Within-plot relationships between tree species occurrences and hydrological soil constraints: an example in French Guiana investigated through canonical correlation analysis

Raphaël Pélissier[1,*], Stéphane Dray[2] and Daniel Sabatier[1]

[1]*IRD, UMR botanique et bioinformatique de l'Architecture des plantes (AMAP), 34398 Montpellier Cedex 5, TA 401P52, France;* [2]*UMR-CNRS 5558, Laboratoire de Biométrie et Biologie Evolutive, Université Lyon 1, 69622 Villeurbanne Cedex, France; *Author for correspondence (e-mail: Raphael.Pelissier@mpl.ird.fr; fax: +33(0)4 676 175 21; phone: +33 (0)4 676 175 23)*

Abstract

Spatial relationships between tree species and hydrological soil constraints are analysed within a 10-ha rainforest plot at Piste de St Elie in French Guiana. We used canonical correlation analysis to cross directly the occurrence-by-species table of 4 992 individuals (d.b.h. ⩾ 10 cm) belonging to 120 species with qualitative soil variables and quantitative spatial data. Firstly, the list of species occurrences was confronted to nine soil descriptors characterising a weathering sequence from the initial well-drained ferralitic cover to transformed hydromorphic soil conditions. This analysis revealed that, apart from some specialised species restricted to the swamps that experience prolonged water saturation, the most abundant species can be ordered along two intermingled gradients of tolerance limiting their niche amplitude: a main gradient of tolerance to prolonged water saturation that appears down slope during the weathering sequence; a second gradient of less importance, displaying the species intolerant of prolonged water saturation according to their tolerance to temporary confinement of the uphill transformed soil systems due to the late appearance of a perched water-table. The results support the hypothesis that at Piste de St Elie, the constraining soil conditions imposed by surface water saturation are more important determinants for tree zonation of many tree species than water shortage. Secondly, the list of species occurrences was confronted to a spatial data table built from a trend surface regression of the tree coordinates. This analysis indicated that soil drainage is the main structuring factor of the local multispecies spatial pattern. After partialling out the soil effect, the multispecies pattern revealed a broader scale of heterogeneity that we supposed to be linked to endogenous factors resulting from population dynamics. Implications of the results are then discussed in the perspective of future research on tree zonation, local diversity pattern and community structuring in tropical rainforests.

Introduction

Complementary environmental and biotic hypotheses are commonly invoked for explaining the spatial structuring of natural ecosystems (see for example Borcard et al. (1992) for an introduction). In tropical rainforests, gap disturbances, species competition, topographic, and edaphic variations are among the driving forces explaining the maintenance of high tree species diversity (Denslow 1987, 1995; He et al. 1996; Gimaret-Carpentier et al. 1998a). These factors are, moreover, expected to act at various spatial scales. The influence of soil conditions (water availability, nutrient content) on the species composition have been emphasised from regional (Baillie et al. 1987; Ashton and Hall 1992) to landscape (Gartlan et al. 1986; Clark et al. 1998, 1999) and to local scales (Newbery and Proctor 1986; Lescure and Boulet

(1985); Basnet (1992); Ter Steege et al. (1993); Sabatier et al. (1997)).

In Amazonia, the soil organisation shows a currently unbalanced status regarding the present tectonic and climatic constraints, which results in a supergene weathering of the initial ferralitic cover, and consequently, in a continuous expansion of the hydromorphic and podzolic conditions (Fritsch et al. 1986; Lucas et al. 1986; Veillon and Soria-Solano 1988). The current transformation process of the initial ferralitic cover has been demonstrated at the local scale in French Guiana by studying hydrological, structural and geochemical modifications of the soil along topographical catenas (Humbel 1978; Guelh 1984; Grimaldi and Boulet 1990; Grimaldi et al. 1994). This transformation can be summarised in four stages (see Fritsch et al. (1986) or Sabatier et al. (1997) for a more detailed introduction). Stage I corresponds to the thick and vertically well-drained initial ferralitic cover. At this stage, only the soils restricted to the edges of the main watercourses experience prolonged water saturation in the upper horizons (surface hydromorphy). At stage II, the profile gets thinner under mechanical and chemical erosion and a compact weathering horizon appears down-slope at very low depth (< 1 m). At stage III the weathering horizon, which is "dry to the touch" in all seasons, is present all along the slope and modifies the soil drainage from deep and vertical to superficial and lateral. Depending on the slope angle, the weathering horizon induces a more or less fleeting water saturation of the upper horizons. Stage IV marks the extension of two transformed hydromorphic systems: (i) a uphill system associated with the formation of closed depressions on the flattop hills (the so called "djougoungpétés" in French Guiana; Fritsch et al. (1986)), where a perched water-table that appears during the rainy season at the bottom of the profile, determines a temporary confined environment in the upper horizons; (ii) a more open downhill system where the upper horizons are more or less permanently saturated by a slow lateral water flow coming from the slope, and in connection with the main drainage axes. These transformed hydromorphic systems represent the first stages of a podzolisation process (Fritsch et al. 1986). The time scale of this transformation is considered to be considerably longer than the lifetime of trees (probably on the order of several thousand years; Grimaldi, M. unpublished data), and therefore affects the spatial pattern of local stand structure and com-

position (Lescure and Boulet 1985; Sabatier et al. 1997).

On another hand, ecophysiological studies carried out in plantations (Huc et al. 1994; Guelh et al. 1998; Bonal et al. 2000a) as well as in natural conditions (Guelh et al. 1998; Bonal et al. 2000b) in French Guiana, mainly focused on water-use efficiency (WUE), but did not enable to clearly elucidate the distribution pattern of species regarding soil conditions. For instance, the very common canopy species *Eperua falcata*, shows high WUE which should allow it to growth in conditions of reduced soil moisture (Bonal et al. 2000a, 2000b), while this species is less abundant than expected on the well-drained initial ferralitic cover which exhibits low water potential in the dry season (Sabatier et al. 1997). There is consequently a need to clarify the species position and tolerance regarding both the weathering transformation sequence of the initial ferralitic cover and the gradient of increasing surface hydromorphy demonstrated by Sabatier et al. (1997).

