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Successional patterns on tropical inselbergs: a case study on the Nouragues inselberg (French Guiana)

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Abstract

A number of plant communities have been described on tropical inselbergs, known as hot spots of plant and animal biodiversity. However, few studies tried to question what drives seral processes in these harsh environments, submitted to natural hazards (violent storms, intense runoff, lightning strikes) which may destroy the vegetation cover and its accumulated organic matter. We analysed quantitative data from the granitic Nouragues inselberg (French Guiana) in order to discern how successional processes featured their variety. We showed that the transition from herbaceous carpets (bromeliaceous mats and grassy meadows) to woody vegetation (shrub thickets) was not conditioned by slope but was truly successional. We also showed that there was a cycle of change in shrub thickets, reinitiated by the destruction of scrub vegetation by fire (lightnings), wood-destroying fungi and termites.

Keywords: Granite; Non-equilibrium Coexistence; Rocky outcrops; Small scale disturbance

Introduction

Tropical inselbergs (rocky outcrops protruding from a plain landscape) are hot spots of plant and animal biodiversity, due to the high turnover of species between sites and the presence of organisms almost restricted to the inselberg habitat (Gasc et al., 1998; Porembski et al., 2000a; Sarthou et al., 2003). They are characterized by isolated patches of vascular vegetation surrounded by bare rock or cryptogamic vegetation (Sarthou et al., 1995; Büdel et al., 2000). The great diversity of slope and aspect

conditions and the high contrasts in temperature and humidity on the bare rock are prone to the development of particular adaptive strategies (Porembski et al., 2000b; Biedinger et al., 2000; Sarthou, 2001) which confer to inselbergs a high biodiversity conservation value (Parmentier, 2005).

Some studies described distinct plant communities on inselbergs without any attempt to classify them into seres (Sarthou and Villiers, 1998; Parmentier, 2003; Parmentier et al., 2005; Oumorou and Lejoly, 2003), while others aimed at discerning successional pathways (Hambler, 1964; Shure and Ragsdale, 1977; Ibisch et al., 1995; Larpin et al., 2000). Dispersal limitation, stochastic processes and past vegetation changes due to climatic fluctuations explain strong disceprancies in floristic composition from an inselberg to another, and between parts of the same inselberg, despite basic similarities in biological traits of dominant plant species (Sarthou and Villiers, 1998; Sarthou et al., 2003; Parmentier et al., 2005). All these features make difficult to assess successional processes by synchronous analysis, each inselberg or even part of an inselberg being unique in its botanical composition.

The present study was a case study, aimed at disentangling the complex successional processes which occur on the Nouragues inselberg (French Guiana), both by putting things in order in a set of vegetation samples by multivariate analysis and by observing and sketching the establishment and death of dominant plant species.

Methods

Study area

The Nouragues inselberg (4°3’N, 52°42’W, maximum altitude 410 m) is located in French Guiana (South America), 100 km south of the Atlantic Coast in the tropical rain forest, a region with a very low level of anthropogenic disturbance (Fig. 1). It is included in the Balenfois Mountains near the Arataye river, in the Nouragues Biological Reserve. It is dome-shaped, of the so-called whaleback type (Bremer and Sander, 2000). Geomorphological features include flat surfaces, steep slopes, depressions and gullies (Fig. 2A). The very old rocky substrate (2.1-2.6 giga-years) belongs to the granodiorite series originating from the Trans-Amazonian orogenesis (Gruau et al., 1985; Théveniaut and Delor, 2004), with smooth pellicular erosion (exfoliation) due to high thermic contrasts and chemical dissolution of plagioclases and potassic feldspars (Sarthou and Grimaldi, 1992). Coarse (1-2 mm) quartz grains, detached from the substratum by mineral weathering, accumulate in small, closed depressions or are flushed away by intense run-off. Scales of granite are exfoliated by differential dilatation and slowly slide down the smooth, convex slopes (Hurault, 1963), leaving edges onto which pioneer plants (Bromeliaceae, Clusiaceae) may fasten at the time of germination.

Mean annual precipitation reaches 3250 mm, with a dry season from July to November and a wet season from December to June, interrupted by a very short dry season in March (Sarthou and Villiers, 1998). The air temperature (screened condition) varies daily from 18 to 55°C and the air moisture varies from 20 to 100% (Sarthou, 1992). The temperature measured directly on the bare rock may reach 75°C in the dry season. Most of the surface is covered by cyanobacteria (Sarthou et al., 1995), which take part in mineral weathering and fix carbon and nitrogen (Sarthou and Grimaldi, 1992). Cyanobacteria, like lichens on inselbergs in drier regions (Büdel et al., 1997), are

the primary factor in the establishment of nutrient cycles on rock surfaces. Vascular vegetation, locally called ‘rock savanna’ (English translation of ‘savane-roche’), is made up of scattered patches of herb and shrub communities, but steep slopes are covered only with cryptogamic vegetation (Fig. 2A). Organic soils (1-20 cm depth), acid (pH 4.0-5.5), with a high faunal and microbial activity, are formed under patches of woody vegetation where humified organic matter is prevented from flushing by a dense root network (Sarthou and Grimaldi, 1992; Kounda-Kiki et al., 2006). The summit of the inselberg, and the ecotone zone surrounding it, are covered with a low forest rich in epiphytes and understory plants (Larpin, 2001).

‘Epilithic’ plant communities have been described on the Nouragues inselberg (Sarthou, 1992; Sarthou and Villiers, 1998; Sarthou, 2001; Sarthou et al., 2003). The common development of soil and vegetation has been studied by Sarthou and Grimaldi (1992), Vaçulik et al. (2004) and Kounda-Kiki et al. (2006, 2008). We will focus our story on the vascular vegetation of ‘rock savanna’, omitting fringe and summit forested areas. ‘Rock savanna’ can be found in (i) a summit plateau called ‘Summit’ (Fig. 2A), rolling gently in south direction, sloping mostly from 0 to 15% (but slopes higher than 20% are also present), (ii) a lower terrace called ‘Les Terrasses’ (Fig. 2A), with slopes mostly between 15 and 40%, (iii) a small savanna (~ 4 ha) included within a forested area occupying a terrace on the north-east face of the inselberg, called ‘Savane Coco’, with gentle slopes, mostly less than 10%. More water flows on lower terraces than on the summit plateau, due to topographical drainage.

Vegetation samples

Vegetation data were taken from previously published studies which described in detail the sampling procedure (Sarthou and Villiers, 1998; Sarthou, 2001; Sarthou et al., 2003). Briefly, vegetation was sampled on the three parts of the inselberg covered by savanna rock, over three consecutuve years, from November 1987 to November 1989. The plot size varied from 4 (2x2 m) to 8 m^2 (2x4 m) according to patch size in 50 disjointed areas covered by herbaceous vegetation, and was fixed to 16 m^2 (2x8 m) in 57 disjointed areas covered by woody vegetation. These areas were selected in order to represent the whole variation in vegetation observed on the inselberg. Cover abundance data were recorded according to the Braun-Blanquet approach (Braun-Blanquet, 1964) then transformed into a numerical scale according to Van der Maarel (1979). Plant species were grouped into growth forms. Mosses and cyanobacteria were registered as present or absent, but were not considered at the species level. Slope and soil depth were measured at the centre of each plot, by using a goniometer and forcing a steel rod down to the granite, respectively.

