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# Contribution to the Knowledge of Plant Succession in the Lesser Antilles: The Case of the Lower Sylvan Vegetation Layer of Martinique

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## Abstract

The forest ecosystems of Martinique, like those of the Lesser Antilles, are diverse and, in some cases, quite complex. The numerous phytocenoses that make up these ecosystems are differentiated in terms of their surface area, floristic composition and age. Alongside the main ecological factors, such as rainfall and topographic facies, which define bioclimates and the layering of forest types, human activities are a determining factor in their structures, functions and spatio-temporal evolutionary processes. Anthropisation is also a significant factor in both the chorology of plant species and their autoecological and synecological dynamics. On the basis of field surveys within the dry bioclimate of Martinique in transects subdivided into quadrats, to which observations of more than two decades were associated, we attempted to decipher the affiliations of species with regard to the different timeframes of plant succession, and therefore phytocenotic succession, in particular sylvatic succession. The results obtained are encouraging, since they indicate that the typical species of this dry bioclimate belong to different stages of plant succession (plant dynamics), depending on their ecological profiles, and that for the same bioclimate and the same dynamic stage, the floristic assemblages can be different. Time, variations in the shape of the landscape and natural and/or anthropogenic changes condition phytocenotic evolution in terms of successions of ecological profiles. Another interesting and surprising aspect is that for two forest ecosystems colonising two contiguous vegetation layers influenced by two bioclimates and having reached their evolutionary maturity, there are transfers of species. This is the case for certain species of the typical tropical seasonal evergreen forest (mesophilous forest) which make up in small numbers the late seasonal, pre-climacic or climacic tropical evergreen forest of lower horizon and xeric facies (xerophilous forest).

**Keywords**

Lesser Antilles, Martinique Dry Bioclimate, Ecosystems, Phytocenoses, Biodiversity, Plant Succession

## 1. Introduction

Tropical forests present numerous physiognomies corresponding to a wide variety of bioclimates [1]-[3]. They develop in the part of the ecosphere most conducive to the development of animal and plant life according to both a vertical and horizontal distribution [4]-[6]. The multiple species assemblages and their relationships within complex trophic networks make habitats and biotopes as diverse as they are unique [7] [8]. Forest resources are exploited separately by local populations for their survival and by companies according to mercantile mining principles [9]-[12]. The decline in the surface area of tropical ecosystems and their loss of diversity are linked to a weakening of resilience processes [13]-[15]. At the international level, tropical forests are the subject of intense debates in major gatherings intended to find solutions for the protection of biodiversity and to combat climate change [16]-[18]. Tropical forests play an important role in biogeochemical cycles, particularly the water and carbon cycles. They are genuine carbon sinks that contribute to the homeostasis of the biosphere. The forest formations of the Antilles are unique because they develop over small areas but nevertheless present a great diversity of species [19]-[22]. The latter makes the Antilles part of one of the hotspots of biological diversity: that of the Caribbean [23] [24]. At all levels of complexity, the phytodiversity of Martinique, like that of the other Lesser Antilles, is subject to erosion due to ongoing human activities [25] [26]. Almost all tropical forest types are found in various phases of temporal evolution, hence their interest in terms of a laboratory allowing the human exploration of their structural characteristics, their functional and evolutionary processes. In this article, based on observations and floristic surveys carried out in the lower vegetation layer of Martinique influenced by the humid subhumid bioclimate, it was possible to classify the species and the floristic combinations they form according to whether they belong to the different stages of forest dynamics. It should be noted that a small number of floristic inventories have been carried out on the islands of Saint-Vincent and Marie-Galante. These are examples that cannot be used as a basis for comparison, since the study mainly concerns Martinique. Nevertheless, the main conclusions of this study are valid for the Lesser Antilles.

## 2. Materials

Martinique, like the other Lesser Antilles, is the result of an intra-oceanic subduction [27]. This has led to a contrasting geomorphology characterised by numerous mountainous structures including Mont Pelé. The general climate and topography create seasonal rainfall patters and lead to bioclimates whose altitudinal limits are not similar between the windward facade (east facade) and the leeward facade (west facade). From the coast to the summits of the mountain ranges, the bioclimatic layering corresponds to a layering of ecosystem potential, particularly in terms of forestry. From the lowest to the highest altitudes, we potentially find the dry subhumid bioclimate, the humid subhumid bioclimate, the humid and hyperhumid bioclimate, which respectively define the limits or ecotones of the seasonal evergreen, sub-montane ombrophilous and montane ombrophilous forests. In our study area, the annual rainfall, which is by far the most decisive factor, is between 1250 mm for the least watered sectors and 1600 mm to 1700 mm or even 1800 mm for the most humid. This variability of precipitation shapes the phytocenoses, but does not call into question the fact that this altitudinal band belongs to the dry bioclimate, nor the sylvatic type which is associated with it. The lower bioclimatic layer is generally located between the mainland coastline, sometimes adjoining the psammophilous component (sandy system) and on average 250 m. In this area, the regional climate seems to present a certain stability, because the factorial gradients are small. In reality, the spatial variations of the climatic factors are not sufficiently significant to create notable stationary differences, but they do lead to particularities in the floristic composition of the formations. The seasonal evergreen forest has been and still is the site of anthropisation of varying frequency and intensity. The vegetation groupings that make up this vegetation layer are the result of a regression of the original, so-called primitive, woodland entities. Consequently, they are considered secondary with regard to the processes of plant dynamics. The many topographical facets of the lower layer of Martinique (which condition as many habitats) combined with the variations of other ecological factors, result in a mosaic of seasonal evergreen sylvatic phytocenoses. The units of the latter correspond to different stages of temporal evolution and are of different ages, surface areas, floristic compositions and physiognomies.

## 3. Method

On the basis of surveys carried out using transects subdivided into quadrants in certain seasonal evergreen sylvatic units, we attempted to associate plant species with the different stages of intra-forest plant succession. In 75 stations (**Table 1**), the species, the number of individuals in the species populations (nb), and the diameters of the individuals at 1.33 m above ground (international standard) were recorded. This made it possible to calculate the relative frequency (fr), density (d), individual and population surface area (basal area), distribution index (Id) and dominance index (ID). The dominance index (ID) made it possible to numerically differentiate the species. Added to this are several decades of observations. Using WEKA and considering the most relevant structural descriptors, processing was carried out. WEKA is a popular open-source software tool for data mining and machine learning, developed at the University of Waikato in New Zealand. It provides a collection of algorithms for data analysis and predictive modelling, which can be applied to tasks such as classification, regression, clustering and association rule extraction [28] [29]. To get an idea of the structure of the data from the inventories we used XLSTAT 2024 software.

Table 1. General characteristics of the survey stations.

| Stations | Municipalities | Exhibitions | Types of soil/ depths (m) | Precipitation (mm/year) | Slopes (˚) |
|---|---|---|---|---|---|
| Aca1 | Rivière-Pilote | Western slope | Ferrisol/1.5 | 1600 | 14 |
| Aca2 | Rivière-Pilote | Western slope | Ferrisol/ > 1.5 | 1600 | 0 |
| Aca3 | Rivière-Pilote | Western slope | Ferrisol/1.5 | 1600 | 10 |
| Aca4 | Rivière-Pilote | Western slope | Ferrisol/1.5 | 1600 | 20 |
| Aca5 | Rivière-Pilote | Western slope | Ferrisol/ < 1 | 1600 | 20 |
| Aca6 | Rivière-Pilote | Western slope | Ferrisol/ < 0.8 | 1600 | 15 |
| Aca7 | Rivière-Pilote | Western slope | Ferrisol/ < 0.8 | 1600 | 22 |
| Aca8 | Rivière-Pilote | Western slope | Ferrisol/ < 0.8 | 1600 | 0 |
| Aca9 | Rivière-Pilote | Western slope | Ferrisol/ < 0.8 | 1600 | 20 |
| Aca10 | Rivière-Pilote | Western slope | Ferrisol/ < 0.8 | 1600 | 20 |
| Aca11 | Rivière-Pilote | Western slope | Ferrisol/ < 0.8 | 1600 | 20 |
| Aca12 | Rivière-Pilote | Western slope | Ferrisol/ < 0.8 | 1600 | 20 |
| Aca13 | Rivière-Pilote | Western slope | Vertisol/ < 0.6 | 1400 | 21 |
| Aca14 | Rivière-Pilote | Western slope | Vertisol/ < 0.6 | 1400 | 20 |
| Aca15 | Rivière-Pilote | Western slope | Vertisol/ < 0.6 | 1400 | 20 |
| Aca16 | Rivière-Pilote | Western slope | Vertisol/ < 0.3 | 1400 | 30 |
| Aca17 | Marin | Western slope | Vertisol/ < 0.8 | 1400 | 0 |
| Aca18 | Marin | Western slope | Vertisol/ < 0.6 | 1400 | 20 |
| Aca19 | Marin | Western slope | Vertisol/ < 0.8 | 1400 | 5 |
| Aca20 | Marin | Western slope | Vertisol/ < 0.6 | 1400 | 20 |
| Aca21 | Marin | East slope | Vertisol/ < 0.6 | 1400 | 20 |
| Aca22 | Marin | East slope | Vertisol/ < 0.5 | 1250 | 30 |
| Aca23 | Marin | East slope | Vertisol/ < 0.8 | 1250 | 15 |
| Aca24 | Marin | East slope | Vertisol/ < 0.8 | 1250 | 20 |
| Aca25 | Marin | East slope | Vertisol/ < 0.8 | 1500 | 30 |
| Pointe Banane | Robert |  | Vertisol/ < 1 | 1500 | 0 |
| Pointe Brumel | Trinité |  | Ferrisol/0.3 | 1250/1500 | 20 |
| Morne Amérique | Sainte-Anne | East slope | Vertisol/ < 0.6 | 1300/1500 | 20 |
| Morne Caritan 1 | Sainte-Anne | Western slope | Vertisol/ < 0.6 | 1300/1500 | 30 |
| Morne Caritan 2 | Sainte-Anne | Crete | Vertisol/ < 0.8 | 1300/1500 | 0 |

**Continued**

| | | | | | |
|---|---|---|---|---|---|
| Morne Caritan 3 | Sainte-Anne | East slope | Vertisol/ < 0.8 | 1300/1500 | 30 |
| Piton Crève Cœur 1 | Sainte-Anne | Western slope | Vertisol/ < 0.6 | 1250/1500 | 25 |
| Piton Crève Cœur 2 | Sainte-Anne | East slope | Vertisol/ < 0.6 | 1250/1500 | 20 |
| Morne Gardier 1 | Diamant | Western slope | Unknown/ < 0.8 | 1500/2000 | 35 |
| Morne Gardier 2 | Diamant | South slope | Unknown/ > 1 | 1500/2000 | 0 |
| Morne Gardier 3 | Diamant | East slope | Unknown/ < 0.8 | 1500/2000 | 30 |
| Morne Gentyl | Anses d'Arlets | Western slope | Vertisol/ < 0.6 | 1300/1500 | 30 |
| Pointe Jean Claude 1 | Trinité | Western slope | Ferrisol/ < 1 | 1500/1600 | 15 |
| Pointe Jean Claude 2 | Trinité | Western slope | Ferrisol/ < 0.8 | 1500/1600 | 35 |
| Pointe Jean Claude 3 | Trinité | South slope | Ferrisol/ > 1 | 1500/1600 | 7 |
| Morne Joli Cœur 1 | Sainte-Anne | East slope | Vertisol/ < 0.8 | 1300/1500 | 25 |
| Morne Joli Cœur 2 | Sainte-Anne | East slope | Vertisol/ < 0.8 | 1300/1500 | 30 |
| Morne Manioc 1 | Sainte-Anne | South slope | Vertisol/ < 0.8 | 1300/1500 | 0 |
| Morne Manioc 2 | Sainte-Anne | East slope | Vertisol/ < 0.8 | 1300/1500 | 20 |
| Morne Manioc 3 | Sainte-Anne | Western slope | Vertisol/ < 0.8 | 1300/1500 | 25 |
| Morne marguerite 1 | Sainte-Anne | South slope | Vertisol/ < 0.8 | 1300/1500 | 0 |
| Morne marguerite 2 | Sainte-Anne | Western slope | Vertisol/ < 0.8 | 1300/1500 | 25 |
| Morne marguerite 3 | Sainte-Anne | Western slope | Vertisol/ < 0.8 | 1300/1500 | 32 |
| Morne Berry 1 | Marin | East slope | Vertisol/ < 0.8 | 1300/1500 | 32 |
| Morne Berry 2 | Marin | East slope | Vertisol/ < 1 | 1300/1500 | 40 |
| Morne Berry 3 | Marin | Crete | Vertisol/ < 0.6 | 1300/1500 | 10 |
| Morne Larcher 1 | Diamant | South slope | Vertisol/ < 0.6 | 1250/1500 | 0 |
| Morne Larcher 2 | Diamant | East slope | Vertisol/ < 0.3 | 1250/1500 | 35 |
| Morne Valentin | François | Western slope | Vertisol/0.7 | 1500/2000 | 35 |
| Montagne du Vauclin | Vauclin | | Ferrisol/ < 0.8 | 1500/1600 | 20 |
| Pointe la Rose 1 | François | | Vertisol/1.5 | 1250/1500 | 20 |
| Pointe la Rose 2 | François | | Vertisol/0.8 | 1250/1500 | 0 |
| Bois Pothau | Robert | East slope | Ferrisol/ > 1 | 1500/2000 | 25 |
| Morne Préfontaine 1 | Sainte-Luce | | Vertisol/ > 1 | 1500/2000 | 0 |
| Morne Préfontaine 2 | Sainte-Luce | | Vertisol/0.8 | 1500/2000 | 25 |
| Rocher Leclerc 1 | François | | Vertisol/ < 0.6 | 1250/1500 | 22 |
| Rocher Leclerc 2 | François | | Vertisol/ < 1.5 | 1250/1500 | 0 |
| Ravine Saint-Pierre 1 | Sainte-Luce | | Vertisol/ > 1 | 1300/1500 | 0 |
| Ravine Saint-Pierre 2 | Sainte-Luce | | Vertisol/ < 0.8 | 1300/1500 | 15 |
| Ravine Saint-Pierre 3 | Sainte-Luce | | Vertisol/ < 0.8 | 1300/1500 | 15 |
| Ravine Saint-Pierre 4 | Sainte-Luce | | Vertisol/ > 0.6 | 1300/1500 | 25 |
| Caravelle 1 | Trinité | | Ferrisol/0.9 | 1250/1500 | 20 |

**Continued**

| | | | | | |
|---|---|---|---|---|---|
| Caravelle 2 | Trinité | | Ferrisol/ > 1.5 | 1250/1500 | 0 |
| Rocher Zombi 1 | Rivière-Pilote | Crete | Vertisol/ < 0.6 | 1300/1500 | 0 |
| Rocher Zombi 2 | Rivière-Pilote | Western slope | Vertisol/ < 0.8 | 1300/1500 | 30 |
| Tête de Singe | Diamant | | Vertisol/0.2 | 1250/1500 | 0 |
| Morne Réduit 1 | Anses d'Arlets | East slope | Vertisol/0.6 | 1250/1500 | 20 |
| Morne Réduit 2 | Anses d'Arlets | East slope | Vertisol/0.2 | 1250/1500 | 35 |
| King's Hill 1 | Île de Saint-Vincent | | Ferrisol/ > 1 | 1800 | 0 |
| King's Hill 2 | Île de Saint-Vincent | | Ferrisol/ > 1 | 1800 | 20 |

## 4. Results and Discussion

### 4.1. Data Structure

For the 75 stations, descriptive statistics produced using XLSTAT 2024 software and the following parameters describe the structure of the populations of 171 species: number of individuals (nb), density (d), relative frequency (fr), phytomass (basal area), distribution (Id) and dominance (ID). It seems from the standard deviations that the degree of dispersion around the mean presents a certain heterogeneity. The number of individuals ranges from very high to very low. The same is true for the presence of species at all 75 stations, indicated by the relative frequency (fr), which ranges from 1.33% to 100%. All this is corroborated by the basal area, the distribution index (Id) and the dominance index (ID). These aspects highlight a population dissimilarity of the species. This is linked to their ecological strategies (Table 2).