On the basis of a re-examination of the data from a 10-ha rainforest plot in French Guiana previously studied by Sabatier et al. (1997), we propose in this paper to analyse within-plot relationships between species occurrences and soil factors using direct canonical correlations (CANCOR; Hotelling (1936)). This multivariate constrained ordination technique, briefly presented in a first section, is particularly well-designed for the analysis of occurrence data. As does the classical Canonical Correspondence Analysis (CCA; Ter Braak (1986, 1987)) from species-by-relevés tables, CANCOR allows finding the axes that maximise the linear correlation between two sets of variables, namely a taxonomic occurrence table and a table of qualitative soil variables. Furthermore, we developed an algorithm to compute from this analysis, canonical scores leading to the dual scaling of species amplitude or tolerance (niche breadth; Carnes and Slade (1982)) and habitat diversity, a strategy equivalent to reciprocal scaling proposed by Thioulouse and Chessel (1992) for species-site correspondence analysis. In a last section, CANCOR is applied to our entirely mapped data and enables to deal with local multispecies spatial pattern in a Canonical Correspondence Trend Surface Analysis (CCTSA) using an environmental table directly built from the geographical coordinates of trees (trend surface; Gittins (1968)). Results are discussed with special emphasis on species tolerance, habitat diversity and multispecies spatial patterns.

Material and methods

Study site and data

The site studied is a 10-ha forest plot of the station Piste de St Elie (5°18′ N; 53°3′ W) in French Guiana. The forest is a lowland tropical rainforest that grows on the Armina series of the volcano-sedimentary substratum of the platform of the Guianas, in Northeast Amazonia (Milési et al. 1995). The site is subjected to a humid tropical climate with annual rainfall ranging from 2 500 to 4 000 mm (Boyé et al. 1979).

A total of 6 134 trees with diameter at breast height (d.b.h.) ⩾ 10 cm and belonging to 459 taxons were mapped and identified (nomenclature follows Boggan et al. (1992)). Three species, *Eperua falcata*, *Lecythis idatimon* and *Lecythis persistens* (species' authorities are given in Appendix 1) were represented by more than 300 individuals, while 400 species were represented by less than 20 individuals.

Following the method introduced by (Boulet et al. 1982); see also (Lescure and Boulet 1985), nine hydrological soil types in the 10-ha plot at Piste de St Elie, were entirely mapped (Sabatier et al. 1997). Height soil classes characterising the transformation of the initial ferralitic cover were considered: DVD = deep vertical drainage; Alt = weathered material (red alloterite) at a depth less than 1.2 m; SLD1 = superficial lateral drainage with "dry to the touch" character (DC) between 1 and 1.2 m; SLD2 = superficial lateral drainage with DC at less than 1 m; UhS = uphill system; UhS+DC = uphill system with DC at less than 1.2 m; DhS = downhill system; DhS+DC = downhill system with DC at less than 1.2 m. The ninth soil class, called SH for surface hydromorphy, characterises thalwegs experiencing prolonged periods of surface water saturation, while being relatively independent of the weathering process. From the superimposition of the soil and tree maps, each tree was then attached to one of the nine soil descriptors. Figure 1 gives the distribution of trees among the soil classes. The DVD class, which represents the initial ferralitic cover, is the most abundant one, while the transformed stages and the SH class are less abundant.

Canonical correlation analysis

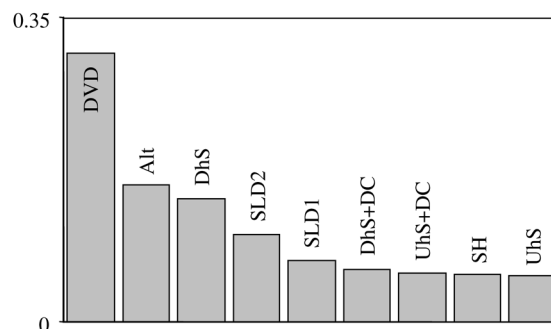Our aim is to perform an ordination of species with the help of environmental variables. When sampling

Figure 1. Frequency distribution of 6 134 trees (d.b.h. ⩾ 10 cm) among 9 hydrological soil classes in a 10-ha forest plot at Piste de St Elie, French Guiana. DVD = deep vertical drainage; Alt = weathered material (red alloterite) at a depth less than 1.2 m; SLD1 = superficial lateral drainage with "dry to the touch" character (DC) between 1 and 1.2 m; SLD2 = superficial lateral drainage with DC at less than 1 m; UhS = uphill system; UhS+DC = uphill system with DC at less than 1.2 m; DhS = downhill system; DhS+DC = downhill system with DC at less than 1.2 m; SH = surface hydromorphy.

units are real relevés, such as spatially independent plots, CCA (Ter Braak 1986, 1987) is a well-suited technique for that purpose which, instead of correlating *a posteriori* a set of environmental variables with the main ordination axes, extracts axes that represent the best linear combination of the environmental variables separating the mean species position (see the bibliographic review of Birks et al. (1996) and the recent paper of Clark et al. (1999) for an example in tropical forest ecology). In principle, CCA can be extended to studying within-plot species-environment relationships by partitioning the plot into more or less arbitrary contiguous quadrats of equal size, a common practice in forest ecology (e.g., Newbery et al. (1996); Pascal and Pélissier (1996); Sabatier et al. (1997)). However, because quadrats defined *a posteriori* are not real relevés, Gimaret-Carpentier et al. (1998b) stressed the interest to consider certain floristic data as lists of species occurrences, where each tree, known by its botanical name and location, is the basic statistical sampling unit. Such lists have been used for a long time in forest ecology for within-plot analysis of tree spatial patterns through methods based on inter-individual distances (e.g., Ripley (1981); Diggle (1983)), but they have been rarely considered as such in ordination techniques. CANCOR (Hotelling 1936), first used in ecology by Austin (1968), gives however an appropriate framework to analyse within-plot relationships between species occurrences and environmental factors.

