From inselberg to inselberg: floristic patterns across scales in French Guiana (South America)

Corinne Sarthou, Sandrine Pavoine, Jean-Pierre Gasc, Jean-Christophe de Massary, Jean-François Ponge

► To cite this version:

Corinne Sarthou, Sandrine Pavoine, Jean-Pierre Gasc, Jean-Christophe de Massary, Jean-François Ponge. From inselberg to inselberg: floristic patterns across scales in French Guiana (South America). *Flora*, 2017, 229, pp.147-158. 10.1016/j.flora.2017.02.025 . hal-01494703

HAL Id: hal-01494703

<https://hal.science/hal-01494703>

Submitted on 23 Mar 2017

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Public Domain

**From inselberg to inselberg: floristic patterns across scales in French
Guiana (South America)**

Corinne Sarthou^{1,*}, Sandrine Pavoine², Jean-Pierre Gasc³, Jean-Christophe de Massary⁴, Jean-François Ponge³

¹*Muséum National d'Histoire Naturelle, Institut de Systématique, Évolution, Biodiversité, ISYEB UMR 7205 – CNRS, MNHN, UPMC, EPHE, Sorbonne Universités, 57 rue Cuvier, CP 39, 75005 Paris, France*

²*Muséum National d'Histoire Naturelle, Département Écologie et Gestion de la Biodiversité, UMR 7204 – CNRS, UPMC, 55-61 rue Buffon, 75005 Paris, France*

³*Muséum National d'Histoire Naturelle, Département Écologie et Gestion de la Biodiversité, UMR 7179 – CNRS, MNHN, 4 avenue du Petit Château, 91800 Brunoy, France*

⁴*Muséum National d'Histoire Naturelle, Service du Patrimoine Naturel, 36 rue Geoffroy Saint-Hilaire, CP 41, 75005 Paris, France.*

*Corresponding author

E-mail addresses of the authors:

C. Sarthou: sarthou@mnhn.fr

S. Pavoine: pavoine@mnhn.fr

J.P. Gasc: gasc@mnhn.fr

J.C. de Massary: jean-christophe.demassary@mnhn.fr

J.F. Ponge: ponge@mnhn.fr

ABSTRACT

Granitic outcrop vegetation was compared in 22 inselbergs of French Guiana, South America, using RLQ and fourth-corner analyses to identify the main relationships between environmental gradients and plant traits. At the scale of the whole territory the distribution of species and species traits was mostly driven by a spatially-structured gradient embracing regional climate (annual rainfall), forest matrix (canopy openness), and inselberg features (altitude, shape, habitats, summit forest, degree of epiphytism, fire events). Biogeographic, environmental and past historical factors contribute to explain the variation observed at coarse scale and two groups of inselbergs are identified. A first group occupies the southern peneplain in a semi-open forest matrix and exhibits a higher representation of suffrutescent species and climbers, a lower representation of upright shrubs, a lower degree of Guiana Shield endemism, and a higher incidence of human use and autochory. All these features suggest an adaptation to more disturbed environments linked to past climate changes and savannization and to human influences. A second group, characterized by opposite plant traits, occupies the northern part of French Guiana and the far south within a closed forest matrix. Within archipelagos (inselbergs at less than 7 km distance), C-score and Mantel tests revealed a random co-occurrence of plant species and an increase of floristic dissimilarity with distance without any concomitant change in plant traits, respectively, suggesting that spatially-structured stochastic factors (limitation by dispersal) were the driving force of vegetation change at fine scale.

Keywords: French Guiana; Inselbergs; RLQ and fourth-corner analysis; Endemism; Human use; Savannas

1. Introduction

Inselbergs are dome-shaped rocky outcrops rising above surrounding plains (Bornhardt, 1900). They have been reviewed worldwide for their geological origin and for their biotic diversity by Porembski and Barthlott (2000). They vary in size and height, being sometimes limited to only a few meters (Bremer and Sander, 2000). They can be considered as analogous to functional islands (Prance, 1996) in a general matrix such as deserts, savannas or forests. Whatever their dimensions, the crystalline rocky surface of inselbergs is covered by a peculiar vegetation growing in a shallow soil layer, a general property of rocky outcrop vegetation adding an ecological dimension to the geomorphological definition of “inselbergs” (Gröger and Barthlott, 1996).

In northern South America, inselbergs are especially frequent in French Guiana within the Guiana Shield (Fig.1). They consist of Precambrian granites. Detailed accounts on their geomorphology and geology were provided by some authors (Hurault, 1973; Teixeira et al., 1989; Delor et al., 2003). French Guianan inselbergs are isolated or clustered in groups called archipelagos. They are mainly distributed in all the southern landscapes (Fig. 1): especially large inland plains, plateaus and mountain chains (Guitet et al., 2013). They are covered with discontinuous vegetation forming a type of mosaic locally called “rock savanna”. This vegetation is characterized by numerous scattered herbaceous and shrubby patches separated by bare rock (de Granville, 1978; Sarthou, 1992; Sarthou and Villiers, 1998; Sarthou et al., 2003). The “rock savanna” vegetation is kept in a dynamic state by erosion and fire events (Kounda-Kiki et al., 2008; Sarthou et al., 2009). It undergoes extreme local climate variation during the day-night cycle: high and frequent variations in temperature (18-55°C) and relative humidity (20-100%; Sarthou, 1992). Cyanobacteria cover the surface of granitic outcrops (Sarthou et al., 1995) and take part in organic matter production and incipient soil formation (Vačulik et al., 2004). Soils are generally shallow, acid with low water-holding capacity

(Sarthou and Grimaldi, 1992). So, inselbergs may be viewed edaphically and climatically as xeric habitats, creating xeric habitat islands in a humid forest matrix.

The influence of past climatic changes in tropical rainforests, especially in South America, has been widely debated (Colinvaux et al. 2000, Willis and Whittaker 2000). The periodic glaciations of the Quaternary corresponded to drier climatic conditions (Hooghiemstra and Hammen 1998). Climatic changes during the last Pleistocene glaciation (between 22 000 and 10 000 years ago) were characterized by a reduction of rainfall and a drop in temperature by up to 5°C compared to the present (Dynesius and Jansson 2000). Consequently, species distributions have been strongly affected (Pennington et al. 2000, Bonaccorso et al. 2006). It has been suggested that these drier and colder periods would have led to the expansion of open vegetation types such as savannas (Hooghiemstra and Hammen 1998). However, climate shifts did not have the same effect over the whole French Guianan territory. During the Holocene, rain forests of the northern part of French Guiana probably remained within the range of more than 2000 mm annual rainfall (Hooghiemstra and van der Hammen, 1998), and soil carbon isotope studies showed that they did not undergo savannization (Freycon et al., 2010). Forest refuges were located in the north while savanna-like vegetation extended in the south (de Granville, 1982; Tardy, 1998). Following de Granville (1982), inselbergs may be interpreted as xeric flora refuges during the present wet period.