Multivariate analysis

Vegetation data were subjected to correspondence analysis (CA), a multivariate method allowing the simultaneous projection of samples and species in a set of factorial axes (Greenacre, 1984). The main (active) variables were the 74 plant species recorded in the plots (Table 1). Additional (passive) variables, describing community parameters (species richness, growth forms), cryptogamic vegetation (mosses, cyanobacteria), environmental conditions (slope, presence of free water, soil depth) and position of plant samples on the inselberg (‘Summit’, ‘Les Terrasses’, ‘Savane Coco’) were projected on factorial axes together with the main variables. Plant species were

classified into growth form groups. For each sample and for each growth form group we summed up the cover values of corresponding plant species. All variables (main and additional) were reweighted and refocused according to Greenacre (1984) in order to (i) avoid discrepancies between contributions to factorial axes and factorial coordinates, (ii) allow quantitative, qualitative and semi-quantitative variables of varying scale to be included in the same analysis. As a consequence, all plant species had the same weight (mean m fixed to 20 and standard deviation s fixed to 1 by tranforming x into X = (x-m)/s) and thus were at the same distance of the origin in the factorial hyperspace. Plant species were doubled into lower and higher values (of cover value) in order to discern also trends of increasing abundance and richness of the community (Peltier et al., 1997). For that purpose, to each plant species (X, mean 20, variance 1), to be projected among samples were it is more abundant, was added a conjugate variable, with same mean (20) and variance (1), measuring the non-occurrence of this species (X' = 40-X). Note that it is quite common, when dealing with large data matrices (here 182 rows and 107 columns), that the first CA factorial axes extract only a little part of the total inertia, which does not preclude them to be highly informative in terms of ecological trends (Benzécri, 1969).

Results and discussion

The numerical analysis of vegetation samples

CA showed three groups of varying botanical composition (Figs. 3A, B), as already described previously (Sarthou and Villiers, 1998). Axis 1 (16% of the total inertia) separated herbaceous vegetation (left side of the horizontal axis), with

Utricularia hispida (UHI) as most characteristic, from woody vegetation (right side of the same axis) with *Clusia minor* (CMI) as most characteristic. Cyanobacteria, mosses, herbs (annual and perennial) and suffrutex were associated with herbaceous vegetation, while shrubs, trees, climbers and hemiparasites were associated with woody vegetation (Fig. 3A). Note that rosettes, by their position not far from the origin along Axis 1, were common to both herbaceous and woody vegetation. More plant species were present in patches of woody vegetation (16-22 species per sample), compared to herbaceous vegetation (5-10 species), as ascertained by the projection of the two extreme categories of species richness on both sides of Axis 1, the intermediate category (11-15 species) being projected not far from the origin. This can be explained by the smaller size of herbaceous plots (4 to 8 m^2) compared to woody plots (16 m^2). The slope did not explain the variation in botanical composition depicted by Axis 1, because the three classes of slope were projected not far from the origin along this axis, but differences were found according to the geographical position of the samples. Herbaceous vegetation was dominant in 'Savane Coco', and to a lesser extent in 'Les Terrasses' while woody vegetation was dominant in 'Summit'. At first sight this could be thought to be an artifact of sample plot selection, however it actually reflected the distribution of vegetation types on the inselberg (Sarthou, 1992). The three vegetation types were present in 'Summit', while only shrub and bromeliaceous vegetation was present in 'Les Terrasses' and only bromeliaceous vegetation in 'Savane Coco' (Fig. 3A).

Axis 2 of total CA (6% of the total inertia) separated two groups within herbaceous vegetation, the one on the positive (upper) side of this axis, with *Pitcairnia geyskesii* (PGE) as most characteristic, the other on the negative (lower) side, with *Axonopus ramosus* (ARA) as most characteristic (Figs. 3A, B). The upper group

(bromeliaceous mats) was comprised of rosettes, cyanobacteria, annuals, suffrutex and creeping perennial herbs, while the lower group (grassy meadows) was comprised of erect perennial herbs and mosses (Fig. 3A). Free water (water running periodically on the granite) was associated with bromeliaceous mats. Axis 2 showed also a gradient within woody vegetation (right side of Axis 1), opposing trees and climbers (with the highest number of plant species) in the lower part of Axis 2 to rosettes and hemiparasites in the upper part of this axis, but this trend was poorly reflected in the botanical composition, as shown by the fact that plant species were grouped in an intermediate position (Fig. 3B), pointing on quantitative rather than qualitative changes in cover values of plant species within woody patches. Contrary to Axis 1, the slope varied along Axis 2, gentle slopes being projected on the lower (negative) part (grassy meadows, woody thickets with trees) while steep slopes were projected on the upper (positive) part of this axis (bromeliaceous mats, woody thickets without trees but with rosettes). As expected, gentle slopes (and corresponding samples) were mostly represented in 'Summit' (negative side of Axis 2) while steep slopes were mostly represented in 'Les Terrasses' (positive side of Axis 2).

The combined effects of slope and succession

On slopes, some vegetation clumps dominated by *P. geyskesii* (bromeliaceous mats) were enriched in *C. minor*, while some vegetation clumps dominated by *C. minor* (shrub thickets) were enriched in *P. geyskesii*. If we examine the respective cover values of *P. geyskesii* and *C. minor* in samples taken on medium and steep slopes (by excluding slopes up to 10%) it appears that the shrub *C. minor* can be found at a low cover value in bromeliaceous carpets dominated by *P. geyskesii*, even when the cover

value of the latter is at its maximum (9), and that the frequency of *C. minor* increases as far as the cover value of *P. geyskesii* decreases from 9 to 7 (Fig. 4). At a cover value of 7 for *P. geyskesii*, *C. minor* can be found either at a lower cover value of 2 (thus as in bromeliaceous mats dominated by *P. geyskesii*) or at a higher value of 8, i.e. at the value commonly observed in shrub thickets, where the cover value of *P. geyskesii* can be observed to decrease step-by-step from 7 to 0. This points to a successional process by which the herb rosette *P. geyskesii* can be replaced by the shrub *C. minor* on slopes. Given that vegetation sampling was done over fixed rectangular areas, the qualitative information on the architecture of vegetation clumps is lacking in our numerical analysis. Fig. 2B pictures the common occurrence of concentric rings of *P. geyskesii* around vegetatively expanding clumps of *C. minor*. On the same photograph, a young individual of *C. minor* can be seen established within a bromeliaceous carpet (to the left), while an older individual of the same shrub species can be seen creeping downslope on the right side. Both *P. geyskesii* and *C. minor* were seen to establish by seed directly on the granite, but a nurse effect of the former in favour of the latter is highly probable. The spatial relationships of these two species within thickets growing on slopes have been sketched in Fig. 5.

