



## A new hypothesis on humid and dry tropical forests succession Una nueva hipótesis sobre la sucesión de los bosques tropicales húmedos y secos

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### ABSTRACT

In this paper 221 forest trees are grouped according to their habitat preferences into species preferring humid or dry and/or saline habitats or indifferent to the habitat type. Eleven functional traits classes (seeds per tree, seed size, seed weight, seeds per fruit, tolerance to shade, selectivity to habitat, sclerophylly, wood density, foliar area, tree height and tree volume) are arranged 1 to 4 according to a successional gradient. The strategies of forest trees are identified by analyzing the species matrices for humid forest ecosystems (joining species preferring humid habitats together with those indifferent to the habitat type) and for dry and/or saline ecosystems (joining species preferring dry and/or saline habitats and the ones indifferent to the habitat type). Both matrices are processed using the average taxonomic distance as the interval coefficient and by clustering analysis to discover successional organization patterns. The complexity of *r-K* continuum is discussed by focusing the *K* behavior of some variables among Pioneers (commonly *r* strategists) or the *r* behavior of some variables among Stabilizers (commonly *K* strategists). A new system of classification is presented as a hypothesis for discovering successional patterns in tropical forests.

### RESUMEN

En el presente artículo agrupamos 221 especies forestales sobre la base de sus preferencias por tipos de hábitat húmedo o seco y/o salino, considerando aparte aquellas que son indiferentes al tipo de hábitat. El sistema de clasificación se sustentó en el empleo de clases de 11 variables funcionales (semillas por árbol, tamaño de las semillas, peso de las semillas, semillas por fruto, tolerancia a la sombra, selectividad al hábitat, esclerofilia, densidad de la madera, área foliar, altura del árbol y volumen del árbol) ordenadas de 1 a 4 de acuerdo con un gradiente sucesional. Las estrategias de las especies arbóreas se identificaron mediante el análisis de las matrices para ecosistemas forestales húmedos (uniendo las especies que prefieren hábitat húmedo con las que son indiferentes al tipo de hábitat) y para ecosistemas secos y/o salinos (uniendo las especies que prefieren hábitat seco y/o salino con las que son indiferentes al tipo de hábitat). Ambas matrices fueron procesadas mediante el uso del coeficiente de distancia taxonómica promedio y por análisis de clasificación para descubrir los patrones de organización sucesional. Se discutieron la complejidad del continuum *r-K* exponiendo el comportamiento *K* de algunas variables entre las Pioneras (que comúnmente son estrategias *r*) y el comportamiento *r* de algunas variables entre las Estabilizadoras (que comúnmente son estrategias *K*). Presentamos el nuevo sistema de clasificación como una hipótesis para descubrir los patrones sucesionales en bosques tropicales.

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## INTRODUCCIÓN

Secondary succession, the change in ecosystem over time following disturbance, is one of the most universal and repeatable of ecological phenomena. In tropical forests, for example, one group of tree species is successful in colonizing recently cleared lands and these species are subsequently replaced by other tree species as the forest matures. Identifying the successional strategy of individual species can be very useful in understanding their response to disturbance and, as a result, extensive efforts have been put into classifying tropical forest tree species into successional strategies, as reviewed by Clark and Clark (1987) and Marquez *et al.* (1990). Most of this work has focused on the humid tropical forest (mostly rain forest) species. General classification schemes are rather scarce in literature. For example, Kageyama and Viana (1989) considered four groups of successional strategies naming them Pioneers, Opportunists, Shade Tolerants and Shade Reproducers. Marquez *et al.* (1990) proposed three groups: Pioneers, Opportunists and Climax. In Cuba, Herrera *et al.* (1988) classified tropical trees in three groups of ecological functioning known as Secondary, Intermediate (or repairing) and Primary species. Subsequently, Torres-Arias *et al.* (1990) and Herrera *et al.* (1991) proposed the functional existence of four big groups (Pioneers, Colonizers, Stabilizers and Stragglers).

These general classification schemes often focus on the extreme tendencies of the *r-K* continuum originally proposed by MacArthur and Wilson (1967), i.e., the reproductive edge (*r*-strategists) and the vegetative one (*K*-strategists). These two major strategy tendencies, *r* and *K*, have made useful contributions to our understanding of the spatial and temporal successional events occurring in forested communities at the ecosystem level (Pielou, 1965; Margalef, 1991; Silvertown *et al.*, 1993). At most, authors have considered one or two, rarely more, successional strategies being intermediate between the *r* and *K* edges of this continuum.

Two approaches have successfully delineated a greater number of groups of species. Hubbell and

Foster (1990) classified 60 tree species into 16 potential functional groups based on their spatial distribution on Barro Colorado Island. These authors used species distribution as characterized by the availability of water, topography, and sunshine exposition. An alternative approach is to focus on aspects of plant morphology. This method has been found to be useful within grasslands of Spain by Gómez-Sal *et al.* (1986), who clustered 52 species into twelve successional strategies based on 39 reproductive, vegetative and ecological variables using multivariate analysis. To our knowledge, a similar multivariate analysis of successional strategies in tropical forest tree species has not been attempted.

In this paper, the classification of 221 tropical forest species into successional strategies is presented based on multivariate clustering analysis of several morphologic and functional characteristics. Species that occur in humid, and dry and/or saline environments are included, but these two groups are analyzed separately. A summary of this analysis has been previously published in Herrera *et al.* (1997). In this paper, the whole classification is fully presented and discussed.

## MATERIALS AND METHODS

### Criteria for the classification of successional strategies

Most of the 221 forest tree species selected for the present study grows naturally in the Neotropics. However, we include several introduced tree species that have been used for fruit production or reforestation in Latin America. With the exception of three species, adults of all species can be found in Cuba, with vouchers located at the *Herbario Nacional de la Academia de Ciencias de Cuba*. *Heliocarpus americanus*, *Anacardium excelsum* and *Decussocarpus rospigliosii* do not occur in Cuba; however, we have studied these species in Mexico or Venezuela.

We have grouped tree species into three key habitat preferences based on their ecological distributions (Appendix I): trees preferring humid habitats (HH), trees preferring dry and/or saline habitats (DSH) or trees being indifferent to the habitat type (IH).

However, these preferences do not reflect restrictions of the species to a particular ecosystem or habitat, as discussed below.

We elucidate successional strategies for two ecosystem types. The first type refers to humid tropical forest ecosystems (HFE) including wet and humid tropical forests, i.e., those forest formations growing on reasonably deep soils, regardless of whether they are oligotrophic or eutrophic systems. Evergreen trees dominate these ecosystems, with less than 30% of tree individuals being deciduous during the drier season. Such locations commonly receive more than 1500 mm annual rainfall, and/or are relatively protected against desiccation. This protection is provided by a high frequency of cloud cover, a high proximity to the water table and/or to water streams, and appropriate sunshine expositions (not directly exposed), or topographic conditions (concave slopes, valleys, etc.). In HFE, forest trees usually reach 15 to 25 m and higher logs may be often found when environment (most humid or nutrient rich topographies or territories) favor their occurrence. This last is particularly common or even general (forests showing trees commonly reaching or surpassing 30 m height) for wet tropical forests or rainforests.

The second type refers either to drier sites, generally with less than 1500 mm annual rainfall and highly influenced by seasonally dry periods (lasting three or more months), or humid to seasonally or permanently flooded sites with high levels of salinity. We will refer to this grouping as dry and/or saline ecosystems (DSE). These locations are influenced by climatic or soil drought and may include sites with a high annual rainfall but reduced water holding capacity (stony substrates, bare shallow soils, extremely exposed topographies, etc.). Semi-deciduous to deciduous forests – both being considered in literature as seasonally dry tropical or simply as tropical dry forests – can be grouped under DSE. A large amount of DSH species are tropical dry forest dwellers. In addition, DSH species commonly thrive at subcoastal to coastal vegetation (on stony or sandy soils), tropical savannas – being subjected to seasonal climatic drought –, xeromorphic spiny or sub spiny shrublands, e.g., Cuban *cuabales* (coastal,

sub-coastal or inland ultramaphic plant communities), or dwarf forests, e.g., Cuban *charrascales* (inland ultramaphic plant communities growing up to 1250 m a.s.l.), and inland spiny or subspiny dry shrublands growing on stony and sandy barrens, e.g., Venezuelan *cardonales*. Mangroves, sand dunes and other coastal plant formations with high salinity usually are dominated by DSH preferring tree species. In DSE, trees commonly reach 5 to 15 m and are rarely higher than 20 m. However, trees in drier or oligotrophic ecosystems (savannas, mangroves, etc.) might be even smaller than 5 m high and might be considered as shrubs. However, several examples of tropical dry forests with trees larger than 25 m can also be found in the Neotropics, particularly those on volcanic soils, and wide pre-mountain valleys.

### Identification and assessment of plant characters

Because our overall goal was to categorize species according to their successional strategy, plant characters that varied across tree species of early to late successional stages were compiled (Table 1). These data were obtained from the literature (León, 1946; León and Alain, 1951, 1953, 1957; Alain, 1964, 1974; Fors, 1965; Roig, 1975; Anonymous, 1983; Mahecha and Echeverri, 1983; National Research Council, 1984; Hoyos, 1987, 1990; Ricardi *et al.*, 1987; Bisse, 1988; Niembro, 1988; Gentry, 1993; Puig, 1993) or based on our own (or our collaborators') taxonomic or field experience.

Variables for the analysis were selected based on 1) our confidence in assessing their categorization, 2) the level of variability of each among tree species, and 3) our ability to arrange the characters into a successional sequence. As a result, eleven reproductive and vegetative variables (i.e., functional traits) were selected.

The level of each plant character was delineated into one of four categories ranging from the early successional extreme (1) to the late successional extreme (4) (see Table 1 for numerical ranges under each category). For example, in the case of seed size, we assigned a low score to early-successional species (e.g., those with small seed size) and a high score to late-successional species (e.g., those with

**Table 1.** Qualification of variables. The categories 1 to 4 follows a successional arrangement: For variables SSZ, SWE, TOL, SHA, SCL, and DEN, the weight of values 1 to 4 increase towards 4 (arrowheads down) being concomitant with the successional arrangement, while for the variables STR, SFR, AFA, HEI and VOL, the weight of values 1 to 4 decrease towards 4 (arrowheads up) being then contrary to the successional arrangement.

Variables	Code	Value	Description of Categories for Qualification
SEEDS PER TREE	STR	1	Commonly, more than 20 000: Type <i>Cecropia</i> spp. Often from 2 000 to 20 000: Type <i>Swietenia</i> spp. Approximately, from 500 to 2 000: Type <i>Brosimum</i> spp. Often less than 500: Type <i>Pouteria</i> spp.
		2	
		3 ▲	
		4	
SEEDS SIZE	SSZ	1	Smaller than 2.0 mm From 2.1 to 5.0 mm From 5.1 to 10.0 mm Larger than 10.1 mm
		2	
		3 ▼	
		4	
SEEDS WEIGHT (air dried seeds)	SWE	1	Less than 20.0 mg From 20.1 to 200.0 mg From 200.1 to 2 000.0 mg More than 2 000.1 mg
		2	
		3 ▼	
		4	
SEEDS PER FRUIT	SFR	1	More than 101 From 11 to 100 From 2 to 10 Commonly 1, rarely 2 or 3
		2	
		3 ▲	
		4	
TOLERANCE TO SHADE, HELIO- AND SCIADOPHILY	TOL	1	Intolerant to shadow Facultative semitolerant to shadow Semitolerant to shadow Tolerant to shadow
		2	
		3 ▼	
		4	
SELECTIVITY TO HABITAT (frequency of occurrence of individuals)	SHA	1	Abundant and low selective with respect to plant formation. Frequent, though restricted to a particular plant formation. Relatively scarce, restricted frequency inside the plant formation. Rare, difficult to be found inside the plant formation, highly selective.
		2	
		3 ▼	
		4	
SCLEROPHYLLY (leaves dry weight : fresh weight ratio)	SCL	1	Lower than 0.300 (SUBSCLEROPHYLLOUS) From 0.301 to 0.380 (MESOSCLEROPHYLLOUS) From 0.381 to 0.450 (SCLEROPHYLLOUS) Higher than 0.451 (EUSCLEROPHYLLOUS)
		2	
		3 ▼	
		4	
WOOD DENSITY (in kg.m <sup>-3</sup> )	DEN	1	Less than 600 From 601 to 800 From 801 to 1 000 More than 1 001
		2	
		3 ▼	
		4	
APPROXIMATED FOLIAR AREA	AFA	1	Larger than 140.1 cm <sup>2</sup> (MEGAFOLIACEOUS) From 60.1 to 140.0 cm <sup>2</sup> (MACROFOLIACEOUS) From 20.1 to 60.0 cm <sup>2</sup> (HEMIFOLIACEOUS) Smaller than 20.0 cm <sup>2</sup> (MICROFOLIACEOUS)
		2	
		3 ▲	
		4	
COMMONLY REACHED MAXIMUM TREE HEIGHT	HEI	1	Higher than 25 m (very high tree) From 16 to 24 m (high tree) From 11 to 15 m (middle height tree) Smaller than 10 m (small tree)
		2	
		3 ▲	
		4	
COMMONLY REACHED MAXIMUM TREE VOLUME	VOL	1	Larger than 10.1 m <sup>3</sup> (very large volume tree) From 2.6 to 10.0 m <sup>3</sup> (large volume tree) From 0.6 to 2.5 m <sup>3</sup> (middle volume tree) Smaller than 0.5 m <sup>3</sup> (small volume tree)
		2	
		3 ▲	
		4	

with small seed size) and a high score to late-successional species (e.g., those with large seed size). Thus, our approach is circular (much like the ordering of character states in cladistic analysis) in that we are using our observations of successional status of trees to order the variables that are then used to group species into successional strategies. Similarly, natural history observations are used to delineate ranges of four categories for continuous variables. For example, early successional the leaf area has a broad range while it rapidly decreases for categories 2 to 4 (Appendix II-A, see Figure II-1). For the description of the selected variables see Appendix II-B. Acronyms for the 11 variables are: STR, seeds per tree; SSZ, seed size, SWE, seed weight, SFR, seeds per fruit; TOL, tolerance to shade; SHA, selectivity to habitat; SCL, sclerophylly; DEN, wood density; AFA, approximated foliar area; HEI, tree height and VOL, tree volume.

#### Identification of successional strategies

A multivariate classification based on successional strategies of tree species was carried out separately for HFE (160 species, joining HH and IH groups) and DSE (148 species, joining DSH and IH groups). We considered our scores for each variable (1 to 4) as multistage quantitative data with logical sequence (Crisci and López, 1983; Rohlf, 1993).

We analyzed HFE and DSE contingency matrices with clustering analysis using the program NTSYSpc Version 2.10j (Rohlf, 1993). This software allows the application of numerous options to find the best clustering analysis. In addition, cophenetic correlations (*CR*) were estimated to compare clustered results from each matrix. The cophenetic correlation evaluates the similarity between the distance values in the dendrogram resulting from a clustering analysis and the observed distances in the original data matrix. Ultimately, we identified the following steps as producing the highest *CR* values. Data were first log transformed ( $\log x$ ), then standardized by the mean and the average taxonomic distance was calculated using the unweighted pair-group method, arithmetic average (the UPGMA method) for the sequential, agglomerative, hierarchical and nested (SAHN) clustering. For each run, the single best tree was

identified using the option FIND. The pivots of the dendrograms were rotated as necessary to improve the presentation of the results.

While most of the measured variables could be quantified continuously, our opinion is that this categorical approach had several strengths. First, in all clustering analysis, the numerical range of each variable influences the outcome. Therefore, the importance of each character within the analysis is scale-dependent. By scoring all plant characters on the same 1-4 scale, no greater weight is given *a priori* to any character. Secondly, the qualitative nature of the 1-4 score allows us to break the continuous variables into successional relevant categories. For some characters, these categories are roughly log-scale (e.g., STR and SWE, Table 1), while for others they can be roughly linear (e.g., DEN and HEI, Table 1). Finally, for several characters (such as TOL) four categories represent accurately the available qualitative level of resolution. Moreover, for all the variables, this four-level approach allows inclusion of a larger number of tree species than that possible if a more precise measure were used.

That the log transformation of a 1 – 4 sequence improved the *CR* values initially struck us as odd. However, in retrospect, the value of this transformation likely results from the biological differences inherent to our scoring system. That is, for most of our variables there is a large difference between the typical character level of early successional species (i.e., a character scored as 1) and the character level scored as 2. For example, in AFA, as depicted in Appendix II-A (see Figure II-1), leaf and leaflets areas were very large for early successional species, and much smaller for plants in the mid to late successional stages. There is, in fact, a larger biological difference between the states identified as 1 and 2 than between the states identified as 3 and 4. The log transformation of the 1 – 4 rank substantially reduces the interval between the 3 and 4 ranks in relation to the interval between the 1 and 2 ranks. Hence, we think that the improved *CR* values for log-transformed ranks resulted from real differences in the underlying biology, rather than from statistical issues.

### Functional characterization of successional strategies

Once the dendrograms for HFE or DSE were obtained, polygrams (radar graphs) were designed to explain strategies functioning under each successional order. An additional argument to search for statistical significance of strategies identification and significance was measuring the polygrams areas as a percentage of the maximal theoretical area (all values for 11 variables matching 4). This area is to be called the Strategy *K* Area (SKA), i.e., the measure of the strategy as a percentage of the maximal theoretical area in the radar graph. The maximal theoretical area corresponds to the maximal *K*-strategist. While a maximal *K*-strategist may not be observed in nature, measuring the strategies as a proportion of the maximal strategy provides a means of comparing sites within a successional sequence, as well as different ecosystem types. We estimate the Strategy *K* area (SKA) with the equation:

$$SKA = \frac{\sum_{i=1}^{10} (\text{Var}_i * \text{Var}_{i+1}) + (\text{Var}_{11} * \text{Var}_1)}{(\text{MVA})^2 * \text{Nr.Vars.}}$$

Where, Var (*i* to *i*+1, 11 or 1) refer to values 1 – 4 for each of 11 variables; MVA refers to the maximal value for the axis, i.e., 4, and Nr.Vars refers to the total number of variables (i.e., 11).

Finally, regression analysis was used to relate the strategy *K* areas for different strategies to the rank order of the successional strategies for HFE and DSE separately.

### Characterization of successional functioning at the community level

Once the dendrograms are obtained for HFE and DSE, the consecutive enumeration of final successional strategies' groups (last order of successional organization) give the possibility of quantifying successional position. We rank order these successional positions (with the earliest successional category receiving rank 1) and call these quantifications Successional Numbers (SNs).

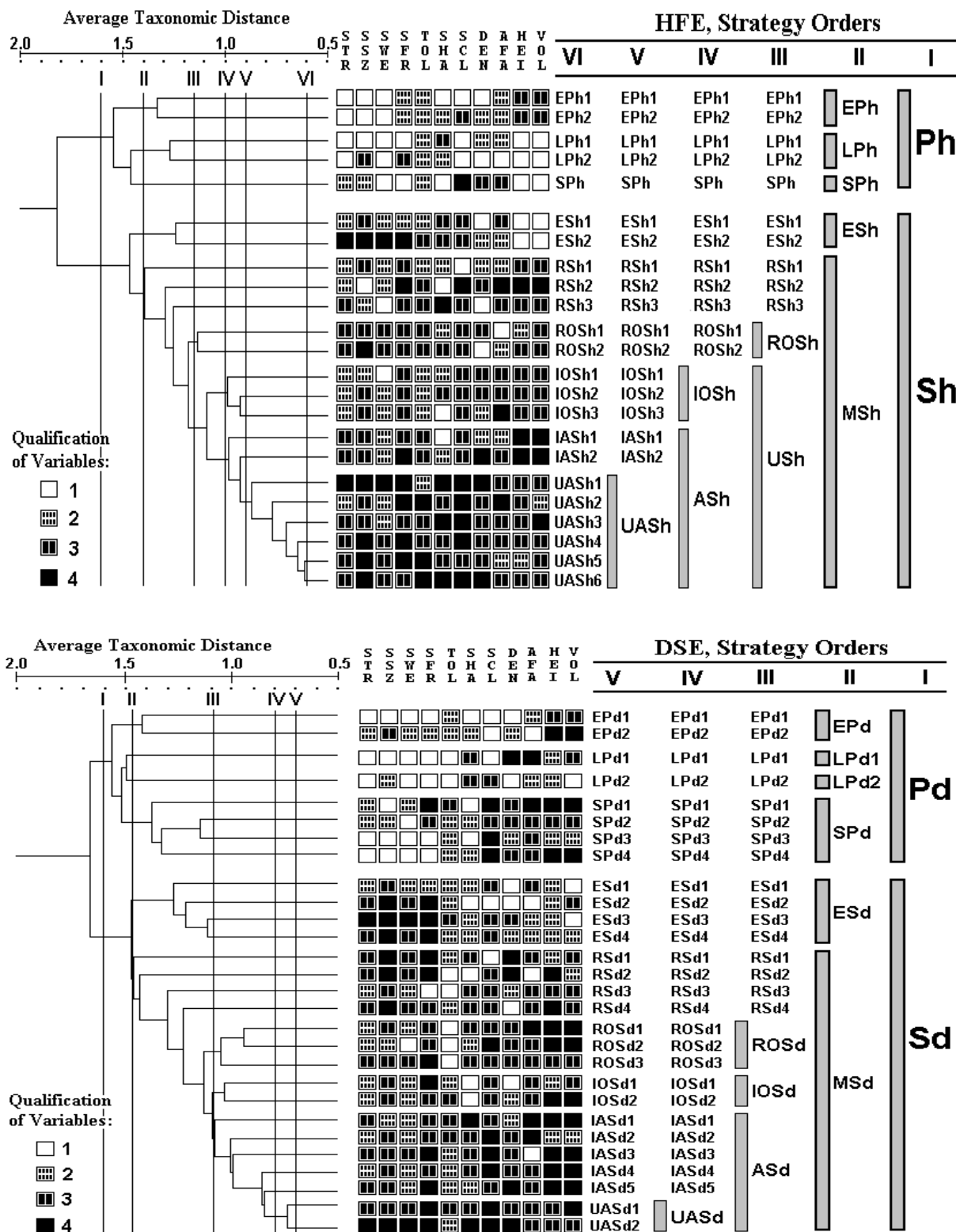
For a particular forest community, screening of individual tree heights and breath height diameters can be measured and their volumes estimated (see above), grouped and added for each species. Subsequently, the species volume proportion with respect to the plot total can be estimated and multiplied by its corresponding SN value. Adding all the products (species proportion in the plot x SN) for the plot and dividing by 100 give a figure here to be considered as Ceno-successional index (CSI) allowing the observer to quantify the average successional stage of a particular forest plot. Appendixes III-A and III-B illustrate how the CSI values of different ecosystems can be estimated for a forest plot belonging to HFE and DSE, respectively.

Once the forest plot species volume proportions are obtained, and the strategies order is chosen (the user is free to choose the successional order considered appropriate, given the previously obtained phenogram) species proportions in the plot are summed according to their similar strategy. Subsequently, the proportion of different strategies' volumes in the plot can be multiplied by the average category for each of the 11 variables previously estimated as rounded average for each strategy. Subsequently, the products corresponding to each variable are separately added and divided by 100 rendering (rounded numbers) the qualification (1 to 4) of each variable for the studied plot. Finally, as for determining SKA values, a similar approach and equation is used here to determine the ecosystems *K*-Strategist areas (EKSA). Appendixes III-A and III-B illustrate how EKSA values can be estimated for a forest plot belonging to HFE and DSE respectively. In addition, once the 11 variables are quantified for a given forest plot, the ecosystems polygrams can be designed to describe their successional functioning.

