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Climax Phase Forest Species of the Lesser Antilles Forests

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***Abstract*-From the low areas to the summits, the Lesser Antilles exhibit a dry sub-wet, sub-wet wet, wet and hyperwet bioclimates with several mesoclimate and microclimatic characteristics. They are mainly due to variations in rainfall. The bioclimatic tiering results in a plant tiering whose potential forest types are diverse both at biocenotic and specific level. In fact the high heterogeneity of the biophysical factors, including the topography and rainfall factors, result in a large number of micro-environments which support a significant floristic, phenological and biocenotic diversity. In these territories, by modifying the biotopes, man has simply increased their biological diversity at all the ecosystem integration (or complexity) levels and particularly the diversity of the species of the rather general secondary plant communities. The dominating tree associations of the Lesser Antilles prehistory (pre-colonial assemblies) are little known because the remaining primitive forests have very small surfaces. Based on our current knowledge regarding vegetation dynamics and the degree of vegetation specialization in relation to the main eco-climatic factors such as light and water, we were able to list the species that formerly comprised the primeval forests of the Amerindian age. Irrespective of the bioclimate, today's so-called advanced old forests are structurally and architecturally different from the pre-Columbian forest formations. Nevertheless, they often suffer from a notable lack of climax stage species resulting both from biotope regression and the changes, over time, of the means of diaspore dissemination. In order to understand the phases of vegetation dynamics, we must know the main taxa of the climatic climax forest vegetation.**

Key words- Lesser Antilles, bioclimates, forests, climax, climax species

I. INTRODUCTION

On all spatial and temporal scales, the Lesser Antilles forest represents a biocenotic mosaic that reveals the heterogeneity of its ecological conditions [1-5]. Irrespective of the taxonomic differences, the main matrix of the so-called climax forest formations, the highly specialized species of the different strata (including the upper and lower ones) have quasi-equivalent (morphogenetic) architectural features and functions [6-7]. The continuous and hummocky forest roof caused by nested crowns is a direct result. In reality, the ecologic matrix units of these climax forests consists of terminal species [8]. They are floristically different, although they belong to the ultimate successional stages and have a matching combinatorial complexity [9-11].

In short, irrespective of their backgrounds and their level of evolution, the various forest types of the Lesser Antilles can be included in a set of interactive characteristics consisting of multiple ecological units identified by functional groups [12-15] (Fig.1). Rather than seeing preponderant groups of two, three or four species, we must now consider a quantitatively more important floristic community. It consists of all taxa which may be dominant in the plural site conditions arising from the heterogeneity of the environment [16-17]. The idea of a pool of tree species characterising each evolutionary stage of the plant floors, in particular the one corresponding to the climax floor, seems more appropriate to explain the large differences observed *in-situ* [18-21]. The floristic combinations depend on environmental variations and interspecific local interactions. The heterogeneity of the (physical, biological, and anthropogenic) factors, specific to each island system, explains the demographic differences of the species of the floristic potential of the archipelago in the plant populations [22-25].

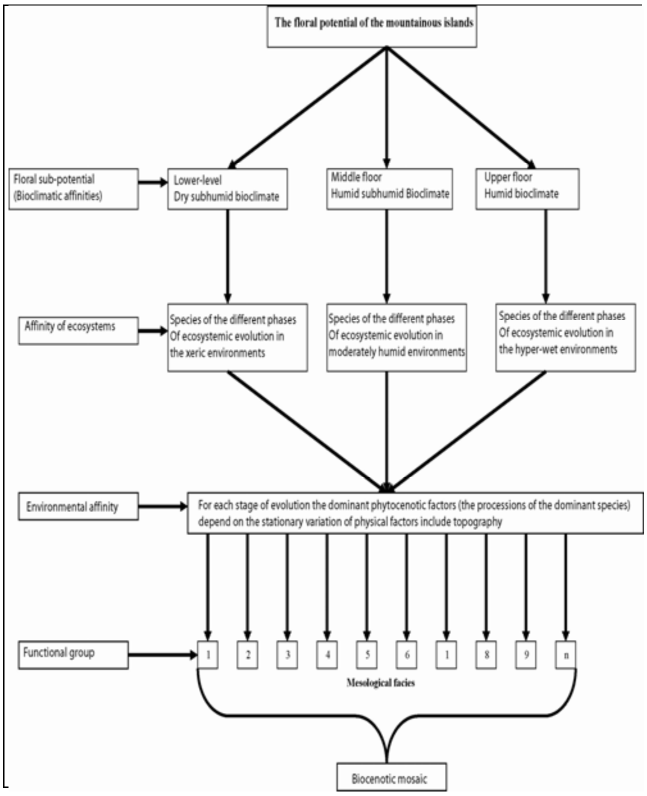


Fig.1 Different aspects of the floristic potential

The species which dominated the Lesser Antilles prehistory survived the first clearings and presented viable although reduced populations. Conversely, those which were weakly represented in the pre-colonial forest floor did not survive the deforestation and the subsequent ecosystem effects especially when they were used for the development of human populations.

For each island unit, the current presence of remaining former climax species must be coordinated with their high levels of distribution and dominance in the primitive forests [13]. Therefore, according to the island territory, the anthropization resulted in regression or even in the more or less rapid disappearance of plant representatives of the original floristic potential whose majority were climax plants. Nowadays we see an unequal distribution of these plant species in the archipelago with highly specialized ecology [26]-27]. However, the absence of taxa cannot be explained only by their lack of ecosystem efficiency. This raises the issue of their degree of rarity and endemism which may be a consequence of the destruction of the original forest environments in which certain species were very little represented. In other words, originally these had a low installation likelihood and were no longer able to ensure their survival in anthropogenic habitats. Today the absence and rarity of a number of infrequent species in the pre-Columbian primitive formations are probably due to the “floristic identity” of the different islands [28-29]. This phenomenon is the result of factorial constraint multiplicity within which we must take into account the history of the geographical units. In this article we will present the main taxa features of the so-called climax primitive forests which, to be followed by further publications on their chorology and their synecology in relation to the plant succession process.

