



The Spatio-Temporal Interfaces within the Lesser Antilles Vegetation (The Example of the Island of Martinique)

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Received 21 February 2016; accepted 5 March 2016; published 10 March 2016

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Abstract

The temporal vegetation dynamics and its spatial distribution cause discontinuities, border areas, ecotones and ecosystem heterogeneities, in other words biocenotics which result in a multitude of shapes and organic combinations. These interfaces are added variations due to vertical stratification involving specific architectures and behaviours towards light. These “interface environments” represent a plurality of plant biodiversity aspects and therefore ecological profiles which form the basis of the resilience processes. In the Lesser Antilles, Man has increased community complexity by increasing the number of eco-units¹. As a result, the number of ecosystem interfaces increased so in some ways, he became the “architect” or “creator” of species biodiversity in the landscape through the ecosystem and the plant communities. Ultimately the current landscape is a mosaic of physiognomic units of unequal dimensions belonging to various successional stages. In the case of Martinique, we will discuss the complexity of the Lesser Antilles forest vegetation. The argument seeks to show its hierarchical organisation, the characteristics of its subsets and their spatial and temporal relationships.

Keywords

Lesser Antilles, Martinique, Vegetation, Forest Ecosystem, Biodiversity, Anthropization, Interface, Ecotone

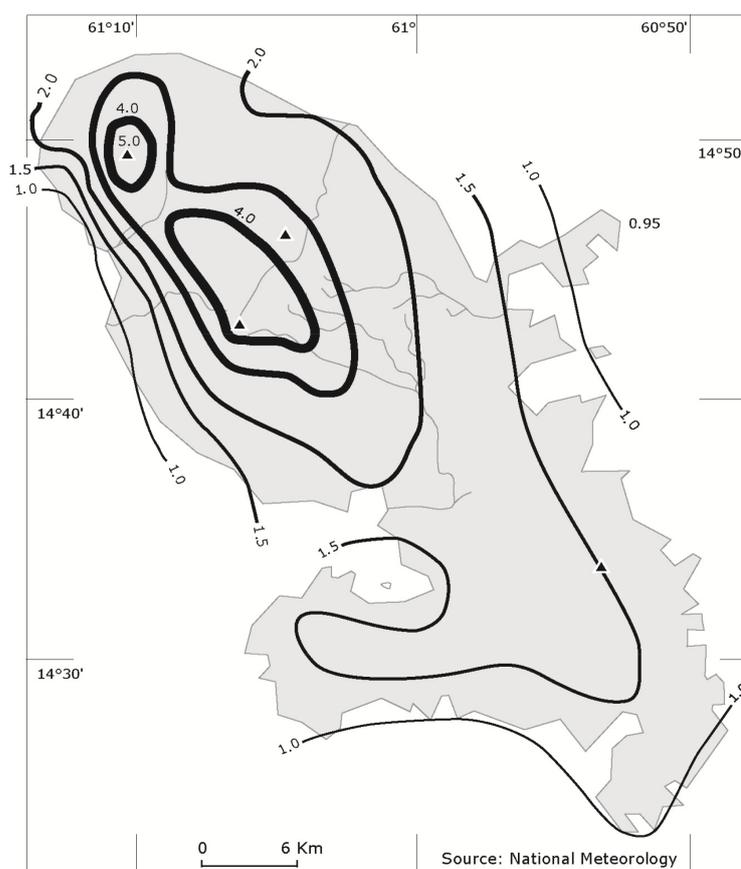
Subject Areas: Biodiversity, Biogeography, Ecology, Ecosystem Science, Environmental Sciences, Natural Geography, Plant Science

¹Eco-units are ecological units that reflect the factor characteristics of biotopes and are specified by preponderant groups and physiognomies.

1. Introduction

Despite the current landscape, characterised predominantly by herbaceous, shrub, and pre-forest units, the Lesser Antilles have forest ecosystem potentiality² [1]. One of the reference points of this archipelago's history is the passage from an "original" vegetation dominated by forest species to cultivated fields consisting of exogenous anthropophyte plants and regressive floristic units composed mainly of shrubs, small trees and native grasses. The mountainous islands create orographic rainfall which varies from the low areas to the top. This rainfall gradient, whose structure differs from one mountain side to another, can roughly be divided into four bioclimates resulting in four potential forest types depending on their subtypes and characteristics (Figure 1). These different forest ecosystems delimit the plant floors and are specified by plant species and combinations.

In the light of recent studies, it seems that in the prehistoric times of the Lesser Antilles, the various plant coverage had reached maximum structural and architectural complexity and their floristic units were composed of highly specialized species from an ecological point of view. The edge of the forest developed formations which were unique both at floristic and biocenotic level. These are ecosystem interfaces created by the spatial overlapping of adjacent ecosystems. Highly layered, these pre-Columbian forest groups had arrived at the end of their evolution and had acquired a certain degree of autonomy from the macroclimate. In fact the exchange surfaces which constituted the crowns of the upper, middle and lower tree strata insulated the intra-forest environment from external fluctuations [2]-[4]. In the past these stratigraphic interfaces between the lower forest environment and the general climate favoured the demographic development of species which were highly specialized especially in their behaviour towards light energy [5]-[8].



Dry bioclimate : annual rain fall < 1.5 m.
 Middle-humid bioclimate : annual rain fall between 1.5 m and 2.5 m.
 Humid bioclimate : annual rain fall between 2.5 m and 4 m.
 Highly-humid bioclimate : annual rain fall > 4 m.

Figure 1. The different bioclimate types of Martinique (P. JOSEPH modified).

²The term of plant succession in this part of the world has resulted in the establishment of forest formations.

The present vegetation is seen as a mosaic of different temporal phases [9]-[12]. All the temporal sequences of the vegetation successions are present and correspond to transitional stages with regard to the climax³ [13] [14]. They can be considered successional intermediaries and represent just as many temporal interfaces [15] [16].

Ultimately, the ecotones (borders) between the large floristic groups, the multiple dynamic stages and their various strata create the plant coverage of the Lesser Antilles with its complex spatio-temporal interfaces [17]-[21]. Despite their small size, they are part of the amazing floristic diversity of the Lesser Antilles, which represent one of the 24 global biodiversity *hot-spots*: that of the Caribbean. For our case study, we will use Martinique's vegetation as reference because this island is subject to very strong human pressure, but nevertheless contains a large number of plant species and communities.

2. The General Context

Located at 14°30' latitude North and 61° longitude West, Martinique occupies a central position in the archipelago. It extends over 1090 km² (65 km long and 35 km at its widest) and has openings as the Bay of Fort-de-France and Robert Bay. It is a rugged island. Mount Pelée (1397 m), the Morne Jacob (884 m), the Pitons du Carbet whose peaks reach higher than 1000 m are the main mountain ranges. In the southern regions, the old volcano-sedimentary and volcanic complexes have a significantly softer terrain: the Vauclin Mountain is the highest one. There are also smaller mountains locally called hills, between which we see plains with various surfaces. The whole gives us a very varied landscape with slopes ranging from 2% to 50% while the average is around 20%. Therefore the great diversity of the topographical aspects represents an important parameter in the establishment of plant communities.

