International Journal of Environmental Studies
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/genv20

The vegetation of the Lesser Antilles: floristic diversity and ecosystemic dynamics
Philippe Joseph a
a Département de géographie, Campus de Schoelcher, UMR ESPACE DEV, Université des Antilles et de la Guyane, Martinique, 97200, France

Version of record first published: 16 Aug 2012

To cite this article: Philippe Joseph (2012): The vegetation of the Lesser Antilles: floristic diversity and ecosystemic dynamics, International Journal of Environmental Studies, DOI:10.1080/00207233.2012.715384

To link to this article: http://dx.doi.org/10.1080/00207233.2012.715384

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: http://www.tandfonline.com/page/terms-and-conditions

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.
The vegetation of the Lesser Antilles: floristic diversity and ecosystemic dynamics

PHILIPPE JOSEPH*

Département de géographie, Campus de Schoelcher, UMR ESPACE DEV, Université des Antilles et de la Guyane, Martinique 97200, France

Human activity in the Lesser Antilles has led to the establishment of secondary herbaceous, shrubby and pre-forest communities. Today, vegetation cover is a mosaic of phisonomic units of varying age, structure and floristic composition. These various components cover a range of specific biocenotic evolution levels. There are many degrees of complexity which correspond to the stages or phases of vegetative succession, the whole of which forms a dynamic gradient. In fact, over the course of time, the generalist species have supplanted those which, at the centre of pre-Columbian climax forest occupied highly specialised sites. The numeric data generated, with the help of macro-ecological and biogeographical methodologies as well as from naturalistic observations, has made possible the identification of the traits of vegetal dynamics. More specific future research, also relating to the dynamics of taxa, could use this general framework as a reference.

Keywords: Antilles; Human activity; Ecosystem; Dynamic; Biodiversity

1. Introduction

The tree cover of the Caribbean is very diverse, but we are far from understanding its functioning in detail. The present ecosystem complexity results from the multiple dynamic changes caused by human beings as well as by the spatial variability of bioclimatic factors [1–3]. To the metastable character of these systems are added natural and ecological unanticipated events which modify their structures and highlight their instability [4,5]. Human beings, by their actions, have increased the intrinsic heterogeneity of plant cover and have enlarged the range of ‘possible successional trajectories’ [6].

Because of human impacts, it is difficult to study the vegetation of the Lesser Antilles. Although forest can flourish to a height of approximately 800–900 m, ignorance of the original conditions makes it difficult to describe the various aspects of vegetation dynamics [7]. The schemas offered below, focused on the stages of the successional gradient, are based on physiognomic units [8,9]. They provide information about the succession of preponderant physiognomies over the course of evolution of the vegetation. Nevertheless, the dominant morphological traits roughly indicate the complexity of the ecological units which make up the landscape. In fact, the ecosystemic potentiality of the Antilles is sylvan, a landscape marked by an abundance of bush communities.

*Email: Joseph.phil@wanadoo.fr
The elements presented below result from naturalist observations and from collected floristic data and are only an attempt at classification of vegetal species on the temporal dynamic scale. In this respect, the specific and community successions that appear are linked to the organisation of the current plant cover. Indeed, the floristic combinations that have been inventoried depend on the species pool (or on the floristic potential) of today. The taxa have an ecological importance, as they provide information on their community strategies. Fundamental elements necessary to understand the process of vegetative succession in the Lesser Antilles will also be explained. Moreover, these explanations will have to be completed in the future by the study of the auto-ecological characteristics of the taxa.

The objective of this paper is to characterise the principle factors which condition the spatial distribution and the regressive or progressive evolution of the multiple units of the vegetation. The bioclimates have been defined in relation to the rainfall gradient between the coasts and the summits, which form what is locally called the island’s hog back. The various vegetal morphologies were mapped using aerial photographs from the ‘Institut Géographique National’ (IGN or National Geographic Institute, French Antilles, figures 1a and 1b).

To the ground readings, we may add more qualitative data from naturalist writers, some from the early colonial days [10–14], our botanist or ecologist predecessors [15,16] and also from colleagues from the ‘Unité de Formation et de Recherche (UFR) Sciences exactes’ [17,18]. To include both qualitative and quantitative approaches, 800 observation points were decided upon. They cover all the vegetal stages and their various physionomic types. Despite the fact that the arguments and general conclusions concern all types of

Figure 1a. Antilles within the Caribbean.
vegetation, most of the maps, tables and figures presented below refer only to the lower layer of the vegetation.

