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RESEARCH ARTICLE

TRIAL TO COMPREHEND THE FUNCTIONING OF THE VEGETATION OF THE LESSER ANTILLES IN THE LIGHT OF THE GENERAL UNDERSTANDING OF VEGETATION DYNAMICS.

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The geomorphology and dynamics of the atmosphere are two elements which determine the diversity of the bioclimates of the Lesser Antilles. These are usually associated with specific forest types: seasonal evergreen rainforests with their subtypes and facies, tropical sub-montane rain forests and tropical montane rain forests. Originally, these forests had many plant species in a plurality of combinations and reflecting the multiplicity of biotopes. Human activities varying in intensity and frequency have, over the centuries caused a reduction of multiple forms in the ecosystem. The phytocenotic canvas of today derives from this phenomenon and is a good example for the study of various structural, architectural and functional features. To decrypt the main spatio-temporal characteristics of plant cover, we used data from the scientific literature specific to this region and from some of our field surveys. It was therefore possible to highlight the different levels of integration (of complexity) of the scale on the site of the installation and expansion of plant species (microsystemic) individuals in various places (macrosystemic): the latter in mesosystems. We have also been able to decrypt the biological traits of different groups of taxa involved in all stages of plant succession.

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Introduction:-

The gradual evolution of the vegetation is a slow and ongoing process, whereby plant ecosystems become more complex and involve a large number of components (Lebrija-Trejos et al. 2010; Foster, Fluet & Boose, 1999; Wright, 2010; Shaheen, Qureshi, & Shinwari, 2011). The resulting factorial constraints evolve in the same direction and are often difficult to determine (Finegan, 1996; Waring & Running 2010). The diversity of plant processions associated with the same level of dynamic stages poses the problem of floristic identification. In the context of establishing a general law of the dynamics of the plant carpets of the Lesser Antilles, only dynamic profiles of taxa (their functions) will be retained as relevant descriptors. They are likely to indicate a step of evolution. In this review, proposals for explanation in the text concerning the evolution of the vegetation of the Lesser Antilles must be regarded as major trends, because at any point in the Caribbean plant cover, there may, due to human activity (anthropisation), successive domination by a set of successional mechanisms.

Method:-

What follows is a summary based on data from the literature to which will be added by way of example, data from surveys of the undergrowth vegetation of Martinique. The elements of the arguments that follow are derived from data from the international literature, as well from our observations and our surveys in the field and the work of other researchers of the flora of the Lesser Antilles (Stehlé, 1936, 1938 & 1947; Beard, 1949; Portecop, 1978). The data is scant and derives from simple experiments (Joseph, 1997, 2012, 2013, 2014 & 2015; Imbert & Portecop, 1992; Doyle, 1981; Lugo et al., 2006). We have retained the following descriptors: diversity of species (ecological profiles), phytocenoses, physiognomic types, architectural and structural types. This has enabled us to propose a

synthesis based on the essential traits of the multiplicity of structures, functions and the process of evolution of the vegetation of the Lesser Antilles.

Plant succession: a complex reality:-

The term plant succession can be defined many ways, depending on the school of thought. Biological succession refers to the set of events that occur during the colonisation of a biotope by organisms (Clements, 1916, 1920, 1928, 1936, 1949, 1977; Holt, Robinson & Gaines, 1995; Watkinson, 1997). This colonisation under defined climatic conditions translates into changes over time, of the composition of the flora and fauna after disturbances have destroyed the (pre-existing) ecosystem totally or partially (Walker et al., 1996; Peterson & Haines, 2000). Changes proper to unregulated ecosystems and consequently those of the environment, are taken into account. In a more general framework, the concept of succession may be apprehended by the transformations of the vegetation under the influence of recurrent natural, and often of anthropogenic, disturbances: these are successive regressions (Mangan et al., 2010). It is worth noting that within this conceptual framework, phenological rhythms (the phases of the life cycle) do not act as disturbances (Figures 1 and 2, Box 1, Whittaker, Levin & Root, 1973).

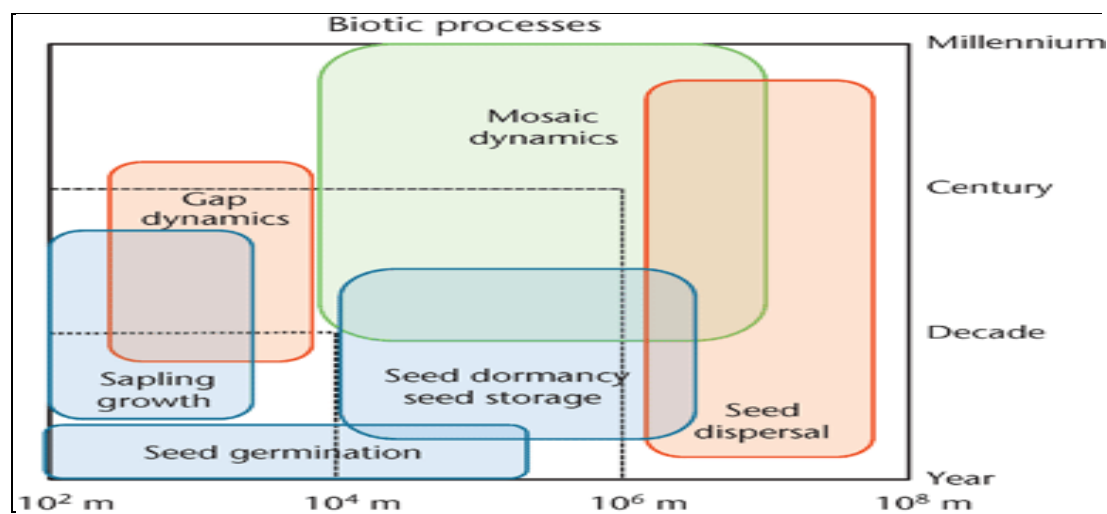


Figure 1: Temporal and spatial scales governing the successional dynamics of forests (Shugart, 2012).

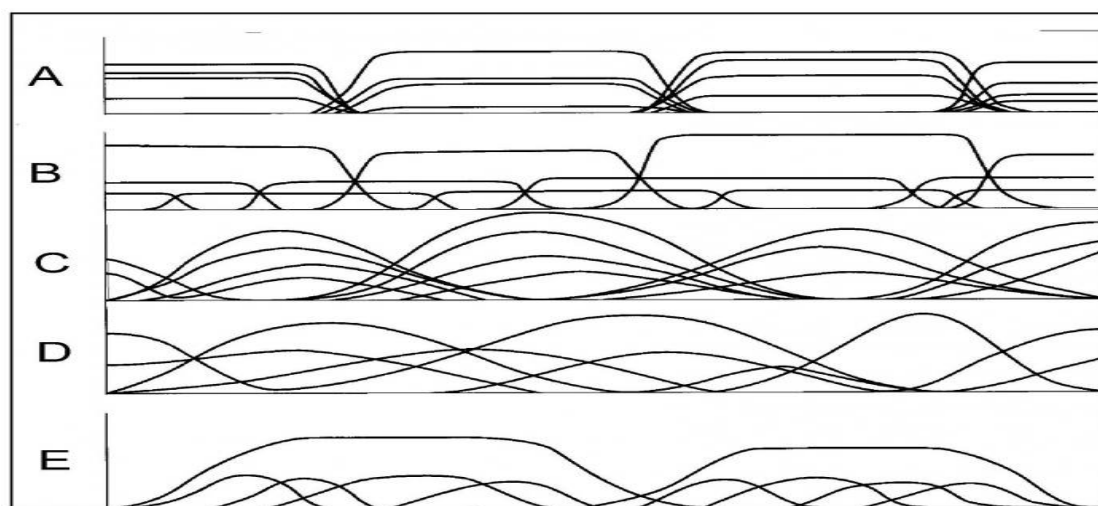


Figure 2: Five assumptions relating to the distribution of the species along an ecological gradient) Abscissae: theoretical ecological gradient; ordinate, theoretical frequency of species (Brown and Lomolino 1998, after Whittaker, 1973).

Box 1

A - Species are distributed in discrete communities; each community replaces another abruptly (hypothesis that corresponds as well to the super-organisms of Clements (1916) as well as the associations of Braun-Blanquet, 1928).