The general climate of Martinique is characterised by two periods of varying duration: one accompanied by a significant decrease in rainfall (Lent), one characterised by a flow of more humid East winds (Wintering). The winter rains are increased by the orography and their quantity varies from the coast at the top of the mountains. All the bioclimatic and forest floors in the Lesser Antilles are represented. Today almost all vegetation is secondary. Due to human impact over time the forest has become "insular" and occupies barely 20% of the territory. Consisting primarily of shrub land, shrub and pre-forest communities, the contemporary vegetation is called regressive. There are few advanced, pre-climax and climax secondary units. Generally, the current flora is typical of open environments and is dominated by heliophile, semi-heliophile and semi-ombrophile species. Relic areas still allow species to reach the optimal phases of dynamic plant development (ombrophile and helio-ombrophile species) to reach all of their pheno-phases (phases of their life cycle) are located in remote areas of the foothills of the island's North mountains [10]. However, within the littoral and the inland forests (in the centre and South), there are marginal units with secondary stage late, pre-climax and climax species [10] [22]. By inference, all these remaining areas allow the reconstruction of the precolonial landscapes. They belong to the ombrophile tropical sub-montane type and the evergreen tropical seasonal type as well as to their tropical seasonal ombro-evergreen ecotone (Figures 2-4).

3. Method

Apart from the climate aspect, the following is an exercise in synthesis using data from the scientific literature. Indeed, the data of our predecessors such as [23]-[26], and as well as the recent works [1] [10] [11] [27]-[31], have allowed us to describe Martinique's structural and functional vegetation units. These data also allow us to assert that the observable physiognomic units in the current vegetation landscape represent as many degrees of biocenotic complexity, in other words dynamic stages [32] [33]. In these studies, the structural, architectural and spatiotemporal dynamic floristic descriptors taken into account regarding the conventional methodologies of botany, biogeography and ecology distinctively refer to autecology, synecology⁴ and chronology [34]-[38]. The floristic data were supplemented by measuring the climatic parameters. In fact, weather devices were installed in the open (witness) and within structured, pre-forest and shrub forest formations. While incomplete, the obtained data helped to highlight the effect of the exchange surfaces formed by the peaks of various the strata, on the macro-climate factors such as temperature, humidity and evaporation [39]-[41].

³It has a forest nature as in many regions of the intertropical zone.

⁴The autecology and synecology correspond respectively to the ecology of the species and communities they form.

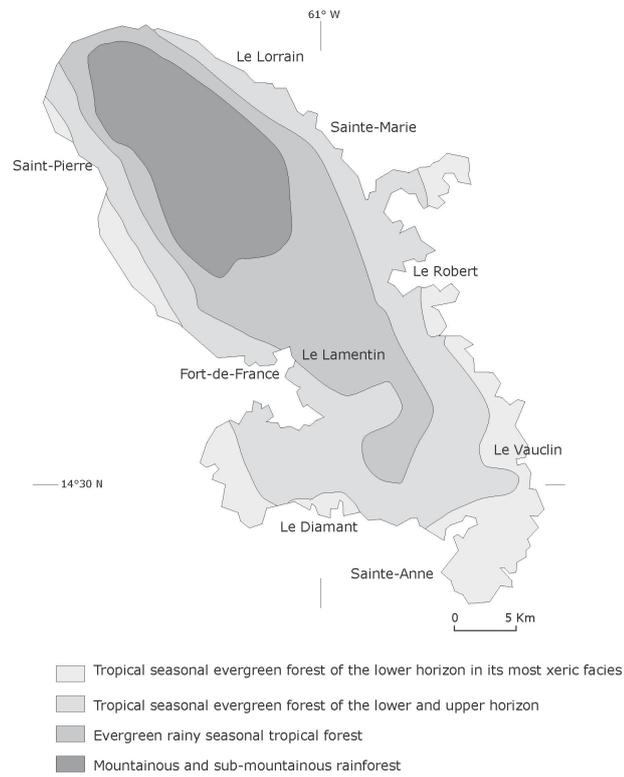


Figure 2. Martinique's vegetation in pre-Columbian times (Source: P. JOSEPH).

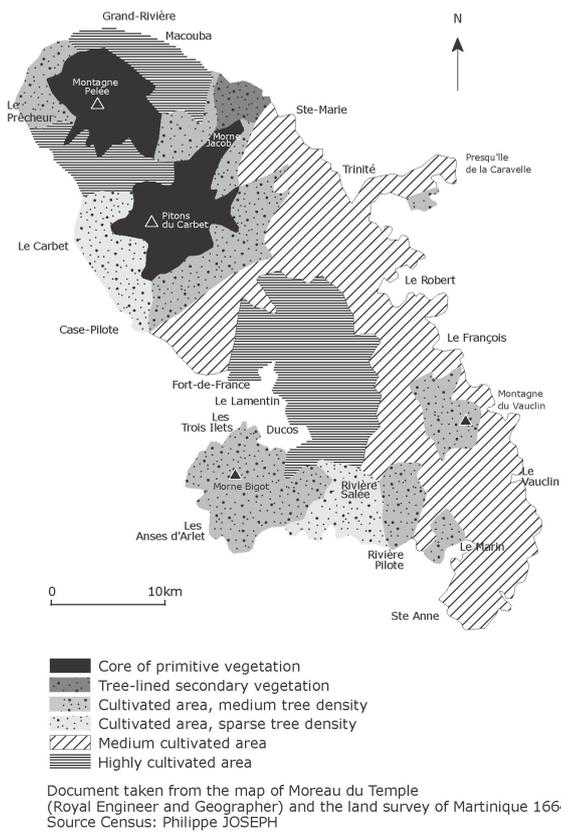


Figure 3. The vegetation state and structuring circa 1770 (Source: P. JOSEPH).

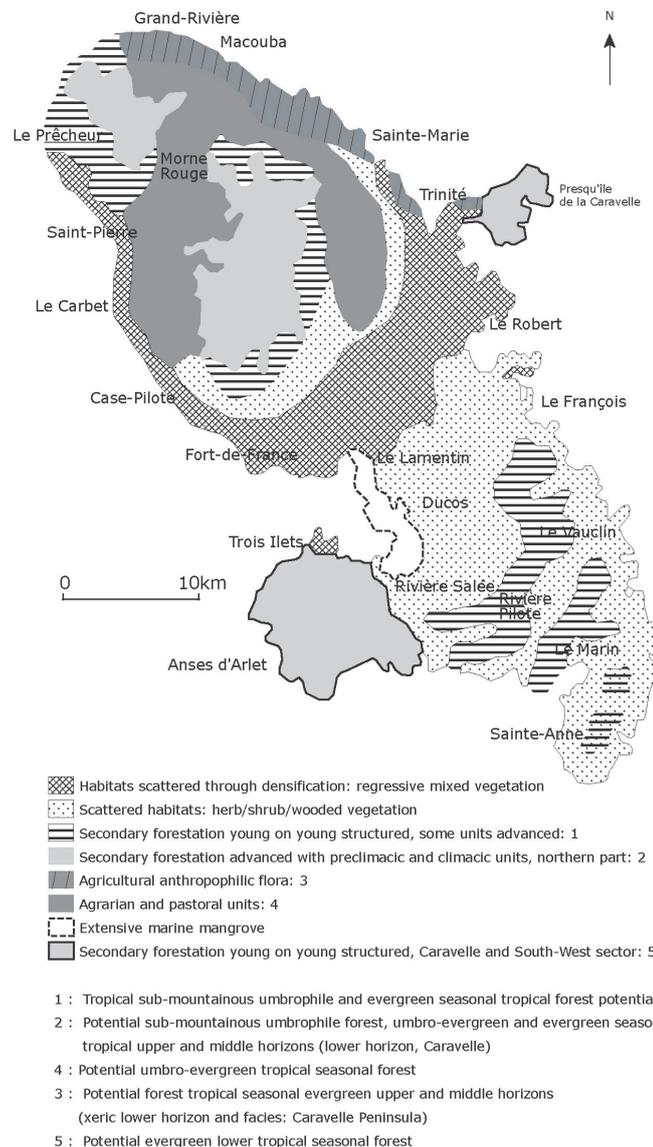


Figure 4. The present landscape (Martinique/ Source: P. JOSEPH).

