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Abstract
The Organismic and the Continuous theories are traditionally considered as antagonist in ecology studies. In this research, we make the floristic characterization of different forest communities and establish the corresponding classification, taking into account the approaches derived from the theories aforementioned. We used 1 ha plots to evaluate individuals bigger than 10 cm dbh (diameter at breast height). In each one of that plots, four sub-plots of 100 m^2 were measured, to study all the spermatophyta in the understory. The data obtained were considered in an Enlarged Importance Index (EII), for each species in each plot. Then, the phytosociological relationships were established, according to the importance and appearance of all the species in all the plots and the results from conglomerate and multivariate analyses. We found a great unit of vegetation where the species *Pentaclethra macroloba* and *Carapa guianensis* are characteristic-dominant. In position of summit and hillside, an *Alexa imperatricis* Forest was identified. A valley type exists where a *Catostemma commune* Forest is present, and there is another valley with a *Mora excelsa* Forest. We found that Organismic and Continuous approaches could be complementary to get a better understanding of the tropical forest ecosystems.

Keywords: *Ecological classification, importance index, forest survey methods, Guayana shield, Imataca Forest Reserve*

Introduction

There are two main focuses that have based the study of the vegetation communities:

The Organismic Theory has its origin in the work of Clements (1916) about forest succession. According to this postulate, vegetal communities are discreet entities and a kind of ''super-organism''. Following this concept, in the classic Phytosociology, each community has its own floristic composition and can acquire a name based on one or two characteristic species (Braun-Blanquet 1979). In addition, the school known as numeric syntaxonomy evaluates the communities in function of its quantitative attributes (Mucina & Van der Maarel 1989). Among these methods, the conglomerates' analyses and the Importance Value Index (IVI) (Curtis & McIntosh 1951) stand out.

The Individualistic Hypothesis of Gleason (1917) promoted from the Continuous Theory (McIntosh 1967). With these perspectives, the vegetation community does not exist, because the environment is continuous and the species are distributed in equal forms along the environmental gradients, independently the some of the other ones. Therefore, the differentiation of communities is arbitrary, and what is recommended is to order the censuses in function of variation axes. From this perspective, multivariate analysis methods have been developed, where it is judged that gradients are so complex that they are considered abstract dimensions of an ecological hyperspace, conformed by a multidimensional cloud of points; the cloud is ''flat'' to take it to two dimensions that can be interpreted (De Cáceres 2005).

There is a direct relationship between the Organismic theory and the phytosociological approach. In neotropical ecosystems, its concepts were applied in the first half of the twentieth-century (Beard 1944, 1955; Fanshawe 1952). In the second half of the twentieth-century, most of the classification based on

phytosociological method was restricted to simple ecosystems like savannas, shrub lands, and "paramos" (Castroviejo & López 1985; Berg & Suchi 2001; Arbelaez & Duivenvoorden 2004). The main reason of this relatively scarce phytosociological work (in a classical sense) could be the "subjectivity" pointed out in this method (Matteucci & Colma 1982; Terradas 2001; Dakskobler 2009). Although several computing methods have been developed in the last decade, the phytosociological indexes could not been used in multivariate analyses such as principal components' analysis and correspondence analysis (Podani 2006).

But, in recent times, works that seem to support the former idea of vegetal communities with an own characteristic floristic composition and with few distinctive species are arising. There are evidences of forests dominated by a low number of species (Connel & Lowman 1989; Johnston & Gillman 1995; Knab-Vispo et al. 1999) and the so-called "oligarch forests" (Peters et al. 1989; Pitman et al. 2001; Vormisto et al. 2004). "Monodominant forests" is another expression that is being related to some tropical communities in a worldwide scope (Hart 1995; Nascimento & Proctor 1997; Martijena 1998; Torti et al. 2001; Degagne et al. 2009). In addition, there are works that use objective and numerical classification methods to sustain phytosociological units (Bruelheide & Chytry 2000; Grabherr et al. 2003; Petrik et al. 2009; Kavgaci et al. 2010).

