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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 estrategas *r*) y el comportamiento *r* de algunas variables entre las Estabilizadoras (que comúnmente son estrategas *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 (l990) 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 *Cecropia* spp.
		2		Often from 2 000 to 20 000: Type *Swietenia* spp.
		3	▲	Approximately, from 500 to 2 000: Type *Brosimum* spp.
		4		Often less than 500: Type *Pouteria* spp.
SEEDS SIZE	SSZ	1		Smaller than 2.0 mm
		2		From 2.1 to 5.0 mm
		3	▼	From 5.1 to 10.0 mm
		4		Larger than 10.1 mm
SEEDS WEIGHT (air dried seeds)	SWE	1		Less than 20.0 mg
		2		From 20.1 to 200.0 mg
		3	▼	From 200.1 to 2 000.0 mg
		4		More than 2 000.1 mg
SEEDS PER FRUIT	SFR	**1**		More than 101
		2		From 11 to 100
		3	▲	From 2 to 10
		4		Commonly 1, rarely 2 or 3
TOLERANCE TO SHADE, HELIO- AND SCIADOPHILY	TOL	1		Intolerant to shadow
		2		Facultative semitolerant to shadow
		3	▼	Semitolerant to shadow
		4		Tolerant to shadow
SELECTIVITY TO HABITAT (frequency of occurrence of individuals)	SHA	1		Abundant and low selective with respect to plant formation.
		2		Frequent, though restricted to a particular plant formation.
		3		Relatively scarce, restricted frequency inside the plant formation.
		4	▼	Rare, difficult to be found inside the plant formation, highly selective.
SCLEROPHYLLY (leaves dry weight : fresh weight ratio)	SCL	1		Lower than 0.300 (SUBSCLEROPHYLLOUS)
		2		From 0.301 to 0.380 (MESOSCLEROPHYLLOUS)
		3	▼	From 0.381 to 0.450 (SCLEROPHYLLOUS)
		4		Higher than 0.451 (EUSCLEROPHYLLOUS)
WOOD DENSITY (in $kg.m^{-3}$)	DEN	1		Less than 600
		2		From 601 to 800
		3	▼	From 801 to 1 000
		4		More than 1 001
APPROXIMATED FOLIAR AREA	AFA	**1**		Larger than 140.1 cm^2 (MEGAFOLIACEOUS)
		2		From 60.1 to 140.0 cm^2 (MACROFOLIACEOUS)
		3	▲	From 20.1 to 60.0 cm^2 (HEMIFOLIACEOUS)
		4		Smaller than 20.0 cm^2 (MICROFOLIACEOUS)
COMMONLY REACHED MAXIMUM TREE HEIGHT	HEI	**1**		Higher than 25 m (very high tree)
		2		From 16 to 24 m (high tree)
		3	▲	From 11 to 15 m (middle height tree)
		4		Smaller than 10 m (small tree)
COMMONLY REACHED MAXIMUM TREE VOLUME	VOL	**1**		Larger than 10.1 m^3 (very large volume tree)
		2		From 2.6 to 10.0 m^3 (large volume tree)
		3	▲	From 0.6 to 2.5 m^3 (middle volume tree)
		4		Smaller than 0.5 m^3 (small volume tree)

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), leafs 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:

$$\mathrm{SKA} = \frac{\sum_{1}^{10}(\mathrm{Var_i} * \mathrm{Var_{i+1}}) + (\mathrm{Var_{11}} * \mathrm{Var_1})}{(\mathrm{MVA})^2 * \mathrm{Nr.Vars.}}$$

