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Structure and floristic pattern of a coastal dunes in southeastern Brazil

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ABSTRACT

The Brazilian shrublands area (*restinga*) is composed of marine coast vegetation on Quaternary sandy plains, where the species composition can vary depending on the surrounding ecosystems. The aims of this study were to describe the structure and floristic composition of a *restinga* near the community of Itaúnas, in the northern part of the state of Espírito Santo, to identify any relationships between this *restinga* and surrounding plant formations, and to determine which are the species that occur preferentially in the coastal forests of Espírito Santo. We sampled woody plants with a diameter at breast height ≥ 2.5 cm, excluding lianas, in 50 plots of 100 m². We selected studies of coastal forests in the states of Espírito Santo and Bahia to prepare a database that would reveal patterns of floristic variation among these areas. We used two-way indicator species analysis for the identification of the species that occur preferentially in the coastal forests of Espírito Santo. We identified 114 species belonging to 38 families. Species richness was greatest for Myrtaceae (26 species), followed by Fabaceae (10). The Shannon index for the study area was 3.96. The estimated total density was 3,330 individuals/ha and basal area was 32.02 m²/ha. The highest importance value (IV) was for *Protium heptaphyllum* (IV, 23.4), indicating that it is characteristic of the Espírito Santo *restinga*. The results of our floristic analysis indicate that the species composition of the Itaúnas *restinga* is influenced by the so-called *tabuleiro* forests (coastal lowland forests on Tertiary deposits), which are most common in northern Espírito Santo. This seems to be the main factor responsible for the gradual reduction in floristic similarity between the *restingas* in the north of Espírito Santo and those in the south of the state, each constituting a distinct floristic block. In addition, we generated lists of species that occur preferentially in the *restinga* and *tabuleiro* forests. Those lists could inform decisions regarding environmental restoration programs.

Key words: phytosociology, phytogeography, Pleistocene *restinga*, Espírito Santo, Itaúnas

Introduction

One of the major factors responsible for the biological diversity in the Atlantic Forest is its environmental heterogeneity, resulting from significant variations in latitude, longitude and altitude, which function as key determinants of such diversity (Scarano 2002; Marques *et al.* 2011). Floristic studies conducted along the southeastern coast of Brazil have demonstrated the heterogeneity of the biome as a whole, revealing considerable similarities between forest formations, even those that are geographically distant from each other (Oliveira-Filho & Fontes 2000). These conclusions were made possible by floristic analyses that considered the Atlantic Forest *stricto sensu*, despite having been recognized, within a broader approach, as a complex of vegetation patterns, including those distributed on the periphery and classified as associated patterns, such as the shrublands, or *restinga* (IBGE 1992).

Distributed along the entire coastline of Brazil and therefore the most extensive vegetation type associated with the Atlantic Forest, the *restinga* is composed of a combination of established vegetation on sandy plains of marine origin formed either during the Quaternary (Menezes & Araujo 2005) and the Pleistocene, constituting the oldest, innermost portions of the plains, or during the Holocene, constituting the most recent, outermost portions (Martin *et al.* 1981. Martin *et al.* 1997). In these environments, the vegetation communities face marked variations in temperature, floods, constant wind, high salinity and nutrient-poor soil, adverse conditions that are reflected in less diversity and structural complexity (Pereira 1990; Scarano 2002; Pimentel *et al.* 2007). The floristic composition of the *restinga* can also vary in function of the adjacent ecosystems (Freire 1990; Scherer *et al.* 2005), acquiring unique characteristics in each region. These characteristics can result in marked floristic and

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structural differences between geographically proximate areas, creating distinct distribution patterns (Araujo 2000).

Phytogeographically, the *restinga* in the state of Espírito Santo is characterized by the fact that there is greater floristic similarity between areas of *restinga* located in the south of the state and those located along the coast of the neighboring state of Rio de Janeiro than between the former and those located in the north of Espírito Santo (Araujo 2000). Floristic studies of the *restinga* in the southern part of Espírito Santo have indicated that the flora of the adjacent hillside forests have a strong influence (Fabris & Cesar 1996; Assis *et al.* 2004b). In fact, the crystalline uplands are closer to the coast in the south of Espírito Santo than in the north of the state. In the north, the most conspicuous geomorphologic feature is constituted by the Tertiary deposits of the Barreiras formation, which extends from the crystalline uplands to near the coastline (Lani *et al.* 2008). The so-called *tabuleiro* forests (semi-deciduous, coastal lowland forests) develop on the Barreiras formation, between the *restinga* and the hillside forests (IBGE 1992; Jesus & Rolim 2005). Phytophysiognomically, this forest is primarily composed of *mata alta* (tall forest) vegetation and the so-called *muçununga* vegetation (similar to that observed in some parts of the *restinga*). The first, which dominates the landscape, is distributed on clay soils with trees up to 35 feet high, and the second, forming enclaves within the *mata alta* vegetation, is on sandy soils of marine origin with some trees of small stature and taller trees reaching approximately 10 m in height (Peixoto *et al.* 2008; Simonelli *et al.* 2008).

Considering that the *restinga* is a geologically recent ecosystem and the colonizing species are from adjacent ecosystems (Freire 1990; Araujo 2000), we can hypothesize that the floristic composition of the *restingas* in the north of Espírito Santo are influenced by *tabuleiro* forest and that similarity diminishes toward the south of the state. In this context, the objectives of this study are to describe the structure and floristic composition of an area of Pleistocene *restinga* in Itaúnas, in northern Espírito Santo; to determine whether relationships exist between the *restinga* and adjacent floristic formations; and to identify the species that occur preferentially in the coastal forests of the state.

Material and methods

Study area

As shown in Fig. 1, the fragment of *restinga* studied is located on private land in Itaúnas, a district of the municipality of Conceição da Barra, located in the northern part of the state of Espírito Santo (18°25’16”S; 39°43’8”W), in an area of 51.3 ha and a border along the edge of the Itaúnas State Park, lying approximately 2 km from the coastline. The forest studied is associated with fields of Pleistocene sand ridges (Kenitiro Suguio, personal communication) that were formed after the peak of the penultimate marine transgression, initiated at approximately 123,000 B.C., when the relative sea level was 8 ± 2 m higher than the present-day level (Suguio & Martin 1978; Suguio *et al.* 1982). The dune ridge extends approximately 10 m above sea level, without any waterlogging of the soil due to fluctuations in the groundwater level. The soil is composed of a surface layer of leaf litter ≤ 15 cm deep; 5 cm further down, there is a network of thin, intertwined roots, below which there is sandy sediment, the initial layer of which is white. The closest weather station is located in the municipality of São Mateus, approximately 35 km from the study area. Climatic data recorded over the last 34 years by the Espírito Santo State Institute for Research, Technical Support and Rural Extension Services/National Meteorology Institute show that average annual temperature ranges from 21.7°C to 26.7°C, with a relative humidity of 83% and an average annual rainfall of 1308 mm. According to the Köppen climate classification system, the study area climate is type Aw (tropical savanna), a humid tropical climate in which rainfall rates are highest during the summer months and lowest during winter months.

Vegetation sampling

Data were collected on 0.5 ha of *restinga* in Itaúnas, divided into 50 plots of 10 × 10 m (Müeller-Dombois & Ellenberg 1974). The plots were delineated systematically with use of a compass in 11 rows in a northwest-southeast orientation, providing the basis for implementation of alternately positioned plots at least 50 m apart.

We sampled all woody plants, except lianas, with a diameter at breast height (DBH) ≥ 2.5 cm, including dead and standing trees. For each sampled individual, we also estimated height with the aid of a pole pruner of known length (6 m). Individuals profiled above ground level and with a DBH < 2.5 cm were marked and measured when one of the branches fit the inclusion criteria, with measurements from all branches then recorded to calculate the basal area. The floristic list was supplemented with individuals collected outside the plots, following the inclusion criteria established for the structural analysis.

All fertile material collected was categorized according to Fidalgo & Bononi (1984) and incorporated into the collection of the Central Herbarium of the Federal University of Espírito Santo (VIES). The botanical identifications were performed by consulting classical works and taxonomic reviews, as well as through expert consultation and by comparisons with material on file at the Central Herbarium of the Federal University of Espírito Santo, the Natural Vale Reserve Herbarium and the Herbarium of the Rio de Janeiro Botanical Gardens. The taxonomic classification system used was that proposed by the Angiosperm Phylogeny Group (APG III 2009). For the abbreviations of the authorities for specific binomials, we followed the example of Brummitt & Powell (1992).

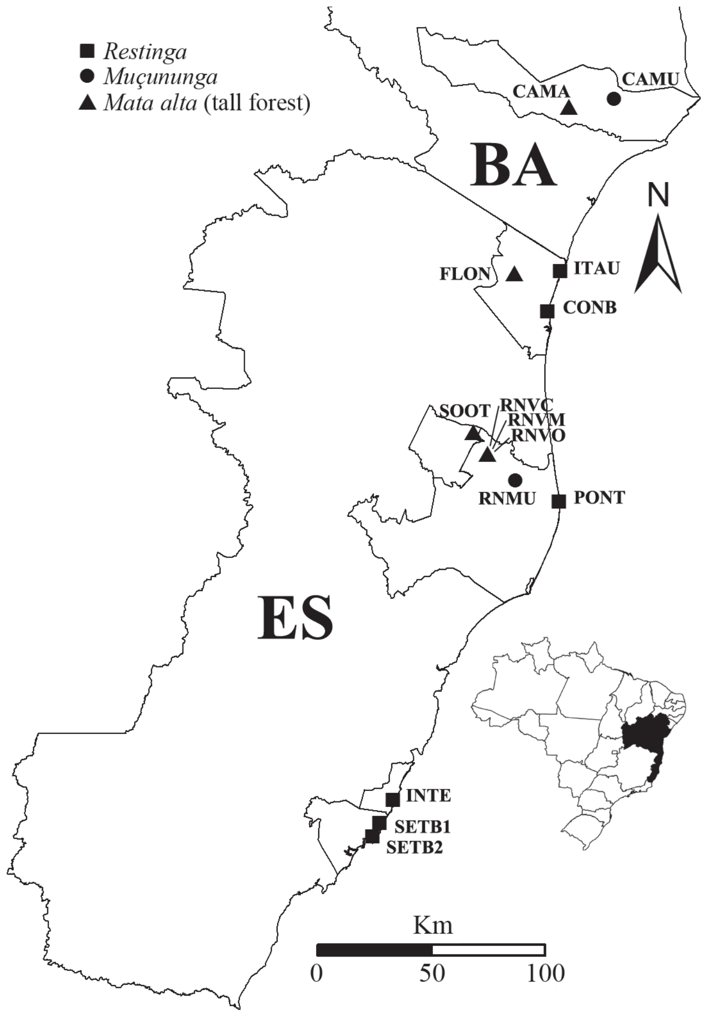

Figure 1. Location of the study area and distribution of sites used in the floristic analyses of the coastal forests in the state of Espírito Santo and in the southern part of the state of Bahia, Brazil.
Restinga – shrublands; *muçununga* – similar to *restinga* but established on Tertiary land, forming enclaves in the *mata alta* (tall forest).