4. Results and Interpretations: General Synthesis

4.1. Some Data on Ecosystem Change

It is quite plausible that prior to colonisation Martinique’s vegetation was almost fully primitive and of the forest type [42]-[48]. Current data seem to confirm this hypothesis [22]. All the pre-Columbian forests of Martinique, like those of the other Lesser Antilles, consisted of pre-climax and climax floristic units. Unlike Mesoamerica and more widely the tropical America [49] the impact of the Native American people on the original forest ecosystems was very low. During the first contacts, the chroniclers described physiognomies and landscapes resulting from various combinations of highly specialized species in the final stages of vegetation dynamics [50]. In reality the pre-Columbian vegetation was divided into three plant floors at the end of their evolution. At the time the inhabitants practiced marginal burnt land agriculture at the lower level. Sometimes they ventured into remote areas to find and cut white gum trees (*Dacryodes excelsa*-Burseraceae) of important size which they shaped on the spot. Transported to the villages on the coast, they received the final touches before the boat was launched. These boats could carry fifty men and allowed long voyages in the Caribbean Sea, between the Islands and the Mainland.

From sea level to the peaks we schematically see [10] [22] [51]: the evergreen seasonal tropical forest of the lower horizon which exhibits xeric features, the tropical seasonal evergreen forest, the sub-montane tropical ombrophile forest and the tropical montane ombrophile forest (**Figure 2**). At large scale these forest formations formed swaths which corresponded to the sub-humid dry, sub-humid damp, wet and hyper-humid bioclimatic areas (**Figure 1**). The plant floors were spatially solidary and their mass effect increased their resistance to severe weather (storms, hurricanes). The species space transfers were effective between these different floors. In fact, from their main areas the middle and upper species colonized the installation and expansion sites of certain formations of the lower floor and developed very low populations [10].

Nowadays, apart from the forest formations that cover the foothills of the mountains and a few areas of their lower third, everywhere the vegetation is regressive and dominated by pre-forest, shrub and herbaceous species. Due to various anthropization means, the present biocenotic net is dense, formed largely of secondary ecological units whose age, structure, floristic composition, physiognomy and dynamic stages are as varied as they are numerous. The units of this floristic mosaic generate many contact areas where it is difficult to create ecological maps even at site level.

4.2. The Contact Areas between the Plant Floors: Forest Ecotones

Of course, logically, the interfaces between adjacent forest types and their horizons do exist [52]. These interfaces reach to the edge of the seasonal evergreen tropical and tropical ombrophile forests as well as that of the sub-montane ombrophile and montane tropical forests. They correspond respectively to the ombro-evergreen seasonal and ombro-ombrophile sub-montane forest. Although more difficult to identify, these ecosystem interfaces are also effective between the horizons of forest types: in particular between the lower and middle horizons (horizon type) of the tropical seasonal evergreen forest. Today, there are few examples of ecosystem continuum allowing us to precisely explore the forest ecotones. We were able to describe their global ecological characteristics only by using synchronic analysis⁵.

4.2.1. The Tiering Generates Spatial Interfaces

[25] proposed the forest xero-mesophilic and hygro-mesophilic ecotones. While improving the floral aspects, [30] used the same concepts in his doctoral thesis and they are still used nowadays. In the early 90s, in his work on the forest formations of the northeast of Martinique, [22] adapted the UNESCO nomenclature to the local context. In the light of analyses of approximately 300 floristic survey sites, he identified the semi-deciduous evergreen seasonal ecotone and the seasonal ombrophile evergreen ecotone. To these forest contact areas we must add those which signal the passage from the sub-montane ombrophile forest to the montane ombrophile forest: the ombro-ombrophile sub-montane ecotone (Philippe JOSEPH, personal unpublished data). Previous designations are ecosystem equivalents corresponding to two distinct classifications, one old and regional designed by [25] and revisited by [30], the other one defined by [51], fairly recent and universal in its outlines. Despite the difficulties of small scale use, the UNESCO forest classification enables comparisons. We have increased the relevance of the ecosystem description by adding the slope, the floristic potentiality and the stage of development [10] (**Figure 5, Table 1**). While we can prove the existence of the seasonal ombro-evergreen ecotone, we cannot say the same for the semi-deciduous - evergreen tropical seasonal ecotone. In fact, in the Lesser Antilles, the existence of this potential semi-deciduous forest type [31] in the tropical dry season has not been demonstrated, not even in the low islands such as the Grande-Terre of Guadeloupe, Marie-Galante, les Saintes, la Desirade, Saint-Barthelemy, etc. And according to the new data [10] [22] the current formations are regressive forms of the climax tropical seasonal evergreen forest which from a phenological as well as a physiognomic point of view is related to the semi-deciduous forest during the tropical dry season as defined by UNESCO. The woody species of xerophytic environments are well represented [for example *Eugenia confusa* (Myrtaceae) and *Randia aculeata* (Rubiaceae)] and 50% of them are deciduous [10] [22].

4.2.2. The General Characteristics of the Tropical Seasonal Ombrophile Evergreen Forest

Unlike other ecotones, the tropical seasonal ombrophile evergreen forest is spatially well represented, both in its climax phase (**Figure 2**) and in its regression stage (**Figure 3**). Its floristic, biocenotic and structural identification

⁵However, differences in levels of development and therefore complexity due to human impact can distort the ecological characterization of these ecotones.

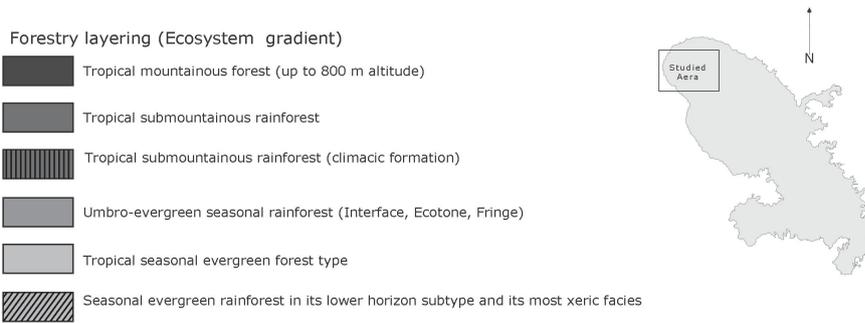
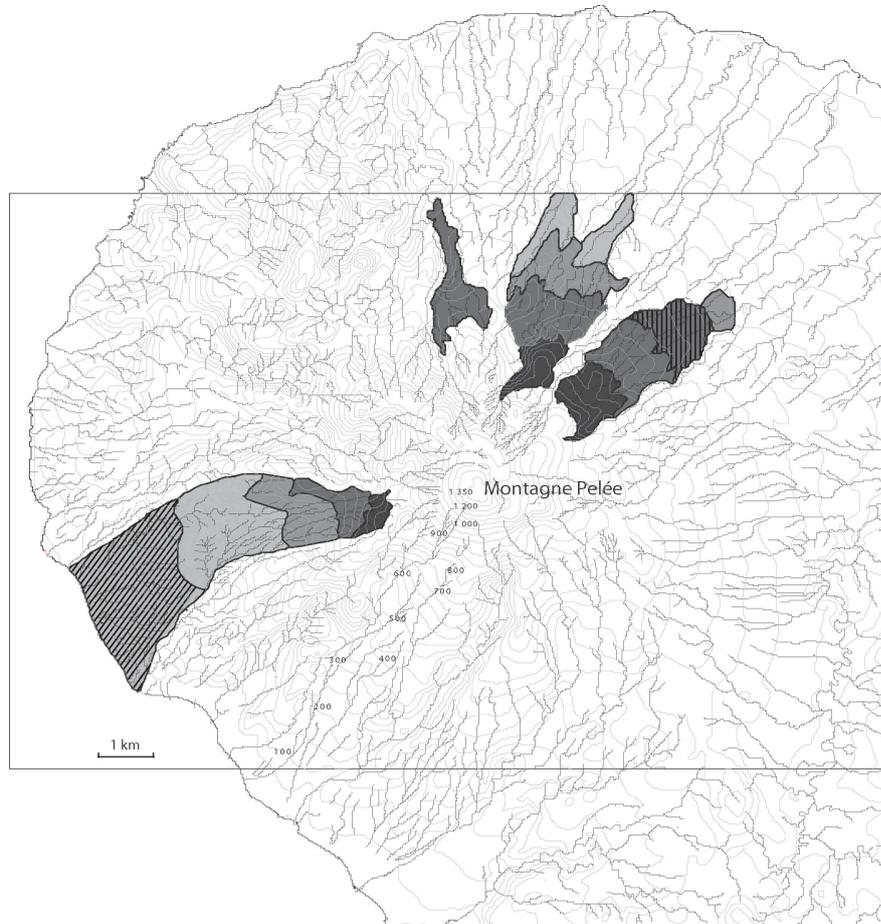