## RESULTS

### Arrangement of successional strategies for HFE and DSE

The dendrograms for humid forest and dry and/or saline ecosystems are presented in [Figure 1](#). In all cases, the option FIND during clustering process produced a single optimal dendrogram of the



**Fig. 1.** Tree species strategies in humid tropical forest ecosystems (HFE, above) and dry or saline ecosystems (DSE, below). Order I strategies are Pioneers (P) and Stabilizers (S), “h” and “d” refers to HFE or DSE, respectively. From order II in advance, the strategies names are: Early (EP), Late (LP) and Sclerophyllous (SP) Pioneers, Exuberant (ES), Major (MS), Restoring (RS), Restoring Opportunist (ROS), Ultimate (US), Invasive Opportunist (IOS), Austere (AS), Invasive Austere (IAS) and Ultimate Austere (UAS) Stabilizers. Functional traits: STR (seeds per tree), SSZ (seed size), SWE (seed weight), SFR (seeds per fruit), TOL (tolerance to shade), SHA (selectivity to habitat), SCL (sclerophylly), DEN (wood density) AFA (approximated foliar area), HEI (tree height) and VOL (tree volume). Species belonging to HFE Order VI and DSE Order V strategies are listed in Appendix IV.

analyzed species. This means that there was a single best clustering arrangement for the variables and species in HFE and DSE, thereby showing the strength of the results due to the absence of ambiguities from equivalent dendrograms, and eliminating the necessity of consensus trees. Cophenetic correlations for HFE and DSE clustered dendrograms were 0.90 and 0.82, and 0.90 and 0.72, for variables and species, respectively.

For convenience in dealing with strategies, we have developed a hierarchical classification system. The system is based on the identification of six Strategy Orders, named I to VI for HFE (Fig. 1) and five Strategy Orders, named I to V for DSE (Fig. 1). The defined Strategy Orders depend on different progressive levels of cutting for each tree defining a gradient that gradually increases affinities between groups. Consequently, in both figures, and from Order II on, some strategies remain as single indivisible and some others are still divisible when the next order is to be considered. Orders I to VI in HFE are represented by 2 (both divisible), 5 (4 divisible), 12 (2 divisible), 14 (2 divisible), 18 (1 divisible) and 23 final strategies, respectively. On the other hand, Orders I to V in DSE are represented by 2 (both divisible), 6 (4 divisible), 19 (3 divisible), 27 (1 divisible), and 28 final strategies, respectively. Appendix IV lists the species composition for 23 strategies in HFE and 28 strategies in DSE, respectively.

Order I levels of cutting are similar for HFE and DSE dendrograms (Fig. 1). The deepest division in the cluster separates the two basic strategies coexisting under tropical forest ecosystems as proposed by Whitmore (1989). We refer to these two strategies as Pioneers and Stabilizers. This Order I classification follows the main division separating Pioneers from the remaining strategies, as observed at left in Figure 1.

Next level of separation, which we call Order II, gives 5 strategies for HFE and 6 for DSE (Fig. 1). The remaining Order II strategies – Early, Late and Sclerophyllous Pioneers, Exuberant Stabilizers and

Major Stabilizers occupy similar positions in both dendrograms. When observing Order II for HFE and DSE, Exuberants clearly separates from the remaining strategies, which, at this level, we have preferred to group under the name of Major Stabilizers.

Under Order III and next orders for HFE, Early Pioneers (EPH1 and 2), Late Pioneers (LPH1 and 2), Sclerophyllous Pioneers (SPH), Exuberant Stabilizers (ESH1 and 2), and Restoring Stabilizers (RSH1 to 3) separate as single strategies whereas Restoring Opportunist Stabilizers (ROSH) and Ultimate Stabilizers (USH) still remain as clustered strategies. Moreover, under Order III and next orders for DSE, Early Pioneers (EPH1 and 2), Sclerophyllous Pioneers (SPH1 to 4), Exuberant Stabilizers (ESH1 to 4), and Restoring Stabilizers (RSH1 to 4) separate as single strategies whereas Restoring Opportunist Stabilizers (ROSD), Invasive Opportunist Stabilizers (IOSd) and Austere Stabilizers (ASd) still remain as clustered strategies.

Under Order IV and next orders for HFE, Restoring Opportunists Stabilizers (ROSH) separate as single strategies (ROSH1 and 2) whereas Invasive Opportunist Stabilizers (IOSH) and Austere Stabilizers (ASH) still remain clustered. Under Order IV and next order for DSE, Restoring Opportunist Stabilizers (ROSD) separate as single strategies (ROSD1 to 3), Invasive Opportunist Stabilizers (IOSd) separate as single strategies IOSd1 and 2 and Invasive Austere Stabilizers (IASd1 to 5) occur as single strategies, only one cluster constituted by Ultimate Austere Stabilizers (UASd) remaining.

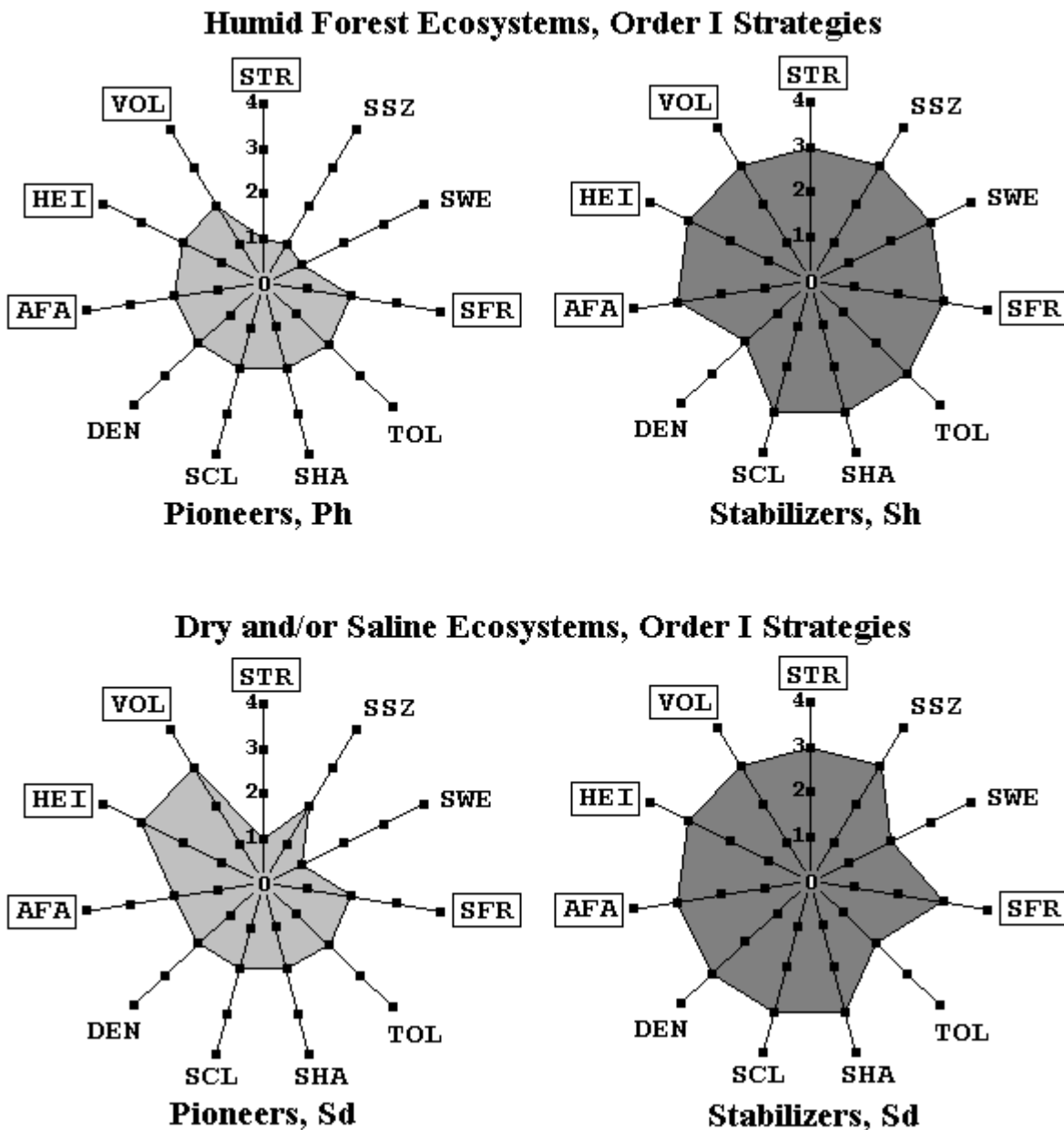
Under Order V and subsequent order for HFE Invasive Opportunist Stabilizers (IOSH1 to 3) separate as single strategies, and at the same time Ultimate Austere Stabilizers (UASH1 to 6) remain still as a clustered strategy. Finally, under Order VI, last for HFE, Ultimate Austere Stabilizers (UASH1 to 6) separate to complete a total of 23 strategies. However, Order V, for DSE is the last, and leads to a total of 28 single strategies.



**Analysis of successional strategies' polygrams for HFE and DSE**

A large amount characters are typical of early successional species (as represented by few shaded areas in Fig. 2) for early successional categories, while the opposite is true for late successional categories, both for HFE and DSE Order I. As observed in Figure 2 most of variables for HFE and DSE Pioneers average 2 (in the 1 to 4 scale). The

prevailing stress for DSE seems to favor smaller trees (HEI and VOL matching 3 in DSE vs. 2 in HFE) producing slightly larger seeds (SSZ matching 2 in DSE vs. 1 in HFE). Majority of characters for Stabilizers match 3, and tree species grouped under this strategy in humid ecosystems tend to produce less dense woods while in dry and/or saline ecosystems seeds tend to be less heavy and trees tend to be less tolerant to shade.

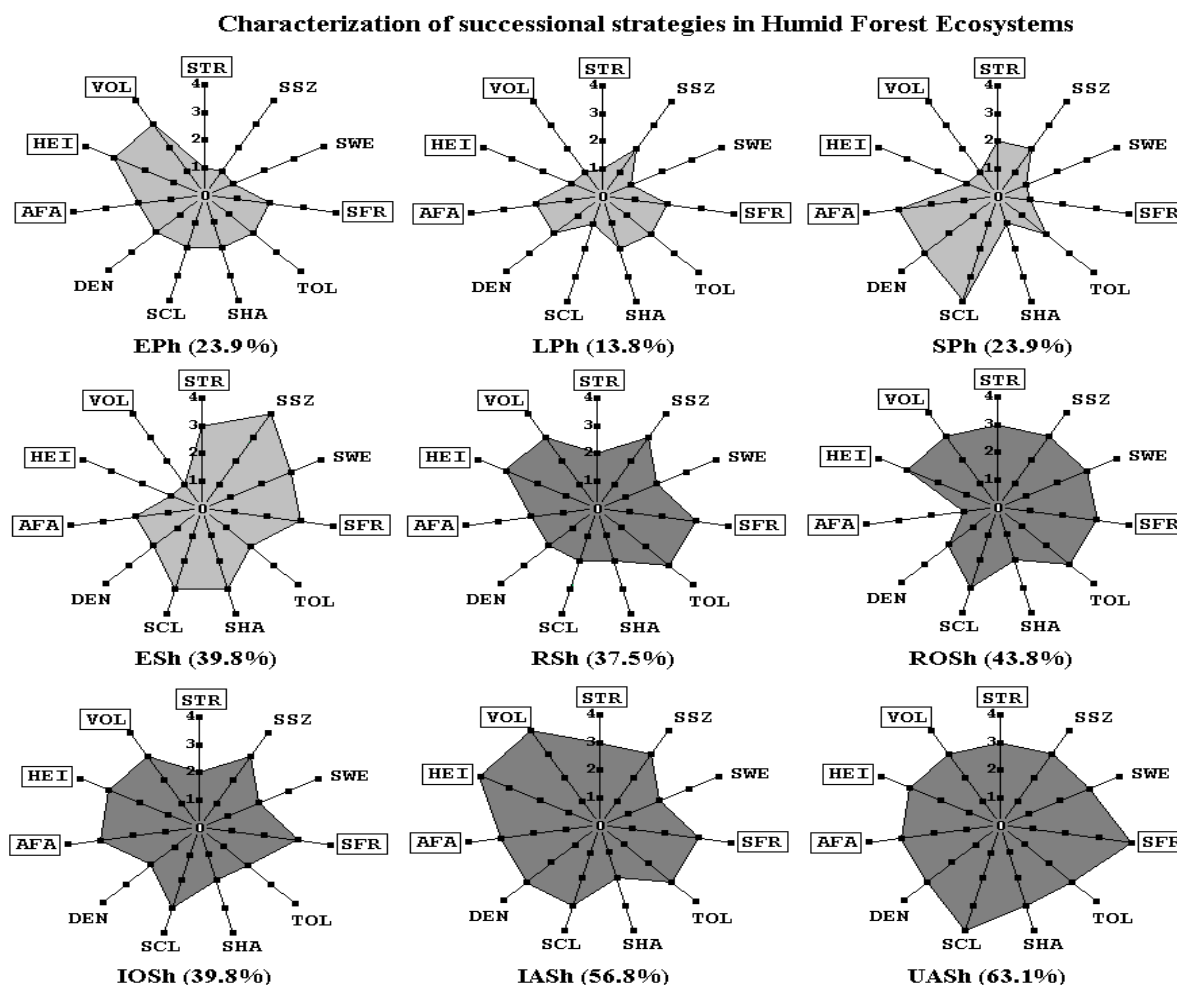


**Fig. 2.** Order I Successional Strategies polygrams for Humid Forest Ecosystems (HFE) and Dry or Saline Ecosystems (DSE). Description of variables see Figure 1.

The corresponding polygrams for HFE Orders II to VI and DSE Orders II to V are illustrated in Appendix V (see Figures V-1, V-2, V-3 and V-4). In this appendix, all the intermediate strategies can be examined to characterize them functionally. While users may choose the strategy Order that is appropriate for their purpose, we have preferred to use and discuss the higher Order strategies because they offer the greater resolution of successional behaviors.

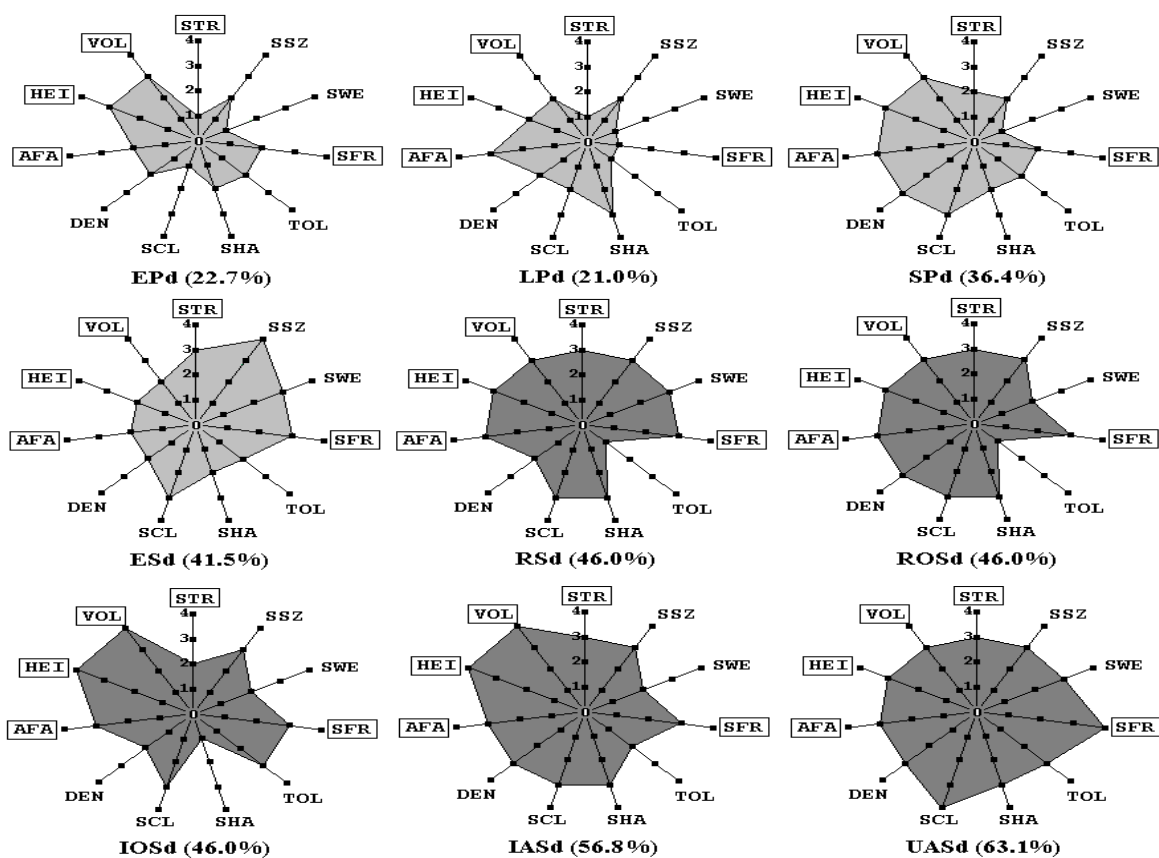
Therefore, we have chosen 9 strategies in accordance with their names and positions in the HFE and DSE dendrograms equivalent; although functionally they can be different (see below). These

strategies correspond to Order VI in HFE and Order V in DSE as follows: Early Pioneers (EP<sub>h</sub> and EP<sub>d</sub>), Late Pioneers (LP<sub>h</sub> and LP<sub>d</sub>), Sclerophyllous Pioneers (SP<sub>h</sub> and SP<sub>d</sub>), Exuberant Stabilizers (ES<sub>h</sub> and ES<sub>d</sub>), Restoring Stabilizers (RS<sub>h</sub> and RS<sub>d</sub>), Restoring Opportunist Stabilizers (ROSh and ROS<sub>d</sub>), Invasive Opportunist Stabilizers (IOS<sub>h</sub> and IOS<sub>d</sub>), Invasive Austere Stabilizers (IAS<sub>h</sub> and IAS<sub>d</sub>) and Ultimate Austere Stabilizers (UAS<sub>h</sub> and UAS<sub>d</sub>). Their polygrams are illustrated in Figure 3 and Figure 4. We note the similarity between Invasive Austeres and Ultimate Austeres both in HFE (Fig. 3) and DSE (Fig. 4) in spite of the changes of species composition in each case (see also Appendix IV).



**Fig. 3.** Polygrams for nine strategies summarizing Order VI in Humid Forest Ecosystems. In parenthesis Strategy *K* Area (SKA) values. Successional strategies: Early (EP), Late (LP) and Sclerophyllous (SP) Pioneers, Exuberant (ES), Restoring (RS), Restoring Opportunist (ROS), Invasive Opportunist (IOS), Invasive Austere (IAS) and Ultimate Austere (UAS). Description of variables see Figure 1.

## Characterization of successional strategies in Dry and/or Saline Ecosystems



**Fig. 4.** Polygrams for nine strategies summarizing Order V in Dry or Saline Ecosystems. In parenthesis Strategy *K* Area (SKA) values. For successional strategies see Figure 3.

When polygrams for the nine strategies in each ecosystem type are compared, it is noted that SKA values are larger in DSE for the strategies LP, SP, ES, RS, ROS and IOS (Fig. 5). On the other hand, the Figure 5 also shows that the proportions of species in using EP, IOS and UAS is greater in HFE than in DSE, while the proportion of species in SP, ROS and IAS is greater in DSE than in HFE.

Figure 6 demonstrates that both for HFE and for DSE, and from early to late successional, SKA values increase significantly. The results show that increasing of SKA values is generally corresponds to the *r*-*K* continuum of successional strategies.

However, the successional strategies do not all fall on a simple *r*-*K* continuum. Rather, the successional strategies vary in multiple dimensions. For example, early successional species can have some characters typical of *K*-strategists and late successional species can have some characters

typical of *r*-strategists. Figure 7 and Table 2 show the proportion of higher (3 and 4) values (*K* behavior) of characters among Pioneers and the proportion of lower (1 and 2) values (*r* behavior) of characters among Stabilizers. Ten to 50% of variables among Pioneers show high *K* values while 5 to 55% of variables among Stabilizers show low *r* ones. Among Pioneers the lowest *K* behavior (being more *r*-strategists) is shown by Late Pioneers in HFE, while the largest *K* behavior is shown by Sclerophyllous Pioneers in DSE. On the other hand, Exuberant, Restoring, and Invasive strategies show a high *r* behavior among Stabilizers, while the lowest *r* behavior is common for Ultimate Austeres, i.e., an extreme *K* behavior.

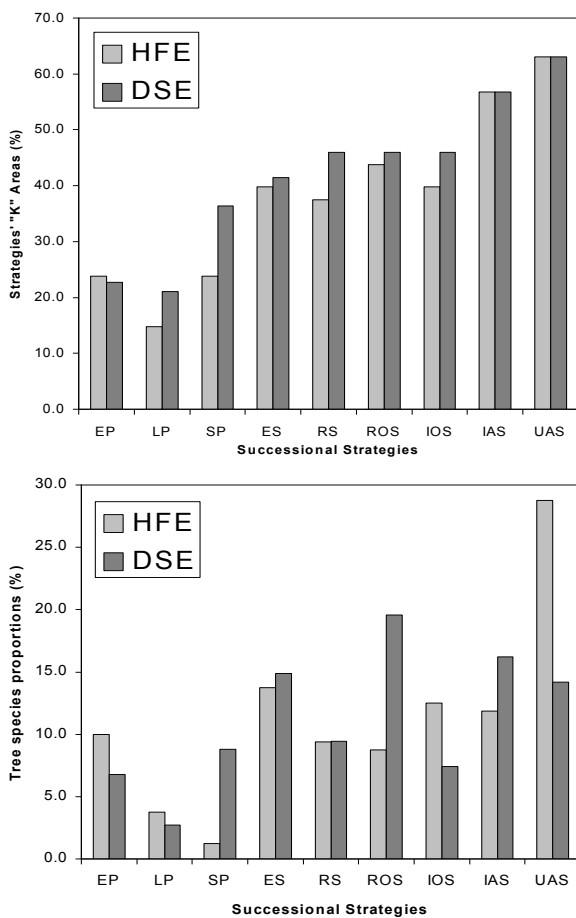
#### Functional shifts of IH species between HFE and DSE

Interestingly, some of the species that occur in both HFE and DSE change their successional strategy between environments. The species shifting

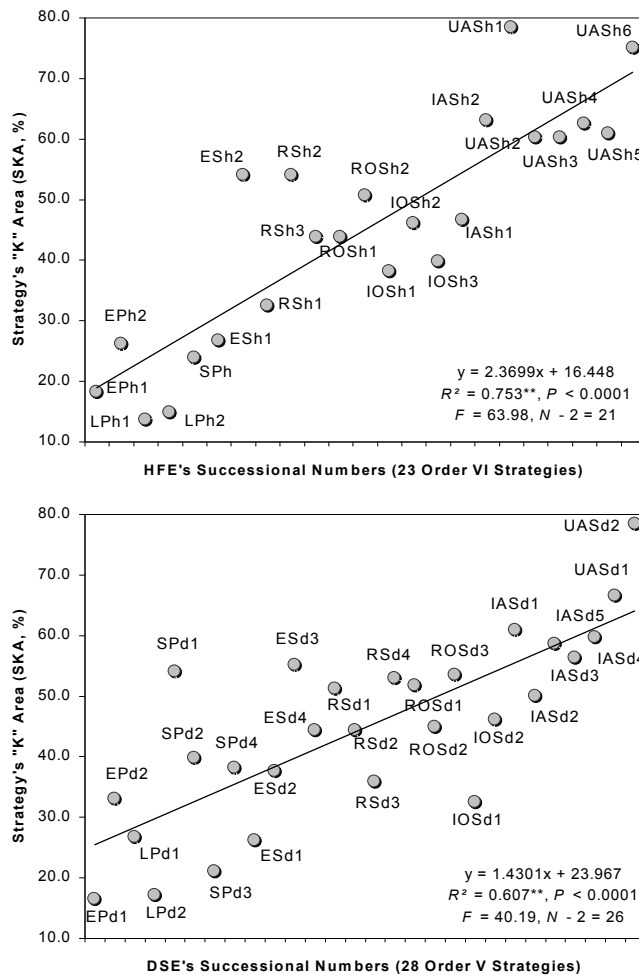
shifting strategies between environments are listed in Table 3. Some IH species advance their successional position (bolded and underlined) when in DSE compared with their grouping in HFE. However, other species can retard their position to occupy earlier successional strategies (normal letters).