Let us consider a list of n trees. Its botanical name, spatial position and environment characterise each tree. The taxonomic information is arranged in a table $\mathbf{T}$ with n rows (trees) and s columns (species). For the i-th tree we have:

$$T_{ij} = \begin{cases} 1 & \text{if the } i\text{-th tree belongs to the } j\text{-th species} \quad (1 \leq j \leq s) \\ 0 & \text{otherwise} \end{cases}$$

Let $\mathbf{E}$ be the trees-by-environment table with the measurements or estimations of m environmental variables as columns for the n individuals (rows). Moreover, let $\mathbf{D}_n$ be the n by n diagonal matrix of weights:

$$\begin{cases} \boldsymbol{D}_n(ii) = \dfrac{1}{n} \\ \boldsymbol{D}_n(ij) = 0 \end{cases} \quad \text{for} \quad ij \in [1j], \quad i \neq j$$

CANCOR of $\mathbf{T}$ and $\mathbf{E}$ corresponds to the analysis of the statistical triplet $(\mathbf{T}^t\mathbf{D}_n\mathbf{E}, (\mathbf{E}^t\mathbf{D}_n\mathbf{E})^{-1}, (\mathbf{T}^t\mathbf{D}_n\mathbf{T})^{-1})$ (see Escoufier (1987) for a comprehensive explanation of statistical triplet analysis). CANCOR requires numerical conditions that are well satisfied by our data set: number of trees (6 134) largely bigger than the number of species (459) and the number of environmental variables (9).

CANCOR of $(\mathbf{T}, \mathbf{E})$ consists in finding the normalised canonical variates $\mathbf{t}^*$ and $\mathbf{e}^*$ representing the linear combinations of each set of variables which are the most correlated (see for example Gittins (1985) for further explanations and examples in ecology). In our case, table $\mathbf{T}$ gives a taxonomic information. Therefore, rows of this table are identical for all trees of the same species, to which the canonical variate $\mathbf{t}^*$ consequently gives the same scores. $\mathbf{e}^*$ represents the linear combination of the variables of $\mathbf{E}$ which is the most correlated with the variables of $\mathbf{T}$. As table $\mathbf{T}$ is engendered by a dummy variable, it follows that $\mathbf{e}^*$ is a linear combination of environmental variables maximising the separation of the species centroids. This part of the analysis is known under the name of canonical variate analysis (Gittins 1985) or discriminant analysis (DA; Lebart et al. (1984)). Lebreton et al. (1988) proved that DA is, in a theoretical point of view, exactly the CCA of Ter Braak (1986), but taking as statistical unit the individual instead of the site (Ter Braak and Verdonschot 1995). The averages of environmental variables by species are thus only computed with realised observations (presence), so that sampling bias caused by the use of quadrats is

excluded and that the much-debated step in classical CCA, which consists in a centring of environmental variables with the species richness of the sampling units, is avoided.

Based on individual occurrences, CANCOR permits also partial analyses in which the effects of covariables are factored out (Ter Braak 1988). Considering a table $\mathbf{E}_1$ of variables of interest and a table $\mathbf{E}_2$ of covariables from which the effects must be eliminated, the principle of partial analysis consists in using the residuals of the regression of $\mathbf{E}_1$ on $\mathbf{E}_2$ in table $\mathbf{E}$. In this paper, we performed partial analyses as explained in Méot et al. (1998), i.e. by constraining the residuals to be linear combinations of the variables of $\mathbf{E}_1$.

Ordination diagram

The difficulty in representing results issued from CANCOR, which concerns two sets of variables, is mentioned in several papers (Gauch and Wentworth 1976; Ter Braak 1990). However, we propose an ordination diagram that seems to be very suitable for species occurrence data.

In a geometrical point of view, CANCOR finds a vector $\mathbf{t}^*$ in the species space, which is the nearest of the environment space and, simultaneously, a vector $\mathbf{e}^*$ in the environment space, which is the nearest of the species space. But it is also possible to define CANCOR by finding in the environment + species space, a normalised vector $\mathbf{s}^*$ which is the nearest of the two spaces. This vector is the bisector of the angle formed by the two canonical variates $\mathbf{t}^*$ and $\mathbf{e}^*$ and can be expressed as: $S^* = (e^* + t^*)/\sqrt{\text{var}(e^* + t^*)}$.

The canonical score $\mathbf{s}^*$ maximises simultaneously, and in the same proportion, the between-species variance and the correlation with the environmental variables. When the environmental variables are qualitative, the proposed graphical representation allows to position the occurrences with uncorrelated scores of unit variance, and to put by averaging, species and environmental categories at the centroid of their occurrences. This strategy corresponds to reciprocal scaling (Thioulouse and Chessel 1992) introduced in the context of traditional species-by-sites contingency tables and that allows representing on the same graph, the notions of species weighted optimum and tolerance (niche width), and within- and between- sample diversity.

Computation

D. Chessel implemented CANCOR analysis in the OccurData module of ADE-4 software (Thioulouse et al. 1997) available with documentation at http://pbi-l.univ-lyon1.fr/ADE-4.html. A multivariate randomisation test (Manly 1991) was also implemented in order to test the statistical significance of the canonical axes obtained by CANCOR. It consists in a comparison of the eigenvalues (or sum of eigenvalues) obtained from the original data set, with the ones obtained after row permutations of the environmental table **E**. We used 1 000 row permutations of the environmental table.

Results

Species-soil relationships

As the rare species induced *de facto* strong correlations with the soil variables, we retained from the initial data, 4 992 trees accounting for 120 species with 10 individuals or more in the 10-ha plot. A multivariate randomisation test (Manly 1991) on the total inertia among the soil classes, computed from the centred-by-species table using the Mahalanobis norm and 1 000 permutations ($P < 0.001$), justified further investigation of the relationships between species occurrences and soil factors.

An analysis of the data set by CANCOR suggested that this relationship was clearly expressed by the two first canonical axes: the sum of the two first eigenvalues representing 63.7% of the total inertia, was highly significant ($P < 0.001$). The first canonical plane (not shown) showed outliers corresponding to the occurrences of *Tabebuia insignis* ($N = 11$) and *Euterpe oleracea* ($N = 33$) exclusively found on SH soil.