B - In the train of changes in net dominant species (landscape discontinuities), species occur along the gradient, each of them starting or stopping abruptly.

C - Species regroup in largely interconnected communities; where it is located in the heart of the community, the vegetation is homogeneous, on its margins, it is heterogeneous.

D - Each species behaves as if it were totally independent of all the others; no plant grouping is discernible (hypothesis that corresponds to the) undisturbed continuum to which Gleason inclined (1926).

E - Most species are grouped within landscapes dominated by a few species. Floral heterogeneity is high in these areas.

In the history of scientific thought there have been a number of theories on the problems of plant succession. The theories that have marked the evolution of ideas in this field are: the autogenic model (Clements, 1916, 1936), the initial floristic composition model (Egler, 1954), the facilitation model (Connell & Slatyer, 1977), the tolerance model and the inhibition model (Connell & Slatyer, 1977). The theories of the Clements School were long dominant and the autogenic succession model was the main setting for the study of the evolution of plant ecosystems. Processions of species present in each phase of gradual succession transform the environment and create more favourable conditions for the introduction of other more specialised kinds of ecology. A competition process was initiated with consequent elimination of the first (Figure 3). According to Clements (1916-1936), all the succession in territory converge to an optimal organisation (climax) completely determined by the local climate: climatic climax (Figures 3, 4 and 5). The climax is reached when the changes generated by the vegetation are more favourable to the species already in place than to other species. It should be noted that to the climatic factors there should be added other elements, particularly human activity. These influencing successional processes result in totally different ecologies, all called physiographic climaxes: subclimax, pseudoclimax, paraclimax, dysclimax (Abi-Saleh et al. 1976; Ponce, Senespleda & Palomares, 2010; Bonney et al. 2010, Drake, 1990).

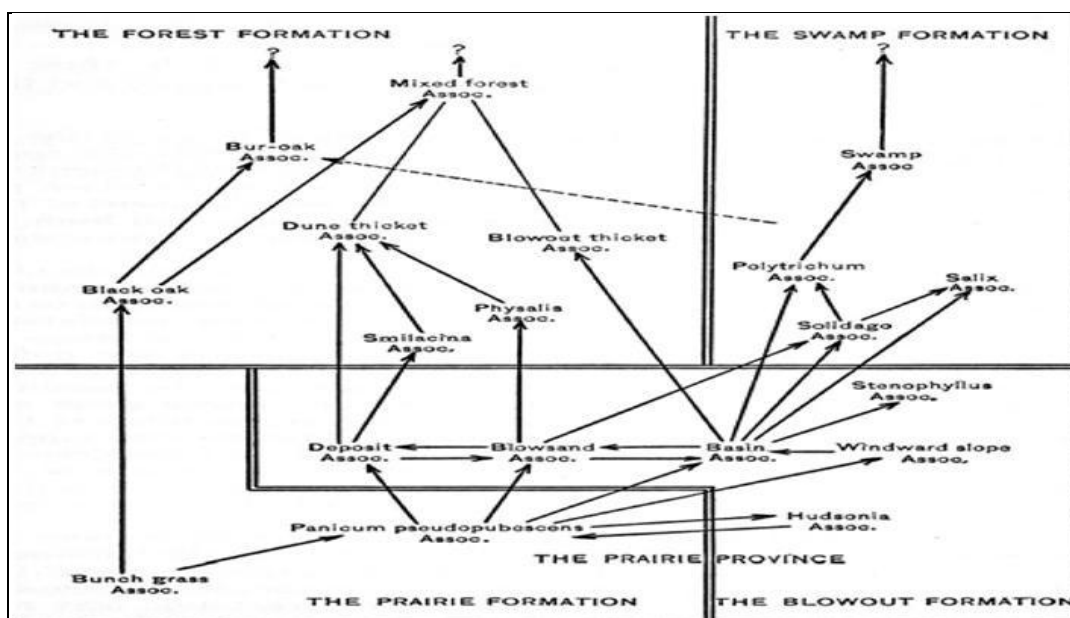


Figure 3: Psammosere in Central Illinois (Gleason, 1907).

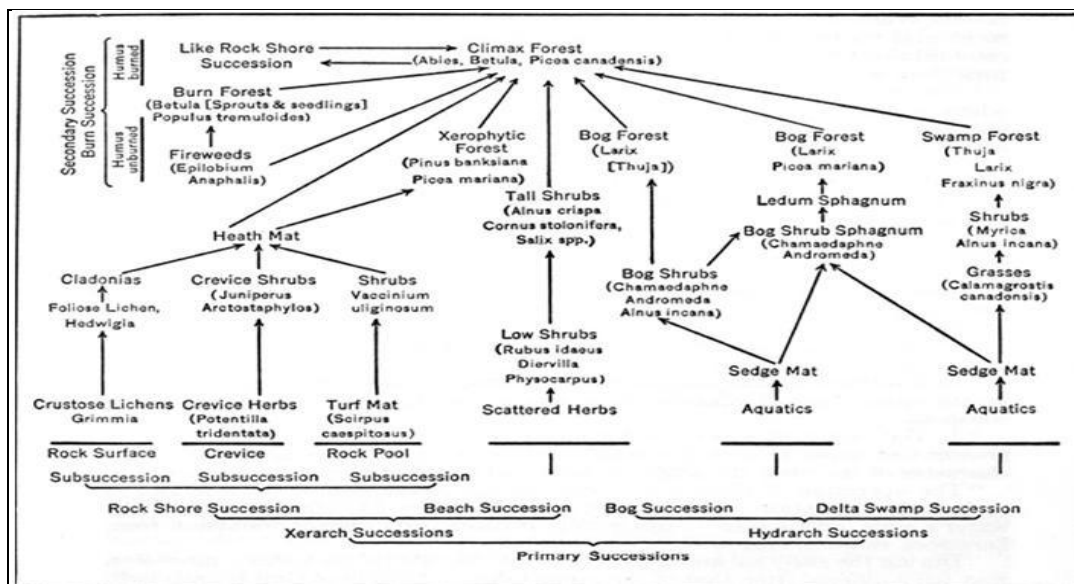


Figure 4: Diagram of development of climax forest on Isle Royale (Cooper, 1912, 1913)

Phytocenotic succession: the result of a process of self-organisation:-

Primary succession and secondary succession are the main concepts developed by Clements (1928, 1949). Primary succession boils down to the dynamics of occupation of naked bedrock by living organisms (Chevennement, 1990). The environment changes over time at the same time as changes take place in the vegetation (Jones & Henry, 2003). The study of this type of succession was made possible by the observation of plant colonisation in dune systems, areas of glacial retreat, volcanic lava fields, islands recently formed or devastated by natural disasters, the environs of silted lakes and bogs (Cutler, 2010; Yarranton & Morrison, 1974; Bazzaz, 1979; Tejesvi et al. 2010). Secondary succession is the process of reconstitution of the pre-existing vegetation among abandoned crops (Knapp, 1992; Huston & Smith, 1987; Horn, 1974; McBride, 1974), in areas subject to deforestation (Corlett, 1991; Walker et al., 2010a; Wright & Fridley, 2010; Junqueira, Shepard & Clement, 2010), in regions heavily degraded after soil sterilisation, plant groupings that have been subject to selective sampling or even following major climate disruptions such as hurricanes or typhoons (Tang, Li & Zhang, 2010; Shafi & Yarranton, 1973; Halpern et al., 1997, Figures 5 & 6).