The present paper makes the first synthetic and comparative overview of the vascular vegetation spread over granitic outcrops of French Guiana. Our aim is to elucidate the patterns of floristic variation in relation to space, local environment, surrounding environment, plant traits, biogeographic affinities and past history. We also postulate, according to Wiens (1989) that factors acting at fine scale (i.e. within archipelagos) differ from those acting at coarse scale (i.e. over the whole territory of French Guiana). Several hypotheses will be tested. First,

we hypothesize that at the scale of French Guiana (coarse scale) differences in floristic composition are mainly explained by environmental factors operating directly and indirectly through the selection of adaptive traits (Hypothesis 1). We also hypothesize that past floristic history (biogeographic affinities, climate changes, human settlements) influenced the present-day composition of inselberg vegetation (Hypothesis 2). At last we hypothesize that at fine scale, i.e. within archipelagos, differences in floristic composition result from dispersal limitation by distance rather than from positive and/or negative species interactions (Hypothesis 3).

2. Materials and methods

2.1. Study area

As part of the Guiana Shield in northern Amazonia, French Guiana (4°13'N, 52°59'W) covers about 85,000 km² and has a mean altitude of about 140 m above sea level with few mountainous peaks exceeding 800 m. Its basement, approximately 2.2–1.9 G years in age, corresponds to the oldest and most homogeneous part of the Guiana Shield (Delor et al., 2003). Its climate is equatorial and is characterized by 3000 mm mean annual rainfall, distributed along a Northeast to Southwest gradient decreasing from about 4000 to 2000 mm (Fig. 1), with rainfall being concentrated mainly between December and July (Héritier, 2011). Granitic inselbergs were mostly concentrated in southern and eastern parts of the territory (Fig. 1). In the extreme south, groups of elevated dome-shaped inselbergs border the Brazilian Amazonian basin. The peneplain in the southern half part of French Guiana (Fig. 1) is characterised by low elevated and slightly slanting rocky slabs in a semi-open forest matrix. The northern half part of French Guiana is covered with a dense rain forest with isolated dome-shaped inselbergs (Gond et al., 2011).

We studied 22 inselbergs (of which 15 are grouped in 4 archipelagos) scattered over the territory of French Guiana (Fig. 1). We carried out field work to analyse the vegetation of 20 granite outcrops from 1988 to 2011: Nouragues, Trinité A, Mont Chauve, Bakra (A, B), Roche Dachine, Arawa, Wanapi (A, B, C, D, E), Haut Marouini (A, B, C, D, F, G), Mont Saint Marcel, Mitaraka Sud (each letter designates an isolated inselberg). The data set was completed for Trinité B and Virginie through an extraction from the Cayenne Herbarium (CAY) database (available at <http://publish.plantnet-project.org/project/caypub>): the sampling effort devoted to Trinité B and Virginie by the collectors allowed us to consider these additional records as comprehensive and fully reliable (Appendix A). Geographic coordinates of each site (longitude, latitude) were recorded by a GPS device and are expressed in decimal degrees (coordinate system WGS 84; Appendix A). Sampling effort was adapted to area and environmental heterogeneity of each site, and was included in data analysis in the form of three scores: 1 from one to two days, 2 from 10 to 14 days, and 3 for more than 14 days.

2.2. Sampling design

A comprehensive inventory of the vascular flora was undertaken on each rocky outcrop. However, we excluded from the analysis: (1) species growing in the ecotone zone between rock-savanna and the surrounding forested matrix; (2) species growing in summit forests (when present). Consequently, the analysis is restricted to the “rock savanna” facies *sensu stricto* characterized by vegetation patches on bare rock. Furthermore, we also exclude epiphytic species because the epiphyte layer requires a peculiar sampling protocol. We estimated that the sampling of epiphytes was insufficient.

The final data set comprises 318 plant species (Appendix B). Voucher specimens were deposited in the Cayenne Herbarium (CAY) and were registered in the Cayenne Herbarium database. Plant identification was performed according to Funk et al. (2007).

2.3. *Environmental data*

To characterize relevant aspects of the environment we used ten parameters: latitude-longitude, mean annual rainfall according to Hritier (2011), maximum altitude, outcrop area, geographical distance between outcrops, openness of the forest matrix surrounding outcrops, dominant savanna facies, habitats, and occurrence of a summit forest and a cliff (Appendix A).

Mean annual rainfall was coded as 1 from 2200 to 2400 mm, 2 from 2400 to 2600 mm, 3 from 2600 to 2800 mm, 4 from 2800 to 3000 mm, 5 from 3000 to 3200 mm, 6 from 3200 to 3400 mm, 7 from 3400 to 3600 mm, and 8 from 3600 to 3800 mm and was treated as an ordinal variable.

Maximum altitude was measured during field survey with a GPS device (Appendix A). The area of each outcrop was calculated from aerial photographs and was measured directly in the field for the smallest inselbergs (Appendix A). Geographical distances between inselbergs were calculated using the GIS program Mapinfo^{} version 9.0.

Canopy openness of the forest matrix surrounding each inselberg was classified as an ordinal variable with three modalities according to data obtained from remote sensing (Gond et al., 2011): dense and regular canopy, mixed canopy and open canopy (Appendix A), coded 1, 2 and 3, respectively. Two facies of savanna (flat-savanna and steep-savanna) were distinguished, their dominance depending on whether the inselberg was flattened or dome-shaped, respectively (Appendix A). Each of these facies was coded as 1 or 0 according to its presence or absence in a given inselberg (nominal variable). Note that when both facies were co-dominant (in the case of Roche Dachine) these variables could thus not be considered as redundant and were treated separately.

The list of habitats available on the rock outcrops was based on Porembski et al. (2000) after refinement from field observations. Twelve types of habitat were retained and treated as nominal variables with two attributes (presence/absence; see Appendix A): cryptogamic vegetation of rock surfaces (habitat 1), wet flush vegetation (habitat 2), vascular epilithic vegetation (habitat 3), vegetation of horizontal or vertical crevices (habitat 4), vegetation of seasonal rock pools in depressions (habitat 5), vegetation on rock debris in depressions (habitat 6), herbaceous vegetation of soil-filled depressions (habitat 7), woody vegetation of soil-filled depressions (habitat 8), ephemeral flush vegetation (habitat 9), monocotyledonous mats on sun-exposed steep rocky slopes (habitat 10), suffrutescent vegetation on sun-exposed rocky slopes (habitat 11) and woody vegetation on sun-exposed rocky slopes (habitat 12). Note that the first habitat type (cryptogamic vegetation = cyanobacteria or lichens in the inselberg context) was present everywhere and thus was not accounted for in the analyses. The number of epiphytic species was measured by an ordinal variable coded as 1 (< 5 epiphyte species), 2 (5-10 species), or 3 (> 10 species).

2.4. Plant traits and biogeographic affinities

To understand the response of outcrop vegetation to environmental variability, we selected seven plant traits and considered biogeographic affinities of each species (Table 1, Appendix B). Growth-form classification was adapted from Ramsay and Oxley (1997). Fruit types were grouped in four major categories according to Lorts et al. (2008). Seed dispersal syndromes were grouped in four categories according to van der Pijl (1982) and Howe and Smallwood (1982). Dispersal mechanisms of species were either recorded in the field or based on fruit and seed morphology. Data were also collected in literature (Roosmalen, 1985). Each plant species was assigned to one or more of these dispersal syndromes, which were treated as distinct dummy variables.

Considering the high xeric environmental constraints on inselberg vegetation, species presenting a crassulacean acid metabolism (CAM) were identified from literature (Lüttge, 2007; Silvera et al., 2009, 2010; Crayn et al., 2015) and succulent species were also identified (personal observations).

Human use of plant species in the Guianas was documented from Grenand et al. (2004), DeFilipps et al. (2004) and Cadamuro (2000) in order to disclose potential human-mediated effects.