In a second step, we thus removed these two species in order to examine the ordination of the remaining species from a reduced data set of 4 948 trees belonging to 118 species. As expected, the canonical correlation coefficients were less than in the previous analysis ($r_1 = 0.380$ *vs*. 0.507; $r_2 = 0.298$ *vs*. 0.318), but the sum of the two first eigenvalues representing 54.8% of the total inertia, remained highly significant ($P < 0.001$). The dual scaling property of CANCOR allows the representation of species and soil classes at the weighted mean position of their occurrences on the first canonical plane (Figure 2). This shows that species were scattered between the vertices of a tri-
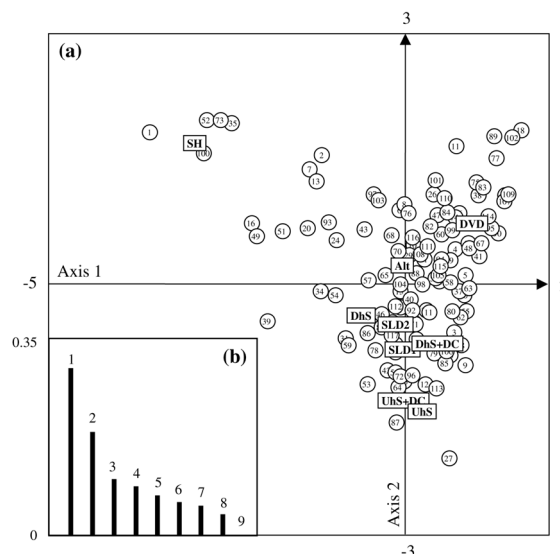

Figure 2. Canonical correlation analysis crossing 4 948 occurrences of trees (d.b.h. $\geq$ 10 cm) belonging to 118 species with 9 hydrological soil classes in a 10-ha forest plot at Piste de St Elie, French Guiana. (a) The circles and squares represent the weighted mean position of the occurrences of the 118 species and the 9 soil classes in the first canonical plane. Species codes are given in Appendix 1. Key for the soil classes is the same as in Figure 1. (b) Percentage of inertia absorbed by the 9 canonical axes.

angle which oppose three poles of constraining soil conditions: prolonged water saturation (SH), temporary confinement during the rainy season (UhS and UhS+DC), and low water potential in the dry season (DVD) (see Figure 4 in Sabatier et al. (1997)).

The between-habitat distance, which corresponds to soil β-diversity, indicates that the species composition in SH differed markedly from the other soil classes, while the transformed soil complex was floristically close to the initial ferralitic cover (DVD). Computation of the multivariate among-group distances using the Mahalanobis norm, confirmed this visual impression (Table 1).

Species optimum and amplitude regarding soil conditions, which can be viewed through the mean and variance of their canonical scores along the ordination axes (given in Appendix 1), are usually summarised by Gaussian curves (see Thioulouse and Chessel (1992)). However, for the sake of clarity, we preferred a different representation (Figure 3) showing separately for axes 1 and 2, the species mean position along a diagonal, with horizontal bars proportional to their amplitude. Figure 3a reveals that species ordination along axis 1 corresponds to a gradient of increasing tolerance to prolonged water saturation

Table 1. Among-group distances (Mahalanobis norm) between nine hydrological soil classes containing 4 948 trees (d.b.h. $\geqslant$ 10 cm) belonging to 118 species in a 10-ha forest plot at Piste de St Elie, French Guiana. Key for the soil classes is the same as in Figure 1.

	SH	DVD	Alt	SLD1	SLD2	DhS+DC	DhS	UhS+DC	UhS
SH	0.00	3.66	2.77	3.33	2.96	4.07	2.35	3.59	4.14
DVD		0.00	0.50	0.89	0.84	1.09	0.91	1.18	1.29
Alt			0.00	0.67	0.59	1.05	0.49	0.95	1.23
SLD1				0.00	0.84	1.24	0.59	0.71	1.15
SLD2					0.00	0.99	0.67	0.92	1.16
DhS+DC						0.00	1.19	1.39	1.49
DhS							0.00	0.82	1.17
UhS+DC								0.00	0.83
UhS									0.00

from positive to negative values: species with high negative scores on axis 1 showed high variances along this axis (they predominated in SH but could also be found in other soil conditions), while species with high positive scores had low variances because they avoided soils experiencing surface hydromorphy (SH, DhS, DhS+DC). This main gradient was combined with a second one (Fig. 3b), which displayed along axis 2 the species that avoided surface hydromorphy, according to an increasing gradient of tolerance to temporary confinement from positive to negative values. Species with high positive scores on both axes exhibited low variances along these two axes: they were intolerant of prolonged water saturation as well as of temporary confinement. They were thus confined to the well-drained soil types (DVD and Alt). Species with negative scores on axis 2 showed high variances along this axis: they were intolerant of prolonged water saturation but could suffer temporary confinement. Frequency distributions among the nine soil classes of the three characteristic species numbered in Figure 3 are given in Figure 4.

Multispecies spatial pattern

The existence of tangible relationships between species occurrences and soil factors is expected to influence the multispecies spatial pattern of the community. A first assessment of this pattern can be made through trend surface analysis (Gittins 1968; Wartenberg 1985; Borcard et al. 1992). We thus confronted in a Canonical Correspondence Trend Surface Analysis (CCTSA), the list of species occurrences to an environmental table containing the terms of a 2-dimensional polynomial regression of the standardised *x* and *y* tree coordinates (trend surface). According to the shape of the plot (100 × 1 000 m), we retained

only 32 orthonormal polynomial variables of order less than 2 on *x* and less than 20 on *y*. The analysis was conducted on the reduced data set of 4 948 trees belonging to 118 species. A preliminary randomisation test on the total inertia among species indicated a highly significant multispecies spatial pattern (1 000 permutations; $P < 0.001$).