In our work, it is considered that the neotropical high forests, in low-lands, are very complex and difficultly some isolated procedure will be efficient to explain its variability. In consequence, the two previous focuses will be used, since they can be complementary for a better understanding of the analyzed ecosystems. We appreciate that tropical forest requires very analytical and precise survey methods, as far as possible from the subjectivity of the appraiser. We accept that ecotones exist, but most of vegetation communities have a particular floristic composition. The objective of this research is to use the physiographic, structural, and floristic elements to characterize different vegetation communities, to evaluate their relationships, and to establish the classification and/or the corresponding ordering.

Materials and methods

Study site

The Imataca Forest Reserve (IFR) covers a surface of 3,822,000 ha (MARN-UCV 2003), and it is located to the east of Venezuela, among the coordinates 6°00′ and 8°30′ N and 59°50′ and 62°10′ W. The evaluated places belong to the Unit C4, located in the central sector of the reserve.

According to the isohyets and isotherm maps (MARN-UCV 2003), it is considered that the annual precipitation is near 1700 mm, and the annual average temperature is 26°C. Although is outside of the IFR, the Tumeremo Climatic Station is representative of this area and shows that precipitation picks exist in December and the May–August period (Figure 1).

The geology is dominated by granitic, basic volcanic, and turbidic metamorphosed rocks of the Precambrian. The physiography is soft or fairly wavy peneplain, with small valleys in the lowest areas. The soils are acid, very leached, and very low in the cation exchange capacity and base saturation (Franco 1988).

More than 80% of the IFR possesses forest covering (MARN-UCV 2003). In the Holdridge System, the study area belongs to tropical humid forest (Ewel et al. 1976). There is still a lack of clarity in relation to the phytogeographical category that should have the area (region, province, etc.) and as for its precise limits. Most of the systems grant the Venezuelan Guayana the category of Region (Cabrera & Willink 1973; Good 1974; Huber & Alarcón 1988; Berry et al. 1995). Only Takhtajan (1986) and Rivas-Martínez and Navarro (2001) consider that this territory is a subordinate province to the Amazon region.

Selection of the work places

Terrestrial journeys were carried out, in non-logged areas, to detect the zones with more ecological variability. Two pathways were traced for ecological interpretation. In each pathway, a topographical mensuration was carried out, and in a preliminary way, different vegetation communities according to


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VENEZUELA ( TUMEREMO )                          187 m.

P= 1236        07°18'N         061°27'W         11/11 y.
T=   26        Ic=  2.0        Tp=  3138        Tn=    0
m=  20.0       M=  30.0        Itc=  762        Io=  3.9
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M'= 38.3

m'= 14.4

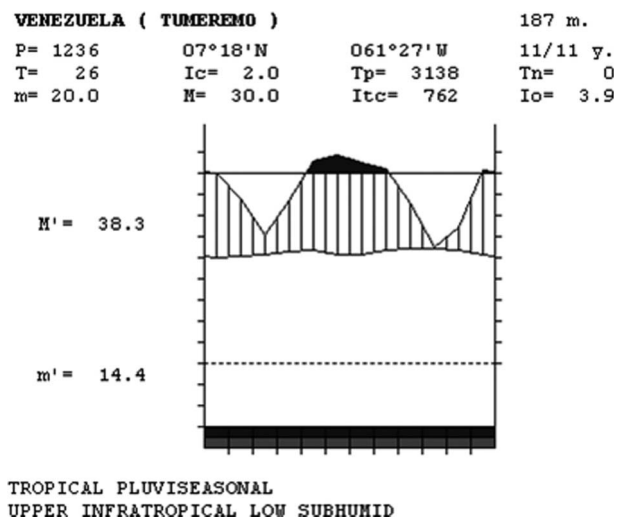TROPICAL PLUVISEASONAL
UPPER INFRATROPICAL LOW SUBHUMID

Figure 1. Ombrothermic diagram of the Tumeremo station (taken from Rivas-Martínez & Rivas y Sáenz 2006).

their height, covering, and physiographic position were identified. Each community represents a work sector, and in each one, three plots for the ecological survey were settled down.

Vegetation survey

We used 100 m × 100 m plots. In each plot, all the trees, palms, and lianas were measured (dbh ≥ 10 cm), and four 10 m × 10 m understory sub-plots were evaluated, and there we made a census of all the spermatophyta species (dbh < 10 cm).

