Munhoz et al. 2008).

In spite of higher organic matter content and higher fertility, environmental conditions in flooded areas are very limiting to the establishment of species in this forest floodplain, in function of the low oxygen availability combined with higher salt concentration.

The negative correlation between richness and soil fertility and positive correlation between richness and drainage suggest that since the Floodplain Forests have flooded soils with higher fertility, flood-tolerant species would be more competitive, resulting in higher abundance of species, with ecological

dominance and lower richness. This condition is similar to one found in monodominant forests of *Vochysia divergens* in the Pantanal wetlands of Brazil, where values for this species greatly increase with flooding, accompanied by a decrease in species richness (Arieira and Cunha 2006). In this regard, Nascimento and Villela (2006) reported an increased dominance of *Peltogyne gracilipes* related to increasing magnesium in the soil, thus excluding other species through competition. According to Scarano (2002), this high dominance of a few species can be considered typical of extreme environments.

In floodplain forests, the species *Bactris setosa*, *Alchornea triplinervia*, *Calophyllum brasiliense*, *Sapium glandulatum*, *Geonoma schottiana*, *Symphonia globulifera*, *Nectandra oppositifolia* and *Myrcia brasiliensis* are generally the most common (Araujo et al. 1998, 2004, Sztutman and Rodrigues 2002, Dorneles and Waechter 2004, Menezes-Silva and Britez 2005, Menezes and Araujo 2005, Guedes et al. 2006, Carvalho et al. 2006, Martins et al. 2008). Less frequent, but also present in studies of floodplain forests are *Sloanea guianensis*, *Alibertia myrciifolia*, *Qualea cryptantha*, *Myrcia racemosa* and *Cyathea phalerata* (Behar and Viégas 1992, Galvão et al. 2002, Goldenberg 2004, Guedes et al. 2006, Sacramento et al. 2007, Martins et al. 2008).

The species present in the Well-drained and Transition Forests are mentioned as being common in similar environments in studies elsewhere (Assis et al. 2004, Fabris and César 1996, Araujo et al. 1998, 2004, Menezes and Araujo 2005, Assumpção and Nascimento 2000, Pereira and Assis 2000,

Menezes-Silva and Britez 2005). Some species that occurred in Transition Forest such as *Calophyllum brasiliense*, *Alchornea triplinervia*, *Nectandra oppositifolia* and *Guarea macrophylla* are among the most common in floristic and phytosociological studies of the Brazilian Riparian forests outside Amazonia (Rodrigues and Nave 2004).

The distribution of the species in the CCA and Indicator Species analyses are consistent with that in the literature. Thus, we infer that these species are indicators of soil conditions (soil types and groundwater level) imposed at each community analyzed, showing greatest abundance where environmental conditions are more favorable for their establishment and development.

The results for the Restinga forests of Jacarenema corroborate those proposed for Riparian forests, which are marked by high plant-species richness (Rodrigues and Nave 2004), accompanied by a significant gradient of soil and drainage (Jacomine 2004).

We found that changes in the floristic composition, richness and species abundance that make up the different forest types form, together with soil and drainage variation, form a complex and heterogeneous enviroment that is characteristic of tropical floodplain/riverine forests.

Thus, we can infer that in the Restinga forests the amounts of aluminum, sodium, and organic matter, as well as soil acidity and flooding regime are the most important determining factors controlling plant richness. Flooding seems to be a more limiting factor for the establishment of plant species than soil fertility attributes.

RESUMO

O objetivo deste estudo foi o de determinar as mudanças na composição, abundância e riqueza de espécies ao longo de um gradiente de floresta com variações de solo e inundações. As florestas localizam-se na margem esquerda do Rio Jucu, no Parque Natural Municipal de Jacarenema, Espírito Santo. O levantamento das espécies arbustivo/arbóreas foi realizado em 80 parcelas de 5x25m, distribuídas equitativamente entre as florestas estudadas. Foram incluídos na amostragem todos os indivíduos com ≥3,2 cm diâmetro à altura do solo (1,30 m). Foram coletadas amostras de solo superficial (0-10 cm) em cada parcela para análise química e física. Os resultados mostraram a existência de gradiente pedológico significativo, que é influenciado pelas variações sazonais do lençol freático. As formações florestais da Restinga apresentaram diferenças significativas na riqueza de espécies, com exceção da Floresta Não Inundável em relação a Floresta Não Inundável de Transição. A Análise de Correlação Canônica (CCA) mostrou que algumas espécies apresentam sua distribuição ao longo do gradiente sob influência da drenagem, das concentrações de nutrientes e das características físicas dos solos. Entre as variáveis testadas, a inundação parece ser o fator mais limitante para o estabelecimento de espécies vegetais nas florestas de Restinga do que os atributos básicos de fertilidade do solo.

Palavras-chave: Vegetação, Florestas inundadas, Ecossistema costeiro, Solos arenosos, Depósitos quaternários, Influência Marinha, Florestas Ciliares.

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