These observations generated floristic, structural and architectural data with the following descriptors [19,20]: species, minimal surfaces, section diameters of over 2.5 cm and 1.33 m from the ground (international standard), crown height, first ramifications and biomass (phytomass or biovolume [21]. The latter was measured according to the basal area. In addition to these descriptors, traditional indices belonging to macro-ecology were used. The distribution index (Id3) and the dominance index (ID4) represent, respectively, the spatial distribution mode of the various species (isolated or clustered individuals) and their ecological importance.

Figure 1b. Observation points (Martinique).
2. Theories about vegetation succession

The succession processes are auto-organisation mechanisms which result from interactions between the organisms themselves and also between the organisms and the environment [22–24]. The biotic relationships could be the motor of the mechanism of species replacement. Through progressive or regressive dynamics, plant species become increasingly adapted to the conditions of successive ecosystemic states [25,26]. This process of substitution implies the existence of a large behavioural diversity in the species stock, therefore of a large floristic and ecological diversity. For example, during a progressive succession, the mature communities in place allow the establishment, in a few sites, of taxa in a superior dynamic stage. Thus, a small number of species contributes over time to the transformation of the original environment and to the setting up of new floristic corteges.

Vegetation succession, while it may fall into different stages or phases, generally results in a process of competition for the environment’s resources, both inter-specific and intra-specific. The action of plant life on the biotope brings about structural modifications which produce micro-sites, more favourable to the regeneration of incoming species. Progressively, those plants which formed the framework for the existing formation become less and less competitive and are eliminated. There are, nevertheless, cases where the pioneer species can continually oppose the establishment of new vegetative associations, thanks to their regeneration modalities. In addition to phenology, climatic conditions and human action, other elements, such as animal predation, can bring about notable ecosystem change. These changes accentuate the factorial constraints, the random appearance of the regeneration sites for the development of the species.

The dispersal of diaspores is also an important factor in vegetation succession. The dispersal vectors specific to various vegetation communities, by their ethology and their level of activity, influence the combinatory modalities of species. The structure of biotic relationships is all-important and determines the ecological niche of each species [27,28] according to habitat (spatial component) and function (biological component). Consequently, a notable structural transformation accompanied by a modification of the interactions between dispersal vectors causes a qualitative and quantitative change in the vectors (from personal observation). The result will be a quantitative and qualitative variation, autecological as well as synecological, of new floristic communities [29].

All the types of models proposed in scientific literature [30] are aspects of what we could consider as the system of succession in which numerous directions are possible [31]. The history of plots, the different forms of disturbances and the ecology of the taxa are fundamental factors [32,33]. Therefore, the systemic approach seems to be the one which allows for the exploration of plant ecosystems on both spatial and temporal levels.

By means of recolonisation or restoration mechanisms, with each notable structural variation of the biosystem, adjustments aid in re-establishing the initial organisation. It is important to study the autecology of taxa and track their quantitative variations during the evolution of vegetation. Requirements for germination and tolerance to certain factors vary with plant succession, particularly light energy, predation and dispersal.

Synecological study or structural dynamics is also fundamental, because it is difficult to separate the taxon studied from the association in which it is an interactive element. The actions of all the species in the plant community partially define the characteristics of individual sites. As a consequence, the species depends on the global organisation incarnate in the vegetal formation and its environment.
3. The floristic potential

The floristic potential can be defined as an ensemble of species present in a given place and for a precise time period. From the shore to the peaks of the mountain ranges: sub-humid dry, sub-humid humid, humid and hyperhumid bioclimates correspond, respectively, to collections of species with identical mesological affinities (figure 2). The history of the sites determines, in terms of disturbances, the components of the floristic potential which will express itself in the form of floristic associations.

There are four types of floristic potential for a given bioclimate, namely:

1. Vegetative floristic potential made up of plants found in a vegetative state on the site.
2. Peripheral or border vegetative floristic potential made up of plants found in a vegetative state on the periphery of the site.
3. Edaphic seminal potential (seed bank) made up of tree species potentially present in the form of seeds in the soil of the site.
4. External or advective potential made up of vegetal species having individuals capable of reproducing outside the site.\(^5\)

For a given site, the predominance of one floristic potential over another depends on the degree of spatial heterogeneity of the units which make up the regional mosaic, their floristic compositions and the characteristics of the disturbance(s). In a mature forest, the canopy is closed. In this case regeneration depends on the vegetative floristic potential. In forest estates, in the ‘sciaphile’ matrix the floristic potential intervenes in the following

![Diagram of floristic potential of the mountainous islands](image)

Figure 2. The floristic potential of the mountainous islands.
order: vegetative floristic potential, peripheral floristic potential and advective floristic potential. In the windfalls, the most common floristic potentials are the edaphic seminal potential and the advective potential. These depend on the size of the openings and the prevalent ecoclimatic conditions (figure 3).