II. MATERIALS AND METHODS

A. Bioclimatic determinism and ecosystem potential of the Lesser Antilles forests

The Lesser Antilles phytocenoses are highly diversified and colonize many topographic units in areas where the pedogenesis, irrespective of its features, has been and remains active, even if sometimes it produced discontinuous soils. With the exception of the cliffs or rock ledges, the variable gradient slopes give birth to forest communities in the terminal stages of plant succession [30-31]. Naturally, the floristic, physiognomic, dynamic and therefore phenologic and ecosystem characteristics will be different depending on the bioclimate [32-33]. In general, the plant ecosystems are conditioned from the coast to the summits of the mountains by the dry subwet, wet subwet, wet and hyperwet bioclimates which delimit all the vegetation floors [34-35]. Respectively these bioclimates occur in the late successional process, where the forest can grow, allowing the existence of tropical seasonal evergreen forests with a lower horizon and xeric, typical evergreen seasonal, submontane and montane tropical rainforest characteristics. Generally the lower areas of the side in the wind exhibit much more xeric bioclimatic conditions (Fig. 2).

Rain-rainforest submontane and evergreen seasonal tropical rainforests can growat the border between the dry sub-wetand wet sub-wet bioclimates as well as between the wet and hyperwet bioclimates. The distribution of indicator species determines the altitudinal limits of these ecotones [36-38]. More rarely and depending to factorial site specific characteristics the lower plant floor includes the seasonal evergreen tropical rainforest species and semi-deciduous species in the tropical dry season (Fig.2). Within the lower plant floor these specific species depend on the topographical model: the glens and valleys bottomand the ridges exposed in dry bioclimate (Fig.2). Actually, on the bottom of the valleys, the containment and the relatively deeper soils created by colluvion allow the system to retain the water for much longer and result in a higher relative humidity. It creates favourable conditions for the installation of species of the sub-montane tropical evergreen rainforests and the seasonal tropical evergreen rainforests distinctively belonging to the wet bioclimatic floor or at the edge of the wet and wet sub-wet bioclimates (Fig.2). These ecosystem singularities correspond to the phenomenon we call vegetation inversion [39]. Like the vegetation, the above mentioned bioclimates will create specific pedogenetic mechanisms leading to soil plurality which form an integral part of the various plant ecosystems.

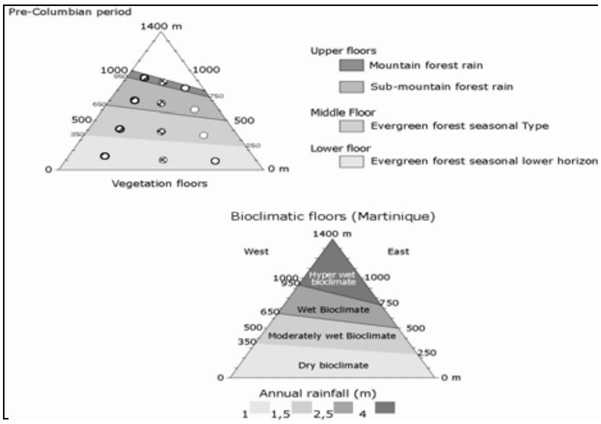


Fig. 2 The vegetation of the mountainous Lesser Antilles (pre-Columbian era)

B. General method

In the light of the results of our research, our predecessors data and information from ancient naturalists who knew these islands before and after the land had owners in the 17th century, we were able to match the various forest units of a given region with a complexity index depending on their structure, architecture and floristic composition [40-41],[9],[27],[33]. Today's plant formations located in remote little or no anthropised areas are regarded as relics of primitive vegetation. The species composing it logically belong to the optimal phases of the forest succession. In fact, the qualitative and quantitative floristic data of the discoverers, naturalists travellers, the administration at the time, the first landowners and other writers [42-46], compared with the more recent ones derived from field surveys allowed us to identify the most significant so-called climax or subclimax species. Those who were demographically dominant in pre-Columbian times and which gave phytocenoses its physiognomy. Ultimately, the synthesis of the floristic data allowed us to identify some traits of the plant floors species which managed to reach the climax phase (including their distribution groups and their stratigraphic position).

III. RESULTS

A. The hypothetical primitive flora

In the absence of pre-anthropic references and despite the existence of remaining climax forest designated as such by many researchers, it is difficult to imagine the various original plant communities which colonized the plant floors of the Lesser Antilles. With the exception of the vegetation inversion phenomena, the taxa mentioned below are the most specialized particularly in relation to the environmental factors (in particular the light, topography, climate and soil). They form the overall forest structure (the forest matrix) and belong to precise stratigraphic levels (Fig. 3a & b) [6]. In general, in the primitive plant layers the topographic classes, the edaphic characteristics, the screen effect, the functional means of the vector wildlife and the plant order of arrival within the biotopes resulted in great plant variety (Fig. 4). Nevertheless many ecological units or eco-units belonged to the terminal or optimal stages.