Vegetation structure

To evaluate the vertical structure, we used the absolute and relative phytosociological parameters described in Brower & Zar (1984). We chose to use the Shannon diversity index (H') and Pielou's evenness index (J').

To analyze the vertical stratification of the forest, we developed an abundance matrix, organizing the sampled individuals into 1-m classes by height. To determine whether our sample was floristically representative of the vegetation formation, we performed a sampling sufficiency analysis using Mao Tau rarefaction curves, with a confidence interval of 95% (Colwell *et al.* 2004), and an abundance matrix by plots, calculated with the program PAST, version 2.0 (Hammer *et al.* 2001). This method consists in sorting the order of entry of the plots or individuals and calculation of the cumulative number of species, thus avoiding the influence that the randomness of the order of the sampling units might have on the construction of the curve (Kersten & Galvão, 2011).

Similarity analysis

For the similarity analysis, we included data from 14 floristic and phytosociological studies conducted areas in that were in a good state of conservation, including the present study, totaling 669 shrub or tree species (Fig. 1). For *restingas* and *tabuleiro* forests (Tab. 1), we included mostly studies conducted in Espírito Santo, the exceptions being two studies conducted in the southern part of the state of Bahia. The forest referred to here as the *muçununga* of Caravelas, in Bahia, is, phytophysiognomically, a poorly drained system (Meira-Neto & 2005). Nevertheless, we treated it in a broader context, in order to elucidate floristic differences in comparison with the *muçununga* forest in Espírito Santo. The 14 studies selected were used in order to compile a binary matrix (presence vs. absence) of tree and shrub species occurring in those two areas, considering only the specific level determinations and verified synonyms in the database from the list of species

Table 1. Information about the sites used in the floristic analyses of 14 coastal forests in the state of Espírito Santo and in the southern part of the state of Bahia, Brazil.

Abbreviation	Location	Municipality	Reference	Vegetation formation	Method	Area	Inclusion criterion	H'
SETB1	Paulo César Vinha State Park* 1	Guarapari (ES)	Assis *et al.* 2004b	*Restinga*	P	1 ha	DBH ≥ 4.8 cm	3.73
SETB2	Paulo César Vinha State Park* 2	Guarapari (ES)	Fabris & César 1996	*Restinga*	P	0.5 ha	DBH ≥ 4.8 cm	—
INTE	Interlagos	Vila Velha (ES)	Pereira & Zambom 1998	*Restinga*/dry tropical forest	F	—	—	—
PONT	Pontal do Ipiranga	Linhares (ES)	Pereira *et al.* 1998	*Restinga*/dry tropical forest	F	—	—	—
ITAU	Itaúnas	Conceição da Barra (ES)	The present study	*Restinga*	P	0.5 ha	DBH ≥ 2.5 cm	3.96
CONB	Conceição da Barra	Conceição da Barra (ES)	Pereira & Gomes 1994	*Restinga*/Myrtaceae-dominated dry tropical forest	F	—	—	—
RNMU	Rio Doce Valley Nature Reserve	Linhares (ES)	Simonelli *et al.* 2008	*Muçunungu*	P	0.93 ha	DBH ≥ 5 cm	3.36
CAMU	Caravelas	Caravelas (BA)	Meira-Neto *et al.* 2005	*Muçunungu*	F	—	—	—
CAMA	Caravelas	Caravelas (BA)	Souza *et al.* 1998	*Mata alta*	P	1.125 ha	DBH ≥ 5 cm	4.71
FLON	Rio Preto National Forest	Conceição da Barra (ES)	Salomão 1998	*Mata alta*	P	10.55 ha	DBH ≥ 10 cm	4.71
SOOT	Sooretama Biological Reserve	Sooretama (ES)	Paula & Soares 2011	*Mata alta*	P	1 ha	DBH ≥ 4.8 cm	4.87
RNVC	Caigá Valley Nature Reserve	Linhares (ES)	Jesus & Rolim 2005	*Mata alta*	P	24 ha	DBH ≥ 4.8 cm	4.98
RNVM	Macanaíba Valley Nature Reserve	Linhares (ES)	Jesus & Rolim 2005	*Mata alta*	P	9.6 ha	DBH ≥ 4.8 cm	4.83
RNVO	Oiticica Valley Nature Reserve	Linhares (ES)	Jesus & Rolim 2005	*Mata alta*	P	6.4 ha	DBH ≥ 4.8 cm	4.79

*Formerly known as Setiba Park, hence the abbreviation.
Restinga – shrublands; *muçunungu* – similar to *restinga* but established on Tertiary land, forming enclaves in the *mata alta* (tall forest); P – Plot; DBH – diameter at breast height; F – Floristics; H' – Shannon diversity index.

of Flora of Brazil (http://floradobrasil.jbrj.gov.br/2012/). This same data set was the basis for the analyses to follow. To calculate similarity, we used the Sørensen coefficient (Müeller-Dombois & Ellenberg 1974), because it is more effective than are other similarity measures, as well as being consistent with the unweighted pair group method with arithmetic mean (McCune Grace & 2002; Magurran 2004), which is employed in order to avoid distortions during the analysis (McCune & Mefford 1999). For all cluster analyses, we used the Multivariate Statistical Package, version 3.1 (Kovach 2004). To identify species that occur preferentially in the coastal forests of Espírito Santo and were responsible for the clusters formed in the similarity dendrogram, we used dichotomous classification by Two-Way Indicator Species Analysis (TWINSPAN; Hill 1979). In order to rank the areas according to the floristic similarity and thus reveal patterns of variation in species composition along an environmental gradient (ter Braak 1995), we performed reciprocity averaging, equivalent to a correspondence analysis, the latter name being chosen due to its wider usage. These analyses were processed with the program PC-ORD, version 4.1 (McCune & Mefford 1999).

Results

Floristics, structure and diversity

The survey of trees and shrubs revealed the presence of 114 species, within 96 genera, among 38 families. The richest families were Myrtaceae (27 species, 23.7%), Fabaceae (10 species, 8.8%), Sapotaceae (8 species, 7%), Lauraceae (7 species, 6%) Annonaceae, Rubiaceae and Rutaceae (4 species each, 3.5% each), collectively representing 56.0% of the species sampled and 68.2% of the samples of living individuals. Samples collected from outside the study area (146 species) added 32 species to the floristic list (Tab. 2).

Table 2. Floristic list of shrub/tree species occurring in the *restinga* (shrublands) in Itaúnas, near the municipality of Conceição da Barra, in the state of Espírito Santo, Brazil.

Family	Species
Achariaceae	*Carpotroche brasiliensis* (Raddi) Endl.
Anacardiaceae	*Schinus terebinthifolius* Raddi
	Spondias macrocarpa Engl.
	Tapirira guianensis Aubl.
Annonaceae	*Annona salzmannii* A. DC.
	Duguetia sessilis (Vell.) Maas
	Unonopsis aurantiaca Maas & Westra
	Xylopia laevigata R.E. Fr.*
	Xylopia sericea A. St.-Hil.
Apocynaceae	*Aspidosperma pyricollum* Müll. Arg.
	Himatanthus phagedaenicus (Mart.) Woods.
	Rauvolfia mattfeldiana Markgr.*
	Tabernaemontana flavicans Willd. ex Roem. & Schult.*
Bignoniaceae	*Jacaranda puberula* Cham.*
	Tabebuia roseoalba (Ridl.) Sandwith
Boraginaceae	*Cordia taguahyensis* Vell.*
Brassicaceae	*Capparis flexuosa* (L.) L.*
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand
	Protium icicariba (DC.) Marchand
	Trattinnickia mensalis Daly
Calophyllaceae	*Kielmeyera albopunctata* Saddi
	Kielmeyera membranacea Casar.
Caricaceae	*Jacaratia heptaphylla* (Vell.) A. DC.*
Celastraceae	*Maytenus* cf. *communis* Reissek
	Maytenus distichophylla Mart.
Chrysobalanaceae	*Couepia schottii* Fritsch
	Couepia sp.
	Licania heteromorpha Benth.
	Licania arianeae Prance*
Clusiaceae	*Clusia hilariana* Saddi
	Garcinia brasiliensis Mart.
Connaraceae	*Connarus blanchetti* Planch.
Ebenaceae	*Diospyros apeibacarpos* Raddi*
Elaeocarpaceae	*Sloanea guianensis* (Aubl.) Benth.
Erythroxylaceae	*Erythroxylum subsessile* (Mart.) O.E. Schulz*
Euphorbiaceae	*Joannesia princeps* Vell.

Continues

Table 2. Continuation.