**Application of the method to different forest communities at Sierra del Rosario**

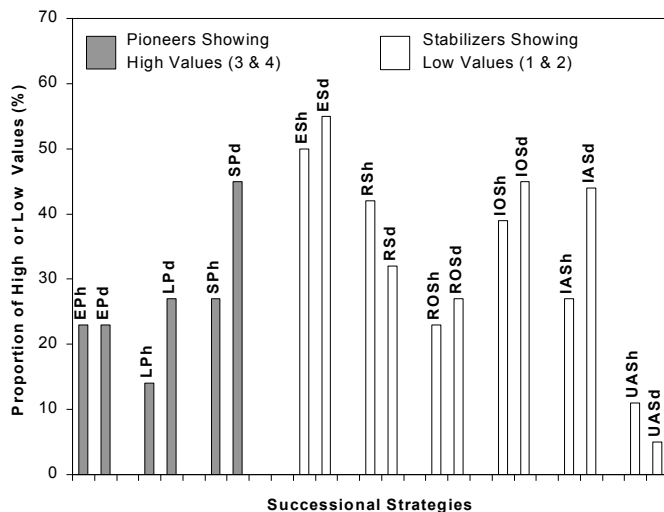
The procedures for the estimation of CSI and EKSA values is mentioned above (see Materials and Methods). On the other hand, Appendixes VI-A and VI-B show the tables resulting from the estimation of CSI values for 13 (4 real and 9 hypothetical) HFE forest plots and 3 hypothetical DSE plots.



**Fig. 5.** Comparison between nine strategies in Humid Forest Ecosystems (HFE) and Dry or Saline Ecosystems (DSE). Above, Strategy K Area (SKA) values, and below, sharing of species proportions among the nine chosen strategies.



**Fig. 6.** SKA (Strategy K Area) vs. SN (Successional Number) regression analysis for HFE Order VI (above) and DSE Order V (below) strategies.



**Fig. 7.** The *r*-*K* continuum expressed to show the proportion of variables that have *K* tendencies among Pioneers and *r* tendencies among Stabilizers.

**Table 2.** The *K* ability among Pioneers and the *r* ability among Stabilizers. Cells marked with “**X**” or “**XX**” refers to those Pioneer strategies (Order VI for HFE and Order V for DSE) where higher values (3 and 4 in the 1 to 4 scale) appears among less or more than 50% of strategies. Cells marked with “x” or “xx” refers to those Stabilizer strategies (Order VI for HFE and Order V for DSE) where lower values (1 and 2 in the 1 to 4 scale) appears among less or more than 50 % of strategies. Double marks, “**XX**” and “**xx**”, are considered as primary variables defining the strategy while simple marks “**X**” and “**x**” are considered as secondary. HFE strategies appear with “h” and DSE strategies appear with “d”.

Functional traits											
	STR	SSZ	SWE	SFR	TOL	SHA	SCL	DEN	AFA	HEI	VOL
EPh							<b>X</b>			<b>XX</b>	<b>XX</b>
EPd	<b>X</b>									<b>XX</b>	<b>XX</b>
LPh	<b>X</b>		<b>X</b>			<b>X</b>					
LPd					<b>XX</b>	<b>X</b>	<b>X</b>	<b>X</b>			<b>X</b>
SPh						<b>XX</b>	<b>XX</b>	<b>XX</b>			
SPd			<b>X</b>	<b>X</b>		<b>XX</b>	<b>XX</b>	<b>XX</b>	<b>XX</b>	<b>XX</b>	<b>XX</b>
ESh	x		x	x	x			xx	x	xx	xx
ESd	x		x	x	xx	xx	x	xx	xx	xx	xx
RSh	xx	xx	xx		x	xx	x	xx	x		
RSd	x		x	x	xx	x	x	x	x	x	x
ROSh						x		x	xx	x	
ROSd	xx	x	xx		xx	x					
IOSh	xx	x	xx		xx	xx		x			
IOSd	xx		xx		x	xx		xx		x	
IASh			xx		xx			x	x		
IASd	x	x	xx		xx			x	x	x	x
UASh	x		x		x	x			x		x
UASd					x						

The resulting polygrams for 13 HFE forest plots in *Sierra del Rosario* are shown in [Figure 8](#). Increasing gray tones from *Yagrumal Joven* and *Yagrumal* to *Cima Macagual* and *El Salón Sur* refer to the variation from early to late successional functioning. When [Figures 8](#) and [3](#) are compared, it is interesting to note that *Yagrumal Joven* and *Yagrumal* almost fit EPh, *Majagual* fits LPh, *Bosque Joven* fits UASh and *El Rubí Sur* almost fit IOSh. Therefore, the ecosystems functioning can be successional described and even named accordingly.

On the other hand, [Table 4](#) describes the successional composition of the forest plots studied in *Sierra del Rosario*. Among them, *Yagrumal Joven*, *Yagrumal* and *Majagual* are three early successional stage plots dominated by EP and LP while *Los Jagüeyes*, *Helechal*, *El Ébano*, *El Mulo Sur* and *Macurijal* constitute primary forest stages where favorable environmental conditions allow the

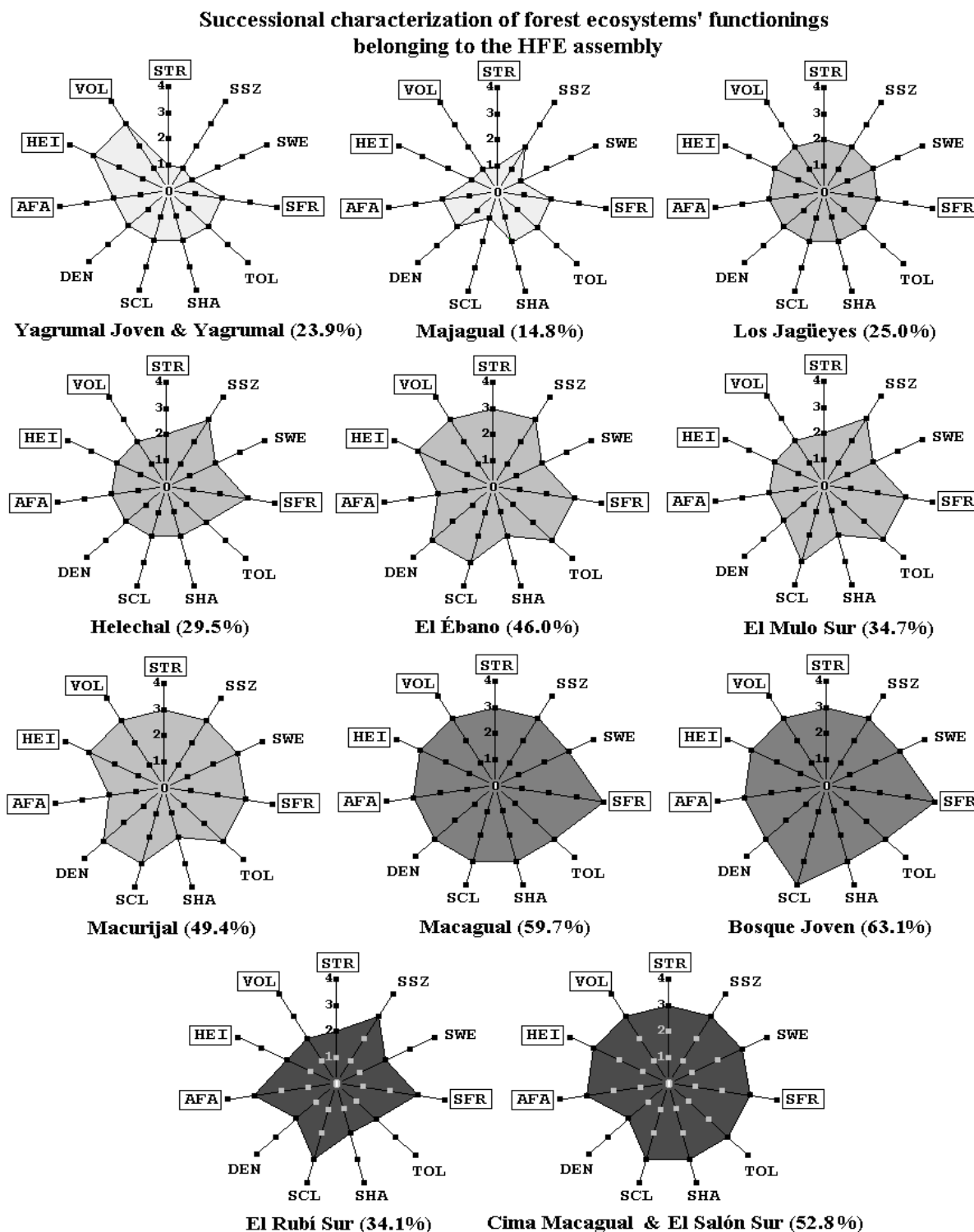
prevailing and successful development of early successional. The formerly mentioned 5 forest plots are evergreen communities fitting the tropical humid forest functioning as a variant of tropical dry forest where the water availability is larger. Appendix VI-A

**Table 3.** Shifts of IH (indifferent to the habitat type) species' from a strategic position in HFE (Appendix IV) to a new position in DSE (Appendix IV). Advancing shifts in DSE in bold and underlined, while other strategies in DSE show delaying shifts.

TREE SPECIES	SHIFTS OF STRATEGIES FROM HFE TO DSE	
	STRATEGY IN HFE	STRATEGY IN DSE
<i>Psidium guajava</i>	EPh2	<b><u>SPd2</u></b>
<i>Tetrazygia bicolor</i>	EPh2	<b><u>SPd2</u></b>
<i>Casuarina equisetifolia</i>	EPh2	<b><u>SPd3</u></b>
<i>Talipariti elatum</i>	LPh2	EPd1
<i>Zanthoxylum martinicense</i>	ESh1	SPd4
<i>Bauhinia monandra</i>	RSh1	EPd2
<i>Plumeria obtusa</i>	RSh1	EPd2
<i>Gmelina arborea</i>	RSh1	ESd2
<i>Cordia collococca</i>	RSh1	ESd4
<i>Eugenia foetida</i>	RSh2	SPd1
<i>Juniperus lucayana</i>	RSh3	<b><u>IASd1</u></b>
<i>Gettarda elliptica</i>	RSh3	<b><u>IASd1</u></b>
<i>Roystonea regia</i>	ROSh1	ESd4
<i>Tectona grandis</i>	ROSh1	ESd4
<i>Hura crepitans</i>	ROSh1	ESd4
<i>Persea americana</i>	ROSh2	ESd4
<i>Anacardium occidentale</i>	ROSh2	RSd4
<i>Annona muricata</i>	ROSh2	RSd4
<i>Maclura tinctoria</i>	IOSh1	SPd4
<i>Zuelania guidonia</i>	IOSh1	SPd4
<i>Cordia gerascanthus</i>	IOSh1	SPd4
<i>Cordia alliodora</i>	IOSh1	SPd4
<i>Clusia rosea</i>	IOSh1	SPd4
<i>Chrysophyllum cainito</i>	IOSh2	ESd4
<i>Calophyllum antillanum</i>	UASh4	ESd4

gives the major characteristics for the examined forest plots. In contrast, *Macagual* and *Bosque Joven*, having the largest EKSA values, fit an Austere functioning (Fig. 8) and, as observed in Table 4, they are super-dominated by Ultimate

Austeres. These two plots are classified as the most stressed tropical humid forests in Sierra del Rosario, although they still are evergreen all year long (see also Appendix VI-A).



**Fig. 8.** Polygrams characterizing 13 Humid Forest Ecosystems (HFE) plots in *Sierra del Rosario* (see Table 4 and also Appendixes III-A and V-A). In parenthesis, the Ecosystems *K* Strategist Area (EKSA) values.

Sites as *El Rubí Sur*, *Cima Macagual* and *El Salón Sur* (Fig. 8 and Table 4; see also Appendix VI-A) can be classified as tropical dry forest plots. Indeed, they show a phytocenosis similar to the ones exhibited by evergreen (tropical humid) variants, but foliar caducity of these three plots is larger than 30% during the dry season. The super-dominant strategies among these forests are firstly Invasive Opportunists and secondly Ultimate Austeres (Table 4).

As shown in Figure 9, tropical dry forests growing at *Carapachibey* and *Punta del Este*, fit the IASd strategy in Figure 4, the only difference being that *Carapachibey* have taller trees than *Punta del Este*. Subsequent analysis of Table 5 allows noting that, as it occurs on tropical humid forests, EP dominates early successional stages. However, super-dominants can not be found in *Carapachibey* whereas they are represented by Invasive Austeres in *Punta del Este* (see also Appendix VI-B).

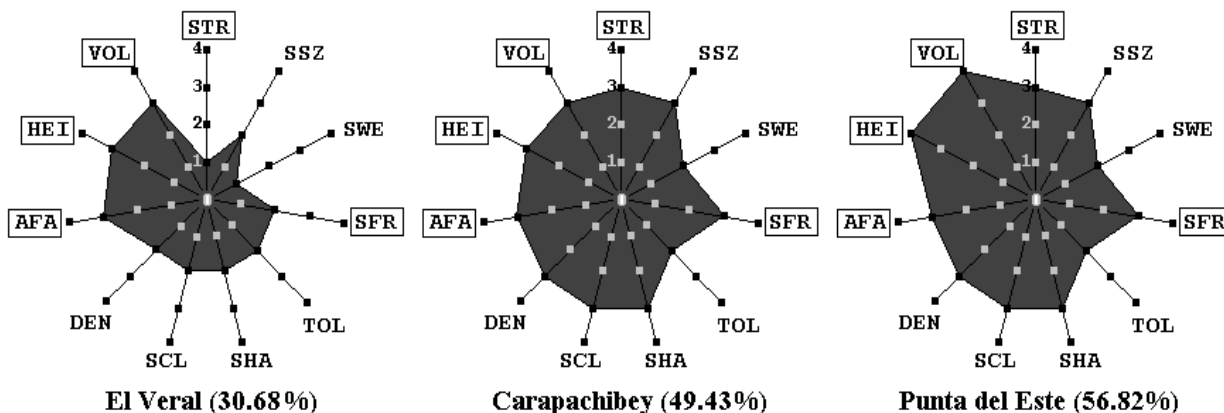
**Table 4.** Characterization of functional groups (successional strategies) along a gradient of successional and/or functionally different forest plots belonging to the assembly of Humid Forest Ecosystems (HFE). Those strategies represented by more than 5% are considered as dominant while those represented by more than 30% are considered to be super-dominants (in bold and underlined, at the table's bottom). H and R, Hypothetical or Real estimations, respectively; SNs, Successional Numbers for each case; CSI, Ceno-Successional Index; EKSA (%), Ecosystem's K-Strategist Areas, where K refers to the functional carrying capacity in the r-K continuum.

	H	H	H	H	R	H	R	H	H	R	H	H	H	H
	Yagrumal Joven	Yagrumal Majagual	Los Jagüeyes	Helechal	El Ebano	El Mulo Sur	Macurijal	Macagual	Bosque Joven	El Rubí Sur	Cima Macagual	El Salón Sur		
SNs														
EPh	1 & 2 <b><u>93.55</u></b>	0.00	4.05	4.28	<b><u>6.16</u></b>	0.00	<b><u>5.52</u></b>	0.00	1.72	0.00	0.00	0.00	0.00	0.00
LPh	3 & 4 3.83	<b><u>62.06</u></b>	<b><u>56.99</u></b>	<b><u>44.86</u></b>	<b><u>18.14</u></b>	<b><u>24.52</u></b>	2.76	4.42	0.00	<b><u>19.29</u></b>	0.67	0.41		
SPh	5 0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
ESh	6 & 7 0.00	0.00	0.07	<b><u>7.66</u></b>	0.32	<b><u>16.13</u></b>	<b><u>15.97</u></b>	2.26	1.90	<b><u>14.79</u></b>	<b><u>20.70</u></b>	<b><u>17.00</u></b>		
RSh	8 to 10 2.62	2.39	<b><u>12.27</u></b>	0.82	0.14	<b><u>20.32</u></b>	2.71	3.87	0.12	4.82	1.85	0.41		
ROSh	11 & 12 0.00	3.50	3.26	3.44	<b><u>18.91</u></b>	3.87	<b><u>26.04</u></b>	<b><u>13.37</u></b>	<b><u>7.01</u></b>	0.00	<b><u>6.28</u></b>	<b><u>7.01</u></b>		
IOSh	13 to 15 0.00	0.00	0.01	0.01	1.05	0.00	1.74	0.00	0.02	<b><u>36.98</u></b>	<b><u>31.49</u></b>	<b><u>31.76</u></b>		
IASh	16 & 17 0.00	3.16	<b><u>8.66</u></b>	<b><u>9.49</u></b>	<b><u>37.21</u></b>	<b><u>9.68</u></b>	<b><u>21.70</u></b>	<b><u>16.59</u></b>	<b><u>20.76</u></b>	<b><u>9.00</u></b>	4.03	<b><u>10.31</u></b>		
UASh	18 to 23 0.00	1.75	<b><u>14.69</u></b>	<b><u>29.44</u></b>	<b><u>18.07</u></b>	<b><u>25.48</u></b>	<b><u>23.56</u></b>	<b><u>59.49</u></b>	<b><u>68.48</u></b>	<b><u>15.12</u></b>	<b><u>34.98</u></b>	<b><u>33.10</u></b>		
CSI	1.26	2.43	7.74	10.38	13.07	10.97	13.16	17.53	19.16	11.82	15.12	15.37		
SKA (%)	23.9	25.6	25.0	29.5	46.0	46.0	49.4	59.7	63.1	39.8	49.4	52.8		
Dominant and Super-Dominant Strategies	<u>EP</u>	<u>EP</u>	LP	LP	EP	LP	ES	ROS	ROS	LP	ES	ES		
		RS	RS	ES	LP	ES	ROS	IAS	IAS	ES	ROS	ROS		
		ROS	IAS	IAS	ROS	RS	IOS	UAS	UAS	IOS	IOS	IOS		
			UAS	UAS	IAS	IAS	IAS	UAS	UAS	UAS	<b><u>UAS</u></b>	IAS		
					UAS	UAS	UAS					UAS		

**Table 5.** Characterization of functional groups (successional strategies) along a gradient of successional and/or functionally different forest plots belonging to the assembly of Dry and/or Saline Ecosystems (DSE). Those strategies represented by more than 5 % are considered as dominant while those represented by more than 30% are considered to be super-dominants (in bold and underlined, at the table's bottom). The three examples are hypothetical estimations; SNs, Successional Numbers for each case; CSI, Ceno-Successional Index; EKSA (%), Ecosystem's K-Strategist Areas, where *K* refers to the functional carrying capacity in the *r-K* continuum.

	SNs	<i>El Veral</i>	<i>Carapachibey</i>	<i>Punta del Este</i>
EPd	1 & 2	<b><u>48.07</u></b>	0.00	0.00
LPd	3 & 4	<b><u>9.09</u></b>	3.60	0.00
SPd	5 to 8	<b><u>24.69</u></b>	<b><u>12.59</u></b>	<b><u>5.85</u></b>
ESd	9 to 12	0.39	<b><u>8.99</u></b>	0.00
RSd	13 to 16	0.00	0.00	<b><u>11.10</u></b>
ROSd	17 to 19	0.00	<b><u>21.05</u></b>	<b><u>22.81</u></b>
IOSd	20 & 21	<b><u>16.58</u></b>	<b><u>11.51</u></b>	<b><u>18.72</u></b>
IASd	22 to 26	1.18	<b><u>23.20</u></b>	<b><u>39.77</u></b>
UASd	27 & 28	0.00	<b><u>19.06</u></b>	1.75
CSI		6.90	18.92	20.12
ESKA (%)		30.68	49.43	56.82
		<b><u>EP</u></b>	SP	SP
		LP	ES	RS
Dominant and Super-dominant Strategies		SP	ROS	ROS
		IOS	IOS	IOS
			IAS	<b><u>IAS</u></b>
			UAS	

**Successional characterization of forest ecosystems' functionings belonging to the DSE assembly**



**Fig. 9.** Polygrams characterizing Dry or Saline Ecosystems (DSE) plots in Western Cuba (see Table 5 for explanation and also Appendixes III-B and V-B). In parenthesis, the Ecosystems “K-Strategist” Area EKSA values.

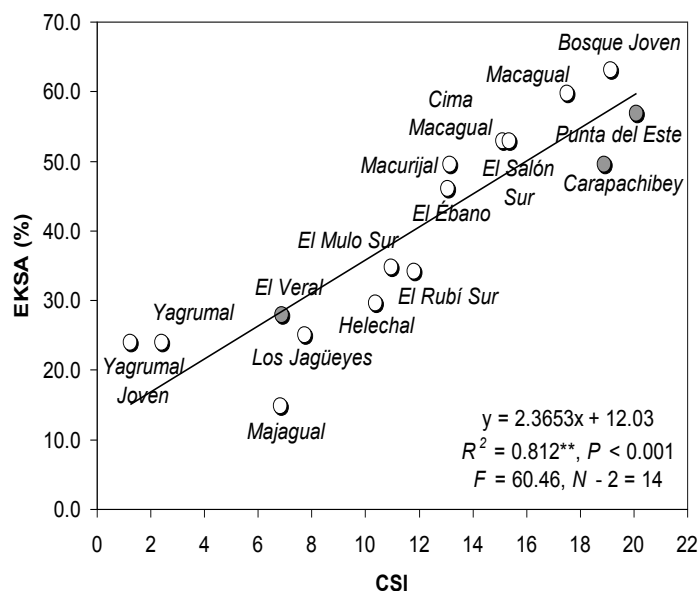
Finally, [Figure 10](#) show the regression analysis resulting from the comparison between CSI and EKSA values for *Sierra del Rosario* forest plots. As shown in the figure, a high  $R^2$  is obtained, demonstrating that CSI and EKSA are significantly correlated, i.e., for a group of forest plots the higher CSI is the higher carrying capacity (EKSA) results.

## DISCUSSION

The numerical values of STR, SFR, AFA, HEI and VOL generally tend to diminish during succession, while values for SSZ, SWE, TOL, SHA, SCL and DEN tend to increase (Clark and Clark, 1987; Jordan 1989; Kageyama and Viana, 1989; Whitmore, 1989; Hubbell and Foster, 1990; Marquez *et al.*, 1990;



Medina *et al.*, 1990; Bazzaz 1991; Gómez-Pompa *et al.*, 1991; Herrera *et al.*, 1991, 1997; Loehle, 2000). We have scored each of the variables from values typical of early successional to values typical of late successional species and then analyzed these variables to create a refined system of classification of successional strategies that can be viewed as the presentation of a hypothesis.



**Fig. 10.** EKSA (Ecosystem “K-Strategist” Area) vs. CSI (Ceno-successional Index) regression analysis for 13 Humid Forest Ecosystems (white dots, see Appendix V-A) and 3 Dry or Saline Ecosystems plots (gray dots, see Appendix V-B).

Classification of species into functional groups can play an important role in the interpretation of biodiversity. As identified by Mooney *et al.* (1995), functional groups are “groups of species that have ecologically similar effects on ecosystem processes.” While classification and comparison between functional groups is a first step in describing ecological processes, “no two species or individuals are ecologically identical, so as our understanding improves we expect to recognize situations where species diversity within functional groups or genetic diversity within species has important ecosystem consequences” (Mooney *et al.*, 1995).

In this paper, we have developed a classification scheme for ecological functions that is explicitly based on quantitative analysis of characters known to vary with succession. We consider this

classification system to be a refined version of the *r*-*K* continuum for tropical forest ecosystems. This classification scheme then presents a hypothesis concerning the dynamics of species replacement following disturbance. As such these groupings can help facilitate the understanding of tropical forest ecological functioning, the occurring forest stands management and conservation and the restoration of disturbed forest landscapes.