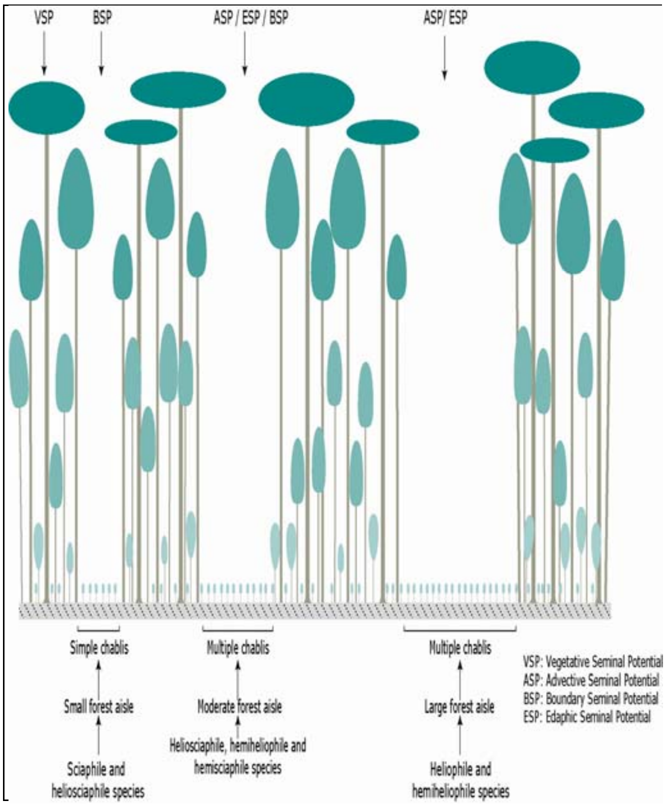


Fig. 3a Ecological profiles of mature forest chablis

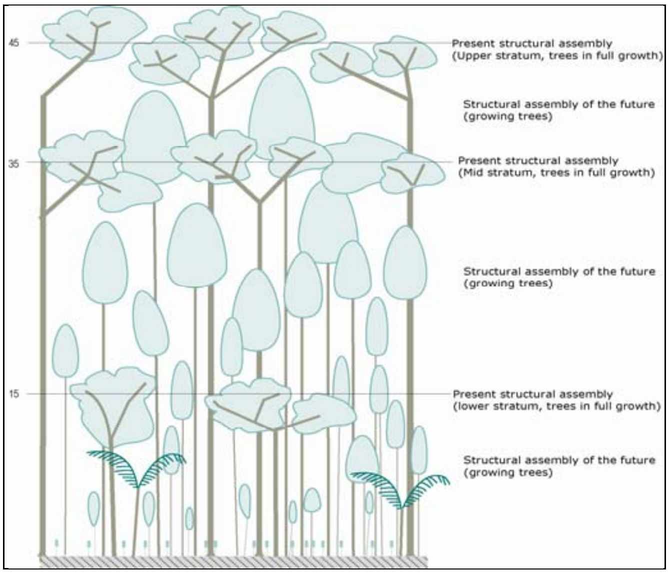
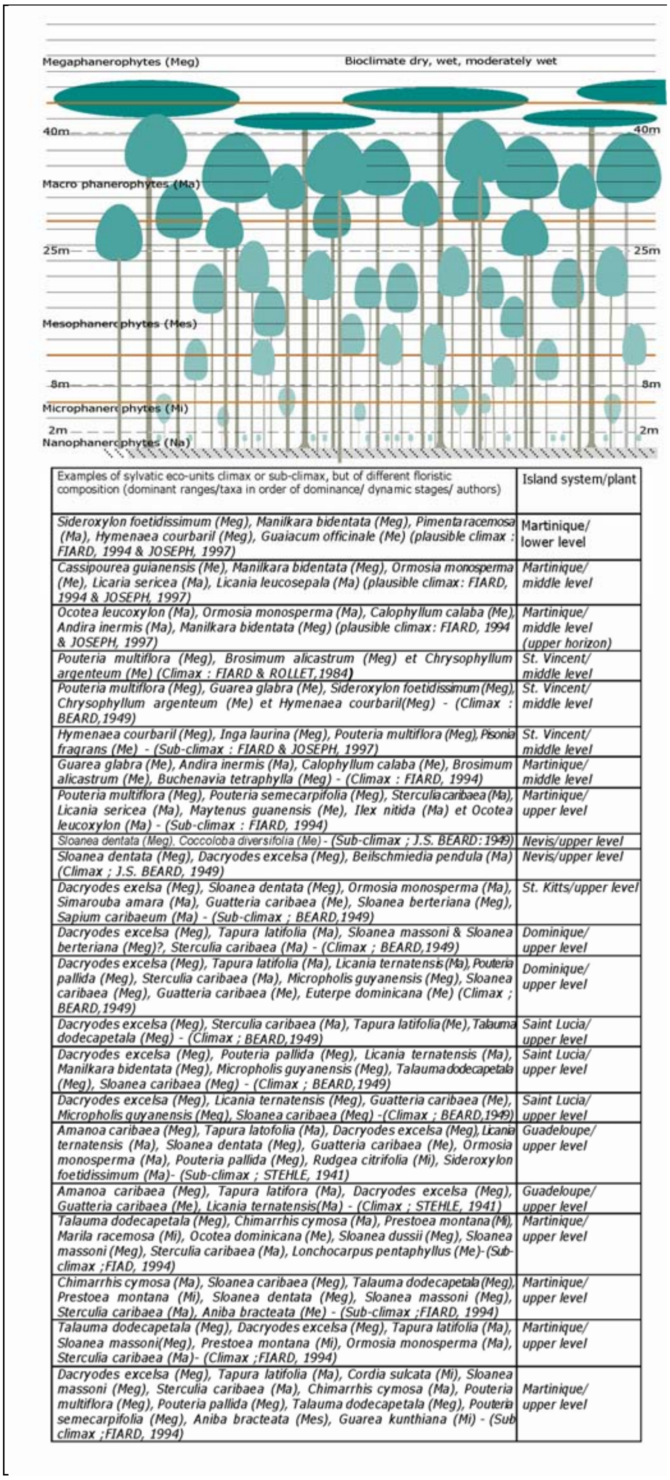


Fig.4 Primary Forest (synthesis diagram of an eco-unit)