Family	Species
Fabaceae	*Abarema filamentosa* (Benth.) Pittier
	Acosmium bijugum (Vogel) Yakovlev*
	Andira fraxinifolia Benth.
	Andira nitida Mart. ex Benth.
	Chamaecrista ensiformis (Vell.) H.S. Irwin & Barneby*
	Inga exfoliata T.D. Penn. & F.C.P. García
	Inga laurina (Sw.) Willd.*
	Inga subnuda Salzm. ex Benth.
	Macrolobium latifolium Vogel
	Pterocapus rohrii Vahl
	Swartzia apetala Raddi
	Swartzia simplex (Sw.) Spreng.
	Zollernia glabra (Spreng.) Yakovlev.
Humiriaceae	*Humiriastrum dentatum* (Casar.) Cuatrec.
Icacinaceae	*Emmotum nitens* Miers.
Lacistemaceae	*Lacistema robustum* Schnizl.
Lamiaceae	*Vitex polygama* Cham.
Lauraceae	*Aiouea saligna* Meisn.
	Aniba firmula (Ness & Mart.) Mez
	Ocotea glaziovii Mez
	Ocotea lobbii (Meisn.) Rohwer
	Ocotea notata (Nees & C. Martius ex Nees) Mez
	Ocotea sp.1
	Ocotea sp.2
Lecythidaceae	*Eschweilera ovata* (Cambess.) Miers
Malpighiaceae	*Byrsonima bahiana* W.R. Andreson
	Byrsonima sericea DC.
Malvaceae	*Eriotheca macrophylla* (K. Schum.) A. Robyns
Melastomataceae	*Miconia* cf. *cinnamomifolia* (DC.) Naudim*
	Miconia prasina (Sw.) DC.*
	Miconia cf. *pusilliflora* (DC.) Naudin
Meliaceae	*Guarea penningtoniana* Pinheiro
Monimiaceae	*Mollinedia glabra* (Sprengel) Perkins.*
Moraceae	*Ficus* cf. *bahiensis* C.C. Berg & Carauta
	Ficus gomelleira Kunth & C.D. Bouché
	Ficus tomentella (Miq.) Miq.*
	Ficus cf. *trigona* L.f.
	Sorocea hilarii Gaudich.*

Continues

Table 2. Continuation.

Family	Species
Myrtaceae	*Calyptranthes brasiliensis* Spreng.
	Campomanesia guazumifolia (Cambess.) O.Berg
	Eugenia astringens Cambess.
	Eugenia bahiensis DC.
	Eugenia brasiliensis Lam.
	Eugenia brejoensis Mazine
	Eugenia dichroma O.Berg
	Eugenia excelsa O.Berg
	Eugenia hirta O.Berg*
	Eugenia ilhensis O.Berg
	Eugenia inversa Sobral
	Eugenia cf. *itapemirimensis* Cambess*
	Eugenia pisiformis Cambess.
	Eugenia punicifolia (Kunth) DC.*
	Eugenia sulcata Spring ex Martius
	Eugenia sp.1
	Eugenia sp.2
	Marlierea neuwiedeana (O.Berg) Nied.*
	Marlierea polygama (O.Berg) D.Legrand*
	Marlierea regeliana O.Berg
	Marlierea sucrei G.M. Barroso & Peixoto
	Marlierea obversa D.Legrand*
	Myrcia bergiana O.Berg
	Myrcia ilheosensis Kiaersk.
	Myrcia cerqueiria (Nied.) E.Lucas & Sobral
	Myrcia splendens (Sw.) DC.
	Myrcia vittoriana Kiaersk.
	Myrciaria floribunda (H.west ex Willd.) O.Berg
	Myrciaria strigipes O.Berg*
	Myrciaria tenella (DC.) O.Berg
	Neomitranthes langsdorffii (O.Berg) Mattos
	Neomitranthes obtusa Sobral & Zambom
	Plinia grandifolia (Mattos) Sobral
	Psidium brownianum DC.
Nyctaginaceae	*Guapira obtusata* (Jacq.) Little
	Guapira opposita (Vell.) Reitz
	Guapira sp.
Ochnaceae	*Ouratea cuspidata* Tiegh.

Continues

Table 2. Continuation.

Family	Species
Olacaceae	*Heisteria perianthomega* (Vell.) Sleumer
	Pera glabrata Baill.
Peraceae	*Pera leandri* Baill.
	Pogonophora schomburgkiana Miers ex Benth.
Picramniaceae	*Picramnia gardneri* Planch.
Primulaceae	*Myrsine guianensis* (Aubl.) Kuntze
	Amaioua intermedia Mart.
	Chiococca nitida Benth.*
Rubiaceae	*Melanopsidium nigrum* Colla
	Psychotria carthagenensis Jacq.
	Simira glaziovii (K. Schum.) Steyerm.
	Conchocarpus insignis Pirani*
	Conchocarpus longifolius (A.St.-Hil.) Kallunki & Pirani
	Esenbeckia grandifolia Mart.
Rutaceae	*Pilocarpus grandiflorus* Engl.
	Rauia cf. *nodosa* (Engl.) Kallunki
	Ravenia infelix Vell.*
Salicaceae	*Casearia commersoniana* Cambess.
	Cupania emarginata Cambess.
Sapindaceae	*Cupania racemosa* (Vell.) Radlk.
	Matayba guianensis Aubl.
	Chrysophyllum splendens Spreng.
	Manilkara subsericea (Mart.) Dubard
	Micropholis venulosa (Mart. & Eichler) Pierre
	Pouteria caimito (Ruiz & Pav.) Radlk.
Sapotaceae	*Pouteria coelomatica* Rizzini
	Pouteria grandiflora (A. DC.) Baehni
	Pouteria peduncularis (Martius & Eichler) Baehni
	Pouteria aff. *psammophila* (Mart.) Radlk.
Simaroubaceae	*Simarouba amara* Aubl.
	Aureliana fasciculata (Vell.) Sendtn*
Solanaceae	*Cestrum retrofractum* Dunal*
	Solanum martii Sendtn.*
Urticaceae	*Cecropia pachystachya* Trécul.

*Species outside the complementary sampling of the floristic list.

The most numerous genera were *Eugenia* (15 species), *Marlierea*, *Myrcia*, *Ocotea* and *Pouteria* (5 species each).

The mean height of the forest was 8 ± 4 m, the lower stratum comprising individuals 2-3 m in height (Fig. 2) and accounting for 44.7% of all sampled species. The most representative species, in terms of the numbers of individuals, were *Unonopsis aurantiaca*, *Ocotea lobbii*, *Myrcia vittoriana*, *Eugenia astringens* and *Ouratea cuspidata*. These species collectively accounted for 7.5% of the individuals and 0.8% of the total basal area. The middle stratum comprised individuals 4-9 m in height, accounting for 76.2% of all sampled individuals, 92% of the species and

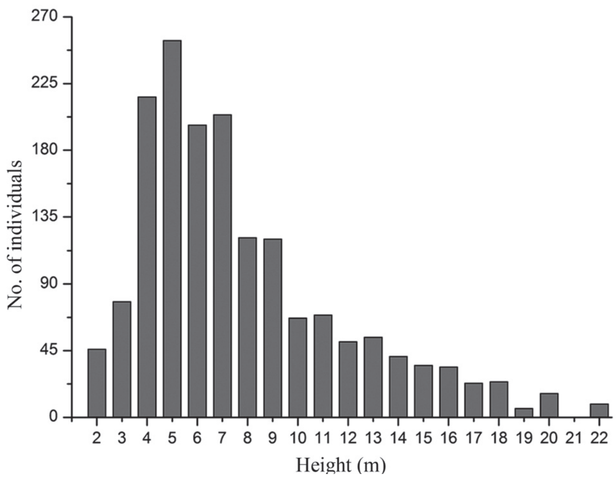

Figure 2. Distribution of frequencies of classes of total height (m) of the individuals in the *restinga* (shrublands) in Itaúnas, near the municipality of Conceição da Barra, in the state of Espírito Santo, Brazil.

17.6% of the total basal area, *O. lobbii*, *U. aurantiaca*, *M. vittoriana*, *E. excelsa* and *E. astringens* showing the greatest density in this stratum. Individuals in the upper stratum (10-22 m in height) accounted for 16.7% of the species, the tallest individuals being those of *Protium heptaphyllum*, *Tapirira guianensis*, *Kielmeyera albopunctata*, *Macrolobium latifolium* and *Aspidosperma pyricollum*. Upper-stratum species accounted for 25.8% of the individuals sampled and covered 81.6% of the total basal area.

The behavior of the species-area rarefaction curve indicated a tendency towards stabilization, given that, by the time half of the allocated plots had been sampled, approximately 85% of the species had been included (Fig. 3). Of the 114 species sampled, 20 (17.5%) were represented by a single individual.

In Itaúnas, the H' was 3.96 and the J' was 0.836. Among trees and bushes, we sampled 1665 living individuals, collectively covering a basal area of 32.02 m^2/ha. We recorded 107 dead individuals totaling 1.10 m^2/ha basal area, with 65.5% of individuals with DBH ≤ 5 cm and 24% ≤ 10 cm DBH. As can be seen in Tab. 3, Burseraceae and Anacardiaceae stood out in that they accounted for a considerable portion of the basal area mainly because of a single species. *P. heptaphyllum* occupied 10.4% of the total basal area, accounting for 64.5% of the basal area covered by *Burseraceae*, and *T. guianensis* occupied 6.1% of the total basal area, accounting for 98.2% of the basal area covered by Anacardiaceae. Myrtaceae was the most important family, accounting for 16% of the total importance value (IV), *E. astringens* and *E. excelsa* showing IVs of 10.8 and 9.9, respectively (Tab. 4).

Taking all of the phytosociological information, as well as the floristic composition and the soil water saturation, into account, we can classify the forest formation analyzed as a dune-ridge forest, according to the classification system devised by Menezes & Araujo (2005) and Silva & Britez (2005).

Similarity analysis

The similarity coefficient between the coastal forests of Espírito Santo and those of southern Bahia ranged from 0.03 to 0.86, which, by TWINSPAN, could indicate that some species were preferential to these forests (Chart 1). According to the similarity dendrogram (Fig. 4), *restingas* constitute a cohesive cluster associated by a similarity coefficient ranging from 0.27 to 0.57, with only *Capparis flexuosa*, *Garcinia brasiliensis*, *P. heptaphyllum* and *Guapira opposita* occurring in all of the *restingas* considered. Within the cluster consisting of *restingas*, one subcluster comprised *restingas* in northern Espírito Santo (Conceição da Barra and Itaúnas) and another comprised *restingas* in the southern and northern parts of the state (Interlagos, as well as two locations with the Paulo César Vinha State Park, previously known as Setiba Park, in the south; and Pontal do Ipiranga in the north).