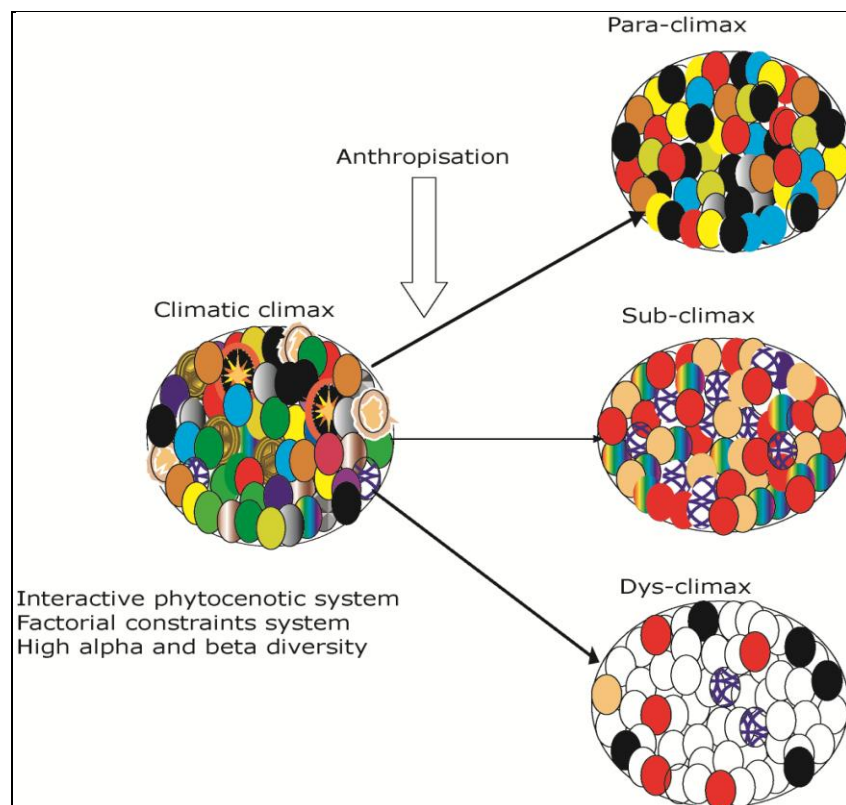


Figure 5: Plausible trajectories of a vegetable ecosystem under anthropogenic stress.

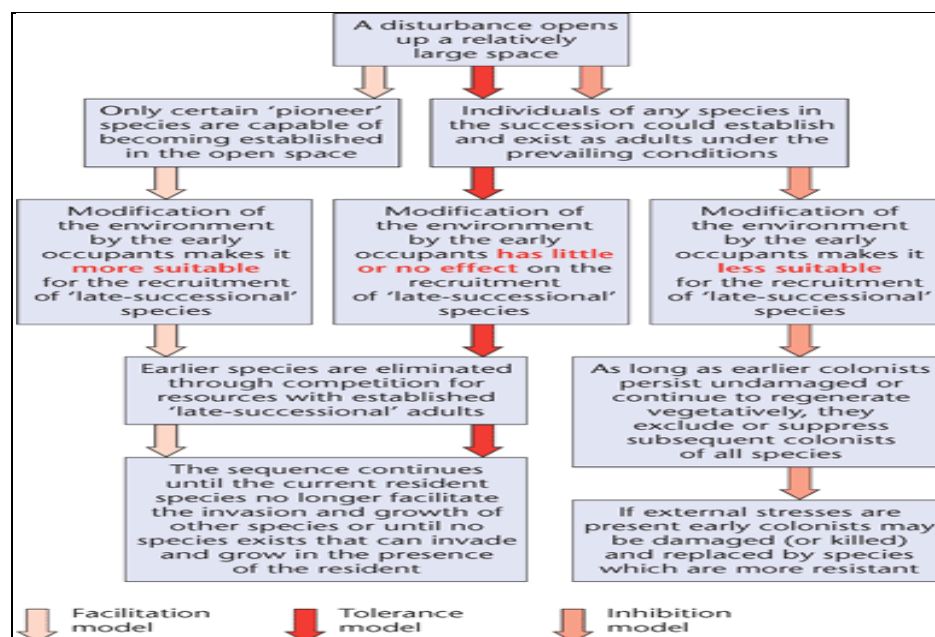


Figure 6: Mechanistic models of ecological succession (Shugart, 2012, Reproduced from Connell and Slatyer, 1977).

The main methodological approaches:-

The methods used for the study of plant succession fit into two approaches: the direct or diachronic approach (Comin et al., 2011, Posey, 1998), the indirect or synchronic approach (Abreu, Llambí & Sarmiento, 2009). The diachronic approach is to observe over time changes that happen in the plant structure (Catorci & Gatti, 2010). It requires periodic monitoring of the experimental plots to detect changes (Arnould, Hotyat & Simon, 2000). If rigorous from the methodological point of view, it nevertheless has a few limitations: the scale of realisation of the succession phenomena is variable and depends on the stage of maturity of the plant ecosystem. As such, the direct or diachronic approach is better to use in the first sequences of plant succession, because transformations are observable in temporal increments corresponding to a decade. This is contrary to succession in older formations that is seen over a much longer scale, such as a century or even several centuries.

This means of investigation is of use when it comes to highlighting slight changes of floristic composition in the first wave of colonisation, particularly when vegetation dynamics are deeply influenced by the initial floristic composition of the area. Therefore, the changes within the plant mantle are perceptible by the physiognomic variations of multiple structuring groups; aerial photographs or satellite images allow appreciation of these transformations across the landscape and analysis of the phenomena of succession (Xie, Sha & Yu, 2008).

The slow pace of changes in vegetation, especially in phases of forestation, requires an alternative approach, an approach based on the spatial and temporal variations of the structure and floristic composition of plant formations. As a result, the phytocenoses can be arranged in series, phases, stages, chrono-sequences and dynamic sequences of vegetation (Miles, 2012; Van Hulst, 1979; Martínez, 1980; Diallo et al., 2011). This procedure for analysing the vegetation corresponds to the indirect or synchronic approach. This principle of vegetation analysis, if it to some extent allows us to go back in time along the dynamic gradient, cannot identify with precision the main features of the succession in a particular space and under specific environmental conditions (Losos & Ricklefs, 2009). Ecosystems where the elements are different to varying degrees are good subjects for the synchronic method. Reconstitution of the dynamic puzzle requires knowledge of the floristic composition, of the abiotic factors of the stations, of the history of the plant communities and of the complex interaction between man and vegetation. The stations must be under the influence of relatively homogeneous physical conditions. This is often not realised. For example, microrelief variations are important in the installation of a great variety of species of flora. This is in contrast to the existence of a uniform soil substrate. The nature of the disturbance is an element that influences the dynamics of the vegetation, since each type of anthropisation initiates a well-defined direction or successional path (Figures 7 & 8). The modes of anthropisation depend on technological developments. Over time they take various forms that change the soil's potential for floral introduction after a discontinuation of disruptive human activity. Three dimensions are, therefore to be considered: time, space and change.

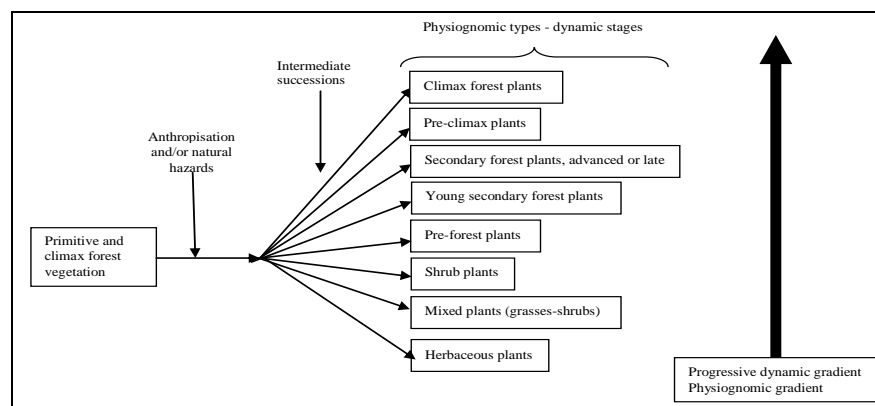


Figure 7: Ecosystemic potential and forms of regression for synchronic analysis.

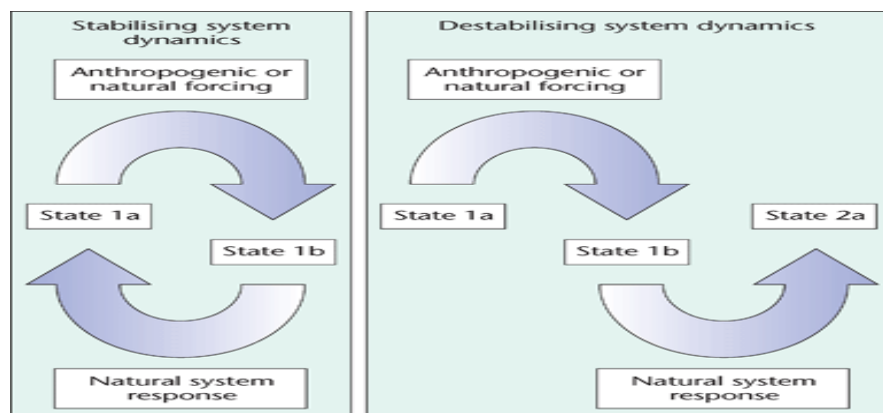


Figure 8: Stabilising and destabilising dynamics of ecosystems. In the case of stabilising system dynamics, a disturbance from humans or natural causes changes the vegetation to a new state or condition (State 1 b in the diagram). Ecological succession eventually returns the vegetation system to its original condition. In destabilising system dynamics, disturbance causes the systems to change but the response of the system brings it to a new condition (State 2a) that is different from the original condition(Shugart,2012).