Over the course of phases preceding the emergence of the forest, processes are not always easy to explain, but it is possible to clarify the specificity of floristic potentials. When profound ecosystem deregulations occur and the edaphic system remains in place, it seems that the seed-bearing potential of the soil becomes very important in the process of reconquering the plant cover. Consequently, the impoverishing of the seed stock of the edaphic system linked to man-made degradation, direct or indirect, progressively leads to the predominance of the advective potential, in which the success of the species depends on the mode and the vectors of diaspore dispersal. In general, in cases of heavy biotope degradation, the advective and edaphic potentials seem the most apt to sustain a dynamic of progressive evolution.

The vegetation of the Lesser Antilles, today, comprises numerous dynamic stages in which all combinations exist, both from a structural and floristic point of view. To varying degrees, all the components of the global floristic potential depend on the anthropogene history of the plots studied and those adjacent. It is difficult to get past this level of analysis given the extreme spatial and temporal heterogeneity of the vegetal mosaic. One may say that the conditions of ‘natural’ vegetative succession are not met everywhere. The implantation of anthropophytes is one of the principal consequences of the permanent human impacts on environments. Even though their ecological dominance is conditioned by humankind, they are ecologically capable of completing their phenologic cycles without human intervention.

The development of human activity has had, as a corollary, the ‘insularisation’ of a number of forest stands and the regression, or even the elimination of tree species. Over the course of progressive or regressive evolution of the tree cover, modification of the original environments changes the factors and consequently the development logic of specific

Figure 3. Multiple windfalls and ecological profiles of taxa in mature forests.
combinations (figure 4). This brings about communities which have an organisation and a floristic combination completely different from those which could have existed following a natural disturbance without previous human activity. If the present-day plant cover became sylvan again, it would be different from that of the Amerindian period on floristic, physiognomic and architectural levels because the spatial distribution and demographic characteristics of contemporary species are different. To this must be added the long-term effects of various climatic hazards.

![Diagram of Mountainous Lesser Antilles](image)

**Figure 4. Diversity of secondary phytocenoses.**
4. A descriptive model of the dynamic functioning of vegetal species

In the sense of an ecosystemic progressive evolution, the gradient dynamics include stages symbolised by morphologically identifiable communities: grasses, shrubs, bushes, presylvans and sylvans. The complexity increases, from the most regressive structures to those that indicate optimal phases. The question here is to estimate the importance or ‘level of expression’ of taxa in the various dynamic phases. In fact, over the course of the vegetative dynamics, it is necessary to define their capacity to implant themselves in sites successively produced by different states of the ecosystem [34,35]. Distinctive signs or symbols (table 1) will be used within a successional stage, to indicate the degree of covariance between a species and the ecological characteristics of the installation or expansion sites.

For each dynamic phase, the colonising power of the taxa is symbolised by a number of choices reflecting their autecological and synecological functions and giving an idea of their dynamic profiles (table 1). The latter must be used with caution because human activity induces local features which often conflict with the global model. It follows that the numerous expressions of floristic potential can be explained by the presence of several determining elements.

First, the dynamic profile of species is linked to the probability of establishment in the sites generated by the physical and biotic constraints which are transformed along with the evolution of the vegetation (tables 2a, 2b and 2c). Then the phenological differences intervene as well as the ecophysiological differences. These confer on the species a specific efficiency for the use of the essential elements of the environment (tables 2a, 2b and 2c). Finally, human activity will indicate a precise direction, from a choice of possible direc-

Table 1. Autecological and synecological descriptors.

<table>
<thead>
<tr>
<th>Importance of the species in the dynamic phase</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>+: Probability of installation very slight, a few sites have the necessary characteristics for the species to settle there. In the case of forest systems, accidental installation related to highly specialised mechanisms</td>
<td></td>
</tr>
<tr>
<td>++: Probability slight, marginal species in the association</td>
<td></td>
</tr>
<tr>
<td>+++: Probability average, species often co-dominant or of secondary importance in the formation</td>
<td></td>
</tr>
<tr>
<td>++++: Probability strong, phasing more and more accentuated between the biology of the species under consideration and the conditions offered by the installation and expansion sites</td>
<td></td>
</tr>
<tr>
<td>++++: Species ecologically dominant which holds an important position in the vegetal formation, by the number of stems, but also in biomass; covariance high between its ecology and the site characteristics</td>
<td></td>
</tr>
</tbody>
</table>