Data concerning the geographic distribution of taxa were mainly obtained from diverse Neotropical floras, especially Steyermark et al. (1995-2005) and Funk et al. (2007), and from the on-line Brazilian Herbarium (available at <http://reflora.jbrj.gov.br/jabot/herbarioVirtual/>). Biogeographic classes were first specified according to de Granville (1992) and Kelloff and Funk (2004), then were grouped in three categories according to their affinity to the Guiana Shield, the Neotropics or elsewhere (Table 1, Appendix B). A nominal variable describing the degree of Guiana Shield endemism was created by assigning to each group a score varying from 1 to 3.

2.5. Statistical analyses

The joint structure of species, species traits and environmental factors at the scale of the whole territory of French Guiana (Hypothesis 1) was analysed by a combination of two methods: RLQ (Legendre et al., 1997) and fourth-corner tests (Dolédec et al., 1996). Both methods are complementary and can be combined in a procedure described by Dray et al. (2014) which allows the graphical representation of species-trait-environment relationships and to test them by a Monte-Carlo simulation method. These calculations were done using the module ade4 package of R (R Core Team, 2016).

Three matrices were created for RLQ: a matrix crossing sites (inselbergs) with environmental variables (matrix R), a matrix crossing sites with species occurrences (matrix L) and a matrix crossing species with species traits (matrix Q). They were simultaneously ordinated, resulting in a factorial hyperspace of reduced dimensions (RLQ factorial axes) in which sites, species, species traits and environmental variables can be simultaneously projected, with permutation procedures to evaluate the significance of their relationships. Taxonomic units, growth forms, fruit types, levels of endemism and carbon metabolic types were considered as nominal variables with 4, 9, 4, 3 and 3 modalities each, respectively. Dispersal types, which are not exclusive, were considered as separate dummy variables. To original spatial variables (longitude as x and latitude as y), which only describe east-west and north-south gradients, respectively, we added polynomial combinations of scaled latitude and longitude (x^2 , y^2 , x^3 , y^3 , x^2y , xy^2) which could potentially reveal a higher variety of spatial patterns (Borcard et al., 1992). In matrices R and Q, ordinal variables were rank transformed and treated as quantitative. Both matrices were then analysed using Principal Component Analysis (PCA) designed for both nominal and quantitative variables (Hill and Smith, 1976).

Fourth corner tests were first used to test the significance of the relationships between each trait modality and each environmental variable. The high number of combinations did not allow finding significant relationships between traits and environment, once significance levels were adjusted for simultaneous comparisons, despite global significance of trait-environment relationships. Thereby the alternative procedure suggested by Dray et al. (2014) was applied. Cross comparisons between traits and environmental variables were replaced by testing directly the links between RLQ axes and both traits and environmental variables, after adjustment for multiple comparisons (Benjamini and Yekutieli, 2001), using the `fourthcorner.rlq` function.

Variance partitioning between space and environment was achieved by the procedure proposed by Borcard et al. (1992), using simple and partial Redundancy Analysis (RDA) with either species or traits as dependent (explained) variables and environmental variables as independent (explanatory) variables. The species matrix was the L matrix used for RLQ. The trait matrix was constructed by assigning to each site (inselberg) the % contribution of each trait modality, which was calculated as the number of species possessing a given trait modality divided by the number of species recorded in the inselberg (Appendix A). Floristic and environmental data were standardized by reweighting and focusing (mean = 0, standard deviation = 1). Calculations were done with XLSTAT[®] version 2016.

The influence of past floristic history (Hypothesis 2) was partly tested by the above procedures (RLQ followed by fourth-corner tests). The human use of plant species and their degree of endemism to the Guiana Shield (biogeographic affinity) were considered as traits, which were thus included in the Q matrix and analysed by RLQ and fourth-corner tests. Other factors could not be introduced as variables but a critical examination of a wide corpus of literature allowed discussing these influences in a special chapter.

Fine-scale patterns of floristic change (Hypothesis 3) were studied by comparing species or trait dissimilarity (Jaccard index and Spearman-rank dissimilarity, respectively) with geographic distance for couples of inselbergs belonging to the same archipelago (Wanapi, Haut Marouini, Trinité, Monts Bakra), using the Mantel test. Monte Carlo simulation (9999 replicates) was performed within each inselberg group (archipelago) before computing a global correlation coefficient according to a procedure implemented in ade4 (R Core Team, 2016).

Departure from random variation in the co-occurrence of plant species was tested both at coarse-scale (the whole set of inselbergs) and at fine-scale (within archipelagos) using checkerboard C-scores (Stone and Roberts, 1990). This measure of community structure

calculates the number of checkerboard units (specimens in which two taxa are not found together) between all possible taxon pairs in a matrix, and calculates a single score for the entire data set. The C-score is the average for all of the possible pairs in the matrix. This measure is compared with a null distribution of random matrices of the same size. If the observed C-score is larger than the score for the null hypothesis, it suggests significant segregation between taxa, and if the observed C-score is smaller than the score for the null hypothesis, it suggests significant aggregation between taxa. Regression tests were done with XLSTAT[®] version 2015, and C-scores were calculated using EcoSim Professional[®].

3. Results

Permutation tests (9999 replicates) showed that there was a global link between traits and environment ($P < 0.01$). The distribution of eigenvalues (1.485, 0.069, 0.046, 0.029, and 0.016 for the first five factorial axes) showed an abrupt shift from the first factorial axis (88.4% of total inertia) to the second one (4.1% of total inertia). Thereby only the first factor (called RLQ1) will be taken into consideration in the following, although two-dimensional plots were thought to be visually more comfortable. Results of RLQ analysis and fourth-corner tests (Hypotheses 1 and 2) were represented by figures 2 to 5. For the sake of clarity, sites, species, traits and environmental variables were represented as separate bi-plots but it should be noted that their projection was simultaneous.

The projection of sites (Fig. 2) showed a clear separation between two groups of inselbergs, (*i*) the southern peneplain (Haut Marouini, Wanapi, Arawa) with negative coordinates, and (*ii*) a group with positive coordinates comprising the far south (Mitaraka, Mont Saint Marcel) and the northern group (Roche Dachine, Monts Bakra, Mont Chauve, Nouragues, Virginie, Trinité).

For the two groups, dominant families and their species numbers are indicated in Table 2. The group including northern inselbergs, Mitaraka and Mont Saint-Marcel inselbergs, exhibits a greater number of families and species than the peneplain group (69 families versus 55 families; 265 species versus 149 species). In the first group, the best represented families are Orchidaceae and Bromeliaceae, including numerous epilithic and terrestrial herbs, and Myrtaceae, Clusiaceae and Rubiaceae, including numerous upright shrubs growing in dense thickets. All these families are poorly represented in inselbergs of the peneplain group (Table 2). In the two groups, Poaceae, Cyperaceae, Fabaceae and Melastomataceae families are well represented.

RLQ1 was significantly and positively associated with rainfall, latitude, squared and cubed latitude, inselberg area, presence of a summit forest, of steep slopes, epiphytism (all with $P < 0.01$), altitude and presence of habitat 10 corresponding to monocotyledonous mats (both with $P < 0.05$). It was significantly and negatively associated with openness of the surrounding forest matrix, longitude, the product of squared latitude with longitude, the presence of flat areas and of habitat 11 corresponding to suffrutescent vegetation (all with $P < 0.01$). The gradient depicted by RLQ1 associated spatial and environmental factors, opposing small, low elevated and flattened inselbergs of the southern peneplain to large, dome-shaped, elevated inselbergs of the northern group and of the extreme south along a gradient of increasingly rainy climate and associated ecological features (closed forest matrix, summit forest, bromeliacean mats, and shrub thickets with epiphytes).