The sum of the first two eigenvalues of the CCTSA, representing 24.9% of the total inertia, appeared highly significant ($P < 0.001$). A partial-CCTSA was then computed in order to partial out the soil effect. When the soil effect was removed, there remained only one significant axis ($P < 0.001$) representing 13.0% of the total inertia (Table 2). The corresponding multispecies spatial patterns can be viewed as maps by drawing contour lines from the canonical scores of each tree positioned in (x,y) coordinates (Thioulouse et al. 1995). The contour lines were computed by interpolation of values estimated at each node of a 10 × 10 m systematic grid using bidimensional lowess regressions (Cleveland 1979) of the canonical scores over the 25 nearest trees, a value minimising the mean smoothing error (Figure 5; Cleveland and Delvin (1988)). Comparing these maps with the one of the soil classes (Fig. 6a) revealed that the multispecies pattern displayed by axis 1 of the CCTSA mainly expressed the soil effect (Fig. 6b), while the pattern displayed by axis 2 exhibited a broader scale of floristic heterogeneity (Fig. 6c). The map computed from scores on the first axis of the partial-CCTSA, i.e. after elimination of the soil effect (Fig. 6d), showed a pattern very similar to the one displayed by axis 2 in the previous analysis. This means that soil heterogeneity plays a major role on the spatial structuring of the species mixture, but that another factor, still unidentified, is responsible for a broader significant floristic heterogeneity in this plot.
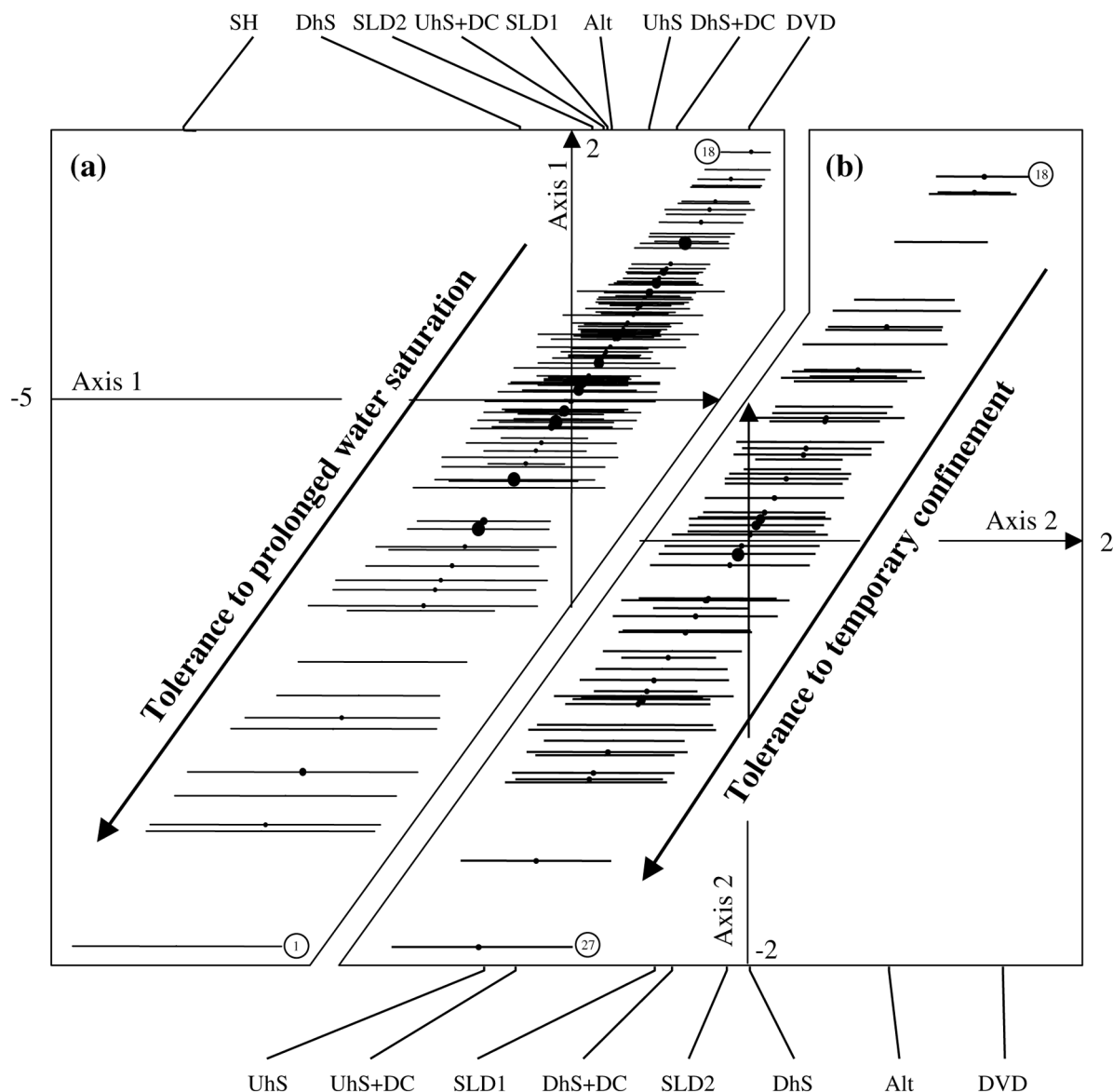
SH   DhS SLD2 UhS+DC SLD1 Alt   UhS DhS+DC DVD

(a)

Axis 1

-5   Axis 1

2

18

(b)

18

Tolerance to prolonged water saturation

Tolerance to temporary confinement

Axis 2

2

1

27

Axis 2

-2

UhS   UhS+DC   SLD1   DhS+DC   SLD2   DhS   Alt   DVD

Figure 3. Species weighted mean position (species optimum) and variance (species amplitude) along axes 1 (a) and 2 (b) issued from the canonical correlation analysis crossing 4 948 occurrences of trees (d.b.h. ⩾ 10 cm) belonging to 118 species with 9 hydrological soil classes in a 10-ha forest plot at Piste de St Elie, French Guiana. Only species avoiding SH soil type have been represented in (b). The circles are proportional to species frequency and the horizontal bars to species amplitude. Frequency distributions among the soil classes of the numbered species are given in Figure 4.

Scrutinising the five most correlated species with the first canonical axis of the partial-CCTSA — *Couepia guianensis* ($N = 18$); *Pourouma villosa* ($N = 12$); *Pouteria egregia* ($N = 28$); *Siparuna decipiens* ($N = 17$); *Theobroma subincanum* ($N = 14$) — revealed that they were mainly present in the upper quarter part of the plot.