The floristic similarity between the *restinga* of Itaúnas and the other *restingas* analyzed ranged from 0.29 to 0.43, varying even when compared with the survey conducted in Conceição da Barra (Gomes Pereira & 1994), which is quite near our study area. Nevertheless, Itaúnas and Conceição da Barra proved to be cohesive in the similarity analysis and consistent in the TWINSPAN divisions (eigenvalue, 0.499), *Eriotheca macrophylla*, *Ficus gomelleira*, *Joannesia princeps*, *M. latifolium* and *Pterocarpus rohrii* being identified as responsible for this clustering. Given the floristic similarities between the *restinga* of Itaúnas and the other formations evaluated (0.08-0.43), the Itaúnas *restinga*, as would be expected, showed greater affinity with the other *restingas*. However, despite the low degree of floristic affinity between the Itaúnas forest and the *tabuleiro* forests (0.15-0.22), Itaúnas was more similar to the *tabuleiro* forest than to the other *restingas* analyzed (0.04-0.16).

According to the similarity dendrogram, the *muçununga* forest in Linhares (Rio Doce Valley Nature Reserve) had greater floristic affinity with the *restinga*. The *muçununga* forest in Caravelas constituted an outlier to all of the other forests analyzed, with a similarity coefficient of 0.06.

Floristically, the areas of *mata alta*formed a very cohesive cluster, generating the highest similarity indices (0.46-0.86). Although the *mata alta* in Caravelas (southern Bahia) is geographically the most remote of the *mata alta* surveyed, the *mata alta* in the Sooretama Biological Reserve showed the least similarity.

The correspondence analysis eigenvalues for the first two axes were 0.739 and 0.604 for axis 1 and axis 2, respectively, the first explaining 17.88% of the total variance, compared with 14.63% for the second, collectively explaining 32.51%. Therefore, the ordination diagram distinguished a cluster that was highly associated by the proximity among the *mata alta* areas (Fig. 5). The *restingas* formed another cluster, which, unlike the *mata alta* areas, comprised formations that were more or less aligned in order. Along axis 1, the *muçununga* forests were in an intermediate position

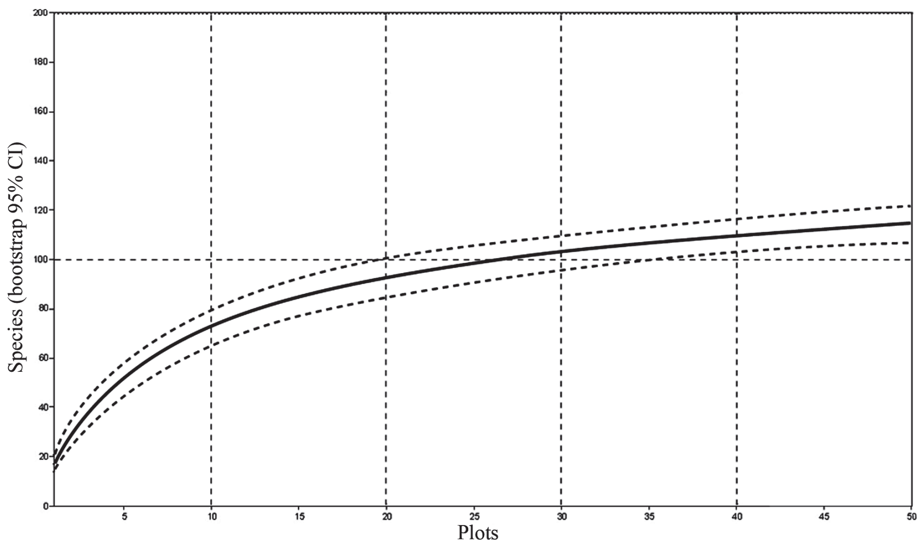

Figure 3. Species-area rarefaction curve, generated with the Mao Tau method, for the *restinga* (shrublands) in Itaúnas, near the municipality of Conceição da Barra, in the state of Espírito Santo, Brazil.
CI – confidence interval.

between *restinga* and *mata alta*. According to axis 2, the *muçununga* forest in Caravelas was floristically distant from the other forests.

Discussion

Floristics, structure and diversity

In floristic surveys of shrub or tree formations in well-drained *restingas* in northern Espírito Santo, 82 species have been observed in Linhares (Pereira *et al.* 1998), comparable to the 83 observed in Conceição da Barra (Pereira & Gomes 1994). In the cities of Vila Velha (Pereira & Zambom 1998) and Guarapari (Assis *et al.* 2004a), coastal communities in the south of the state, 74 and 103 species, respectively, were observed. In the state of Rio de Janeiro, which has the longest tradition of studying *restinga* communities, species richness has been shown to range from 26 to 108 species (Assumpção & Nascimento 2000; Lobão & Kurtz 2000; Sá & Araujo 2009). The Itaúnas forest presented even higher species richness, indicating that it is an important forest remnant that should be preserved.

The great species richness of Myrtaceae is commonly known and has also been detected in other *restingas* along the Brazilian coast (Araujo 2000; Assumpção & Nascimento 2000; Scherer *et al.* 2005; Sacramento *et al.* 2007; Amaral *et al.* 2008). This might be related to the adaptability of Myrtaceae species to low fertility soils (Ashton 1988), such as those of the *restinga* (Scarano 2002).

The high species richness of the Itaúnas *restinga* is attributable to the presence of families that are also plentiful in other neotropical formations (Leitão-Filho 1987). Along the southern coast of Brazil, where Waechter *et al.* (2000) and Guedes *et al.* (2006) each found only one Sapotaceae species (*Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn. and *Manilkara Subsericea*, respectively), Sapotaceae is the family that has had the highest VI. Along the northern and northeastern coasts, Sapotaceae is also not among the most species-rich families, only four species or fewer having been observed (Freire 1990; Sacramento *et al.* 2007; Santos-Filho *et al.* 2011). Studies addressing the structural contribution of these species in the communities of the northern and northeastern Brazil are scarce, which precludes comparisons across studies. On the coast of the state of São Paulo, in southeastern Brazil, Guedes *et al.* (2006) found that a single Sapotaceae species was the most important species in a flooded *restinga* and the fifth most important in a terra firme forest. In the *restinga* within Paulo César Vinha State Park, on the southern coast of Espírito Santo, Assis *et al.* (2004b) found that the Sapotaceae family was also important, *Pouteria coelomatica* having the second highest IV. Unlike the authors of the aforementioned studies, those authors also found Sapotaceae to be one of the most species-rich families, being represented by nine species. Similarly, in that study, Sapotaceae stood out for its contribution to the structure and species richness of the community. Sapotaceae has also been identified as being among the most species-rich families in the *restinga* in the state of Rio de Janeiro (Pereira & Araujo 2000). Given its wide distribution along the Brazilian coast, Sapotaceae can also be considered characteristic of nutrient-poor soils such as that of the *restinga*. In the northern and northeastern regions, with the data currently available, Sapotaceae can be identified as being of key importance for the flora of the *restinga* forests. For the southern and southeastern regions, Sapotaceae is of relevant structural importance. In the southeast, Sapotaceae plays an important role in the flora and structure of *restinga* forests in the

Table 3. Phytosociological parameters of families sampled in the *restinga* (shrublands) in Itaúnas, near the municipality of Conceição da Barra, in the state of Espírito Santo, Brazil.

Family	S	Ni	Ab	AF	AD	ADo	RF	RD	RDo	IV
Myrtaceae	27	447	1.986	96	894	3.971	8.972	26.847	12.406	48.225
Burseraceae	3	121	3.327	74	242	6.654	6.916	7.267	20.788	34.971
Lauraceae	7	231	1.615	88	462	3.231	8.224	13.874	10.093	32.191
Sapotaceae	8	148	1.179	90	296	2.358	8.411	8.889	7.366	24.666
Anacardiaceae	3	43	2.000	44	86	3.999	4.112	2.583	12.494	19.189
Fabaceae	10	75	1.206	66	150	2.411	6.168	4.505	7.533	18.206
Apocynaceae	2	54	0.692	58	108	1.383	5.421	3.243	4.322	12.985
Annonaceae	4	92	0.218	62	184	0.435	5.794	5.526	1.360	12.680
Humiriaceae	1	53	0.541	56	106	1.082	5.234	3.183	3.379	11.796
Rutaceae	5	82	0.116	36	164	0.232	3.364	4.925	0.725	9.014
Nyctaginaceae	3	36	0.457	40	72	0.915	3.738	2.162	2.858	8.758
Calophyllaceae	2	38	0.228	32	76	0.455	2.991	2.282	1.423	6.696
Chrysobalanaceae	3	23	0.213	32	46	0.426	2.991	1.381	1.332	5.704
Sapindaceae	2	16	0.274	28	32	0.549	2.617	0.961	1.715	5.293
Lecythidaceae	1	21	0.224	26	42	0.448	2.430	1.261	1.399	5.090
Ochnaceae	1	31	0.032	32	62	0.064	2.991	1.862	0.199	5.052
Peraceae	3	22	0.137	20	44	0.273	1.869	1.321	0.853	4.044
Rubiaceae	4	19	0.063	26	38	0.125	2.430	1.141	0.391	3.962
Clusiaceae	2	6	0.388	10	12	0.776	0.935	0.360	2.424	3.719
Celastraceae	2	12	0.066	22	24	0.132	2.056	0.721	0.412	3.188
Moraceae	3	7	0.216	14	14	0.432	1.308	0.420	1.348	3.077
Meliaceae	1	13	0.153	12	26	0.306	1.121	0.781	0.957	2.859
Malpighiaceae	2	6	0.196	10	12	0.392	0.935	0.360	1.224	2.519
Olacaceae	1	9	0.027	16	18	0.053	1.495	0.541	0.166	2.202
Bignoniaceae	1	9	0.053	12	18	0.107	1.121	0.541	0.333	1.995
Malvaceae	1	4	0.152	8	8	0.304	0.748	0.240	0.950	1.938
Salicaceae	1	12	0.023	10	24	0.045	0.935	0.721	0.141	1.796
Simaroubaceae	1	5	0.085	8	10	0.171	0.748	0.300	0.533	1.581
Melastomataceae	1	9	0.010	6	18	0.020	0.561	0.541	0.063	1.164
Elaeocarpaceae	1	5	0.014	8	10	0.028	0.748	0.300	0.087	1.135
Connaraceae	1	5	0.005	8	10	0.011	0.748	0.300	0.033	1.081
Lamiaceae	1	3	0.035	4	6	0.070	0.374	0.180	0.219	0.773
Icacinaceae	1	2	0.036	4	4	0.072	0.374	0.120	0.225	0.719
Lacistemaceae	1	2	0.022	4	4	0.045	0.374	0.120	0.141	0.634
Achariaceae	1	1	0.009	2	2	0.019	0.187	0.060	0.058	0.305
Urticaceae	1	1	0.003	2	2	0.007	0.187	0.060	0.021	0.268
Primulaceae	1	1	0.003	2	2	0.006	0.187	0.060	0.020	0.267
Picramniaceae	1	1	0.001	2	2	0.003	0.187	0.060	0.009	0.256

S = number of species; Ni = number of individuals sampled; Ba = basal area; AF = absolute frequency; AD = absolute density; ADo = absolute dominance; RF = relative frequency, RD = relative density, RDo = relative dominance, IV = importance value.