Among plant traits, RLQ1 was significantly and positively associated with the highest degree of Guianan endemism ($P < 0.05$), upright shrubs ($P < 0.01$), and was significantly and negatively associated with human use, autochory, suffrutescence (all with $P < 0.01$) and climbers ($P < 0.05$).

The decomposition of the total variance in environmental, spatial and spatially-structured (shared) variation (Table 3) showed that traits compared to species displayed a higher (x 2) contribution of spatially-structured environment and a lesser contribution of pure space (x 0.74). Both species and traits showed a higher contribution of pure environment than of pure space, the ratio being higher for traits (1.9) than for species (1.5).

At fine scale (Hypothesis 3), Figure 6 showed a discrepancy between species and traits when their dissimilarity was plotted against geographical distances: dissimilarity between inselbergs included within archipelagos increased with distance when species were considered (Mantel correlation coefficient $r_M = 0.53$; $P = 0.019$), while the correlation between trait and geographical matrices was feeble ($r_M = 0.10$) and not significant ($P = 0.62$) when traits were considered.

Checkerboard scores (Table 4) showed that plant species co-occurred at random at fine scale (among inselbergs located within the same archipelago) but did not at coarse scale (over the whole set of inselbergs), pointing to stochastic factors explaining changes in floristic composition within archipelagos, while floristic changes between archipelagos are mainly explained by non-stochastic factors.

4. Discussion

4.1. Abiotic parameters and response traits at coarse and fine scale

RLQ and fourth-corner analyses support our Hypothesis 1 and reflect how at coarse scale, differences in floristic composition are mainly explained by environmental factors operating directly and indirectly through the selection of adaptive traits. Species trait distribution changed according to a composite, spatially-structured gradient, embracing variations in climate (annual rainfall, and associated vegetation features: epiphytism, summit forest, habitats), inselberg shape (flattened versus dome-shaped, low versus high elevation),

composition of the surrounding forest (semi-open versus closed canopy) and human influences. Among traits, suffrutescence, climbers, and autochory are drought-adaptive traits (Monneveux and Belhassen, 1996; Schnitzer, 2005). These traits are better represented at a lower level of annual rainfall on peneplain inselbergs by *Ernestia* spp. *Spermacoce* spp., *Dioclea guianensis*, *Cissus erosa*, *Omphalea diandra* (Fig.3). Conversely, upright shrubs represented by *Clusia* spp. and *Myrcia* spp. (Fig. 3), which constitute dense thickets on northern inselbergs (Sarhou et al., 2003; Fonty et al., 2009), and Guianan endemics, adapted to a more rainy climate than Central Amazonian species (Ter Steege et al., 2000), are better represented at a higher level of annual rainfall, showing the importance of climate in the composite gradient depicted by RLQ. A similar situation has been recorded in a study performed on African inselbergs by Parmentier et al. (2005), showing rainfall as the second main driver of floristic heterogeneity at regional scale, after altitude.

Among habitats, annual-perennial herbaceous mats, the dominant vegetation type of inselberg savannas (Porembski et al., 2000) show a southwards shift from epilithic bromeliacean mats (habitat 10) on slopes with flowing water, dominated by *Pitcairnia geyskesii* (Fig. 3) to grassy suffrutescent meadows (habitat 11) on flat areas with shallow mineral soil, dominated by suffrutescent species such as *Stylosanthes guianensis*, *Chamaecrista desvauxii*, *Ernestia* spp., *Unxia camphorata*, *Sinningia incarnata*, *Sipanea pratensis*, *Spermacoce* spp. and graminaceous species such as *Ischaemum guianense* and *Axonopus ramosus* (Fig. 3). Habitat 11 is reminiscent of the dominant inselberg vegetation of less rainy countries both in the Neotropics (Porembski et al., 1998) and in Africa (Parmentier et al., 2005) which have in common poikilohydric sedges belonging to the genera *Trilepis* and *Afrotrilepis*, respectively.

The climate effect, mediated by adaptive traits, does not preclude the existence of other indirect effects of climate, such as those mediated by surrounding cryptogamic

vegetation (biological crusts), known to affect germination and survival of vascular plants and nutrient availability (Belnap et al., 2001; Sarthou et al., 2009): the lower biomass of cyanobacteria or the replacement of cyanobacteria by lichens along the southwards aridity gradient has probably influenced the floristic composition to some extent.

Climate influences also the structure of the forest matrix (the rain forest) and thus influences regional species pools from which inselberg floras are filtered (Burke, 2002). A noticeable difference in floristic composition (beta diversity) was reported between the forest located in the northern part and the southern part of French Guiana, in relation to geomorphology (Sabatier and Prévost, 1990), and a general pattern may be described at a regional scale (Gond et al., 2011; Guitet et al., 2015). At present, southern forests, with their lower level of annual rainfall, are characterized by their almost open aspect (discontinuous canopy), especially in the southern peneplain where numerous local clearings are found, while northern forests show a continuous canopy typical for rain forests (Gond et al., 2011).

Elevation may also yield contrasting effects on floristic composition. If present and past climate prove to be important factors, local environmental variables (shape, elevation, presence of summit forest) also contribute strongly to explain inselbergs' floristic composition. As evidence, all dome-shaped and elevated inselbergs with summit forest are quite similar in composition even if far in the (drier) south, like St Marcel and Mitaraka, or in the (wetter) north, like Nouragues. We suppose that this local environmental effect which contributes to the observed floristic variation (Table 3) could be related to micro-climate. In fact it has been shown that at mid-elevation water condensation favours fern diversity (Kluge et al. 2006) and a higher biomass and diversity of epiphytes (Gehrig-Downie et al., 2011, 2013). The frequent mists we observed on the most elevated inselbergs (Mitaraka) in the dry season, together with relatively low temperature (19°C), may explain why inselbergs of the far south, while being in a lower precipitation zone (Fig. 1) share more species and species

traits with the northern group than with the southern group. Montane species settled during glacial (drier) periods may have survived here under these conditions, making Mitaraka and Saint Marcel important refuges for Pleistocene floras.

At fine scale, C-scores (Table 4) showed that inselbergs of the same archipelago did not display any checkerboard pattern of floristic composition. There was no segregation of species due to competition (Bowker and Maestre, 2012) and/or priority effects (Fukami, 2015), as well as no positive interspecific interactions (López et al., 2016). However, floristic dissimilarity within archipelagos increased with distance, while trait dissimilarity did not change (Fig. 6), supporting our Hypothesis 3 of dispersal limitation by distance in a common environmental context, i.e. when inselbergs share similar environmental conditions and have most probably undergone a common history (Flinn et al., 2010). Parmentier and Hardy (2009) also showed that differences in floristic composition result from dispersal limitation by distance on African inselbergs.

4.2. Influence of past climate changes and human use

RLQ and fourth-corner analyses also allowed checking part of our second hypothesis while taking Guiana Shield endemism and human use as proxies for past history.