Examples of sylvatic eco-units climax or sub-climax, but of different floristic composition (dominant ranges/taxa in order of dominance/ dynamic stages/ authors)	Island system/plant
Sideroxylon foetidissimum (Meg), Manilkara bidentata (Meg), Pimenta racemosa (Ma), Hymenaea courbaril (Meg), Guaiacum officinale (Me) (plausible climax : FIARD, 1994 & JOSEPH, 1997)	Martinique/ lower level
Cassipourea guianensis (Me), Manilkara bidentata (Meg), Ormosia monosperma (Me), Licaria sericea (Ma), Licania leucosepala (Ma) (plausible climax: FIARD, 1994 & JOSEPH, 1997)	*Martinique/ middle level*
Ocotea leucoxylon (Ma), Ormosia monosperma (Ma), Calophyllum calaba (Me), Andira inermis (Ma), Manilkara bidentata (Meg) (plausible climax: FIARD, 1994 & JOSEPH, 1997)	*Martinique/ middle level (upper horizon)*
Pouteria multiflora (Meg), Brosimum alicastrum (Meg) et Chrysophyllum argenteum (Me) (Climax : FIARD & ROLLET,1984)	*St. Vincent/ middle level*
Pouteria multiflora (Meg), Guarea glabra (Me), Sideroxylon foetidissimum (Meg), Chrysophyllum argenteum (Me) et Hymenaea courbaril(Meg) - (Climax : BEARD,1949)	*St. Vincent/ middle level*
Hymenaea courbaril (Meg), Inga laurina (Meg), Pouteria multiflora (Meg), Pisonia fragrans (Me) - (Sub-climax : FIARD & JOSEPH, 1997)	*St. Vincent/ middle level*
Guarea glabra (Me), Andira inermis (Ma), Calophyllum calaba (Me), Brosimum alicastrum (Me), Buchenavia tetraphylla (Meg) - (Climax : FIARD, 1994)	*Martinique/ middle level*
Pouteria multiflora (Meg), Pouteria semecarpifolia (Meg), Sterculia caribaea (Ma), Licania sericea (Ma), Maytenus guanensis (Me), Ilex nitida (Ma) et Ocotea leucoxylon (Ma) - (Sub-climax : FIARD, 1994)	*Martinique/ upper level*
Sloanea dentata (Meg), Coccoloba diversifolia (Me) - (Sub-climax ; J.S. BEARD: 1949)	*Nevis/upper level*
Sloanea dentata (Meg), Dacryodes excelsa (Meg), Beilschmiedia pendula (Ma) (Climax ; J.S. BEARD, 1949)	*Nevis/upper level*
Dacryodes exelsa (Meg), Sloanea dentata (Meg), Ormosia monosperma (Ma), Simarouba amara (Ma), Guatteria caribaea (Me), Sloanea berteriana (Meg), Sapium caribaeum (Ma) - (Sub-climax ; BEARD,1949)	*St. Kitts/upper level*
Dacryodes excelsa (Meg), Tapura latifolia (Ma), Sloanea massoni & Sloanea berteriana (Meg)?, Sterculia caribaea (Ma) - (Climax ; BEARD,1949)	*Dominique/ upper level*
Dacryodes excelsa (Meg), Tapura latifolia (Ma), Licania ternatensis (Ma), Pouteria pallida (Meg), Sterculia caribaea (Ma), Micropholis guyanensis (Meg), Sloanea caribaea (Meg), Guatteria caribaea (Me), Euterpe dominicana (Me) (Climax ; BEARD,1949)	*Dominique/ upper level*
Dacryodes excelsa (Meg), Sterculia caribaea (Ma), Tapura latifolia (Me), Talauma dodecapetala (Meg) - (Climax ; BEARD,1949)	*Saint Lucia/ upper level*
Dacryodes excelsa (Meg), Pouteria pallida (Meg), Licania ternatensis (Ma), Manilkara bidentata (Meg), Micropholis guyanensis (Meg), Talauma dodecapetala (Meg), Sloanea caribaea (Meg) - (Climax ; BEARD,1949)	*Saint Lucia/ upper level*
Dacryodes excelsa (Meg), Licania ternatensis (Meg), Guatteria caribaea (Me), Micropholis guyanensis (Meg), Sloanea caribaea (Meg) -(Climax ; BEARD,1949)	*Saint Lucia/ upper level*
Amanoa caribaea (Meg), Tapura latofolia (Ma), Dacryodes excelsa (Meg), Licania ternatensis (Ma), Sloanea dentata (Meg), Guatteria caribaea (Me), Ormosia monosperma (Ma), Pouteria pallida (Meg), Rudgea citrifolia (Mi), Sideroxylon foetidissimum (Ma)- (Sub-climax ; STEHLE, 1941)	*Guadeloupe/ upper level*
Amanoa caribaea (Meg), Tapura latifora (Ma), Dacryodes excelsa (Meg), Guatteria caribaea (Me), Licania ternatensis(Ma) - (Climax ; STEHLE, 1941)	*Guadeloupe/ upper level*
Talauma dodecapetala (Meg), Chimarrhis cymosa (Ma), Prestoea montana (Mi), Marila racemosa (Mi), Ocotea dominicana (Me), Sloanea dussii (Meg), Sloanea massoni (Meg), Sterculia caribaea (Ma), Lonchocarpus pentaphyllus (Me)-(Sub-climax ;FIAD, 1994)	*Martinique/ upper level*
Chimarrhis cymosa (Ma), Sloanea caribaea (Meg), Talauma dodecapetala (Meg), Prestoea montana (Mi), Sloanea dentata (Meg), Sloanea massoni (Meg), Sterculia caribaea (Ma), Aniba bracteata (Me) - (Sub-climax ;FIARD, 1994)	*Martinique/ upper level*
Talauma dodecapetala (Meg), Dacryodes excelsa (Meg), Tapura latifolia (Ma), Sloanea massoni(Meg), Prestoea montana (Mi), Ormosia monosperma (Ma), Sterculia caribaea (Ma)- (Climax ;FIARD, 1994)	*Martinique/ upper level*
Dacryodes excelsa (Meg), Tapura latifolia (Ma), Cordia sulcata (Mi), Sloanea massoni (Meg), Sterculia caribaea (Ma), Chimarrhis cymosa (Ma), Pouteria multiflora (Meg), Pouteria pallida (Meg), Talauma dodecapetala (Meg), Pouteria semecarpifolia (Meg), Aniba bracteata (Mes), Guarea kunthiana (Mi) - (Sub climax ;FIARD, 1994)	*Martinique/ upper level*

Fig. 3b Schematic representation of the structural units of a climax forest

B. The lower floor

The frequently listed or observed upper and middle strata species are (TABLE I): *Hymenaea courbaril, Pimenta racemosa, Guaiacum officinale, Ocotea coriacea, Sideroxylon obovatum, Sideroxylon foetidissimum, Sideroxylon salicifolia, Genipa americana, Ormosia monosperma*, *Krugiodentron ferreum, Maytenus laevigata, Maytenus grenadensis, Coccothrinax barbadensis.*

In the relatively less xeric sectors the species of the upper horizon of the middle plant floor or horizon or of the lower horizon of the upper floor participate in various floristic units in small populations [13]: *Antirhea coriacea, Chione venosa, Cupania triquetra, Cupania americana, Pouteria multiflora, Pouteria semecarpifolia, Guarea glabra, Maytenus guinensis, Sterculia caribaea, Cassipourea guianensis, Cherimolia leucosepala, Andira inermis, Ilex nitida, Licaria sericea, Pithecellobium jupunba, Brosimum alicastrum, Swartzia simplex, Protium attenuatum, Diospyros ebenaster, Manilkara bidentata, Callophyllum calaba, Buchenavia tetraphylla, Cedrela odorata.*