Discussion

Species tolerance to soil water saturation

Direct analysis of species-soil relationships using canonical correlations confirmed the previous results obtained at Piste de St Elie by Lescure and Boulet (1985) and Sabatier et al. (1997) concerning the ma-
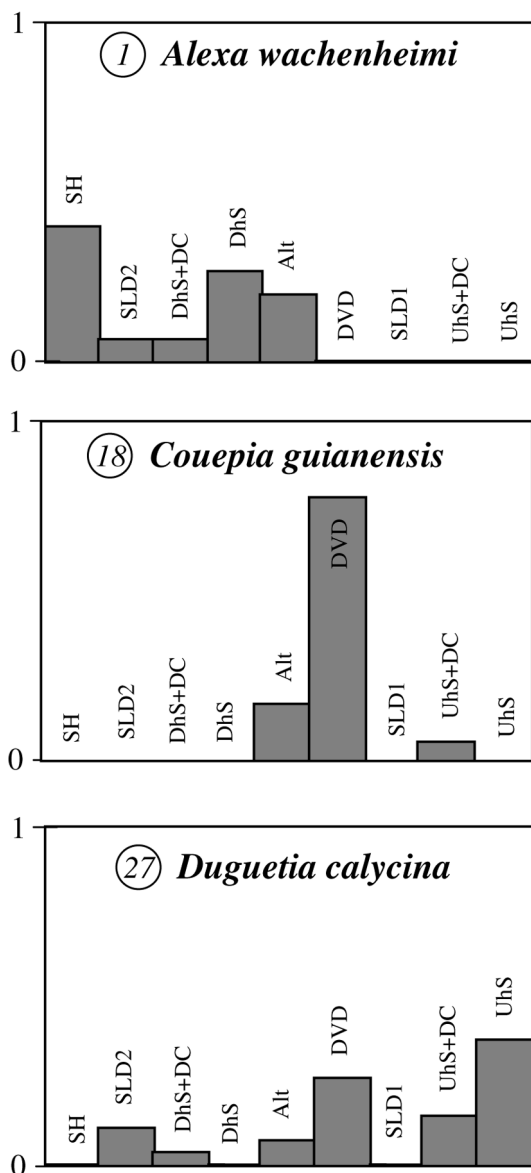
Figure 4. Frequency distributions among the nine hydrological soil classes of some characteristic species. Species codes (encircled numbers) are the same as in Figure 2 and Figure 3. Key for the soil classes is the same as in Figure 1.

jor effect of the hydrological soil characteristics on species composition at the local scale. Apart from some specialised species (*Tabebuia insignis* and *Euterpe oleracea*, exclusively found in hydromorphic thalwegs), the most abundant species can be ordered along two intermingled soil gradients. The predominant one opposes the soils experiencing prolonged surface hydromorphy to the other soil types, which are ordered along a second gradient displaying the
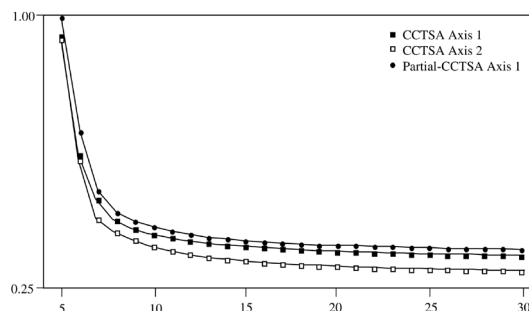

Figure 5. Mean smoothing error (sum of the squared differences between the observed and estimated values) as a function of the number of nearest neighbours taken into account in the lowess regressions conducted on the canonical scores issued from CCTSA and Partial-CCTSA (see Table 2).
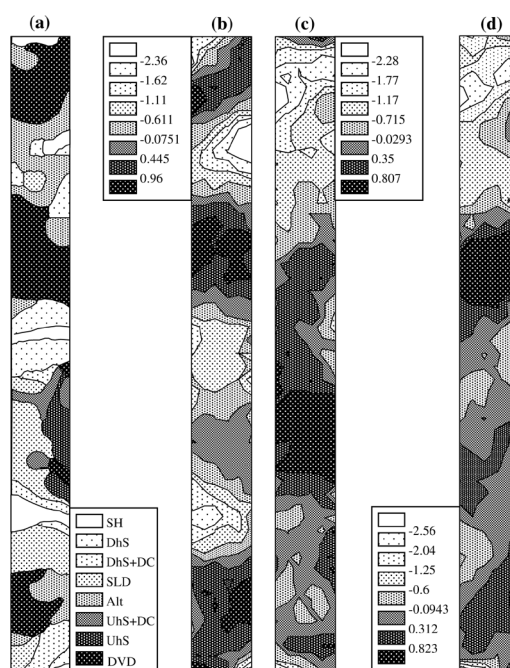

Figure 6. Map of the soil classes (a) and of the multispecies spatial patterns displayed by axes 1 (b) and 2 (c) of the CCTSA and axis 1 (d) of the partial-CCTSA (see Table 2). The contour lines of maps (b) to (d) were drawn by interpolation of values estimated at each node of 10 × 10 m systematic grid using bidimensional lowess regressions of the canonical scores over the 25 nearest trees.

weathering sequence from the initial ferralitic cover to the transformed hydromorphic soil systems. These two gradients are organised between three poles of constraining hydrological soil conditions: prolonged surface water saturation (SH), temporary confinement during the rainy season (UhS and UhS+DC), and low water potential in the dry season (DVD).

Table 2. Canonical correspondence trend surface analysis (CCT-SA) of 4 948 occurrences of trees (d.b.h. $\geq$ 10 cm) and orthonormal polynomial variables of the standardised x and y tree coordinates (trend surface) in a 10-ha forest plot at Piste de St Elie, French Guiana. Partial-CCTSA corresponds to the same analysis after partialling out the soil effect. r_k^2 = squared canonical correlation coefficient for axis k; % inertia = percentage of total inertia absorbed by axis k.

| | Axis (k) | | | |
	1	2	3	4
CCTSA (32 orthonormal variables)				
r_k^2	0.199	0.142	0.093	0.091
% inertia	14.55	10.37	6.79	6.62
Partial-CCTSA (24 orthonormal variables)				
r_k^2	0.147	0.072	0.062	0.057
% inertia	13.06	8.20	7.11	6.54