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

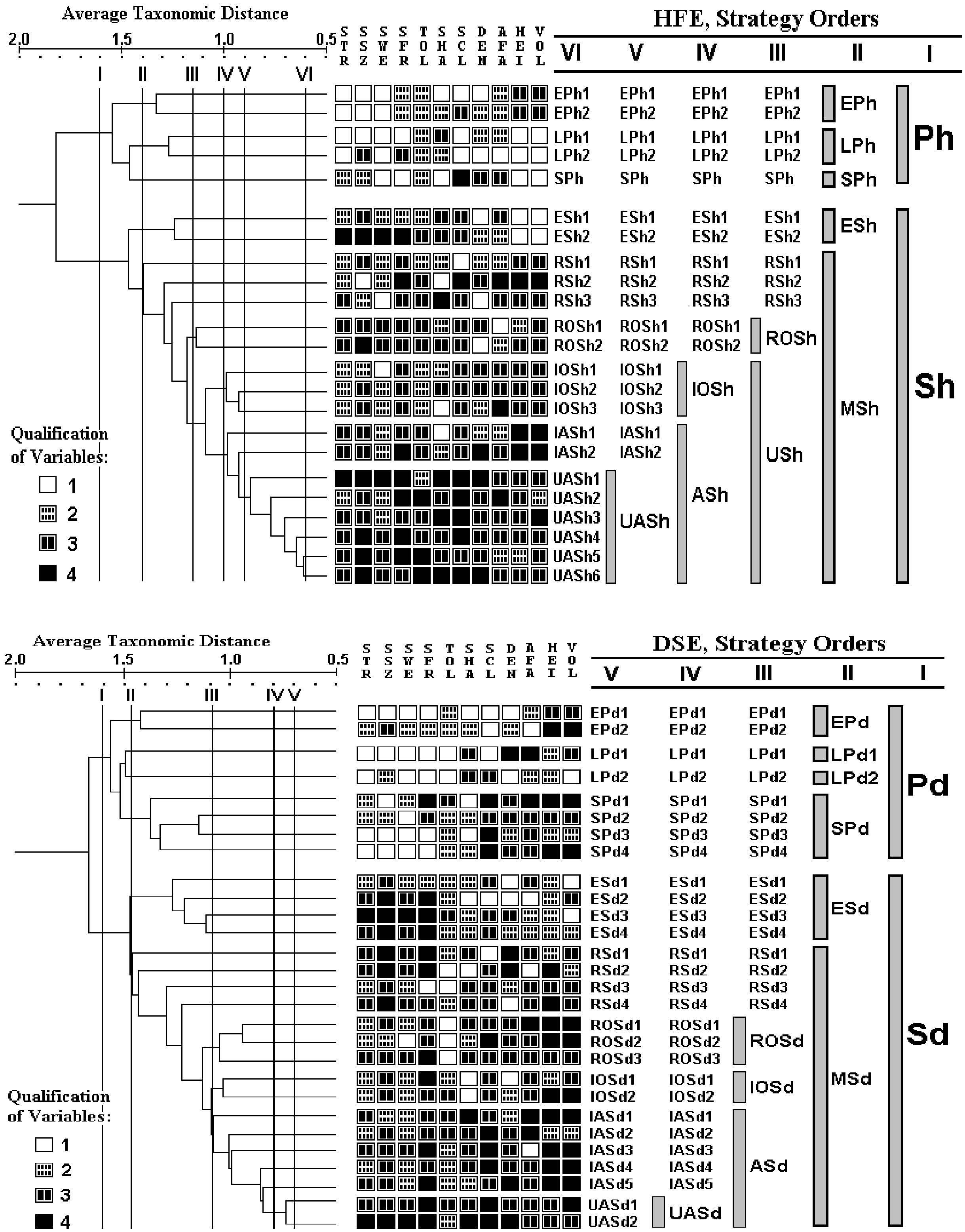

Fig. 1. Tree species strategies in humid tropical forest ecosystems (HFE, above) and dry or saline ecosystems (DSE, below). Order I strategies are Pioneers (P) and Stabilizers (S), "h" and "d" refers to HFE or DSE, respectively. From order II in advance, the strategies names are: Early (EP), Late (LP) 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.