Table 4. Parameters of the species sampled in the *restinga* (shrublands) in Itaúnas, near the municipality of Conceição da Barra, in the state of Espírito Santo, Brazil.

Species	Ni	AD	AF	ADo	RD	RF	RDo	IV
Protium heptaphyllum	82	164	58	4.831	4.925	3.380	15.093	23.398
Ocotea lobbii	148	296	80	1.861	8.889	4.662	5.813	19.364
Tapirira guianensis	35	70	40	3.928	2.102	2.331	12.272	16.705
Eugenia astringens	85	170	60	0.728	5.105	3.497	2.274	10.876
Eugenia excelsa	77	154	56	0.662	4.625	3.263	2.068	9.956
Humiriastrum dentatum	53	106	56	1.082	3.183	3.263	3.379	9.826
Macrolobium latifolium	29	58	30	1.923	1.742	1.748	6.006	9.496
Unonopsis aurantiaca	87	174	56	0.285	5.225	3.263	0.891	9.380
Pouteria caimito	52	104	60	0.873	3.123	3.497	2.728	9.347
Myrcia vittoriana	86	172	44	0.311	5.165	2.564	0.970	8.699
Himatanthus phagedaenicus	42	84	48	1.031	2.523	2.797	3.222	8.542
Protium icicariba	30	60	22	1.328	1.802	1.282	4.148	7.232
Eugenia bahiensis	36	72	44	0.586	2.162	2.564	1.832	6.558
Ocotea glaziovii	27	54	30	0.800	1.622	1.748	2.498	5.868
Micropholis venulosa	21	42	24	0.871	1.261	1.399	2.721	5.380
Guapira obtusata	20	40	28	0.776	1.201	1.632	2.425	5.258
Marlierea regeliana	28	56	34	0.258	1.682	1.981	0.805	4.468
Rauia cf. *nodosa*	43	86	24	0.112	2.583	1.399	0.351	4.332
Eschweilera ovata	21	42	26	0.448	1.261	1.515	1.399	4.176
Ouratea cuspidata	31	62	32	0.064	1.862	1.865	0.199	3.926
Esenbeckia grandiflora	36	72	24	0.116	2.162	1.399	0.363	3.923
Marlierea sucrei	17	34	26	0.425	1.021	1.515	1.329	3.865
Kielmeyera albopunctata	22	44	22	0.251	1.321	1.282	0.785	3.388
Ocotea notata	21	42	24	0.220	1.261	1.399	0.687	3.347
Pouteria coelomatica	18	36	24	0.197	1.081	1.399	0.617	3.096
Pouteria grandiflora	19	38	26	0.137	1.141	1.515	0.429	3.085
Cupania emarginata	8	16	16	0.483	0.480	0.932	1.508	2.921
Trattinnickia mensalis	9	18	12	0.495	0.541	0.699	1.547	2.787
Aspidosperma pyricollum	12	24	16	0.352	0.721	0.932	1.100	2.753
Myrcia ilheosensis	18	36	24	0.080	1.081	1.399	0.250	2.730
Guapira opposita	14	28	24	0.136	0.841	1.399	0.425	2.664
Manilkara subsericea	18	36	20	0.115	1.081	1.166	0.359	2.605
Campomanesia guazumifolia	15	30	16	0.246	0.901	0.932	0.768	2.602
Guarea penningtoniana	13	26	12	0.306	0.781	0.699	0.957	2.437
Ocotea sp.1	16	32	18	0.134	0.961	1.049	0.418	2.428
Kielmeyera membranacea	16	32	14	0.204	0.961	0.816	0.638	2.415
Couepia schottii	8	16	14	0.318	0.480	0.816	0.995	2.291
Maytenus distichophylla	11	22	20	0.130	0.661	1.166	0.407	2.233
Aniba firmula	12	24	18	0.127	0.721	1.049	0.396	2.166
Abarema filamentosa	14	28	10	0.214	0.841	0.583	0.667	2.091
Pouteria peduncularis	13	26	18	0.047	0.781	1.049	0.148	1.978

Continues

Table 4. Continuation.

Species	Ni	AD	AF	ADo	RD	RF	RDo	IV
Byrsonima sericea	5	10	8	0.375	0.300	0.466	1.170	1.937
Eugenia dichroma	9	18	16	0.145	0.541	0.932	0.452	1.925
Garcinia brasiliensis	4	8	8	0.351	0.240	0.466	1.095	1.802
Plinia grandifolia	10	20	18	0.048	0.601	1.049	0.150	1.800
Simira glaziovii	11	22	14	0.102	0.661	0.816	0.318	1.795
Pera glabrata	12	24	8	0.184	0.721	0.466	0.575	1.762
Clusia hilariana	2	4	4	0.425	0.120	0.233	1.329	1.682
Eriotheca macrophylla	4	8	8	0.304	0.240	0.466	0.950	1.657
Heisteria perianthomega	9	18	16	0.053	0.541	0.932	0.166	1.639
Tabebuia roseoalba	9	18	12	0.107	0.541	0.699	0.333	1.573
Eugenia sulcata	10	20	14	0.034	0.601	0.816	0.105	1.522
Cupania racemosa	8	16	14	0.066	0.480	0.816	0.206	1.503
Casearia commersoniana	12	24	10	0.045	0.721	0.583	0.141	1.444
Swartzia apetala	9	18	14	0.022	0.541	0.816	0.068	1.424
Eugenia sp.1	10	20	12	0.040	0.601	0.699	0.124	1.424
Myrcia splendens	8	16	14	0.038	0.480	0.816	0.119	1.415
Couepia sp.	10	20	10	0.071	0.601	0.583	0.223	1.406
Pera leandri	7	14	12	0.067	0.420	0.699	0.209	1.329
Simaruba amara	5	10	8	0.171	0.300	0.466	0.533	1.300
Aiouea saligna	6	12	10	0.084	0.360	0.583	0.262	1.205
Ficus cf. *trigona*	4	8	8	0.149	0.240	0.466	0.466	1.173
Spondias macrocarpa	7	14	10	0.050	0.420	0.583	0.157	1.160
Pterocarpus rohrii	5	10	10	0.058	0.300	0.583	0.181	1.064
Licania heteromorpha	5	10	10	0.037	0.300	0.583	0.115	0.998
Ficus gomelleira	1	2	2	0.259	0.060	0.117	0.808	0.985
Neomitranthes langsdorffii	4	8	6	0.122	0.240	0.350	0.382	0.972
Sloanea guianensis	5	10	10	0.028	0.300	0.583	0.087	0.970
Miconia cf. *pusilliflora*	9	18	6	0.020	0.541	0.350	0.063	0.953
Neomitranthes obtusa	4	8	8	0.074	0.240	0.466	0.232	0.939
Andira fraxinifolia	6	12	8	0.035	0.360	0.466	0.108	0.935
Pouteria aff. *psammophila*	4	8	8	0.060	0.240	0.466	0.189	0.895
Inga subnuda	4	8	6	0.091	0.240	0.350	0.286	0.876
Myrciaria floribunda	4	8	8	0.038	0.240	0.466	0.118	0.824
Amaioua intermedia	5	10	8	0.018	0.300	0.466	0.057	0.824
Annona salzmannii	2	4	4	0.145	0.120	0.233	0.453	0.807
Connarus blanchetii	5	10	8	0.011	0.300	0.466	0.033	0.799
Zollernia glabra	4	8	8	0.015	0.240	0.466	0.046	0.752
Eugenia pisiformis	5	10	6	0.023	0.300	0.350	0.071	0.721
Eugenia brasiliensis	5	10	6	0.013	0.300	0.350	0.042	0.692
Vitex polygama	3	6	4	0.070	0.180	0.233	0.219	0.633
Chrysophyllum splendens	3	6	4	0.056	0.180	0.233	0.176	0.589

Continues

Table 4. Continuation.