Analysis of floristic succession in the Lesser Antilles:-

Complex phytocenotic strategies

The proposal of an explanatory model is not a simple task because of the great complexity of plant ecosystems of the Lesser Antilles. Their floristic dynamics involve many factors that make the study of their detailed operation particularly delicate (Walker et al. 2010b; Tognetti et al., 2010). It is very unlikely a model will be found to take into account all the elements acting on all the levels of specific integrations (Joseph, 2012; Godin & Sinoquet, 2005). According to the environment and the nature of the disturbance, the above mentioned models are more or less applicable. We must therefore work with flexibility and simplicity. Emphasis is placed on the important, even crucial, role of interspecific plant and animal competition (Tilman, 1994). However also the action of wildlife in the relation to predations and the dispersal of diaspores (seeds and pollen). These models take into account stresses such as anthropisation and cyclonic phenomena, not to mention mechanism of regulation of populations, internal mechanisms in ecosystems: autecological processes (uprooted trees, teleotoxic processes).

Despite this great conceptual diversity which specifically does not translate into a unified theory of plant succession, it seems however that models taken in isolation are individual cases of a general function. Often, conflicts over terminology obscure the reality of the succession, and we should therefore find a framework in which all the predictable modalities can be retained. Regardless of the dynamic characteristics of vegetation, taxa are immersed in an interactional fabric, in which they themselves are the regulators. This fabric, from the constraints imposed by each factor, can be seen through the multiple interactions (Tilman, 1990). This brings us to the theories related to systems (Margalef, 1958, 1963, 1968; Odum, 1969).

The processes of succession are mechanisms of self-organisation resulting from the interactions between the organisms themselves, but also between them and the environment (Lobo, Castro & Moreno, 2001). The latter, by its characteristics determines the kinetics and the development of the phenomenon of succession (Walker et al. 2010b; Lebrija-Trejos et al. 2010; Archer et al., 1988). Biotic relationships constitute the mechanism for the replacement of species (Prach et al., 2001; Prach & Walker, 2011). In the different plant ecosystems of the Lesser Antilles, during progressive or regressive dynamics, taxa are more adapted to the conditions offered by the successive ecosystemic states. It is logical that this substitution implies the existence in the stock of species, of behavioural diversity, and great diversity of flora and of ecological profiles [Figure 9; (Ruiz-Jaén & Aid, 2005)].

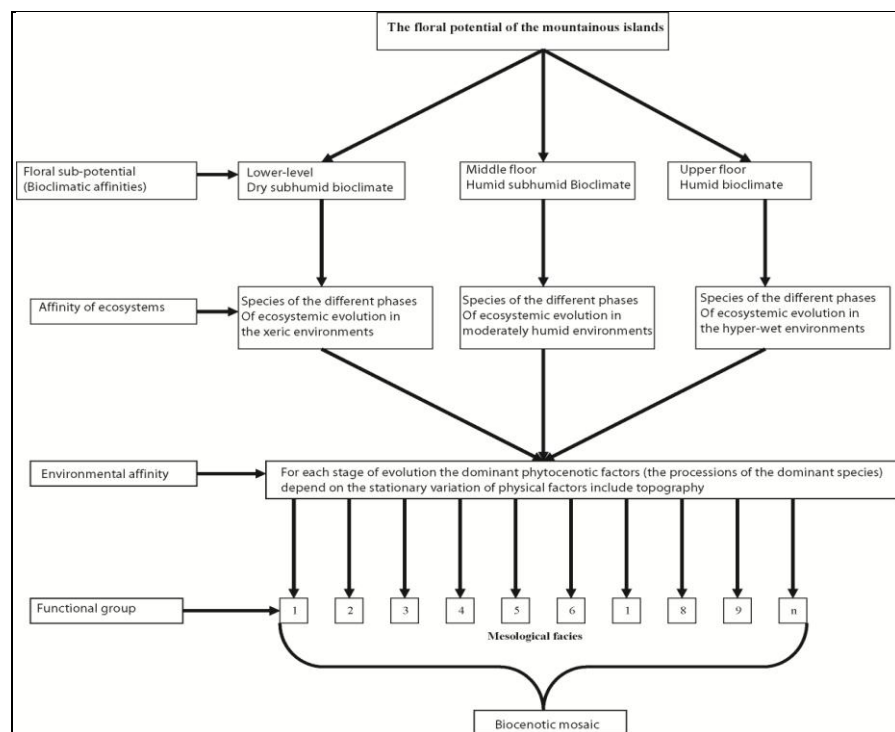


Figure 9: Various aspects of floristic potential.

The installation of various species is conditioned by their ecological strategy, which is in turn a direct reflection of their biology and therefore their genetic potential (Appendix). In theory two diametrically opposed but deeply reductive strategies appear to be able to explain the relevance of the successional phenomenon. Firstly, the species belonging to the first phases of vegetable colonisation are subject to a selection process, called 'r' selection. This is characterised by a rapid growth rate, diaspores adapted to ammechore dissemination (spread by the wind), low longevity and high reproduction (MacArthur & Wilson, 1967; MacArthur, Recher and Cody, 1966; Planka, 1987). Secondly, those in the terminal stages of succession have a selection mode qualified as 'K'. This is characterised by low growth, zoochore dissemination (spread by animals), low reproduction related to environments that vary less from a factorial point of view (Table 1, Figures 10 & 11). If physiological aspects such as stress and disturbance are to be taken into account, other strategies should be considered (Table 2; Grime et al., 1997).

Table 1: r-selected and K- selected (life history adaptations)

Adaptation	r-Selected Populations	K-Selected Populations
Age at first reproduction	Early	Late
Homeostatic capability	Limited	Often extensive
Life span	Short	Long
Maturation time	Short	Long
Mortality rate	Often high	Usually low
Number of offspring produced per reproductive episode	Many	Few
Number of reproductions per lifetime	Usually one	Often several
Parental care	None	Often extensive
Size of offspring or eggs	Small	Large

(Planka, 1987).

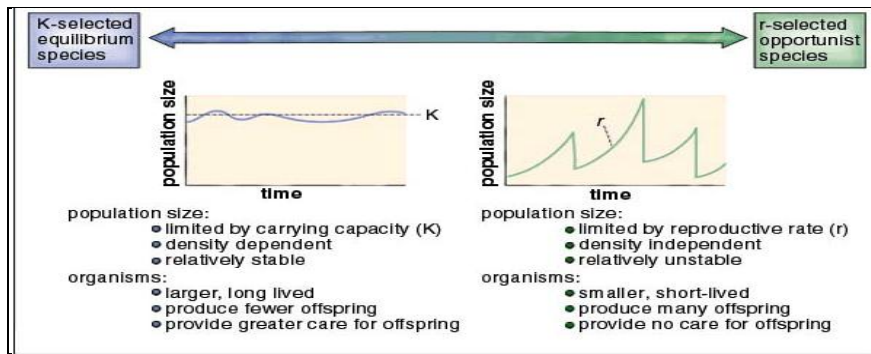


Figure 10: Characteristics of K-selected and r-selected species (Planka, 1987).

Table 2: Typical life histories of plants in environments with different selective factors (Grime et al., 1997).