Table 2. Descriptive statistics for all stations.

| Variable | Observations | Observations without missing data | Minimum | Maximum | Average | Standard deviation |
|---|---|---|---|---|---|---|
| nb (number) | 171 | 171 | 1000 | 3082,000 | 321,503 | 566,535 |
| fr (relative frequency) | 171 | 171 | 1333 | 100,000 | 20,452 | 22,345 |
| Density (d) | 171 | 171 | 0.000 | 0.056 | 0.006 | 0.010 |
| Basal area | 171 | 171 | 0.000 | 30,186 | 1626 | 3676 |
| Id (distribution index) | 171 | 171 | 0.000 | 4683 | 0.300 | 0.754 |
| ID (dominance index) | 171 | 171 | 0.000 | 81,308 | 1825 | 7895 |

### 4.2. Structural Characteristics of Species Populations at All Stations

By comparing the Distribution Index and the Basal area, the processing of population data for 171 species relating to the 75 survey stations shows a fairly tangible separability (Figures 1-3). In Figure 1, the clusters differentiate species profiles. Firstly, and generally speaking, the majority of species are around the origin of the axes (species in clusters 1 and 3 and some in clusters 2 and 4), have low population biomasses (Basal areas) and are poorly distributed (Id). **Figure 1**, in decreasing quantitative order, also shows that the species in cluster 2 can have low, medium and high basal areas (phytomass) distinctively associated with low, medium and high distributions (Id). These two parameters combined (Id and basal area) using the WEKA software give us a fairly clear idea of the ecological importance of the species in relation to each other. For the same ecological data, on the basis of density (d) and relative frequency (fr), which make up the distribution index (Id), **Figure 2** indicates fairly marked discriminations. The most widely distributed species have higher densities and relative frequencies. The same is true for **Figure 3**, in which several clusters stand out in with regard to the dominance index (ID). Clusters 2, 3 and 4 in **Figure 3** correspond to most of the species whose dominance index (ID) is low or even very low. With regard to the inventory stations, a small number of species dominate from the point of view of distribution (Id) and phytomass (basal area), as confirmed by **Table 3** of the predominant ecological species.

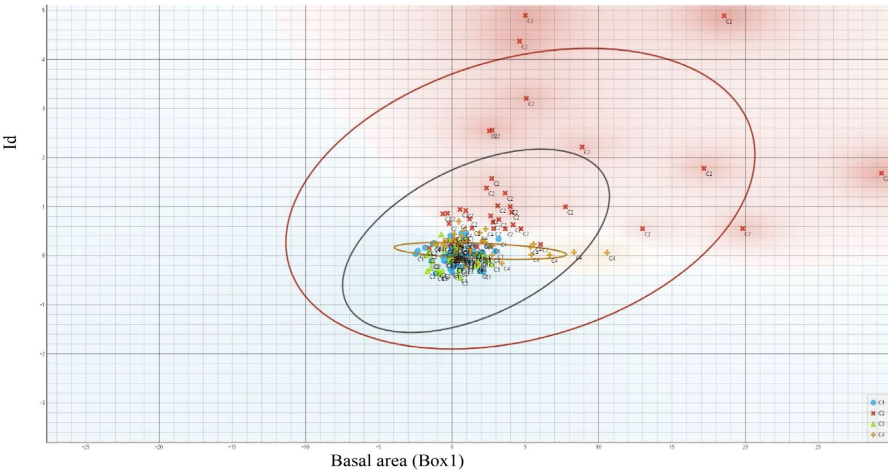

**Figure 1.** Discrimination of species populations with regard to Id and basal area.

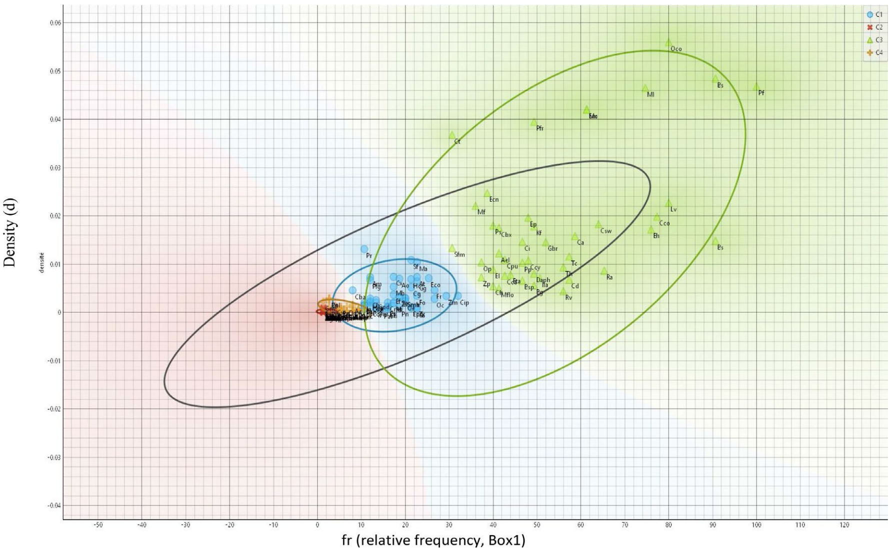

**Figure 2.** Discrimination of species with regard to relative frequency (fr) and density.

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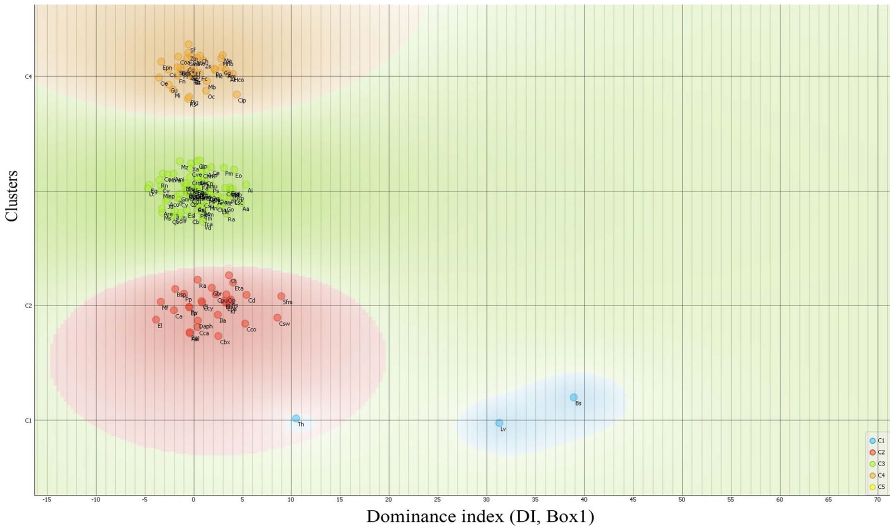

**Figure 3.** Groups discriminated using the dominance index (DI).

[*Pisonia fragrans* (*Pf*) is not visible]

Box 1

*Acacia muricata* (*Am*) / *Acacia sp*(*Asp*) / *Acacia tamarindiflolia*(*At*) / *Acatinostemon caribaeus*(*Ac*) / *Aiphanes*(*Ae*) / *Aiphanes minima*(*Ami*) / *Allophyllus recemosus*(*Ar*) / *Amyris elemifera* (*Ael*) / *Andira inermis* (*Ai*) / *Annona muricata* (*Amu*) / *Annona reticulata* (*Are*) / *Anthirhea coriacea* (*Aco*) / *Ardisia obovata* (*Ao*) / *Artocarpus altilis* (*Aa*) / *Bourreria succulenta*(*Bs*) / *Brosimum alicastrum* (*Ba*) / *Buchenavia tetraphylla* (*Bt*) / *Bunchosia glandulosa* (*Bg*) / *Bursera simaruba* (*Bs*) / *Byrsonima spicata* (*Bsp*) / *Calliandra tergemina* (*Ct*) / *Calyptranthes elegans* (*Ce*) / *Canella winterana* (*Cw*) / *Capparis baduca* (*Cb*) / *Capparis cynophallophora*(*Cc*) / *Capparis hastata* (*Ch*) / *Capparis indica* (*Ci*) / *Casearia decandra*(*Cd*) / *Cassine xylocarpa*(*Cx*) / *Cassipourea guianensis*(*Cg*) / *Cecropia schreberiana*(*Cs*) / *Cedrela odorata* (*Co*) / *Ceiba pentandra* (*Cp*) / *Cestrum sp* (*Csp*) / *Chamaecrista nictitans* (*Cn*) / *Chionanthus compacta* (*Cco*) / *Chione venosa* (*Cv*) / *Chrysophyllum argenteum* (*Ca*) *Citharexylum spinosum* (*Cip*) / *Citrus sp* (*Cisp*) / *Coccoloba publescens* (*Cpu*) / *Coccoloba swartzii* (*Csw*) / *Coccoloba venosa*(*Cve*) / *Coccothrinax barbadensis* (*Cba*) / *Conostegia calyptrata*(*Cca*) / *Cordia alliodora* (*Coa*) / *Cordia collococca*(*Ccl*) / *Cordia martinicensis* (*Cmt*) / *Cordia sulcata*(*Csu*) / *Cornutia pyramidata* (*Cy*) / *Crateva tapia*(*Cta*) / *Crossopetalum rhacoma* (*Crm*) / *Croton bixoides* (*Cbx*) / *Croton corylifolius* (*Ccy*) / *Croton flavens*(*Cfv*) / *Croton guildinguii*(*Cg1*) / *Croton hircinus* (*Chn*) / *Cupania americana* (*Cma*) / *Dapnopsis americana*(*Daph*) / *Erithalis fructicosa* (*Ef*) / *Erythroxylum havanense* (*Eh*) / *Erytrhina corallodendrum* (*Ec*) / *Eugenia axillaris* (*Ea*) / *Eugenia biflora* (*Eb*) / *Eugenia confusa* (*Ecn*) / *Eugenia cordata* (*Eco*) / *Eugenia gregii* (*Eg*) / *Eugenia hodgei*(*Ehd*) / *Eugenia ligustrina* (*El*) / *Eugenia monticola* (*Em*) / *Eugenia oerstedeana* (*Eo*) / *Eugenia pseudopsidium* (*Ep*) / *Eugenia tapacumensis* (*Eta*) / *Exostema sanstae-luciae* (*Esl*) / *Exothea paniculata* (*Epn*) / *Faramea occidentalis* (*Fo*) / *Ficus americana* (*Fa*) / *Ficus citrifolia*(*Fc*) / *Ficus nymphaeifolia* (*Fn*) / *Forestiera rhamnifolia* (*Fr*) / *Garcinia Guaiacum officinale* (*Go*) / *Guarea glabra* (*Gg*) / *Guarea* *macrphylla (Gm) / Guazuma ulmifolia (Gu) / Guettarda odorada (Go) / Guettarda scabra (Gbr) / Gyminda latifolia(Gl) / Haematoxylon campechianum (Hc) / Hymenaea courbaril(Hco) / Ilex nitida(In) / Inga ingoides(Ii) / Inga laurina(Ila) / Ixora ferrea(If) / Jacquinia armillaris(Ja) / Krugiodendron ferreum(Kf) / Laetia thamnia(Lt) / Leuceana leucocephala (Ll) / Licania leucosepala (Lle) / Licaria sericea(Ls) / Lonchocarpus sericeus(Lsc) / Lonchocarpus pentaphyllus(Lp) / Lonchocarpus violaceus(Lv) / Maclura tinctoria(Mt) / Malpighia martinicensis(Mm) / Mangifera indica(Mi) / Manilkara bidentata(Mb) / Manilkara zapota(Mz) / Margaritaria nobilis(Mn) / Maytenus laevigata(Ml) / Melicoccus bijugatus (Mb) / Miconia laevigata (Mlv) / Morisonia americana (Ma) / Myrcia citrifolia(Mc) / Myrcia fallax(Mf) / Myrcia leptoclada(Mlep) / Myrcia splendens (Ms) / Myrcianthes fragrans (Mfra) / Myrciaria floribunda (Mflo) / Ocotea cernua(Oc) / Ocotea coriacea(Oco) / Ocotea eggersiana(Oe) / Ocotea leucoxylon (Ole) / Ocotea patens (Op) / Ormosia monosperma(Om) / Ouratea guildenguii(Og) / Palicourea crocea(Pc) / Pavonia spinifex(Ps) / Persea americana(Pa) / Picramnia pentandra(Pp) / Picrasma excelsa(Pe) / Pilocarpus racemosus(Pr) / Pimenta racemosa(Pfr) / Pisonia fragrans(Pf) / Pisonia suborbiculata(Ps) / Pithecellobium unguis-cati(Pig) / Plinia pinnata(Ppl) / Plumeria alba(Pal) / Pouteria multiflora (Pm) / Pouteria semecarpifolia(Ps) / Psychotria nervosa(Pn) / Quararibea turbonata(Qt) / Randia aculeata(Ra) / Randia nitida(Rn) / Rauvolfia viridis(Rv) / Rhyticocos amara (Ra) / Rochefortia spinosa(Rs) / Schaefferia frutescens (Sf) / Scheopfia schreberi (Ss) / Sideroxylon foetidissimum(Sfm) / Sideroxylon obovatum(So) / Simaruba amara(Sa) / Spondias mombin(Sm)Sterculia caribaea (Sc) / Swartzia simplex(Ss) / Swietenia macrophylla(Sma) / Swietenia mahagoni(Smh) / Tabebuia heterophylla(Th) / Tabebuia insignis var. Monophylla(Tm) / Tabernaemontana cirifolia(Tc) / Tamarindus indica(Ti) / Theobroma cacao (Tca) / Vitex divaricata (Vd) / Ximenia americana(Xa) / Zanthoxylum caribaeum(Zc) / Zanthoxylum flavum (Zf) / Zanthoxylum monophyllum(Zm) / Zanthoxylum punctatum (Zp) / Zanthpxylum spinifex(Zs).*