Among the previously listed tree species, some have strong affinities to calcareous soils or are quasi-calciphilic: *Sideroxylon obovatum, Sideroxylon foetidissimum, Sideroxylon salicifolia, Guaiacum officinale, Krugiodendron ferreum.* For example in Martinique, in order of importance, on the bleak limestones of the south (the municipalities of Marin and Sainte-Anne) the climax floristic combination for the structuring trees would be*: Sideroxylon foetidissimum, Sideroxylon obovatum, Krugiodendron ferreum, Guaiacum officinale, Coccothrinax barbadensis.*

In the light of our lists and observations and based on those of other specialists (mainly [40],[9],[27],[41]) on the volcanic soils of the Guadeloupe archipelago, in Martinique and the British Islands, we have reason to propose the following dominant climax order: *Sideroxylon foetidissimum, Manilkara bidentata, Pimenta racemosa, Hymenaea courbaril.* This data obtained by inference must not ignore the multiplicity of floral formations within the terminal eco-units, subsequent to site changes, even minimal ones, in the environmental factors.

There is no mandatory covariance of these four species. They can participate, isolated in binomials or trinomials, to subclimax or climax groups in combination with other less specialised taxa of advanced or late forest stages. These dominant plant variants are determined by the site absence of the taxa of the above mentioned climax stage as well as by their inability to be competitive and therefore ecologically dominant. In the absence of reliable data, everything suggests that the tentative ecosystem-based description of the pre-anthropic real forest is a mere guess.

At maturity the majority of these species have an average height of circa 20-40 meters and belong to the macrophanerophyte and of mesophanerophyte class (TABLE I). The canopy seems continuous due to crest or nested crowns [31]. Lianas with significant diameters(between 10 and 15 cm) such as *Macfadyena unguiscati,Tournefortia bicolor, Heteropteris purpurea,* can be found in climax units just like heliophile plants and grow through a gap or an ecosystem regression. Unlike the epiphylls which are not represented, the epiphytes are present in a very small number of quantitatively little representative taxa: bromeliads, ferns, herbs, orchids.

TABLE I
Main tree species of the successional terminal phases of the lower floor floristic potential

Plant species (Box 1)	Families	SEM/Chorology (Box 1)
Amyris elemifera	Rutaceae	S3. SK, Mt, BT, St, D, M, SL, SV, Gs, Gr, Ag, SM, SB, Ba, At, GT, De, MG
Andira inermis	Fabaceae	S1. S, SE, SK, Mt, BT, D, M, SL, SV, Gr
Antirhea coriacea (*)	Rubiaceae	S3 / Mt, BT, D M, ST (?), Gs, At, GT,
Brosimum alicastrum (*)	Moraceae	S1. M, SV, Gs
Buchenavia tetraphylla (*)	Combretaceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr, At, MG
Callophyllum calaba (*)	Clusiaseae	S2. SK, Mt, At, N, D, SL, SV, BT, Gs, Ba, Gr, GT, M, MG, De, B
Cassipourea guianensis	Rhizophoraceae	S3. Mt, BT, D, M, SL SV Gr MG
Chione venosa (*)	Rubiaceae	S3. SK, Mt, BT, D, M, SL, SV, Gs (?), Gr, At
Cupania americana (*)	Sapindaceae	S2. D, M, SL, B
Cupania tiquetra (*)	Sapindaceae	S2. D, M, SL, At
Diospyros revoluta	Ebenaceae	S2. SK, N, Mt, BT, D, SL, MG
Eugenia tapacumensis	Myrtaceae	S3. BT, M, SL
Genipa americana	Rubiaceae	S2. M, SV, Gr, MG
Guaiacum officinale	Zygophyllaceae	S2.Mt, D, M, SV, Gr, Ag, SM, SB, Ba, At, GT, MG
Guarea glabra (*)	Meliaceae	S2. SK, N, Mt, BT, D, M, SL, SV, Gr, SM, At, MG
Homalium racemosum (*)	Flacourtiaceae	S1. SK, LV, D, M, At, GT
Hymenaea courbaril	Caesalpinioideae	S1. S, SE, SK, LV, Mt, St, D, M, SL, SV, Gs, Gr, SM, Ba, At, GT, MG, B
Ilex nitida (*)	Aquifoliaceae	S1.
Krugiodendron ferreum	Rhamnaceae	S2. SE, SK, BT, ST, D, M, SL, SV, Gs, Ag, SM, SB, Ba, At, GT, De, MG
Cherimolia leucosepala (*)	Chrysobalanceae	S1. BT, D, M, SL, SV
Licaria sericea (*)	Lauraceae	S1. BT, D, M, SL,
Manilkara bidentata (*)	Sapotaceae	S1. BT, M, SL, SV, Gr, GT, D, B
Maytenus grenadensis	Celastraceae	? / GR
Maytenus guianensis (*)	Celastraceae	? / BT, D, M, SM
Maytenus laevigata	Celastraceae	S1. SE, SK, Mt, BT, St, D, M, SL, SV, Gs, Gr, Ag, SM, SB, GT, MG, B
Myrcianthes fragrans	Myrtaceae	S2. S, SK, Mt, BT, M, SL, Gr; SM, SB, Ba, At, De, MG
Ocotea coriacea	Lauraceae	S2. S, SE, Mt, BT, St, D, M, SL, SV, Gs, Gr, SM, Ba, At, GT, in, MG, B
Ormosia monosperma	Fabaceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr
Pimenta racemosa	Myrtaceae	S1. S, SE, SK, LV, Mt, St, D, M, SL, SV, Gs, Gr, Ag, SM, SB, Ba, At, GT, in, MG, B
Pithecellobium jupunba	Mimosaceae	S3. BT, D, SL, SV, Gr
Pouteria multiflora (*)	Sapotaceae	S1 / S SE SK N Mt BT, D, M, SL, SV, Gr, GT (Grands-Fonds: P. JOSEPH)
Pouteria semecarpifolia (*)	Sapotaceae	S1. BT, D, M, SL, SV
Protium attenuatum	Burseraceae	S2. BT, D, M, SL, SV
Sideroxylon foetidissimum	Sapotaceae	S1. S, SE, SK, Mt, BT, St, D, M, SL, SV, Gs, At, GT, MG, B
Sideroxylon obovatum	Sapotaceae	S2. S, SE, SK, Mt, D, M, SL, Gs
Sideroxylon salicifolia	Sapotaceae	S3. SE, N, BT, D, M, SL, SK, SV, Gs (?)
Sterculia caribaea	Sterculiaceae	S1. Mt, BT, D, M, SL, SV
Swartzia simplex	Caesalpinioideae	S2 / D, M, SL, SV, Gs