The peripheral exclusion of light-demanding herbs by shrubs expanding their crowns is a well-known process (Watt, 1955) which can be discerned easily on the Nouragues inselberg. However, we may wonder whether the enrichment of shrub thickets in woody and climber species, as depicted by Axis 2 of CA (Fig. 3) is truly successional or due to decreasing slope, as suggested by CA. If we discard samples taken on gentle slopes, the cover value of *P. geyskesii* in woody vegetation was negatively correlated (r_s = -0.50, P<0.01, n = 26) with the number of woody species.

This points to an increasing variety of shrubs, trees and woody climbers as far as the abundance of *P. geyskesii* decreases, when slope was not allowed to vary. When analysing the whole set of samples of woody vegetation (n = 57), simple regression analysis showed that slope did not account for the number of woody species ($t = -0.993$, $P = 0.33$) while the abundance of *P. geyskesii* did ($t = -3.69$, $P = 5.10^{-4}$). Although we cannot discard without eradication experiments a possible interference of *P. geyskesii* with the establishment of woody species, the most plausible hypothesis is that the establishment of shrubs, trees and climbers within clumps of *C. minor* causes the retreat of prostrated light-demanding species such as *P. geyskesii*.

Small gap disturbances occurring within *C. minor* thickets might be the way by which they become colonized by a more diversified woody flora, among which *Myrcia sylvatica* (Myrtaceae) is most frequently observed. At the border of shrub thickets (mostly upslope) patches (1-10 m^2) can be seen devoid of living woody vegetation, with an accumulation of dead wood, still standing or transformed into humus and covered with mosses (Fig. 2C). A closer examination of advancing zones of destruction reveals intense wood-rotting and xylophagous termite activity (Fig. 2D) and charcoal has been found in all samples taken in the topsoil of destruction zones (Kounda-Kiki et al., 2008). Whether wood-destroying fungi and xylophagous termites occur concurrently after fire (due to lightning strikes) or, more probably, according to a substrate succession starting with death of woody branches and stems and subsequent fungal development, is still a matter of conjecture, but we always found rotten wood associated with termite consumption. In areas where aerial parts of *C. minor* have been destroyed in this way, the ground is often covered with a cryptogamic vegetation made of mosses and/or lichens (Fig. 2C), the rhizoids of which are known to prevent soil particles to be flushed

away by water (Leach, 1931). However, other places can be seen without any cryptogamic vegetation, maybe as an earlier stage of colonization. This exposes the root system of *C. minor*, which locally dies in the absence of a vegetation cover. The establishment by seed of phanerogamic vegetation can be observed in such places when they are protected from intense runoff (Fig. 2E). Laterally, destruction zones, when not rapidly penetrated by moss and lichen rhizoids, can be easily flushed away, exposing the granitic substrate at a place previously occupied by vegetation. Zones destroyed by fire, fungi and termites are bordered by a species-rich ecotone where herbaceous and woody species cohabit (Fig. 2F), pointing to their role in the botanical enrichment of *C. minor* thickets. The advance of succession can thus be seen as a cyclical process when and where a primary sere is reinitiated on bare granite or an 'helicoidal process' when and where the organic soil accumulated under woody vegetation increases in thickness at each cycle of building and destruction.

Fig. 3 shows an opposition between the Bromeliaceae *P. geyskesii* and the Poaceae *A. ramosus* along Axis 2 of CA. Axis 2 was explained by slope, which discriminated between negative and positive sides of this axis and *A. ramosus* was mainly present on slopes $\leq$ 10% ($t = -3.89$, $P = 3.10^{-4}$). If we take into account only gentle slopes (thereby excluding the effect of slope), there appears a positive relationship between the cover value of *A. ramosus* and soil depth ($t = 19$, $P < 10^{-4}$), and a negative relationship with the cover value of *P. geyskesii* ($r_s = -0.71$, $P = 5.10^{-8}$), which was itself negatively influenced by soil depth ($t = -26$, $P < 10^{-4}$). Soil (mostly sand and gravel issuing from the weathering of granite) was shown to accumulate in small depressions periodically filled up by water during storms, more especially near the summit of the inselberg ('Summit'). These results point to a successional process,

governed by the increase in thickness of the mineral soil in the absence of slope. Here, too, *P. geyskesii* was observed to grow in concentric rings around *A. ramosus* meadows but in this case the spatial discrimination was due to the epilithic behaviour of the bromeliad, maybe reinforced by some interference with *A. ramosus*. Several Cyperaceae (*Rhynchospora fallax*, *Rhynchospora tenella*, *Rhynchospora subdicephala*, *Scleria cyperina*) have been shown to accompany *A. ramosus*. At a micro-scale we observed that the deposition of gravel and sand was not uniform but rather formed a mosaic with Cyperaceae growing in gravelly parts of the depressions while *A. ramosus* grew in sandy parts. The interplay between the segregated deposition of mineral particles by water flushes, the immobilization of sand within the basal parts of sedges and the clonal growth of *A. ramosus* is at the origin of a parallel development of soil and vegetation which has been sketched in Fig. 6 as described by Sarthou (1992). Depressions may become invaded by *C. minor*, which establishes both by seed and vegetatively, thus starting the development of woody vegetation, with associated soil formation (8-20 cm), depressions becoming finally enclosed in *Clusia* thickets.

This successional scheme does not explain how early as well as late seral stages are still observable on the inselberg. Before deeper, more stable soils are formed under the development of woody vegetation, a return to early stages of vegetation development can be effected by a flush effect during violent storms, destructing sand/gravel deposits with their accompanying vegetation. An alternative explanation could be the formation of dissolution pans on flat parts of the granite, but the slow rate at which such depressions may form in granite makes this hypothesis highly improbable (Hurault, 1963; Bremer and Sander, 2000).

Comparisons with other inselbergs

Bromeliaceous mats have been described on other South American inselbergs, with some degree of variation in their botanical composition at the genus or species level (Granville and Sastre, 1974; Ibisch et al., 1995; Sarthou and Villiers, 1998; Meirelles et al., 1999). In West Africa, monospecific mats of the sedge *Afrotrilepis pilosa* (W.C. Boeck) J. Raynal have been widely reported (Hambler, 1964; Jeník and Hall, 1976; Parmentier, 2001, 2003; Oumorou and Lejoly, 2003). Their seral development exhibits many features in common with bromeliaceous mats, although they seem to be much more stable (Hambler, 1964; Porembski et al., 1996).