The hierarchical nature of our functional classification proposal (i.e., description of functional groups) is intended to provide adequate flexibility to fit an appropriate level of resolution. Dendrogram branches shape suggests homogeneity or heterogeneity of groups resulting from each cut. Trees showing many clusters at low levels of cutting, branching into many long single lines might indicate larger community heterogeneity. However in our resulting trees, both in HFE and DSE (Fig. 1), a gradient of step-by-step branching is observed at low cutting levels. Those branches are composed by few long and many short single lines (strategies) suggesting the occurrence of very clear and believable functional groups or strategies inside each ecosystem type.

Cutting levels and resulting strategies under each order are approximately the same for HFE and DSE (Fig. 1), suggesting that functional groups exist independently of ecosystem types. Both for HFE and DSE, there are several strategies becoming single and indivisible as early as Order II on. However, Exuberant Stabilizers, Major Stabilizers, Restoring Opportunist Stabilizers, Ultimate Stabilizers, Invasive Opportunist Stabilizers, Austere Stabilizers and Ultimate Austere Stabilizers are still recognizable, from Order II on, as divisible intermediate strategies both in HFE and DSE.

Influence of environment seems to cause humid ecosystems tendencies to be more austere (six Ultimate Austere functional groups) while dry and/or saline ecosystems tend to be more opportunists (two Ultimate Austere functional groups). A reduced number of orders, lack of Ultimate Stabilizers and a delay in the apparition of Austere strategies, the reduction of Ultimate Austere Stabilizers, subdivision

of Late Pioneers as early as Order II and an increased richness of Sclerophyllous Pioneers, Exuberants, Restorers, Restoring Opportunists, Invasive Opportunists and Invasive Austeres are significant arguments to reinforce the idea that forest species functional groups in DSE are functionally more opportunist and invasive than those flourishing under humid forest ecosystems.

The Order I classification into Pioneers and Stabilizers (Fig. 1 and 2) is reminiscent of the two strategies for tropical forests distinguished by other authors (e.g., Whitmore, 1989): pioneers and climax (non-pioneers). Indeed, we consider that Pioneer species are the first to colonize forest gaps, subsequently being replaced by Stabilizers. The functional roles of Pioneers and Stabilizers might be described as follows: Pioneers are fast growing species that establish themselves readily in gaps early during succession. They are able to replace grasses and shrubs constituting the immediate phase after the gap opening. Stabilizers might occur in the gap as seedlings or saplings already occurring as a bank of survivor individuals after the gap opening, or might arrive, during gap cicatrisation by dispersal mechanisms. Due to their slower growth rate and larger capabilities to tolerate shade, they

are capable of growing underneath and afterwards competitively replace Pioneers. This group includes the so-called "climax" species. However, we avoid this name (climax species) because, depending upon forest functioning and successional stages a smaller or larger proportion of Pioneers can frequently occur in primary forests.

Stabilizers make up the majority of the mature community in humid and dry and/or saline environments. For Stabilizers, the prevailing stress for DSE seems to favor a reduction of SWE and TOL whereas for HFE reduced DEN are favored, due perhaps to a larger water availability.

As mentioned before, users of the present system of classification are free to choose the level of cutting (strategies for a given Order) they believe more appropriate. From a biological point of view, all the orders are valuable and useful to identify different

strategic levels. However, we have preferred to use the final strategies (23 for HFE and 28 for DSE), which can be summarized into 9 main strategies but we advise that present results should be accepted rather as a new system of classification based on real or hypothetical data. Once users are convinced of the methods utility they should prepare their own matrix for the species growing in a particular territory and use the system for discovering their own strategies.

A simple look at species listed in Appendix IV tables allow us to observe the causes for the nomenclature used for strategies, as they are based on the species successional behavior in nature. We understand that there might be no doubts about Early, Late and Sclerophyllous Pioneers once the grouped species under these names are considered. We used the name Exuberant with the intention to refer to those species that commonly produce large logs, consequently requiring large nutrient sources to grow and develop.

Restorer Stabilizers include species with the ability to behave as second cycle pioneers and also having the ability to increase their tolerance to shade, but in most cases they are competitively weak. On the other hand, Restoring Opportunists behave reproductively as Austeres, but they seem to keep high growth rates (see Appendix IV's tables).

Many species have invasive abilities and are very well known in Neotropics, e.g., *Abarema obovalis*, *Albizia lebbeck*, *Bursera simaruba*, *Caesalpinia violacea*, *Chrysophyllum cainito*, *Clusia rosea*, *Cordia alliodora*, *Cordia gerascanthus*, *Leucaena leucocephala*, *Pithecellobium obovale*, *Savia sessiliflora*, *Swietenia mahagoni* and *Zuelania guidonia*. In our study, these species are grouped under the name of Invasive Opportunist Stabilizers (Appendix IV). Particularly, their intermediate values (2 to 3) for most variables probably grant their abilities to behave like invading opportunists. They are able to invade man-made gaps easily and belong to the so-called anthropic pioneers (Budowski, 1961). Exceptionally, when favored by environment and low plant competition, they might grow to form large logs being then easily taken for Exuberants.

Invasive and Ultimate Austere Stabilizers behave equally for HFE and DSE. The specialization of UAS lies on their ability to show maximal values for SFR and SCL while the other variables match 3. On the other hand, IAS are just intermediate between IOS and UAS, their particular specialization being based on the production of smaller trees.

A deeper analysis of these nine strategies demonstrates that the successional potentials are similar for HFE and DSE. However, the increased values of SKA for LP, SP, ES, RS, ROS and IOS in DSE, suggest again that this last type of ecosystem constitutes a flourishing environment for early and restoring and invasive strategies (Fig. 5). This last is also demonstrated by the fact that species richness in SP, ES, ROS and IAS is larger in DSE than in HFE.

As shown in Figures 6 and 7, the occurrence of the biologically relevant *r-K* continuum is demonstrated by the strategies resulting from our classification system. However, the continuum is not so simple. In fact, it results from many combinations of *r* and *K* tendencies among the biological variables we studied. Consequently, pioneer strategies can be *K* strategists in some respects and stabilizer strategies can be *r* strategists in other respects. Therefore, it seems to be obligatory from a biological standpoint to consider the coexistence of *r* and *K* behaviors not only as a particular property of a given strategy, but also as different levels of biological organization.

The system of classification presented here proves to be useful both for characterizing ecosystem functional groups and for differentiating functioning at the ecosystem level. Using successional numbers is interesting for quantifying mathematically the successional stage (CSI values) at a given forest plot.

In addition, the EKSA values represent the successional status of a particular ecosystem (forest community functioning *sensu* Whittaker, 1975). We also suspect that the EKSA values may relate to the potential energy of the ecosystem (standing crop given by living plant individual components in addition to the un-decomposed necromass), and that

the remaining percentage to fill 100% of the polygram area might be related with the kinetic energy, i.e., with the plant community turnover rate (observed in a 0 to 100 scale instead of the commonly used 0 to 1 scale). While this connection is speculative at this point, we know that *Bosque Joven* and *Majagual* show turnover rates of about 45% and 80%, respectively (Herrera *et al.*, 1988; actual figures are 0.45 and 0.80 in a 0 to 1 scale), while those suggested by their EKSA values (Fig. 8) are 39.6% and 85.2% (actual figures might be 0.40 and 0.85 in a 0 to 1 scale), respectively. Consequently, the values resulting from 100 - EKSA seems to correlate with the real standing crop turnover rates for *Bosque Joven* and *Majagual*. The generality of this relationship requires further investigation.

The classification system also demonstrates that species composition grouped inside a given strategy or growing together as a plant community assembly gives enough information to characterize forest ecosystems successional and functional processes. On the other hand, SN, CSI, SKA, and EKSA values, in addition to the advantage of describing successional strategies dominating a particular ecosystem, challenge us for new research directions dealing with mathematical modeling and ecosystems' thermodynamics.

## SUPPLEMENTARY INFORMATION

Additional supporting information (six appendices) may be found in the online version of this article.

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## APPENDIX I

**Appendix I.** Species included in the present study listed according to their preferential habitat.

**I-A. Humid Habitats.** Sites with annual rainfall > 1500 mm and/or relatively to completely protected against desiccation by a higher frequency of cloudiness, a higher proximity to water table and/or water streams, and appropriate sunshine expositions (not directly exposed) or topographies (concave slopes, valleys, etc.).

Scientific Name	Common Name	Family
<i>Albizia berteriana</i> (Balbis) Maza	Abey macho	Mimosaceae
<i>Alchornea latifolia</i> Sw.	Aguacatillo	Euphorbiaceae
<i>Anacardium excelsum</i> (Bert.et Bald.)S.Keels	Mijao, Nariz	Anacardiaceae
<i>Beilschmiedia pendula</i> (Sw.) et Hook	Aceitunillo	Lauraceae
<i>Brosimum alicastrum</i> Sw.	Guáimaro	Moraceae
<i>Brunellia comocladifolia</i> H. et B.	Unknown	Brunelliaceae
<i>Bucida buceras</i> L.	Júcaro negro	Combretaceae
<i>Buchenavia capitata</i> (Vahl) Eichl.	Júcaro amarillo	Combretaceae
<i>Calycophyllum candidissimum</i> (Vahl) DC.	Dagame	Rubiaceae
<i>Carapa guianensis</i> Aubl.	Najesí	Meliaceae
<i>Cinnamomum triplinerve</i> (R. et P.) Kosterm	Boniato blanco	Lauraceae
<i>Coffea arabica</i> L.	Cafeto	Rubiaceae
<i>Cojoba arborea</i> (L.) Britton et Rose	Moruro rojo	Mimosaceae
<i>Cynometra cubensis</i> A. Rich.	Pico de gallo	Caesalpiniaceae
<i>Cyrilla racemiflora</i> L.	Barril	Cyrtillaceae
<i>Chionanthus domingensis</i> Lam	Bayito	Oleaceae
<i>Chione cubensis</i> A. Rich.	Vigueta naranjo	Rubiaceae
<i>Decussocarpus rospiglosii</i> (Pilger) de Laub.	Pino liso	Podocarpaceae
<i>Dendropanax arboreus</i> (L.) Dec. et Planch.	Víbona	Araliaceae
<i>Diospyros caribaea</i> (A. DC.) Standl.	Ébano	Ebenaceae
<i>Diospyros philippensis</i> (Desr.) Guercke	Mabolo	Ebenaceae
<i>Erythrina berteriana</i> Urb.	Piñón de pito	Fabaceae
<i>Erythrina poeppigiana</i> (Walp.) O.F. Cook	Búcare	Fabaceae
<i>Ficus obtusifolia</i> Kunth	Jagüey	Moraceae
<i>Ficus subscabrida</i> Warb.	Jagüey macho	Moraceae
<i>Fraxinus cubensis</i> Griseb.	Búfano	Oleaceae

## I-A. Humid Habitats. (cont.)

Scientific Name	Common Name	Family
<i>Guarea guidonia</i> (L.) Sleumer	Yamagua	Meliaceae
<i>Guatteria moralesi</i> (Maza) Urb.	Purio prieto	Annonaceae
<i>Guettarda combsii</i> Urb.	Jagüilla de monte	Rubiaceae
<i>Guibourtia hymenifolia</i> (Moric.) J. Leonard	Quiebra hacha	Caesalpiniaceae
<i>Heliocarpus americanus</i> L.	Majagua	Tiliaceae
<i>Hymenaea courbaril</i> Griseb.	Curbaril	Caesalpiniaceae
<i>Inga vera</i> Willd.	Guabá	Mimosaceae
<i>Juglans insularis</i> Griseb.	Nogal del país	Juglandaceae
<i>Licaria triandra</i> (Sw.) Kostermans	Leviza	Lauraceae
<i>Magnolia cubensis</i> Urb.	Magnolia	Magnoliaceae
<i>Manilkara jaimiquí</i> (Wr. ex Griseb.) Dubard	Jaimiquí	Sapotaceae
<i>Manilkara valenzuelana</i> (A. Rich.) T. D. Penn.	Ácana	Sapotaceae
<i>Manilkara zapota</i> (L.) P. Royen	Níspero	Sapotaceae
<i>Margaritaria nobilis</i> L. f.	Azulejo	Euphorbiaceae
<i>Matayba apetala</i> Sw.	Macurije	Sapindaceae
<i>Miconia elata</i> (Sw.) DC	Cordobán	Melastomataceae
<i>Micropholis polita</i> (Griseb.) Pierre	Sapotillo árbol	Sapotaceae
<i>Ocotea cuneata</i> (Griseb.) Urb.	Canelón	Lauraceae
<i>Ocotea leucoxydon</i> (Sw.) Mez	Judío	Lauraceae
<i>Ochroma lagopus</i> L.	Balsa	Bombacaceae
<i>Oxandra laurifolia</i> (Sw.) A. Rich.	Purio	Annonaceae
<i>Pera bumeliaefolia</i> Griseb.	Jiquí	Euphorbiaceae
<i>Piscidia piscipula</i> (L.) Sargent	Guamá candelón	Fabaceae
<i>Podocarpus angustifolius</i> Griseb.	Sabina cimarrona	Podocarpaceae
<i>Poeppigia procera</i> Presl.	Tengue	Caesalpiniaceae
<i>Pouteria dictyoneura</i> (Griseb.) Radlk.	Cocuyo	Sapotaceae
<i>Pouteria dominigensis</i> (Gaertn.) Baehni	Sapote culebra	Sapotaceae
<i>Protium cubense</i> (Rose) Urb.	Copal	Burseraceae
<i>Prunus myrtifolia</i> (L.) Urb.	Cuajani hembra	Rosaceae
<i>Prunus occidentalis</i> Sw.	Cuajani	Rosaceae
<i>Pseudolmedia spuria</i> (Sw.) Griseb.	Macagua	Moraceae
<i>Rheedia aristata</i> Griseb.	Manajú	Clusiaceae
<i>Sapindus saponaria</i> L.	Jaboncillo	Sapindaceae
<i>Sapium jamaicense</i> Sw.	Piniche, Lechero	Euphorbiaceae
<i>Schefflera morototonii</i> (Aubl.) Magu., Stey. et Frodin	Yagruma macho	Araliaceae

**I-A. Humid Habitats. (cont.)**

Scientific Name	Common Name	Family
<i>Sloanea amygdalina</i> Griseb.	Pico de gallo	Elaeocarpaceae
<i>Syzygium jambos</i> (L.) Alston	Pomarrosa	Myrtaceae
<i>Tabebuia angustata</i> Britt.	Roble blanco	Bignoniaceae
<i>Tabebuia shaferi</i> Britt.	Roble blanco	Bignoniaceae
<i>Talauma orbicularis</i> Britt. et Wils.	Marañón de la Maestra	Magnoliaceae
<i>Theobroma cacao</i> L.	Cacaotero	Sterculiaceae
<i>Trema micrantha</i> (L.) Blume	Guasimilla macho	Ulmaceae
<i>Trichilia havanensis</i> Jacq.	Siguaraya	Meliaceae
<i>Trichospermum grewifolium</i> (A. Rich.) Kosterm.	Majagüilla	Tiliaceae
<i>Trophis racemosa</i> (L.) Urb.	Ramón	Moraceae
<i>Wallenia laurifolia</i> Sw.	Guacamari	Myrsinaceae
<i>Zanthoxylum elephantiasis</i> Macfd.	Bayúa	Rutaceae

**I-B. Dry-Saline Habitats.** Prevalently terrestrial sites with annual rainfall < 1500 mm, enduring seasonally dry periods three or more months. Coastal habitats or highly influenced by salinity are also included. Species growing in semi-deciduous (canopy foliar caducity more than 30%) and deciduous forests commonly reaching 10 to 15 m high and rarely higher than 25 m.

Scientific Name	Common Name	Family
<i>Adelia ricinella</i> L.	Jía blanca	Euphorbiaceae
<i>Albizia cubana</i> Britt. et Wilson	Bacona	Mimosaceae
<i>Alvaradoa amorphoides</i> Liebm.	Tamarindillo	Simaroubaceae
<i>Amyris balsamifera</i> L.	Cuaba	Rutaceae
<i>Ateleia apetala</i> Griseb.	Mierda de gallina	Fabaceae
<i>Avicennia germinans</i> (Jacq.) L.	Mangle prieto	Verbenaceae
<i>Bauhinia divaricata</i> L.	Pata de vaca	Caesalpiniaceae
<i>Belairia mucronata</i> Griseb.	Yamaquey	Fabaceae
<i>Bombacopsis cubensis</i> A. Robyns	Ceibón	Bombacaceae
<i>Bourreria succulenta</i> Jacq.	Ateje de costa	Boraginaceae
<i>Byrsonima crassifolia</i> (L.) HBK	Peralejo	Malpighiaceae
<i>Cameraria retusa</i> Griseb.	Maboa de sabana	Apocynaceae
<i>Canella winterana</i> (L.) Gaertn.	Cúrbana	Canellaceae
<i>Carpodiptera cubensis</i> Griseb.	Majagüilla	Tiliaceae
<i>Casasia calophylla</i> A. Rich.	Jicarita	Rubiaceae
<i>Casearia hirsuta</i> Sw.	Raspa lengua	Flacourtiaceae
<i>Cassia ekmaniana</i> Urb.	Guacamaya	Caesalpiniaceae
<i>Cedrela cubensis</i> Bisse	Cedro macho	Meliaceae



## I-B. Dry-Saline Habitats. (cont.)

Scientific Name	Common Name	Family
<i>Celtis trinervia</i> Lam.	Ramón de costa	Ulmaceae
<i>Citharexylum fruticosum</i> L.	Penda	Verbenaceae
<i>Coccoloba uvifera</i> L.	Uva caleta	Polygonaceae
<i>Colubrina arborescens</i> (Mill.) Sarg.	Bijáguara	Rhamnaceae
<i>Conocarpus erectus</i> L.	Yana	Combretaceae
<i>Cordia sebestena</i> L.	Vomitel colorado	Boraginaceae
<i>Curatella americana</i> L.	Vacabuey	Dilleniaceae
<i>Chrysobalanus icaco</i> L.	Icaco	Chrysobalanaceae
<i>Diospyros crassinervis</i> (Krug. et Urb.) Standl.	Ébano	Ebenaceae
<i>Erythroxylum alaternifolium</i> A. Rich.	Arabo prieto	Erythroxylaceae
<i>Ficus aurea</i> Nutt.	Jagüey hembra	Moraceae
<i>Forestiera rhamnifolia</i> Griseb.	Almorránilla	Oleaceae
<i>Genipa americana</i> L.	Jagua	Rubiaceae
<i>Guaiacum officinale</i> L.	Guayacán	Zygophyllaceae
<i>Guaiacum sanctum</i> L.	Guayacán santo	Zygophyllaceae
<i>Haematoxylum campechianum</i> L.	Palo campeche	Caesalpiniaceae
<i>Hamelia patens</i> Jacq.	Ponasí	Rubiaceae
<i>Haematoxylum campechianum</i> L.	Palo campeche	Caesalpiniaceae
<i>Hamelia patens</i> Jacq.	Ponasí	Rubiaceae
<i>Hebestigma cubense</i> (HBK) Urb.	Frijolillo	Fabaceae
<i>Hippomane mancinella</i> L.	Manzanillo	Euphorbiaceae
<i>Hypelate trifoliata</i> Sw.	Hueso de costa	Sapindaceae
<i>Jacaranda coerulea</i> (L.) Griseb.	Abey macho	Bignoniaceae
<i>Krugiodendron ferreum</i> (Vahl.) Urb.	Carey de costa	Rhamnaceae
<i>Laguncularia racemosa</i> (L.) Gaertn.	Patabán	Combretaceae
<i>Luehea speciosa</i> Willd.	Guásima amarilla	Tiliaceae
<i>Lysiloma latisiliqua</i> (L.) Benth.	Soplillo	Mimosaceae
<i>Metopium brownei</i> (Jacq.) Urb.	Guao de costa	Anacardiaceae
<i>Ottoschulzia cubensis</i> (Wr. et Griseb.) Urb.	Cogote de toro	Icacinaceae
<i>Pachyanthus cubensis</i> A. Rich.	Hierro	Melastomataceae
<i>Peltophorum adnatum</i> Griseb.	Moruro abey	Caesalpiniaceae
<i>Phyllostylon brasiliensis</i> Capanema	Jatía	Ulmaceae
<i>Picrodendron macrocarpum</i> (A. Rich..) Britt.	Yana prieta	Euphorbiaceae
<i>Pinus tropicalis</i> Morelet	Pino hembra	Pinaceae
<i>Pithecellobium lentiscifolium</i> (A. Rich.) Wr.	Humo	Mimosaceae

**I-B. Dry-Saline Habitats. (cont.)**

Scientific Name	Common Name	Family
<i>Polygala cuneata</i> (Griseb.) Blake	Cocuyo blanco	Polygalaceae
<i>Prosopis juliflora</i> (Sw.) DC.	Mezquite	Mimosaceae
<i>Quercus cubana</i> A. Rich.	Encino	Fagaceae
<i>Rhizophora mangle</i> L.	Mangle rojo	Rhizophoraceae
<i>Simarouba glauca</i> DC.	Gavilán	Simaroubaceae
<i>Swartzia cubensis</i> (Britt. et Wils.) Standl.	Pico de gallo	Caesalpiniaceae
<i>Thespesia populnea</i> (L.) Soland	Majagua de Florida	Malvaceae
<i>Ximenia americana</i> L.	Yaná	Olacaceae
<i>Xylopia aromatica</i> (Lam.) Mart.	Malagueta	Annonaceae
<i>Zanthoxylum fagara</i> (L.) Sargent	Chivo	Rutaceae

**I-C. Species Indifferent to Habitat.** Species able to grow equally on humid or dry and/or saline habitats.

Scientific Name	Common Name	Family
<i>Abarema obovalis</i> (A. Rich.) Wr.	Encinillo	Mimosaceae
<i>Albizia lebbbeck</i> (L.) Benth.	Algarrobo de olor	Mimosaceae
<i>Albizia procera</i> Benth.	Algarrobo de la India	Mimosaceae
<i>Allophylus cominia</i> (L.) Sw.	Palo de caja	Sapindaceae
<i>Anacardium occidentale</i> L.	Marañón	Anacardiaceae
<i>Andira inermis</i> (Sw.) HBK	Yaba	Fabaceae
<i>Annona muricata</i> L.	Guanábana	Annonaceae
<i>Bauhinia monandra</i> Kurz	Pata de vaca	Caesalpiniaceae
<i>Brya microphylla</i> Bisse	Granadillo	Fabaceae
<i>Bunchosia media</i> (Ait.) DC	Mierda gallina	Malpighiaceae
<i>Bursera simaruba</i> (L.) Sargent	Almácigo	Burseraceae
<i>Caesalpinia violacea</i> (Mill.) Standl.	Yarúa	Caesalpiniaceae
<i>Calophyllum antillanum</i> Britt.	Ocuje	Clusiaceae
<i>Cassia grandis</i> L.	Cañandong	Caesalpiniaceae
<i>Casuarina equisetifolia</i> Forst.	Casuarina	Casuarinaceae
<i>Cecropia schreberiana</i> Miq.	Yagruma	Cecropiaceae
<i>Cedrela odorata</i> L.	Cedro	Meliaceae
<i>Ceiba pentandra</i> (L.) Gaertn.	Ceiba	Bombacaceae
<i>Chrysophyllum cainito</i> L.	Caimito	Sapotaceae
<i>Chrysophyllum oliviforme</i> L.	Caimitillo	Sapotaceae
<i>Citrus aurantium</i> L.	Naranja agrio	Rutaceae

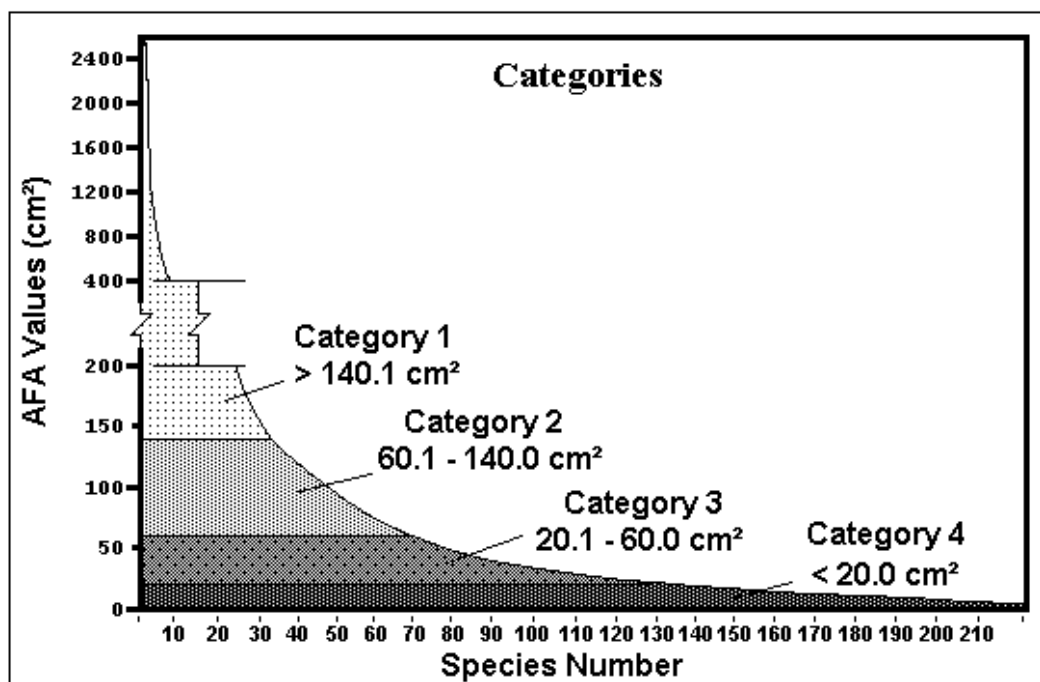
## I-C. Species Indifferent to Habitat. (cont.)