Box 1

(*): late or climax species of the middle floor in marginal area in eco-units of the lower floor. SEM: Maximal Expansion Stratum / S1: upper stratum / S2: middle stratum / S3: lower floor. Chorology: distribution within the archipelago. S (Saba - 13 Km^2), SE (Saint-Eustache - 21 Km^2), SK (Saint-Kitts - 176 Km^2), N (Nevis - 92 Km^2), Mt (Montserrat - 101 Km^2), BT (Basse Terre of Guadeloupe - 880 Km^2), St (the Saintes - 13 Km^2), D (Dominique - 790 Km^2), M (Martinique - 1100 Km^2), SL (Sainte-Lucie - 616 Km^2), SV (Saint Vincent 344), Gs (the Grenadines 91), Gr (Granada 310), Ag (Aguila 88), SM (Saint-Martin 87), SB (Saint-Barthélemy - 21 Km^2) , Ba (Barbuda - 160 Km^2) At (Antigua - 276 Km^2), GT (Grande Terre of Guadeloupe - 610 Km^2), De (Désirade - 21 Km^2), MG (Marie-Galante - 158 Km^2), B (Barbados - 430 Km^2. ^{2}. The absence of a species in some islands does not mean it has never been present. We have reason to think that in many cases this absence is the result of biotope disappearance (especially if they were few in number) or/and the weakness of the population numbers.

C. The middle floor

The middle floor environmental conditions are optimal and allow the development of a greater characteristics diversity of tree species which comprise the tropical seasonal evergreen forest type irrespective of its degree of maturity (TABLE II). During the Lesser Antilles prehistory, the deciduous species and their population were very marginal. Apart from flowering and fruiting, the phenophases were little noticeable. The joined crowns and the photosynthetic evergreen apparatus exhibited small physiognomic (chromatic) annual variations. This forest type originally had no or almost no physiognomic seasonality. In addition, its operation in terms of “water resource management“ allowed it to deal with the short period of physiological drought. Some remaining climax forests as well as old-growth forests such as those of King's Hill in Saint-Vincent and the northwest slopes of the Mount Pelée in Martinique allow us to understand the autecological and synecologic characteristics of the primitive forest species of the middle floor. The overall biomass as well as their specific and community diversity were higher. The average height of the tree crowns equalled that of pre-colonial seasonal evergreen rainforest groups of the upper floor.

These elements are corroborated by the accounts of early explorers who described the original vegetation of this area (which they named temperate zone) of cathedral forests where trees were monstrous and very varied. In Native American times, at the scale of large floristic groups, this floor differed little from the upper floorin what regards the architectural and structural characteristics. Logically on one hand the differences were at the plant and phenology level and on the other hand at the level of the intra-forest climate. Overall, the more frequent flowering and fruiting resulted in a more diverse and quantitatively most important vector fauna ensuring diaspora dissemination.

TABLE II

Main tree species of the successional terminal phases of the middle plant floor floristic potential