Competitors	Ruderals	Stress tolerators
Herbs, shrubs, or trees	Herbs, usually annuals	Lichens, herbs, shrubs, or trees; usually evergreen
Large, with a fast potential growth rate	Fast potential growth rate	Potential growth rate slow
Reproduction at a relatively early age	Reproduction at an early age	Reproduction at a relatively late age
Small proportion of production to seeds	Large proportion of production to seeds	Small proportion of production to seeds
Seed bank sometimes, vegetative spread often important	Seed bank and/or highly vagile seeds	Vegetative spread important

This theory of demographic strategies highlights the selective action of the environment at each stage of its evolution (Figure 11). It is a simplistic vision of reality, since the early successional species (the pioneer species) and the late successional species (terminal, climax or balanced), are not confined to extremely specific conditions (Appendices). Instead they exhibit respectively a certain ecological plasticity and can colonise biotopes (or establish themselves) well beyond their main area (Appendices). Between the pioneer and terminal (climax) species, one of the main objections lies at the level of the environmental spectrum which is much wider for the former (Figure 11).

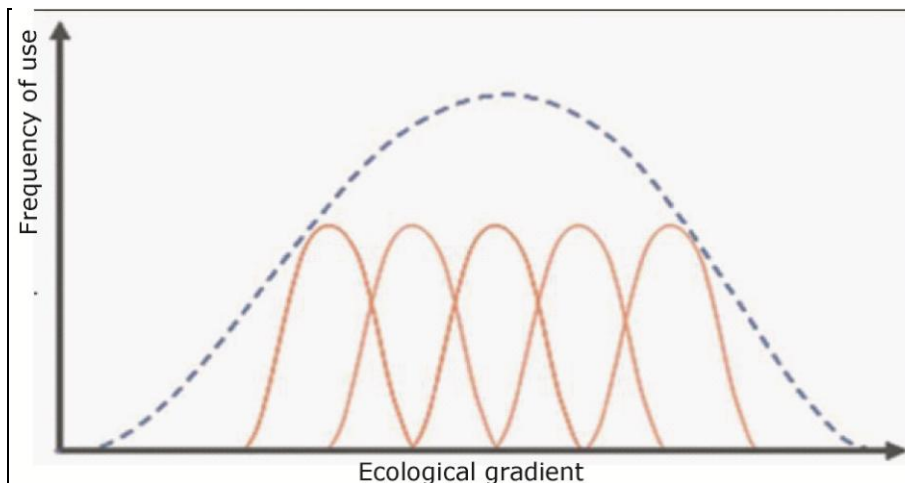


Figure 11: Graphical representation of the concept of individual specialisation. The dotted blue curve represents the global niche of the species and the curved red one, individuals belonging to that species (Bolnick et al., 2003).

Proposal for a descriptive model of plant succession:-

During a progressive succession, a mature formation allows the installation of taxa at a higher dynamic stage in a few places. Initially marginal, they are pioneers which in the long term will contribute to the transformation of the environment and in implementing new floristic successions, identified by their physiognomic, phenological and landscape aspects (Joseph, 2015).

Vegetation dynamics if it can be broken down into stages, dynamic phases, chrono-sequences or successional stages, which taken as whole can be seen as a process of competition and interaction for the biotope's resources. The action of plants on it causes structural alterations producing microsites, more favourable to the regeneration of species at installation. Gradually those which form the backbone of the pre-existing formation become less competitive and will be eliminated.

The autogenic succession model easily explains the primary succession, meaning that taxa pioneers, by modifying the environment, can stimulate the installation of ever more specialised taxa which will subsequently form dense populations. This mechanism is of delicate application when it comes to secondary succession, particularly when the sylvatic state has been reached. Changes induced by vegetation frequently translate into decreased resources, particularly of light energy (Joseph, 1997). In this case the tolerance and inhibition mechanisms are better able to explain the process of replacement. The autogenic succession mode, even if it is not dominant, nevertheless plays a role at the lower levels in all the mechanisms that underlie plant succession. Generally a vegetation ecosystem will favour one dynamic mode over another, according to the ecological characteristics related to its level of development.

Reconquest by vegetation depends on initial plant formation, primary or secondary, and mobilises specific processes that rely on the biology of the species and therefore on their ecological strategy (Westoby et al., 2002; Grime, 1977; Baraloto et al., 2010). Interspecific or even intra-specific interactions cause competition phenomena, leading in some cases to blocking of the vegetation, at a specific floristic and physiognomic successional stage. Indeed the pioneer species can permanently oppose the installation of new plant associations, by their modes of regeneration. For example, some grasses and shrubs by vegetative propagation or stump sprouts (suckers) have a dynamic of rapid occupation. They often impede the establishment of other species in the stock of flora. These species often form monospecific units capable of indefinite reproduction, and these block the evolution of the plant cover.

This phenomenon is noticeable in areas where slash-and-burn is very common, but also on land where the soil is stripped before agricultural production (of plants or of animals). In all these cases, the evolution of the vegetation depends on the exterior seminal potential, since these modes of soil preparation have as a consequence the destruction of the edaphic seminal potential (the soil seed bank). Efficiency in the dynamic of installation and differences in growth are key elements in the initiation of the cycles of succession.

We can add to the biology of the species (phenology), weather conditions and human impacts, other elements that will accentuate the factorial constraints and the randomness of the sites of regeneration and development of species. For example, animal predation can induce significant ecosystem changes. Selective consumption and trampling act to select specific phytocenoses from a structural, architectural, floristic and dynamic perspective. Animal predation, often guided by man, called zoo-anthropisation, is currently one of the driving forces of the organisation of some plant landscapes (Terborgh & Estes, 2013). The release of the diaspores is an important factor in plant succession. It is dependent on vectors which depending on the evolution of the vegetal mantle will be essential and will determine the balance in a particular plant stock. In the Lesser Antilles of today, regardless of the dynamic stages, anemochoric and zoochoric, and specifically ornithochoric, appear to be the main modes of dissemination (Appendices).

Barochoric dissemination becomes an essential mechanism when the efficiency of some elements of faunal vector decreases. This is dissemination without apparent adaptation. The diaspores mature and fall by gravity, creating a phenomenon in steep areas of "aggradation", which transfers by accumulation bulky and heavy seeds to the bottom of slopes. These can be drained by permanent or seasonal water courses of all sizes that ensure a spread well beyond the original plant [e.g. *Jatobá* *Hymenaea courbaril* (Caesalpinioideae), *Angelin* *Andirá inermis* (Fabaceae), Appendices].

Zoochore, and ornithochore, dissemination, is a way to increase the efficiency of long-distance spread (Vittoz & Engler, 2007; Charles-Dominique, 1986). Generally the faunal vector, whatever the animal, disseminates with

greater efficiency. Thanks to a strong directionality, it places the diaspores in the most favourable sites for germination and development of the organisms that they generate (Lakshmi et al., 2011). Although the data are non-existent or incomplete in the Lesser Antilles, covariance between the feeding behaviour of animal species and the regenerative capacity of plant species seems plausible (Appendices). In vegetation dynamics, plant succession is consubstantial with the changes in the components of the faunal vector (Appendices).

Accordingly, the concepts of coevolution and coadaptation are in many cases used to explain this phenomenon (Lankinen & Larsson, 2009;). This covariance exists in some cases, however it is difficult to demonstrate its features (Occhipinti, 2013; Corlett, 2009). The fact that it is possible to do, in light of the work done and available in the literature and from our studies and observations, has several aspects. First, it appears that ornithochore dissemination is dominant in advanced plant communities, more precisely in the middle of a succession. However in a shrub matrix, as trees emerge, they serve as a perches for birds, and bring about a sylvan diaspore system, which is the point of departure for the next successional stage. Other vertical elements, like a pile of stones that attracts birds, are also sites which develop the same initiating mechanisms for the higher dynamic stages. These are significant in anthropogenic grassland and facilitate tree colonisation. Secondly, the dispersal vectors, by their ethology and their level of activity, which generally depend on the type of plant, strongly influence the specific combinations of species (Clark et al., 1999; Vences et al., 2009). From this there follows an extreme specificity of floristic compositions. The structure of the biotic relationships is crucial and determines the ecological niche of each species: its habitat (the spatial component) and its function (the biological component). It seems there a scalable covariance between the vectors of dissemination and vegetation cover.

Therefore, a notable structural transformation accompanied by a change in interactions between the vectors of dissemination results in a qualitative and quantitative change in the latter. The result will be a quantitative and qualitative variation, both autoecological as synecological, in the new vegetation. Finding in this complexity a model for succession, with a universal dimension, poses many problems. Because of the exceptional artificialisation of plant ecosystems of the Lesser Antilles, the initial state is not always definable, except with formations whose primitive character is demonstrable. Given the number of factors, there are as many models as successional processes. Here we should lay down the conceptual groundwork for any subsequent modelling attempts.