Figure 5. Ecosystem gradient and ecotones (the example of Martinique/Source: P. JOSEPH).

Table 1. The main species of the late seasonal ombro-evergreen forests in Northern Martinique (Source: P. JOSEPH).

Taxa/families	Vernacular names	Qualitative prevalence	Ecological strategy	Dynamic stages	Ecosystem-based affinity
<i>Guatteria caribaea</i>	Corossol grand bois	R	M	FST, FPC, CF	OBS
<i>Oxandra laurifolia</i>	Bois de lan	TR	M	FT, FPC, CF	Ecotone OBS - SS
<i>Tabernaemontana citrifolia</i>	Milkwood	R	Tr	FS	OBS
<i>Prestoea montana</i>	Palm	TAB	M & Ch	FS, FST	OBS
<i>Quararibea turbinata</i>	Lele tree	TAB	M & Ch	FS, FST	SS
<i>Hirtella triandra</i>	Hairy Zicaque	TR	M	FST, FPC, CF	OBS
<i>Tapura latifolia</i>	Bois-cote	R	M	FPC, CF	OBS
<i>Sloanea caribaea</i>	Acomat boucan	R	M	FPC, CF	OBS

Continued

<i>Sloanea dentata</i>	Large leaf chestnut	TAB	M	FST, FPC, CF	OBS
<i>Sloanea massoni</i>	Small leaf chestnut	R	M	FST, FPC, CF	OBS
<i>Erythroxylum squamatum</i>	Red seeds	R	M & Ch	FS	OBS
<i>Sapium caribaeum</i>	Glue tree	AB	M & Ch	FS	OBS
<i>Dussia martinicensis</i>	Bois la gamelle	AB	M & Ch	FS	OBS
<i>Lonchocarpus pentaphyllus</i>	Savonette grand bois	AR	CH	FS	OBS
<i>Ormosia monosperma</i>	Red Caconnier	AB	M	FS, FST	SS
<i>Inga ingoides</i>	Hairy sweet peas	R	Ch	FS	OBS
<i>Casearia decandra</i>	Egg yolk	R	Ch	FS	SS
<i>Homalium racemosum</i>	Hybrid Acomat	TR	Ch	FS, FST	PEMS
<i>Aniba bracteata</i>	Yellow Laurel	TAB	M	FS, FST	OBS
<i>Ocotea cernua</i>	Isabelle Laurel	R	M & Ch	FS, FST	SS
<i>Ocotea dominicana</i>	Okra Laurel	TR	Ch	FS	SS
<i>Ocotea leucoxydon</i>	Fine Laurel	TAB	M	FPC, CF	OBS
<i>Ocotea martinicensis</i>	Laurier-root	R	M	FS, FST	SS
<i>Ocotea patens</i>	Gros grain laurel	R	Ch	FS	OBS
<i>Cinnamomum elongatum</i>	Cinnamon Laurel	R	Ch	FS, FST	PEMS
<i>Talauma dodecapetala</i>	Pine tree	TR	M	FPC, CF	OBS
<i>Guarea glabra</i>	Gun tree	TR	M	FPC, CF	SS
<i>Guarea macrophylla</i>	Gun tree	TAB	M	FPC, CF	Ecotone OBS - SS
<i>Trichilia pallida</i>	Black chestnut	R	M & Ch	FS	SS
<i>Ficus americana</i>	The small leaf fig tree	TR	CH	FS	OBS
<i>Ficus insipida</i>	Agouti Fig tree	TAB	M & Ch	FS, FST	OBS
<i>Stylogyne canaliculata</i>	Bois-petite chique	AR	M	FST, FPC, CF	OBS
<i>Eugenia gregii</i>	Ash tree	R	M	FS, FST, FPC	SS
<i>Eugenia pseudopsidium</i>	Hybrid guava	R	M & Ch	FS, FST	SS
<i>Myrcia fallax</i>	Hybrid guava	R	M & Ch	FS, FST	SS
<i>Plinia pinnata</i>	Nutmeg tree	R	M	FS, FST	OBS
<i>Pisonia fragrans</i>	Mapou	TR	Ch	FS	SS
<i>Piper reticulatum</i>	Rat tail	AC	Ch	FS	OBS
<i>Heisteria coccinea</i>	Partridge tree	R	M	FS, FST, FPC	OBS
<i>Cassipourea guyanensis</i>	Garlic tree	TR	M	FS, FST	SS
<i>Chimarrhis cymosa</i>	River tree	TAB	M	FS, FST, FPC	OBS
<i>Faramia occidentalis</i>	Arrow tree	TR	M & Ch	FS, FST	SS
<i>Ixora ferrea</i>	Coffee-tree	R	M & Ch	FS, FST	SS
<i>Psychotria mapourioides</i>	Coffee-tree	R	Ch	FS	OBS
<i>Psychotria tenuifolia</i>	Brown Coffee	R	Ch	FS	OBS
<i>Zanthoxylum caribaeum</i>	White pine	TR	Ch	FS	SS
<i>Chrysophyllum argenteum</i>	Petit boui	TR	M	FS, FST, FPC	SS
<i>Micropholis guyanensis</i>	Golden leaves	TR	M	FST, FPC, CF	OBS
<i>Pouteria multiflora</i>	Gingerbread	R	M	FST, FPC, CF	OBS
<i>Pouteria semecarpifolia</i>	Contrevent	R	M	FST, FPC, CF	OBS
<i>Simarouba amara</i>	White wood	AR	M & Ch	FS, FST	OBS
<i>Cestrum laurifolium</i>	Forest Jasmine	AR	Ch	FS	OBS
<i>Sterculia caribaea</i>	Machot-pig	AR	M	FS, FST	OBS
<i>Philodendron scandens</i>	Siguine (epiphyte)		M	FS, FST, FPC, CF	OBS
<i>Amphilophium paniculatum</i>	Boat vine (vine)		M	FS, FST, FPC, CF	Ecotone OBS - SS
<i>Macfadyena unguis-cati</i>	Cat claw (vine)		M	FS, FST, FPC, CF	Ecotone OBS - SS
<i>Petrea kohautiana</i>	Great vine (vine)		Ch	FS, FST	SS