Several authors described primary plant successions on exposed granite in temperate regions, especially in the United States (Whitehouse, 1933; Oosting and Anderson, 1939; Keever et al., 1951; Burbanck and Platt, 1964; Burbanck and Phillips, 1983). In their dynamic schemes, lichens are pioneer organisms which weather the rock and constitute microsites favouring seedling establishment. These authors insisted on the slow rate of the observed successional processes and the absence of any equilibrium in the establishment of the late-successional ‘shrubby’ stage. They showed that the high mortality rate of woody plants was due to dry conditions and instability of the soil substrate, the local disappearance of the final stage initiating a new cycle of vegetation dynamics. Shure and Ragsdale (1977) studied a primary succession on a granitic outcrop in Georgia (USA), involving both plant and soil animal communities, but they did not question the reasons for the absence of a forested stage. Parmentier (2003), studying three inselbergs in Central Africa, did not describe any woody vegetation except summit and fringe forest areas. Jeník and Hall (1976) and Oumorou and Lejoly

(2003) described woody plant communities on slopes of inselbergs in West Africa, but they attributed the existence of woody areas to thickness of the soil which, based on our own observations, should not be considered as a cause but rather as a consequence of shrub development (Vaçulik et al., 2004; Kounda-Kiki et al., 2006). Hambler (1964) and later Isichei and Longe (1984) described the seral and seasonal development of *Afrotrilepis* mats on Nigerian inselbergs, but without any appearance of woody vegetation except in particular areas such as ravines and fringes of the summit forest, probably because of recurrent fires during the dry season. However Ibisch et al. (1995), working in Bolivia, described concentric circles of woody, herbaceous and cryptogamic vegetation, as a spatial projection of a seral process. They reported also the occurrence of termite nests in shrub canopies, and postulated their role in the formation of pristine soils, but they did not identify them as wood destroyers.

Conclusion

To the light of our observations it is highly probable that climatic fluctuations and biological interactions between plants, microbes and animals, rather than invariant environmental factors such as aspect and slope, drive the cycle of change of the ‘rock savanna’ vegetation (Houle and Phillips, 1989). Despite variation in the species composition of vegetation patches, which we observed to occur on the same inselberg according to aspect and altitude (Sarthou, 1992, 2001), a common sequence of vegetation and soil development, involving a limited number of dominant plant species, can be described (Fig. 7). Several well-known mechanisms of plant succession play probably a role in the dynamics of ‘rock savanna’, in particular facilitation (establishment of plant species on cyanobacterial crusts, sand deposit around

Rhynchospora tufts), tolerance (establishment of *C. minor* within bromeliaceous mats, of Myrtaceae within *Clusia* thickets), and small-scale disturbance (colonization of cyanobacterial crusts by enchytraeids, destruction of *Clusia* thickets by fire, fungi and termites). However, the random establishment of plant and animal species, exemplified by a high turnover rate of species between seasons (Porembski et al., 2000a), vegetation patches (Kounda-Kiki et al., 2004) and inselbergs (Porembski et al., 2000a; Sarthou et al., 2003; Parmentier et al., 2005), should not be overlooked. The non-equilibrium co-existence of a variety of organisms in a permanently changing environment (Connell, 1978; Briske et al., 2003) probably contributes to explain the high level of biodiversity exhibited by inselbergs, despite harshness of life conditions. They may also explain why so few authors attributed unambiguously to dynamic processes the wide variety of plant communities observed on isolated rock outcrops (Hambler, 1964; Shure and Ragsdale, 1977; Houle and Phillips, 1989; Larpin et al., 2000).

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1

Table 1. List of plant species which were sampled on the Nouragues inselberg, together with their codes for CA and potential life forms

Code	Species	Family	Life form
APE	*Actinostachys pennula* (O.P. Swartz) W.J. Hooker and J.G. Baker	Schizaeaceae	Erect perennial herb
AAQ	*Aechmea aquilega* (Salisbury) Grisebach	Bromeliaceae	Rosette
AME	*Aechmea melinonii* Hooker	Bromeliaceae	Rosette
APU	*Aganisia pulchella* Lindley	Orchidaceae	Climber herb
AJE	*Anthurium jenmanii* Engler	Araceae	Erect perennial herb
ARA	*Axonopus ramosus* Swallen	Poaceae	Erect perennial herb
BCA	*Borreria capitata* (Ruiz et Pavon) de Candolle	Rubiaceae	Suffrutex
BUC	*Burmannia capitata* (Walter ex Gmelin) Martius	Burmanniaceae	Annual
CBE	*Catopsis berteroniana* (Schultes f.) Mez	Bromeliaceae	Rosette
CCA	*Cavendishia callista* Donnell-Smith	Ericaceae	Woody climber
CDE	*Chamaecrista desvauxii* (Colladon) Killip var. *saxatilis* (Amshoff) Irwin et Barneby	Caesalpiniaceae	Suffrutex
CAL	*Chelonanthus alatus* (J.B. Aublet) Pulle	Gentianaceae	Erect perennial herb
CPU	*Chelonanthus purpurascens* (J.B. Aublet) Struwe, S. Nilsson and V.A. Albert	Gentianaceae	Erect perennial herb
CRO	*Cleistes rosea* Lindley	Orchidaceae	Erect perennial herb
CMI	*Clusia minor* Linnaeus	Clusiaceae	Shrub
CNE	*Clusia nemorosa* G.F.W. Meyer	Clusiaceae	Shrub
CRU	*Commelina rufipes* Seubert var. *glabrata* (D.R. Hunt) Faden et D.R. Hunt	Commelinaceae	Creeping perennial herb
CLA	*Coussapoa latifolia* Aublet	Cecropiaceae	Tree
CHO	*Croton hostmannii* Miquel	Euphorbiaceae	Shrub
CBL	*Cuphea blackii* Lourteig	Lythraceae	Suffrutex
CGU	*Cybianthus guianensis* (de Candolle) Miquel subsp. *pseudoicacoreus* (de Candolle) Agostini	Myrsinaceae	Tree
EGR	*Encyclia granitica* (Lindley) Schlechter	Orchidaceae	Erect perennial herb
EIO	*Encyclia ionosma* (Lindley) Schlechter	Orchidaceae	Erect perennial herb
ENO	*Epidendrum* cf. *nocturnum* N.J. Jacquin	Orchidaceae	Erect perennial herb
ESU	*Eriotheca surinamensis* (Uittien) A. Robyns	Bombacaceae	Tree
ECO	*Ernestia confertiflora* Wurdack	Melastomataceae	Suffrutex
EGI	*Ernestia granvillei* Wurdack	Melastomataceae	Shrub
ECI	*Erythroxylum citrifolium* Saint-Hilaire	Erythroxylaceae	Shrub
GLI	*Guzmania lingulata* (Linnaeus) Mez	Bromeliaceae	Rosette
IAN	*Ipomoea angulata* Martius ex Choisy	Convolvulaceae	Climber herb
IPU	*Irlbachia purpurescens* (Aublet) Maas	Gentianaceae	Erect perennial herb
MCR	*Macrocentrum cristatum* (de Candolle) Triana	Melastomataceae	Suffrutex
MSA	*Matelea sastrei* Morillo	Asclepiadaceae	Climber herb
MCI	*Miconia ciliata* (L.C. Richard) de Candolle	Melastomataceae	Shrub
MFA	*Myrcia fallax* (L.C. Richard) de Candolle	Myrtaceae	Shrub
MGU	*Myrcia guianensis* (Aublet) de Candolle	Myrtaceae	Shrub
MSS	*Myrcia saxatilis* (Amshoff) Mc Vaugh	Myrtaceae	Shrub
MSY	*Myrcia silvatica* (G.F.W. Meyer) de Candolle	Myrtaceae	Shrub
MSP	*Myrciaria* sp. Desvaux	Myrtaceae	Tree
NFL	*Neea floribunda* Poeppig et Endlicher	Nyctaginaceae	Shrub
POY	*Paepalanthus oyapokensis* Herzog	Eriocaulaceae	Annual
PRI	*Panicum rivale* Swallen	Poaceae	Erect perennial herb
PHI	*Perama hirsuta* Aublet	Rubiaceae	Annual
PLI	*Phragmipedium lindleyanum* (Schomburgk) Rolfe	Orchidaceae	Erect perennial herb
PPY	*Phtirusa pyrifolia* (Humboldt, Bonpland et Kunth) Eichler	Loranthaceae	Hemiparasite
PSC	*Piptocoma schomburgkii* (Schultz Bipontinus) Pruski	Asteraceae	Shrub
PGE	*Pitcairnia geyskesii* L.B. Smith	Bromeliaceae	Rosette
PAD	*Polygala adenophora* de Candolle	Polygalaceae	Annual
PRE	*Psittacanthus redactus* Rizzini	Loranthaceae	Hemiparasite
PHO	*Psychotria hoffmannseggiana* (Roemer et Schultes) Müller-Argoviensis	Rubiaceae	Shrub
RSP	*Racinea spiculosa* (Grisebach) Spencer et L.B. Smith	Bromeliaceae	Rosette
RBA	*Rhynchospora barbata* (Vahl) Kunth	Cyperaceae	Erect perennial herb
RCE	*Rhynchospora cephalotes* (Linnaeus) Vahl	Cyperaceae	Erect perennial herb
RFA	*Rhynchospora fallax* Uittien	Cyperaceae	Erect perennial herb
RSU	*Rhynchospora subdicephala* Koyama	Cyperaceae	Erect perennial herb
RTE	*Rhynchospora tenella* (C.G.D. Nees) Böckeler	Cyperaceae	Erect perennial herb
RCR	*Rudgea crassiloba* (Bentham) B.L. Robinson	Rubiaceae	Shrub
SCE	*Satyria cerander* (Dunal) A.C. Smith	Ericaceae	Woody climber
SAL	*Sauvasegia aliciae* Sastre	Ochnaceae	Suffrutex
SCY	*Scleria cyperina* Kunth	Cyperaceae	Erect perennial herb
SPR	*Selaginella producta* Baker	Selaginellaceae	Creeping perennial herb
SPA	*Sipanea pratensis* Aublet	Rubiaceae	Suffrutex
SGU	*Souroubea guianensis* Aublet	Marcgraviaceae	Woody climber
SSU	*Stelestylis surinamensis* Harling	Cyclanthaceae	Erect perennial herb
SPS	*Sterculia pruriens* K. Schumann	Sterculiaceae	Tree
SGU	*Stylosanthes guianensis* (Aublet) Swartz	Fabaceae	Suffrutex
TCA	*Tabebuia capitata* (Bureau et K. Schumann) Sandwith	Bignoniaceae	Tree
TDE	*Ternstroemia dentata* (Aublet) Swartz	Theaceae	Tree
UAM	*Utricularia amethystina* Saint-Hilaire	Lentibulariaceae	Annual
UCH	*Utricularia choristotheca* P. Taylor	Lentibulariaceae	Annual
UHI	*Utricularia hispida* Lamarck	Lentibulariaceae	Annual
USU	*Utricularia subulata* Linnaeus	Lentibulariaceae	Annual
VPL	*Vriesea pleiosticha* (Grisebach) Gouda	Bromeliaceae	Rosette
VSP	*Vriesea splendens* (Brongniart) Lemaire	Bromeliaceae	Rosette