Undeniably for each type of succession there is an approach that more or less faithfully represents the functional reality. All these proposed models are aspects of what might be called: the system of succession within which many directions are possible. The history of the plots of land, the different types of disturbance and the ecology of the taxa will define and punctuate the succession (Figure 12).

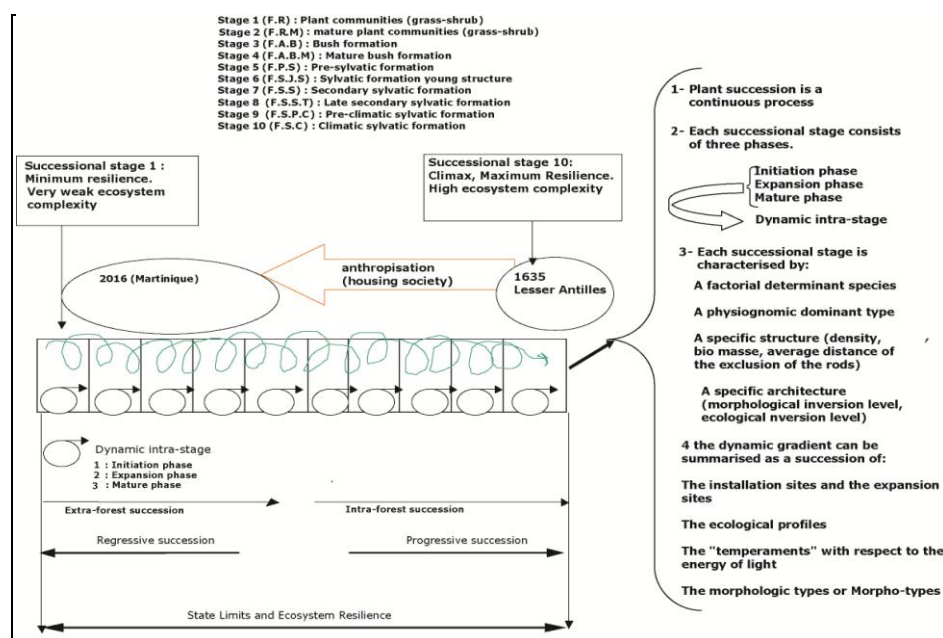


Figure 12: Dynamic gradient (descriptive model).

Therefore the systemic approach seems to be one that allows us to explore plant ecosystems both spatially and temporally. As stated previously, temporal dynamics are divided into respective degrees of evolution of diverse appellation: phases, stages, steps or even chrono-sequences, define floristic compositions and defined architectures and physiologies, corresponding to distinct landscape units (Figure 12). The main elements that influence the spatial and temporal dynamics of plant ecosystems are: climate, floristic potential, soil, topographic heterogeneity, exposure, the plant itself (its ecological profile reflecting its biology). Secondly there is dissemination and its associated vectors, anthropisation (intensity, frequency, mode), disturbances of natural origin, intra- and inter-species competition. The plant is located, somehow, and plunged into a fabric of factorial constraints resulting from interactions between all elements of the ecosystem. Installation involves a covariance between the characteristics of the installation site and its ecological potential (Figure 13).

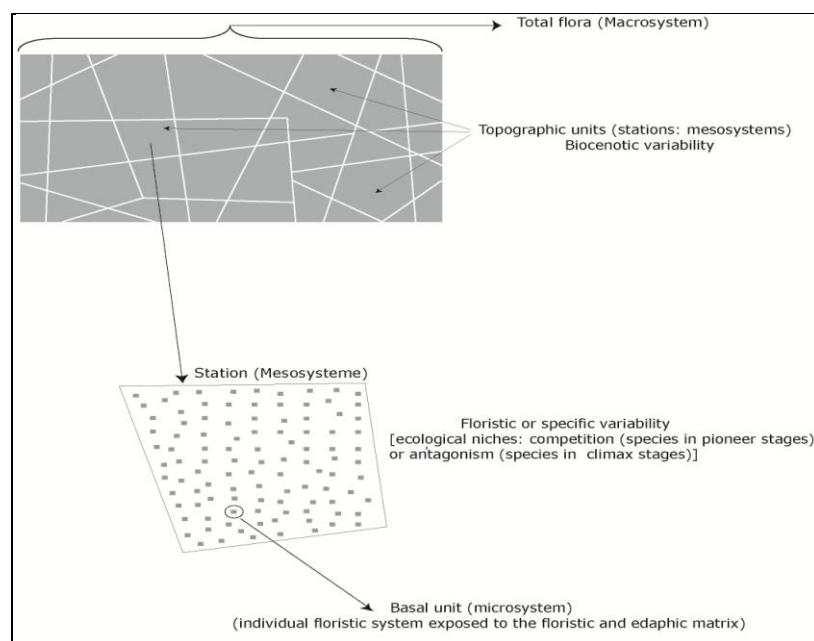


Figure 13: Example of levels of integration within the ecosystem.

Through mechanisms of recolonisation or restoration, for every significant structural variation of the system, adjustments contribute to restore the initial organisation. It is important to take the level of the autecologic study to research along the dynamic gradient for quantitative variations of the species (appearance, disappearance). This is more relevant during plant succession than germination requirements, tolerances for certain variable factors in particular light energy, predation and dispersal (Appendix 3, Van der Valk, 1981; Walker & del Moral, 2009; Hyatt & Casper, 2000). Synecological study or structural dynamics is also crucial, because it is difficult to separate the taxon being studied from the association of which it is an interactive element. The action of all species in the plant community defines the characteristics of the installation sites (Joseph, 1997). So, an isolated species, even if it has its own ecological identity, is dependent on the overall organisation embodied by vegetable formation and the environment. Therefore, a plant which aspires to become part of the general floristic composition, when it is immersed in the interactive system, represented by the plant ecosystem, is somehow a particular expression of all the functional modes of the entire system.

Appendix 1: Ecological dominance of the major taxa in the undergrowth vegetation of Martinique.