Scientific Name	Common Name	Family
<i>Clusia rosea</i> Jacq.	Copey	Clusiaceae
<i>Coccoloba diversifolia</i> Jacq.	Uvilla	Polygonaceae
<i>Coccoloba retusa</i> Griseb. Cat.	Uvilla	Polygonaceae
<i>Comocladia dentata</i> Jacq.	Guao	Anacardiaceae
<i>Cordia alliodora</i> (R. et P.) Cham.	Baría prieta	Boraginaceae
<i>Cordia collococca</i> L.	Ateje	Boraginaceae
<i>Cordia gerascanthus</i> L.	Baría	Boraginaceae
<i>Cupania americana</i> L.	Guara	Sapindaceae
<i>Cupania glabra</i> Sw.	Guara de costa	Sapindaceae
<i>Delonix regia</i> (Bojer.) Raf.	Flamboyant	Caesalpiniaceae
<i>Drypetes alba</i> Poit.	Hueso	Euphorbiaceae
<i>Ehretia tinifolia</i> L.	Roble prieto	Boraginaceae
<i>Enterolobium cyclocarpum</i> (Jacq.) Gris.	Oreja de judío	Mimosaceae
<i>Erythroxylum areolatum</i> L.	Arabo jibá	Erythroxylaceae
<i>Erythroxylum confusum</i> Britt.	Arabo colorado	Erythroxylaceae
<i>Erythroxylum havanense</i> Jacq.	Arabo	Erythroxylaceae
<i>Eucalyptus citriodora</i> Hook	Eucalipto	Myrtaceae
<i>Eugenia axillaris</i> (Sw.) Willd.	Guairaje	Myrtaceae
<i>Eugenia foetida</i> Poir.	Guairaje	Myrtaceae
<i>Exothea paniculata</i> (Juss.) Radlk.	Yaicuaje	Sapindaceae
<i>Faramea occidentalis</i> (L.) A. Rich.	Nabaco	Rubiaceae
<i>Gliricidia sepium</i> (Jacq.) Steud.	Piñón florido	Fabaceae
<i>Gmelina arborea</i> Roxb.	Gemelina	Verbenaceae
<i>Guazuma ulmifolia</i> Lam.	Guásima	Sterculiaceae
<i>Guettarda calyptrata</i> A. Rich.	Guayabillo	Rubiaceae
<i>Guettarda elliptica</i> Sw.	Cigüilla	Rubiaceae
<i>Gymnanthes lucida</i> Sw.	Yaití	Euphorbiaceae
<i>Hura crepitans</i> L.	Salvadera	Euphorbiaceae
<i>Juniperus lucayana</i> Britt.	Sabina	Cupressaceae
<i>Khaya nyassica</i> Stapf.	Caoba africana	Meliaceae
<i>Leucaena leucocephala</i> (Lam.) de Wit	Leucaena	Mimosaceae
<i>Lysiloma sabicu</i> A. Rich	Sabicú	Mimosaceae
<i>Maclura tinctoria</i> (L.) Don	Mora	Moraceae
<i>Mammea americana</i> L.	Mamey Sto. Domingo	Clusiaceae
<i>Mangifera indica</i> L.	Mango	Anacardiaceae

## I-C. Species Indifferent to Habitat. (cont.)

Scientific Name	Common Name	Family
<i>Melia azedarach</i> L.	Paraiso	Meliaceae
<i>Muntingia calabura</i> L.	Capulí	Elaeocarpaceae
<i>Nectandra coriacea</i> (Sw.) Griseb.	Sigua	Lauraceae
<i>Oxandra lanceolata</i> (Sw.) Bail.	Yaya	Annonaceae
<i>Persea americana</i> Mill.	Aguacate	Lauraceae
<i>Picramnia pentandra</i> Sw.	Aguedita	Simaroubaceae
<i>Pinus caribaea</i> Morelet	Pino macho	Pinaceae
<i>Plumeria obtusa</i> L.	Lirio	Apocynaceae
<i>Pouteria sapota</i> (Jacq.) H.E. Moore & Stearn.	Mamey colorado	Sapotaceae
<i>Psidium guajava</i> L.	Guayaba	Myrtaceae
<i>Roystonea regia</i> (HBK) O.F. Cook	Palma real	Arecaceae
<i>Samanea saman</i> (Jacq.) Merr.	Algarrobo	Mimosaceae
<i>Savia sessiliflora</i> (Sw.) Willd.	Carbonero	Euphorbiaceae
<i>Sideroxylon foetidissimum</i> (Jacq.) Cronquist	Jocuma	Sapotaceae
<i>Sideroxylon salicifolium</i> (L.) Lam.	Sangre doncella	Sapotaceae
<i>Spathodea campanulata</i> Beauv.	Tulipán africano	Bignoniaceae
<i>Spondias mombin</i> L.	Jobo	Anacardiaceae
<i>Sterculia apetala</i> (Jacq.) Karst.	Anacahuita	Sterculiaceae
<i>Swietenia macrophylla</i> King.	Caoba de Honduras	Meliaceae
<i>Swietenia mahagoni</i> (L.) Jacq.	Caoba antillana	Meliaceae
<i>Talipariti elatum</i> (Sw.) Fryxell	Majagua	Malvaceae
<i>Tamarindus indica</i> L.	Tamarindo	Caesalpiniaceae
<i>Tectona grandis</i> L. f.	Teca	Verbenaceae
<i>Terminalia catappa</i> L.	Almendro de la India	Combretaceae
<i>Terminalia eryostachia</i> A. Rich.	Chicharrón	Combretaceae
<i>Terminalia intermedia</i> (A.Rich.) Urb.	Chicharrón	Combretaceae
<i>Tetrazygia bicolor</i> (Mill.) Cogn.	Cordobancillo	Melastomataceae
<i>Trichilia hirta</i> L.	Cabo de hacha	Meliaceae
<i>Vitex divaricata</i> Sw.	Roble guayo	Verbenaceae
<i>Zanthoxylum martinicense</i> (Lam.) DC.	Ayúa	Rutaceae
<i>Zuelania guidonia</i> (Sw.) Britt. et Millsp.	Guaguasí	Flacourtiaceae

## APPENDIX II



**Appendix II-A. Figure II-1.** Categorization of approximated foliar area (AFA) values. Categories 1 to 4 are not shared in four equal ranges, but in ranges which follow the successional placement of forest species.

**Appendix II-B.** Description of reproductive and vegetative variables.

**Seeds per tree (STR).** In estimating STR values, we mainly drew upon our practical experience as well as the experience of our collaborators. We estimated the means of species seed productions rather than productions during mast years (Ramírez, 1978; Howe, 1990). We have assumed here that the value given for this variable decreases from early to late successional.

**Seed size (SSZ), Seed weight (SWE) and Seeds per fruit (SFR).** Data for SSZ, SWE and SFR were obtained from the literature (see references above), of the *Herbario Nacional de la Academia de Ciencias de Cuba* and from field sampling. For practical reasons, we measured the size (length, width, and thickness) and dry weight of seeds in a strict sense, i.e., the seed coat surrounding the endosperm, the cotyledons and the embryo. The fruit attributes commonly remaining around the seed after air-dried, e.g. the dried, originally fleshy, cover surrounding the seed in *Andira inermis* and *Calophyllum antillanum* drupes, or seed attributes as wings, trichomas, arils, etc., were not considered within our measure of seeds. According to our experience, SSZ and SWE increase from early to late successional, while SFR decreases.

**Tolerance to shade (TOL).** Tolerance to shade tends to increase from early to late successional (Clark and Clark, 1987; Whitmore, 1989; Marquez *et al.*, 1990; Medina *et al.*, 1990; Bazzaz, 1991; Gómez-Pompa *et al.* 1991; Herrera *et al.* 1991). Our assessment of tree species TOL

values was subjective and based on our experience with these species. The deepest shade in which trees grow is in the understory of HFE. In this environment, light intensity penetrating through the forest canopy can be reduced to about 10% of incident sunlight (Vilamajó *et al.* 1988). We decided to reserve values 4 of TOL only for those species, which preferring humid habitats are able to fully develop from seedlings to saplings in the understory under reduced sources of sunlight (Appendix I). For species preferring humid habitats value 1 of TOL was not used because they cannot be omniheliofilous. For these species, the minimal level of TOL, i.e., their maximal degree of heliophily, was 2, since in humid forest environments shade-intolerant species are able to survive and grow when partially shaded. Following similar reasoning, values 4 for TOL were not assigned to species preferring DSE. In these environments – including dry forests, subdeciduous forests, mangrove, savannas, etc. – sunlight reaching the understory or topsoil is surely more intense than in tropical wet or humid forest environments.

**Selectivity to habitat (SHA).** Selectivity to habitat was subjectively assigned based on the establishment success of a species under different environments. It therefore refers to the water and nutrient requirements of the species and other environmental conditions necessary for their successful establishment. We have assumed that the selectivity of tree species to habitat increases successional, since generalists are commonly considered to be successional earlier than specialists (e.g., Gómez-Sal *et al.*, 1986).

**Sclerophylly (SCL).** Causes of sclerophylly among plants have been commonly associated with the lack of water or nutrients (Medina *et al.*, 1990). In addition, it has been generally accepted that in tropical forest SCL tends to increase from early to late successional species (Herrera *et al.*, 1991). In a very broad sense the categories defined for SCL are concurrent with the classification of leaves and leaflet texture into membranaceous, papyraceous, chartaceous and coriaceous, though different authors do not consistently use these terms. However, careful consideration is to be had when classifying SCL based on the texture of leaves and leaflets since species as *Clusia rosea* and *Coccoloba retusa* may falsely appear to be sclerophyllous and hard-leaved due to their thick cuticles, epidermis thickness, brightness and dark glossy green color, though they show low SCL values according to our definition (Herrera *et al.*, 1991, see also comments below).

Our measure of SCL was based on fresh weight: dry weight (FW:DW) ratios. The FW:DW ratios were obtained by collecting mature leaves or leaflets from sunshine exposed branches of three individuals for each species. Depending upon their size 10 to 100 leaves or leaflets were collected for each of the three replicates. Leaves were collected prior to midday and the plant material was stored inside a sealed polyethylene bag. All bags were refrigerated prior to being weighed (maximum two days). Condensed water adhering to the inner plastic bag wall was included in the measurement of fresh weights. Petioles and rachis were eliminated except for very small ones, *e.g.* in *Matayba apetala*. Dry weights were assessed after oven drying at 90°C to constant weight. The FW:DW ratios were assessed for 158 (72%) of 221 analyzed species and published in Herrera and Rodríguez (1988) and Herrera *et al.* (1991). For the remaining species the level of SCL was estimated according to the characteristics observed on the herbarium vouchers, available literature and practical field experience of the authors and collaborators.

**Wood density (DEN).** The values of DEN for 183 of our species were obtained from a published work (Fors, 1965). The rest of the values were estimated based on our experience and that of Rigoberto Pérez (pers. comm.). In general, DEN seems to correlate with SCL, *i.e.*, wood density increases from early to late successional species.

**Approximated foliar area (AFA).** Generally AFA (*i.e.*, the area of a leaf or leaflet) and SCL are negatively correlated (Medina *et al.* 1990; Herrera *et al.*, 1991), *i.e.*, foliar area decreases while sclerophylly increases from early to late successional. In the case of AFA, the values were estimated from published or observed field and herbarium mean values for leaves or leaflets length (l) and width (w). With these values, we estimated foliar area using the equation for the area of an ellipse ( $= \pi \times l \times w$ ). If the categories listed for this variable in Table 1 are going to be used in botanical nomenclature, we recommend the

Greek suffix *-foliaceus* instead of *-phyllus* to avoid comparisons with Raunkiaer's classification (Raunkiaer, 1934).

**Tree height (HEI) and Tree volume (VOL).** According to our experience and the published literature (Leigh *et al.*, 1990; Gómez-Pompa *et al.*, 1991; McDade *et al.*, 1994; Bullock *et al.*, 1995), HEI and VOL decrease from early to late successional species. Tree volumes were estimated from the maximal height and diameter at breast height (*i.e.*, 1.30 m). Approximate tree volume was then calculated according to the equation for the volume of a cylinder ( $=\pi \times r^2 \times h$ , where h and 2r are the height and diameter respectively). In this calculation, we assumed that the whole volume of a tree log, branches and leaves fit a cylinder volume of constant diameter. The ranges for tree height and tree volume qualification are listed in Table 1. As individual tree species grow differently when growing in HFE or DSE, their values for HEI and VOL were emended accordingly when necessary.

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### APPENDIX III

**Appendix III-A.** Estimation of ceno-successional index (CSI) and the ecosystem *K*-strategist area (EKSA, %) for a particular forest plot belonging to the HFE (humid forest ecosystems) assembly.

Once the forest plot is examined and the trees heights and BHD (breath height diameters) are listed in a table, data are grouped by species and the trees phytomass (as trees volumes) estimated in m<sup>3</sup>. For tree volume (*V*) the equation of a cylinder is considered to be  $V = \pi r^2 h$ , where  $r = \text{BHD}/2$ .

The following table gives an example corresponding to a 20 x 20 m forest plot named "El Ébano", Reserve of Biosphere *Sierra del Rosario, Pinar del Río*, Western Cuba. SP refers to the species proportion, in %, with respect to the total phytomass for the plot (100%), SN refers to the successional number according to the present study, SP x SN list the products resulting from multiplying SP and SN, and CSI (ceno-successional index) is estimated by dividing the products total for the plot (SP x SN) by 100.

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Guazuma ulmifolia</i>	0.004	0.016	1	0.0	
<i>Tabebuia shaferi</i>	1.336	6.143	2	12.3	
<i>Ficus subscabrida</i>	0.182	0.837	3	2.5	
<i>Talipariti elatum</i>	3.763	17.298	4	69.2	
<i>Sideroxylon foetidissimum</i>	0.070	0.321	7	2.2	
<i>Dendropanax arboreus</i>	0.031	0.141	8	1.1	
<i>Alchornea latifolia</i>	3.344	15.371	11	169.1	
<i>Trophis racemosa</i>	0.705	3.239	11	35.6	13.07
<i>Ocotea floribunda</i>	0.066	0.303	12	3.6	
<i>Lonchocarpus domingensis</i>	0.227	1.045	14	14.6	
<i>Matayba apetala</i>	8.095	37.211	16	595.4	
<i>Syzygium jambos</i>	0.001	0.003	16	0.0	
<i>Margaritaria nobilis</i>	0.001	0.004	20	0.1	
<i>Calophyllum antillanum</i>	0.304	1.395	21	29.3	
<i>Nectandra coriacea</i>	0.100	0.459	21	9.6	
<i>Oxandra lanceolata</i>	0.001	0.005	21	0.1	

Table. Cont.

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Beilschmiedia pendula</i>	0.002	0.008	22	0.2	
<i>Pseudolmedia spuria</i>	2.272	10.442	22	229.7	
<i>Chionanthus domingensis</i>	0.053	0.243	22	5.4	
<i>Diospyros caribaea</i>	1.199	5.513	23	126.8	
<i>Pouteria chrysophyllifolia</i>	0.001	0.003	23	0.1	
	21.754	100.000		1307.0	

In humid forest ecosystems CSI lower values mean that the forest plot is integrated mostly by pioneers and or exuberants while higher values mean that the forest plot is dominated by opportunists and/or austeres *sensu lato*. In a second step, the phytomass values for the considered species are grouped according to their particular

strategies. In the example we use the Order VI strategies for HFE which include one to several successional numbers (SN) as showed in the column for "Grouped SN values" in the next table. Consequently, the strategies' proportions for each case are grouped as showed in the column "Strategy proportions in the plot" (next table).

Chosen Order VI Strategies	Grouped SN values	Strategy's proportions in the plot	Average Reproductive and Vegetative Variables for each Order VI Strategy										
			STR	SSZ	SWE	SFR	TOL	SHA	SCL	DEN	AFA	HEI	VOL
EPh	1 & 2	6.16	1	1	1	2	2	2	2	2	2	3	3
LPh	3 & 4	18.14	1	2	1	2	2	2	1	2	2	1	1
SPh	5	0.00	2	2	1	1	2	1	4	3	3	1	1
ESh	6 & 7	0.32	3	4	3	3	2	3	3	2	2	1	1
RSh	8 to 10	0.14	2	3	2	3	3	2	2	2	2	3	3
ROSh	11 & 12	18.91	3	3	3	3	3	2	3	2	1	3	3
IOSh	13 to 15	1.05	2	3	2	3	2	2	3	2	3	3	3
IASh	16 & 17	37.21	3	3	2	3	3	2	3	3	3	4	4
UASh	18 to 23	18.07	3	3	3	4	3	3	4	3	3	3	3
Total		100.00											

Once the "Strategies proportions in the plot" (third column in former table) are grouped, the resulting values are multiplied by the corresponding category (1 to 4) for each of the considered variables (average reproductive and vegetative variables for each Order VI Strategy in the former table). The results appear in the next table:

	STR	SSZ	SWE	SFR	TOL	SHA	SCL	DEN	AFA	HEI	VOL
EPh	6.2	6.2	12.3	12.3	12.3	12.3	12.3	12.3	12.3	18.5	18.5
LPh	18.1	36.3	18.1	36.3	36.3	36.3	18.1	36.3	36.3	18.1	18.1
SPh	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ESh	1.0	1.3	1.0	1.0	0.6	1.0	1.0	0.6	0.6	0.3	0.3
RSh	0.3	0.4	0.3	0.4	0.4	0.3	0.3	0.3	0.3	0.4	0.4
ROSh	56.7	56.7	56.7	56.7	56.7	37.8	56.7	37.8	18.9	56.7	56.7
IOSh	2.1	3.2	2.1	3.2	2.1	2.1	3.2	2.1	3.2	3.2	3.2
IASh	111.6	111.6	74.4	111.6	111.6	74.4	111.6	111.6	111.6	148.8	148.8
UASh	54.2	54.2	54.2	72.3	54.2	54.2	72.3	54.2	54.2	54.2	54.2
Σ	250.2	269.9	219.2	293.8	274.3	218.4	275.5	255.3	237.4	300.3	300.3
Σ/100	2.5	2.7	2.2	2.9	2.7	2.2	2.8	2.6	2.4	3.0	3.0
Rounded	3	3	2	3	3	2	3	3	2	3	3



Finally, the EKSA (ecosystem *K*-strategist area, in %) is estimated from rounded values at the table bottom using the same equation as for the strategy *K* area (SKA):

$$EKSA = \frac{\sum_{i=1}^{10} (\text{Var}_i * \text{Var}_{i+1}) + (\text{Var}_{11} * \text{Var}_1)}{(\text{MVA})^2 * \text{Nr. Vars.}}$$

The EKSA value in the given example from rounded values is 46.02%.

**Appendix III-B.** Estimation of ceno-successional index (CSI) and the ecosystem *K*-strategist area (EKSA, %) for a particular forest plot belonging to the DSE (dry and/or saline ecosystems) assembly.

Once the forest plot is examined and the trees heights and BHD (breath height diameters) are listed in a table, data are grouped by species and the trees phytomass (as trees volumes) estimated in m<sup>3</sup>. For tree volume (*V*) the equation of a cylinder is considered to be  $V = \pi r^2 h$ , where  $r = \text{BHD}/2$ .

The following table gives a hypothetical example corresponding to a forest plot named “*Punta del Este*”, localized in the Southeast of *Isla de la Juventud*, Western Cuba. SP refers to the species proportion, in %, with respect to the total phytomass for the plot (100%), SN refers to the successional number according to Figure 3 showing the strategies for dry and or saline ecosystems (DSE), SP x SN list the products resulting from multiplying SP and SN, and CSI (ceno-successional index) is estimated by dividing the products’ total for the plot (SP x SN) by 100.

Punta del Este (Hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Cordia gerascanthus</i>	1.00	5.85	8	46.78	
<i>Ateleia apetala</i>	1.00	5.85	15	87.72	
<i>Simarouba glauca</i>	0.90	5.26	16	84.21	
<i>Citharexylum fruticosum</i>	0.20	1.17	17	19.88	
<i>Adelia ricinella</i>	2.00	11.70	18	210.53	
<i>Krugiodendron ferreum</i>	0.50	2.92	18	52.63	
<i>Lysiloma latisiliqua</i>	1.20	7.02	19	133.33	
<i>Swietenia mahagoni</i>	2.00	11.70	20	233.92	20.12
<i>Gymnanthes lucida</i>	1.20	7.02	21	147.37	
<i>Lysiloma sabicu</i>	2.00	11.70	23	269.01	
<i>Bursera simaruba</i>	3.00	17.54	23	403.51	
<i>Diospyros crassinervis</i>	0.20	1.17	26	30.41	
<i>Amyris balsamifera</i>	1.60	9.36	26	243.27	
<i>Guaiacum sanctum</i>	0.30	1.75	28	49.12	
	17.10	100.00		2011.70	

In dry and/or saline ecosystems, CSI lower values mean that the forest plot is integrated mostly by pioneers and/or exuberants while higher values means that the forest plot is dominated by opportunists and/or austeres *sensu lato*. In a second step, the Phytomass values for the considered species are grouped according to their particular

strategies. In the example we use the Order V strategies for DSE which include one to several successional numbers (SN) as showed in the column for “Grouped SN values” in the next table. Consequently, the strategies proportions in each case are grouped as showed in the column “Strategy proportions in the plot” (next table).