R: Rare; TR: Very Rare; AR: fairly rare; TAB: Very abundant; AB: abundant; AC: Fairly common; M: Forest Matrix; Ch: Chablis; FS: Secondary Forest; FST: Late or advanced Secondary Forest; FPC: Pre-climax forest; CF: Climax forest; OBS: Sub-mountain ombrophile; SS: Evergreen seasonal.

criteria are also very specific. It is a contact environment where the humid and sub-humid wet bioclimates overlap and it also contains the vegetation of the lower horizon of the sub-montane ombrophile forest and that of the upper horizon of the tropical seasonal evergreen forest (Figure 1 & Figure 2). Actually like all ecotones, this group offers a partial mix of both forest types (Table 1). Among the dominant climax or sub-climax species we mention *Sloanea dentata* (Big leaf Chestnut) and the *Chimarrhis cymosa* (River tree) for the sub-montane ombrophile forest, *Ocotea leucoxylon* (Fine laurier) and *Ormosia monosperma* (Caconnier) for the seasonal evergreen forest [22]. The ecological forest edge species are joined by others that characterize the ecotone. They are few in number, nevertheless they are indicators of the transition between two bioclimatic floors (between two plant floors), in this case the middle and lower floor. *Cherimolia ternatensis* (Devil tree), *Guarea marophylla* (the gun tree), *Quararibea turbinata* (the lélé tree) and *Stylogyne canalicuta* (bois petite chique) are among the most significant. The latter taxon is a relevant bio-indicator because it is inseparable from the climax. Vines, herbs and epiphytic or terrestrial ferns also exhibit the same interference of ombrophile and evergreen taxa. Indeed, the typical vines of the seasonal evergreen forests, such as *Amphilophium paniculatum* (the boat vine), *Macfadyena unguis-cati* (the cat claw vine) and *Petrea kohautiana* (big vine), those of the sub-montane ombrophile forests such as *Marcgavia umbellata* (the josé tree) and the *Philodendron scandens* cover the same trees. Sometimes they throw ramifications with centimetre-thick sections from the crowns of the upper and middle strata. The undergrowth is frequently colonized by low populations of herbaceous species⁶ which are purely ombrophile in nature, including the *Thelypteris reticulata* and the Sélaginelle (*Selaginella flabellata*) ferns.

From a structural and architectural point of view, in its mature stage, the ombro-evergreen tropical seasonal forest is closer to the sub-montane ombrophile forest. Nevertheless it retains some traits of the seasonal tropical evergreen type. They are equivalent in their overall appearance. The generally hooped peaks are evergreen: the canopy is always green. Only a few species marginal in biomass and density lose their leaves during the dry season which, occurring at the interface of the sub-humid humid and sub-humid dry bioclimates, is very short or non-existent. The main ones are *Dussia martinicensis* (bois-gamelle), *Ceiba pentandra* (Fromager), *Lonchocarpus pentaphyllus* (Savonette grand-bois) and *Vitex divaricata* (Bois-lezard). Compared to the seasonal evergreen tropical forest the trees have a greater average distance of exclusion. They are between 30 and 40 meters high and have powerful buttresses. These, like the *Slonea*, *Dussia*, *Ceiba* and *Chimarrhis* genera give these “juggernauts” a very stable footing. As for the other forest types, the structuring trees of the final stages of this ecotone are more resistant to hurricanes. The herbaceous stratum is mainly occupied by more ombrophile species⁷ such as the terrestrial ferns (example: *Thelypteris reticulata*, *Polybotria cervina*) and the Clyclantacees (example: *Asplundia rigida*, *Asplundia dussii*).

The regressive forms of this forest type are plural. Most ombrophile species disappear before those of the secondary evergreen tropical seasonal groups. Somehow, the forest canopy opening favours an increase in pioneer or secondary taxa of the middle floor upper horizon.

Ultimately, it seems that in marginal areas as the mature tropical seasonal ombro-evergreen ecotone corresponds to an extension of the species of the lower horizon of the sub-montane ombrophile forest to the upper horizon of the evergreen seasonal forest. Conversely after the anthropogenic or natural degradation the species of the upper horizon of the seasonal evergreen forest colonize the lower horizon of the sub-montane ombrophile forest (Figure 2).

4.3. Successional Intermediaries: Temporal Interfaces

In the Lesser Antilles the anthropization diversified in frequency and intensity has produced a dense floral mosaic. Irrespective of their bioclimatic classification, the multiple landscape units result from the regression of the almost primitive and climax pre-Columbian forests. Today the shrubland, herbaceous, shrub and pre-forest phytocenoses develop alongside young secondary forest communities and rare advanced or climax forest relics. These physiognomic types represent as many stages of evolution and degrees of ecosystem complexity. During a gradual evolution, all transitional phases determine the optimal forest organisation at structural and architectural levels as well as at biocenotic level. As a result, the dynamic or successional gradient composed of stages, phases or chronologies is divided into two periods: the extra-forest successional cycles and intra-forest succes-

⁶They are often species with broad leaves adapted to the crepuscular conditions of the undergrowth.

⁷In the undergrowth of the tropical seasonal evergreen forest the herbaceous species such as the Bois-genou (*Odontonema nitidum*) are very abundant.

sional cycles (Figure 6). In reality these cycles delimit two unique bio-systemic stages. They correspond, respectively, to a degree of greater complexity (the climax forest) and low complexity (the herbaceous stage) below which the ecosystem disappears as such. We were able to identify eleven dynamic stages which correspond to strict ecosystem characteristics (Figure 6): the herbaceous Formations⁸ the Shrubbery, the mature Shrubbery, the shrub Formation, the mature shrub Formation, the pre-forest Formation, the structured young forest Formation, the secondary forest Formation, the late secondary forest Formation, the pre-climax forest Formation and the climax forest Formation.

All the ecological profiles can be found in the floristic potential⁹. These refer to affinities for bioclimates and even biotic or environmental factors. The light seems to be the most relevant factor to consider. Close to the climax the species become increasingly ombrophile, particularly those of the medium and low forest strata. On the contrary, the regression of a mature forest translates into the progressive establishment of increasingly heliophile taxa. Irrespective of the bioclimate, the vegetation dynamics translates into physiognomic and floristic, structural and architectural changes. The vegetation's internal environment is also affected by significant factor changes, particularly temperature, evaporation, humidity and saturation deficit. From the shrubbery stage to the climax forest stage we move from morpho-type shrubs which are low and weakly branched to morpho-types of highly branched trees, some of which may peak at over 40 metres, passing through all the shrub morpho-types. These physiognomic changes are accompanied by a floristic succession corresponding to a succession of ecological profiles. The successive phytocenoses consist of species more specialized for the various biophysical factors. Thus, during the vegetation dynamics we successively see the development of the first rank heliophiles¹⁰ the second rank heliophiles, the semi-heliophiles, the semi-ombrophiles, the ombrophiles, and finally the helio-ombrophiles.