Essences	nb	fa	fr	densité	Ld	Aire basale	LD
<i>Pisonia fragrans</i>	2578	75	100	0,04683015	4,68301544	17,362218	81,307535
<i>Bursera simaruba</i>	816	68	90,6666667	0,01482289	1,34394187	30,186213	40,5685156
<i>Lonchocarpus violaceus</i>	1250	60	80	0,02270663	1,81653043	16,470831	29,9197657
<i>Maytenus laevigata</i>	2558	56	74,6666667	0,04646685	3,46952468	6,9462584	24,1002149
<i>Bourreria succulenta</i>	2666	68	90,6666667	0,0484287	4,39086891	4,7602596	20,9016759
<i>Ocotea coriacea</i>	3082	60	80	0,05598547	4,47883742	3,9315548	17,6087948
<i>Pimenta racemosa</i>	2173	37	49,3333333	0,03947321	1,94734484	8,6791759	16,9013484
<i>Tabebuia heterophylla</i>	513	42	56	0,0093188	0,52185286	19,738256	10,3004654
<i>Coccoloba swartzii</i>	1006	48	64	0,0182743	1,16955495	8,4171233	9,84428822
<i>Chionanthus compacta</i>	1092	58	77,3333333	0,01983651	1,53402362	4,4138391	6,77093341
<i>Eugenia monticola</i>	2311	46	61,3333333	0,04198002	2,57477445	2,3457174	6,03969322
<i>Sideroxylon foetidissimum</i>	735	23	30,6666667	0,0133515	0,40944596	10,527929	4,31061798
<i>Eugenia cordata</i>	1360	29	38,6666667	0,02470481	0,9552528	4,49177	4,29077587
<i>Myrcia citrifolia</i>	2313	46	61,3333333	0,04201635	2,57700273	1,5360684	3,95845245
<i>Krugiodendron ferreum</i>	982	37	49,3333333	0,01783833	0,88002422	3,9985153	3,51879031
<i>Erythroxylum havanense</i>	946	57	76	0,01718438	1,30601272	2,2336979	2,91723786
<i>Guettarda scabra</i>	801	39	52	0,01455041	0,75662125	3,5595433	2,69322611
<i>Calliandra tergemina</i>	2024	23	30,6666667	0,03676658	1,12750833	1,96	2,20991632
<i>Eugenia pseudopsidium</i>	1080	36	48	0,01961853	0,94168937	2,3365329	2,2002882
<i>Inga laurina</i>	390	38	50,6666667	0,00708447	0,35894641	5,8409888	2,09660197
<i>Byrsonima spicata</i>	360	35	46,6666667	0,00653951	0,30517711	6,8034969	2,07627153
<i>Coccoloba pubescens</i>	599	32	42,6666667	0,01088102	0,46425674	3,933321	1,82607077
<i>Myrcia fallax</i>	1215	27	36	0,02207085	0,79455041	1,9984334	1,58785608
<i>Chrysophyllum argenteum</i>	870	44	58,6666667	0,01580382	0,92715713	1,4942083	1,38536588
<i>Tabernaemontana cirifolia</i>	636	43	57,3333333	0,01155313	0,66237966	1,903468	1,26081848
<i>Amyris elemifera</i>	673	31	41,3333333	0,01222525	0,50531032	1,99	1,00556755
<i>Croton bixoides</i>	963	31	41,3333333	0,01749319	0,72305177	1,1655288	0,84273766
<i>Capparis indica</i>	804	35	46,6666667	0,01460491	0,68156222	1,1914534	0,81204962
<i>Dapnopsis americana</i>	442	37	49,3333333	0,00802906	0,39610052	1,8625695	0,73776474
<i>Pisonia suborbiculata</i>	990	30	40	0,01798365	0,71934605	0,9888056	0,7112934
<i>Haematoxylon campechianum</i>	378	16	21,3333333	0,00686649	0,14648501	4,784575	0,70086853
<i>Croton corylifolius</i>	592	36	48	0,01075386	0,51618529	1,2338041	0,63687152
<i>Ocotea patens</i>	570	28	37,3333333	0,01035422	0,38655768	1,3236866	0,51168121
<i>Manilkara bidentata</i>	292	13	17,3333333	0,00530427	0,09194066	4,9359426	0,45381382
<i>Casearia decandra</i>	373	43	57,3333333	0,00677566	0,38847109	0,9606634	0,37318996
<i>Acacia muricata</i>	400	9	12	0,00726612	0,08719346	3,79	0,33046322
<i>Eugenia tapacumensis</i>	429	33	44	0,00779292	0,34288828	0,7950676	0,27261937
<i>Randia aculeata</i>	474	49	65,3333333	0,00861035	0,56254314	0,4676411	0,26306829
<i>Hymenaea courbaril</i>	124	9	12	0,0022525	0,02702997	8,5684909	0,23160608
<i>Eugenia ligustrina</i>	490	30	40	0,008901	0,35603996	0,6017418	0,21424413
<i>Picramnia pentandra</i>	566	35	46,6666667	0,01028156	0,47980624	0,4347919	0,20861587
<i>Schaefferia frutescens</i>	597	16	21,3333333	0,01084469	0,23135332	0,8305889	0,1921595
<i>Morisonia americana</i>	572	17	22,6666667	0,01039055	0,23551923	0,8153403	0,19202832

Conostegia calyptrata	418	32	42,6666667	0,0075931	0,32397215	0,564159	0,1827718
Bunchosia glandulosa	306	37	49,3333333	0,00555858	0,27422343	0,66	0,18098747
Ficus citrifolia	56	16	21,3333333	0,00101726	0,02170148	8,0879531	0,17552058
Pilocarpus racemosus	721	8	10,6666667	0,01309718	0,1397033	1,2396131	0,17317804
Zanthoxylum punctatum	399	28	37,3333333	0,00724796	0,27059037	0,5854923	0,15842858
Acacia tamarindifolia	402	17	22,6666667	0,00730245	0,16552225	0,921	0,152446
Citharexylum spinosum	188	24	32	0,00341508	0,10928247	1,1151318	0,12186436
Capparis hastata	299	30	40	0,00543143	0,21725704	0,5171188	0,1123477
Ocotea eggersiana	123	15	20	0,00223433	0,04468665	2,5019324	0,11180297
Guarea glabra	353	17	22,6666667	0,00641235	0,14534666	0,7645568	0,11112577
Cassine xylocarpa	404	13	17,3333333	0,00733878	0,12720557	0,8253098	0,104984
Forestiera rhamnifolia	253	20	26,6666667	0,00459582	0,12255525	0,8230529	0,10086946

nb: number of individuals / fa: absolute frequency / fr = fa / 75 stations (relative frequency).

I.d. = fr × density (index distribution) / I. D = basal area × I.d. (dominance index)

Appendix 2: Ecological profiles of the main species of the undergrowth vegetation of Martinique.

Espèces	FR	FRM	FAB	FABM	FPS	FSJS	FSS	FSST	FSPC	FSC
Pisonia fragrans			+	++	+++	+++	++++	++		
Bursera simaruba		+	++	+++	+++++	+++	++			
Lonchocarpus violaceus			+	++	+++	++++	+++++	++		
Maytenus laevigata				+	+	++	++	+++	++++	++++
Bourreria succulenta		+	+++	++++	+	+				
Ocotea coriacea						+	++++	+++		
Pimenta racemosa				+	++	+++	++++	+++	++	++
Tabebuia heterophylla	+	++	+++	+++	++++	+++	++			
Coccoloba swartzii				+	++	+++	+++++	+++	+	
Chionanthus compacta			+	++	+++	++++	+++++	++		
Eugenia monticola	+	++	+++	+++	+++++	+++	++	+		
Sideroxylon foetidissimum						+	++	++++	+++	++
Eugenia cordata	+	++	++++	+++++	+					
Myrcia citrifolia	+	++	++++	+++++	++	+				
Krugiodendron ferreum				+	+	++	+++	++++	+++	++
Erythroxylum havanense	+	+++	++++	+++++						
Guettarda scabra			+	++++	+++++	++	+			
Calliandra tergemina	+	++	++++	+++++						
Eugenia pseudopsidium					+	+++	++++	++	+	
Inga laurina					+	++	++++	+++	+	
Byrsonima spicata					+	++	+++++	++	+	
Coccoloba pubescens		+	++	++	++++	+++	++			
Myrcia fallax						+++	+++++	++		
Chrysophyllum argenteum					+	++	+++	++	+	
Tabernaemontana					+	++	++++	+		

<i>cirifolia</i>										
<i>Amyris elemifera</i>				+	++	+++	+++	+	+	
<i>Croton bixoides</i>	+	++	++++ +	++++	+					
<i>Capparis indica</i>			+	+++	+++++	++++	+			
<i>Dapnopsis americana</i>			+	++	+++	++++	++++	+		
<i>Pisonia suborbiculata</i>		+	+++	++++	+++++	++	+			
<i>Haematoxylon campechianum</i>	+	++	+++	+++++	+++	++	+			
<i>Croton corylifolius</i>					+++	+++	+			
<i>Ocotea patens</i>						+++	++++	+++		
<i>Manilkara bidentata</i>						+	++	++++	++++	++
<i>Casearia decandra</i>			+	+++	+++++	+++	++	+		
<i>Acacia muricata</i>		+	+++	++++	+++++	+++	++			
<i>Eugenia tapacumensis</i>				+	++	++++	+++	++	+	+
<i>Randia aculeata</i>	++	+++	++++	++++	++					
<i>Haematoxylon campechianum</i>	+	++	+++	+++++	+++	++	+			
<i>Eugenia ligustrina</i>	+	+++	++++	++++	+					
<i>Picramnia pentandra</i>						+++	++++	+		
<i>Schaefferia frutescens</i>			+	+++	++++	++				
<i>Morisonia americana</i>				+++	+++++	++	+			
<i>Conostegia calyptata</i>			+	++	+++	++++	++	+		
<i>Bunchosia glandulosa</i>			+	++	+++	++++	++	+		
<i>Ficus citrifolia</i>						+	+++	+		
<i>Pilocarpus racemosus</i>			+	+++	++++	+++	++	+		
<i>Zanthoxylum punctatum</i>				+	++++	+++	+			
<i>Acacia tamarindifolia</i>	+	++	+++	++++	+++	++	+	+		
<i>Citharexylum spinosum</i>			+	++	++++	+++	+			
<i>Capparis hastata</i>				+	+++	+++++	++++	+		
<i>Ocotea eggersiana</i>						+	+++	++++	+	
<i>Guarea glabra</i>							+	+++	++++	+++
<i>Cassine xylocarpa</i>					++	+++	+++	++++	++	+
<i>Forestiera rhamnifolia</i>			+	++++	+++	++	+			

(F.R.: fruticetum / (F.R.M): mature fruticetum / (F.A.B): bushy formation / (F.A.B.M): mature bushy formation / (F.P.S): pre-sylvan formation / (F.S.J.S): structured immature sylvan formation / (F.S.S): secondary sylvan formation / (F.S.S.T): late secondary sylvan formation / (F.S.P.C): pre-climax sylvan formation / (F.S.C): climax sylvan formation / (+): Importance of the descriptor

Appendix 3: Temperaments (light) and modes of dissemination of the main species in the undergrowth of Martinique.