**Table 3.** Predominant ecological species (Box 1).

| | Number of individuals (nb) | Relative frequency (fr) (%) | Density (d) d = nb/m$^2$ | Basal area (Ab, m$^2$) | Id = fr × d | ID = Id × Ab |
|---|---|---|---|---|---|---|
| Pf | 2578 | 100 | 0.04683015 | 17.362218 | 4.683015 | 81.3075273 |
| Bs | 816 | 90.6666667 | 0.01482289 | 30.186213 | 1.34394203 | 40.5685203 |
| Lv | 1250 | 80 | 0.02270663 | 16.470831 | 1.8165304 | 29.9197652 |
| Ml | 2558 | 74.6666667 | 0.04646685 | 6.9462584 | 3.4695248 | 24.1002158 |
| Bs | 2666 | 90.6666667 | 0.0484287 | 4.7602596 | 4.3908688 | 20.9016754 |
| Oco | 3082 | 80 | 0.05598547 | 3.9315548 | 4.4788376 | 17.6087955 |
| Pfr | 2173 | 49.3333333 | 0.03947321 | 8.6791759 | 1.94734503 | 16.90135 |
| Th | 513 | 56 | 0.0093188 | 19.738256 | 0.5218528 | 10.3004642 |

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| | | | | | | |
|---|---|---|---|---|---|---|
| Csw | 1006 | 64 | 0.0182743 | 8.4171233 | 1.1695552 | 9.84429032 |
| Cco | 1092 | 77.3333333 | 0.01983651 | 4.4138391 | 1.53402344 | 6.77093264 |
| Em | 2311 | 61.3333333 | 0.04198002 | 2.3457174 | 2.57477456 | 6.03969348 |
| Sfm | 735 | 30.6666667 | 0.0133515 | 10.527929 | 0.409446 | 4.31061842 |
| Ecn | 1360 | 38.6666667 | 0.02470481 | 4.49177 | 0.95525265 | 4.29077521 |
| Mc | 2313 | 61.3333333 | 0.04201635 | 1.5360684 | 2.5770028 | 3.95845257 |
| Kf | 982 | 49.3333333 | 0.01783833 | 3.9985153 | 0.88002428 | 3.51879055 |
| Eh | 946 | 76 | 0.01718438 | 2.2336979 | 1.30601288 | 2.91723823 |
| Gbr | 801 | 52 | 0.01455041 | 3.5595433 | 0.75662132 | 2.69322635 |
| Ct | 2024 | 30.6666667 | 0.03676658 | 1.96 | 1.12750845 | 2.20991657 |
| Ep | 1080 | 48 | 0.01961853 | 2.3365329 | 0.94168944 | 2.20028836 |
| Ila | 390 | 50.6666667 | 0.00708447 | 5.8409888 | 0.35894648 | 2.09660237 |
| Bsp . | 360 | 46.6666667 | 0.00653951 | 6.8034969 | 0.30517713 | 2.07627168 |
| Cpu | 599 | 42.6666667 | 0.01088102 | 3.933321 | 0.46425685 | 1.82607123 |
| Mf | 1215 | 36 | 0.02207085 | 1.9984334 | 0.7945506 | 1,58785646 |
| Ca | 870 | 58.6666667 | 0.01580382 | 1.4942083 | 0.92715744 | 1.38536634 |
| Tc | 636 | 57.3333333 | 0.01155313 | 1.903468 | 0.66237945 | 1.26081809 |
| Ael | 673 | 41.3333333 | 0.01222525 | 1.99 | 0.50531033 | 1.00556756 |

### 4.3. Descriptive Model of Plant Succession

The temporal evolution of vegetation is subdivided into phases related to its self-organisation. Ten phases or stages of plant succession were considered, bearing in mind that this process normally begins with herbaceous communities (**Figure 4**). Each stage is made up of three temporal processes: initiation, expansion and maturity. The whole corresponds to the intra-stage dynamics. Each stage of succession is characterised by a determining factorial space; a physiognomic type, horizontal distributions of stems, densities of individuals, biomasses and distances of woody exclusion. In addition, there is a vertical organisation known as architectural. Generally speaking, within the plant matrix, a specimen of an erect woody species in its development reaches its level of morphological inversion corresponding to the establishment of the first ramifications and which is related to its level of ecological inversion. Ultimately, the dynamic gradient or plant succession can be likened to a succession of installation and expansion sites, of ecological profiles, in particular of temperaments in relation to light and species, and therefore of morphological types.

### 4.4. Phases in the Morphogenesis of Tree Species

As shown in **Figure 5**, in each phase of succession we find trees that have reached maturity and that continue until senescence (the trees of the present that will become the trees of the past) and trees that are in a phase of morphogenetic development (the trees of the future).

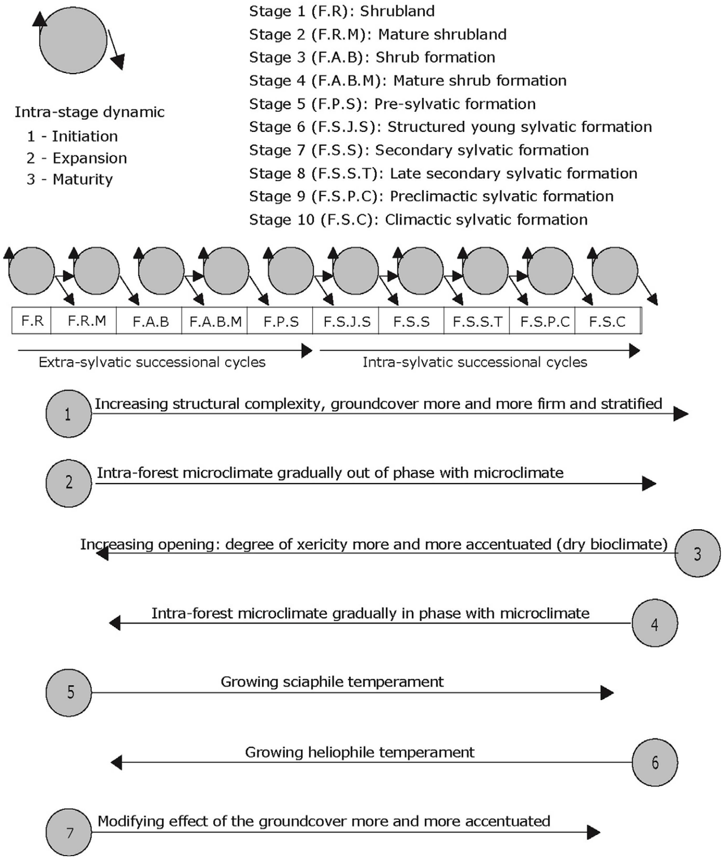

**Figure 4.** Self-Organisation process in plant life.

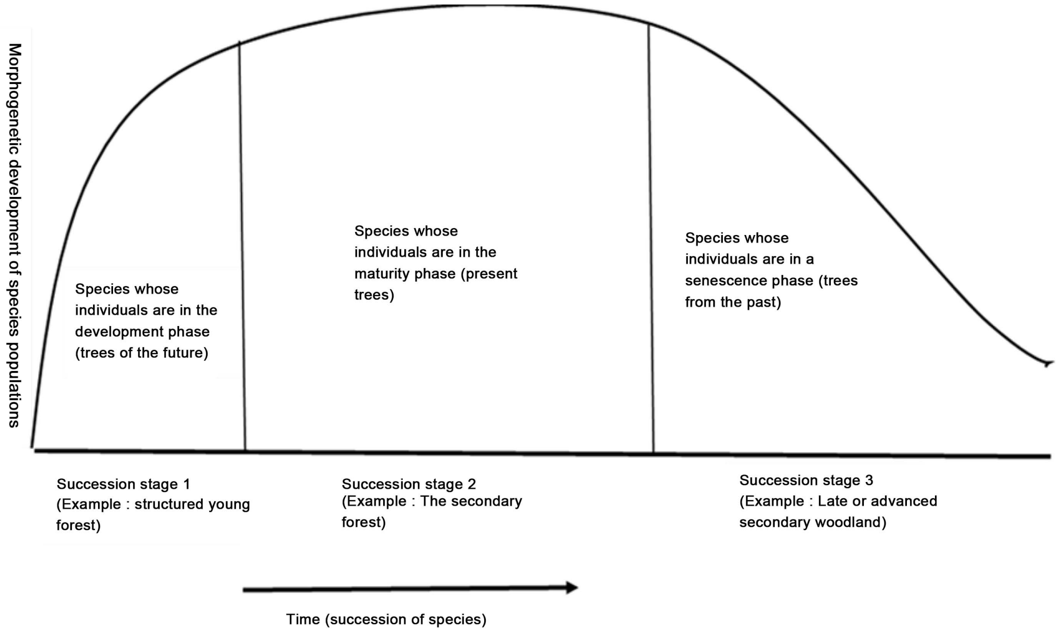

**Figure 5.** Phases in the morphological evolution of species populations.

## 4.5. Sylvatic Stages

### 4.5.1. Young Structured Sylva (Figure 4)

This dynamic stage is made up of young sylvatic associations; it is the initiation state in which tree species are predominant and some of which are at the beginning of their expansion. The sylva is young and structured, since the intra-forest climate and the installation and expansion sites are essentially suited to forest species with "secondary heliophilous" temperament. It (the young sylva) still preserves in its structure some relict representatives of the last rank of the dynamic intra-shrub stage process. Windthrow is not yet the main method of renewing the forest cover or forest matrix. It is very difficult to distinguish the different strata because the structured young sylvatic formation is still very compact. For reasons of intellectual ease and to understand its overall architecture, we will consider the existence of stratification. Among the most predominant and characteristic species of this stage,[1] we can distinguish, in order of ecological dominance and stratigraphic importance [Trees of the present (AP), trees of the future (AF); Figure 5]:

***a) The upper strata:***

*Pisonia fragrans* (*AP*) / *Mayteanus laevigata* (*AF*) / *Pimenta racemosa* (*AF*) / *Lonchocarpus violaceus* / *Chionanthus compacta* / *Bursera simaruba* / *Coccoloba swartzii* / *Eugenia confusea* / *Tabebuia heterophylla* / *Krugiodendron ferreum* / *Inga laurina* / *Byrsonima spicata* / *Coccoloba pubescens* / *Myrcia fallax* / *Amyris elemifera* / *Pisonia suborbiculata* / *Acacia muricata* / *Hymenaea courbaril* / *Citharexylum spinosum* / *Ocotea eggersiana* / *Cassine xylocarpa* / *Sideroxylon foetidissimum* / *Sideroxylon obovatum* / *Cordia alliodora* / *Buchenavia tetraphylla* / *Swietenia mahagoni* / *Swietenia macrophylla* / *Gyminda latifolia* / *Zanthoxylum spinifex* / *Cornutia pyramidata* / *Cannella winterana* / *Cordia sulcata* / *Spondias mombin* / *Ouratea guildingii* / *Cordia Ceiba* / *Ceiba pentandra* / *Brosimum alicastrum* / *Exostema sanctae-luciae* / *Garcinia humilis* / *Crateva tapia* / *Cedrela odorata* / *Zanthoxylum flavum* / *Myrthiantes Fragrans* / *Maclura tinctoria* / *Inga ingoides* / *Coccoloba venosa* / *Magaritaria nobilis* / *Cupania americana* / *Cecropia schreberiana* / *Guazuma ulmifolia*.

In addition to these species: *Picrasma exelsa* (Marie-Galante), *Sideroxylon salicifolia* (Marie-Galante), *Tabebuia pallida* (Marie-Galante), *Swartzia simplex* (Saint Vincent).

***b) The lower strata:***

*Ocotea cernua* / *Bourreria succulenta* / *Myrcia citrifolia* / *Eugenia monticola* / *Guettarda scabra* / *Eugenia pseudopsidum* / *Chrysophyllum argenteum* / *Tabernaemontana citrifolia* / *Capparis indica* / *Daphnopsis americana* / *Haematoxylon campechianum* / *Croton corylifolius* / *Casearia decandra* / *Eugenia tapacumensis* / *Hymenaea coubaril* / *Picramnia pentandra* / *Schaefferia frutescens* / *Conostegia calyptrata* / *Morisonia americana* / *Bunchosia glandulosa* / *Ficus citrifolia* / *Pilocarpus racemosus* / *Zanthoxylum punctatum* / *Acacia tamarindifolia* / *Cassine xy-*

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[1] In bioclimatic conditions already specified.

*locarpa* / *Forestieria rhamnifolia* / *Myrciaria floribunda Ardisia obovata* / *Rauvolfia viridis* / *Zanthoxylum monophyllum* / *Erithalis fruticosa* / *Zanthoxylum caribaeum* / *Guettarda odorata* / *Capparis baduca* / *Cordia martinicensis* / *Capparis Cynophallophora* / *Coccothrinax barbadensis* / *Jacquinia armillaris* / *Eugenia axillaris* / *Actinostemon caribaeus* / *Leucaena leucocephala* / *Malpighia martinicensis* / *Rhyticocos amara* / *Psychotria nervosa* / *Plumeria alba* / *Annona reticulata* / *Ximenia americana* / *Annona muricata* / *Eugenia hodgeï* / *Erythrina collarodendrum* / *randia nitida* / *Melicoccus bijugatus* / *Crossopetalum rhacoma* / *Myrcia spendens* / *Calyptranthes elegans* / *Aiphanes erosa* (*Saint Vincent*).

***c*) *Regenerations*:** species whose sites are suitable for their germination phase, their seedling state and the start of their ligneous development (in the form of small sprigs).

*Pisonia fragrans* / *Ocotea coriacea* / *Maytenus laevigata* / *Pimenta racemosa* / *Chionanthus compacta* / *Coccoloba swartzii* / *Sideroxylon foetidissimum* / *krugiodendron ferreum* / *Eugenia sp* / *Inga laurina* / *Byrsonima spicata* / *Coccoloba pubescens* / *Myrcia fallax* / *Chrysophyllum argenteum* / *Tabernaemontana citrifolia* / *Daphnopsis americana* / *Croton corylifolius* / *Ocotea patens* / *Manilkara bidentada* / *Eugenia tapacumensis* / *Hymenaea courbaril* / *Picramnia pentandra* / *Ocotea eggersiana* / *Cassine xylocrapa* / *Sideroxylon obovatum* / *Cassipourea guianensis* / *Ardisia obovata* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Simaruba amara* / *Zanthoxylum caribaeum* / *Ocotea cernua* / *Ormosia monosperma* / *Pouteria multiflora* / *Ixora ferrea* / *Garcinia humilis* / *Guaiacum officinale* / *Picrasma exelsa*.

#### 4.5.2. Secondary Forest (Figure 4)

This is the result of the morphogenetic development of tree species forming the young structured forest. In this case, there is a physiognomic transformation of the vegetation cover correlating with an increase in the colonising capacity of certain species which are already installed and which will persist in the late or advanced secondary sylvatic stage. Some of them may be marginally present in the pre-climacic and climacic stages. Overall, the ecological inversion surface and the morphological inversion surface are reached for the species of the present structural group, whatever strata they belong to (**Figure 5**). The aerial organisation that is being established is at the beginning of its development and is concretely translated on the architectural level by the appearance of the first ramifications and therefore by the expansion of the foliar phytomass. The growth of the epigeal biomass is accompanied by an increase in the photosynthetic surface area. Whatever the position of the taxa in the vertical organisation, the morphological inversion surface represents the stratigraphic level where the characteristics of the vertical factorial gradients give the species the most favourable development conditions (**Figure 5**). Some species consolidate their presence in the structure by increasing their density and biomass and are often in a metastable situation due to their demographic dynamics, which are related to the scale of the intra-stage cycles (**Figure 4**). Consequently, they are represented in the majority of age classes. The forest matrix is favourable to the installation and expansion of these species, allowing them to carry out all of their phenophases (the different stages of their biology). Other woody species belonging to the lower (or earlier) dynamic stages are represented either by senescent individuals or by individuals at the end of their biological cycle. Diaspores germinate at certain sites but do not complete all of their phenophases. Since the ecological conditions are profoundly unfavourable to them, in particular the distribution of photic energy and the loss of competitiveness with regard to environmental resources, dieback occurs shortly after the appearance of the seedlings.