Data analysis

According to the following equation, the IVI of each species was calculated (Curtis & McIntosh 1951):

$$IVI = Abundance\% + Dominance\% + Frequency\%$$

The IVI is one of the most used indexes in the analysis of tropical forest ecosystems (Dezzeo et al. 2000; Aymard et al. 2009; Cielo-Filho et al. 2009; Lin et al. 2010; Thakur & Khare 2010). Its main advantage is that it is quantitative and precise; not ready to subjective interpretations. In the IVI, the dominance is evaluated by the covering or the basal area. The covering presents serious problems of "appreciation" since the tropical forest is very diverse, the crowns are very high and intensely blended. For this, in forest studies, the basal area is usually employed, that is to say, the surface that occupies a bole that possesses a determined diameter or circumference. The disadvantage of this procedure is that it requires individuals with an appreciable dbh. Palms and trees usually have been surveyed, and it has been done without other life forms like lianas, ferns, and others that do not possess a defined or big bole (herbs).

The rejected life forms can, as a whole, represent a small fraction of the community biomass. But it is obvious that their ecological function is not worthless. With this procedure, there is a restricted vision of the ecosystem diversity and of the biotic relationships among their components. Understory contains 25%–46% of species diversity in tropical forests (Gentry & Dodson 1987). Aymard et al. (2009) tried to solve this problem by measuring individuals ≥2.5 cm dbh, but this procedure would leave out important groups like *Calathea* spp. in our Imataca forests.

Therefore, in this study an Enlarged Importance Index (EII) was used, and it is calculated by means of the following formula:

$$EII = IVI + UA\% + UF\%$$

where UA% is understory relative abundance and UF% is understory relative frequency.

In addition, an equivalence between this quantitative method and the indexes of the phytosociological method of Braun-Blanquet (1979) was carried out. This was done because, in the phytosociological school, the measure of abundance is appreciative ("little", "enough or very abundant", "variable number") and it is based on the experience of the appraiser. In the tropics, this is very complicated since, for the high diversity, the species-area curve establishes big sample units (1 ha), where it is very difficult to make appreciative surveys. Even, the estimate of the covering is hindered by some life forms (for example, lianas), because of the intense mixture of the foliages and the canopy height (often above 25 m). So, in this study, the correspondence among dominance% (basal area) and EII% was evaluated (Figure 2), the limits pointed out by the
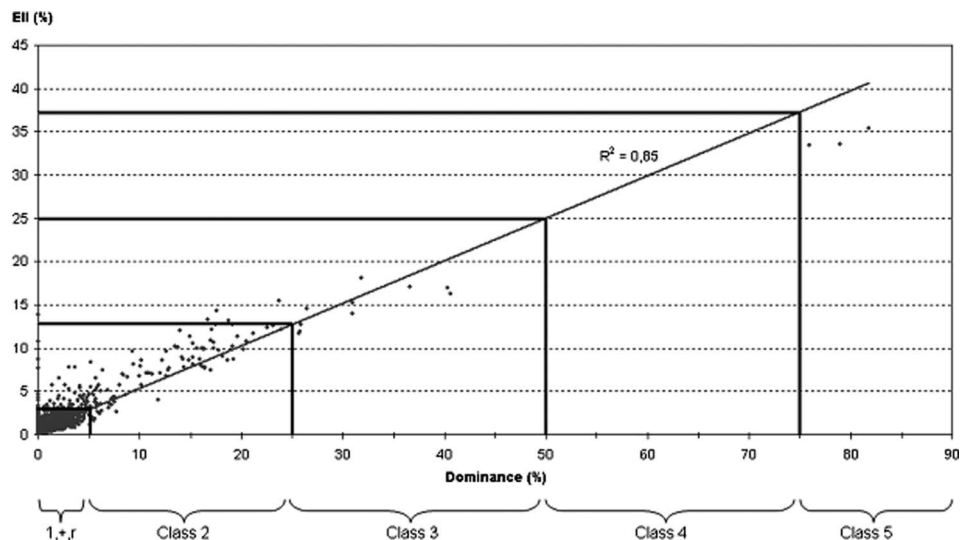

Figure 2. Correspondence between the dominance and the EII%.

Sigmatism Phytosociology (for the dominance) were applied, and together with them the corresponding limits in EII% were defined (graphically).