Espèces	HP	HS	HTS	HéSc	S	HémSc	VDP	PSEM	C	D	DE
<i>Pisonia fragrans</i>		+++	++			+	ORNI	S1	NC	G	G
<i>Bursera simaruba</i>	+++	+	+				ORNI	S2	T	M	G
<i>Lonchocarpus violaceus</i>	+	+++					ANEMO	S1	T	M	M
<i>Maytenus laevigata</i>					+++		ORNI	S1	NC	G	M
<i>Bourreria succulenta</i>	+++	+					ORNI	S3	T	G	M
<i>Ocotea coriacea</i>		+	+++				ORNI	S2	NC	G	M
<i>Pimenta racemosa</i>		+	+	+++			ORNI	S1	NC	M	M
<i>Tabebuia heterophylla</i>	+++	++	++				ANEMO	S1	T	F	M
<i>Coccoloba swartzii</i>		+++	+				ORNI	S1	P	M	F
<i>Chionanthus compacta</i>		+++	+				ORNI	S2	NC	M	F
<i>Eugenia monticola</i>	+	+++	+				ORNI	S2	NC	G	F
<i>Sideroxylon foetidissimum</i>			+	+++			ORNI	S1	P	F	F
<i>Eugenia cordata</i>	+++	+					ZOOCH	S3	NC	EF	EF
<i>Myrcia citrifolia</i>	+	+++					ORNI	S3	NC	G	F
<i>Krugiodendron ferreum</i>		+	+	+++			ORNI	S2	NC	F	F
<i>Erythroxylum havanense</i>	+++	+					ORNI	S3	T	M	F
<i>Guettarda scabra</i>	++	+++	+				ORNI?	S2	T	F	F
<i>Calliandra tergemina</i>	+++	+					BARO	S3	T	M	F
<i>Eugenia pseudopsidium</i>		+	+++				ORNI	S2	NC	F	F
<i>Inga laurina</i>			+++				ZOOCH	S1	NC	F	F
<i>Byrsonima spicata</i>	+	+	+++				ZOOCH	S1	P	TF	F
<i>Coccoloba pubescens</i>	+++	++					ZOOCH	S2	P	TF	F
<i>Myrcia fallax</i>		+++	++				ZOOCH	S2	NC	F	F
<i>Chrysophyllum argenteum</i>			+++			++	ZOOCH	S3	NC	F	F
<i>Tabernaemontana cirifolia</i>		++				++	ZOOCH	S3	NC	F	F
<i>Amyris elemifera</i>	+	++	+++				ZOOCH	S2	NC	F	F
<i>Croton bixoides</i>	+++							S3	T	F	F
<i>Capparis indica</i>	+	+++					ZOOCH	S3	NC	F	F
<i>Dapnopsis americana</i>	+	+++	+				ZOOCH	S2	T	F	F
<i>Pisonia suborbiculata</i>	+++	+					ZOOCH	S3	T	F	F
<i>Haematoxylon campechianum</i>	+++						ZOOCH	S2	T	TF	TF
<i>Croton corylifolius</i>	+	+++						S3	T	TF	TF
<i>Ocotea patens</i>		+	+++	+			ZOOCH	S2	NC	F	TF
<i>Manilkara bidentata</i>			+	+++			ZOOCH	S1	NC	TF	TF
<i>Casearia decandra</i>	+	+++	+				ZOOCH	S2	T	TF	TF
<i>Acacia muricata</i>	+++	+					BARO	S2	T	TF	TF
<i>Eugenia tapacumensis</i>		+++	+				ZOOCH	S2	NC	TF	TF

<i>Randia aculeata</i>	+++						ZOOCH	S3	T	TF	TF
<i>Hymenaea courbaril</i>	+	++	+++				BARO/ ZOOCH	S1	T	TF	TF
<i>Eugenia ligustrina</i>	+++						ZOOCH	S3	NC	TF	TF
<i>Picramnia pentandra</i>		++				+	ZOOCH/ BARO	S3	NC	TF	TF
<i>Schaefferia frutescens</i>	+	+++						S3	NC	TF	TF
<i>Morisonia americana</i>		+++	+				ZOOCH	S3	NC	TF	TF
<i>Conostegia calyptrata</i>		+++	+					S3	NC	TF	TF
<i>Bunchosia glandulosa</i>	+	+++	+					S2	T	TF	TF
<i>Ficus citrifolia</i>	+	++	+				ZOOCH	S1	NC	TF	TF
<i>Pilocarpus racemosus</i>	+	+++					BARO	S3	NC	TF	TF
<i>Zanthoxylum punctatum</i>	+	+++	+				ZOOCH	S3	NC	TF	TF
<i>Acacia tamarindifolia</i>	++	++	+				BARO	S3	T	TF	TF
<i>Citharexylum spinosum</i>	+	+++					ZOOCH	S2	T	TF	TF
<i>Capparis hastata</i>		+++	+				ZOOCH/ BARO	S2	NC	TF	TF
<i>Ocotea eggersiana</i>			+++	+			ZOOCH	S1	NC	TF	TF
<i>Guarea glabra</i>				+++	+		BARO/ ZOOCH	S2	NC	TF	TF
<i>Cassine xylocarpa</i>		+++	++				ZOOCH/ BARO	S2	NC	TF	TF
<i>Forestiera rhamnifolia</i>	+++	+					ZOOCH	S2	T	TF	TF

HP: primary heliophile / **HS:** secondary heliophile / **HTS:** heliophile in forest clearing.

HESC: heliosciaphile / **S:** Sciaphile/ **Hemsc:** hemisciaphile / **VDP:** potential dissemination vector (**BARO:** barochore, **ORNI:** ornithochore, **ZOOCH:** zoochore, **ANEMO:** anemochore) / **PSEM:** maximum expansion stratigraphic position (**S1:** upper stratum, **S2:** average stratum, **S3:** lower stratum) / **C:** Caducity (**T:** totally, **NC:** not deciduous, **P:** partially) / **D:** distribution / **DE:** ecological dominance / **G:** great, **M:** average, **F:** low, **TF:** very low.

Conclusion:-

The vegetation of the Lesser Antilles of today is composed of a plural set of dynamic levels in which all structural and floral combinations exist. To varying degrees, all the components of the overall floristic potential are mobilised by and depend on land worked by man and the adjacent areas. However, in the case of severe degradation of biotopes, advective and seminal potentials soil seem best suited to support a dynamic of progressive evolution. They can hardly exceed this level of analysis taking into account the extreme spatial and temporal heterogeneity of the vegetable mosaic. As such, in the strictest sense of the term, it is based said that the conditions of "natural" plant succession are no longer required. The establishment of anthropophyte species is one of the main consequences of permanent artificial environments. Currently, the ecological dominance of species is strongly defined by humans, although they are environmentally capable of providing their full phenological cycles without their involvement. Somehow the development of human activities has had as a corollary, the islandification of a number of forest formations and the regression or eradication of plant species. Generally progressive or regressive of vegetation evolution, anthropogenic modification of the original environment changes the structure factors and by implication the logic of specific or plant combinations. This results in completely different organisation and floristic composition of formations that might exist after a natural disturbance or in the absence of any human impacts. This was and remains a major structuring factor in the plant landscape of the Caribbean and will have some repercussions in its future development. In the event where the plant cover becomes climax forest, it would be different from those of the Amerindian epoch, in their floristic form and their physiognomy and architecture.

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