***a) The upper and middle strata***

*Pisonia fragrans / Maytenus laevigata / Pimenta racemosa / Lonchocarpus violaceus / Chionanthus compactus / Bursera simaruba / Coccoloba swartzii /Eugenia confusa / Tabebuia heterophylla / Sideroxylon foetidissimum / Krugiodendron ferreum / Inga laurina / Byrsonima spicata / Coccoloba pubescens / Myrcia citrifolia / Manilkara bidentata / Acacia muricata / Hymenaea courbaril / Ficus citrifolia / Ocotea eggersiana / Cassine xylocarpa / Mangifera indica / Sideroxylon obovatum / Cassipourea guianensis / Buchenavia tetraphylla / Cordia alliodora / Simaruba amara / Zanthoxylum caribaeum / Gyminda latifolia / Ficus nymphaeifolia / Exothea paniculata / Guazuma ulmifolia / Ormosia monosperma / Pouteria multiflora / Licaria service / ILex nitida / Spondias mombin / Cordia sulcata / Quararibea turbinata / Cordia collococca / Lonchocarpus pentaphyllus / Guarea macrophylla / Pouteria semecarpifolia / Brosimum alicastrum / Exostema sanctae-luciae / Rhyticocos amara / Garcinia humilis / Crateva tapia / Cedrela odorata / Zanthoxylum flavum / Margaritaria nobilis / Tabebuia monophylla / Maclura tinctoria / Cupania americana / Cecropia schreberiana / Antirhea coriacea / Allophyllus racemosus / Manilkara zapota / Sterculia caribaea / Melicoccus bijugatus / Swartzia simplex / Vitex divaricata / Inga ingoides / Ocotea leucoxylon / Ficus americana / Ceiba pentandra / Myrcianthes fragrans.*

***b) The lower strata***

*Ocotea coriacea / Eugenia monticola / Guettarda scabra / Chrysophyllum argenteum / Tabernaemontana citrifolia / Amyris elemifera / Capparis indica / Daphnopsis americana / Pisonia suborbiculata / Haematoxylon campechianum / Croton corylifoilus / Ocotea patens / Casearia decandra / Eugenia tapacumensis / Picramnia pentandra / Conostegia calyptrata / Morisonia americana / Bunchosia glandulosa / Pilocarpus racemosus / Zanthoxylum punctatum / Eugenia pseudopsidium / Acacia tamarindifolia / Capparis hastata / Guarea glabra / Forestieria rhamnifolia / Myrciaria floribunda / Ardisia obovata / Rauvolfia viridis / Zanthoxylum monophyllum / Swietenia macrophylla / Swietenia mahagoni / Faramea occidentalis / Guettarda odorata / Rochefortia spinosa / capparis baduca / Cornutia pyramidata / Capparis Cynophallophora / Canella winterana / Coccothrinax barbadensis / Jacquinia armillaris / Eugenia axillaris / Ouratea guildinguii / Actinostemon caribaeus / Ixora ferrea / Eugenia gregii / Leucaena leucocephala / Psychotria nervosa / Annona reticulata / Ximenia americana / Annona muricata /*

*Eugenia hodgei* / *Guaiacum officinale* / *Crossopetalum rhacoma* / *Myrcia splendens* / *Calyptranthes elegans* / *Eugenia biflora* / *Aiphanes erosa* / *Pricrasma exelsa* / *Coccoloba venosa*.

Apart from a small number of new species, the plant community representative of this dynamic stage is almost identical to that of the previous stage (structured young sylvatic stage). The transformations that have taken place are only physiognomic in nature and are not without consequence for the interactional fabric. Due to the morphogenetic expansion of secondary forest plants, the installation sites have changed somewhat. The reduction in the number of sites suitable for their ecology means that existing species are becoming demographically less and less competitive. On the other hand, the new web of constraints resulting from these modifications is much more favourable to plant species with greater ecological specialisation. Some species of the final stages[2], timidly installed in this stage, will see their populations strengthen over time in terms of regeneration and young stems.

***c*) Regenerations**

*Pisonia fragrans* / *Ocotea coriacea* / *Maytenus laevigata* /*Pimenta racemosa* / *Coccoloba swartzii* / *Sideroxylon foetidissimum* / *Krugiodendron ferreum* / *Eugenia pseudopsidium* / *Ocotea patens*/ *Manilkara bidentata* /*Eugenia tapacumensis* / *Hymenaea courbaril*/ *Ocotea eggersiana* / *Guarea glabra* / *Cassine xylocarpa* / *Sideroxylon obovatum* / *Cassipourea guianensis* / *Buchenavia tetraphylla* / *Ocotea cernua* / *Exothea paniculata* / *Rochefortia spinosa* / *Ormosia monosperma* / *Pouteria multiflora* / *Licaria sericea* / *Ilex nitida* / *Coccothrinax barbadensis* /*Eugenia axillaris* / *Quararibea turbinata* /*Ixora ferrea* / *Guarea macrophylla* /*Eugenia gregii* / *Pouteria semecarpifolia* / *Brosimum alicastrum* / *Exostema sanctae-luciae* / *Rhyticocos amara* / *Garcinia humilis* / *Cedrela odorata* / *Guaiacum officinalis* / *Cupania americana* / *Antirhea coriacea* / *Myrcia leptoclada* /*Eugenia oerstedeana* / *Sterculia caribaea* / *Swartzia simplex* / *Chione venosa* / *Calyptranthes elegans*/ *Eugenia biflora* / *Aiphanes erosa*.

### 4.5.3. Late or Advanced Secondary Forest

This stage can to some extent be characterised by what has been mentioned above except that it corresponds to an important temporal interface. Indeed, optimal ecosystem organisation is almost reached and thus prefigures the conditions that prevail in the climax: the apogee of the plant cover in terms of physiognomy, architecture, flora and ecosystems. The difference already initiated between a preponderant matrix composed of ecologically more demanding species and the entities of renewal of the forest (the gaps), is definitively affirmed. This duality of structure (matrix-gaps) is matched by a duality of function signified by differences in spatio-temporal expression, both phytocenotic and logically floristic. We therefore move from a barely differentiated secondary forest to a late secondary forest

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[2] Although they only develop significant populations in the climax, certain species with a fairly broad dynamic range can install themselves as early as the secondary forest stage.

characterised by a "matrix-gaps" system which is distinctively composed of heliophilous and hemi-heliophilous species and helio-sciaphilous species (structuring the upper strata) and sciaphilous species (structuring the lower strata, **Figure 6**). Depending on their geometric characteristics (implying particular ecological conditions), the gaps are composed of hemi-heliophilous or primary heliophilous species. Where there has been little change in the forest cover, such as in the case of windsnap, secondary heliophilous or even hemi-sciaphilous species are the most common.

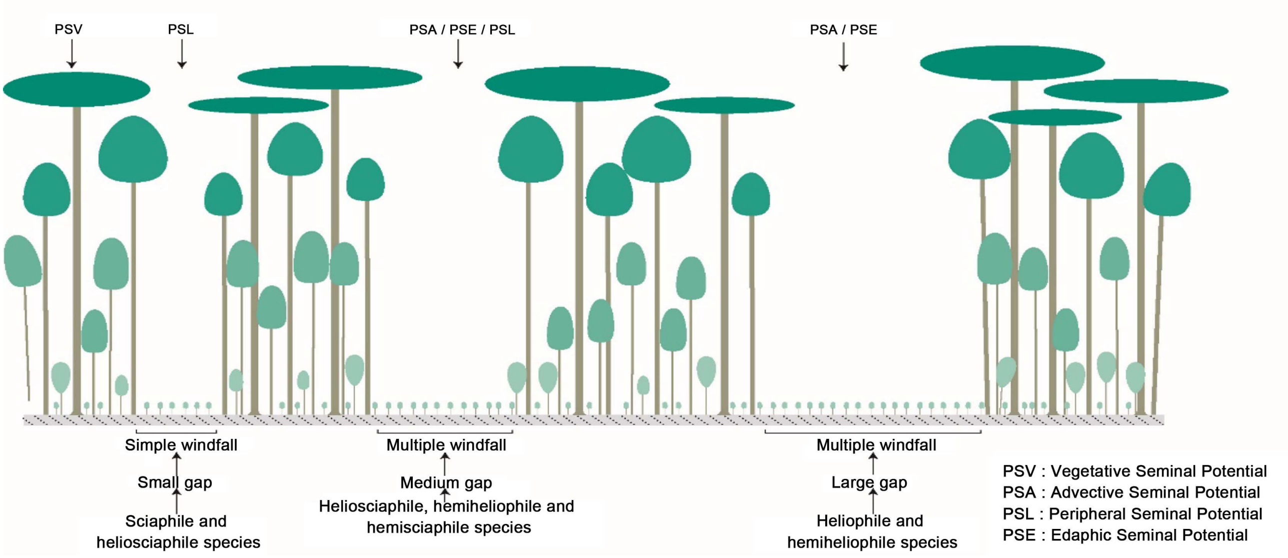

**Figure 6.** Regenerations in the primary forest matrix and in gaps.

### a) *The upper and middle strata*

*Pisonia fragran* / *Maytenus laevigata* / *Pimenta racemosa* / *Lonchocarpus violaceus* / *Chionanthus compacta* / *Coccoloba swartzii* / *Eugenia confusa* / *Sideroxylon foetidissimum* / *Krugiodendron ferreum* / *Inga laurina* / *Manilkara bidentata* / *Hymenaea courbaril* / *Ocotea eggersiana* / *Guarea glabra* / *Sideroxylon obovatum* / *Cassipourea guianensis* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Simaruba amara* / *Zanthoxylum caribaeum* / *Gyminda latifolia* / *Ficus nymphaeifolia* / *Exothea paniculata* / *Guazuma ulmifolia* / *Rechefortia spinosa* / *Ormosia monosperma* / *Pouteria multifora* / *Licaria sericea* / *Ilex nitida* / *Cordia sulcata* / *Lonchocarpus pentaphyllus* / *Guarea macrophylla* / *Pouteria semecarpiflia* / *Brosimum alicastrum* / *Exostema sacntae-luciae* / *Rhyticocos amara* / *Crateva tapia* / *Cedrela odorata* / *Zanthoxylum flavum* / *Myrcianthes fragrans* / *Margarita nobilis* / *Tabebuia heterophylla* / *Tabebuia monophyllum* / *Maclura tinctoria* / *Cupania americana* / *Antirhea coriacea* / *Cecropia schreberiana* / *Allophyllus racemosus* / *Manilkara zapota* / *Lonchocarpus cericeus* / *Myrcia Leptoclada* / *Sterculia caribaea* / *Melicoccus bijugatus* / *Swartzia simplex* / *Vitex divaricata* / *Licania leucosepala* / *Chione venosa* / *Inga ingoides* / *Picrasma exelsa* / *Ocotea leucoxylon* / *Ficus americana* / *Ficus citrifolia.*

***b*) *The lower strata***

*Ocotea coriacea* / *Eugenia monticola* / *Eugenia confusa* / *Eugenia pseudopsidium* / *Myrcia fallax* / *Chrysophyllum argenteum* / *Tabernaemontana citrifolia* / *Amyris elemifera* / *Daphnopsis americana* / *Ocotea patens* / *Casearia dacandra* / *Eugenia tapacumensis* / *Picramnia pentandra* / *Conostegia calyptrata* / *Bunchosia glandulosa* / *Pilocarpus racemosus* / *Acacia tamarindifolia* / *Capparis hastata* / *Cassine xylocarpa* / *Forestiera rhamnifolia* / *Mangifera indica* / *Myrciaria floribunda* / *Ardisia obovata* / *Zanthoxylum monophyllum* / *Ocotea cernua* / *Capparis Cynophallophora* / *Canella winterana* / *Coccotrhinax barbadensis* / *Eugenia axillaris* / *Quararibea turbinata* / *Plinia pinnata* / *Ixora ferrea* / *Eugenia gregii* / *Garcinia humilis* / *Eugenia hodgei* / *Guaiacum officinale* / *Randia nitida* / *Eugenia oerstedeana* / *Aiphanes erosa*.

The late or advanced sylvatic stage is a state of the vegetation cover corresponding to ecological conditions profoundly different from those of the less complex preceding stages, even if it still includes plant species typical of the latter. Compared to the young structured secondary stage, the characteristics of the installation and expansion sites of the species are similar to those associated with sites of the pre-climacic and climacic stages. In other words, they can only accommodate the most specialised plant species, known as terminal species: this phenomenon is observable at the level of regenerations.

***c*) *Regenerations***

*Ocotea coraicea* / *Maytenus laevigata* / *Pimenta racemosa* / *Sideroxylon foetidissimum* / *Krugiodendron ferreum* / *Manilkara bidentata* / *Eugenia tapacumemsis* / *Hymenaea courbaril* / *Guarea glabra* / *Sideroxylon obovatum* / *Cassipourea guianensis* / *Rochefortia spinosa* / *Ormosia monosperma* / *Pouteria multiflora* / *Licaria sericea* / *Ilex nitida* / *Coccothrinax barbadensis* / *Quararibea turbinata* / *Guarea macrophylla* / *Pouteria semecarpifolia* / *Guaiacum offinal* / *Cupania americana* / *Myrcia leptoclada* / *Eugenia oerstedeana* / *Licania leukosispala*.

### 4.5.4. The Pre-Climacic and Climacic Sylvatic Stages

The following assemblage of species is composed of species that are potentially the most specialised. In other words, they are the most likely to be part of climacic floristic compositions. These plant species have notable populations as early as the pre-climacic stage, thanks to the sites provided by the late sylvatic formation that has reached its final phase; they consolidate and stabilise in the climacic stage.

*Maytenus laevigata* / *Pimenta racemosa* / *Sideroxylon foetidissimum* / *Krugiodendron ferreum* / *Manilkara bidentata* / *Eugenia tapacumemsis* / *Hymenaea courbaril* / *Guarea glabra* / *Sideroxylon obovatum* / *Pouteria multiflora* / *Coccothrinax barbadensis* / *Guarea macrophylla* / *Pouteria semecarpifolia* / *Brosimum alicastrum* / *Rythicocos amara* / *Ocotea leucoxylon*.

In many combinations, these species will form the heliosciaphilous matrix. The main component of the climacic forest, this stable and balanced matrix is a mosaic of ecologically and structurally similar patches or ecological units (eco-units).