Plant species	Families	SEM /Chorology (see box 1)
Aiphanes erosa	Arecaceae	S2. BT (?), B
Andira inermis	Fabaceae	S1. S, SE, SK, Mt, BT, St, D, M, SL, SV, Gr, Ba, At, MG, B
Andira sapindoides	Fabaceae	S1. BT, D, M, SL, Gr, At, B
Aniba bracteata	Lauraceae	S2. SK, N, Mt, BT, D, M, SL, SV
Antirhea coriacea	Rubiaceae	S3. Mt, BT, D, M, SL (?), SV, At, GT
Brosimum alicastrum	Moraceae	S1. M, SV, Gs
Buchenavia tetraphylla	Combretaceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr, At, MG
Byrsonima spicata	Malpighiaceae	S1. S, SE, SK, LV, Mt, St, D, M, SL, SV, Gs (?), Gr, At, GT, MG, B
Calophyllum calaba	Clusiaceae	S2. SK, Mt, At, N, D, SL, SV, BT, Gs, Ba, Gr, GT, M, MG, De, B
Chione venosa	Rubiaceae	S3. SK, Mt, BT, D, M, SL, SV, Gs (?), Gr, At
Chrysophyllum argenteum	Sapotaceae	S2. S, SE, SK, N, Mt, BT, D, M, SL, SV, Gr, At, MG, B
Coccoloba swartzii	Polygonaceae	S2. S, SE, SK, LV, Mt, St, D, M, SL, SV, At, GT, MG, B
Cordia alliodora	Boraginaceae	S1. Mt, BT, D, M, SL, SV, Gs, At, GT, B
Cupania americana	Sapindaceae	S2. D, M, SL, B
Cupania triquetra	Sapindaceae	S2. D, M, SL, At
Diospyros revoluta	Ebenaceae	S2. SK, N, Mt, BT, D, SL, MG
Eugenia gregii	Myrtaceae	S3. BT, D, M, SL, B (?)
Eugenia speudosidium	Myrtaceae	S2. Mt, BT, D, M, SL, B (?)
Exostea paniculata	Sapindaceae	S2. SE, GT, SV, De, M
Exostema sanctae-luciae	Rubiaceae	S3. BT, D, M, SL, SV, MG
Framea occidentalis	Rubiaceae	S3. S, SE, SK, Mt, BT, D, M, SL, SV, Gr, At, B
Genipa americana	Rubiaceae	S2. M, SV, Gs, Gr, MG
Guarea glabra	Meliaceae	S2. SK, N, Mt, BT, D, M, SL, SV, Gr, SM, At, MG
Guarea macrophylla	Meliaceae	S1. Mt, BT, D, M, SL, SV, Gr, At
Guazuma tomentosa	Sterculiaceae	S2. M (?)
Guazuma ulmifolia	Sterculaiceae	S2. SK, LV, D, M, SL, Gs, Gr, Mt, At, GT, MG, B, N, SV
Homalium racemosa	Flacourtaiceae	S1. SK, LV, D, M, At, GT
Hura crepitans	Euphorbiaceae	S1. SE, SK, Mt, BT, D, M, SL, SV, Gs, Gr, Ag, SM, Ba, At, GT, MG, B
Hymenaea courbaril	Caesalpinioideae	S1. S, SE, SK, LV, Mt, St, D, M, SL, SV, Gs, Gr, SM, SB, At, GT, MG, B
Ilex nitida	Aquifoliaceae	S1. Mt, BT, M, SL, At, MG (?)
Cherimolia leucosepala	Chrysobalanaceae	S1.BT, D, M, SL, SV
Cherimolia ternatensis	Chrysobalanaceae	S1. BT, D, M, SL, SV, Gr
Licaria sericea	Lauraceae	S1. BT, D, M, SL
Manilkara bidentata	Sapotaceae	S1. BT, M, SL, SV, Gr, GT, D, B
Maytenus guyanensis	Celastraceae	S2.BT, D, M, SM
Myrcia fallax	Myrtaceae	S1. Mt, BT, D, M, SL, SV, Gr
Myrcia leptoclada	Myrtaceae	S3. BT, D, M, SV
Myrcia platiclada	Myrtaceae	S2. BT, St, D, M, SL, SV, Gr
Ocotea leucoxylon	Lauraceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr, At
Ormosia monosperma	Fabaceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr, MG
Oxandra laurifolia	Annonaceae	S2. SK, N, BT, D (?), M
Picramnia pentandra	Simaroubaceae	S3. Mt, BT, D, M, SL, SM, At, GT
Picrasma excelsa	Simaroubaceae	S3. S, SE, SK, N, Mt, BT, D, M, SL, SV, SM, At, GT, in, MG, B
Pithecellobiumjupunba	Mimosaceae	S3. BT, D, SL, SV, Gr, Ag
Pouteria multiflora	Sapotaceae	S1. S, SE, SK, N, Mt, BT, D, M, SL, SV, Gr, GT , MG (?)
Pouteria semecarpifolia	Sapotaceae	S1. BT, D, M, SL, SV
Prestoea montana	Arecaceae	S3. SE, SK, N, Mt, BT, D, M, SL, SV, Gr, SM, SB
Quararibea turbinata	Bombacaceae	S3. SE, SK, N, Mt, BT, D, M, SL, SV, Gr, At, MG, B
Rhytococos amara	Arecaceae	S2. Mt, BT, D, M, SL, At (?)
Simaruba amara	Simaroubaceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr, B
Sterculia caribaea	Sterculiaceae	S1. Mt, BT, D, M, SL, SV
Swartzia simplex	Caesalpinioideae	S2. D, M, SL, SV, Gs
Vitex divaricata	Verbenaceae	S1. SK, Mt, BT, D, M, SL, SV, Gr, SB, At, GT, MG, B
Zanthoxylumflavum	Rutaceae	S1. Mt, BT, St, D, M, SL, Ba, De, Ag, SB, SM, At, GT, MG

D. The upper floor

Despite significant rainfall, which sometimes becomes a limiting factor, compared to the previous floor, the vegetation on this floor is a little less diversified (TABLE III), irrespective of the ecosystem scale and considered stage of development. Yet the topographic and edaphic characteristics are just as numerous. As with other forest floors, the upper and lower limits vary from one mountain island to the other. Nevertheless in the increasing altitude direction, this floor allows the respective development of the potential sub-montane rainforests and tropical montane forests.

The sub-montane primary rainforest was characterised by high aboveground and below ground biomass, a structure consisting primarily of large or medium-diameter trees and a global architecture formed of “mastodon trees“ at the level of the upper strata. They had shallow roots but developed winged buttresses which spanned an area at least equal to the one occupied by the foliage biomass.

As regards the montane rainforest, it was undisturbed by human activity and has retained much of its primitive character. Its upper altitudinal limit does not exceed 800 to 900 meters. It undergoes the full assault of the elements. The rains are very heavy throughout the year, the wind is steady and often strong, and the slopes are usually steep. In reality this forest type develops in conditions of climate and soil instability. The consequences are important and occur at several levels: low biomass, structure exhibiting a high density of small-diameter stems, overall architecture consisting of stunted little branched trees present mostly in the tropical sub-montane rainforest, smaller associative as well as specific biodiversity. In their majority, the trees of the previous forest type (sub-montane rainforest) form the floristic units of the montane rainforest (TABLE III). However, irrespective of their maturity level, their morphogenesis is different and is characterised by trunks with smaller sections, less spreading crowns, lower branching, a significantly higher density of stems and, when it occurs, reduced stratification having two-components at the most. In general, compared to the tropical sub-montane rainforest, the forest roof is less high and discontinuous. We note architectural simplification accompanied by a forest structure characterised by the undeniable predominance of small diameters.

The more difficult climate conditions (wind, rainfall, cloudiness) render the environment unstable. As such, this montane rainforest is in some ways similar to a regressive stage of the sub-montane rainforest to be seen in some sites exposed to the wind, with hydromorphic soil and subject to frequent landslides. The species diversity is lower, the groups are multiple and it is more difficult than elsewhere to define the relevant plant markers. The structural and architectural differences are the main descriptors of this forest type which however remains marginal from the spatial point of view. Within the archipelago, the most representative assemblies of this ecosystem vary from one system to the other. In each island, the plant combinations, which depend on site conditions, are based on the same species fund.