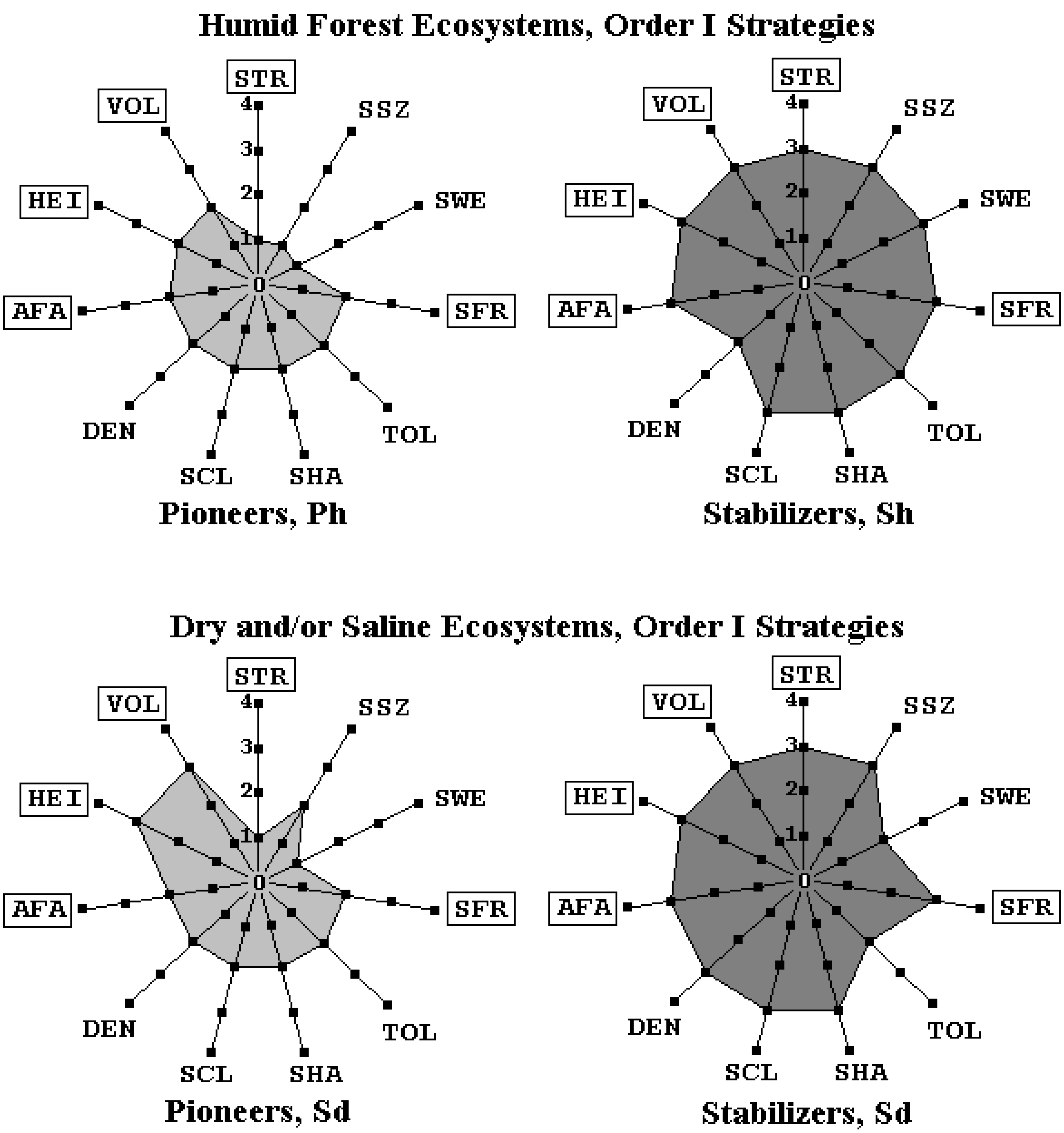

Fig. 2. Order I Successional Strategies polygrams for Humid Forest Ecosystems (HFE) and Dry or Saline Ecosystems (DSE). Description of variables see Figure 1.