Other species with different dynamic profiles prefer to live in windthrows or forest gaps. This category includes the large heliophilous plants (sylvatic builders) and a good number of species whose existence in the forest entity depends on the size of the windthrow.

### 4.5.5. Synecological or Community Facets of the Lower Bioclimatic Layer

Given the variability of rainfall, three sectors can therefore be defined in which climatic conditions present some differences and lead to selectivity with respect to the representatives of the floristic potential of the lower layer. This selectivity entails the existence of three subsets of the floristic potential or collection of plant species. Firstly, a floristic sub-potential associated with zones with an annual rainfall of less than or equal to 1250 mm; these are mostly zones close to the coast and some sites on exposed slopes. Secondly, a floristic sub-potential associated with zones with an annual rainfall of between 1250 mm and 1600 mm and thirdly, a floristic sub-potential associated with zones with rainfall equal to or greater than 1600 - 1700 mm and rarely exceeding 1800 mm. The proposed subdivision into rainfall bands is a simplified version of reality, since other factors may come into play and act in conjunction to increase or decrease the xericity of the stations. For example, valley bottoms, whatever the sector under consideration and the potential rainfall, often have greater water resources: here we are talking about potential rainfall and not the water available for plants.

These different zones have their own characteristics in terms of annual water useful for vegetation and could be broken down into a horizontal rainfall gradient. This phenomenon is related to the duration of the period of rainfall deficit or climatic drought, but also with the water storage capacity of plant formations, which depends on the plant component and the evolution of the edaphic system. This refers to the dynamics of plant systems in its broadest definition; that based on the interactive complex of soil and vegetation, evolving *a priori* in the same direction under natural conditions. The biology of the different species gives them a capacity for colonisation which is enhanced to a greater or lesser extent by the mesological or ecological characteristics of the stations. Moreover, this is even before the various successional processes influencing the identity of the installation and expansion sites take place. The ecological success of taxa, in fact their demographic efficiency, is conditioned by their biology and the biophysical parameters of the biotopes.

**(1) Floristic potential of the least watered sectors: annual rainfall less than or equal to 1250 mm, rarely less than 1000 mm**

*Lonchocarpus violaceus* / *Busera simaruba* / *Erythroxylum havanense* / *Eugenia confusa* / *Tabebuia heterophylla* / *Sideroxylon foetidissimum* / *Coccoloba pubescens* / *Amyris elemifera* / *Maytenus laevigata* / *Pisonia subcordata* / *Haematoxylon campechianum* / *Acacia muricata* / *Eugenia tapacumemsis* / *Randia aculeata* / *Eugenia ligustrina* / *Schaefferia frutescens* / *Morisonia americana* / *Acacia tamarindifolia* / *Forestiera rhamnifolia* / *Pithecellobium unguis-cati* / *Sideroxylon obovatum* / *Krugiodendron ferreum* / *Eugenia cordata* / *Rauvolfia viridis* / *Eri-*

*thalis fruticosa* / *Gyminda latifolia* / *Zanthoxylum spinifex* / *Guettarda odora* / *Rochefortia spiniosa* / *Cornutia pyramidata* / *Cordia martinicensis* / *Capparis Cynophallophora* / *Canella winterana* / *Acacia sp* / *Jacquinia armillaris* / *Eugenia axillaris* / *Ouratea guildinguii* / *Actinostemon caribaeus* / *Croton flavens* / *Leucaena leucocephala* / *Malpighia martinicensis* / *Plumeria alba* / *Ximenia americana* / *Schoepfia schreberi* / *Eugenia hodgei* / *Guaiacum officinale* / *Maclura tinctoria* / *Erythrina corallodendrum* / *Crossopetalum rhacoma* / *Laetia thamnia* / *Cestrum sp* / *Coccoloba venosa* / *Croton hircinus* / *chamaecrista nictitans* / *Croton guildinguii* / *Pavonia spinifex*.

The species of this sub-potential have a capacity to colonise the most xeric zones of the study area, from the fruticose stage to the sylvatic stage. The geological substratum, through pedogenesis, favours certain species. In fact, it appears that soils on calcareous formations, in a small number of stations, favour an assemblage of species known as calciphilous species. Consequently, it was important to propose two dynamic directions, on calcareous and volcanic formations respectively, corresponding to strict floristic sub-potentials. In Martinique, unlike Guadeloupe and some of its dependencies, the calcareous bedrock is very marginal; it is present on the calcareous hills of Sainte-Anne and Le Marin as well as on a very small portion of the Caravelle peninsula.

**1) Dynamic pattern on volcanic substratum**

**a) *Fruticose and shrub stages* (Box 2a, Figure 4)**

*Erithroxylum havanese* / *randia aculeata* / *Aacacia tamarindifolia* / *Eugenia ligustrina* / *Pithecellobium unguis-cati* / *Eugenia cordata* / *Rauvolfia viridis* / *Cordia martinicensis* / *Acacia sp* / *Jacquinia armillaris* / *Actinostemon caribaeus* / *Croton flavens* / *Malpighia martinicensis* / *Plumeria alba* / *Schoepfia schreberi* / *Laetia thamnia* / *Cestrum sp* / *Croton hircinus* / *Chamaecrista nictitans* / *Croton guildinguii* / *Pavonia spinifex*.

**b) *Young structured secondary, secondary and late secondary sylvatic stages* (Box 2b, Figure 4)**

*Lonchocarpus violaceus* / *Bursera simaruba* / *Tabebuia heterophylla* / *Coccoloba pubescens* / *Amyris elemifera* / *Pisonia suborbiculata* / *Haematoxylon campechianum* / *Acacia muricata* / *Eugenia tapacumensis* / *Morisonia americana* / *Forestiera rhamnifolia* / *Erithalis fruticosa* / *Gyminda latifolia* / *Guettarda odorata* / *Cornutia pyramidata* / *Eugenia axillaris* / *Ouratea guildinguii* / *Leuceana leucocephala* / *Ximenia americana* / *Eugenia hodgei* / *Maclura tinctoria* / *Erythrina corallodendrum* / *Coccoloba venosa*.

***Pre-climacic and climacic sylva stage***

*Sideroxylon foetidissimum* / *Amyris elemifera* / *Maytenus laevigata* / *Eugenia tapacumemsis* / *Gyminda latifolia*.

**2) Dynamic pattern on calcareous substratum**

Species with a high affinity for this type of environment and in which their distinctive populations may be of overwhelming ecological importance with regard to the other species of the floristic sub-potential will be mentioned. These so-called calciphilous species form communities in the stations with calcareous substratum in which they constitute the majority of the structuring elements.

***a) Fruticose and shrub stages*** (Box 2a, Figure 1)

*Schaefferia frutescens* / *Crossopetalum rhacoma*.

***b) Secondary sylvatic stage*** (Box 2b, Figure 1)

*Gyminda latifolia* / *Zanthoxylum spinifex* / *Capparis Cynophallophora* / *Canella winterana*.

***Pre-climactic and climactic stages***

*Guaiacum officinale* / *Rochefortia spinosa* / *Sideroxylon obovatum* / *Sideroxylon foetidissimum* / *krugiodendron ferreum*.

All taxa associated with the pre-climacic and climacic successional phases have virtually the same ecological profile. Depending on the soil substratum, some will be favoured by small phenological differences: in this case the physicochemical composition of the soil. On a calcareous bedrock, this causes changes within the installation sites that favour calciphilous species. This does not prevent non-calciphilous species from occupying some installation sites, which makes them auxiliary elements in the structural and functional organisation of the phytocenoses.

Box 2

*a) Ecological conditions associated with shrub and fruticose formations*

- *Species adapted to drought and presenting a fairly wide range of mechanisms. Apart from caducity, which remains an important adaptive feature, there is a whole series of strategies allowing species to complete their biological cycle (morphological and anatomical transformations).*
- *Seminal dormancy is a distinctive characteristic.*
- *In general, the edaphic system is pellicular, although the phytocenoses of these stages can colonise the sectors with deep soils compacted by cattle (significant structural modifications).*
- *Physiological rhythms are in phase with climatic rhythmicity: very pronounced seasonality of the groundcover.*
- *Species among the most generalist in terms of floristic potential.*
- *There is no matrix/gap bipolarity. The groundcover is still open and interspecific competition is fierce. Dominance of primary heliophiles (pioneers).*
- *Zoochore, anemochore and barochore dissemination. It is difficult to find a hierarchy of importance between these three modes of dispersion. However, it seems that anemochory is efficient.*

*b) Young structured and expanding secondary sylvatic conditions*

*The species belonging to these stages have been previously mentioned and analysed from an ecological point of view. In what follows we will only state the main principles associated with this crucial phase of dynamics, particularly in the lower layer and in dry bioclimates:*

- *Species with a certain ability to withstand drought and with some* *adaptations, notably caducity. Diaspores capable of resisting, within particular limits, desiccation.*

- *Existence of dormancy, the extent of which depends on the position of the species on the successional gradient.*
- *Inherited soils, more or less deep depending on the characteristics of erosion. Soils of medium to shallow depth, in the case of a co-evolution of edaphic system-vegetation.*
- *The intra-forest microsystem is still in phase with the macroclimate.*
- *Start of vertical structuring: one or two strata.*
- *Moderately specialised installation and expansion sites.*
- *Species still exhibiting generalist behaviour (transitional post-pioneers).*
- *Initiation of a bipolarity of the matrix/gap sylvatic ecosystem: predominantly hemi-heliophile "proto-matrix" with a weakly represented hemi-sciaphilous component. Gaps composed of primary heliophiles.*

*Zoochore dissemination accompanied by an anemochore dissemination that is still active.*

**(2) Floristic potential of sectors with annual rainfall between 1250 mm and 1600 - 1700 mm**

The regions that are under the influence of the dry bioclimate and have these rainfall criteria are frequent and occupy larger areas. The subset of the floristic potential thus selected is composed of a greater number of plant species and can be considered representative of this vegetation layer:

*Pisonia fragrans / Ocotea coriacea / Bourreria succulenta / Maytenus laevigata / Tabebuia heterophylla / Myrcia citrifolia / Eugenia Monticola / Pimenta racemosa / Lonchocarpus violaceus / Chionanthus compacta / Coccola swartzii / Calliandra tergemina / Eugenia confusa / Tabebuia heterophylla / Sideroxylon foetidissimum / Krugiodendron ferreum / Guettarda scabra / Byrsonima spicata / Amyris elemifera / Croton bixoides / Capparis indica / Haematoxylon campechianum / Croton corylifolius / Manilkara bidentata / Casearia decandra / Eugenia tapacumensis / Hymenaea courbaril / Picramnia pentandra / Bunchosia glandulosa / Ficus citrifolia / Pilocarpus racemosus / Zanthoxylum punctatum / Citharexylum spinosum / Capparis hastata / Cassine xylocarpa / Forestiera rhamnifolia / Myrciaria floribunda / Ardisia obovata / Rauvolfia viridis / Zanthoxylum monophyllum / Swietenia macrophylla / Swietenia mahagoni / Coccothrinax barbadensis / Cordia Ceiba / Ceiba pentandra / Rhyticocos amara / Garcinia humilis/ Crateva tapia / Psychotria nervosa / Cedrela odorata / Zanthoxylum flavum / Myrcianthes fragrans / Eugenia hodgei / Tabebuia pallida / Maclura tinctoria / Buchenavia tetraphylla / Picrasma exelsa / Ficus americana / Zanthoxylum caribaeum.*

***a) Fruticose and shrub stages***

*Bourreria succulenta / Myrcia citrifolia /Eugenia monticola / Calliandra* *tergemina* / *Croton bixoides* / *Capparis indica* / *Haematoxylon campechianum* / *Croton corylifolius* / *Pilocarpus racemosus* / *Zanthoxylum punctatum* / *Rauvolfia viridis* / *Psychotria nervosa*.

***b*) Secondary sylvatic stages (*young structured, secondary and late secondary sylva*)**

*Pisonia fragrans* / *Ocotea coriacea* / *Tabebuia heterophylla* / *Pimenta racemosa* / *Lonchocarpus violaceus* / *Chionanthus compacta* / *Coccoloba swartzii* / *Eugenia confusa* / *Tabebuia pallida* / *Guettarda scabra* / *Byrsonima spicata* / *Amyris elemifera* / *Casearia decandra* / *Eugenia tapacumensis* / *Picramnia pentandra* / *Bunchosia glandulosa* / *Ficus citrifolia* / *Citharexylum spinosum* / *Capparis hastata* / *Cassine xylocarpa* / *Forestieria rhamniflolia* / *Myrciaria floribunda* / *Ardisia obovata* / *Zanthoxylum monophyllum* / *Swietenia macrophylla* / *Swietenia mahagoni*/ *Coccothrinax barbadensis* / *Cordia Ceiba* / *Ceiba pentandra* / *Rhyticocos amara* / *Garcinia humilis* / *Crateva tapia* / *Cedrela odorata* / *Zanthoxylum flavum* / *Myrcianthes fragrans* / *Eugenia hodgei* / *Maclura tinctoria* / *Aiphanes erosa* / *Picrasma exelsa* / *Zanthoxylum caribaeum*.

The "secondary sylvatic" stages correspond to "primordial states" of sylvigenesis and are located between the young, barely structured sylva and the late or advanced secondary sylva. The "matrix-gaps" bipolarity exists from the very beginning of the forest entity. As the forest progresses towards its optimal organisation, it becomes more complex and induces an increasing specialisation of species. Unlike windthrows, which are renewal cells, the sylvan matrix is predominant in terms of surface area, species and biomass. Differentiated floristic functional groups are associated with the various "matrix-gaps" binomials of the intra-sylvatic successional cycles (**Figure 4**). Throughout the evolution of forest vegetation, depending on their ecology, hemisciaphilous and hemiheliophilous or even heliophilous plant species form the assemblages either in the matrix or in the gaps. Particularly during a positive or progressive succession, generalist species and their regenerations, tolerant to varying degrees of light, are eliminated from the matrix and can install themselves in the gaps. We have named this phenomenon: floristic transfer from the stable, balanced sylvatic matrix for the dynamic stage under consideration towards the renewal units represented by the windthrows.

**Sylvatic matrix species for the secondary stage:**

**(*The notion of secondary stage encompasses all states of forest formation before the climacic stage can be defined*)**

*Pisonia fragrans* / *Ocotea coriacea* / *Tabebuia heterophylla* / *Pimenta racemosa* / *Lonchocarpus violaceus* / *Chionanthus compacta* / *Coccoloba swartzii* / *Eugenia confusa* / *Byrsonima spicata* / *Amyris elemifera* / *Eugenia tapacumensis* / *Picramnia pentandra* / *Ficus citrifolia* / *Capparis hastata* / *Cassine xylocarpa* / *Swietenia macrophylla* / *Swietenia mahagoni* / *Coccothrinax barbadensis* / *Cordia collococca* / *Rhyticocos amara* / *Garcinia humilis* / *Crateva tapia* / *Cedrela odorata* / *Zanthoxylum flavum* / *Myrcianthes fragrans* / *Eugenia hodgei* / *Maclura tinctoria* / *Picrasma exelsa* (*Marie-Galante*) / *Myrciaria floribunda* / *Zanthoxylum mono-*

*phyllum* / *Zanthoxylum caribaeum*.