Under a dominance value of 5%, the dispersion of the points is very big, being impossible to separate the classes. Also, the phytosociological method specifies that, in that level, the classes "1", "+", and "r" separate according to the abundance, pointing out respectively: "quite abundant", "not very abundant", and "strange or isolated". Therefore, an analysis of the correspondence between abundance and EII% was carried out, for the data where the dominance is inferior to 5% (Figure 3). The data of EII% were obtained in 1 ha plots, for it was assumed that 5 and 10 are convenient values of abundance to separate the classes "r", "+", and "1". Then, in a graphic way, the respective limits of importance were designated.

The result of the whole previous process leads to the equivalences that are shown in Table I.

Ordering and classification

Analysis of conglomerates was developed by means of the program MVSP© (Kovach Computer Services 2004), by using the following procedures:

- Method of Ward, with the Squared Euclidean Distance.
- UPGMA (unweighted pair group method average), with the Sorensen's coefficient.

For the ordering, the program PC-ORD (McCune & Mefford 1999) was used, and the principal components analysis method was applied.

Results

Floristic composition and classification

We identified a total of five communities. In each community, we evaluated three plots and got a total of 15 ha for ecological assessment. We recognized a total of 232 species and made a full identification for 90.6% of them. The total list was reported by Lozada (2008). Following the style of Braun-Blanquet (1979), the species and the plots have been ordered so that the possible floristic associations are evidenced. These associations become very remarkable when observing the summary presented in Tables II and III.

According to these data, it is interpreted that the whole study area belongs to a vegetation unit characterized by *Pentaclethra macroloba* (Willd.) Kuntze. and *Carapa guianensis* Aubl. Inside this floristic entity, there are the following forests:

- *Alexa imperatricis* (R.H. Schomb.) Baill., in the hillside and summit plots (smf, hmf, hlf).
- *Mora excelsa* Benth., in plots of valley 1 (vf1).
- *Catostemma commune* Sandwith, in plots of valley 2 (vf2).

In the classic Phytosociology, we could understand an association named *Carapo guianensis-Pentaclethretum macrolobae* and the *A. imperatricis* Facies, the *M. excelsa* Facies, and the *C. commune* Facies.

In the full vegetation unit, the species *P. macroloba* and *C. guianensis* stand out on all the other ones for their frequency and importance. To these two species, *Clathrotropis brachypetala* (Tul.) Kleinhoonte, *Eschweilera chartacea* (O. Berg) Eyma,
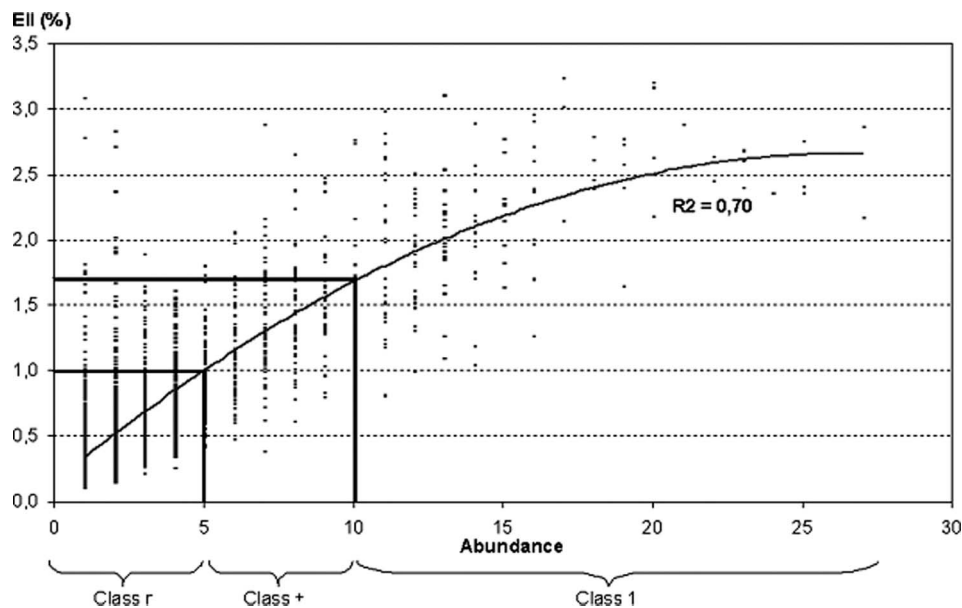

Figure 3. Correspondence between the abundance and the EII%.