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 (EPh and EPd), Late Pioneers (LPh and LPd), Sclerophyllous Pioneers (SPh and SPd), Exuberant Stabilizers (ESh and ESd), Restoring Stabiliziers (RSh and RSd), Restoring Opportunist Stabilizers (ROSh and ROSd), Invasive Opportunist Stabilizers (IOSh and IOSd), Invasive Austere Stabilizers (IASh and IASd) and Ultimate Austere Stabilizers (UASh and UASd). 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).

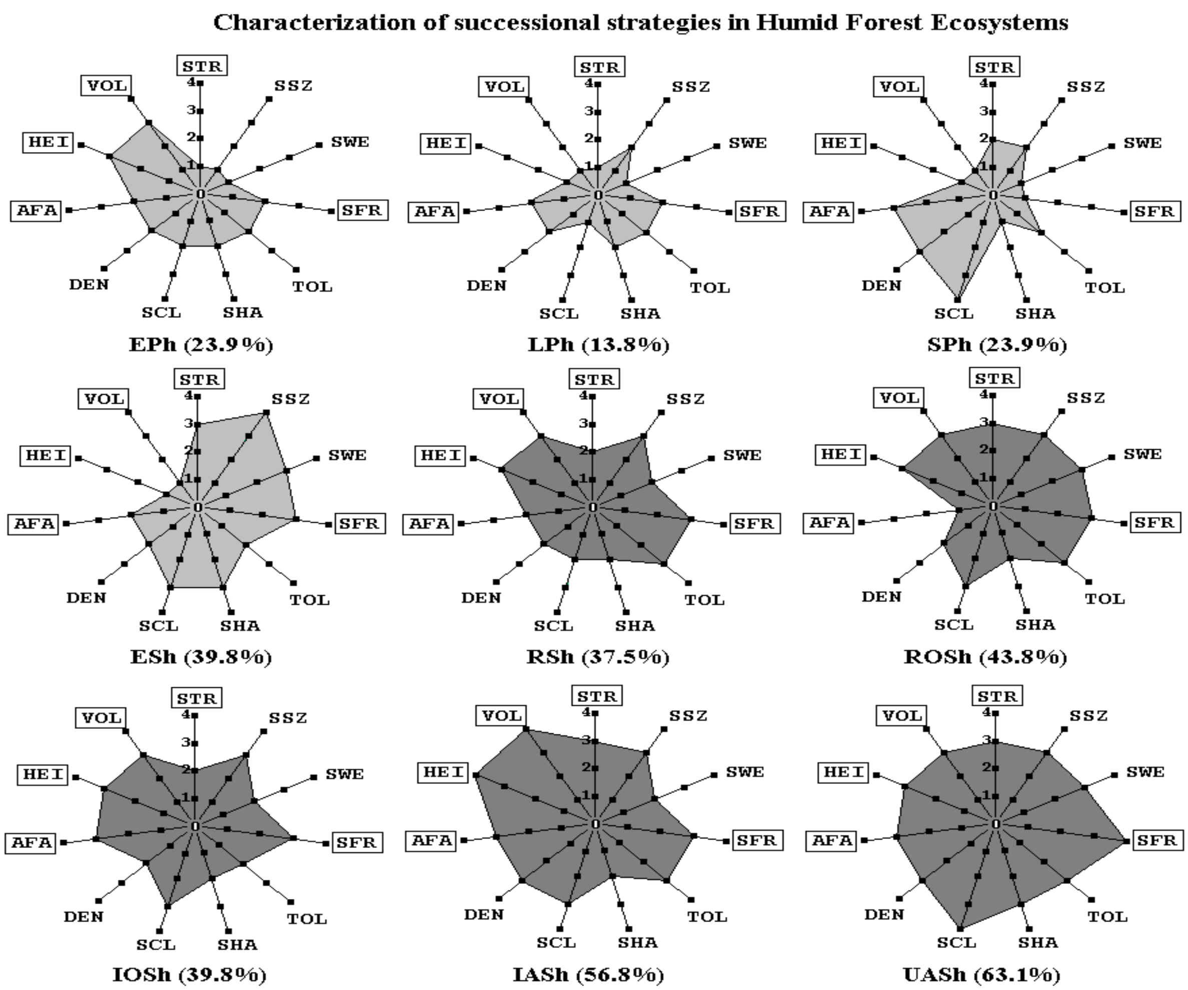