**Species of small disturbed areas considered to be windthrows or gaps**

*Guettarda scabra* / *Casearia decandra* / *Citharexylum spinosum*/ *Forestiera rhamnifolia* / *Ardisia obovata* / *Bunchosia glandulosa* / *Ceiba pentandra*.

In addition to these taxa from destabilised zones, there are those that are typical of fruticose and shrub formations (Box 2); logically, their presence depends on the surface area of the windthrow. At this stage of evolution, this matrix-gap dichotomy, in the spatial organisation of the forest is not always easy to see. All the species and morphological types appear to belong to both the matrix and the renewal cells (windthrow or gaps). Nevertheless, even if all the species are represented in terms of absolute frequency (their presence or absence with respect to the stations), the study of their spatial distribution and their dominance shows that those that belong to the component called the matrix have a high probability of installing themselves in this entity. They therefore find a significant number of sites for installation and expansion and develop a much larger phytomass. The same applies to species that are preferentially dependent on gaps.

This phenomenon is mainly due to the ecology of the species, which gives them a certain plasticity in terms of their ability to occupy installation and expansion sites, the biophysical characteristics of which are dictated by the degree of structuring of the plant communities. In this dynamic stage, the sylvatic matrix is made up of secondary heliophiles and hemi-heliophiles and sometimes hemi-sciaphiles. On the other hand, windthrow species are primary heliophiles whose expansion is favoured by the more xeric conditions that prevail in these entities of "maintenance" and forest restructuring.

***c) Pre-climacic and climacic sylvatic stages***

*Maytenus laevigata* / *Pimenta racemosa* / *Sideroxylon foetidissimum* / *Krugiodendron ferreum* / *Byrsonima spicata* / *Amyris elemifera* / *Manilkara bidentata* / *Eugenia tapacumemsis* / *Hymenaea courbaril* / *Guarea glabra* / *Myrciaria floribunda* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Zanthoxylum flavum* / *Exothea paniculata* / *Coccothrinax Barbadensis* / *Eugenia axillaris* / *Garcinia humilis* / *Cedrela odorata* / *Zanthoxylum caribaeum* / *Myrcianthes Fragrans* / *Picrasma exelsa*.

**Matrix species of climacic and pre-climacic forests**
**(Helio-sciaphilous/sciaphilous matrix)**

*Maytenus laevigata* / *Pimenta racemosa* / *Sideroxylon foetidissimum* / *Manilkara bidentata* / *Guarea glabra* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Eugenia tapacumensis* / *Coccothrinax barbadensis* / *Garcinia humilis* / *Exothea paniculata* / *Krugiodendron ferreum*.

**Species associated with windthrow in climacic and pre-climacic forests**

*Amyris elemifera* / *Byrsonima spicata* / *Hymenaea courbaril* / *Myrciaria floribunda* / *Zanthoxylum caribaeum* / *Eugenia axillaris* / *Cedrelala odorata* / *Zanthoxylum flavum* / *Myrcianthes Fragrans* / *Picrasma exelsa*.

As vegetation evolves, species, to ensure their sustainability, colonise areas whose environmental conditions suit their biology. When we progress towards climacic forest formation, the dynamic profile of species with a purely heliophilous temperament becomes increasingly unsuited to the ecological characteristics of the matrix.

**(3) Floristic potential of sectors with annual rainfall greater than 1600-1700 mm and only exceptionally exceeding 1800 mm**

These significantly more watered sectors are, in reality, very poorly represented and can be considered marginal. Despite their rarity, they are proving to be valuable assets. Analysis of their vegetation suggests that they are interface environments that would probably be associated with a change in macro-climatic conditions. A certain number of species from the other rainfall areas defined above are represented there. Taxa from the more humid subhumid bioclimatic layer (mesophilous plants) find it difficult to install themselves in these intermediate spaces. Together with other taxa, they form original plant associations, somewhat different from those that traditionally specify vegetation developing in a dry bioclimate.

*Eugenia pseudopsidium* / *Myrcia fallax* / *Daphnopsis americana* / *Ocotea patens* / *Manilkara bidentata* / *Picramnia pentandra* / *Conostegia calyptrata* / *Ocotea eggersiana* / *Guarea glabra* / *Cassipourea guianenis* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Simaruba amara* / *Zanthoxylum caribaeum* / *Faramea occidentalis* / *Ocotea cernua* / *Ficus nymphaeifolia* / *Exothea paniculata* / *Guazuma ulmifolia* / *Ormosia monosperma* / *Pouteria multiflora* / *Capparis baduca* / *Licaria sericea* / *Ilex nitida* / *Spondias mombin* / *Cordia sulcata* / *Quararibea turbinata* / *Plinia pinnata* / *Lonchocarpus pentaphyllus* / *Ixora ferrea* / *Guarea macrophylla* / *Eugenia gregii* / *Pouteria semecarpifolia* / *Brosimum alicastrum* / *Exostema sanctae-luciae* / *Rhyticocos amara* / *Cedrela odorata* / *Margaritaria nobilis* / *Palicourea crocea* / *Cupania americana* / *Randia nitida* / *Cecropia schreberiana* / *Antirhea coriacea* / *Allophyllus racemosus* / *Lonchocarpus sericeus* / *Myrcia leptoclada* / *Eugenia oerstedeana* / *Inga laurina* / *Sterculia caribaea* / *Swartzia simplex* / *Vitex divaricata* / *Licania leucosepala* / *Chione venosa* / *Myrcia splendens* / *Inga ingoides* / *Calyptranthes elegans* / *Eugenia biflora* / *Ocotea leucoxylon* / *Miconia laevigata* / *Gonzalagunia hisurta*.

***a) Fruticose and shrub stages***

*Conostegia calyptrata* / *Capparis baduca* / *Palicourea crocea* / *randia nitida* / *Miconia laevigata* / *Gonzalagunia hisurta* / *Myrcia splendens*.

***b) Secondary sylvatic stages***

*Eugenia pseudossidium* / *Myrcia fallax* / *Daphnopsis americana* / *Ocotea patens* / *Picramnia pentandra* / *Ocotea eggersiana* / *Cassipourea guianensis* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Simaruba amara* / *Zanthoxylum caribaeum* / *Faramea occidentalis* / *Ocotea cernua* / *Ficus nymphaeifolia* / *Exothea paniculata* / *Guazuma ulmifolia* / *Ilex nitida* / *Spondias mombin* / *Cordia sulcata* / *Quararibea turbinata* / *Plinia pinnata* / *Lonchocarpus pentaphyllus* / *Ixora ferrea* / *Eugenia gregii* / *Exostema sanctae-luciae* / *Rhyticocos amara* / *Cedrela odorata* / *Margaritaria nobilis* / *Cupania americana* / *Cecropia schreberiana* / *Antirhea coriacea* /

*Allophyllus racemosus* / *Lonchocarpus sericeus* / *Eugenia oerstedeana* / *Vitex divaricata* / *Inga ingoides* / *Inga laurina* / *Calyptranthes elegans* / *Eugenia biflora*.

**Matrix species of secondary formation**

*Eugenia pseudopsidium* / *Myrcia fallax* / *Ocotea coriacea* / *Picramnia pentandra* / *Ocotea eggersiana* / *Cassipourea guianensis* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Simaruba amara* / *Zanthoxylum caribaeum* / *Faramea occidentalis* / *Ficus nymphaeifolia* / *Exothea paniculata* / *Guazuma ulmifolia* / *Ilex nitida* / *Spondias mombin* / *Quararibea turbinata* / *Plinia pinnata* / *Lonchocarpus pentaphyllus* / *Ixora ferrea* / *Eugenia gregii* / *Rhyticocos amara* / *margaritaria nobilis* / *Cupania americana* / *Antirhea coriacea* / *Allophyllus racemosus* / *Eugenia oerstedeana* / *Inga laurina* / *Inga ingoides* / *Calyptranthes elegans* / *Eugenia biflora*.

**Species associated with windthrow in secondary sylva**

*Cordia sulcata* / *Cedrela odorata* / *Cecropia schreberiana* / *Lonchocarpus sericeus* / *vitex divaricata*.

***c) Climacic and pre-climacic formations***

*Manilkara bidentata* / *Ocotea eggersiana* / *Guarea glabra* / *Cassipourea guianensis* / *Buchenavia tetraphylla* / *Cordia alliodora* / *Simaruba amara* / *Exothea paniculata* / *Ormosia monosperma* / *Pouteria multiflora* / *Licania sericea* / *Ilex nitida* / *Guarea macrophylla* / *Pouteria semecarpifolia* / *Brosimum alicastrum* / *Exostema sanctae-luciae* / *Eugenia gregii* / *Rhyticocos amara* / *margaritaria nobilis* / *Cupania americana* / *Antirhea coriacea* / *Myrcia leptoclada* / *Eugenia oerstedeana* / *Sterculia caribaea* / *Swartzia simplex* / *Licania leucosepala* / *Chione venosa* / *Eugenia biflora* / *Ocotea leucoxylon*.

**Matrix climacic species**

*Manilkara bidentata* / *Guarea glabra* / *Cassipourea guianensis* / *Ormosia monosperma* / *Pouteria multiflora* / *Guarea macrophylla* / *Pouteria semecarpifolia* / *Brosimum alicastrum* / *Cupania americana* / *Myrcia leptoclada* / *Eugenia oerstedeana* / *Sterculia caribaea* / *Licania leucosepala* / *Chione venosa* / *Eugenia biflora* / *Ocotea leucoxylon*.

**Species associated with windthrow in climacic forest**

*Ocotea eggersiana* / *Buchenavia tretaphylla* / *Cordia alliodora* / *Simaruba amara* / *Exothea paniculata* / *Licaria sericea* / *Ilex nitida* / *Exostema sanctae-luciae* / *Eugenia gregii* / *Rhyticoos amara* / *margaritaria nobilis* / *Antirhea coriacea*.

## 5. Discussion

### 5.1. Vegetation in the Humid Subhumid Bioclimate (Dry Bioclimate): A Complex Biosystem

Due to their multi-faceted nature, the plant cover of the dry bioclimate of Martinique is a good subject for scientific study, but we are far from being able to understand how it works [30] [31]. The ecosystem complexity of the present results from the multiple dynamic directions caused by man and the spatial variability of bioclimatic factors [32] [33]. In addition to the metastable nature of these biosystems, many natural and anthropogenic hazards modify their structures and accentuate their instability. In a way, man, through his actions, increases the intrinsic heterogeneity of plant cover and thus broadens the scope of possible successional trajectories. Under anthropogenic influence, the multifactorial entity that vegetation represents becomes a hyperspace that is difficult, if not almost impossible, to penetrate. Although the potential of this vegetation layer is, like the others, forest, the lack of knowledge of the initial conditions makes it difficult to easily describe the various aspects of plant dynamics [34]-[36]. **Figure 4** above, showing the stages of the successional gradient, has meaning and reality only on the physiognomic level. It provides information on the succession of the predominant physiognomies during the evolution of the vegetation and not on the constituent floristic elements. However, the dominant physiognomic features roughly indicate the complexity of the ecological units that structure the landscape. Indeed, a landscape marked by the abundance of shrub communities corresponds to regressive vegetation.

By inference, we can say that the ecosystem as a whole[3] will generate installation and expansion sites that are constantly changing. These sites reflect the factorial reality of the ecosystem and present a great deal of spatio-temporal diversity in our study area, as in the archipelago as a whole. This observation reveals the real problem facing biogeographers and ecologists when it comes to finding a common ecosystem analysis framework for the Lesser Antilles. What has been proposed above is merely an attempt to classify candidate species on the time scale of plant succession. From this perspective, the dynamic paths that emerge are linked to the organisation of the current groundcover. The floristic combinations inventoried effectively depend on the current species base (floristic potential). The ecological importance of the species provides information on the potential of the plant formations and, consequently, on their biocenotic complexity.

Fundamental units, installation and expansion sites correspond to the smallest analysable systems and are typical of the spatio-temporal configurations of the plant formation under consideration. They are at the root of the extreme diversity in the organisation of the vegetation, as evidenced by the great multiplicity of floristic combinations. The foregoing highlights two fundamental elements emerge for understanding succession processes: firstly, the great difference in the plasticity of species due to their multiple dynamic profiles, and secondly, the existence of a change in the status of taxa during successional processes, in relation to their ecological importance.

## 5.2. Main Features of Plant Succession

From the "fruticose" stage to the so-called climacic stage, the ecological aptitudes necessary for participation in the "dynamic ballet" change (**Figure 4**). Species with a primary heliophilous temperament, which are the majority at the beginning of plant colonisation in regressive structures such as fruticose and shrub formations,

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[3] Namely, the regional climate, the groundcover in its many phytocenotic facets, the different topographic classes, the various components of the edaphic substratum, anthropogenic energy and the dissemination processes (physical and biological).

become unsuitable as we move towards the most complex vegetation organisations. Secondary heliophiles and hemiheliophiles are better suited to presylvatic and young structured sylvatic formations. In late and climacic sylvatic secondary formations, hemisciaphilous, sciaphilous and heliosciaphilous temperaments give species a very high degree of installation or colonisation efficiency. Considering the biophysical characteristics of the biotopes, the ecological importance of the taxa in the various floristic groupings (their intrinsic ecological potential) is modulated by intra- and interspecific interactions.

Thus, during the plant dynamics, species of different ecology and demographic importance (distribution and dominance) come together. The families of "photic temperament" succeed each other in time and define, at each major stage of succession, periods in which one family dominates the others. From the beginning of the dynamic to its end, we could schematically define: the era of heliophiles, the era of hemiheliophiles, the era of hemisciaphiles, and finally the era of heliosciaphiles and sciaphiles (climacic sylva). Theoretically, at the end of the plant succession, in pre-climacic and climacic sylva, the gaps become sanctuaries within which some of the most heliophilous species survive, as they are unable to install and expand elsewhere. As a result of the way the forest ecosystem functions, it carries within its structure all the possible responses to any degradations; provided that its integrity (or resilience) is not compromised by excessive disruption or deregulations[4]. Apart from their function of sylvigenetic renewal, windthrows are floristic reserves from which restoration mechanisms can be initiated. In small forest patches, new gaps, depending on their size, are colonised by diaspores from peripheral degraded zones and/or gaps already in place and engaged in a "healing" process. Conversely, within large forest massifs, new windthrows are mainly colonised by anemochore and/or zoochore (often ornithochore) seeds from their own gaps.

The geometry of gaps is a primary silvigenetic factor. From the centre to the periphery, they induce a more or less significant variation in physical factors and condition the spatial distribution of floristic assemblages. Over time, restoration mechanisms result in a floristic succession ranging from short-lived to long-lived scar species, passing through a whole series of degrees of longevity. In general, long-lived cicatricial species arrive at the end of restoration (at the end of the restorative succession) and can persist for a long time in the sylvan matrix.

### 5.3. Floristic Transfers from Mesophilous[5] Forest Formations (Humid Subhumid Bioclimate, Middle Vegetation Layer) to Late Pre-Climacic and Climacic Xerophilous[6], Forest Formations (Dry Subhumid Bioclimate, Lower Vegetation Layer, Box 3)

Species transfers from one plant layer to another require specific conditions.