2

3

Legends for figures

Figure 1. Map of French Guiana, indicating the localization of inselbergs (modified after Descamps et al. (1978))

Figure 2.

A South overview of the 'rock savanna' on the Nouragues inselberg, showing the summit plateau (called 'Summit'), the cliff and the lower terrace (called 'Les Terrasses')

B A young ramet of *Clusia minor*, surrounded by *Pitcairnia geyskesii*. Note the adventitious development of *C. minor* on the right side of the photo

C An advancing destruction zone in a *Clusia* thicket (advance from left to right). In the right part, dead wood has been already transformed into humus, now covered with mosses, while branches of *C. minor* are still living on the left, with fallen wood and standing dead wood as intermediates

D A macro-view of the wood of *C. minor*, infested by the basidiomycete *Lentinus* gr. *villosus* (see sporocarp), then colonized by a termite society (*Nasutitermes*). Note the deposition of wood transformed into excrements along the branches, bark being not or only poorly consumed

E A destruction zone now colonized by a variegated flora, dominated by saplings of the shrub *Ernestia granvillei*. Note the absence of litter from *Clusia minor*, dead roots of this species being apparent at the ground surface, indicating erosion of the accumulated humus

F A destruction zone now partly colonized by mosses (foreground), herbaceous species (*Pitcairnia geyskesii*, *Scleria cyperina*) and woody species (Myrtaceae)

Figure 3. Total correspondence analysis

A Projection of samples and passive variables (growth forms, sites, slope classes, species richness) in the plane of the first two axes

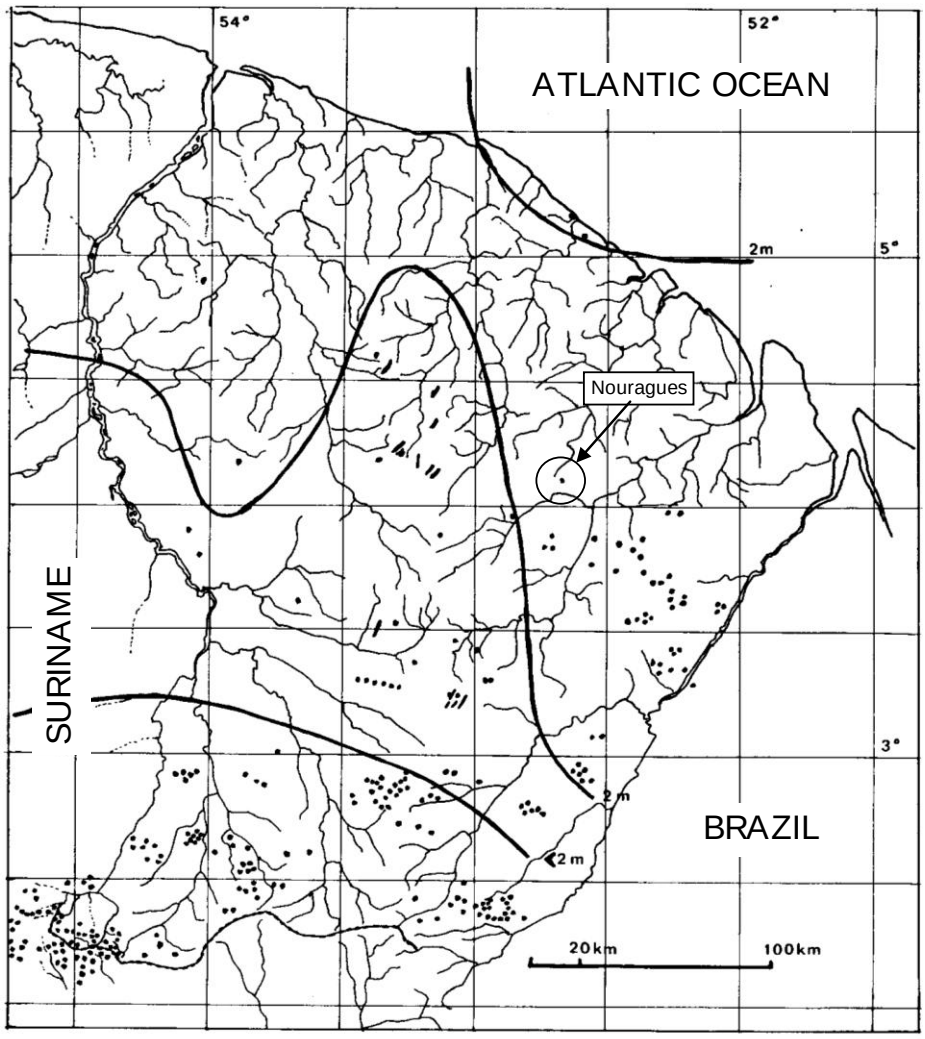
B Projection of active variables (plant species) in the plane of the first two axes