Fig. 3. Polygrams for nine strategies summarizing Order VI in Humid Forest Ecosystems. In parenthesis Strategy *K* Area (SKA) values. Successional strategies: Early (EP), Late (LP) and Sclerophyllous (SP) Pioneers, Exuberant (ES), Restoring (RS), Restoring Opportunist (ROS), Invasive Opportunist (IOS),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

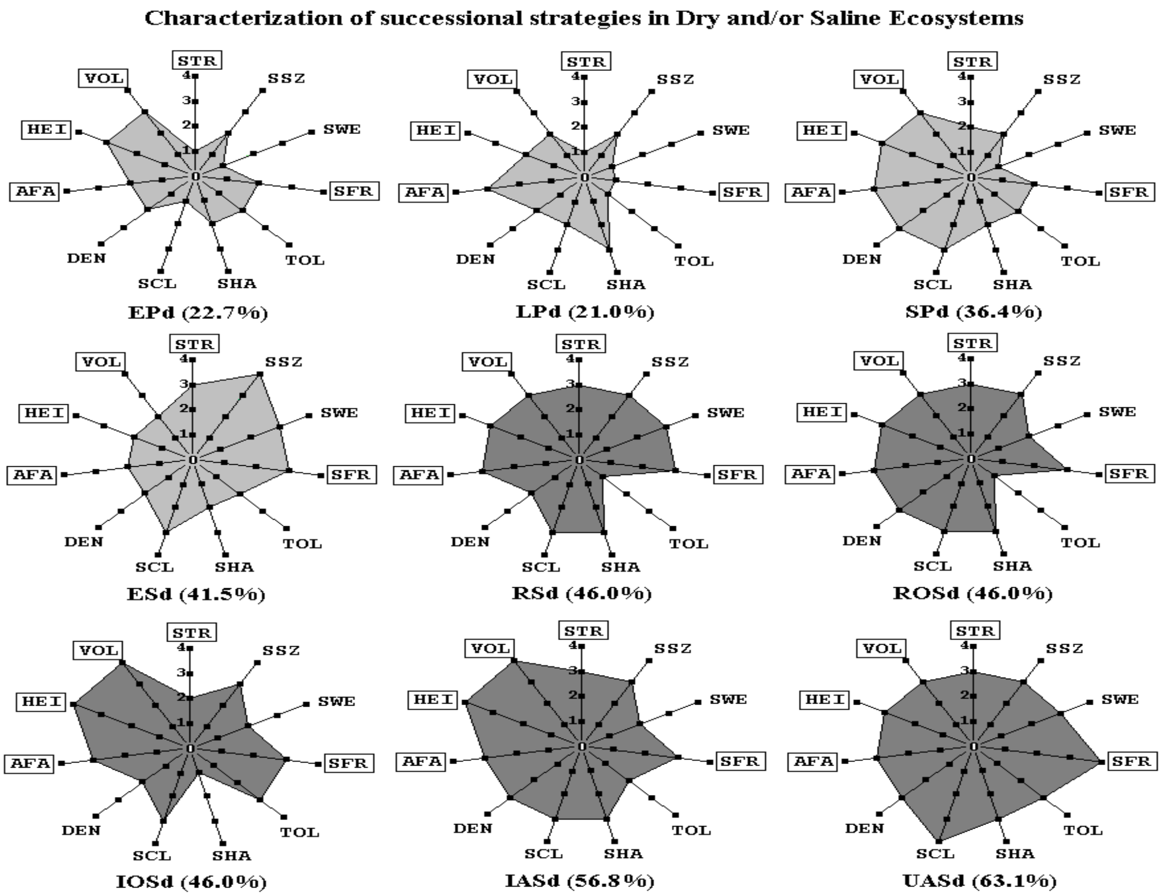

Fig. 4. Polygrams for nine strategies summarizing Order V in Dry or Saline Ecosystems. In parenthesis Strategy *K* Area (SKA) values. For successional strategies see Figure 3.