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[4] Ecosystem integrity refers to resilience and therefore the ability to absorb fluctuations in the external environment. These fluctuations can be natural and/or anthropogenic.

[5] Typical tropical seasonal evergreen forest formations.

[6] Terminal phase of plant succession in seasonal tropical evergreen vegetation in a dry bioclimate.

These transfers can take place from the lower to the middle vegetation layer and vice versa. The transfer of species from the typical seasonal evergreen forest formations of the middle storey to the seasonal evergreen forest formations of the lower horizon and xeric facies of the lower storey requires the host forests of this lower storey to have reached a very high level of organisation close to the climax. The seasonal evergreen forest units of the lower horizon and xeric facies of the lower climacic vegetation layer have several strata from the ground to the canopy. These strata are all exchange surfaces that cause a phase shift between the intra-forest environment and the external environment. This attenuates the strong nycthemeral variations of certain factors such as temperature. As a result of this phenomenon, the interior environment of the lower forest floor becomes more humid and can support mesophilous forest species from adjacent areas at higher altitudes. The vector fauna is generally responsible for these transfers between these two levels of vegetation.

Box 3: Characteristics of advanced secondary and climacic seasonal evergreen sylva of the lower horizon in its xeric facies (maximum homeostasis)

a) Species not adapted to drought, very pronounced evergreen character, diaspores sensitive to desiccation.
b) Absence of dormancy except for some gap species, particularly large builders.
c) Deep soils.
d) Internal microclimatic autonomy of the forest ecosystem.
e) Maximum structuring: polystratified system (3 to 4 strata or more).
f) Hyper-specialised installation and expansion sites (pronounced antagonism).
g) Balanced species, the most specialised in the associated floristic potential.
h) Bipolarity of the sylvatic system (matrix/gaps) well established and functional: sciaphilous and helio-sciaphilous matrix, hemi-sciaphilous and hemi-heliophilous gaps.
i) Zoochore dissemination, mainly ornithochore and secondarily barochore in the matrix; but also zoochore in small gaps and anemochore in large ones.

### 5.3.1. Species in the Main Range in the Humid Subhumid Middle Layer

***Matrix species***

*Ilex sideroxyloides* / *Prestoea montana* / *Pouteria semecarpifolia* / *Antirhea coriacea* / *Eugenia oerstedeana* / *Licania leucosepala* / *Brosimum alicastrum* / *Exostema sanctae-luciae* / *Maytenus guianensis* / *Calophyllum calaba* / *Andira inermis* / *Ormosia monosperma* / *Ocotea leucoxylon* / *Guarea glabra* / *Eugenia biflora* / *Eugenia coffeifolia* / *Cassipourea guianensis* / *Chimarrhis cymosa* / *Chione venosa* / *Pouteria multiflora* / *Chrysophyllum argenteum* / *Manilkara bidentata* / *Sterculia caribaea* / *Tabernaemontana citrifolia* / *Guarea macrophylla*.

***Species of disturbed spatial units (windsnap and windthrows of variable size)***

*Rhyticocos amara* / *Tabebuia heterophylla* / *Ceiba pentandra* / *cordia alliodora* / *Hymenaea courbaril* / *Erythroxylon squamatum* / *Margaritaria nobolis* / *Sapium caribaeum* / *Lonchocarpus pentaphyllus* / *Homalium racemosum* / *Cinnamomum elongatum* / *Licaria sericea* / *Ocotea cernua* / *Ocotea eggersiana* / *Ocotea membranacea* / *Ocotea patens* / *Conostegia calyptrata* / *Cedrela odorata* / *Inga laurina* / *Inga ingoides* / *Ficus americana* / *Ficus nymphaeifolia* / *Eugenia gregii* / *Eugenia lambertiana* / *Eugenia pseudopsidium* / *Myrcia citrifolia var.imrayana* / *Myrcia fallax* / *Pisonia fragrans* / *Coccoloba swartzii* / *Faramea occidentalis* / *Ixora ferrea* / *Neolaugeria resinosa* / *Zanthoxylum caribaeum* / *Picramnia pentandra* / *Simarouba amara* / *Guazuma ulmifolia* / *Daphnopsis americana* / *Pimenta racemosa* / *Ilex nitida*.

### 5.3.2. Species in a Marginal Area in the Lower Layer, Coming from the Middle Layer and Developing in the Very Advanced or Climacic Organisations of the Lower Layer with Different Structural Aspects

*Manilkara bidentata* / *Calophyllum calaba* / *Ormosia mosnosperma* / *Andira inermis* / *Ocotea leucoxylon* / *Guarea macrophylla* / *Guarea glabra* / *Cassipourea guianensis* / *Pouteria multiflora* / *Licaria sericea* / *Pouteria semecarpifolia* / *Rhyticocos amara* / *Cordia alliodora* / *Margaritaria nobilis* / *Homalium racemosum* / *Inga laurina* / *Ocotea cernua* / *Ocotea eggersiana* / *Ocotea patens* / *Ocotea membranacea* / *Eugenia gregii* / *Simarouba amara* / *Guazuma ulmifolia* / *Eugenia oerstedeana* / *Sterculia caribaea* / *Licania leucosepala* / *Exostema sanctae-luciae* / *Antirhea coriacea* / *Brosimum alicastrum* / *Eugenia biflora* / *Ilex nitida*.

### 5.3.3. Species in the Main Range in the Lower Layer

*Sideroxylon foetidissimum* / *Amyris elemifera* / *Eugenia tapacumensis* / *Gyminda latifolia* / *Maytenus laevigata* / *Guaiacum officinale* / *Rochefortia spinosa* / *Sideroxylon obovatum* / *Pimenta racemosa* / *Krugiodendron ferreum* / *Byrsonima spicata* / *Hymenaea courbaril*/ *Myrciaria floribunda* / *Buchenavia tetraphylla* / *Zanthoxylum flavum* / *Exothea paniculata* / *Coccothrinax barbadensis* / *Cedrela odorata* / *Zanthoxylum caribaeum* / *Myrcianthes Fragrans* / *Picrasma exelsa* / *Garcinia humilis*/ *Ilex nitida* / *Cupania americana* / *Myrcia Leptoclada* / *Canella winterana*.

***Matrix species*** (***all dynamic facies***)

*Sideroxylon foetidissimum* / *Maytenus laevigata* / *Guaiacum officinale* / *Rochefortia spinosa* / *Sideroxylon obovatum* / *Pimenta racemosa* / *Krugiodendron ferreum* / *Exothea paniculata* / *Coccothinax barbadensis* / *Myrcianthes Fragrans* / *Picrasma exelsa* / *Garcinia humilis* / *Cupania americana* / *Myrcia leptoclada* / *Eugenia tapacumensis* / *Buchenavia tetraphylla* / *Hymenaea courbaril*.

***Gaps species*** (***all dynamic facies***)

*Gyminda latifolia* / *Amyris elemifera* / *Byrsonima spicata* / *Hymenaea courbaril* / *Myrciaria floribunda* / *Buchenavia tetraphylla* / *Zanthoxylum flavum* / *Cedrela odorata* / *Zanthoxylum caribaeum* / *Ilex nidita* / *Canella winterana*.

## 5.4. Main Ecological Traits of Plant Species

Depending on the bioclimatic layer and the dynamic level reached by the plant community, the concept of sciaphilous species and heliophilous species should be used with great caution. A species can have several temperaments with respect to photic energy. For example, for the same dynamic stage, a middle layer gap species with a heliophilous tendency can, in the main matrix of the lower layer, act as a secondary heliophilous species or a hemisciaphilous species. Conversely, in the same vegetation layer and for two distinct dynamic phases, a species can have two opposing behaviours with respect to light energy and find opportunities to install itself either in the matrix or in the gaps. It is clear that sciaphilous and heliophilous characteristics are relative and depend on the following fundamental parameters: the intensity and distribution of photic energy within the vegetation units[7] and the photosynthetic profile of the species of floristic potential. The latter is a reflection of their biology.

For a species to be in optimal conditions for development, the light energy available in the forest formation must correspond to its photosynthetic efficiency. This condition is more likely to be met if the other factors are non-limiting. Light temperament alone does not explain the ecosystem behaviour of species of floristic potential; it participates with the other factors in the definition of the different ecological profiles, which are therefore dynamic. In a forest entity, species are in strong competition with each other, so that their population and morphogenetic development determine the quantitative relationships between installation and expansion sites. At each degree of evolution, the most represented species will be those that find the most sites for installation and expansion. Consequently, they will be balanced for a given formation and during the period in which the latter is stable, if it constitutes a transition stage.

The dominance (or preponderance) of a species or, more broadly, of a group of species, is a reflection of the great differences that exist between installation and expansion sites. The latter are subdivided into families with distinct characteristics. Depending on the factorial conditions prevailing in the ecosystem, certain families take on significant importance and host the most ecologically adapted species. These species, through their ecological profiles, are indicators of the ecosystem state of the vegetation cover and have a high dominance index. The other taxa are associated with a small number of sites and constitute the auxiliary or marginal group, which it is not essential to take into account in the analysis of the structure and floristic combination of the formation studied.

### 5.5. The Final Phases of Plant Dynamics or Approaching the Structural Apogee of Vegetation

It is possible to end this section without mentioning the optimum stage of vegetation. Without impoverishing the subject, we could overlook the ultimate potential of the plant cover, which we know to be sylvatic. Nevertheless, all the problems that were raised, and which in many cases have not been resolved, suggest that we

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[7] The intensity and distribution of light energy are a function of the degree of organisation and the successional phase of the phytocenoses.

should reflect on climax. There are many different definitions, analyses and assertions regarding this concept, which, depending on the school of thought, takes on various forms and is the subject of controversy. The climax of a type of vegetation is the end of a successional process which has taken place over a long period, during which successive and not always continuous associations of species with very varied ecological strategies have been mobilised. In the climacic entity, maximum organisation is achieved and the most specialised floristic assemblages are dominant. The intra-forest microclimatic conditions are different from those that characterise the macroclimate. The degree of stability (resilience) of the system is high. It is said to be homeostatic and that variations, particularly daily variations, in the regional climate are strongly buffered. In the absence of disturbances that are not solely linked to turnover in windthrows, the conditions are favourable to the reiteration of the structure in place.

At the level of the edaphic component, things seem to be identical. There is theoretically a hyper-organisation of the soil from the abiotic (depth, texture, water dynamics, nutrient potential [fertility], water potential) and biotic (micro-fauna, macro-fauna, meso-fauna, root tissue) point of view. The climax is characterised above all by great complexity and diversity. In fact, a pedoclimax corresponds to a phytoclimax.

It is true that in the climax, the most specialised species are preferentially expressed. However, in the matrix-gap climacic entity, differentiated from a structural, functional and floristic point of view, all dynamic strategies are represented. This could be described as a dynamic climax [37] [38]. In the absence of anthropogenic and/or climatic disturbances that do not jeopardise the stability of the ecosystem, these terminal communities are self-sustaining.

This maintenance of the climacic forest is similar to that of the graminaceous herbaceous formation, which can be repeated over a long period. However, it is different because it is subject to elimination by substitution. Indeed, when shrubs install themselves within the graminaceous cover, they gradually become denser and develop increasingly large biomasses. In a way, they initiate a plant succession. The climacic formation, on the other hand, is stable over time in the absence of any profound natural or anthropogenic stress. This maximum homeostatic character means that changes are extremely slow. Therefore, the inertia of the climacic forest allows it to perpetuate itself in new climatic conditions, different from those of the original climate, under the influence of which it developed. In this state of affairs, it is obvious that human activity is very harmful and can lead to irreversible deregulation, resulting in the definitive disappearance of floristic organisations that bear witness to past eco-climatic conditions.

The autonomy of the intra-forest environment with respect to the macroclimate, and the structural and floristic integrity ensured mainly by the inertia of the system[8], are all elements that are specific to the pre-Columbian sylva of the Lesser

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[8] The climactic forest is like a hyperorganism endowed with autonomy with regard to the surrounding environment and capable of perpetuating itself when the initial conditions for its emergence no longer exist.

Antilles, particularly the lower vegetation layer of Martinique. Today, there are no more examples of primitive seasonal evergreen sylvan formations. Regarding the sub-montane and montane ombrophile vegetation layers, there are some severely weakened relicts on landforms unsuitable for the development of human societies (Martinique, Dominica, Guadeloupe, Saint Lucia).

The concept of climax must be put into perspective and should not be understood dogmatically as a perfect balance between plant ecosystems and the climate [39] [40]. The high degree of structuring of plant communities results in a phase shift between the intra-forest microclimate and the macroclimate. This phase shift leads to significant transfers of species from their main areas to their marginal areas: for example, from the middle layer to the lower layer. The climax can then be seen as a maximum balance between eco-units and specific mesological or ecological conditions. The biocenotic mosaic reflecting the underlying ecosystem heterogeneities is composed of little differentiated matrix patches to which gaps of different, or even very different, ages, structures, sizes and floristic compositions are added. At the regional level, the characteristics of the topo-sequences, the various microclimates and the edaphic variants accentuate the multi-faceted character of the climax. Moreover, it is this phenomenon which is at the root of the great biodiversity of climacic sylvatic formations. The various floristic arrangements or combinations reveal the variability of the ecological factors. In reality, the climax is a polyclimax, since it corresponds to a great number of highly specialised matrix-like terminal plant units.

At the optimum stage, however, there is a tendency for this intrinsic factorial heterogeneity to diminish. For example, differences due to the edaphic system and topography, which create unique microclimates, can be compensated for by the hyper-organisation of climacic plant communities. Furthermore, it is these ecosystem corrections that condition the spatial floristic transfers described above. In the past, this resulted in a certain homogenisation of the contiguous vegetation layers. Currently, the vegetation is in a state of collapse and regression. Most of the phytocenoses that make it up are both physiognomic types and dynamic facies that contribute to the very diverse landscape. Despite the lack of relevant data, there is every reason to believe that in the absence of the original climatic conditions, the inertia necessary for the maintenance of primitive plant ecosystems no longer exists because of anthropisation. In reality, the formations from which contemporary plant units are derived were, even in their primitive state, relicts of a distant climatic era.

It therefore appears that the climax or even polyclimax of primitive pre-colonial vegetation represented a singularity in the evolution of vegetation at the level of climate change. That is to say that the dynamic directions which made this possible were part of a particular history of the biosphere, in very specific environmental and climatic conditions. Consequently, the physiognomic aspects indicate as many dynamic stages. In the Lesser Antilles today, particularly in Martinique, the evolution of the plant world is marked by a highly diversified anthropisation.