Figure 4. Relationships between cover values (Van der Maarel scale) of *Pitcairnia geyskesii* and *Clusia minor* in patches of 'rock savanna' on slopes. Black dot size is proportional to the number of superposed samples (from 1 to 9)

Figure 5. Four stages of the seral development of *Clusia minor* thickets on moderate slopes (modified after Sarthou (1992))

Figure 6. Three stages of the development of vegetation and sediments in granite depressions (modified after Sarthou 1992). Arrows indicate the advance of sand deposits

Figure 7. Successional relationships between main vegetation types of the 'rock savanna' on slopes and depressions, and the parallel development of (organic) soils and (mineral) sediments


54°
52°
ATLANTIC OCEAN
2m
5°
Nouragues
SURINAME
3°
2m
BRAZIL
2m
20km
100km

1

2 **Fig. 1.**

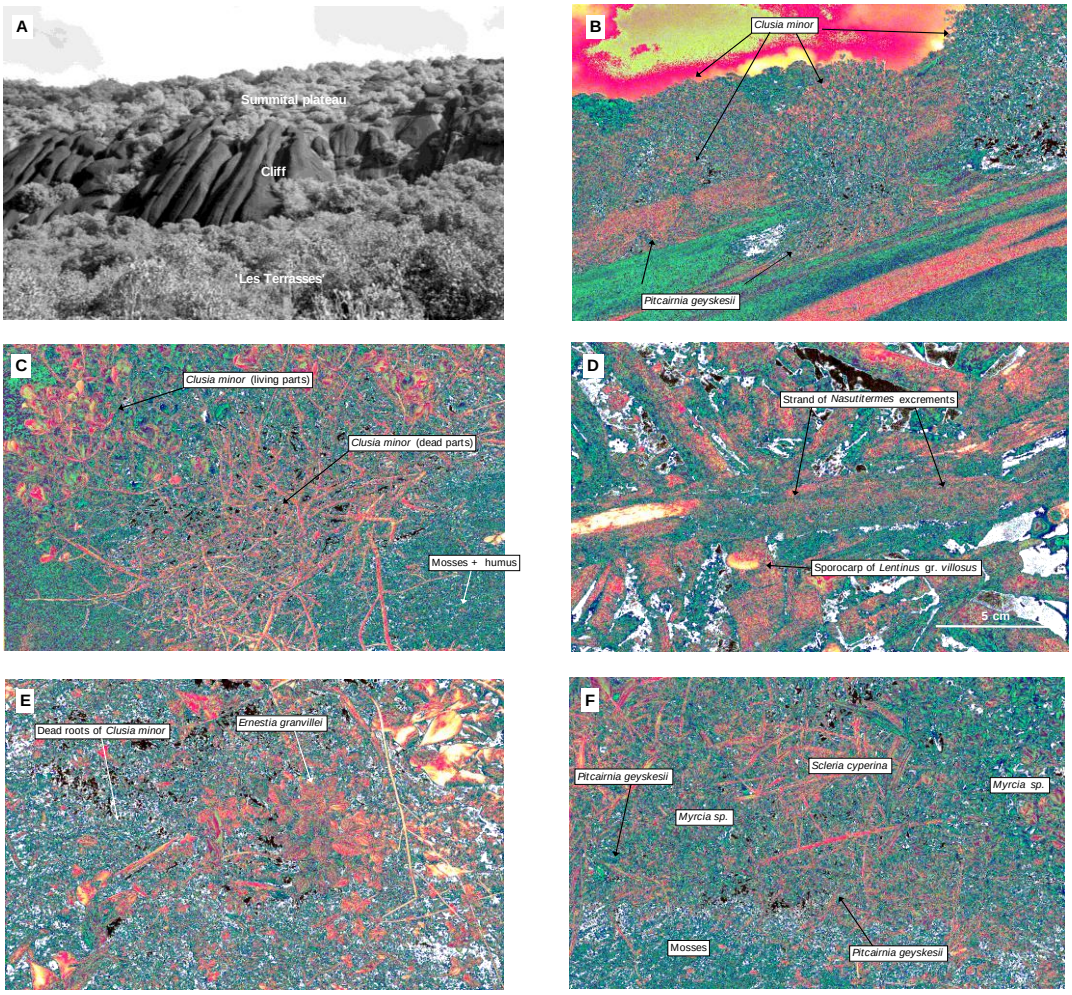
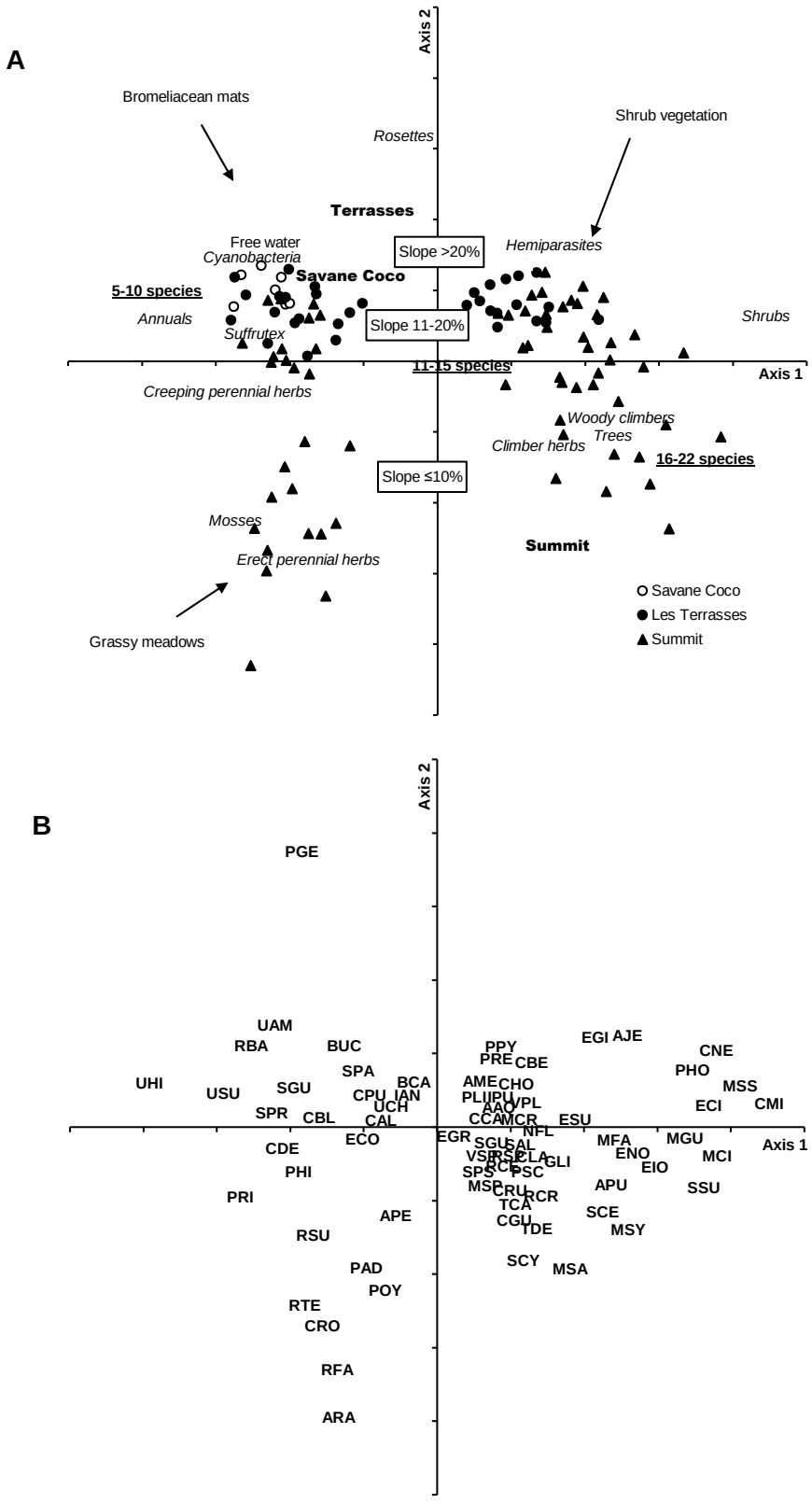