Sterculia pruriens (Aubl.)K. Schum., *Inga punctata* Willd., *Trichilia lepidota* subsp *leucastera* (Sandwith) T. D. Penn., *Neea spruceana* Heimerl, *Brosimum alicastrum* Sw., *Drypetes variabilis* Uittien and *Unonopsis glaucopetala* R. E. Fr. can be added to form a group that presents small to medium trees (they rarely overcome 80 cm dbh), and they are in the medium and inferior strata of almost all the evaluated plots.

The EII data (for 232 species) were processed by means of a conglomerates' analysis, and the obtained classification is shown in Figure 4. The Squared Euclidean Distance does not have an ecological interpretation, and it spreads to exaggerate the differences. In any event, it can be observed that, according to the EII of each species, all the summit and hillside plots are very similar, while those of valley are very different. Two types of valley communities were identified, and they show marked differences to each other.

When only considering the appearance/absence of the species, according to the Sorensen's Index (Figure 5), it can be observed that how a similarity bigger than 50% among all the plots exists. The likeness between the summit and hillside plots (smf, hmf, hlf) and the separation of two valley communities (vf1 and vf2) is confirmed. Each one of these groups has internal similarities near or larger than 70%.

The principal components analysis (Figure 6) confirms again the validity of the cluster carried out. It was executed with the 15 evaluated plots and the 232 registered species, where 81% of accumulated variance was explained by axes one and two. In Figure 6, the plots of the hills (smf, hmf, hlf) are gathered in the inferior left sector; those of the valley 1 (vf1) are on the right and those of the valley 2 (vf2) are on the left superior part.

Description of the identified communities

A. imperatricis Forest.   It is present in the summits and sides of the small elevations of the study areas. It was observed that these areas correspond to Soft and Fairly Wavy Peneplain, where the maximum slopes reach 10%. These are forests with a medium canopy (15–25 m height) and frequent high individuals (>25 m); they are evergreen, and in general, they possess three to four strata.

A. imperatricis is a tree that grows to medium sizes (near to 80 cm dbh). At the canopy, *Protium neglectum* Swart, *P. decandrum* (Aubl.) Marchand, *Eschweilera decolorans* Sandwith, and *E. grata* Sandwith are also very important. The low stratum

Table I. Adjusted scale for the mixed evaluation of the phytosociological indexes and the EII%.

Phyto-indexes	EII%
5	>37.5
4	25–37.4
3	12.5–24.9
2	3–124
1	1.7–29
+	1.0–1.6
r	<1.0

Table II. Determination of the floristic units according to EII% values.