If we accept the systemic functioning of plant formations at station level, it must also be admitted at a higher level of integration. It results from the interaction of biocenoses and mature ecosystems of different natures, maintaining the major regional biological balances [41]-[43]. The recent history of the vegetation of Martinique and the Lesser Antilles has been characterised by human activities of varying frequency and intensity. Moreover, if anthropisation disappears, in particular in protected areas, the vegetation will produce, in the sectors where it can reach its dynamic peak, multifaceted sylvan ensembles: structural analogues of the polyclimax of pre-Columbian times. What will differentiate this next hypothetical climax will be linked mainly to floristic compositions. Thus, in protected zones, based on the current severely depleted floristic potential, the newly formed climacic floristic combinations will be totally different from those of the old climax. This future terminal stage will result from the occurrence of all the specific combinations specific to the different phases of the dynamic gradient. At each of them, the characteristics of the installation and expansion sites depend largely on the structure of regional physical factors: more precisely, the geomorphological shape and the climate. The latter are associated with important parameters that interact and create a factorial space (precipitation, cloud cover, evaporation, evapotranspiration, topography, circulation of pellicular and underground water, pedogenesis and vegetation). This evolves in correlation with changes in the floristic cover and the edaphic system: in general, these two components of the ecosystem vary in parallel. Theoretically, future climaxes of protected areas will not correspond to pre-colonial ones, since the successive factorial spaces that mark out the dynamic gradient will differ from the old ones.

In the best non-anthropised forest relicts, ongoing plant successions will result in floristic groupings different from those found in the plant cover of Amerindian times, despite a plausible architectural and structural analogy. Many biological types belonging to ancient (mature) ecosystems have disappeared or are today in sharp decline. Successional processes make selections from the contemporary floristic potential, which is extremely diverse for species in the pioneer and young secondary stages and not very diverse for those in the advanced and climacic secondary stages. It should also be noted that species from the advanced secondary and relict climacic phases of the primitive forest most often form populations composed of a small number of individuals.

In the event that certain inaccessible sectors unsuitable for human activities reach climax, the latter will certainly be poly-facies and the architecture of the sylvatic plant units will be close to that of the climax of pre-colonial times. However, they will be made up of species with dynamic profiles of lower successional stages: rather generalist. Logically, the complexity of the assumed future climax will be much lower than that which corresponded to the conditions that generated the primitive sylva.

In general, plant succession reaches its final phase when it has used, in the form of plant assemblages, all the species of the floristic potential. The maximum structuring associated with it depends on the great diversity of dynamic profiles. When they are sufficiently numerous, as in Amerindian times, they give the groundcover a high degree of biocenotic plasticity, both in the restoration and complexification processes. In the past, natural hazards, such as hurricanes, constituted sylvigenetic factors in their own right that occurred over a long period of time: they are said to have a structuring effect. From the 17th century onwards, human activities of low occurrence led to an insularisation of the forest and over-expressed the impacts of natural hazards: destructuring elements.

After a few hundred years or even a millennium, in the absence of any disturbance, the polyclimax generated will be based on a greatly diminished floristic potential, consisting mainly of species with dynamic profiles adapted to secondary vegetation. A few relict climacic species may also be present in small numbers, timidly ensuring their sustainability in marginal and non-climacic forest groupings. Many stations with these characteristics are located in zones sensitive to human pressure. Given the insufficiently comprehensive (systemic) environmental management of these island territories, they are at risk of disappearance in the short to medium term.

Over time, the decrease in the complexity of the groundcover has resulted in greater fragility of the structures in place. In this regard, many taxa that currently participate in the most advanced eco-units, and some of which will participate in those of the next climax, are much less resistant and have a shorter life cycle. These rather generalist matrix species of the present could only perpetuate themselves in the gaps or windthrows of the old climacic sylva.

The fragility of today's forests means that climatic hazards are of greater significance, and in certain situations their effects are paroxysmal. For example, hurricanes David (1979), Hugo (1989) and DEAN (2007) caused a significant loss of epigeal biomass in the different forest types. The first hit the north of Martinique and caused heavy damage in the weakly structured secondary forests, particularly in the heavily anthropised hills. Hurricane DEAN is a typical example because the secondary sylva of the ACA hill (commune of Marin, south of the island) were devastated. The forest formations still bear the scars of these recent catastrophic cyclonic episodes. Generally speaking, many trees that built the sylva of the time were "cyclonised". They were broken or fell, thus increasing the density of the gaps. The excessive increase in the number of windthrows is a destabilising factor that prevents the structural integrity of forest formations from being maintained.

These natural degradations were not comparable to those suffered by the forest units of Guadeloupe during hurricane Hugo (1989). All forest groupings were affected. The violence of the winds was such in Guadeloupe that in many forest sectors the quantity of mutilated trees was astonishingly high. On the other hand, in Martinique, Guadeloupe and Puerto Rico, hurricanes David and Hugo caused little damage to the most advanced sylvatic ecosystems: mature or old-growth forests as well as those known as climacic or subclimacic. The destructuring resulted in windsnap, partial or total but temporary defoliation and probably an increase in gaps following the fall of trees. Moreover, this occurred without the architectural and structural integrity of the eco-units being compromised [44] [45]. The importance of the mass effect, which reduces the influence of strong winds, is clear to see. From an aerial and root point of view, the mechanical resistance of forest massifs is all the greater when the structuring species are in the terminal stage [46] [47].

The forest ecosystem that has reached its maximum complexity seems to be less vulnerable to climatic hazards. The degradation of the crowns of the upper strata has as a corollary a decrease in the overall leaf index of the affected forest communities and a gain in light energy for their internal environment [48]. Under these conditions, the heliosciaphilous matrix species, which are on standby, can develop or, on the contrary, some heliophiles can find installation and expansion sites. In the Lorrain valley (Martinique), within the advanced tropical sub-montane ombrophilous eco-units, the regular distribution of the Mahot *grandes feuilles* (*Cordia sulcata*: Boraginaceae), a heliophilous species of secondary seasonal evergreen groups, raises a number of questions. This species seems to have installed itself as a result of openings in the canopy due to a cyclonic phenomenon. A whole range of factors point to a regular opening up of the sylvatic groundcover: firstly, the quasi-random distribution of the stems; secondly, all the individuals of the population of Mahot grandes feuilles belong to the same diametric class. It is therefore plausible that this population of "Mahot grandes feuilles" corresponds to a single wave of colonisation of sites which were surely created by an atmospheric phenomenon.

When the reduction in aerial biomass has not been too significant, the trees reiterate their structure and regain their full development in their installation and expansion sites (nano-systems similar to Holdeman's ecotopes [49]. The reconstitution of the epigeal phytomass is effective on a decade-long scale and leads to a regression in the regeneration of exogenous heliophilous trees that had installed themselves thanks to modifications of the canopy due to cyclonic winds. The overall organisation of the climacic eco-units is maintained, with minimal variations in specific abundance. The terminal or climacic species remain dominant and are mainly regenerated in the sylvatic matrix. These transformations due to climatic hazards are essential for the forest. In addition to renewal in the gaps[9], there are major climatic disturbances[10] that seem to temporarily lower the level of complexity of the climacic formations.

Consequently, the structural transformations of the forest roof mobilise terminal species that are in a stationary state. This renewal mechanism applies as much to the matrix and the gaps and can, like the latter, be considered a sylvigenetic engine. In terms of its temporal dynamics, its mechanisms and the affected sylvatic surface, this *turnover*, linked to aerological disturbances, differs from that which occurs in windthrows. It follows that the climacic forest formations, in par-

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[9] Continuous process with low occurrence.

[10] Discontinuous process with high occurrence.

ticular seasonal evergreen forest formations in Martinique and the Lesser Antilles, present notable differences compared to those that are not subject to destructive hurricanes, in particular those of the equatorial zone (the Guianas).

The climax oscillates between two distinct levels of organisation. The first corresponds to a hyper-structuring of maximum complexity. That is to say that in the absence of powerful hurricanes over a fairly long period, the most specialised floristic and biocenotic interactions would take place. This would lead to high stability, a great self-protective capacity with regard to climatic hazards, a buffered internal environment or microclimate and a high level of ecosystem inertia (high resilience capacity). The second would be similar to the lowest possible complexity of the climacic sylvatic ecosystem without its integrity being compromised. Cyclones are the main determinants and act as a sylvigenetic process. This mechanism is important for the development of certain mature forest-building species, in particular heliosciaphiles [50]. In hyper-structured forest groupings (poly-climaxes), due to the excessive specialisation of the installation and expansion sites, heliosciaphilous species have difficulty in perpetuating in a stationary state, or even in a state of regeneration.

Today, things are diametrically opposed because the floristic potential has been weakened. Due to the impossibility of finding sufficiently extensive and evolved host formations, the most specialised taxa, witnesses of the ancient climax, are for the most part almost absent or in danger of extinction. The sylvatic stations sheltering these relict species are frequently enclosed within a regressive plant cover composed, in order of importance, of shrub, pre-sylvatic and young secondary sylvatic phytocenoses (**Figure 4**). The discontinuity or fragmentation of mature sylvan units, combined with the low efficiency of today's vector fauna, limits the possibilities of dissemination of terminal species. In the hypothesis of a progressive future evolution, the climax will be achieved with the most specialised species of the current floristic potential. The result will be an ecosystem organisation called climacic, but of a complexity much lower than that of the primitive Amerindian forest.

This new hypothetical sylvatic climax will be formed by species whose dynamic profiles would make them similar to the windthrows of pre-Columbian sylva. These species are highly sensitive and vulnerable to cyclones, both from a root point of view and from the point of view of the epigeal phytomass. They are not very dense and their longevity is low to average. Unlike the pre-Columbian period, future climacic forest formations will be much more similar to para-climaxes and climatic disturbances will be, even at low levels, highly destructive and will cause profound, sometimes irreversible, degradation[11].

This results from the loss of interaction possibilities[12] linked to the disappearance or anthropogenic regression of populations of highly specialised species of

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[11] In general, these will call into question the integrity of the newly formed climacic formations.

[12] Here the notion of interaction refers to the notion of connectivity, the degree of which, which is a function of the number of species, defines the hierarchical modes of these species and of the biocenoses within the ecosystem.

the terminal stage: those that normally occupy hyperstructured installation and expansion sites[13]. Like the original primitive forest, ecosystem modifications due to cyclonic winds will not result in a slight rejuvenation, mobilising the climacic plant potential to obtain a hyperclimax after a climacic phase of lower complexity. On the contrary, they will induce a regression that will depend on the intensity of the deregulating elements and the dynamic stages. The damage in terms of broken and fallen trees will be such that the subclimactic vegetation cover will not be able to maintain itself. Since its integrity is not ensured by the new eco-climatic conditions, the vegetation that develops will belong to lower, extra or intra-sylvatic successional stages. In this case of disturbance of a para-climacic forest composed of secondary species with respect to the pre-Columbian climax, there may be dynamic jumps between stages with significant deviations[14] in the direction of regressive succession. Conversely, in the case of the primitive climactic forest, there is an intra-stage regressive succession with small deviations[15] (**Figure 4**).

The vegetation of the lower and middle layers is the result of all the destructive events that have occurred since the beginning of the history of the Lesser Antilles, and therefore of Martinique. It still suffers today from the aggressive impact of human activity, which reinforces the effects of increasingly frequent cyclonic phenomena. All these destabilising factors in the present are not conducive to a positive evolution of the groundcover, which is very far from its maximum organisation (the climax). The persistence of the factors promoting its degradation means that it (the plant cover) is engaged in a permanent process of collapse. This thus leads to the establishment of assemblages of plant species whose dominance is due to anthropisation. These species could be called “anthropophytes” or “anthropophiles” because their ecological prevalence today is facilitated by humans. They indicate the degree of artificialisation of the floristic communities.

Across several generations, significant changes in the overall vegetation would be barely perceptible, even in protected zones. Anthropogenic factors must now be considered as constraints in their own right, influencing the overall dynamics of the ecosystem. As a result, they characterise, as much as the other biophysical factors, the factorial space and will have a very strong “weight” in the identity of the sites of installation and expansion. Anthropisation imposes new ecosystem limits. Indeed, the formerly sylvatic potential of the groundcover is now, for the most part, pre-sylvatic and shrub.

In the dry bioclimate in particular, the slowness of discontinuous successional processes is offset, over a short period of time, by an active and continuous anthropisation of forest formations. Today’s vegetation oscillates between the fruticose, shrub, pre-sylvatic and young, barely structured sylvatic stages. The ad-

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[13] The most complex from a factorial point of view.

[14] From a paraclimacic forest and following a hurricane, we can move to a herbaceous, shrub or fruticose phytocenosis.

[15] The transformations of the forest organisation do not jeopardise the integrity of the dynamic stage, which is sub-climacic or weakened climacic.

vanced or late secondary stages, pre-climacic and climacic, are marginal, particularly in the middle and lower layers[16]. Graminaceous grass formations resulting from profound zoo-anthropic degradation[17] in the driest sectors are very poorly represented. The compaction of the soil by animals changes its characteristics and thus induces atypical plant successions which, during the ligneous pioneer phases, favour species that are naturally scarce. *Mimosa pigra* (Amourette, Mimosaceae) is an eloquent example. Inherited from the first waves of shrub colonisation, it develops preferentially on soils which were the site of agricultural and pastoral practices.

## 6. Conclusions

The concepts that have been developed on the organisation of temporal dynamics, punctuated by specific events, refer to well-defined floristic organisations. Implicitly, these refer to unique autoecological and synecological functions. These organisations can be classified into families of particular physiognomic types corresponding to several degrees of ecosystem complexity. What has been proposed does not constitute. Given the existence of a large number of factors, the primary goal here is to try to explain the functioning of extremely complex plant biosystems. Whatever the exploration tools used, the large number of mesological (ecological), biological and anthropogenic parameters generate factorial spaces which impose limits on the overall analysis: in particular the impossibility of knowing the initial state of the plant cover, the difference between the scale of their evolution and that of human observation, and the large number of direct and induced anthropogenic factors.

Currently, knowledge of the many biocenotic facies does not provide a clear understanding of the evolution of the vegetation. At most, we are able to analyse the "plant dynamics" system in terms of its large subdivisions, which correspond to several levels of integration. This is due to the almost non-existence of precise information on the ancient climax. Traced back over time, the evolution of the vegetation cover in a dry bioclimate (lower layer) assumes that all the successional stages are known, from the most regressive to the most advanced. In contrast to the forest, late secondary, pre-climacic and climacic stages, the shrub and secondary sylvatic stages are currently widely represented. The late secondary forest formation, although very marginal, is the only formation that can be considered the most complex or most evolved representative.

In light of the factors mentioned above, it appears that the evolution of the current vegetation towards its most complex organisation has been blocked or significantly slowed by anthropisation. Consequently, significant ecosystem transformations due to progressive dynamics, particularly in protected areas, will only be observable after several decades, or even on a timescale exceeding a hundred years. This state of affairs has permeated and continues to permeate mentalities and con-

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[16] This is true throughout the Lesser Antilles.

[17] Sometimes the damage caused by pastoral activities is almost irreversible.

tributes to a singular perception of the physiognomy and functioning of the plant world. For example, low-lying zones influenced by a dry bioclimate, such as the northern Caribbean fringe and the extreme south of Martinique, are considered to be areas of low, dry and non-forest vegetation, although there may exist in these places small zones where the relief has made it possible to preserve sylvatic units, some of which bear witness to the forest ecosystems of the early days of colonisation. In regions where the anthropogenic factor continues to prevail, the future climax or paraclimax, even with the current floristic potential, will never be reached. The profound deregulation of the middle and lower layers must be compensated for by responsible environmental policies relating to conservation biology, as they could become irreversible and catastrophic in a few decades.

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## Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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