Chosen Order V Strategies	Grouped SN values	Strategy's proportions in the plot	Average Reproductive and Vegetative Variables for each Order VI Strategy											
			STR	SSZ	SWE	SFR	TOL	SHA	SCL	DEN	AFA	HEI	VOL	
EPd	1 & 2	0.00	1	2	1	2	2	2	2	1	2	2	3	3
LPd	3 & 4	3.60	1	2	1	1	1	3	2	2	3	2	2	2
SPd	5 to 8	12.59	2	2	1	2	2	2	3	3	3	3	3	3
ESd	9 to 12	8.99	3	4	3	3	2	2	3	2	2	2	2	2
RSd	13 to 16	0.00	3	3	3	3	1	3	3	2	3	3	3	3
ROSd	17 to 19	21.05	3	3	2	3	1	3	3	3	3	3	3	3
IOSd	20 & 21	11.51	2	3	2	3	3	1	3	2	3	4	4	4
IASd	22 to 26	23.20	3	3	2	3	2	3	3	3	3	4	4	4
UASd	27 & 28	19.06	3	3	3	4	3	3	4	3	3	3	3	3
Total		100.00												

Once the "Strategies proportions in the plot" (third column in former table) are grouped, the resulting values are multiplied by the corresponding category (1 to 4) for each

of the considered variables (average reproductive and vegetative variables for each Order V Strategy in the former table). The results appear in the next table:

	STR	SSZ	SWE	SFR	TOL	SHA	SCL	DEN	AFA	HEI	VOL
EPh	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LPh	3.6	7.2	3.6	3.6	3.6	10.8	7.2	7.2	10.8	7.2	7.2
SPh	25.2	25.2	12.6	25.2	25.2	25.2	37.8	37.8	37.8	37.8	37.8
ESh	27.0	36.0	27.0	27.0	18.0	18.0	27.0	18.0	18.0	18.0	18.0
RSh	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
ROSh	63.2	63.2	42.1	63.2	21.1	63.2	63.2	63.2	63.2	63.2	63.2
IOSh	23.0	34.5	23.0	34.5	34.5	11.5	34.5	23.0	34.5	46.0	46.0
IASh	69.6	69.6	46.4	69.6	46.4	69.6	69.6	69.6	69.6	92.8	92.8
UASh	57.2	57.2	57.2	76.2	57.2	57.2	76.2	57.2	57.2	57.2	57.2
Σ	268.7	292.8	211.9	299.3	205.9	255.4	315.5	275.9	291.0	322.1	322.1
Σ/100	2.7	2.9	2.1	3.0	2.1	2.6	3.2	2.8	2.9	3.2	3.2
Rounded	3	3	2	3	3	2	3	3	2	3	3

Finally, the EKSA (ecosystem *K*-strategist area, in %) is estimated from rounded values at the table's bottom using the same equation as for the strategy *K* area (SKA):

$$EKSA = \frac{\sum_{i=1}^{10} (\text{Var}_i * \text{Var}_{i+1}) + (\text{Var}_{11} * \text{Var}_1)}{(MVA)^2 * \text{Nr. Vars.}}$$

The EKSA value in the given example from rounded values is 49.43%.

## APPENDIX IV

**Appendix IV-A.** Clustering of species belonging to each of 23 Order VI strategies for humid (h) forest ecosystems. TD (taxonomic distance) values at each major differentiation tie are in underlined. SN, Successional Number; EPh, Early Pioneers; LPh, Late Pioneers; SPh, Sclerophyllous Pioneers; ESh, Exuberant Stabilizers; RSh, Restoring Stabilizers; ROSh & IOSh, Restoring & Invasive Opportunist Stabilizers; IASh & UASh, Invasive and Ultimate Austere Stabilizers. Pr, species preference for humid habitats (H) or being indifferent (I) to the habitat type.

SN	O-VI	TREE SPECIES	Pr	TD	SN	O-VI	TREE SPECIES	Pr	TD		
1	EPh1	<i>Cecropia schreberiana</i>	I	0.56	7	ESh2	<i>Hymenaea courbaril</i>	H	0.42		
		<i>Heliocarpus americanus</i>	H	0.80			<i>Micropholis polita</i>	H	0.87		
		<i>Ochroma lagopus</i>	H	1.01			<i>Juglans insularis</i>	H	0.67		
		<i>Guazuma ulmifolia</i>	I	0.76			<i>Mammea americana</i>	I	<u>1.46</u>		
		<i>Muntingia calabura</i>	I	0.55			8	RSh1	<i>Bauhinia monandra</i>	I	1.28
		<i>Spathodea campanulata</i>	I	1.13					<i>Dendropanax arboreus</i>	H	1.04
		<i>Trema micrantha</i>	H	<u>1.33</u>					<i>Guarea guidonia</i>	H	1.18
2	EPh2	<i>Brunellia comocladifolia</i>	H	0.90			<i>Erythrina berteriana</i>	H	0.71		
		<i>Calycophyllum candidissimum</i>	H	0.70			<i>Cordia collococca</i>	I	0.92		
		<i>Cyrilla racemiflora</i>	H	0.98			<i>Plumeria obtusa</i>	I	1.07		
		<i>Casuarina equisetifolia</i>	I	1.09			<i>Shefflera morototonii</i>	H	0.59		
		<i>Psidium guajava</i>	I	0.63			<i>Gmelina arborea</i>	I	1.20		
		<i>Tetrazygia bicolor</i>	I	0.86			<i>Melia azedarach</i>	I	<u>1.39</u>		
		<i>Tabebuia angustata</i>	H	0.43	9	RSh2	<i>Eugenia foetida</i>	I	<u>1.29</u>		
		<i>Tabebuia shaferi</i>	H	1.21	10	RSh3	<i>Sloanea amygdalina</i>	H	0.71		
		<i>Miconia elata</i>	H	<u>1.54</u>			<i>Sapium jamaicense</i>	H	0.90		
3	LPh1	<i>Ficus subscabrida</i>	H	0.65			<i>Juniperus lucayana</i>	I	0.81		
		<i>Ficus cf. obtusifolia</i>	H	1.03			<i>Guettarda elliptica</i>	I	0.98		
		<i>Ceiba pentandra</i>	I	<u>1.27</u>			<i>Fraxinus cubensis</i>	H	<u>1.25</u>		
4	LPh2	<i>Trichospermum grewiifolius</i>	H	0.93	11	ROSh1	<i>Roystonea regia</i>	I	0.62		
		<i>Talipariti elatum</i>	I	1.05			<i>Tectona grandis</i>	I	0.84		
		<i>Erythrina poeppigiana</i>	H	<u>1.46</u>			<i>Hura crepitans</i>	I	0.99		
5	SPh	<i>Eucalyptus citriodora</i>	I	0.90			<i>Alchornea latifolia</i>	H	0.60		
		<i>Pinus caribaea</i>	I	<u>1.81</u>			<i>Trophis racemosa</i>	H	0.84		
6	ESh1	<i>Cedrela odorata</i>	I	0.58			<i>Diospyros philippensis</i>	H	0.93		
		<i>Zanthoxylum martinicense</i>	I	0.88			<i>Guettarda combsii</i>	H	0.87		
		<i>Albizia procera</i>	I	0.89			<i>Coccoloba diversifolia</i>	I	<u>1.12</u>		
		<i>Samanea saman</i>	I	0.35	12	ROSh2	<i>Cinnamomum triplinerve</i>	H	0.53		
		<i>Enterolobium cyclocarpum</i>	I	0.65			<i>Ocotea leucoxyton</i>	H	0.65		
		<i>Khaya nyassica</i>	I	0.56			<i>Persea americana</i>	I	0.82		
		<i>Swietenia macrophylla</i>	I	0.74			<i>Theobroma cacao</i>	H	0.56		
		<i>Spondias mombin</i>	I	1.20			<i>Annona muricata</i>	I	0.96		
		<i>Cassia grandis</i>	I	<u>1.24</u>			<i>Anacardium occidentale</i>	I	<u>1.18</u>		
7	ESh2	<i>Prunus occidentalis</i>	H	0.72	13	IOSh1	<i>Maclura tinctoria</i>	I	0.70		
		<i>Carapa guianensis</i>	H	0.89			<i>Albizia berteriana</i>	H	0.61		
		<i>Anacardium excelsum</i>	H	0.56			<i>Zuelania guidonia</i>	I	0.89		
		<i>Sterculia apetala</i>	I	0.69			<i>Cordia gerascanthus</i>	I	0.74		
		<i>Pouteria sapota</i>	I	0.98			<i>Cordia alliodora</i>	I	0.93		
		<i>Mangifera indica</i>	I	0.92			<i>Clusia rosea</i>	I	<u>0.99</u>		
		<i>Terminalia catappa</i>	I	1.10			14	IOSh2	<i>Piscidia piscipula</i>	H	0.50
<i>Sideroxylon foetidissimum</i>	I	0.83	<i>Savia sessiliflora</i>	I	0.60						
		<i>Decussocarpus rospigliosii</i>	H	0.60			<i>Vitex divaricata</i>	I	0.74		

## Appendix IV-A. (cont.)

SN	O-VI	TREE SPECIES	Pr	TD	SN	O-VI	TREE SPECIES	Pr	TD
14	IOSh2	<i>Poeppigia procera</i>	H	0.49	20	UASh3	<i>Guettarda calyprata</i>	I	0.50
		<i>Abarema obovalis</i>	I	0.60			<i>Bunchosia media</i>	I	0.18
		<i>Caesalpinia violacea</i>	I	0.36			<i>Coccoloba retusa</i>	I	0.29
		<i>Swietenia mahagoni</i>	I	0.78			<i>Sideroxylon salicifolium</i>	I	0.41
		<i>Bucida buceras</i>	H	0.59			<i>Faramea occidentalis</i>	I	0.66
		<i>Chrysophyllum cainito</i>	I	<u>0.93</u>			<i>Magnolia cubensis</i>	H	0.45
15	IOSh3	<i>Leucaena leucocephala</i>	I	0.62	21	UASh4	<i>Talauma orbicularis</i>	H	0.53
		<i>Albizia lebeck</i>	I	0.19			<i>Protium cubense</i>	H	<u>0.71</u>
		<i>Trichilia hirta</i>	I	0.42			<i>Drypetes alba</i>	I	0.48
		<i>Delonix regia</i>	I	0.73			<i>Exothea paniculata</i>	I	0.21
		<i>Bursera simaruba</i>	I	<u>1.09</u>			<i>Oxandra lanceolata</i>	I	0.37
16	IASh1	<i>Allophylus cominia</i>	I	0.60	22	UASh5	<i>Tamarindus indica</i>	I	0.40
		<i>Cupania americana</i>	I	0.43			<i>Chione cubensis</i>	H	0.37
		<i>Cupania glabra</i>	I	0.66			<i>Rheedia aristata</i>	H	0.54
		<i>Chrysophyllum oliviforme</i>	I	0.48			<i>Calophyllum antillanum</i>	I	0.37
		<i>Syzygium jambos</i>	H	0.77			<i>Nectandra coriacea</i>	I	0.63
		<i>Coffea arabica</i>	H	0.64			<i>Buchenavia capitata</i>	H	0.38
		<i>Trichilia havanensis</i>	H	0.85			<i>Guibourtia hymenifolia</i>	H	0.46
		<i>Matayba apetala</i>	H	0.77			<i>Andira inermis</i>	I	<u>0.65</u>
		<i>Gymnanthes lucida</i>	I	0.65			<i>Sapindus saponaria</i>	H	0.34
17	IASh2	<i>Citrus aurantium</i>	I	<u>0.98</u>	23	UASh6	<i>Prunus myrtifolia</i>	H	0.41
		<i>Erythroxylum areolatum</i>	I	0.45			<i>Licaria triandra</i>	H	0.46
		<i>Picramnia pentandra</i>	I	0.69			<i>Ocotea cuneata</i>	H	0.28
		<i>Wallenia laurifolia</i>	H	0.62			<i>Beilschmiedia pendula</i>	H	0.00
		<i>Erythroxylum havanense</i>	I	0.48			<i>Brosimum alicastrum</i>	H	0.36
		<i>Erythroxylum confusum</i>	I	0.77			<i>Oxandra laurifolia</i>	H	0.25
		<i>Brya microphylla</i>	I	0.55			<i>Pseudolmedia spuria</i>	H	0.58
		<i>Comocladia dentata</i>	I	0.28			<i>Chionanthus domingensis</i>	H	0.47
		<i>Eugenia axillaris</i>	I	0.47			<i>Manilkara zapota</i>	H	<u>0.60</u>
18	UASh1	<i>Gliricidia sepium</i>	I	<u>0.93</u>	<i>Pera bumeliaefolia</i>	H	0.41		
		<i>Terminalia intermedia</i>	I	0.37	<i>Cojoba arborea</i>	H	0.50		
19	UASh2	<i>Terminalia eryostachia</i>	I	<u>0.87</u>	<i>Cynometra cubensis</i>	H	0.52		
		<i>Lysiloma sabicu</i>	I	0.70	<i>Manilkara valenzuelana</i>	H	0.29		
20	UASh3	<i>Guatteria moralesi</i>	H	<u>0.77</u>	<i>Diospyros caribaea</i>	H	0.33		
		<i>Ehretia tinifolia</i>	I	0.50	<i>Manilkara jaimiqui</i>	H	0.37		
		<i>Zanthoxylum elephantiasis</i>	H	0.40	<i>Pouteria dominigensis</i>	H	0.25		
		<i>Inga vera</i>	H	0.42	<i>Pouteria dictyoneura</i>	H	----		
		<i>Margaritaria nobilis</i>	H	0.59					
		<i>Podocarpus angustifolius</i>	H	0.44					

**Appendix IV-B.** Clustering of species belonging to each of 28 Order V strategies for dry (d) and/or saline forest ecosystems. TD (taxonomic distance) values at each major differentiation tie are in underlined. SN, Successional Number; EPd, Early Pioneers; LPd, Late Pioneers; SPd, Sclerophyllous Pioneers; ESd, Exuberant Stabilizers; RSd, Restoring Stabilizers; ROSd & IOSd, Restoring & Invasive Opportunist Stabilizers; IASd & UASd, Invasive and Ultimate Austere Stabilizers. Pr, species preference for dry and/or saline habitats (DS) or being indifferent (I) to the habitat type.

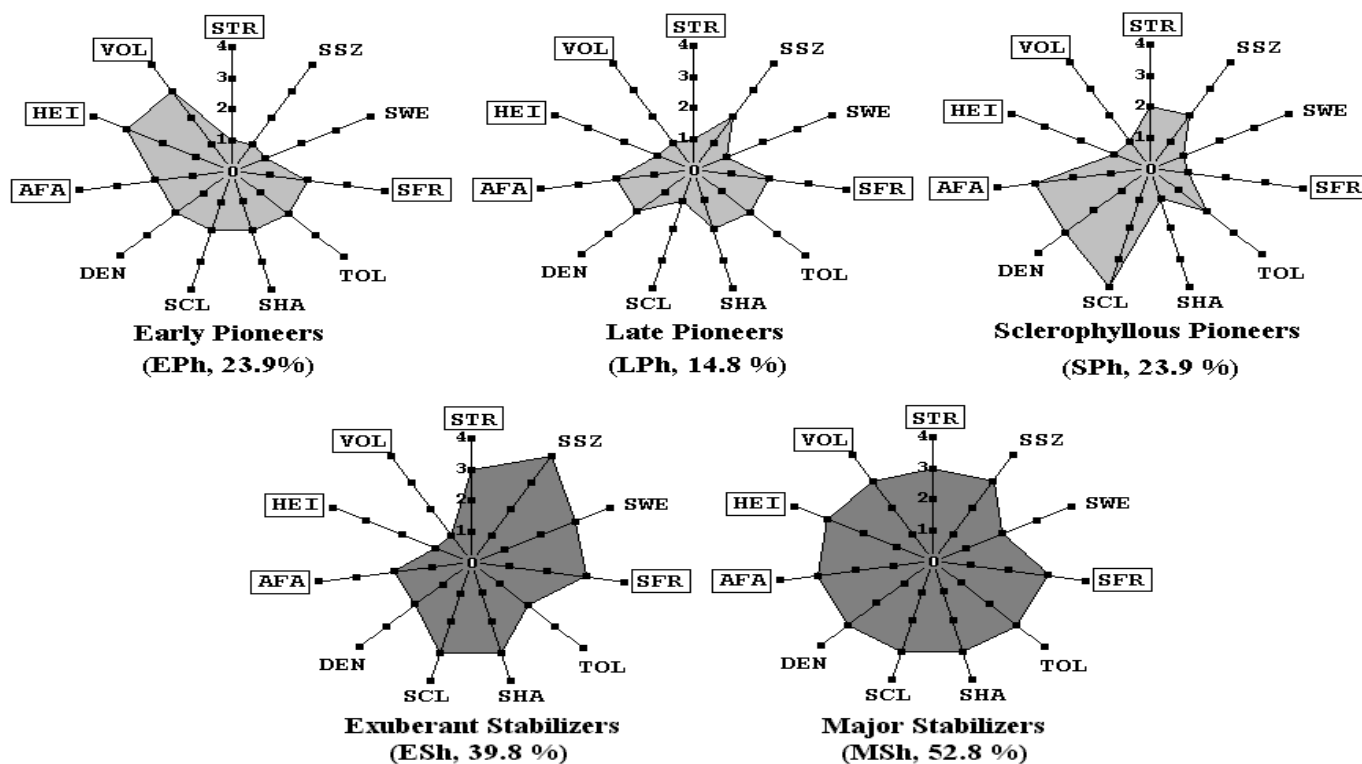
SN	O-V	TREE SPECIES	Pr	TD	SN	O-V	TREE SPECIES	Pr	TD		
1	EPd1	<i>Cecropia schreberiana</i>	I	1.00	12	ESd4	<i>Persea americana</i>	I	0.44		
		<i>Talipariti elatum</i>	I	1.12			<i>Pouteria sapota</i>	I	<u>1.47</u>		
		<i>Guazuma ulmifolia</i>	I	0.80			13	RSd1	<i>Melia azedarach</i>	I	1.18
		<i>Muntingia calabura</i>	I	0.66					<i>Avicennia germinans</i>	DS	1.02
		<i>Spathodea campanulata</i>	I	<u>1.42</u>					<i>Laguncularia racemosa</i>	DS	0.41
2	EPd2	<i>Bauhinia monandra</i>	I	1.23	14	RSd2	<i>Rhizophora mangle</i>	DS	<u>1.46</u>		
		<i>Plumeria obtusa</i>	I	0.55			15	RSd3	<i>Coccoloba uvifera</i>	DS	<u>1.43</u>
		<i>Hamelia patens</i>	DS	0.99			<i>Ateleia apetala</i>		DS	0.58	
		<i>Luehea speciosa</i>	DS	0.71			<i>Hippomane mancinella</i>		DS	0.81	
		<i>Thespesia populnea</i>	DS	<u>1.56</u>			<i>Phyllostylon brasiliensis</i>		DS	0.58	
3	LPd1	<i>Conocarpus erectus</i>	DS	<u>1.50</u>			<i>Pinus tropicalis</i>	DS	1.03		
4	LPd2	<i>Ceiba pentandra</i>	I	0.98	16	RSd4	<i>Genipa americana</i>	DS	<u>1.30</u>		
		<i>Ficus aurea</i>	DS	1.17			<i>Anacardium occidentale</i>	I	0.75		
		<i>Cedrela cubensis</i>	DS	<u>1.52</u>			<i>Annona muricata</i>	I	1.08		
5	SPd1	<i>Eugenia foetida</i>	I	<u>1.38</u>			<i>Bombacopsis cubensis</i>	DS	0.73		
6	SPd2	<i>Psidium guajava</i>	I	0.70	17	ROSd1	<i>Simarouba glauca</i>	DS	<u>1.23</u>		
		<i>Tetrazygia bicolor</i>	I	0.94			<i>Citharexylum fruticosum</i>	DS	0.66		
		<i>Pachyanthus cubensis</i>	DS	<u>1.34</u>			<i>Cordia sebestena</i>	DS	0.62		
7	SPd3	<i>Casuarina equisetifolia</i>	I	0.75			<i>Hebestigma cubense</i>	DS	0.50		
		<i>Eucalyptus citriodora</i>	I	0.93			<i>Metopium brownei</i>	DS	0.81		
		<i>Pinus caribaea</i>	I	<u>1.16</u>			<i>Polygala cuneata</i>	DS	0.51		
8	SPd4	<i>Clusia rosea</i>	I	0.81			<i>Picrodendron macrocarpum</i>	DS	0.42		
		<i>Cordia gerascanthus</i>	I	0.88			<i>Quercus cubana</i>	DS	0.71		
		<i>Cordia alliodora</i>	I	0.75			<i>Ximenia americana</i>	DS	0.90		
		<i>Zanthoxylum martinicense</i>	I	0.66			<i>Albizia cubana</i>	DS	0.57		
		<i>Zuelania guidonia</i>	I	0.93			<i>Peltophorum adnatum</i>	DS	0.69		
		<i>Maclura tinctoria</i>	I	<u>1.67</u>			<i>Celtis trinervia</i>	DS	<u>1.05</u>		
9	ESd1	<i>Albizia procera</i>	I	0.93	18	ROSd2	<i>Byrsonima crassifolia</i>	DS	0.40		
		<i>Cedrela odorata</i>	I	0.89			<i>Colubrina arborescens</i>	DS	0.55		
		<i>Enterolobium cyclocarpum</i>	I	0.66			<i>Curatella americana</i>	DS	0.79		
		<i>Samanea saman</i>	I	0.78			<i>Adelia ricinella</i>	DS	0.43		
		<i>Khaya nyassica</i>	I	0.59			<i>Zanthoxylum fagara</i>	DS	0.52		
		<i>Swietenia macrophylla</i>	I	1.08			<i>Krugiodendron ferreum</i>	DS	0.70		
		<i>Cassia grandis</i>	I	<u>1.27</u>			<i>Belairia mucronata</i>	DS	<u>0.93</u>		
10	ESd2	<i>Gmelina arborea</i>	I	<u>1.21</u>	19	ROSd3	<i>Alvaradoa amorphoides</i>	DS	0.71		
11	ESd3	<i>Sideroxylon foetidissimum</i>	I	0.90			<i>Cassia ekmaniana</i>	DS	0.45		
		<i>Terminalia catappa</i>	I	<u>1.12</u>			<i>Prosopis juliflora</i>	DS	0.58		
12	ESd4	<i>Hura crepitans</i>	I	0.37			<i>Forestiera rhamnifolia</i>	DS	0.43		
		<i>Sterculia apetala</i>	I	0.91			<i>Xylopia aromatica</i>	DS	0.52		
		<i>Tectona grandis</i>	I	0.98			<i>Jacaranda coerulea</i>	DS	0.63		
		<i>Roystonea regia</i>	I	0.63			<i>Lysiloma latisiliqua</i>	DS	0.49		
		<i>Calophyllum antillanum</i>	I	0.50			<i>Pithecellobium lentiscifolium</i>	DS	0.70		
		<i>Chrysophyllum cainito</i>	I	0.70			<i>Cameraria retusa</i>	DS	0.58		
		<i>Mammea americana</i>	I	0.79			<i>Haematoxylum campechianum</i>	DS	0.84		
		<i>Cordia collococca</i>	I	0.60			<i>Carpodiptera cubensis</i>	DS	<u>1.13</u>		
		<i>Spondias mombin</i>	I	0.93	20	IOSd1	<i>Bursera simaruba</i>	I	<u>1.03</u>		
		<i>Mangifera indica</i>	I	0.79							