Species	Ni	AD	AF	ADo	RD	RF	RDo	IV
Emmotum nitens	2	4	4	0.072	0.120	0.233	0.225	0.579
Myrciaria tenella	3	6	6	0.004	0.180	0.350	0.013	0.543
Lacistema robustum	2	4	4	0.045	0.120	0.233	0.141	0.494
Matayba guianensis	2	4	4	0.039	0.120	0.233	0.122	0.475
Eugenia sp.2	3	6	4	0.016	0.180	0.233	0.048	0.462
Inga exfoliata	2	4	4	0.025	0.120	0.233	0.080	0.433
Ficus cf. *bahiensis*	2	4	4	0.024	0.120	0.233	0.074	0.427
Melanopsidium nigrum	2	4	4	0.004	0.120	0.233	0.012	0.366
Pogonophora schomburgkiana	3	6	2	0.022	0.180	0.117	0.068	0.365
Psidium brownianum	2	4	4	0.004	0.120	0.233	0.012	0.365
Xylopia sericea	2	4	4	0.004	0.120	0.233	0.012	0.365
Guapira sp.	2	4	4	0.003	0.120	0.233	0.008	0.361
Myrcia cerqueiria	2	4	2	0.019	0.120	0.117	0.059	0.296
Andira nitida	1	2	2	0.025	0.060	0.117	0.078	0.254
Schinus terebinthifolius	1	2	2	0.021	0.060	0.117	0.065	0.242
Carpotroche brasiliensis	1	2	2	0.019	0.060	0.117	0.058	0.234
Byrsonima bahiana	1	2	2	0.017	0.060	0.117	0.053	0.230
Eugenia brejoensis	1	2	2	0.010	0.060	0.117	0.031	0.207
Cecropia pachystachya	1	2	2	0.007	0.060	0.117	0.021	0.198
Myrsine guianensis	1	2	2	0.006	0.060	0.117	0.020	0.196
Myrcia bergiana	1	2	2	0.006	0.060	0.117	0.019	0.196
Ocotea sp.2	1	2	2	0.006	0.060	0.117	0.018	0.195
Swartzia simplex	1	2	2	0.005	0.060	0.117	0.014	0.191
Picramnia gardneri	1	2	2	0.003	0.060	0.117	0.009	0.186
Eugenia inversa	1	2	2	0.003	0.060	0.117	0.008	0.185
Maytenus cf. *communis*	1	2	2	0.002	0.060	0.117	0.005	0.182
Conchocarpus longifolius	1	2	2	0.001	0.060	0.117	0.004	0.181
Pilocarpus grandiflora	1	2	2	0.001	0.060	0.117	0.004	0.181
Conchocarpus insignis	1	2	2	0.001	0.060	0.117	0.004	0.180
Duguetia sessilis	1	2	2	0.001	0.060	0.117	0.003	0.180
Psychotria carthagenensis	1	2	2	0.001	0.060	0.117	0.003	0.180
Calyptranthes brasiliensis	1	2	2	0.001	0.060	0.117	0.003	0.180

Ni = number of individuals sampled; AF = absolute frequency; AD = absolute density; ADo = absolute dominance; RF = relative frequency, RD = relative density, RDo = relative dominance, IV = importance value.

region. The pattern observed allows us to conclude that the environmental conditions of the areas evaluated, including climatic conditions generated by latitude, proximity to other vegetation types and the influence of human activity, might explain the similarities and differences found for this family along the coast (Guedes *et al.* 2006).

Although there was considerable density of Annonaceae species, mainly *U. aurantiaca*, in the lower and middle strata, the great numbers of Myrtaceae species in these strata made the latter family predominant. However, in the upper strata, Myrtaceae species become less representative for all parameters, confirming that it is a family typical of the lower strata, as stated by Tabarelli & Mantovani (1997). The middle stratum is representative of species in development, which are also present in the upper strata, thus contributing to the maintenance of species diversity in this forest. However, individuals in the upper stratum contribute little to the richness and density, although they are primarily responsible

Chart 1. Selection of shrub/tree species of the coastal forests of the state of Espírito Santo (ES), Brazil, based on the classification of 14 areas by two-way indicator species analysis.

Preferentials of *restingas* in northern ES: *Abarema filamentosa*, *Acosmium bijugum*, *Chrysophyllum splendens*, *Clavija spinosa*, *Couepia schottii*, *Eriotheca macrophylla*, *Eugenia brasiliensis*, *Ficus gomelleira*, *Humiriastrum dentatum*, *Joannesia princeps*, *Lacistema robustum*, *Macrolobium latifolium*, *Picramnia gardneri*, *Piptadenia adiantoides*, *Pogonophora schomburgkiana*, *Protium icicariba*, *Pterocarpus rohrii*, *Simarouba amara*, *Tabebuia roseoalba.*
Preferentials of *restingas* in southern ES: *Abarema jupumba*, *Annona acutifolia*, *Buchenavia tetraphylla*, *Cathedra rubricaulis*, *Coussapoa microcarpa*, *Crataeva tapia*, *Daphnopsis coriacea*, *Dulacia singularis*, *Eriotheca pentaphylla*, *Eugenia speciosa*, *Exostyles venusta*, *Ficus hirsuta*, *Hymenaea rubriflora*, *Marlierea glabra*, *Myrcia racemosa*, *Pseudobombax grandiflorum*, *Trichilia pallens*, *T. pseudostipularis.*
Broad distribution in the *restingas* of ES: *Anacardium occidentale*, *Byrsonima sericea*, *Andira fraxinifolia*, *A. nitida*, *Aspidosperma pyricollum*, *Bactris vulgaris*, *Calyptranthes brasiliensis*, *Capparis flexuosa*, *Chamaecrista ensiformis*, *Chiococca alba*, *Clusia hilariana*, *C. spiritu-sanctensis*, *Coccoloba alnifolia*, *Cupania emarginata*, *Eschweilera ovata*, *Erythroxylum subsessile*, *Esenbeckia grandiflora*, *E. astringens*, *Eugenia excelsa*, *E. punicifolia*, *E. sulcata*, *Garcinia brasiliensis*, *Guapira opposita*, *Guarea guidonia*, *Heisteria perianthomega*, *Himatanthus phagedaenicus*, *Inga subnuda*, *Jacaranda puberula*, *Kielmeyera albopunctata*, *Manilkara subsericea*, *Matayba guianensis*, *Maytenus obtusifolia*, *Melanoxylum nigrum*, *Micropholis venulosa*, *Mollinedia glabra*, *Myrcia bergiana*, *M. splendens*, *M. vittoriana*, *Myrciaria floribunda*, *Ocotea lobbii*, *O. notata*, *Opuntia brasiliensis*, *Ouratea cuspidata*, *Pera glabrata*, *P. leandri*, *Piper arboreum*, *Pouteria caimito*, *P. coelomatica*, *Protium heptaphyllum*, *Psidium brownianum*, *P. cattleianum*, *Rhodostemonodaphne capixabensis*, *Schinus terebinthifolius*, *Stigmaphyllon paralis*, *Simaba cuneata*, *Sorocea hilarii*, *Swartzia apetala*, *Xylopia sericea*, *X. laevigata*, *Ziziphus platiphylla*, *Zollernia glabra.*
Preferentials of the *tabuleiro* forests of northern ES: *Allophylus petiolutatus*, *Andira ormosioides*, *Annona cacans*, *Aspidosperma ilustre*, *Astronium concinmum*, *A. graveolens*, *Banara brasiliensis*, *Blepharocalyx eggersii*, *Bombacopsis stenopetala*, *Brosimum guianense*, *Buchenavia rabelloana*, *Calyptranthes lucida*, *Campomanesia espiritosantensis*, *Carpotroche brasiliensis*, *Caryocar edule*, *Caryodendron grandifolium*, *Casearia commersoniana*, *C. decandra*, *Cecropia glaziovi*, *Cedrela odorata*, *Chrysophyllum lucentifolium*, *C. splendens*, *Citronella paniculata*, *Clarisia racemosa*, *Cordia sellowiana*, *Couepia carautae*, *Couratari asterotricha*, *Cupania rugosa*, *Deguelia longeracemosa*, *Dialium guianensis*, *Diplotropis incexis*, *Ecclinusa ramiflora*, *Eriotheca macrophylla*, *Eugenia pisiformis*, *E. pruinosa*, *E. ternatifolia*, *Exellodendron gracile*, *Faramea bahiensis*, *Garcinia gardneriana*, *Geissospermum laeve*, *Guarea penningtoniana*, *Guettarda angelica*, *Helicostylis tomentosa*, *Hidrogaster trinervis*, *Hirtella hebeclada*, *Inga flagelliformis*, *I. hispida*, *Jacaratia heptaphylla*, *Joannesia princeps*, *Lacistema recurvum*, *Lecythis lanceolata*, *L. lurida*, *Licania kunthiana*, *L. octandra*, *L. salzmanii*, *Luehea mediterranea*, *Machaerium fulvovenosum*, *M. ovalifolium*, *Manilkara bella*, *M. salzmannii*, *Margaritaria nobilis*, *Marlierea estrellensis*, *M. sucrei*, *Melanoxylon brauna*, *Micropholis crassipedicelata*, *M. cuneata*, *Mollinedia marquetiana*, *Myrcia lineata*, *M. multiflora*, *Myrocarpus fastigianus*, *Neoraputia alba*, *Ocotea argentea*, *O. conferta*, *O. confertiflora*, *O. elegans*, *O. odorifera*, *O. velutina*, *Ormosia nitida*, *Parapiptadenia pterosperma*, *Piptadenia paniculata*, *Plinia involucrata*, *Polyandrococos caudescens*, *Pouteria bangii*, *P. cuspidata*, *Pradosia lactescens*, *Protium warmingianum*, *Pseudopiptadenia contorta*, *Psychotria carthagenensis*, *Quararibea penduliflora*, *Randia armata*, *Rinorea bahiensis*, *Schefflera morototoni*, *Schoepfia oblongifolia*, *Sclerolobium striatum*, *Senefeldera multiflora*, *Simarouba amara*, *Simira glaziovii*, *S. grazielae*, *Siparuna reginae*, *Sorocea guilleminiana*, *Spondias venulosa*, *Stephanopodium blanchetianum*, *Sterculia speciosa*, *Swartzia simplex*, *Sweetia fruticosa*, *Tabebuia obtusifolia*, *T. roseoalba*, *Thyrsodium schomburgkianum*, *Vatairea heteroptera*, *Virola gardneri*.

Restinga – shrublands; *tabuleiro* forests – coastal lowland forests on Tertiary

for biomass stocks, given their high representation in terms of basal area. Because the low nutrient content in the soil of the *restinga* makes biomass the principal nutritional reserve maintained through nutrient cycling (Guedes *et al.* 2006), the upper and lower strata are both quite important for maintaining the structural complexity of this type of forest.

For the species-area curve, our sampling can be considered sufficient despite the high proportion of species represented by only one individual. In *restingas*, this does not necessarily indicate that the species are rare. For example, in a *restinga* in southern Espírito Santo, *Schinus terebinthifolius* was found to be represented by a single individual (Assis *et al.* 2004b). In shrub formations along the backshore, as well as in disturbed environments, *S. terebinthifolius* has a higher density (Assumpção & Nascimento 2000; Lobão & Kurtz 2000; Menezes & Araujo 2005). In previous studies, the number of shrub and tree species observed in *restinga* vegetation formations has varied considerably, species richness typically being highest in terra firme forest, although rarely exceeding 150 species (Pereira 1990, Pereira & Araujo 2000; Silva & Britz 2005; Menezes & Araujo 2005; Amaral *et al.* 2008). In the present study, we observed a high number of species with low density, in comparison with other *restingas* of Brazil, which might be an intrinsic characteristic of the community evaluated and could be responsible for the increase in species diversity.