Plausible dispersal
Ornitochory: ORNI (dispersal by birds)
Barochory: BARO (dispersal without defined vectors, most often gravity is the unique dispersal agent)
Zoochory: ZOOCH (dispersal by animals)
Anemochory: ANEMO (dispersal by the wind)
Stratigraphic position
S1: Structuring of the first order (upper layers)
S2: Structuring of the second order (middle layers)
S3: Structuring of the third order (lower layers)
Distribution and abundance
G: distribution high
M: distribution average
F: distribution weak
TF: distribution very weak
ET: distribution extremely weak (species with no biodemographic importance, nevertheless sometimes able to be a spatio-temporal ecological indicator)

Degree of affiliation to a family of temperament ecological specialisation
+: Affiliation weak
++: Affiliation average
+++: Affiliation strong
Table 2a. Ecological dominance of principal species of the lower layer (Martinique, figure 1b).

<table>
<thead>
<tr>
<th>Species</th>
<th>$N_b$</th>
<th>$f_a$</th>
<th>$f_r$</th>
<th>density</th>
<th>Id</th>
<th>Basal area (m$^2$)</th>
<th>ID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pisonia fragrans</td>
<td>2578</td>
<td>75</td>
<td>100</td>
<td>0047</td>
<td>4.68</td>
<td>17.36</td>
<td>81.3</td>
</tr>
<tr>
<td>Bursera simaruba</td>
<td>816</td>
<td>68</td>
<td>90.7</td>
<td>0015</td>
<td>1.34</td>
<td>30.19</td>
<td>40.6</td>
</tr>
<tr>
<td>Lonchocarpus violaceus</td>
<td>1250</td>
<td>60</td>
<td>80</td>
<td>0023</td>
<td>1.82</td>
<td>16.47</td>
<td>29.9</td>
</tr>
<tr>
<td>Maytenus laevigata</td>
<td>2558</td>
<td>56</td>
<td>74.7</td>
<td>0046</td>
<td>3.47</td>
<td>6.95</td>
<td>24.1</td>
</tr>
<tr>
<td>Bouerrera succulenta</td>
<td>2666</td>
<td>68</td>
<td>90.7</td>
<td>0048</td>
<td>4.39</td>
<td>4.76</td>
<td>20.9</td>
</tr>
<tr>
<td>Ocotea coriacea</td>
<td>3082</td>
<td>60</td>
<td>80</td>
<td>0056</td>
<td>4.48</td>
<td>3.93</td>
<td>17.6</td>
</tr>
<tr>
<td>Pimenta racemosa</td>
<td>2173</td>
<td>37</td>
<td>49.3</td>
<td>0039</td>
<td>1.95</td>
<td>8.68</td>
<td>16.9</td>
</tr>
<tr>
<td>Tabebuia heterophylla</td>
<td>513</td>
<td>42</td>
<td>56</td>
<td>0009</td>
<td>0.52</td>
<td>19.74</td>
<td>10.3</td>
</tr>
<tr>
<td>Coccoloba swartzii</td>
<td>1006</td>
<td>48</td>
<td>64</td>
<td>0017</td>
<td>1.17</td>
<td>8.42</td>
<td>9.8</td>
</tr>
</tbody>
</table>

$N_b$: number of individuals; $f_a$: absolute frequency; $f_r$ =$f_a/75$ stations (relative frequency); $Id = f_r \times$ density (distribution index); $ID$ = Basal area $\times$ Id (dominance index) and total survey area: 55,050 m.

Table 2b. Ecological and dynamic profiles of the dominant species of the lower layer (Martinique, figure 1b).

<table>
<thead>
<tr>
<th>Species</th>
<th>FR</th>
<th>FRM</th>
<th>FAB</th>
<th>FABM</th>
<th>FPS</th>
<th>FSJS</th>
<th>FSS</th>
<th>FSST</th>
<th>FSPC</th>
<th>FSC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pisonia fragrans</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td>+</td>
<td>+</td>
<td>++</td>
</tr>
<tr>
<td>Bursera simaruba</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td>++</td>
</tr>
<tr>
<td>Lonchocarpus violaceus</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>++</td>
</tr>
<tr>
<td>Maytenus laevigata</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td>+++</td>
</tr>
<tr>
<td>Bouerrera succulenta</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>++</td>
</tr>
<tr>
<td>Ocotea coriacea</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>++</td>
</tr>
<tr>
<td>Pimenta racemosa</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Tabebuia heterophylla</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Coccoloba swartzii</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>++++</td>
<td>++++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+</td>
</tr>
</tbody>
</table>


Table 2c. Temperaments and dissemination modes of the dominant species of the lower layer (Martinique, figure 1b).