## Appendix IV-B. (Cont.)

SN	O-V	TREE SPECIES	Pr	TD	SN	O-V	TREE SPECIES	Pr	TD		
21	IOSd2	<i>Albizia lebbbeck</i>	I	0.20	26	IASd5	<i>Eugenia axillaris</i>	I	0.47		
		<i>Trichilia hirta</i>	I	0.49			<i>Erythroxylum confusum</i>	I	0.39		
		<i>Delonix regia</i>	I	0.70			<i>Erythroxylum alaternifolium</i>	DS	0.51		
		<i>Leucaena leucocephala</i>	I	0.87			<i>Gliricidia sepium</i>	I	0.68		
		<i>Allophylus cominia</i>	I	0.60			<i>Erythroxylum areolatum</i>	I	0.45		
		<i>Chrysophyllum oliviforme</i>	I	0.66			<i>Picramnia pentandra</i>	I	<u>0.84</u>		
		<i>Cupania americana</i>	I	0.45			27	UASd1	<i>Bunchosia media</i>	I	0.19
		<i>Cupania glabra</i>	I	0.81					<i>Coccoloba retusa</i>	I	0.38
		<i>Gymnanthes lucida</i>	I	0.68					<i>Sideroxylon salicifolium</i>	I	0.45
		<i>Citrus aurantium</i>	I	<u>1.10</u>					<i>Faramea occidentalis</i>	I	0.56
22	IASd1	<i>Guettarda elliptica</i>	I	0.85	<i>Guettarda calyptata</i>	I	0.63				
		<i>Juniperus lucayana</i>	I	<u>1.08</u>	<i>Amyris balsamifera</i>	DS	0.37				
23	IASd2	<i>Caesalpinia violacea</i>	I	0.35	<i>Canella winterana</i>	DS	0.51				
		<i>Swietenia mahagoni</i>	I	0.76	<i>Hypelate trifoliata</i>	DS	0.69				
		<i>Lysiloma sabicu</i>	I	0.77	<i>Drypetes alba</i>	I	0.58				
		<i>Diospyros crassinervis</i>	DS	<u>1.01</u>	<i>Exothea paniculata</i>	I	0.21				
24	IASd3	<i>Coccoloba diversifolia</i>	I	<u>0.99</u>	<i>Oxandra lanceolata</i>	I	0.39				
25	IASd4	<i>Ehretia tinifolia</i>	I	0.63	<i>Tamarindus indica</i>	I	0.46				
		<i>Vitex divaricata</i>	I	0.72	<i>Nectandra coriacea</i>	I	<u>0.74</u>				
		<i>Abarema obovalis</i>	I	0.42	28	UASd2	<i>Andira inermis</i>	I	0.57		
		<i>Bourreria succulenta</i>	DS	0.38			<i>Terminalia eryostachia</i>	I	0.35		
		<i>Casasia calophylla</i>	DS	0.57			<i>Swartzia cubensis</i>	DS	0.48		
		<i>Savia sessiliflora</i>	I	0.51			<i>Terminalia intermedia</i>	I	0.42		
		<i>Bauhinia divaricata</i>	DS	0.28			<i>Guaiacum officinale</i>	DS	0.62		
<i>Casearia hirsuta</i>	DS	<u>0.85</u>	<i>Chrysobalanus icaco</i>	DS	0.40						
26	IASd5	<i>Brya microphylla</i>	I	0.52	<i>Ottoschulzia cubensis</i>	DS	0.46				
		<i>Erythroxylum havanense</i>	I	0.63	<i>Guaiacum sanctum</i>	DS	-----				
		<i>Comocladia dentata</i>	I	0.29							

APPENDIX V

Humid Forest Ecosystems, Order II Strategies



Dry and/or Saline Ecosystems, Order II Strategies

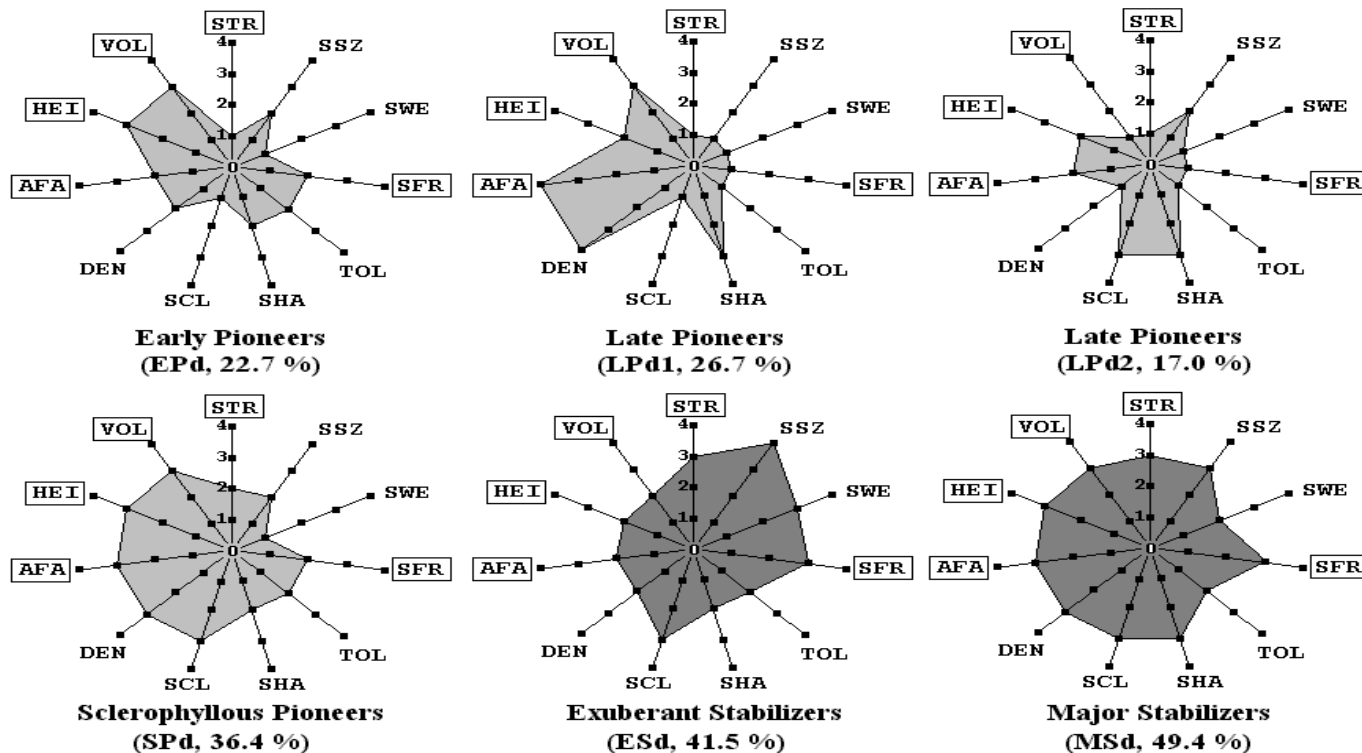
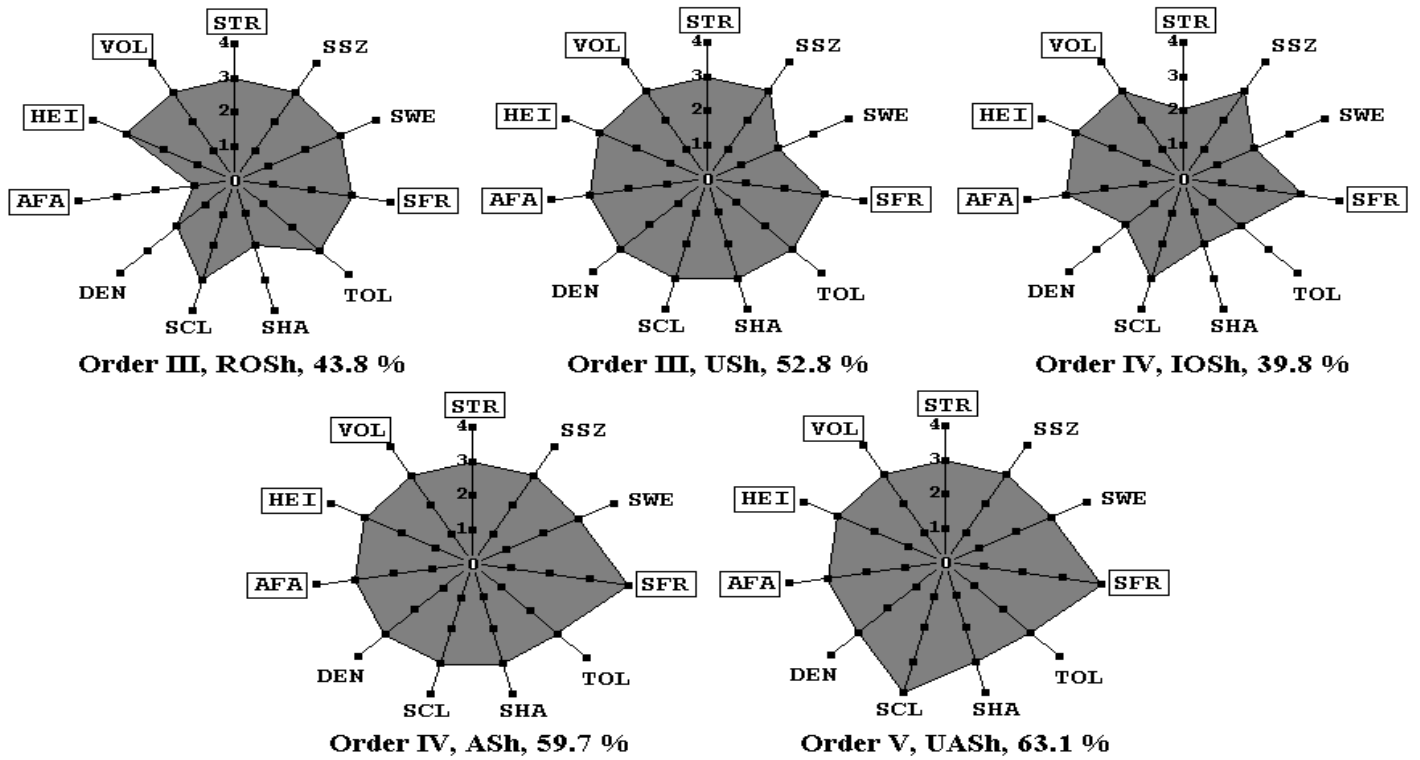
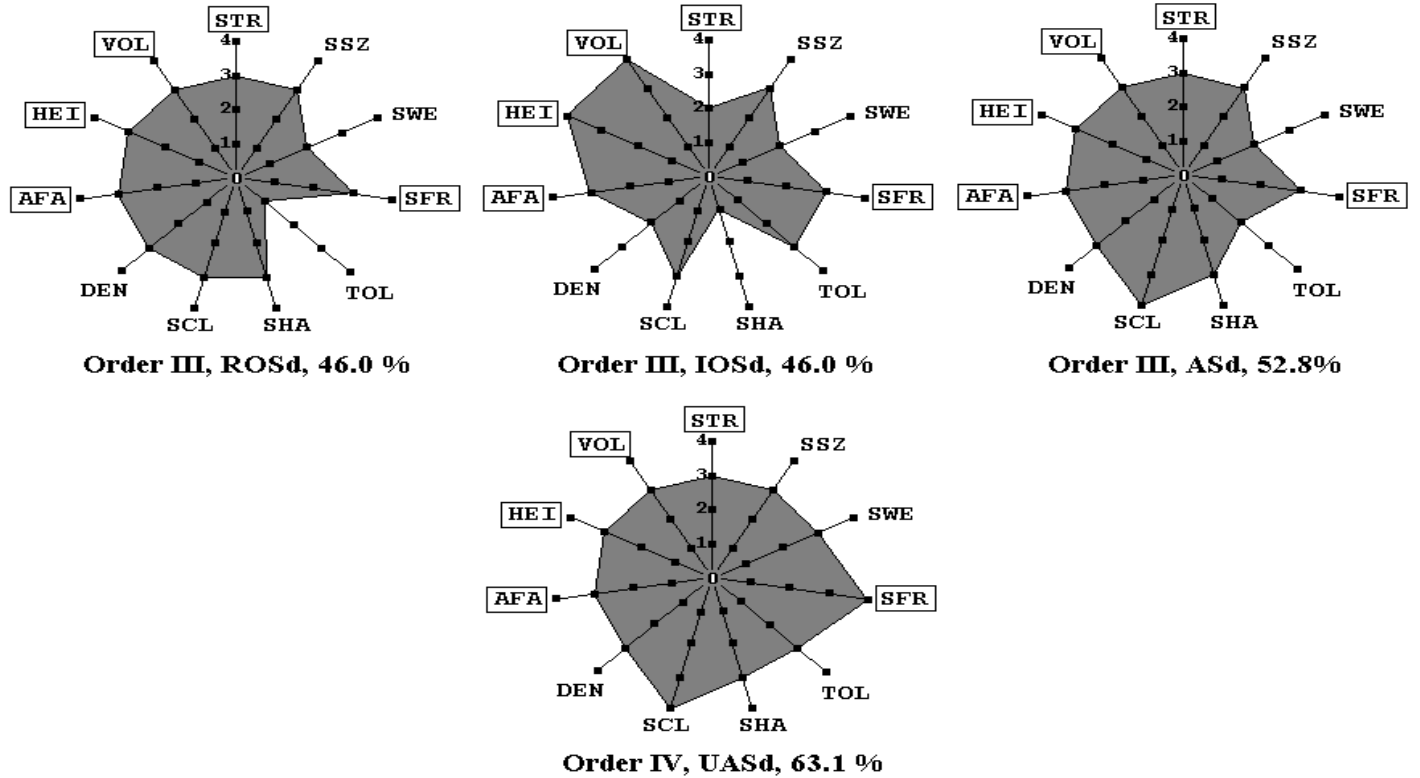


Figure V-1. Order II successional strategies for humid forest (HFE) and dry and/or saline ecosystems (DSE).

**Humid Forest Ecosystems: Grouping Strategies Belonging to Intermediate Orders**



**Dry and/or Saline Ecosystems: Grouping Strategies Belonging to Intermediate Orders**



**Figure V-2.** Intermediate strategies Orders polygrams for humid forest (above) and dry and/or saline ecosystems (below).



Humid Forest Ecosystems, Order VI Strategies

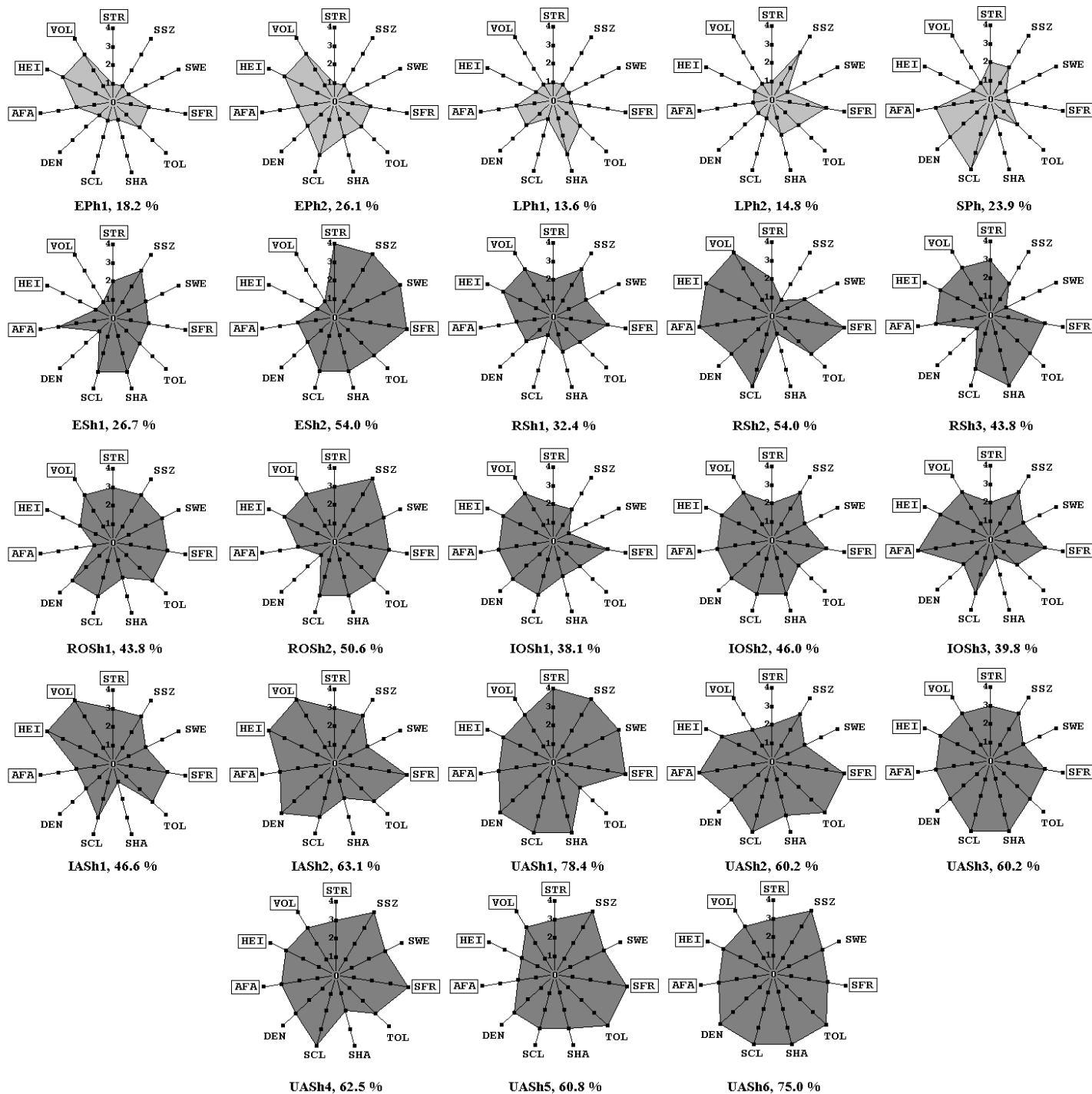


Figure V-3. Twenty three final strategies (Order VI) polygrams for humid forest ecosystems.

Dry and/or Saline Ecosystems, Order V Strategies

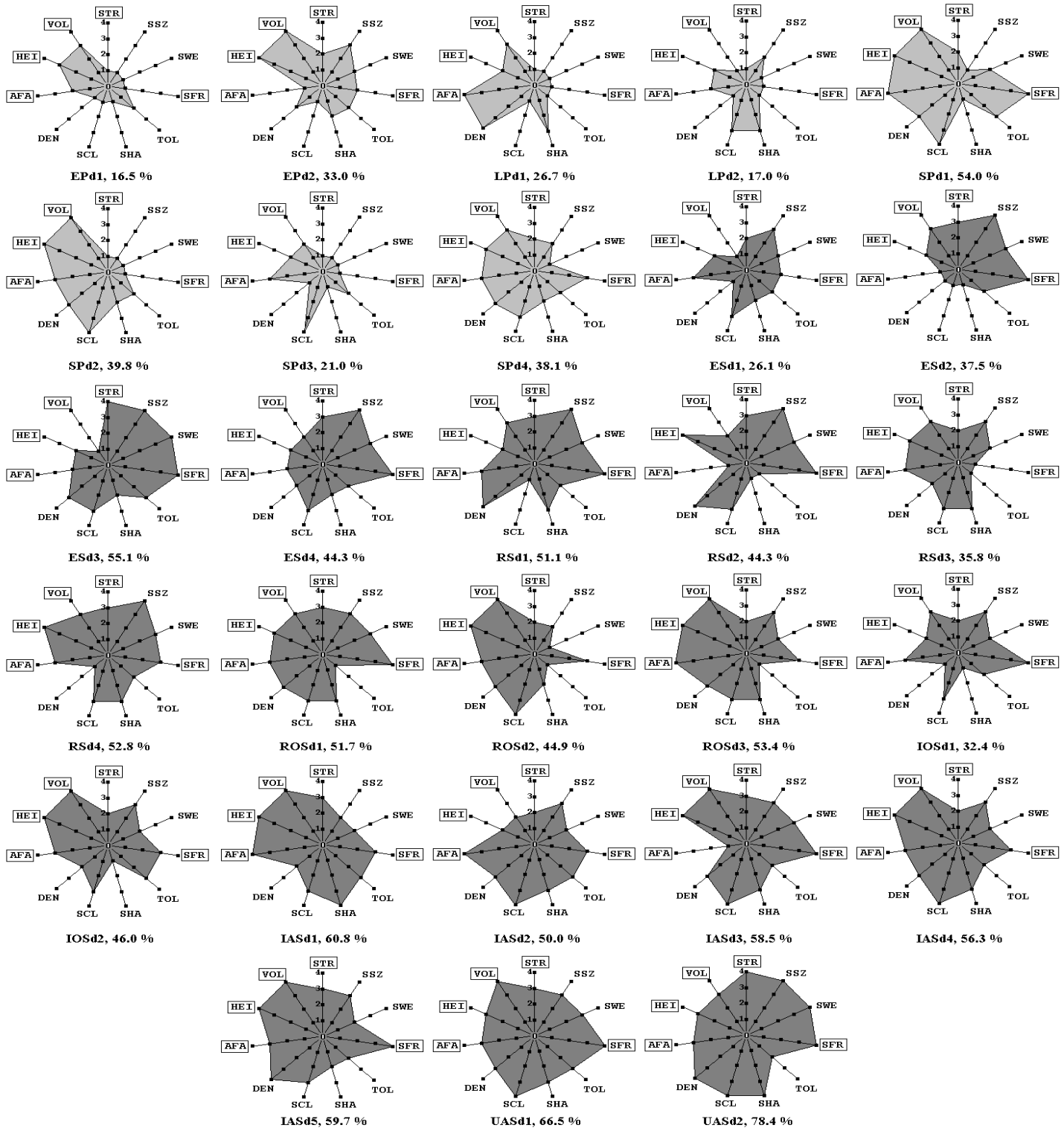


Figure V-4. Twenty eight final strategies (Order V) polygrams for dry and/or saline ecosystems.

## APPENDIX VI

**Appendix VI-A.** Estimation of ceno-successional index (CSI) for several hypothetical or real forest variants belonging to the assembly of humid forest ecosystems (HFE).

Note: *Yagrumal Joven*, *Yagrumal*, *Majagual*, *Los Jagüeyes*, *Helechal*, *El Ébano*, *El Mulo Sur*, *Macurijal*, *Macagual* and *Bosque Joven* belong to the HFE assembly and can be considered as Tropical Humid Forests functioning as more humid variants within a region of mostly Tropical Dry Forests. On the other hand, *Cima Macagual*, *El Salón Sur* and *El Rubí Sur*, belonging also to the HFE assembly, might be considered as a functional frontier between HFE and DSE (Dry and/or Saline Ecosystems). However, these last three plots function rather as Tropical Dry Forests. At the Reserve of Biosphere *Sierra del Rosario*, annual rainfall varies between 2014 and 2300 mm. On the other hand, the plot *Cima Macagual* is relatively drier than the remaining plots because it grows on a summit (convex topography) while the plots *El Salón Sur* and *El Rubí Sur* grow on topographies directly exposed to the South, on a hill and in a wide open valley, respectively. Note that in these cases successional numbers (SN) vary between 1 and 23, according to the Order VI strategies demonstrated in Figure 1.

*Yagrumal Joven* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Cecropia schreberiana</i>	12.69	93.55	1	93.55	
<i>Ficus subscabrida</i>	0.52	3.83	3	11.50	
<i>Dendropanax arboreus</i>	0.02	0.18	8	1.43	1.26
<i>Guarea guidonia</i>	0.33	2.43	8	19.46	
	13.56	100.00		125.95	

Note: The forest plot (trees less than 10 m high) is at 400 m a.s.l. on a lightly concave slope with exposition to North. *Cecropia schreberiana* was a super-dominant species during 1984 while saplings or small trees represented other tree species. Root mats do not occur on the soil. The plot is humid all year long.

*Yagrumal* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Cecropia schreberiana</i>	12.69	85.69	1	85.69	
<i>Ficus subscabrida</i>	0.52	3.51	3	10.53	
<i>Dendropanax arboreus</i>	0.02	0.16	8	1.31	
<i>Guarea guidonia</i>	0.33	2.23	8	17.83	2.43
<i>Trophis racemosa</i>	0.52	3.51	11	38.62	
<i>Matayba apetala</i>	0.47	3.17	16	50.78	
<i>Pseudolmedia spuria</i>	0.26	1.76	22	38.62	
	14.81	100.00		243.38	

Note: The forest plot (trees less than 15 m high) is at 360 m a.s.l. on a concave slope along an intermittent creek with W-NW exposition. *Cecropia schreberiana* was a super-dominant species during 1984. Root mats do not occur on the soil. The plot is highly humid all year long.