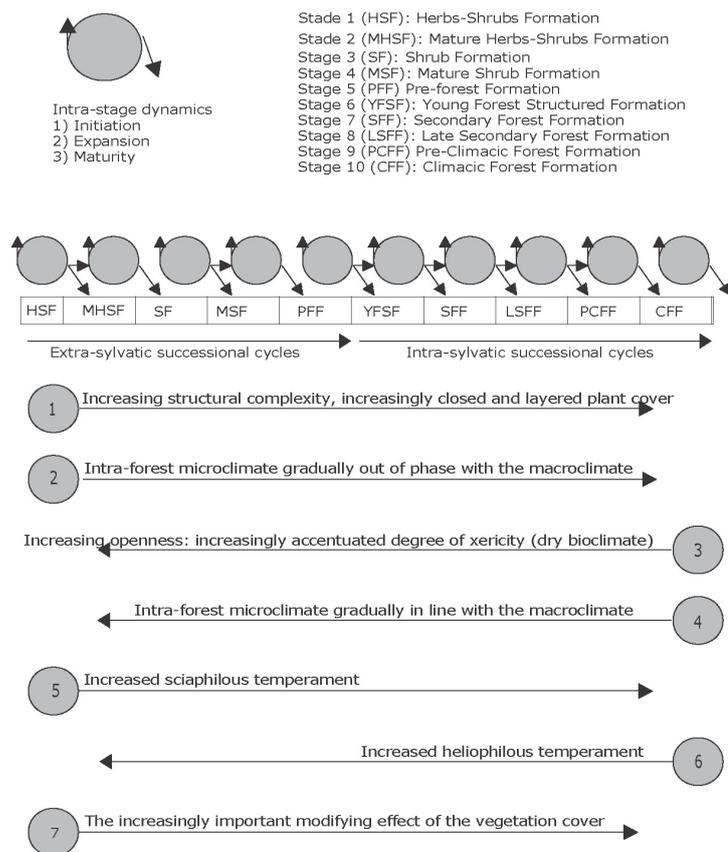


Figure 6. The dynamic gradient (Source: P. JOSEPH).

⁸In Figure 6, the herbaceous formation is not represented: it is also characterized by complex cycles.

⁹The collection of plant species, the stock or species fund.

¹⁰Those that appear with the first waves of floristic colonization.

A dynamic stage consists of a succession of three events: the initiation, expansion and maturity (**Figure 6**). This intra-stage dynamic allows the passage from a successional stage to another. For example, in the adult shrub formations, the shrub species appear in small numbers. Marginal at the beginning¹¹ they regularly increase their density and biomass¹² as they move closer to the pre-forest stage. In the mature phase of the shrub stage, the shrubs are dominant and occupy almost all of the installation and expansion sites¹³. As a general rule, the species of a stage in its maturity phase optimise the installation of the plants that will take precedence in the next stage. All the dynamic stages as well as their internal phases are vegetation evolution stages, all of which represent temporal interfaces.

4.4. The Exchange Surfaces of the Vegetation's Vertical Stratification: The Interfaces between the External Environment and the Intra-Vegetation Environment

4.4.1. The Architectural and Structural Changes during Plant Succession

The average height of the plant eco-units, their architectural organisation and biomass vary significantly especially from the mono-layer regressive phases to the advanced forest phases with three or four strata or exchange surfaces, sometimes even five in old-growth forests [53]. The result is an increasingly strong physical constraint reflected by the progressive rise of the morphological inversion level (the first branches, **Figure 7(a)**): especially for the upper and middle strata trees (the elective or structuring ones). The progressive dynamics is characterised by a succession of physiognomic types. In order of importance we see: the nanophanerophytes (from 0.5 to 2 m), the microphanerophytes (from 2 to 8 m), the mesophanerophytes (from 8 to 25 m), the macrophanerophytes (from 25 to 40 m), the megaphanerophytes (>40 m). Until the late secondary forest stage characterised by joined crowns forming a nearly continuous roof, the vegetal coverage is discontinuous and presents a low number of exchange surfaces. For example in weakly structured young secondary stages, the forest communities are little structured. They have a roof with gaps which nevertheless catches much of the incident energy (**Figure 7(b)**).

4.4.2. The Intra-Vegetation Microclimate: The Example of the Lower Floor

The vegetation's gradual evolution leads to floristic, physiognomic and landscape changes, but also to microclimatic ones. In other words, the plant structure is the initiator of the intra-vegetation microclimate by modifying the macro-climate factors more specifically in its lower part, between 0 and 2 m [54] [55]. This essential area for maintaining the formation in place transforms with the evolution of the vegetation cover. This vegetation regulatory force gradually evolving towards its optimal stage first serves to protect the regeneration from too strong factorial variations which are harmful for their survival (**Figure 8**). In the indoor environments of forest formations (including the oldest), the macroclimate fluctuations are not eliminated. They are more or less damped in space and time depending on the density of the exchanging surfaces formed by the leaf surfaces (**Figure 7**). Compared with a control station, the measurements at 2 m from the ground, within various plant formations in the same bioclimatic conditions, clearly show the modifying effect of the forest architecture on the main climate factors (except rainfall): temperature, humidity, and evaporation (**Figures 8(a)-(e)**). From the pioneer to the climax stage, there seems to be a gradual shift between the general climate and the intra-vegetation environment. Its purpose is a more efficient water resources management.

5. Conclusion

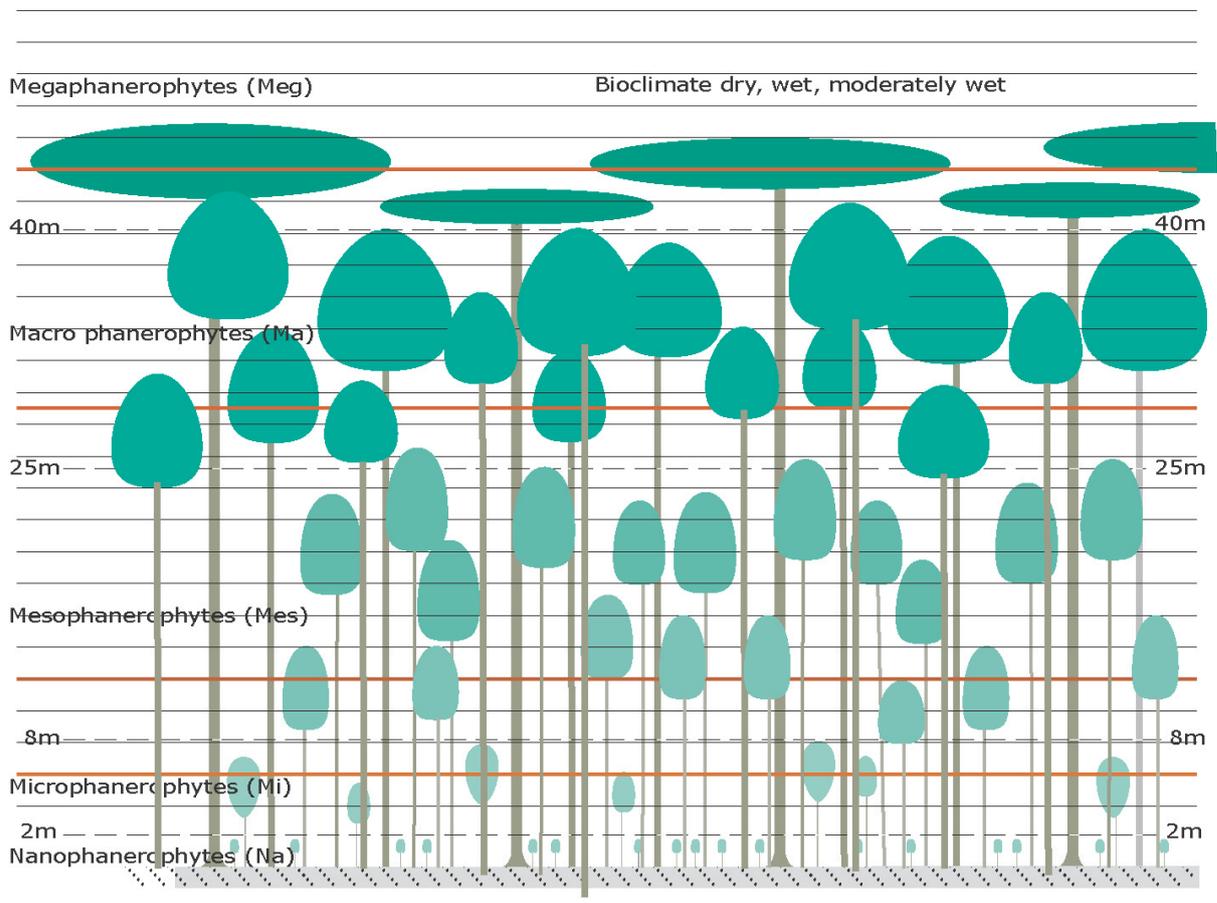
The vegetation cover in the Lesser Antilles is a true laboratory for the study of ecosystem interfaces. From a time or space point of view, they are characterised by specific plant communities. The eco-units that comprised the pre-Columbian forest formations were identical in age and sometimes had a different floristic composition. Their contact areas showed little variation. In contrast, the edges of climax forests and those that existed within the latter between the matrix and the gaps (chablis)¹⁴ were clearly differentiated. From the beginning of colonization to the present day human activities had contributed to the increase in biocenotic interfaces. The climax and subclimax forests of the Amerindian period had gradually been replaced by herbaceous, shrub and pre-forest