Our results completes this figure in an interesting way. Indeed, CANCOR leads to an ordination diagram so that species mean canonical scores and their variances represent species optimum and amplitude along the soil gradients. From the point of view of species, canonical axis 1 corresponds to a gradient of increasing tolerance to prolonged surface water saturation: intolerant species, *i.e.* the ones exhibiting a low amplitude, are found at one extreme of the gradient because they were never found in prolonged hydromorphic soil conditions (SH or even DhS and DhS+DC); tolerant species found in more varied soil conditions, including SH, exhibit a higher amplitude and are found at the opposite extreme of the gradient (e.g., *Alexa wachenheimi, Eschweilera coriacea, Jessenia bataua, Myrcia decorticans, Sclerolobium melonii*). Species intolerant of prolonged surface water saturation display a similar pattern along canonical axis 2 according to their tolerance to temporary confinement of the transformed hydromorphic soil systems: species intolerant of prolonged water saturation and intolerant of temporary confinement, *i.e.* the ones exhibiting a low amplitude along axis 1 as well as along axis 2 (e.g., *Couepia guianensis, Sloanea sp., Thyrsodium guianense, Tetragastris panamensis, Micropholis obscura*), are found at one extreme of the gradient because their distribution is restricted to the well-drained initial ferralitic cover (DVD or DVD and Alt); species intolerant of prolonged surface water saturation but tolerant of temporary confinement (low amplitude along axis 1 but high amplitude along axis 2; e.g., *Duguetia calycina, Pouteria grandis*) are at the opposite extreme of this gradient.

It is notable that the species restricted to the initial ferralitic cover (DVD) does not seem to endure water shortage during the dry season, because in the reverse case they should also be found on the moister soils of the weathering sequence. We can thus support the hypothesis that, at Piste de St Elie, the soil conditions imposed by surface water saturation are more important determinants for niche breadth limitation of many tree species than water shortage. Water saturation excludes oxygen from the soil pore space and imposes constraining, and sometimes lethal, anoxic conditions for seed establishment and plant growth (Kozlowski 1986; Vartapetian and Jackson 1997; Siebel and Blom 1998). It can also induce modifications of the soil chemical properties along the drainage gradients (Sabatier et al. 1997).

Since excessively wet soils are common in tropical rainforests, poor soil aeration is recognised to be an important factor for tree zonation (Joly 1991; Ter Steege 1994). But the effects of water excess have been explored much less in tropical rainforests than has the effects of water shortage. From an ecophysiological point of view, this perspective is surely an interesting direction for future research that could help in explaining the species zonation in natural conditions.

Pattern of diversity and community structuring

Soil heterogeneity has been demonstrated to be an important factor influencing the local distribution of tree species in several tropical rainforests (Basnet 1992; Ter Steege et al. 1993; Newbery et al. 1996; Sabatier et al. 1997). At Piste de St Elie, prolonged water saturation is a major discriminant factor of species composition that leads to a high β-diversity between SH and the other soil types. This confirms the floristic singularity of the extreme environments experiencing water excess in tropical forests (Clark et al. 1998, 1999). This floristic singularity seems, in French Guiana, to go hand in hand with a singular canopy structure that may be viewed from aerial photographs (M. Pain-Orcet & P. Couteron *pers. com.*). This has been little investigated.

The influence of soil heterogeneity on diversity patterns has also not been clearly stated. Soil conditions are often linked to topography (Basnet 1992; Newbery et al. 1996; Sabatier et al. 1997) and topography is recognised to increase the frequency of the natural disturbances (treefall gaps), which in turn increases species diversity (Denslow 1987; Gimaret-

Carpentier et al. 1998a). Our results suggest that well-drained soils contain more species (both species tolerant and intolerant of surface water saturation) than transformed and hydromorphic soils, which could lead to higher diversity on hilltops. This means that different factors could have opposite effects on local diversity patterns. It could thus be very informative to quantify the relative importance of these factors in order to decompose the diversity measure accordingly.

From our results, it is already plausible to support that soil heterogeneity, and probably the depth and the length of the period of soil water saturation, is a predominant factor playing on the spatial structuring of the multispecies community. Indeed, we showed that the first axis of the Canonical Correspondence Trend Surface Analysis (CCTSA) displays a significant multispecies spatial pattern at a scale very similar to the pattern of soil heterogeneity. More than that, this pattern disappears when the soil effect is removed by partial-CCTSA. On the contrary, the second axis of the CCTSA displays a pattern whose scale does not correspond to the scale of soil heterogeneity. More-over, a very similar pattern was displayed by the first canonical axis of the partial-CCTSA, after partialling out the soil effect. Some specific spatial patterns give flimsy arguments to hypothesise that this broad scale of floristic heterogeneity could be due to endogenous factors resulting from temporal fluctuations of population abundance (Condit et al. 1996). Further studies on population dynamics are however needed in this way.

Acknowledgements

Appendix 1

Table A1. Species codes, names and authorities for 118 species in a 10-ha plot at Piste de St Elie, French Guiana. *N* corresponds to the number of trees. *MCS* and *VCS* correspond to the mean species canonical scores (species optimum) and their variances (species amplitude) on axes 1 (*A1*) and 2 (*A2*) issued from canonical correlation analysis crossing species occurrences with nine hydrological soil classes (see text).

Code	TAXON	N	MCS A1	MCS A2	VSC A1	VSC A2
1	*Alexa wachenheimi* Benoist	15	−3.5779	1.8209	0.9508	0.5722
2	*Ambelania acida* Aubl.	11	−1.1778	1.541	0.9983	0.3621
3	*Andira coriacea* Pulle	11	0.6869	−0.5853	0.0914	0.3327
4	*Astrocaryum sciophilum* (Miq.) Pulle	113	0.7069	0.408	0.1696	0.2799
5	*Bocoa prouacensis* Aubl.	69	0.838	0.0975	0.1233	0.3196
6	*Brosimum guianense* (Aubl.) Huber	13	−0.0844	0.8827	0.5482	0.3041
7	*Carapa procera* A. DC.	47	−1.3451	1.3748	1.0948	0.5551
8	*Caryocar glabrum* (Aubl.) Pers.	20	−0.0098	0.9583	0.6238	0.4452
9	*Casearia javitensis* Kunth	12	0.8396	−0.9832	0.1152	0.6005
10	*Cassipourea guianensis* Aubl.	58	0.1219	0.46	0.4591	0.4025
11	*Catostemma fragrans* Benth.	17	0.7178	1.646	0.4632	0.2471
12	*Chaetocarpus schomburgkianus* (Kuntze) Pax & K. Hoffm.	35	0.2905	−1.2059	0.1021	0.4152
13	*Chrysophyllum argenteum* Jacq. *ssp. Nitidum* (G. Mey.) Pennington	17	−1.2413	1.2305	0.8901	0.4302
14	*Chrysophyllum prieurii* A. DC.	10	−0.118	−0.8146	0.1777	0.2738
15	*Chrysophyllum sanguinolentum* (Pierre) Baehni	17	−0.0677	−0.0882	0.1237	0.1671
16	*Conceveiba guianensis* Aubl.	12	−2.1562	0.7313	0.9497	0.544
17	*Couepia caryophylloides* Benoist	12	−0.1419	−0.8225	0.1456	0.2518
18	*Couepia guianensis* Aubl.	18	1.6294	1.8442	0.0818	0.1586
19	*Couratari multiflora* (J.E. Smith) Eyma	12	0.6367	0.2784	0.1912	0.2392

Table A1. Continued.