*Majagual* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Ficus subscabrida</i>	0.18	0.81	3	2.43	
<i>Talipariti elatum</i>	13.76	61.25	4	244.99	
<i>Sideroxylon foetidissimum</i>	0.07	0.31	7	2.18	
<i>Dendropanax arboreus</i>	2.65	11.79	8	94.34	
<i>Alchornea latifolia</i>	2.34	10.41	11	114.55	
<i>Trophis racemosa</i>	1.70	7.57	11	83.22	
<i>Matayba apetala</i>	1.09	4.85	16	77.61	
<i>Calophyllum antillanum</i>	0.30	1.35	21	28.37	6.84
<i>Nectandra coriacea</i>	0.10	0.44	21	9.33	
<i>Oxandra lanceolata</i>	0.01	0.01	21	0.10	
<i>Beilschmiedia pendula</i>	0.01	0.01	22	0.17	
<i>Pseudolmedia spuria</i>	0.27	1.20	22	26.43	
	22.47	100.00		683.72	

Note: The forest plot (trees less than 18 m high) is at 380 m a.s.l. along a flat to concave hill slope with W exposition. *Talipariti elatum* as a super-dominant species during 1984 after felling interrupted the successional natural process. Root mats do not occur on the soil. The plot is highly humid all year long.

*Macagual* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Ficus subscabrida</i>	1.18	3.00	3	9.01	
<i>Talipariti elatum</i>	0.56	1.42	4	5.70	
<i>Sideroxylon foetidissimum</i>	0.89	2.26	7	15.85	
<i>Dendropanax arboreus</i>	1.52	3.87	8	30.94	
<i>Alchornea latifolia</i>	1.56	3.97	11	43.66	
<i>Trophis racemosa</i>	3.69	9.39	11	103.28	
<i>Matayba apetala</i>	6.52	16.59	16	265.45	
<i>Calophyllum antillanum</i>	2.65	6.74	21	141.60	17.53
<i>Nectandra coriacea</i>	3.62	9.21	21	193.44	
<i>Oxandra lanceolata</i>	5.23	13.31	21	279.47	
<i>Beilschmiedia pendula</i>	2.52	6.41	22	141.07	
<i>Pseudolmedia spuria</i>	9.36	23.82	22	523.97	
	39.30	100.00		1753.44	

Note: The forest plot (trees less than 18 m high) is at 350 m a.s.l. along a convex hill slope with SE exposition. At present *Pseudolmedia spuria*, *Oxandra lanceolata* and *Matayba apetala* dominate the plot. Root mats on the soil surface are permanent along the year reaching about 10 cm thick or more. The plot is humid enough all year long but soil dries and deeply cracks during the drier season.

## Los Jagüeyes (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Tabebuia shaferi</i>	1.88	4.05	2	8.10	
<i>Ficus subscabrida</i>	26.53	56.99	3	170.97	
<i>Sideroxylon foetidissimum</i>	0.03	0.07	7	0.46	
<i>Dendropanax arboreus</i>	0.02	0.05	8	0.42	
<i>Guarea guidonia</i>	5.69	12.22	8	97.78	
<i>Trophis racemosa</i>	1.52	3.26	11	35.84	
<i>Ocotea leucoxylon</i>	0.01	0.01	12	0.05	
<i>Cordia gerascanthus</i>	0.01	0.01	13	0.07	
<i>Matayba apetala</i>	4.03	8.65	16	138.42	
<i>Trichilia havanensis</i>	0.01	0.01	16	0.03	7.74
<i>Syzygium jambos</i>	0.01	0.01	16	0.19	
<i>Calophyllum antillanum</i>	0.01	0.01	21	0.18	
<i>Drypetes alba</i>	0.89	1.91	21	40.06	
<i>Beilschmiedia pendula</i>	0.01	0.01	22	0.03	
<i>Pseudolmedia spuria</i>	5.93	12.74	22	280.24	
<i>Chionanthus domingensis</i>	0.01	0.01	22	0.21	
<i>Pouteria chrysophyllifolia</i>	0.01	0.03	23	0.58	
	46.55	100.00		773.62	

Note: The forest plot (trees over 25 m high) is at 450 m a.s.l. along a flat to concave hill slope with W exposition. At present *Ficus subscabrida* is a super-dominant species. Root mats do not occur on the soil. The plot is highly humid all year long.

## Helechal (real 20 x 20 m forest plot)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Tabebuia shaferi</i>	1.88	4.28	2	8.56	
<i>Ficus subscabrida</i>	19.75	44.86	3	134.58	
<i>Sideroxylon foetidissimum</i>	0.03	0.07	7	0.49	
<i>Prunus occidentalis</i>	3.34	7.59	7	53.12	
<i>Dendropanax arboreus</i>	0.02	0.06	8	0.44	
<i>Guarea guidonia</i>	0.32	0.73	8	5.82	
<i>Sloanea amygdalina</i>	0.01	0.03	10	0.34	
<i>Trophis racemosa</i>	1.52	3.44	11	37.89	
<i>Ocotea leucoxylon</i>	0.01	0.01	12	0.05	
<i>Cordia gerascanthus</i>	0.01	0.01	13	0.08	
<i>Matayba apetala</i>	4.03	9.15	16	146.36	
<i>Trichilia havanensis</i>	0.01	0.01	16	0.03	
<i>Citrus aurantium</i>	0.12	0.28	16	4.51	
<i>Chrysophyllum oliviforme</i>	0.01	0.01	16	0.01	10.38
<i>Syzygium jambos</i>	0.01	0.01	16	0.20	
<i>Eugenia confusa</i>	0.01	0.03	17	0.52	
<i>Eugenia farameoides</i>	0.01	0.01	17	0.22	
<i>Casearia sylvestris</i>	0.01	0.01	20	0.01	
<i>Faramea occidentalis</i>	0.12	0.28	20	5.68	
<i>Calophyllum antillanum</i>	0.01	0.01	21	0.19	
<i>Drypetes alba</i>	0.89	2.02	21	42.36	
<i>Nectandra coriacea</i>	0.01	0.01	21	0.01	
<i>Beilschmiedia pendula</i>	0.01	0.01	22	0.03	
<i>Pseudolmedia spuria</i>	11.93	27.09	22	596.09	
<i>Chionanthus domingensis</i>	0.01	0.01	22	0.22	
<i>Pouteria chrysophyllifolia</i>	0.01	0.03	23	0.61	
	44.03	100.00		1038.41	

Note: The forest plot (trees over 25 m high) is at 450 m a.s.l. along a flat to concave hill slope with N exposition. At present *Ficus subscabrida* is a super-dominant species. Root mats commonly do not occur on the soil or if present they are extremely thin and appear in small patches. The plot is highly humid all year long.

*El Ébano* (real 20 x 20 m forest plot)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Guazuma ulmifolia</i>	0.01	0.02	1	0.02	
<i>Tabebuia shaferi</i>	1.34	6.14	2	12.29	
<i>Ficus subscabrida</i>	0.18	0.84	3	2.51	
<i>Talipariti elatum</i>	3.76	17.30	4	69.19	
<i>Sideroxylon foetidissimum</i>	0.07	0.32	7	2.25	
<i>Dendropanax arboreus</i>	0.03	0.14	8	1.13	
<i>Alchornea latifolia</i>	3.34	15.37	11	169.08	
<i>Trophis racemosa</i>	0.70	3.24	11	35.63	
<i>Ocotea floribunda</i>	0.07	0.30	12	3.64	
<i>Lonchocarpus domingensis</i>	0.23	1.05	14	14.63	
<i>Matayba apetala</i>	8.09	37.21	16	595.37	
<i>Syzygium jambos</i>	0.01	0.01	16	0.04	13.07
<i>Margaritaria nobilis</i>	0.01	0.01	20	0.08	
<i>Calophyllum antillanum</i>	0.30	1.40	21	29.30	
<i>Nectandra coriacea</i>	0.10	0.46	21	9.64	
<i>Oxandra lanceolata</i>	0.01	0.01	21	0.10	
<i>Beilschmiedia pendula</i>	0.01	0.01	22	0.18	
<i>Pseudolmedia spuria</i>	2.27	10.44	22	229.72	
<i>Chionanthus domingensis</i>	0.05	0.24	22	5.36	
<i>Diospyros caribaea</i>	1.20	5.51	23	126.79	
<i>Pouteria chrysophyllifolia</i>	0.01	0.01	23	0.06	
	21.75	100.00		1307.00	

Note: The forest plot (trees about 20 m high) is at 475 m a.s.l. along a flat to concave hill slope with SE exposition. At present *Matayba apetala* is a super-dominant species. Root mats on the soil surface are rather seasonal, and when appearing, commonly at the beginning of the rainy period, it is often less than 3 cm thick. The plot is humid enough all year long but soil dries and cracks during the drier season.

*El Mulo Sur* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Ficus aurea</i>	1.50	4.84	3	14.52	
<i>Ficus subscabrida</i>	1.90	6.13	3	18.39	
<i>Ceiba pentandra</i>	2.10	6.77	3	20.32	
<i>Trichospermum grewiifolius</i>	2.10	6.77	4	27.10	
<i>Zanthoxylum martinicense</i>	2.50	8.06	6	48.39	
<i>Samanea saman</i>	1.00	3.23	6	19.35	
<i>Cedrela odorata</i>	1.50	4.84	6	29.03	
<i>Cordia collococca</i>	2.00	6.45	8	51.61	
<i>Guarea guidonia</i>	3.00	9.68	8	77.42	
<i>Eugenia foetida</i>	0.50	1.61	9	14.52	10.97
<i>Sapium jamaicense</i>	0.80	2.58	10	25.81	
<i>Alchornea latifolia</i>	1.20	3.87	11	42.58	
<i>Matayba apetala</i>	3.00	9.68	16	154.84	
<i>Calophyllum antillanum</i>	2.50	8.06	21	169.35	
<i>Andira inermis</i>	1.10	3.55	21	74.52	
<i>Pseudolmedia spuria</i>	3.00	9.68	22	212.90	
<i>Bursera simaruba</i>	1.20	3.87	23	89.03	
<i>Manilkara jaimiqui</i>	0.10	0.32	23	7.42	
	31.00	100.00		1097.10	

Note: The forest plot is at 300 m a.s.l. with a SE exposition. It occurs along a deep concave "V" valley and along the intermittent creeks at the superior basin of *San Juan* River. At present large logs reach over 30 m high. Root mats on the soil surface do not occur. The plot is humid enough all year long but soil dries and cracks during the drier season.

## Macurijal (real 20 x 20 m forest plot)

## Bosque Joven (real 20 x 20 m forest plot)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Tabebuia shaferi</i>	1.839	5.52	2	11.04	
<i>Ceiba pentandra</i>	0.440	1.32	3	3.97	
<i>Ficus aurea</i>	0.479	1.44	3	4.31	
<i>Cedrela odorata</i>	4.335	13.01	6	78.07	
<i>Zanthoxylum martinicense</i>	0.016	0.02	6	0.10	
<i>Sideroxylon foetidissimum</i>	0.978	2.94	7	20.56	
<i>Dedropanax arboreus</i>	0.344	1.03	8	8.27	
<i>Guarea guidonea</i>	0.561	1.68	8	13.48	
<i>Alchornea latifolia</i>	6.590	19.78	11	217.58	
<i>Roystonea regia</i>	1.299	3.90	11	42.88	
<i>Trophis racemosa</i>	0.779	2.34	11	25.73	
<i>Ocotea leucoxylo</i>	0.018	0.03	12	0.30	
<i>Cordia gerascanthus</i>	0.047	0.14	13	1.83	
<i>Lonchocarpus domingensis</i>	0.477	1.43	14	20.03	
<i>Savia sessiliflora</i>	0.055	0.17	14	2.31	
<i>Cupania glabra</i>	0.012	0.01	16	0.08	
<i>Chrysophyllum oliviforme</i>	0.015	0.02	16	0.25	13.16
<i>Gymnanthes lucida</i>	0.187	0.56	16	8.98	
<i>Matayba apetala</i>	6.691	20.08	16	321.30	
<i>Trichilia havanensis</i>	0.027	0.08	16	1.28	
<i>Eugenia axillaris</i>	0.046	0.14	17	2.35	
<i>Wallenia laurifolia</i>	0.271	0.81	17	13.84	
<i>Casearia sylvestris</i>	0.016	0.02	20	0.36	
<i>Faramea occidentalis</i>	0.030	0.09	20	1.83	
<i>Margaritaria nobilis</i>	0.104	0.31	20	6.23	
<i>Drypetes alba</i>	0.061	0.18	21	3.87	
<i>Nectandra coriacea</i>	0.029	0.09	21	1.83	
<i>Oxandra lanceolata</i>	0.014	0.04	21	0.88	
<i>Beilschmiedia pendula</i>	0.501	1.50	22	33.09	
<i>Chionanthus domingensis</i>	1.657	4.97	22	109.40	
<i>Ocotea cuneata</i>	1.896	5.69	22	125.20	
<i>Pseudolmedia spuria</i>	3.548	10.65	22	234.28	
<i>Diospyros caribaea</i>	0.014	0.01	23	0.28	
	33.32	100.00		1315.78	

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Cecropia schreberiana</i>	0.31	1.72	1	1.7	
<i>Sideroxylon foetidissimum</i>	0.32	1.80	7	12.6	
<i>Prunus occidentalis</i>	0.02	0.10	7	0.7	
<i>Dendropanax arboreus</i>	0.02	0.12	8	1.0	
<i>Trophis racemosa</i>	1.27	7.00	11	77.0	
<i>Ocotea leucoxylo</i>	0.01	0.01	12	0.0	
<i>Trichilia havanensis</i>	0.01	0.02	15	0.2	
<i>Cupania americana</i>	0.01	0.01	16	0.0	
<i>Chrysophyllum oliviforme</i>	0.01	0.01	16	0.1	
<i>Matayba apetala</i>	3.73	20.62	16	330.0	
<i>Eugenia axillaris</i>	0.01	0.02	17	0.3	
<i>Wallenia laurifolia</i>	0.02	0.12	17	2.0	
<i>Margaritaria nobilis</i>	0.20	1.08	20	21.7	19.16
<i>Faramea occidentalis</i>	0.06	0.35	20	7.1	
<i>Andira inermis</i>	0.24	1.32	21	27.8	
<i>Calophyllum antillanum</i>	0.17	0.92	21	19.4	
<i>Drypetes alba</i>	0.63	3.50	21	73.5	
<i>Nectandra coriacea</i>	0.01	0.01	21	0.3	
<i>Oxandra lanceolata</i>	1.35	7.46	21	156.8	
<i>Beilschmiedia pendula</i>	0.15	0.85	22	18.8	
<i>Chionanthus domingensis</i>	0.01	0.02	22	0.5	
<i>Prunus myrtifolia</i>	1.02	5.67	22	124.7	
<i>Pseudolmedia spuria</i>	8.52	47.14	22	1037.0	
<i>Pouteria dictyoneura</i>	0.03	0.14	23	3.2	
	18.07	100.00		1916.2	

Note: The forest plot (trees about 20 m high) is at 475 m a.s.l. along a rather flat hill slope with S exposition. At present *Matayba apetala* is a super-dominant species. Root mats on the soil surface are rather seasonal, and when appearing, commonly at the beginning of the rainy period, they are often less than 3 cm thick. The plot is humid enough all year long but soil dries and cracks during the drier season.

Note: The forest plot (trees less than 20 m high) is at 400 m a.s.l. along a convex hill slope with NE exposition. At present *Pseudolmedia spuria*, *Oxandra lanceolata* and *Matayba apetala* dominate the plot. Root mats on the soil surface are permanent along the year reaching less than 5 cm thick. The plot is humid enough all year long but soil dries and cracks during the drier season.

## Cima Macagual (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Ficus subscabrida</i>	0.18	0.67	3	2.02	
<i>Sideroxylon foetidissimum</i>	1.52	5.62	7	39.33	
<i>Cedrela odorata</i>	2.52	9.31	7	65.20	
<i>Spondias mombin</i>	1.56	5.77	7	40.36	
<i>Dendropanax arboreus</i>	0.50	1.85	8	14.78	
<i>Trophis racemosa</i>	1.70	6.28	11	69.12	
<i>Bursera simaruba</i>	8.52	31.49	15	472.36	15.12
<i>Matayba apetala</i>	1.09	4.03	16	64.46	
<i>Calophyllum antillanum</i>	0.30	1.12	21	23.56	
<i>Nectandra coriacea</i>	2.89	10.68	21	224.32	
<i>Oxandra lanceolata</i>	3.62	13.38	21	280.98	
<i>Pseudolmedia spuria</i>	2.65	9.79	22	215.48	
	27.06	100.00		1511.96	

Note: The forest plot (trees less than 15 m heights) is at 350 m a.s.l. along a convex summit directly exposed to sunlight. At present *Bursera simaruba* and *Oxandra lanceolata* dominate the plot. Root mats are absent as in other observed tropical dry forests, perhaps due to litter fall not being constant along the year but concentrated during the drier season. The plot is dry enough all year long and soil dries and cracks during drought.

## El Salón Sur (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Ficus subscabrida</i>	0.10	0.41	3	1.24	
<i>Sideroxylon foetidissimum</i>	1.52	6.27	7	43.89	
<i>Cedrela odorata</i>	0.60	2.47	7	17.32	
<i>Spondias mombin</i>	2.00	8.25	7	57.75	
<i>Dendropanax arboreus</i>	0.10	0.41	8	3.30	
<i>Trophis racemosa</i>	1.70	7.01	11	77.13	
<i>Abarema obovalis</i>	0.60	2.47	14	34.65	
<i>Caesalpinea violacea</i>	1.20	4.95	14	69.30	
<i>Trichilia hirta</i>	0.90	3.71	15	55.68	
<i>Bursera simaruba</i>	5.00	20.62	15	309.36	15.37
<i>Gymnanthes lucida</i>	0.50	2.06	16	33.00	
<i>Matayba apetala</i>	2.00	8.25	16	131.99	
<i>Faramea occidentalis</i>	0.30	1.24	20	24.75	
<i>Andira inermis</i>	0.80	3.30	21	69.30	
<i>Calophyllum antillanum</i>	0.30	1.25	21	26.29	
<i>Nectandra coriacea</i>	1.00	4.12	21	86.62	
<i>Oxandra lanceolata</i>	3.62	14.93	21	313.57	
<i>Pseudolmedia spuria</i>	2.00	8.25	22	181.49	
	24.24	100.00		1536.63	

Note: The forest plot (trees less than 20 m high) is at 250 m a.s.l. along a convex and highly stony hill slope directly exposed to the South. At present *Bursera simaruba* and *Oxandra lanceolata* dominate the plot. Root mats are absent as in other observed tropical dry forests, perhaps due to litter fall not being constant along the year but concentrated during the drier season. The plot is dry enough all year long and soil dries and cracks during drought.

*El Rubí Sur* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Ficus aurea</i>	3.00	9.65	3	28.94	
<i>Ceiba pentandra</i>	3.00	9.65	3	28.94	
<i>Cedrela odorata</i>	4.00	12.86	6	77.17	
<i>Samanea saman</i>	0.60	1.93	6	11.58	
<i>Eugenia foetida</i>	1.50	4.82	9	43.41	
<i>Cordia gerascanthus</i>	2.00	6.43	13	83.60	
<i>Swietenia mahagoni</i>	3.00	9.65	14	135.05	
<i>Caesalpinia violacea</i>	1.50	4.82	14	67.52	
<i>Bursera simaruba</i>	5.00	16.08	15	241.16	11.82
<i>Gymnanthes lucida</i>	0.50	1.61	16	25.72	
<i>Matayba apetala</i>	2.00	6.43	16	102.89	
<i>Erythroxylum havanense</i>	0.30	0.96	17	16.40	
<i>Oxandra lanceolata</i>	1.90	6.11	21	128.30	
<i>Andira inermis</i>	2.00	6.43	21	135.05	
<i>Pseudolmedia spuria</i>	0.80	2.57	22	56.59	
	31.10	100.00		1182.32	

Note: The forest plot (trees over 30 m high) is at 200 m a.s.l. along a highly stony, wide valley directly exposed to the South. The plot is a part of the superior basin of *San Francisco* river. At present *Bursera simaruba*, *Cedrela odorata* and *Oxandra lanceolata* dominate the plot. Root mats are absent as in other observed tropical dry forests, perhaps due to litter fall not being constant along the year but concentrated during the drier season. The plot is humid during the rainy season and running water additionally increases water availability. However, it is dry enough all year long and soil dries and cracks during drought.

**Appendix VI-B.** Estimation of ceno-successional index (CSI) for several hypothetical forest variants belonging to the assembly of dry and/or saline ecosystems (DSE).

*El Veral* is a plot comprising a Pioneer Stage of medium-height trees (15 to 20 m high) Tropical Dry Forest at the Reserve of Biosphere *Guanahacabibes*, *Pinar del Río* province, Western Cuba; *Punta del Este* is a plot growing a Primary Stage of small trees (less than 10 m high) in a Tropical Dry Forest in the Southeast of *Isla de la Juventud*; and *Carapachibey* is a plot growing a Primary

Stage of medium-height trees (15 to 20 m high) in a Tropical Dry Forest in the South of *Isla de la Juventud*.

*El Veral* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Cecropia schreberiana</i>	5.23	20.31	1	20.31	
<i>Talipariti elatum</i>	2.25	8.74	1	8.74	
<i>Hamelia patens</i>	3.25	12.62	2	25.24	
<i>Luehea speciosa</i>	1.65	6.41	2	12.81	
<i>Ficus aurea</i>	2.34	9.09	4	36.34	
<i>Eugenia foetida</i>	1.70	6.60	5	33.01	6.90
<i>Cordia gerascanthus</i>	4.66	18.09	8	144.76	
<i>Cedrela odorata</i>	0.10	0.39	9	3.49	
<i>Swietenia mahagoni</i>	0.30	1.18	20	23.57	
<i>Bursera simaruba</i>	4.27	16.58	23	381.35	
	25.75	100.00		689.62	

*Punta del Este* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Cordia gerascanthus</i>	1.00	5.85	8	46.78	
<i>Ateleia apetala</i>	1.00	5.85	15	87.72	
<i>Simarouba glauca</i>	0.90	5.26	16	84.21	
<i>Citharexylum fruticosum</i>	0.20	1.17	17	19.88	
<i>Adelia ricinella</i>	2.00	11.70	18	210.53	
<i>Krugiodendron ferreum</i>	0.50	2.92	18	52.63	
<i>Lysiloma latisiliqua</i>	1.20	7.02	19	133.33	
<i>Swietenia mahagoni</i>	2.00	11.70	20	233.92	20.12
<i>Gymnanthes lucida</i>	1.20	7.02	21	147.37	
<i>Lysiloma sabicu</i>	2.00	11.70	23	269.01	
<i>Bursera simaruba</i>	3.00	17.54	23	403.51	
<i>Diospyros crassinervis</i>	0.20	1.17	26	30.41	
<i>Amyris balsamifera</i>	1.60	9.36	26	243.27	
<i>Guaicum sanctum</i>	0.30	1.75	28	49.12	
	17.10	100.00		2011.70	



*Carapachibey* (hypothetical example)

FOREST TREE SPECIES	Phytomass (m <sup>3</sup> )	SP	SN	SP x SN	CSI
<i>Ficus aurea</i>	1.00	3.60	4	14.39	
<i>Eugenia foetida</i>	1.50	5.40	5	26.98	
<i>Cordia gerascanthus</i>	2.00	7.19	8	57.55	
<i>Cedrela odorata</i>	2.50	8.99	9	80.94	
<i>Metopium brownei</i>	2.25	8.09	17	137.59	
<i>Pithecellobium lentiscifolium</i>	3.60	12.95	19	246.04	
<i>Swietenia mahagoni</i>	2.00	7.19	20	143.88	
<i>Gymnanthes lucida</i>	1.20	4.32	21	90.65	18.92
<i>Lysiloma sabicu</i>	1.65	5.94	23	136.51	
<i>Bursera simaruba</i>	2.30	8.27	23	190.29	
<i>Erythroxylum havanense</i>	0.90	3.24	26	84.17	
<i>Eugenia axillaris</i>	1.60	5.76	26	149.64	
<i>Andira inermis</i>	3.20	11.51	28	322.30	
<i>Guaiaacum sanctum</i>	2.10	7.55	28	211.51	
	27.80	100.00		1892.45	