¹¹The initiation phase.

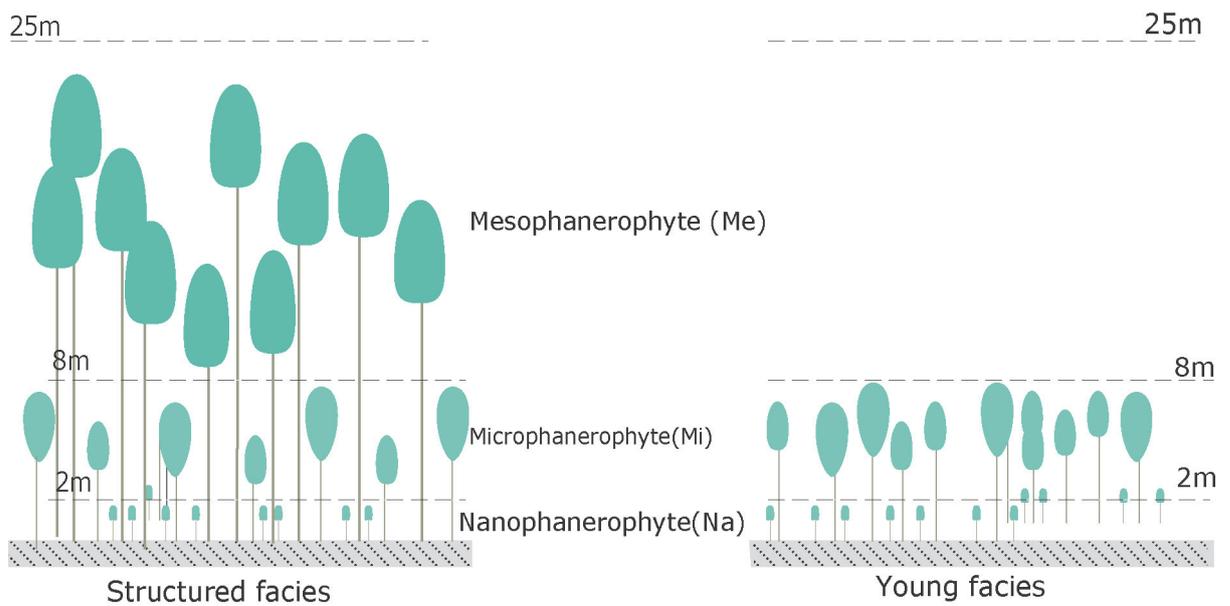
¹²They optimize their ability to use the resources of the environment: this is the expansion phase.

¹³A plant community is a microsystem consisting of basal units named nano-systems [10]. The nano-system can be likened to the plant and its corresponding ground volume: it is its installation and expansion site. Within the latter all the plant's phenological phases take place.

¹⁴The gaps (characterized by secondary species) in relation to the forest matrix (composed of climax eco-units) are very marginal.

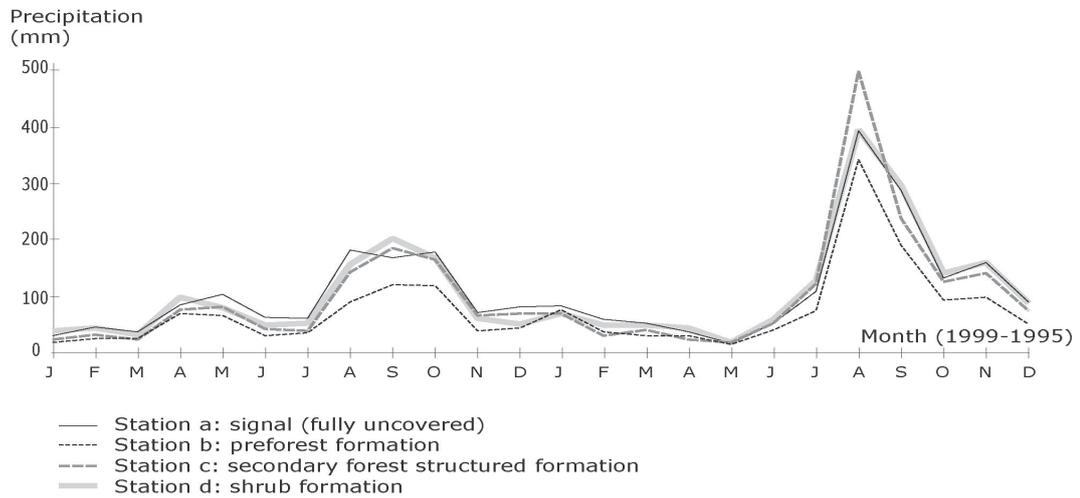


(a)

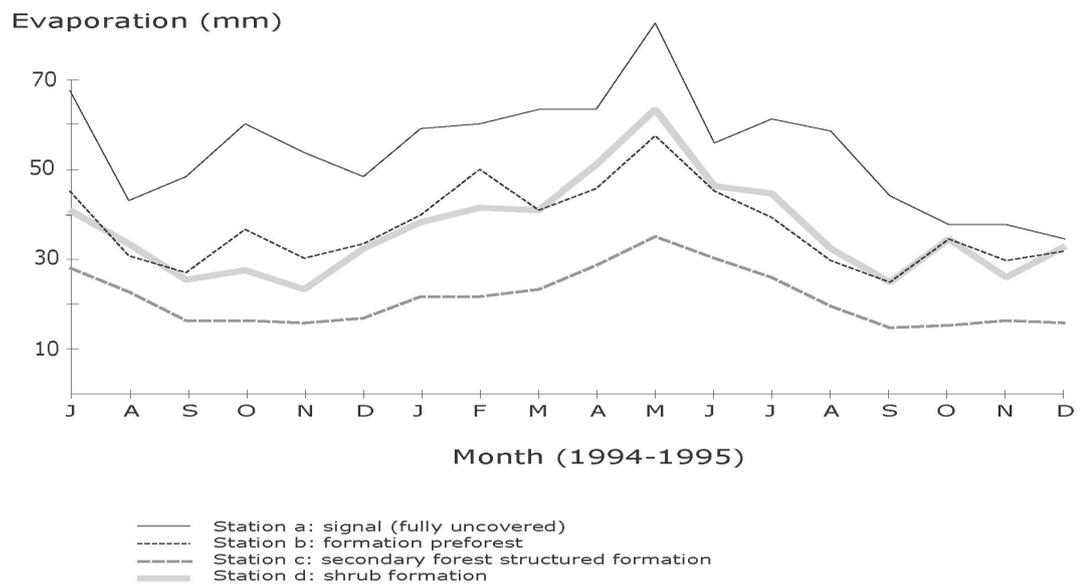


(b)