Species							Plots								
	smf1	smf2	smf3	hlf1	hlf2	hlf3	hmf1	hmf2	hmf3	vf11	vf12	vf13	vf21	vf22	vf23
Pentaclethra macroloba	12.1	9.6	9.9	15.5	12.7	13.1	3.9	5.4	7.5	0.4	1.4	0.0	13.3	8.9	1.7
Carapa guianensis	2.4	2.5	1.9	1.4	2.2	3.0	2.8	1.3	2.8	4.2	3.4	7.1	8.7	3.2	8.6
Clathrotropis brachypetala	1.2	1.2	1.6	2.7	2.0	1.5	0.3	0.9	1.4	3.1	2.7	4.5	2.0	1.4	2.0
Eschweilera chartacea	1.8	0.7	0.5	0.7	0.7	0.8	2.5	1.2	1.3	1.2	0.9	1.3	3.4	3.7	4.4
Sterculia pruriens	1.9	1.3	1.0	1.8	1.7	1.3	1.2	1.3	1.7	0.5	0.6	0.8	1.2	2.4	2.9
Alexa imperatricis	12.7	8.6	15.2	17.0	16.3	17.3	2.2	5.8	9.9	1.1	0.2	0.0	1.6	0.3	0.6
Eschweilera decolorans	7.6	2.9	3.5	0.6	0.1	0.5	8.6	9.9	8.7	2.0	0.7	1.0	0.3	0.4	0.4
Protium decandrum	3.8	7.3	5.1	1.7	2.6	3.5	1.2	0.8	1.8	0.4	0.2	0.4	1.6	7.7	1.3
Protium neglectum	2.4	5.7	3.1	0.9	1.6	2.5	3.1	3.5	2.7	0.6	1.6	0.0	0.1	0.2	0.0
Mabea piriri	3.2	1.4	5.7	2.4	3.0	4.5	1.1	1.2	2.9	0.0	0.0	0.0	0.5	0.7	0.1
Mora excelsa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	3.0	33.6	35.4	33.4	0.0	0.0	0.0
Adiantum petiolatum	0.2	0.0	0.1	0.2	0.0	0.5	0.0	0.2	0.3	1.7	1.7	13.8	0.4	0.0	0.3
Brownea latifolia	0.7	0.7	0.2	0.6	0.7	0.4	0.3	0.4	0.7	3.8	3.2	3.3	1.2	0.9	1.9
Inga myriantha	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	3.8	3.4	0.0	0.0	0.0
Eschweilera subglandulosa	0.0	0.0	0.0	0.0	0.3	1.2	0.6	0.0	0.5	0.6	1.5	2.0	0.9	1.4	0.6
Catostemma commune	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.1	0.9	0.0	0.4	12.6	18.9	11.3
Pterocarpus officinalis	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	4.6	3.4	3.5	12.1	4.6	12.3
Calathea sp.	0.4	0.1	0.2	0.3	0.5	0.3	0.0	0.0	0.0	0.9	0.0	0.0	5.0	3.4	4.5
Euterpe oleracea	0.6	0.4	0.9	0.9	1.0	0.1	0.4	0.3	0.1	0.5	0.0	0.0	1.9	1.8	2.3
Tabebuia stenocalyx	0.0	0.0	0.0	0.5	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	2.8

Table III. Determination of the floristic units according to the Braun-Blanquet phytosociological indexes.

| Species	smf1	smf2	smf3	hlf1	hlf2	hlf3	hmf1	hmf2	hmf3	vf11	vf12	vf13	vf21	vf22	vf23
Pentaclethra macroloba	2	2	2	3	3	3	2	2	2	r	+	−	3	2	2
Carapa guianensis	1	1	1	+	1	2	1	+	1	2	2	2	2	2	2
Clathrotropis brachypetala	+	+	+	1	1	+	r	r	+	2	1	2	1	+	1
Eschweilera chartacea	1	r	r	r	r	r	1	+	+	+	r	+	2	2	2
Sterculia pruriens	1	+	+	1	1	+	+	+	1	r	r	r	+	1	1
Alexa imperatricis	3	2	3	3	3	3	1	2	2	+	r	−	+	r	r
Protium neglectum	1	2	2	r	+	1	2	2	1	r	+	−	r	r	−
Eschweilera decolorans	2	1	2	r	r	r	2	2	2	+	r	+	r	r	r
Protium decandrum	2	2	2	1	1	2	+	r	+	r	r	r	+	2	+
Mabea piriri	2	+	2	1	1	2	+	+	1	−	−	−	r	r	r
Mora excelsa	−	−	−	−	−	−	−	2	2	4	4	4	−	−	−
Adiantum petiolatum	r	−	r	r	−	r	−	r	r	2	2	3	r	−	r
Brownea latifolia	r	r	r	r	r	r	r	r	r	2	2	2	+	r	1
Inga myriantha	−	−	−	−	−	−	−	−	−	1	2	2	−	−	−
Eschweilera subglandulosa	−	−	−	−	r	+	r	−	r	r	+	1	r	+	r
Catostemma commune	−	−	−	−	−	+	−	−	r	r	−	r	3	3	2
Calathea sp.	r	r	r	r	r	r	−	−	−	r	−	−	2	2	2
Pterocarpus officinalis	−	−	−	−	−	+	−	−	−	2	2	2	2	2	2
Euterpe oleracea	r	r	r	r	+	r	r	r	r	r	−	−	1	1	1
Tabebuia stenocalyx	−	−	−	r	r	−	−	−	−	−	−	−	−	+	1
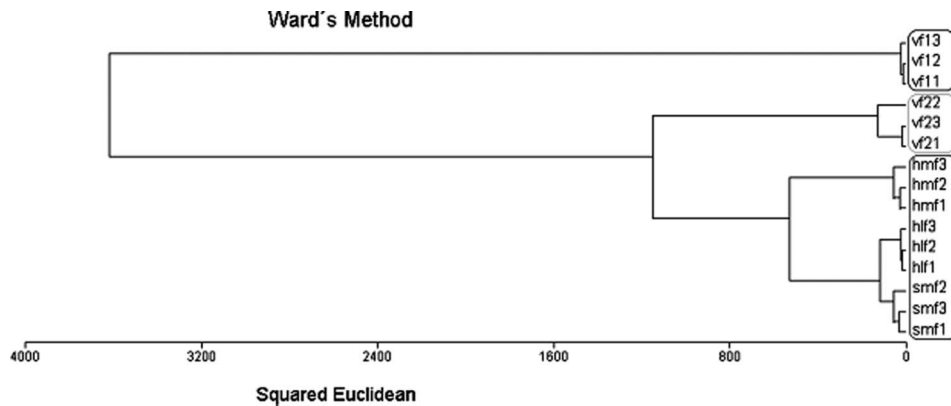
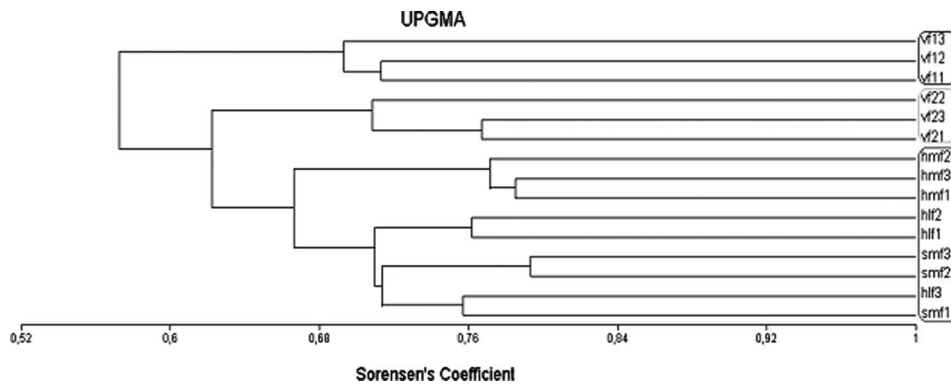Figure 4. Conglomerates' analysis using the Ward method.