<table>
<thead>
<tr>
<th>Species</th>
<th>HP</th>
<th>HS</th>
<th>HTS</th>
<th>HeSc</th>
<th>S</th>
<th>HémSc</th>
<th>VDP</th>
<th>PSEM</th>
<th>C</th>
<th>D</th>
<th>DE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pisonia fragrans</td>
<td>+++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>ORNI</td>
<td>S1</td>
<td>NC</td>
<td>G</td>
<td>G</td>
<td>G</td>
<td></td>
</tr>
<tr>
<td>Bursera simaruba</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>ORNI</td>
<td>S2</td>
<td>T</td>
<td>M</td>
<td>G</td>
<td>G</td>
<td></td>
</tr>
<tr>
<td>Lonchocarpus violaceus</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td>ANEMO</td>
<td>S1</td>
<td>T</td>
<td>M</td>
<td>M</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maytenus laevigata</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>+++</td>
<td>ORNI</td>
<td>S1</td>
<td>NC</td>
<td>G</td>
<td>M</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bouerrera succulenta</td>
<td>+++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>ORNI</td>
<td>S3</td>
<td>T</td>
<td>G</td>
<td>M</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ocotea coriacea</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>ORNI</td>
<td>S2</td>
<td>NC</td>
<td>G</td>
<td>M</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pimenta racemosa</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>ORNI</td>
<td>S1</td>
<td>NC</td>
<td>M</td>
<td>M</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tabebuia heterophylla</td>
<td>+++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>ANEMO</td>
<td>S1</td>
<td>T</td>
<td>F</td>
<td>M</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coccoloba swartzii</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>ORNI</td>
<td>S1</td>
<td>P</td>
<td>M</td>
<td>F</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

HP: Primary Heliophile; HS: Secondary Heliophile; HTS: Heliophile of Sylvan Gaps; HeSc: HelioSciaphile; S: Sciaphile; HémSc: hemisciaphile; +: importance of descriptor; VDP: Potential Dissemination Vector (BARO: Barochory; ORNI: Ornithochory; ZOOCH: Zoodochy; ANEMO: Anémochory); PSEM: Stratigraphique Position in Maximal Expansion (S1: Higher layer; S2: Middle layer, S3: Lower layer); C: deciduousness (T: Total; NC: Non-deciduous; P: partial); D: Distribution; DE: Ecological Dominance; G: Strong; M: Average; F: Weak and TF: Very Weak.
tions. It mobilises a part of the global floristic potential in the form of specific phytocenoses which result in the particular history of a plant cover unit [36].

The entire ecosystem will generate settling and expansion sites that are in perpetual mutation [37]. Fundamental units, the establishment and expansion sites, correspond to smaller analysable systems and are typical of spatio-temporal configurations of the phytocenosisis considered. They are at the base of the multiple forms of organisation in the vegetation. These sites present a large spatio-temporal diversity throughout the archipelago. This fact reveals the real problem for biogeographers and ecologists when trying to find a framework for ecosystemic analysis common to the whole of the Lesser Antilles.

Thus, the biological specifics of the species will confer on them a particular dynamic profile and will define, in space and time, their capacity to implant themselves in introductory and expansion sites. In addition, this dynamic profile will condition their assignment to a sub-group of floristic potential. Concerning biological specifics we can mention more particularly the physiological parameters such as growth differential, nutritional kinetics and the efficiency of use of abiotic elements, notably light energy, are determining factors in the intra- and inter-specific competition. The level of selectivity of taxa is increased by the historical relationship between human beings and the vegetation in terms of soil use (variable in frequency and in intensity). We can summarise the concurrent elements as follows:

- the floristic potential guaranteeing the diversity of the candidates for the occupation of biotopes freed during a possible disturbance;
- the floristic composition of the zone under consideration;
- the structure of the formation as seen from the point of view of architectural complexity as logically related to its position on the gradient dynamic;
- the eco-climatic characteristics of systems stemming from degradation (gaps or windfalls) and
- the dynamic of physical and biotic vectors concerning the dispersal of diaspores (tables 2a, 2b and 2c).

All these elements will contribute to the expression of particular traits of vegetal communities (structural, floristic and physionomic). Regeneration depends on natural or anthropoge-netic degradations, which affect floristic potential differently [38]. The spatio-temporal heterogeneity of the disturbances leads to a group of vegetation successions [5]. Moreover, each chronosequence is represented by vegetal units of floristic composition and well-defined organisation.