A
Summital plateau
Cliff
Les Terrasses
B
Clusia minor
Pitcairnia geyskesii
C
Clusia minor (living parts)
Clusia minor (dead parts)
Mosses + humus
D
Strand of Nasutitermes excrements
Sporocarp of Lentinus gr. villosus
5 cm
E
Dead roots of Clusia minor
Ernestia granvillei
F
Pitcairnia geyskesii
Scleria cyperina
Myrcia sp.
Myrcia sp.
Mosses
Pitcairnia geyskesii

Fig. 2.


A
Axis 2
Axis 1
Bromeliacean mats
Shrub vegetation
Rosettes
Terrasses
Free water
Cyanobacteria
Savane Coco
Slope >20%
Hemiparasites
5-10 species
Annuals
Suffrutex
Slope 11-20%
Shrubs
11-15 species
Creeping perennial herbs
Woody climbers
Trees
Climber herbs
16-22 species
Slope ≤10%
Mosses
Erect perennial herbs
Summit
Grassy meadows
Savane Coco
Les Terrasses
Summit
B
Axis 2
Axis 1
PGE
UAM
RBA
BUC
EGI
AJE
PPY
PRE
CBE
CNE
PHO
SPA
UHI
USU
SGU
BCA
AME
CHO
MSS
CPU
IAN
PLI
IPU
VPL
ECI
CMI
UCH
AAO
SPR
CBL
CAL
CCA
MCR
ESU
NFL
EGR
ECO
MFA
MGU
SGU
SAL
ENO
MCI
CDE
VSP
RSC
CLA
GLI
EIO
PHI
BCE
PSC
SPS
APU
SSU
MSP
CRU
PRI
TCA
SCR
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PAD
MSA
POY
RTE
CRO
RFA
ARA

Fig. 3

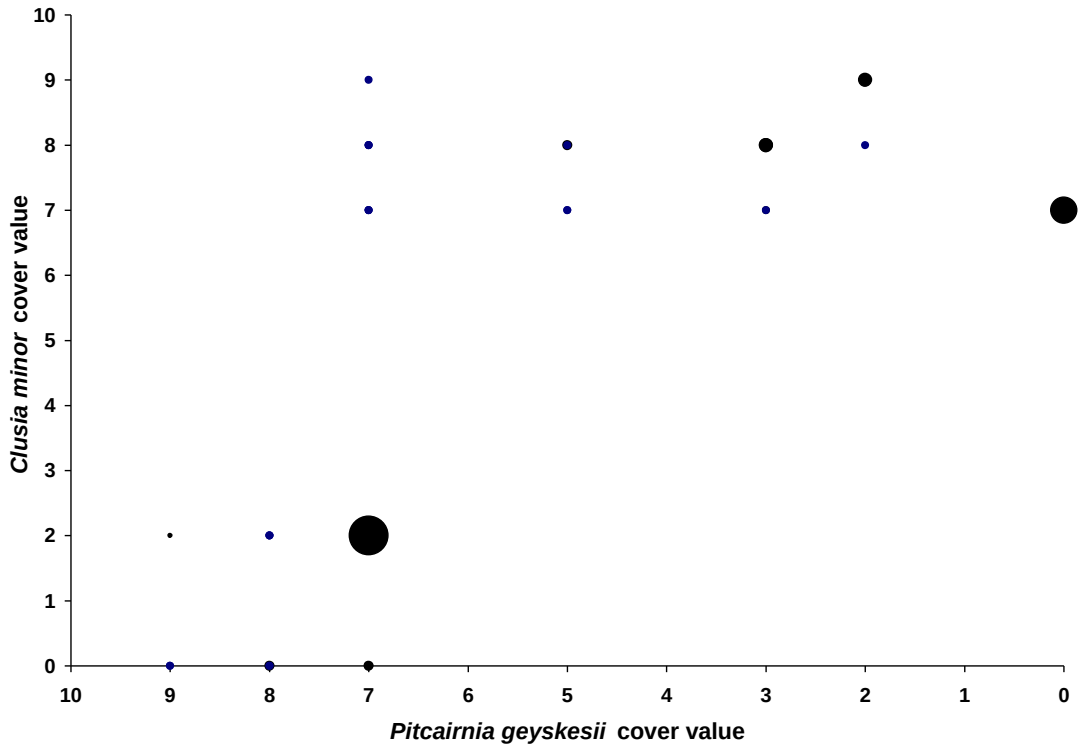
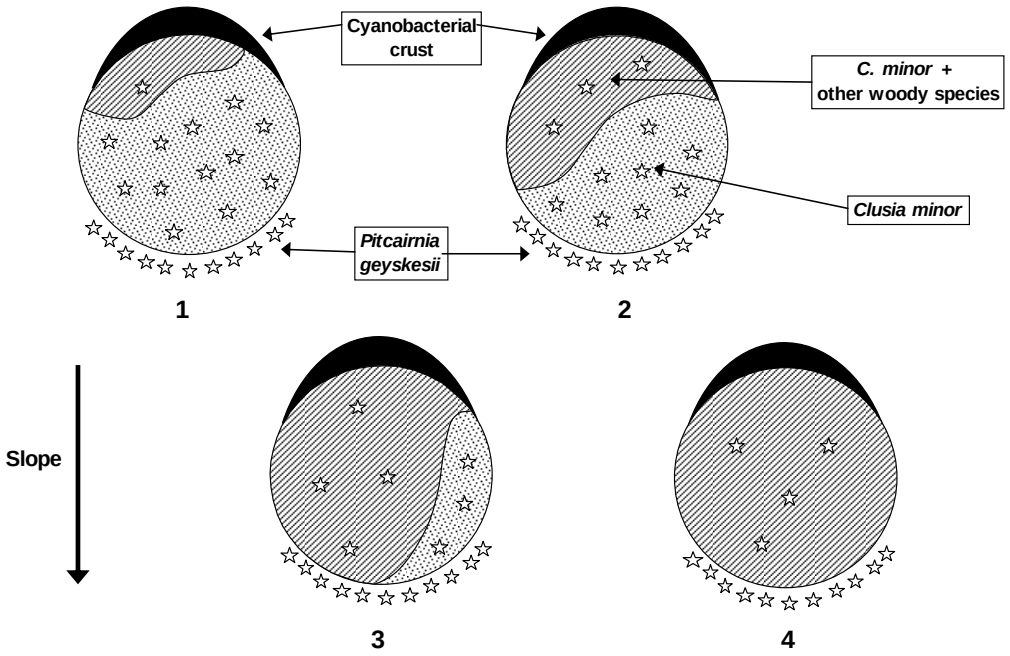