TABLE III

Main species of the terminal successional stages of the upper floor floristic potential

Plant species	Families	S.E.M./Chorology (see box 1)
Amano acaribaea	Euphorbiaceae	S2. BT, D
Aniba ramageana	Lauraceae	S3. D, M (?)
Beilschmiedia pendula	Lauraceae	S1. SK, N, Mt, BT, D, M, SL, SV, At, MG (?)
Calyptranthes fasciculata	Myrtaceae	S3. D, M
Chimarrhis cymosa	Rubiaceae	S1.BT, D, M, SL, SV, At
Cyathea tenera	Cyatheaceae	S3. Mt, BT, D, M, SL, SV, Gr
Cyathea muricata	Cyatheaceae	S3. S, SK, N, Mt, BT, D, M, SL, SV
Dacryodes excelsa	Burserarceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr
Drypetes dussii	Euphorbiaceae	S3. M
Endlicheria sericea	Lauraceae	S3. SK, LV, D, M, SL, SV
Eugenia albicans	Myrtaceae	S3. BT, D, M
Eugenia chrysobalanoides	Myrtaceae	S3. N, BT, St, M, B
Eugenia coffeifolia	Myrtaceae	S3. BT, D, M, SL, SV
Eugenia domingensis	Myrtaceae	S1. D, M, SL, SV
Eugenia gyrospermea	Myrtaceae	S3. M
Eugenia octopleura	Myrtaceae	S3. BT, D, M
Eugenia oerstedeana	Myrtaceae	S3. M, SL, SV, At
Euterpe dominicana	Arecaceae	S3. BT, D, M, SV, Gr
Geonoma dussiana	Arecaceae	S3. BT, D, M
Geonoma martinicensis	Arecaceae	S3. BT, D, M, SL, SV
Guatteria caribaea	Annonaceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr
Heisteria coccinea	Olacaceae	M, SL
Hirtella triandra	Chrysobalanaceae	S2. S, SE, SK, N, Mt, BT, D, M, SL, SV, Gr, MG, B
Ilex sideroxyloides	Aquifoliaceae	S2. SK, N, Mt, BT, D, M, SL, SV, Gr
Cherimolia leucosepala	Chrysobalanaceae	S1. BT, D, M, SL, SV
Cherimolia ternatensis	Chrysobalanaceae	S1. BT, D, M, SL, SV, Gr
Meliosma herbertii	Sabiaceae	S1. SK, Mt, BT, D, M, SL, SV, Gr
Meliosma pardonii	Sabiaceae	S2. BT
Micropholis guyanensis	Sapotaceae	S1. SK, N, Mt, BT, D, M, SL, SV, Gr, At
Ocotea martinicensis	Lauraceae	S2. SK, Mt, BT, D, M, SV
Oxandra laurifolia	Annonaceae	S2. SK, N, BT, St, D (?), M
Phyllanthus mimosoides	Euphorbiaceae	S3. BT, D, M
Podocarpus coriacea	Podocarpaceae	S2. Mt, BT, D, M
Pouteria multiflora	Sapotaceae	S1. S, SE, SK, N, Mt, BT, D, M, SL, SV, Gr, GT, MG
Pouteria pallida	Sapotaceae	S1. BT, D, M, SL, SV, Gr
Pouteria semecarpifolia	Sapotaceae	S1. BT, D, M, SL, SV
Prestoea montana	Arecaceae	S2. S, SK, N, Mt, BT, D, M, SL, SV, Gr, SM
Prunus pleuradenia	Rosaceae	S1. SK, LV, D, M, SV, Gr
Richeria grandis	Euphorbiaceae	S2. Mt, BT, D, SL, SV, Gr, At
Sloanea berteriana	Elaeocarpaceae	S1. SK, Mt, BT, D, N, M
Sloanea caribaea	Elaeocarpaceae	S1. BT, D, M, SL, SV, Gr
Sloanea dentata	Elaeocarpaceae	S1. SE, SK, Mt, BT, D, M, SV (?), Gr
Sloanea dussii	Elaeocarpaceae	S1. M
Sloanea massoni	Elaeocarpaceae	S1. S, SK, N, Mt, BT, D, M, SV, Gr
Sterculia caribaea	Sterculiacaeae	S1. Mt, BT, D, M, SL, SV
Styrax glaber	Styracaceae	S2., SK, Mt, BT, D, M, SL, SV (?)
Swartzia caribaea	Caesalpinioideae	S2. BT, D, SL
Talauma dodecapetala	Magnoliaceae	S1. BT, D, M, SL, SV
Tapura latifolia	Dichapetalaceae	S1. BT, D, M, SL
Tovomita plumieri	Clusiaceae	S3. D, M, SL
Weinmannia pinnata	Cunoniaceae	S3. SK, Mt, BT, D, M, SL, SV

IV. DISCUSSION

This general presentation of the structural organisation of forest ecosystems shows their complexity and the difficulty of their characterization. For simplification reasons and due to the need of an international classification in a comparative context, all the past and present specialists of the Lesser Antilles forests have sought to identify them using “floristic signatures”. These are called dominant assemblies or preferential groupings [47][48]. They sought to define the montanerainforests, sub-montane rainforests and evergreen seasonal forests as well as their mixed forms using plant associations built in significant markers of the eco-climatic conditions (Fig. 4). In the end, in these territories, the history of forest ecology and phytogeography research is rich in data based on plural lists which were however based on different methodologies. Often they simply do not allow a comparative analysis. With the quantitative data available, it is extremely difficult to perceive similarities, homologies and even less, structural and functional differences. The survey methods and the results use are very briefly mentioned in the scientific papers of the majority of authors preceding us. Nevertheless, within the ecological units and between them, for comparison reasons it is important that the exploratory procedures should be identical or at least equivalent. In the previous paper this fact justified a more qualitative than quantitative description which does not detract from the conclusions, at least relevant, of the work of the scientists preceding us.

V. CONCLUSION

The principle of the list site ecological uniformity poses undeniable problems which prohibit any theorizing, conceptualization and modelling. It is almost impossible to establish a general law for the functioning of the Lesser Antilles forest ecosystems. If the bioclimate notion is relevant in this archipelago to try to explain the different types of vegetation, the idea of the main assemblies identifying them is less obvious and unlikely. In fact, the distribution of the isohyets, particularly in the mountainous islands, creates a bioclimatic gradient on the west sides and defines the biogeographic limitations of plant species. These bioclimates are also affected by spatial variations whose biocenotic consequences are significant. The frequently rugged terrain accentuates the environmental heterogeneity which results in vertical and horizontal eco-climatic variations. In pre-Columbian times where the plant coverage were mostly forest and homeostatic, these conditions resulted in a multiplicity of biotopes forming a dense biocenotic canvas consisting of specialized species. They occupied ecological niches which in their turn were also very specific. Apart from the chablis, the so-called matrix forest assemblies of this period reduced the environmental fluctuations, however the same forest unit consisted of several climax eco-units. This calls into question the idea of a “unique phytocenotic signature” for the characterization of forest types and legitimates the existence of functional groups which render the forest ecosystem more flexible from the point of view of the great degree of physical factor heterogeneity.

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