Endemism is better represented at a higher level of annual rainfall. Past climate changes during the Pleistocene and the Holocene are generally evoked to explain this. These climatic changes have modified the floristic composition of the matrix, the rain forest being replaced by open forests or even savannas, relative elevation being increased by lowering of the sea level, with mountain taxa coming into lowland forest (Hooghiemstra and Hammen 1998, Pennington et al. 2004; Rull, 2005; Pinter et al., 2011). However, in French Guiana, a clear difference appears between northern and southern forests. The northern part revealed a

high degree of tolerance during Holocene drier climatic periods (Hooghiemstra and van der Hammen, 1998; Tardy, 1998; Freycon et al., 2010) and constituted rain forest refuges which remained genetically isolated (Granville, 1982; Tardy, 1998; Boisselier-Dubayle et al., 2010). This continuous-in-time isolation may be considered as a reason for a high degree of endemism (Vuilleumier, 1970). Our data (Appendix A) showed that inselbergs of the northern part had on average $30.1 \pm 1.4\%$ (mean $\pm$ SE) Guianan endemics (Guiana Shield + Guianas + French Guiana) against only $19.7 \pm 0.8\%$ for the southern group, the Mitaraka group being intermediate with $23.6 \pm 0.4\%$ endemics.”

In contrast, the southern part displays much disturbance and fire witnesses (Tardy, 1998), suggesting the occurrence of a past savanna-like matrix (and thus numerous exchanges of diaspores) around the numerous inselbergs present today in the peneplain zone. Human use, autochory as characteristic dispersal type, suffrutescence and climbers as characteristic growth types, all these features being associated with the ‘negative’ side of the gradient, are indicators of disturbance of the environment. Autochory, i.e. the absence of dispersal, does not facilitate avoidance in space but generates an abundant soil seed bank, an adaptive strategy used by plant communities when faced to recurrent destruction and regeneration of the vegetation cover (Valbuena and Trabaud, 2001). Suffrutescence and climbers are also associated to such environments, with a high power of post-disturbance regeneration from subterranean organs (Keeley et al., 2006; Schnitzer, 2005). Among causes of disturbance, in addition to seasonal and inter-annual abrupt changes in climate conditions, human activities probably play a non-negligible role, with concomitant increases in trampling, fire, erosion and deletion of species (Pinter et al., 2011). The low elevated and flattened inselbergs of the peneplain are of easy access and Hurault (1989) indicates a high density of Indian tribes in this southern zone.

Otherwise, the ancient and long-time occurrence of Indian populations in the peneplain was considered. Convergent data integrate the southern plain of French Guiana within a large continuous savanna zone spreading from the Venezuelan Llanos, including Roraima, Rupununi, Sipaliwini savannas (Fig. 1) to the upper and middle parts of the northern tributaries of the Amazon River during drier periods of the Holocene (Mayle and Power, 2008). This zone also played the role of a corridor for human dispersal (Plew, 2005; Piperno, 2011). In this context, men probably lived in open areas and used slash-and-burn technics only in the nearby forest, exploiting ecotone plant diversity (Plew, 2005). The fact that wild manihot (*Manihot esculenta* ssp. *flabellifolia*) found on southern inselbergs displays a striking genetic homogeneity (Duputié et al., 2009) is a probable legacy of ancient human management by fire and cultivation in a savanna-like context. This created repeated contacts between inselbergs and temporary colonization of open space in the plain by wild stems of several cultivated plants. Floristic affinities between rock savannas of the peneplain and savannas also suggest the occurrence of an ancient connection between them. Thus, we evaluate that the peneplain inselbergs share 30% of species with Sipaliwini savanna (van Donselaar, 1968; Oldenburger et al., 1973).

5. Conclusion

Our study provides evidence that regional climate, surrounding forest matrix and inselberg features (altitude, shape, habitats, summit forest, epiphytism, fire events) are associated to shifts in the distribution of species and functional traits and determine floristic patterns on French Guianan inselbergs. The study also improves our understanding on how past climatic changes leading to savannization events in the South and how humans using outcrop plants can affect the species composition of inselbergs in the southern peneplain. The high degree of Guiana Shield endemism of inselbergs located within the northern rainforest,

which were seemingly neither affected by past climatic changes nor by human uses points to the need to protect them.

Acknowledgements

This research paper is the end-product of several projects and was mainly supported by a grant from Feder n°1348 (Contrat Plan Etat Région with Ecofor/Gis Silvolab-Guyane, IRD, MNHN as partners). We are grateful to Jean-Jacques de Granville for his field contribution, help in species identification and fruitful discussions. We also thank two anonymous reviewers for their constructive comments on the manuscript. We acknowledge the curator of the Cayenne Herbarium (CAY), Sophie Gonzalez for providing database information. We also thank G. Cremers, F. Crozier, L. Alier, P. Gaucher for their assistance in field work. M. Boudrie, T. Deroin, P. Grenand, V. Guérin, P. Héritier, P. Joubert and B. Lefeuvre have also provided interesting data in their respective scientific domains.

Appendix A. Spatial and environmental data

Appendix B. Floristic data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/xxxx>.

References

- Belnap, J., Prasse, R., Harper, K.T., 2001. Influence of biological soil crusts on soil environments and vascular plants, in Belnap, J., Lange, O.L. (Eds.), Biological soil crusts: structure, function, and management. Springer, Berlin, pp. 281-300.
- Benjamini, Y., Yekutieli, D., 2001. The control of the false discovery rate in multiple testing under dependency. *Ann. Statist.* 29, 1165-1188.
- Boisselier-Dubayle, M.C., Leblois, R., Samadi, S., Lambourdière, J., Sarthou, C., 2010. Genetic structure of the xerophilous bromeliad *Pitcairnia geyskesii* on inselbergs in French Guiana: a test of the forest refuge hypothesis. *Ecography* 33, 175-184.
- Bonaccorso, E, Koch, I., Townsend Peterson, A., 2006. Pleistocene fragmentation of Amazon species' ranges. *Divers. Distrib.* 12, 157-164.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045-1055.
- Bornhardt, W., 1900. *Zur Oberflächengestaltung und Geologie Deutsch-Ostafrikas*. Reimer, Berlin.
- Bowker, M.A., Maestre, F.T., 2012. Inferring local competition intensity from patch size distributions: a test using biological soil crusts. *Oikos* 121, 1914-1922.
- Bremer, H., Sander, H., 2000. Inselbergs: geomorphology and geoecology, in Porembski, S., Barthlott, W. (Eds.), *Inselbergs: Biotic Diversity of Isolated Rock Outcrops in Tropical and Temperate Regions*. Springer, Berlin, pp. 7-35.
- Burke, A., 2002. Island-matrix relationships in Nama Karoo inselberg landscapes. I. Do inselbergs provide a refuge for matrix species? *Plant Ecol.* 160, 79-90.
- Cadamuro, L., 2000. *Plantes Comestibles de Guyane*. Ecocart, Toulouse.