Figure 5. Conglomerates' analysis using the UPGMA method.

(between 7 and 12 m) is dominated by small trees of *Paypayrola longifolia* Tul., *Mabea piriri* Aubl., and *Duguetia pycnastera* Sandwith.

Liana Forest. When considering the physiographic position and the structure of the forest, this community corresponds to a Hillside Low Forest (hlf).
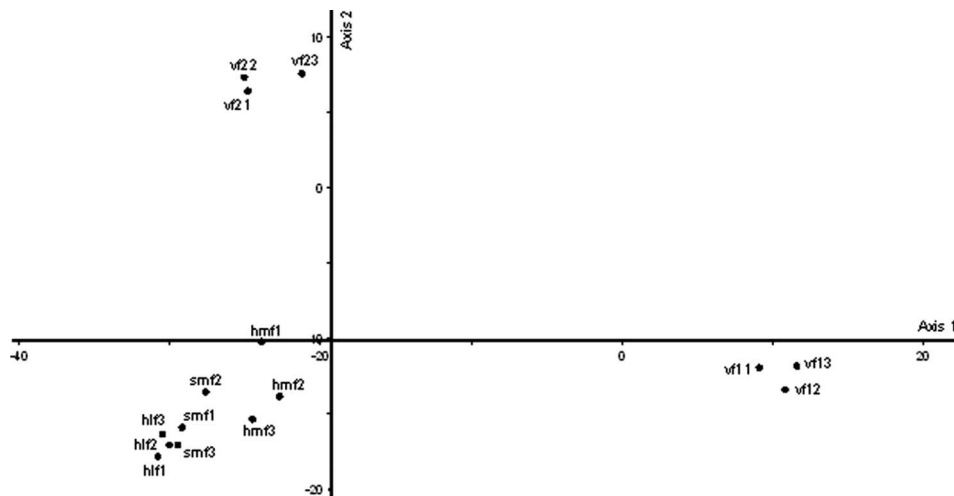
Figure 6. Ordering of the structural plots, according to the principal components analysis.