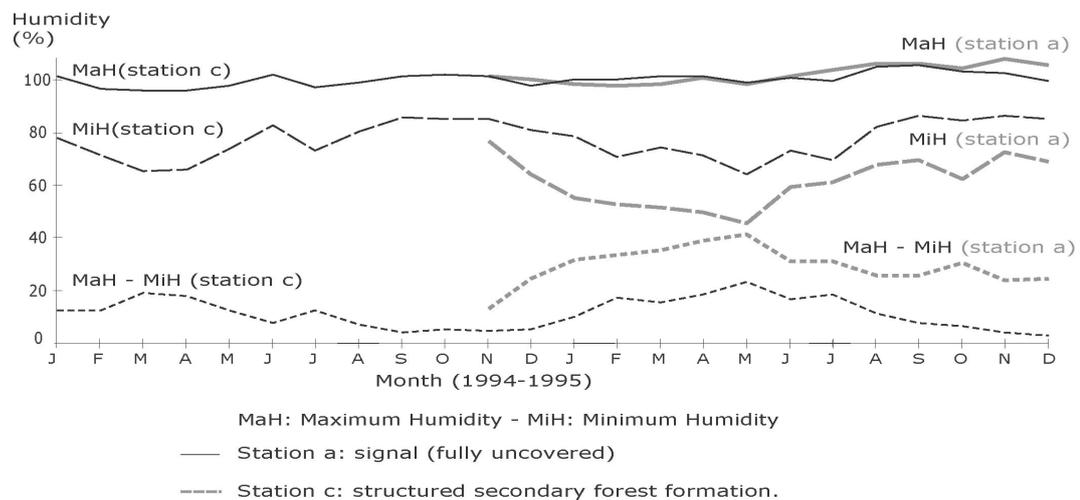
Figure 7. (a) Primary forest (synthesis of an eco-unit plan/Source: P. JOSEPH); (b) secondary forest (synthetic figure/Source: P. JOSEPH).



(a)



(b)



(c)

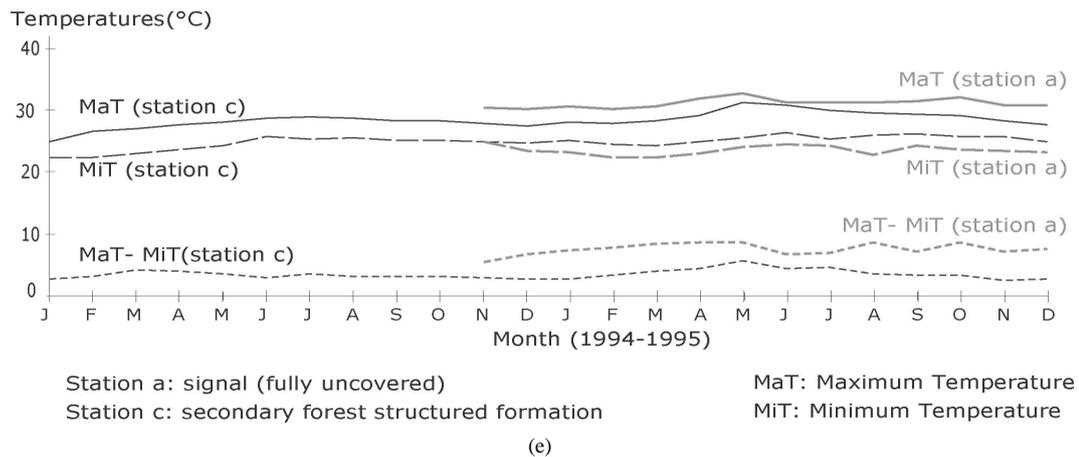
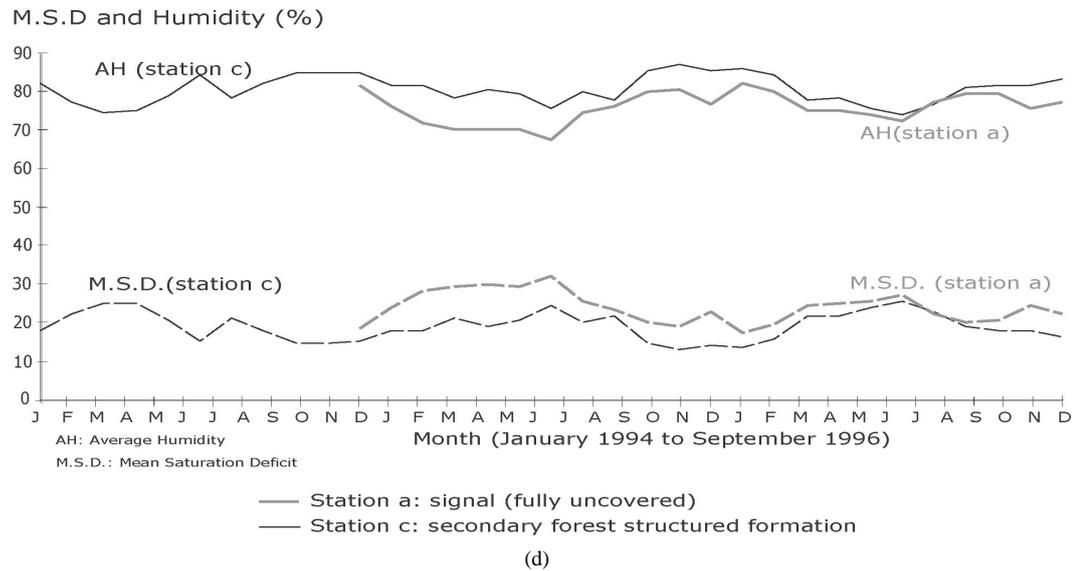


Figure 8. (a) Monthly rainfall variations; (b) monthly evaporation (Piche); (c) average monthly humidity; (d) monthly average saturation deficit and average humidity; (e) monthly mean temperature.

formations. The ecosystem potential being of the forest type, the floristic units of the present plant mosaic therefore represent as many dynamic stages as temporal interfaces. The forest ecosystem regression is also accompanied by the simplification of the plant grouping architecture. In fact, unlike the original multi-layer forests (4 or 5 layers), the current secondary phytocenoses are mostly mono-layered and have no impact on the main climate factors. Their phenology is dictated by fluctuations in their external environment. Nowadays, only mature forests¹⁵ exhibit internal environments with characteristics that differentiate them from the macroclimate. Due to their numerous strata, they significantly change the overall climate factors and create little fluctuating internal environments. These intra-forest microclimates are necessary for the development of specialized ombrophile and helio-ombrophile species. Ultimately, while the vegetation evolves towards the climax, the exchange surfaces increase and become as many interfaces with the external environment. All these specific aspects of the functioning of the Lesser Antilles vegetation are derived from the high degree of biotope heterogeneity which allows for strong biological diversity.

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¹⁵The rare secondary late, pre-climax and climax forests.

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