- 511 Colinvaux, P.A., de Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant
512 communities on glacial time-scales: the failure of the aridity and refuge hypotheses.
513 Quaternary Sci. Rev. 19, 141-169.
- 514 Crayn, D.M., Winter, K., Schulte, K., Smith, J.A.C., 2015. Photosynthetic pathways in
515 *Bromeliaceae*: phylogenetic and ecological significance of CAM and C3 based on
516 carbon isotope ratios for 1893 species. Bot. J. Linn. Soc. 178, 169-221.
- 517 DeFilipps, R.A., Maina, S.L., Crepin, J., 2004. Medicinal Plants of the Guianas (Guyana,
518 Surinam, French Guiana). Smithsonian Institution, Washington.
519 http://botany.si.edu/bdg/medicinal/Medicinal_plants_master.pdf (accessed 11.05.16).
- 520 Delor, C., Lahondère, D., Egal, E., Lafon, J.M., Cocherie, A., Guerrot, C., Rossi, P., Truffert,
521 C., Théveniaut, H., Phillips, D., de Avelar, V.G., 2003. Transamazonian Crustal
522 Growth and Reworking as Revealed by the 1:500,000-Scale Geological Map of French
523 Guiana. Bureau de Recherches Géologiques et Minières, Orléans.
- 524 Dolédec, S., Chessel, D., ter Braak, C.J.F., Champely, S., 1996. Matching species traits to
525 environmental variables: a new three-table ordination method. Environmental and
526 Ecological Statistics 3, 143-166.
- 527 Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak,
528 C.J.F., 2014. Combining the fourth-corner and the RLQ methods for assessing trait
529 responses to environmental variation. Ecology 95, 14-21.
- 530 Duputié, A., Delêtre, M., de Granville, J.J., McKey, D., 2009. Population genetics of *Manihot*
531 *esculenta* ssp. *flabellifolia* gives insight into past distribution of xeric vegetation in a
532 postulated forest refugium area in northern Amazonia. Mol. Ecol. 18, 2897-2907.
- 533 Dynesius, M., Jansson, R., 2000. Evolutionary consequences of changes in species'
534 geographical distributions driven by Milankovitch climate oscillations. Proc. Nat.
535 Acad. Sci. USA 97, 9115-9120.

- 536 Flinn, K.M., Gouhier, T.C., Lechowicz, M.J., Waterway, M.J., 2010. The role of dispersal in
 537 shaping plant community composition of wetlands within an old-growth forest. *J.*
 538 *Ecol.* 98, 1292-1299.
- 539 Fonty, E., Sarthou, C., Larpin, D., Ponge, J.F., 2009. A 10-year decrease in plant species
 540 richness on a neotropical inselberg: detrimental effects of global warming? *Global*
 541 *Change Biol.* 15, 2360-2374.
- 542 Freycon, V., Krencker, M., Schwartz, D., Nasi, R., Bonal, D., 2010. The impact of climate
 543 changes during the Holocene on vegetation in northern French Guiana. *Quaternary*
 544 *Res.* 73, 220-225.
- 545 Fukami, T., 2015. Historical contingency in community assembly: integrating niches, species
 546 pools, and priority effects. *Ann. Rev. Ecol. Evol. Syst.* 46, 1-23.
- 547 Funk, V., Hollowell, T., Berry, P., Kelloff, C., Alexander, S.N., 2007. Checklist of the Plants
 548 of the Guiana Shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana,
 549 Surinam, French Guiana). Smithsonian Institution, Washington.
- 550 <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.454.3269&rep=rep1&context=pdf>. (accessed 11.05.16).
- 551
- 552 Gehrig-Downie, C., Obregón, A., Bendix, J., Gradstein, S.R., 2011. Epiphyte biomass and
 553 canopy microclimate in the tropical lowland cloud forest of French Guiana. *Biotropica*
 554 43, 591-596.
- 555 Gehrig-Downie, C., Obregón, A., Bendix, J., Gradstein, S.R., 2013. Diversity and vertical
 556 distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of
 557 French Guiana. *J. Bryol.* 35, 243-254.
- 558 Gond, V., Freycon, V., Molino, J.F., Brunaux, O., Ingrassia, F., Joubert, P., Pekel, J.F.,
 559 Prévost, M.F., Thierron, V., Trombe, P.J., Sabatier, D., 2011. Broad-scale spatial

- 560 pattern of forest landscape types in the Guiana Shield. *Int. J. Appl. Earth Obs. Geoinf.*
 561 13, 357-367.
- 562 de Granville, J.J., 1978. *Recherches sur la Flore et la Végétation Guyanaise*. PhD thesis,
 563 Université des Sciences et Techniques de Montpellier, Montpellier.
- 564 de Granville, J.J., 1982. Rain forest and xeric flora refuges in French Guiana, in Prance, G.T.
 565 (Ed.), *Biological Diversification in the Tropics*. Columbia University Press, New
 566 York, pp. 159-181.
- 567 de Granville, J.J., 1992. Un cas de distribution particulier: les espèces forestières péri-
 568 amazoniennes. *C. R. Soc. Biogéogr.* 68, 1-33.
- 569 Grenand, P., Moretti, C., Jacquemin, H., Prévost, M.F., 2004. *Pharmacopées Traditionnelles*
 570 *en Guyane: Créoles, Wayapi, Palikur*. Institut de Recherche pour le Développement,
 571 Paris.
- 572 Gröger, A., Barthlott, W., 1996. Biogeography and diversity of the inselberg (Laja) vegetation
 573 of southern Venezuela. *Biodivers. Lett.* 3, 165-179.
- 574 Guitet, S., Comu, J.F., Brunaux, O., Betbeder, J., Carozza, J.M., Richard-Hansen, C., 2013.
 575 Landform and landscape mapping, French Guiana (South America). *J. Maps* 9, 325-
 576 335.
- 577 Guitet, S., Péliissier, R., Brunaux, O., Jaouen, G., Sabatier, D., 2015. Geomorphological
 578 landscape features explain floristic patterns in French Guiana rainforest. *Biodivers.*
 579 *Conserv.* 24, 1215-1237.
- 580 Héritier, P., 2011. *Le Climat Guyanais: Atlas Climatique de la Guyane Française*. Météo-
 581 France, Cayenne.
- 582 Hill, M.O., Smith, A.J.E., 1976. Principal component analysis of taxonomic data with multi-
 583 state discrete characters. *Taxon* 25, 249-255.

- 584 Hooghiemstra, H., van der Hammen, T., 1998. Neogene and Quaternary development of the
585 neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth*
586 *Sci. Rev.* 44, 147-183.
- 587 Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13, 201-
588 228.
- 589 Hurault, J., 1973. Les inselbergs rocheux des régions tropicales humides, témoins de
590 paléoclimats. *CR Soc. Biogéogr.* 439, 49-54.
- 591 Hurault, J., 1989. Français et Indiens en Guyane: 1604-1972. Guyane Presse Diffusion,
592 Cayenne.
- 593 Keeley, J.E., Fotheringham, C.J., Baer-Keeley, M., 2006. Demographic patterns of postfire
594 regeneration in Mediterranean-climate shrublands of California. *Ecol. Monogr.* 76,
595 235-255.
- 596 Kelloff, C.L., Funk, V.A., 2004. Phytogeography of the Kaieteur Falls, Potaro Plateau,
597 Guyana: floral distributions and affinities. *J. Biogeogr.* 31, 501-513.
- 598 Kluge, J., Kessler, M. and Dunn, R.R., 2006. What drives elevational patterns of diversity? A
599 test of geometric constraints, climate and species pool effects for pteridophytes on an
600 elevational gradient in Costa Rica. *Global Ecol. Biogeogr.* 15, 358-371.
- 601 Kounda-Kiki, C., Ponge, J.F., Mora, P., Sarthou, C., 2008. Humus profiles and successional
602 development in a rock savanna (Nouragues inselberg, French Guiana): a
603 micromorphological approach infers fire as a disturbance event. *Pedobiologia*, 52, 85-
604 95.
- 605 Legendre, P., Galzin, R., Harmelin-Vivien, M.L., 1997. Relating behavior to habitat: solutions
606 to the fourth-corner problem. *Ecology* 78, 547-562.