In the Itaúnas *restinga*, the diversity index, density and basal area were higher than in other Brazilian *restingas* (Assumpção & Nascimento 2000; Waechter *et al.* 2000; Scherer *et al.* 2005; Guedes *et al.* 2006; Sá & Araujo 2009), which could be indicative of a good state of preservation. In addition to the higher diversity index, Myrtaceae richness and overall species richness were higher in our sample than in those of other studies of the vegetation of *restingas* in Espírito Santo (Fabris & César 1996; Assis *et al.* 2004b). However, this result might have been influenced by the fact that our inclusion criteria were broader than were those of some of the aforementioned studies, resulting in a more inclusive sample. By adopting a DBH ≥ 5 cm as an inclusion criteria, we eliminated 16 species (three Myrtaceae) and 850 individuals (51% of the total) from our sample, the final sample therefore totaling 98 species. Nevertheless, the values of H' and J' (3.93 and 0.856, respectively) were still higher than those obtained for other *restingas* in Espírito

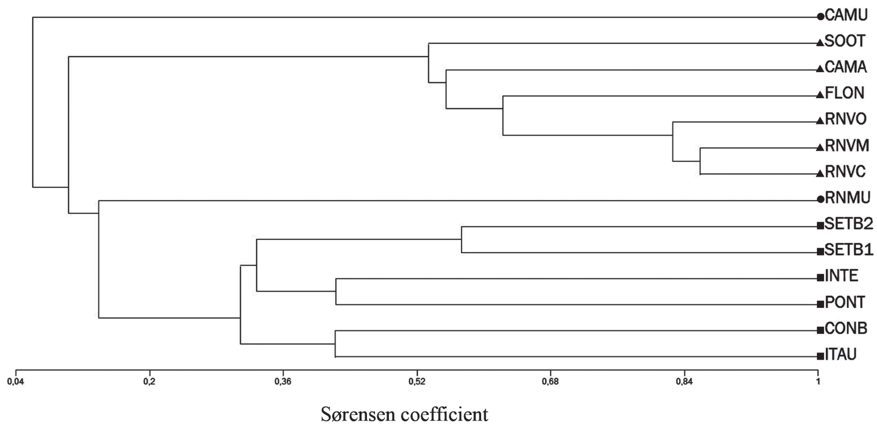

Figure 4. Dendrogram of similarity (unweighted pair group method with arithmetic mean), using the Sørensen coefficient, generated through qualitative data related to 14 coastal forests in the state of Espírito Santo and in the southern part of the state of Bahia, Brazil.
▪ = *restinga*, ● = *muçununga*; ▲ = *mata alta* (tall forest).
Restinga – shrublands; *muçununga* – similar to *restinga* but established on Tertiary land, forming enclaves in the *mata alta* (tall forest); CAMU – *muçununga* in the municipality of Caravelas (state of Bahia); SOOT – Sooretama Biological Reserve (state of Espírito Santo—ES); CAMA – *mata alta* in Caravelas; FLON – Rio Preto National Forest; RNVO – Oiticica Natural Vale Reserve; RNVM – Macanaíba Natural Vale Reserve; RNVC – Caigá Natural Vale Reserve; RNMU – *muçununga* in Natural Vale Reserve; SETB2 – 2nd location within Setiba Park (now Paulo César Vinha State Park); SETB1 – 1st location within Setiba Park; INTE – Interlagos; PONT – Pontal do Ipiranga; CONB – Conceição da Barra; ITAU – Itaúnas.

Santo and for those in other Brazilian states. Therefore, the exclusion of individuals with a DBH < 5 cm implied partial exclusion of the undergrowth, interfering little in the total number of species, given that the middle stratum comprises the largest portion of the wealth of this forest.

Tree death is a natural process triggered by biotic or abiotic conditions that contribute to the forest dynamics of tropical ecosystems (Franklin *et al.* 1987). In the Itaúnas *restinga*, dead trees, if they were to be considered in a specific category, would rank 4th in IV, with a density of 214 ind./ha. This value is higher than that found for *restingas* with well-drained soils along the coast—such as the 58.9 ind./ha reported for the Tavares *restinga*, in the state of Rio Grande do Sul (Dorneles & Waechter 2004); the 67.0 ind./ha and 104.0 ind./ha reported for the *restingas* in Paulo César Vinha State Park, in Espírito Santo (Assis *et al.* 2004b; Fabris 1995); and the 120.0 ind./ha reported for the Armação de Buzios *restinga*, in the state of Rio de Janeiro (Lobão & Kurtz 2000)—as well as that found for poorly drained *restingas*, such as the 152.0 ind./ha reported for the Marambaia *restinga*, in the state of Rio de Janeiro (Menezes *et al.* 2010). However, the basal area of dead trees in Itaúnas was similar to that found for those well-drained *restingas* and lower than that found for the poorly drained Marambaia *restinga* (1.28 m^2/ha). This can be attributed to the fact that flooding creates soil conditions that restrict tree development (Menezes *et al.* 2010). In addition, the significant difference between our findings and those of other studies of *restingas*, in terms of the density of dead trees, can be attributed to the inclusion criterion adopted in our study (DBH ≥ 2.5, a diameter smaller than that used in other studies). This allowed for the inclusion of a high density of thin individuals, as evidenced by the concentration of individuals in the first two diameter classes, which are more susceptible to disease, climate change and senescence due to competition for light (Franklin *et al.* 1987).

The concentration of the IV in a few species is common in Brazilian *restinga*s. In the present study, this became apparent when we summed the IVs of the 13 most important species, which were found to account for approximately 50% of the total density of IV and approximately 60% of the total dominance, as reported for other *restingas* along the coast (Assumpção & Nascimento 2000; Assis *et al.* 2004b). This indicates that environmental factors regulate the composition of species, limiting their establishment and development, resulting in a highly oligarchic structure that can reflect severe environmental conditions, such as the highly porous and nutrient-poor nature of the *restinga* soil, which is unfavorable for the establishment of many species (Scarano 2002). However, some species seem to flourish in these environmental conditions, particularly those belonging to the family Myrtaceae, which stood out in this forest due to their high density, which is common in *restingas*. Trindade (1991), studying a shrub/tree *restinga* near the city of Natal, noted the predominance of Myrtaceae in the sample, attributing this to some power over other species or to a better ability to take advantage of available resources.

The low similarity coefficients found for the coastal forests of Espírito Santo showed high floristic diversity, given that similarity coefficients greater than or equal to 0.5 indicate high floristic similarity (Kent & Coker 1992). These conclusions must be interpreted with caution, because this floristic heterogeneity might, in part, reflect differences among the sampling methods employed for the various areas evaluated. Nevertheless, this does not invalidate the results showing that, despite their proximity to each other,

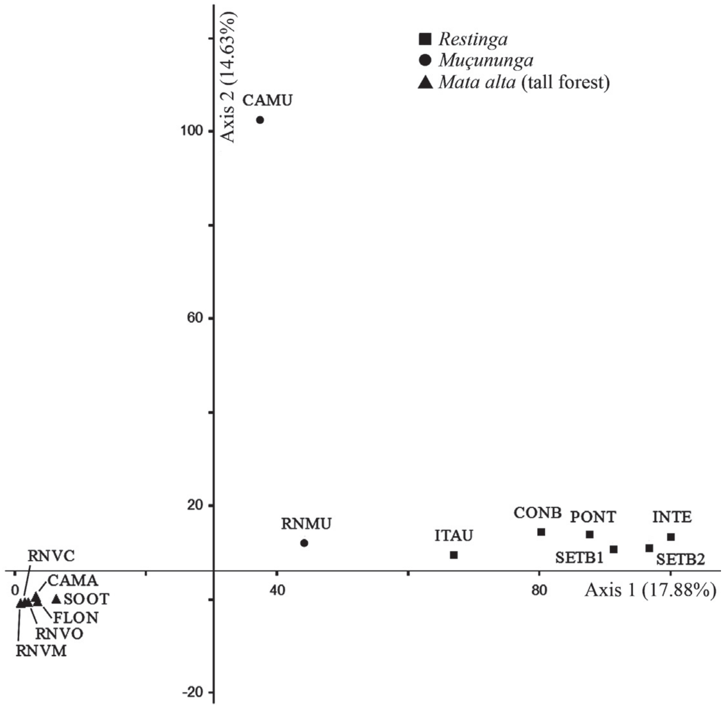

Figure 5. Ordination diagram by correspondence analysis for qualitative data related to 14 coastal forests in the state of Espírito Santo and in the southern part of the state of Bahia, Brazil.
Restinga – shrublands; *muçununga* – similar to *restinga* but established on Tertiary land, forming enclaves in the *mata alta* (tall forest); CAMA – *mata alta* in Caravelas; FLON – Rio Preto National Forest; RNVO – Oiticica Natural Vale Reserve; RNVM – Macanaíba Natural Vale Reserve; RNVC – Caigá Natural Vale Reserve; RNMU – *muçununga* in Natural Vale Reserve; SETB2 – 2nd location within Setiba Park (now Paulo César Vinha State Park); SETB1 – 1st location within Setiba Park; INTE – Interlagos; PONT – Pontal do Ipiranga; CONB – Conceição da Barra; ITAU – Itaúnas.

these forests show floristic characteristics that are particular to each region, a pattern commonly found in Brazilian *restingas* (Pereira 1990; Assis *et al.* 2004a; Scherer *et al.* 2005; Amaral *et al.* 2008). This high floristic heterogeneity complicates the implementation of environmental restoration programs, because of uncertainties over which species to be used, given that the introduction of an exotic species can harm the ecological system (Lani *et al.* 2008). Therefore, the identification of preferentially occurring species in this region is aimed at facilitating this process.

According to the TWINSPAN, *C. flexuosa*, *G. brasiliensis* and *P. heptaphyllum* were identified as preferential to *restinga* and as characteristic of the *restinga* of Espírito Santo, in relation to its *tabuleiro* forests, the latter making an important contribution to the structure of the *restinga* tree community (Assis *et al.* 2004b). In the TWINSPAN division, we found *G. opposita* to be non-preferential, which is in agreement with studies indicating that it is a generalist species (Oliveira-Filho & Fontes 2000).