As the disturbances cause the emergence of dominant physical conditions, they mobilise the various floristic potentials which act either alone or together to ‘heal’ the opening thus created. For a large majority of data collecting stations of the lower layer, found at varying degrees in the extra-sylvan succession cycles, it seems that the vegetative and advective potentials are the most active. Conversely, the edaphic seminal potential takes on vital importance when degradation is severe.

Another set of factors affect the stations colonised by forest communities, namely intra-sylvan successional cycles. Indeed, beginning in the secondary structured forest phase, gaps or windfalls restore the vegetational cover, even if the healing mechanisms are still operating in the most stable matrix. In this case, the exterior potential (vegetative potential or peripheral potential) is preponderant for gaps of small diameters. The latter are rapidly restored by the matrix species (heliosciaphile⁹). The morphologic expansion of the heliosciaphiles is caused by successive small gaps.¹⁰ Generally, new development is accompanied by a new phase of transitory stagnation. The mechanism allows these taxa to reach the canopy.
When the ‘wound’ in the canopy is large, the advective potential becomes superior to the others. From the edge to the centre of the windfall, taxa are found which are increasingly heliophilous. To a lesser degree, the advective potential can be added to the edaphic seminal potential conditioned by modifications in the micro-relief of the soil (localised destruction of the radicular tissue) when trees fall. Generally in large windfalls, the disturbances of the edaphic system can be excessive. In addition, if the ecological conditions are of the sort that initiate resuscitation of the diaspores, the edaphic seminal potential will be vitally important. Over the course of evolution of the vegetal cover in a progressive succession, there are spectral variations of the light which result from the organisational level of the vegetal communities (their stratification). From shrubs to secondary advanced forests pre-climax or climax, the ecoclimatic conditions are decreasingly unfavourable to the action of the edaphic seminal potential (figures 5a and 5b). In the heliosciaphile sylvan matrix and also in gaps of small and medium dimensions, there is random seed germination (diaspores).

These temporal dynamics can be used as global and theoretical descriptive models, proceeding from natural observations and from some ecological experiments (figures 5a and 5b). Nevertheless, they relate to the vegetation of the Lesser Antilles. The principal traits of this vegetal succession are united by physisonomic, landscape and ecosystemic aspects and at the same time separated by the diversity of floristic potentials and vegetal combinations (or habitat associations) generally distinguished in the Caribbean islands. In the absence of significant wind in the Lesser Antilles, the vegetal cover is highly structured and influenced by the separation of the diaspores, which is significant in the vegetation of the forest. This separation may lead to the establishment of the juvenile stage of the vegetal cover in the matrix and the invasion of the secondary forest. In the case of the Greater Antilles, such a separation is occasionally disturbed by the wind, and therefore, the species and functional composition of the vegetal cover is more likely to be determined by the climatic conditions (climatic separation of diaspores).

The vegetation of the Lesser Antilles

Figure 5a. Different aspects of the floristic dynamics.
arrangements). The large variety of floristic compositions reveals the human and natural histories of these islands. In fact, the vegetal succession requires transformations that are floristic, biocenotic and ecological as well as structural and architectural which occur between the successional stages, but also within them.

4.1. The intra-phase dynamic

4.1.1. General considerations

Dynamic phases are made up of little successions termed as intra-phase dynamic cycles, defined by specific criteria such as vertical and horizontal configuration, floristic composition, dominant biological types and the global physiognomy of the communities. The latter modify the factors of the macroclimate, thereby creating microclimatic particularities defining the characteristics of installation sites or nano-systems.

The floristic potential linked to the sylvan types can be divided into several sub-groups or floristic sub-potentials corresponding to the multiple dynamic phases (figures 5a and 5b). For a dynamic phase, the species of the floristic sub-potential have dynamic profiles which are overall identical. Differences between them are not significant enough to allow them to be placed in a different phase. Even so, in the phase under consideration, the differences are sufficient for there to be a hierarchy in the order of appearance and regression of the vegetal associations. Therefore, for an implanting cortege of species of the same

Figure 5b. The gradient dynamic.

Philippe JOSEPH, GEODE Caraïbe, UAG
dynamic profile, the efficiency of the arrival in the installation sites and the greater germinal efficiency will be decisive and will create, on a fairly short time scale, a number of small successive settling and expansion phases. Thus, at the end of this intra-phase succession, the state of maturity is reached when the most specialised association for the defined dynamic phase is ecologically dominant, high density and maximum biomass. It is physiognomically identifiable and constitutes a particular landscape unit. From that point on, the conditions are ripe for the subsequent phase to begin.