- 607 López, R.P., Squeo, F.A., Armas, C., Kelt, D.A., Gutiérrez, J.R., 2016. Enhanced facilitation
608 at the extreme end of the aridity gradient in the Atacama Desert: a community-level
609 approach. *Ecology* 97, 1593-1604.
- 610 Lorts, C.M., Briggeman, T., Sang, T., 2008. Evolution of fruit types and seed dispersal: a
611 phylogenetic and ecological snapshot. *J. Syst. Evol.* 46, 396–404.
- 612 Lüttge, U., 2007. *Clusia: a Woody Neotropical Genus of Remarkable Plasticity and Diversity*.
613 Springer, Berlin.
- 614 Mayle, F.E., Power, M.J., 2008. Impact of a drier Early–Mid-Holocene climate upon
615 Amazonian forests. *Phil. Trans. R. Soc. B* 363, 1829-1838.
- 616 Monneveux, P., Belhassen, E., 1996. The diversity of drought adaptation in the wide. *Plant*
617 *Growth Regul.* 20, 85-92.
- 618 Oldenburger, F.H.F., Norde, R., Riezebos, H.T., 1973. Ecological Investigations on the
619 Vegetation of the Sipaliwini Savanna Area in Southern Surinam. University of
620 Utrecht, Laboratory of Physical Geography, Internal Report.
- 621 http://www.sipaliwinisavanna.com/docs/ecological_investigations_vegetation_sipaliwi
622 [ni_savanna.pdf](http://www.sipaliwinisavanna.com/docs/ecological_investigations_vegetation_sipaliwi). (accessed 11.05.16).
- 623 Parmentier, I., Hardy, O.J., 2009. The impact of ecological differentiation and dispersal
624 limitation on species turnover and phylogenetic structure of inselberg's plant
625 communities. *Ecography* 32, 613-622.
- 626 Parmentier, I., Stévant, T., Hardy, O.J., 2005. The inselberg flora of Atlantic Central Africa. I.
627 Determinants of species assemblages. *J. Biogeogr.* 32, 685-696.
- 628 Pennington, R.T., Prado, D.E, Pendry, C.A. 2000. Neotropical seasonally dry forests and
629 Pleistocene vegetation changes. *J. Biogeogr.* 27, 261-273.
- 630 Pennington, R. T., Lavin, M., Prado, D.E, Pendry, C.A., Pell, S.K, Butterworth, C.A., 2004.
631 Historical climate change and speciation: Neotropical seasonally dry forest plants

- 632 show patterns of both Tertiary and Quaternary diversification. *Phil. Trans. R. Soc. B*
 633 359, 515-538.
- 634 Pinter, N., Fiedel, S., Keely, J. E., 2011. Fire and vegetation shifts in the Americas at the
 635 vanguard of Paleoindian migration. *Quaternary Sci. Rev.* 30, 269-272.
- 636 Piperno, D.R., 2011. The origins of plant cultivation and domestication in the New World
 637 tropics. *Curr. Anthropol.* 52, 453-470.
- 638 Plew, M.G., 2005. The archaeology of Iwakrama and North Rupununi. *Proc. Acad. Nat. Sci.*
 639 Philadelphia 154, 7-28.
- 640 Porembski, S., Barthlott, W., 2000. Inselbergs: Biotic Diversity of Isolated Rock Outcrops in
 641 Tropical and Temperate Regions. Springer, Berlin.
- 642 Porembski, S., Becker, U., Seine, R., 2000. Islands on islands: habitats on inselbergs, in
 643 Porembski, S., Barthlott, W. (Eds.), *Inselbergs: Biotic Diversity of Isolated Rock*
 644 *Outcrops in Tropical and Temperate Regions*. Springer, Berlin, pp. 49-67.
- 645 Porembski, S., Martinelli, G., Ohlemüller, R., Barthlott, W., 1998. Diversity and ecology of
 646 saxicolous vegetation mats on inselbergs in the Brazilian Atlantic rainforest. *Divers.*
 647 *Distrib.* 4, 107-119.
- 648 Prance, G.T., 1996. Islands in Amazonia. *Phil. Trans. Roy. Soc. London B* 351, 823-833.
- 649 R Core Team (2016) R: a Language and Environment for Statistical Computing. R foundation for
 650 Statistical Computing, Vienna.
- 651 Ramsay P.M., Oxley, E.R.B., 1997. The growth form composition of plant communities in
 652 the Ecuadorian paramos. *Plant Ecol.* 131, 173-192.
- 653 Roosmalen, M., 1985. *Fruits of the Guianan Flora*. Institute of Systematic Botany, Utrecht.
- 654 Rull, V., 2005. Biotic diversification in the Guayana Highlands: a proposal. *J. Biogeogr.* 32,
 655 921-927.

- 656 Sabatier, D., Prévost, M.F., 1990. Quelques données sur la composition floristique et la
 657 diversité des peuplements forestiers de Guyane Française. *Bois For. Trop.* 219, 31-55.
- 658 Sarthou, C., 1992. Dynamique de la Végétation Pionnière sur un Inselberg en Guyane
 659 Française. PhD thesis, Université Pierre-et-Marie-Curie, Paris.
- 660 Sarthou, C., Grimaldi, C., 1992. Mécanisme de colonisation par la végétation d'un inselberg
 661 granitique en Guyane française. *Rev. Écol. Terre Vie* 47, 329-349.
- 662 Sarthou, C., Villiers, J.F., 1998. Epilithic plant communities on inselbergs in French Guiana.
 663 *J. Veg. Sci.* 9, 847-860.
- 664 Sarthou, C., Thérézien, Y., Couté, A., 1995. Cyanophycées de l'inselberg des Nouragues.
 665 *Nova Hedwigia* 61, 85-109.
- 666 Sarthou, C., Villiers, J.F., Ponge, J.F., 2003. Shrub vegetation on tropical granitic inselbergs
 667 in French Guiana. *J. Veg. Sci.* 14, 645-652.
- 668 Sarthou, C., Kounda-Kiki, C., Vačulik, A., Mora, P., Ponge, J.F., 2009 Successional patterns
 669 on tropical inselbergs: a case study on the Nouragues inselberg (French Guiana). *Flora*
 670 204, 396-407.
- 671 Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and
 672 distribution. *Am. Nat.* 166, 262- 276.
- 673 Silvera, K., Santiago, L.S., Cushman, J.C., Winter, K., 2009. Crassulacean acid metabolism
 674 and epiphytism linked to adaptive radiations in the Orchidaceae. *Plant Physiol.* 149,
 675 1838-1847.
- 676 Silvera, K., Santiago, L.S., Cushman, J.C., Winter, K., 2010 The incidence of crassulacean
 677 acid metabolism in Orchidaceae derived from carbon isotope ratios: a checklist of the
 678 flora of Panama and Costa Rica. *Bot. J. Linn. Soc.* 163, 194-222.
- 679 Spjut, R.W., 1994. A Systematic Treatment of Fruit Types. New York Botanical Garden, New
 680 York.