It possesses a canopy inferior to 15 m height, with some emergent individuals that get to 25 m height. However, from the floristic point of view, this community is equivalent to the summit and hillside forests described above (*A. imperatricis* Forest). In their inferior strata, the Liana Forest is dominated by climbers in a very striking way. Besides their great abundance, these individuals are very gnarled, and they constitute a huge part of the forest covering.

M. excelsa Forest. This forest is a medium forest (canopy between 15 and 25 m), dominated by *M. excelsa*. This species has its optimum in strait valleys and in the low zone of some hills (with very soft slopes), and then goes diminishing toward the highest parts. *C. guianensis* and *Pterocarpus officinalis* Jacq. possess trees of great size that share the canopy with *M. excelsa*. In the intermediate strata, the most important species are *Brownea latifolia* Jacq. and *Inga myriantha* Poepp. that present trees of medium size.

A peculiar aspect of this community is that the understory is quite homogeneous. It is considered that there are not very favorable conditions for the establishment of other species, due to the abundant regeneration of *M. excelsa* and due to the thick layer of fallen leaves of this species that impedes other seeds to get to the floor and germinate. But, there is a considerable quantity of *Adiantum petiolatum* Desv. This little fern is also seen in other plots, but with low abundance. Therefore, it seems to be very well adapted to the unusual conditions of this forest.

C. commune Forest. It is a medium forest (canopy between 15 and 25 m) that occupies wide valleys with very little slope. In the canopy, *C. commune* is accompanied by *C. guianensis* and *E. chartacea* that are characteristic in the whole vegetation unit. It was also considered convenient to include *P. officinalis*-like

differential species in this forest, although it has the same phytosociological index in the *M. excelsa* Forest, due to their high regeneration values in this sector.

The intermediate and inferior strata are quite heterogeneous, but stand out the presence of *Euterpe oleracea* Mart. This palm is frequent in the whole study area, but it has its optimum in these valley sectors. In the understory, the presence of herbs such as *Calathea* spp. is very conspicuous. Besides having very high abundance, it possesses a great covering that should represent a strong competition for the regeneration establishment of other species.

Discussion

It is difficult to make comparisons between this work and other studies. This is due to the lack of phytosociological research in the neotropics, mentioned at the beginning of this article, which is scarcer in the Guayana shield. However, some comments can be made.

The work of Fanshawe (1952) in British Guiana has similarities with our findings related to some communities dominated by characteristic species, such as: *P. macroloba* Community in marsh forests, *C. guianensis* Facies in marsh and swamp forests, *A. imperatricis* Faciation in rain forests, and *M. excelsa* Consociation in swamp forests.

There are profuse reports about forests dominated by some species mentioned in this research: *P. macroloba* (Webb & Peralta 1998; McKenna & McKenna 2006), *C. guianensis* (Klimas et al. 2007), *A. imperatricis* (Huber 1995; Dezzeo & Briceño 1997; ter Steege & Zondervan 2000), and *M. excelsa* (Beard 1946; Finol 1992; ter Steege 1994; Oatham & Jodhan 2002; Huber 2005).

Related to *C. commune*, there are references about its high abundance in Guianan forests (ter Steege

et al. 2002; Arets 2005), but there are no cites on forests dominated by this species.

Regarding Liana Forests, there are no current evidences, but it is believed that this community is linked to a very strong wind that destroyed most of the forest covering, similar to the cases reported by Webb (1958), Rollet (1971), and Allen et al. (2005). There are relict emergent individuals from the original forest; therefore, it should not have environmental limitations for the trees' development at a great height. The low canopy (15 m) should be the expression of a contemporary mass that was developed after the interference.

Based on the results presented here, we conclude that our work has allowed to identify a great vegetation unit where the species *P. macroloba* and *C. guianensis* are characteristic-dominant. In position of summit and hillside, there is an *A. imperatricis* Forest. A valley type exists where a *C. commune* Forest is present, and there is another valley with a *M. excelsa* Forest. A superior understanding of these ecosystems was possible by combining the Organismic and the Continuous approaches. In addition, it is necessary to highlight the understory survey as a tool to make better ecosystems' studies.

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