During the process of internal succession, the characteristics of settling and expansion sites vary. Nevertheless, they keep their factorial identity which specifies their affiliation with the dynamic phase under consideration. The modifications, though small, create selections in the formation of species – in the floristic sub-potential – belonging to the same dynamic phase. This selectivity, based on infinitesimal differences, is the motor of the intra-phase successional processes. It seems, however, that these processes come from mechanisms which are identical to those that govern the inter-phase dynamics. Indeed, the inter-phase differences, unlike those which exist between the chronosequences of the intra-phase dynamic, are linked to the phenology of the species of sub-groups of the floristic potential, to the great mesological specificity of establishment and expansion sites of the dynamic phases and finally to a time scale punctuated by much longer units. In each dynamic stage, all of that translates into a specific complexity which is easily defined by the morphology of phytocenoses. This complexity continually increases in the framework of a progressive succession.

4.1.2. Actual case: the example of the shrub and bush phases (lower layer)

Given the field data, the gradient dynamics are subdivided into 10 phases which are structurally, physiognomically and functionally identifiable (figures 5a and 5b). In the case of a progressive succession, the shrub phase supplants the graminaceous phase which has reached its maximum level of organisation. When the settling conditions are achieved in the graminaceous cover, by the existence of a few adequate establishment and expansion sites, shrubs implant themselves marginally. Through localised regression of the grass structure, they create conditions for installation of other shrubs of the same ecology which make up the first population of the ligneous colonisation. This begins the shrub phase (figure 6).

At this phase of succession, the vegetation population mainly comprises grasses, associated with a small number of shrubs. Progressively, the biomass of the ligneous population grows and favours the installation of shrubs which have a higher ecological efficiency for the new characteristics of the installation and expansion sites. When all of the ligneous species belonging to this shrub phase (phase number 1) are selected, the transformations are mostly morphological. This is the expansion phase of the shrub phase.

When the highest degree of organisation is reached, the establishment sites are no longer appropriate for shrub taxa. This ultimate state, where all the species of the sub-group of the floristic potential associated with this formation have expressed themselves in waves, corresponds to the biocenotic maturity of this phase (figure 6). In fact, this phenomenon is identified with a process of senescence. This shows that a successional phase, definable by floristic, architectural and functional criteria, may not be reduced to a mere set position on the gradient dynamic.

Unlike mechanisms allowing the transition of one phase to another, the intra-phase dynamic is much faster. It determines the great variety of floristic compositions and
Initiation State

1 Chamaecrista nictitans, 2 Croton guiltingui, 3 and 4 Pavonia spinifex.

Expansion State

1 et 2 Randia aculeata, 3 Chamaecrista nictitans, 4 Croton guiltingui, 5 Myrcia citrifolia, 6 Pavonia spinifex, 7 Eugenia confusa, 8 Chamaecrista nictitans, 9 Erythroxylon havanense, 10 Croton guiltingui, 11 Croton flavens, 12 Pavonia spinifex, 13 Chamaecrista nictitans, 14 Calliandra tergemina, 15 Chamaecrista nictitans, 16 Laetia thamnia, 17 Pavonia spinifex, 18 Croton guiltingui, 19 Tabebuia heterophylla, 20 Croton bixoide, 21 Chamaecrista nictitans, 22 Haematoxylon campechianum, 23 Croton guiltingui, 24 Eugenia lingustrina, 25 Acacia tamarindifolia, 26 Pavonia spinifex, 27 Eugenia cortada, 28 Rauwolfia viridis.

Mature State

1 Chamaecrista nictitans, 2 Eugenia confusa, 3 Erithalis fructicosa, 4 Erythroxylon havanense, 5 Laetia thamnia, 6 Croton hircinus, 7 Pavonia spinifex 8 Acacia muricata, 9 Croton bixoide, 10 Psionia suborbicula, 11 Randia aculeata, 12 Bourreria succulenta, 13 Calliandra tergemina, 14 Croton guiltingui, 15 Cordia martinicensis, 16 Myrcia citrifolia, 17 Bursera simaruba, 18 Erythroxylum havanense, 19 Haematoxylon campechianum, 20 Chamaecrista nictitans, 21 Eugenia cordata, 22 Eugenia monticola, 23 Croton flavens, 24 Pavonia spinifex, 25 Acacia tamarindifolia, 26 Randia aculeata, 27 Rauwolfia viridis, 28 Croton guiltingui, 29 Tabebuia heterophylla, 30 Eugenia ligustrina, 31 Leucaena leucocephala, 32 Chamaecrista nictitans, 33 Pithecellobium unguis-cati, 34 Eugenia ligustrina, 35 Schoepfia schreberi, 36 Pavonia spinifex, 37 Miconia laevigata.