The similarity dendrogram shows that the *restingas* of Espírito Santo do not form clusters clearly distinguishing those in the north of the state from those in the south. For example, the Pontal do Ipiranga *restinga*, along the northern coast, showed greatest floristic similarity to the Interlagos *restinga*, located on the southern coast. However, this finding should also be interpreted with caution, because, despite sharing characteristics with the southern *restinga* cluster, the Pontal do Ipiranga *restinga* has few species in common with those forests, which precludes any hierarchical divisions in the TWINSPAN. Therefore, the inclusion of the Pontal do Ipiranga *restinga* weakens the structure of that cluster, because it is an artifact of the analysis, probably attributable to differences in methodology and sampling power among the studies.

The low floristic similarity between the Itaúnas and Conceição da Barra *restingas* denotes an intrinsic character of the *restingas*, reflecting the high heterogeneity among the sites surveyed, in terms of species composition. This uniqueness provides evidence that the *tabuleiro* forest, given its proximity, had an influence on the Itaúnas *restinga*, providing seedlings of uncommon species that find conditions favorable to their establishment in the *restingas*. Other species identified by the TWINSPAN as preferential to the *tabuleiro* forests of northern Espírito Santo can also be found in the Itaúnas *restinga*, including *Eugenia pisiformis*, *Jacaratia heptaphylla*, *Marlierea sucrei*, *Swartzia simplex* and *Tabebuia roseoalba* (Chart 1).

Although the *muçununga* forest in Linhares (Natural Vale Reserve) was established on Tertiary land, forming enclaves in the *mata alta*, it features soil conditions similar to those observed in the *restingas* analyzed, the soil being essentially sandy and well-drained (Simonelli *et al.* 2008), which justifies its position in the dendrogram. The *muçununga* forest in Caravelas is flooded periodically (Meira-

-Neto *et al.* 2005), which explains the low degree of floristic similarity between this and the other formations. Chief among the species identified by the TWINSPAN as preferential is *Tabebuia cassinoides* (Lam.) DC., which is known to tolerate poorly drained environments (Scarano 2002).

The northern Espírito Santo/southern Bahia region is a recognized focus of plant species diversity (Peixoto & Silva 1997), presenting a unique biogeographic pattern in that it constitutes an area within which semideciduous lowland forests and northern rainforests overlap, which could generate floristic affinities even between geographically distant areas, given the strong floristic links with *tabuleiro* forests in that region (Oliveira-Filho & Fontes 2000; Rolim *et al.* 2006). Some of the species identified by the TWINSPAN as responsible for the clustering have also been cited for Atlantic Forest, in the northern lowlands of Espírito Santo (Oliveira-Filho & Fontes 2000), including *Brosimum guianense*, *Carpotroche brasiliensis*, *Caryocar edule*, *Cedrela odorata*, *J. princeps*, *Melanoxylon brauna*, *T. roseoalba* and *Virola gardneri*, as well as in the lowlands to the south, including *Allophylus petiolulatus*, *Ecclinusa ramiflora*, *Micropholis crassipedicellata*, *Pouteria venosa*, *Psychotria carthagenensis* and *Sweetia fruticosa*.

In the correspondence analysis, we obtained eigenvalues that are considered high and therefore indicative of good separation of areas, as well as indicating complete turnover of species along its axes (ter Braak 1995). According to the ordination diagram, the *restingas* formed an ordered cluster that was essentially aligned toward a gradient of floristic similarities, graphically illustrating the possibility that the distance between the *restingas* of Espírito Santo and the *tabuleiro* forests (in the north of Espírito Santo and the south of Bahia) creates gradual variations in species composition, in which the Itaúnas *restinga* was notable for its degree of similarity with the *tabuleiro* forests. In addition,

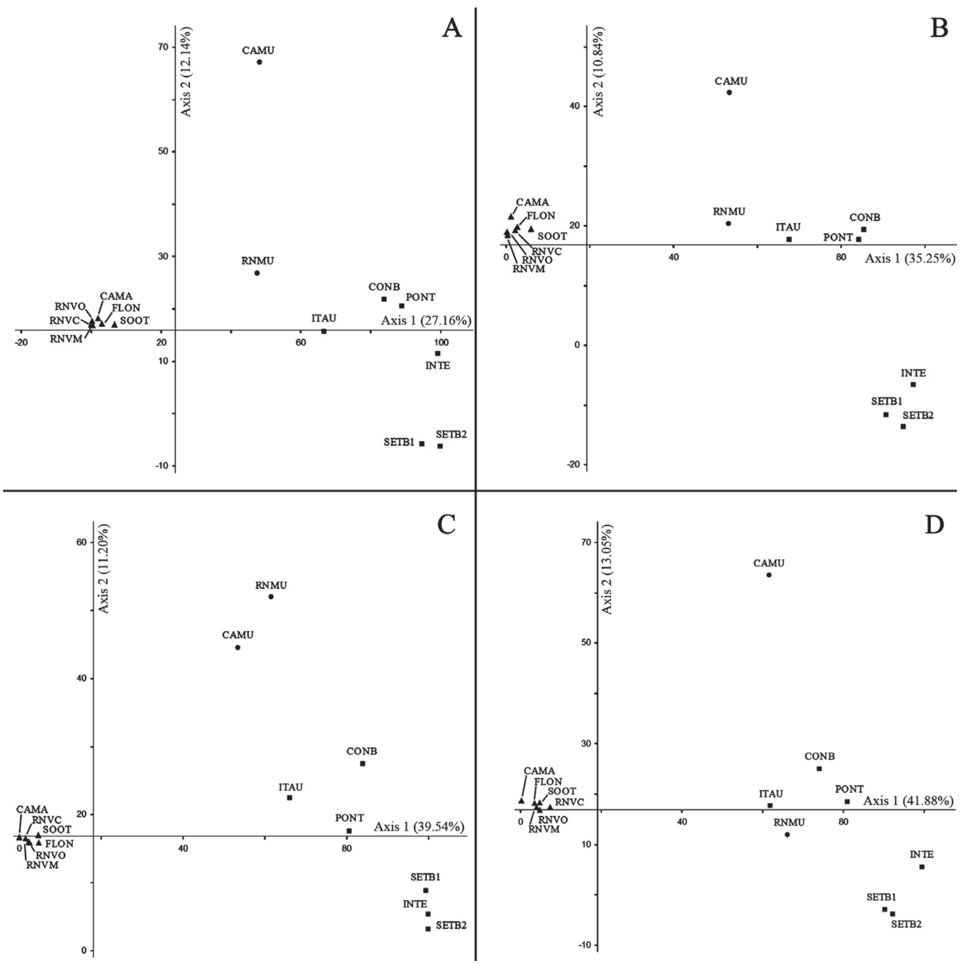

Figure 6. Ordination diagrams generated by correspondence analysis for qualitative data from 14 coastal forests in the state of Espírito Santo and in the southern part of the state of Bahia, Brazil, resulting from the exclusion of species occurring in only one area (A); in only two areas (B); in only three areas (C); and in only four areas (D).

▪ = *restinga*, ● = *muçununga*; ▲ = *mata alta* (tall forest).

Restinga – shrublands; *muçununga* – similar to *restinga* but established on Tertiary land, forming enclaves in *mata alta* (tall forest); CAMA – *mata alta* in Caravelas; FLON – Rio Preto National Forest; RNVO – Oiticica Natural Vale Reserve; RNVM – Macanaíba Natural Vale Reserve; RNVC – Caigá Natural Vale Reserve; RNMU – Natural Vale Reserve; SETB2 – 2nd location within Setiba Park (now Paulo César Vinha State Park); SETB1 – 1st location within Setiba Park; INTE – Interlagos; PONT – Pontal do Ipiranga; CONB – Conceição da Barra; ITAU – Itaúnas.

the difference between the Itaúnas *restinga* and the southern *restingas*, in terms of floristic composition, might reflect the latitudinal position of the former, which is influenced by the dense tropical rain forest on Precambrian terranes that is more common in this region (Fabris & Cesar 1996; Assis *et al.* 2004a). However, this result should be interpreted with caution given the sensitivity of the correspondence analysis to species of low occurrence, and it is suggested that those be given less weight, because they can introduce noise and tend to contribute little to the patterns generated by the analysis (ter Braak 1995). Therefore, when species occurring in only one area were excluded from the analysis, the ordering pattern became conservative, even when species occurring in two, three or four areas were excluded (Fig. 6). Furthermore, the division of the *restingas* of southern and northern Espírito Santo into two floristic blocks became more evident, providing evidence of a historical separation that was probably caused by the influence of the surrounding vegetation on the floristic composition of the *restinga*.

In the ordination diagram, the *muçununga* forest in Linhares can be seen to be in close floristic proximity to the *restingas* and the influence of the *mata alta* on species composition in the *muçununga* forest is evident. The TWINSPAN confirmed this pattern of differentiation, allowing the identification of species responsible for the division between the *muçununga* forest and the *mata alta*. Those species include *Andira nitida*, *Cupania emarginata*, *Eugenia astringens*, *G. brasiliensis*, *Myrcia splendens* and *Rhodostemonodaphne capixabensis*, all of which are commonly found in the *restingas* of Espírito Santo (Pereira & Araujo 2000). As in the similarity dendrogram, the *muçununga* forest in Caravelas, in southern Bahia, was found to be distant from all other forests in the ordination diagram, confirming that the species composition of the community is quite distinct from that of the others analyzed here.

The Itaúnas forest retains unique floristic characteristics because of many factors, among which is its high diversity. The floristic affinity between the Itaúnas *restinga* and *tabuleiro* forests revealed important floristic patterns, suggesting that the species composition of the *restingas* of Espírito Santo is a reflection of distinct environmental and geomorphological conditions, the surrounding vegetation having a decisive influence. This seems to be the main factor responsible for the gradual reduction in floristic similarities between the *restingas* of the north and south. In addition, the indication of preferential species generated by the TWINSPAN can inform the preparation of species lists used in environmental restoration programs, mainly in the *restinga*, given its naturally limiting conditions and the intense process of fragmentation that it is undergoing.

Acknowledgments

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