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 successionals, 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.

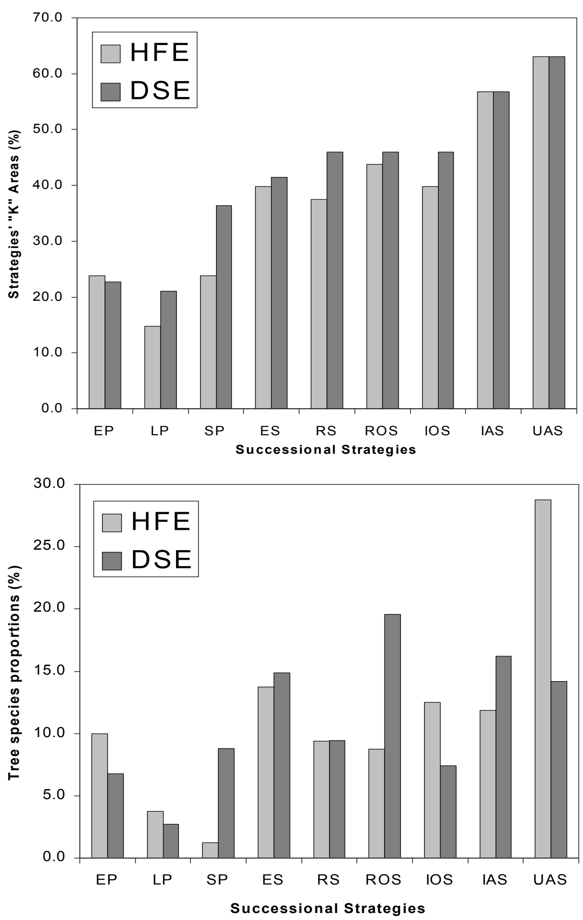

Fig. 5. Comparison between nine strategies in Humid Forest Ecosystems (HFE) and Dry or Saline Ecosystems (DSE). Above, Strategy *K* Area (SKA) values, and below, sharing of species proportions among the nine chosen strategies.