- 681 Steyermark, J.A., Berry, P.E., Yatskievych, K., Holst, B.K., 1995-2005. Flora of the
 682 Venezuelan Guayana, Volumes I-IX. Timber Press, Portland and Missouri Botanical
 683 Garden Press, St. Louis.
- 684 Stone, L., Roberts, A., 1990. The checkerboard score and species distribution. *Oecologia* 85,
 685 74-79.
- 686 Tardy, C., 1998. Paléoincendies Naturels, Feux Anthropiques et Environnements Forestiers de
 687 Guyane Française du Tardiglaciaire à l'Holocène Récent: Approches Chronologiques
 688 et Anthracologiques. PhD thesis, Université Montpellier 2, Montpellier.
- 689 Teixeira, W., Tassinari, C.C.G, Cordani, U.G., Kawashita, K., 1989. A review of the
 690 geochronology of the Amazonian craton: tectonic implications. *Precambrian Res.* 42,
 691 213-227.
- 692 Ter Steege, H., Sabatier, D., Castellanos, H., Van Andel, T., Duivenvoorden, J., Adalardo de
 693 Oliveira, A., Ek, R., Lilwah, R., Maas, P., Mori, S., 2000. An analysis of the floristic
 694 composition and diversity of Amazonian forests including those of the Guiana Shield.
 695 *J. Tropic. Ecol.* 16, 801-828.
- 696 Vaçulik, A., Kounda-Kiki, C., Sarthou, C., Ponge, J.F., 2004. Soil invertebrate activity in
 697 biological crusts on tropical inselbergs. *Eur. J. Soil Sci.* 55, 539-549.
- 698 Valbuena, L., Trabaud, L., 2001. Contribution of the soil seed bank to post-fire recovery of a
 699 heathland. *Plant Ecol.* 152, 175-183.
- 700 van der Pijl, L., 1982. Principles of Dispersal in Higher Plants. Springer, New York.
- 701 van Donselaar, J., 1968. Phytogeographic notes on the savanna flora of Southern Surinam
 702 (South America). *Acta Bot. Neerland.* 17, 363-404.
- 703 Willis, K. J., Whittaker, R. J. 2000. The refugial debate. *Science* 287, 1406-1407.
- 704 Vuilleumier, F., 1970. Insular biogeography in continental regions. I. The northern Andes of
 705 South America. *Am. Nat.* 104, 373-388.
- 706 Wiens, J.A., 1989. Spatial scaling in ecology. *Funct. Ecol.* 3, 385-397.

707 **Table 1.** Traits and biogeographic affinities of plant species used in RLQ and fourth-corner tests.
 708 Numbers between brackets are the scores used for the ordinal variable describing the degree of Guiana
 709 Shield endemism

Taxonomic unit		Fruit type	
	Fern		Fleshy fruit
	Magnoliid		Dry dehiscent fruit
	Monocot		Dry indehiscent fruit
	Eudicot		Sporangium
Growth form	Erect herb	Seed dispersal syndrome	Anemochory
	Rosette		Zoochory
	Cespitose		Autochory
	Suffrutex		Hydrochory
	Upright shrub	Carbon fixation pathway	C3
	Trailing shrub		C4
	Parasitic shrub		CAM
	Small tree	Biogeographic affinity	Pantropical or cosmopolite (1)
	Climber		Endemic of the Neotropics (2)
	Succulent		Endemic of the Guiana Shield (3)

710

711

Table 2. Number of species in dominant plant families over all inselbergs and in each of the two inselberg groups

	All inselbergs	Northern/Mitaraka/Saint Marcel group	Peneplain group
	74 families 318 species	69 families 265 species	55 families 149 species
Bromeliaceae	15	12	6
Clusiaceae	10	11	4
Cyperaceae	19	18	10
Euphorbiaceae	10	9	5
Fabaceae	14	11	8
Melastomataceae	20	17	11
Myrtaceae	15	13	2
Orchidaceae	20	19	6
Poaceae	21	16	14
Rubiaceae	18	15	7

712

713

714

Table 3. Decomposition of the total variance of species and species traits according to environmental and spatial factors, using simple and partial RDA (Borcard et al., 1992)

	Species	Traits
Pure environment	50.4%	45.4%
Pure spatial	33.3%	24.5%
Spatially-structured environment	10.0%	19.9%
Total explained variation	93.7%	89.8%
Unexplained variation	6.3%	10.2%

715

716

Table 4. Checkerboard scores (C-scores) for co-occurrence of plant species on Guianan inselbergs. Numbers of inselbergs for all inselbergs and for Wanapi and Haut Marouini archipelagos are indicated between parentheses

	Observed index	Simulated index	P (obs < sim)	P (obs > sim)	Standardized effect size	Null hypothesis
All inselbergs (22)	7.71	7.11	1	0	31.12	Rejected
Wanapi (5)	0.040	0	0.54	0.47	-0.057	Accepted
Haut Marouini (6)	0.097	0.096	0.85	0.15	0.94	Accepted

717

718

Figure captions

Fig. 1. Map of French Guiana, showing the 22 studied inselbergs (red triangles; each letter designates an isolated inselberg), among the whole set of inselbergs (black dots), the water system and rainfall isohyets. Inserts at the top of the figure indicate the position of French Guiana within South America (left) and within the Guiana Shield (right), with country limits. Country names are indicated by their capitalized initial: B: Brazil; C: Colombia; FG: French Guiana; G: Guyana; S: Suriname; V: Venezuela. Savanna-like vegetation zones are colored. 1: Roraima; 2: Rupununi; 3: Sipaliwini; 4: Coastal savannas; 5: Llanos.

Fig. 2. RLQ multivariate analysis. Projection of sites (inselbergs) in the plane of the first two main components RLQ1 and RLQ2. Insert: distribution of eigenvalues in order of decreasing importance. WAN A to WAN E = Wanapi archipelago; HMA to HMG = Haut Marouini archipelago; ARA = Arawa; DAC = Roche Dachine; MIT = Mitaraka; SMA = Mont saint Marcel; NOU = Nouragues; VIR = Virginie; CHAU = Mont Chauve; TRI A and TRI B = Trinité archipelago; BAK A and BAK B = Monts Bakra archipelago. See Fig. 1 for their localization.

Fig. 3. RLQ multivariate analysis. Projection of plant species in the plane of the first two main components RLQ1 and RLQ2. The number of plant species is much higher than the number of dots indicated on the bi-plot, because many of them are superposed. Some important species have been stamped (for abbreviations see Appendix B).

Fig. 4. RLQ multivariate analysis and fourth-corner tests. Projection of species traits in the plane of the first two main components RLQ1 and RLQ2. Variables with significant relationships with RLQ1 (fourth-corner tests) are indicated with arrows. Each trait name is centered on the corresponding point.

Fig. 5. RLQ multivariate analysis and fourth-corner tests. Projection of environmental variables in the plane of the first two main components RLQ1 and RLQ2. Variables with significant relationships with RLQ1 (fourth-corner tests) are indicated with arrows. Each trait name is centered on the corresponding point.

Fig. 6. Relationship between floristic dissimilarity (Jaccard index for species, Spearman rank dissimilarity index for species traits) and geographical distance for inselbergs located within archipelagos (less than 7 km distance). y = floristic dissimilarity; x = geographic distance (km); r_M = Mantel coefficient of correlation; * = $P < 0.05$; NS = not significant.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6