Figure 6. Shrubs.
Figure 7. The bush formation.
introduces a higher degree of complexity into the analysis of these ecosystems. This intra-phase succession is effective in all the phases of our succession gradient (figure 6), although it is not easily visible. The intra-phase successional cycles can only be understood by diachronic study of the various communities and their multiple floristic combinations in bioclimatic conditions which are considered stable.

Irrespective of the successional processes (extra- or intra-sylvan), it is reasonable to say that a dynamic phase is subdivided into three main states namely initiation, expansion and mature.

When the shrub phase becomes mature, the ecological conditions, in terms of specificity of establishment sites, are favourable for the arrival of a few species of bushes which will constitute the beginning of bush formation (figure 7). Then, little successions will start, like those of the shrub. From the initiation state to the mature state, selection will appear through species which are progressively more specialised in this dynamic phase (the bush phase). The establishment sites will also undergo small modifications while continuing to welcome taxa of bush morpbo-types. Over the course of this intra-phase dynamic, the bush species will be selected according to their ecological demands. This is shown by the constancy of the physiognomy. Only a subtle and diachronic floristic analysis can allow one to perceive a succession in the very short times of the vegetal bush associations. The bush units become mature and carry in their structures, at a few sites, the necessary conditions for the implantation of species or groups of species of tree morpho-types. Initially these symbolise the pre-sylvan entity. Progressively, while reinforcing themselves qualitatively and quantitatively in species and in phytomass, they form the sylvan population in its multiple states of complexity.

5. Conclusion

The succession within and between the dynamic phases seems to proceed from ‘ecosystemic solidarity’ [39]. From the most regressive phase to the most evolved, the vegetal ecosystems organise increasingly complex factorial interactions [40]. This produces gradually more specific environmental conditions resulting in progressively more specialised sites of establishment. As the site progresses towards the sylvan phase, it hosts plant species [40]. The vegetation dynamic in its widest definition is extremely complex [41][42]. It is multidirectional, but the initial conditions and the various disturbances, whether natural or anthropogenic, favour only a few directions [43]. Associated with these are components of the floristic potential of the zone being studied, called sub-groups or floristic sub-potentials. The field of expression of the floristic potential allows the ecosystem to react to random events, either anthropogenic or natural, throughout its history because of the number of vegetal combinations possible. Nevertheless, these possibilities are finite and disturbances which are too severe can initiate irreversible processes of regression or regressive evolution that may result in partial or total disappearance of the vegetation. All this has to be seen in relation to the capacity for resilience of the vegetation of the Lesser Antilles which is not measurable today.

Notes

1. These results summarise abundant data collected over 15 years of observations and surveys, to which must be added the data of the researchers before us.
2. It is somewhere between 300 and 2000 m² and depends on the stage of evolution of the floristic survey station under consideration.

3. \( \text{Id} = f_r \times d \) \([f_r: \text{relative frequency} (f_a / \text{number of stations or quadrat in a transect}); d: \text{density} (\text{number of individuals/survey surface})]. \)

4. \( \text{ID} = \text{Id} \times A \) \([A: \text{basal area in m}^2]). \)

5. In this case, the dispersal vectors are the wind and animals (birds or more rarely certain chiroptera and mammals).

6. The pre-Columbian landscapes, and even those which existed over 4000 years ago, were the results of unique singular evolutionary processes.

7. This probability depends on the degree of organisation of the vegetal formations and consequently on their dynamic levels.

8. In fact, the ecological profile of the taxa gives them, for the different factors of the biotope, a unique aptitude generally called mesological or bioclimatic affinity, etc.

9. In the mature matrix, they are associated with sciaphile species.

10. During atmospheric disturbances (hurricanes and tropical storms), the broken branches also allow for the morphogenetic development of heliosciaphiles.

11. The diaspores of the large windfalls are sensitive to the intensity of photic energy and also to its spectral characteristics.

12. The small ecological differences are brought to the foreground by inference because the chosen protocol does not permit the measurement of their characteristics.

13. In fact, the grass phase is phase 1. After a succession of taxa of various ecological strategies, the formations reach maturity and in certain conditions permit the progressive implantation of shrubs, themselves of varying ecological profiles.

14. It is very plausible that the first shrubs implant themselves, in the graminaceae cover, in favour of discontinuities.

References


[31] Pardon, N., 1877, The island of Martinique from its discovery to the present day (Paris: Challamel).