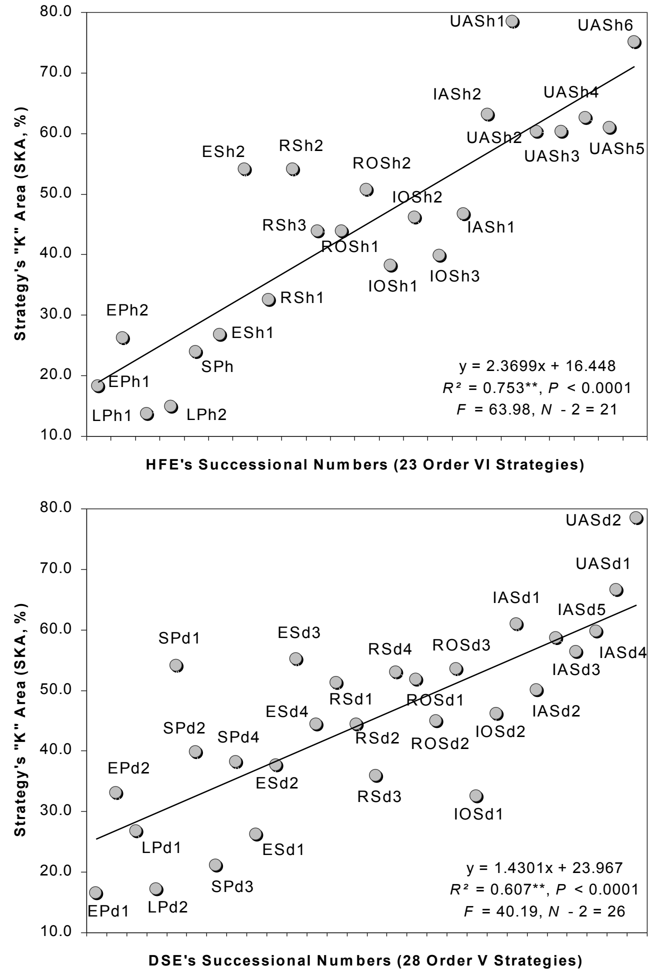

Fig. 6. SKA (Strategy *K* Area) *vs.* SN (Successional Number) regression analysis for HFE Order VI (above) and DSE Order V (below) strategies.

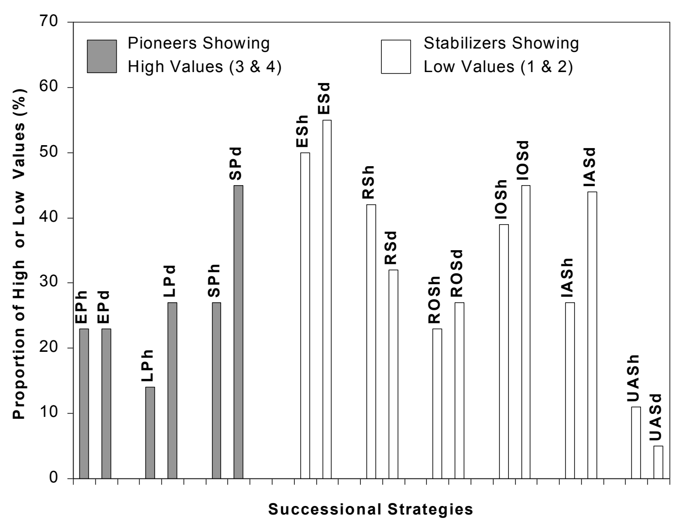

Fig. 7. The *r-K* continuum expressed to show the proportion of variables that have *K* tendencies among Pioneers and *r* tendencies among Stabilizers.

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							**X**			**XX**	**XX**
EPd		**X**								**XX**	**XX**
LPh		**X**		**X**		**X**					
LPd						**XX**	**X**	**X**	**X**		**X**
SPh							**XX**	**XX**	**XX**		
SPd				**X**	**X**		**XX**	**XX**	**XX**	**XX**	**XX**
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 successionally 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 successionals. 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
Psidium guajava	EPh2	**SPd2**
Tetrazygia bicolor	EPh2	**SPd2**
Casuarina equisetifolia	EPh2	**SPd3**
Talipariti elatum	LPh2	EPd1
Zanthoxylum martinicense	ESh1	SPd4
Bauhinia monandra	RSh1	EPd2
Plumeria obtusa	RSh1	EPd2
Gmelina arborea	RSh1	ESd2
Cordia collococca	RSh1	ESd4
Eugenia foetida	RSh2	SPd1
Juniperus lucayana	RSh3	**IASd1**
Gettarda elliptica	RSh3	**IASd1**
Roystonea regia	ROSh1	ESd4
Tectona grandis	ROSh1	ESd4
Hura crepitans	ROSh1	ESd4
Persea americana	ROSh2	ESd4
Anacardium occidentale	ROSh2	RSd4
Annona muricata	ROSh2	RSd4
Maclura tinctoria	IOSh1	SPd4
Zuelania guidonia	IOSh1	SPd4
Cordia gerascanthus	IOSh1	SPd4
Cordia alliodora	IOSh1	SPd4
Clusia rosea	IOSh1	SPd4
Chrysophyllum cainito	IOSh2	ESd4
Calophyllum antillanum	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).