10
9
8
7
6
5
4
3
2
1
0
Clusia minor cover value
10
9
8
7
6
5
4
3
2
1
0
Pitcairnia geyskesii cover value

Fig. 4


Cyanobacterial crust
C. minor + other woody species
Clusia minor
Pitcairnia geyskesii
1
2
Slope
3
4

1

2 **Fig. 5**

3

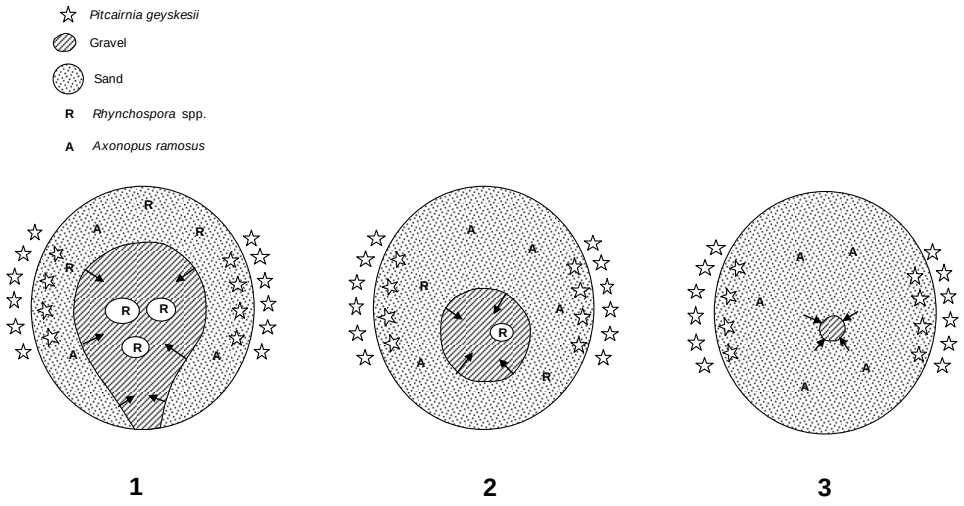

Pitcairnia geyskesii
Gravel
Sand
R Rhynchospora spp.
A Axonopus ramosus
1
2
3

Fig. 6

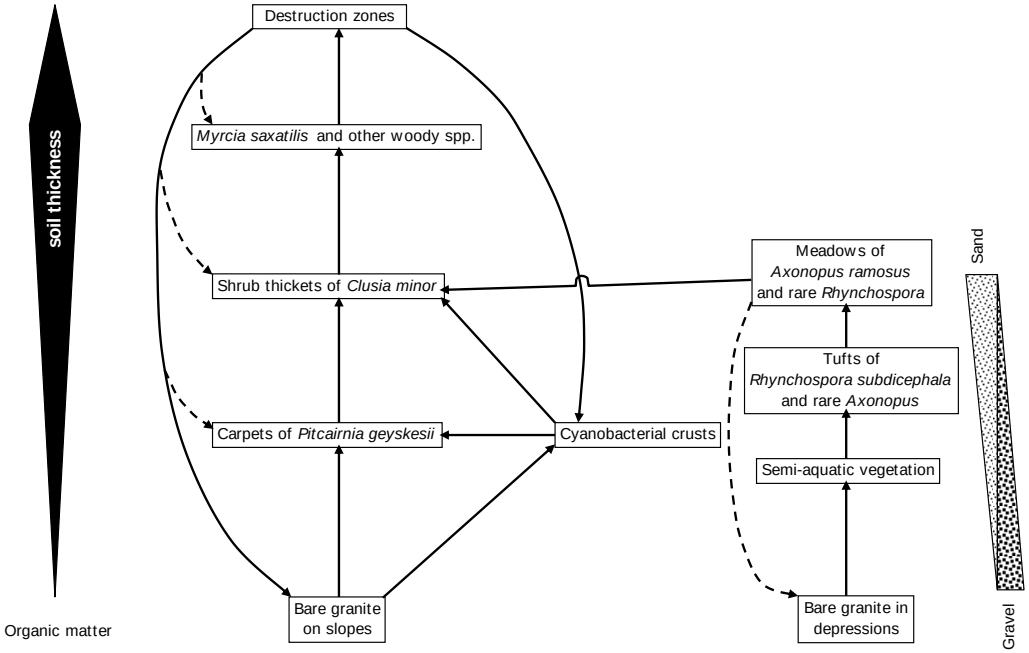

soil thickness
Organic matter
Destruction zones
Myrcia saxatilis and other woody spp.
Shrub thickets of Clusia minor
Carpets of Pitcairnia geyskesii
Bare granite on slopes
Cyanobacterial crusts
Meadows of Axonopus ramosus and rare Rhynchospora
Tufts of Rhynchospora subdicephala and rare Axonopus
Semi-aquatic vegetation
Bare granite in depressions
Sand
Gravel

Fig. 7