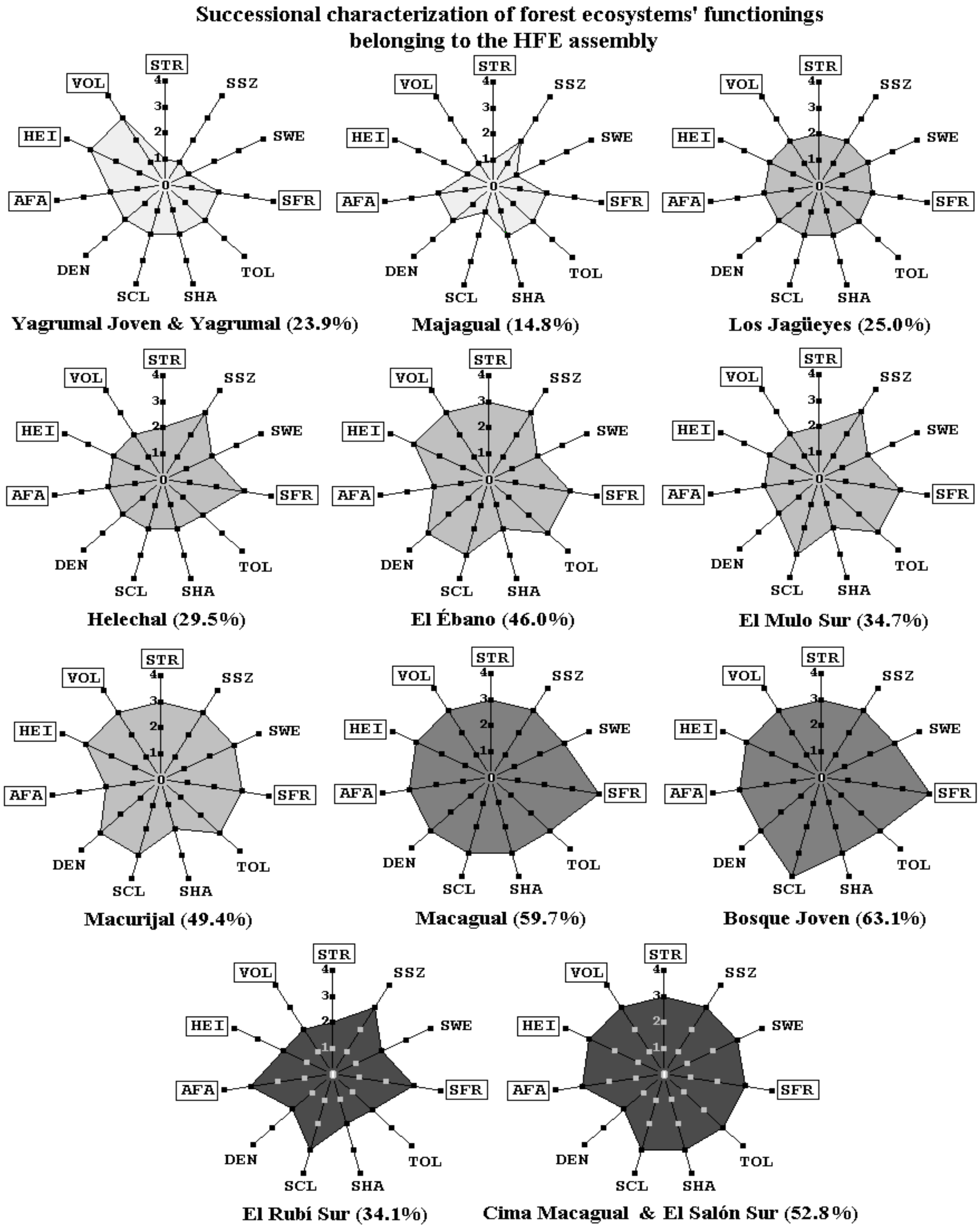

Fig. 8. Polygrams characterizing 13 Humid Forest Ecosystems (HFE) plots in *Sierra del Rosario* (see Table 4 and also Appendixes III-A and V-A). In parenthesis, the Ecosystems *K* Strategist Area (EKSA) values.