Code	TAXON	N	MCS A1	MCS A2	VSC A1	VSC A2
20	*Crudia aromatica* (Aubl.) Willd.	10	−1.3727	0.6691	0.4916	0.2425
21	*Crudia bracteata* Benth.	171	−0.0663	−0.2827	0.2818	0.3613
22	*Cupania scrobiculata* L.C. Rich.	12	0.1249	−0.4764	0.1548	0.2808
23	*Dacryodes nitens* Cuatrec.	19	0.6321	−0.8584	0.1226	0.3415
24	*Dendrobangia boliviana* Rusby	44	−0.9581	0.5208	0.6859	0.4904
25	*Dicorynia guianensis* Amsh.	79	−0.1798	−0.4635	0.2978	0.4095
26	*Drypetes variabilis* Uittien	25	0.3962	1.0751	0.3538	0.2112
27	*Duguetia calycina* Benoist	27	0.6219	−2.0971	0.0781	0.5686
28	*Duguetia surinamensis* R.E. Fries	32	0.795	−0.7334	0.1124	0.4278
29	*Duroia aquatica* (Aubl.) Bremek.	14	0.0566	0.3444	0.196	0.1623
30	*Ecclinusa guianensis* Eyma	25	0.8291	−0.1423	0.1074	0.4097
31	*Eperua falcata* Aubl.	378	−0.8407	−0.6553	0.4083	0.4114
32	*Eperua grandiflora* (Aubl.) Benth.	78	−0.1372	−0.7279	0.2364	0.3522
33	*Eschweilera apiculata* (Miers) A.C. Smith	16	0.2959	−0.3201	0.1144	0.3241
34	*Eschweilera cf. chartaceifolia* Mori	25	−1.179	−0.0913	0.6033	0.4779
35	*Eschweilera coriacea* (A.P. DC.) Mori	67	−2.4319	1.9269	1.0953	0.4343
36	*Eschweilera decolorans* Sandw.	47	−0.003	−1.1669	0.2368	0.4079
37	*Eschweilera micrantha* (Berg) Miers	199	0.7655	−0.0863	0.1438	0.3781
38	*Eschweilera parviflora* (Aubl.) Miers	269	1.0256	1.061	0.1561	0.2132
39	*Eschweilera pedicellata* (Rich.) Mori	12	−1.9328	−0.4479	0.5824	0.5092
40	*Eschweilera sagotiana* Miers	176	0.0685	−0.1911	0.2698	0.3375
41	*Eugenia sp. 10*	10	1.0398	0.326	0.0918	0.2596
42	*Goupia glabra* Aubl.	10	−0.2461	−1.0437	0.168	0.3419
43	*Gustavia hexapetala* (Aubl.) J.E. Smith	15	−0.5691	0.6516	0.8048	0.4938
44	*Hebepetalum humiriifolium* (Planch.) Benth.	14	0.4812	0.0306	0.1923	0.275
45	*Hirtella bicornis* Mart. & Zucc.	15	0.8901	0.4835	0.1251	0.2563
46	*Humiriastrum subcrenatum* (Benth.) Cuatrec.	11	−0.3281	−0.3668	0.1478	0.1613
47	*Inga fanchoniana* O. Poncy	10	0.4478	0.8251	0.1394	0.1323
48	*Inga sp.4*	20	0.8941	0.4245	0.1287	0.3044
49	*Iryanthera hostmanni* (Benth.) Warb.	26	−2.0779	0.5698	0.8053	0.5724
50	*Iryanthera sagotiana* (Benth.) Warb.	107	0.418	0.0654	0.1552	0.287
51	*Jacaranda copaia* (Aubl.) D. Don	13	−1.7124	0.6273	0.621	0.3547
52	*Jessenia bataua* (Mart.) Burret	54	−2.7765	1.9654	1.1049	0.481
53	*Lacmellea floribunda* (Poepp.) Benth. & J.D. Hook.	21	−0.5328	−1.2091	0.0845	0.1383
54	*Laetia procera* (Poepp.) Eichl.	11	−0.9781	−0.1384	0.4966	0.3077
55	*Lecythis holcogyne* (Sandw.) Mori	23	0.8642	−0.3267	0.1249	0.4566
56	*Lecythis idatimon* Aubl.	375	−0.1406	−1.0571	0.2638	0.4051
57	*Lecythis persistens* Sagot *ssp. persistens*	306	−0.5173	0.0425	0.5214	0.4595
58	*Lecythis poiteaui* Berg	30	0.6321	0.0128	0.1503	0.3937
59	*Licania alba* (Bernoulli) Cuatrec.	122	−0.7956	−0.7383	0.3558	0.382
60	*Licania canescens* Benoist	53	0.5047	0.5969	0.1587	0.1964
61	*Licania densiflora* Kleinh.	21	0.2735	0.2997	0.2038	0.2522
62	*Licania granvillei* Prance	39	0.773	−0.4071	0.1273	0.4327
63	*Licania heteromorpha* Benth. *var. heteromorpha*	41	0.8958	−0.0485	0.1096	0.3812
64	*Licania laxiflora* Fritsch	23	−0.0945	−1.2395	0.1448	0.3515
65	*Licania membranacea* Sagot ex Laness.	26	−0.2755	0.1078	0.4818	0.3692
66	*Licania parvifructa* Fanshawe & Maguire	12	0.7592	0.8507	0.1957	0.2874
67	*Maquira guianensis* Aubl.	12	1.0678	0.4871	0.1408	0.3673
68	*Micropholis guyanensis* (A. DC.) Pierre	39	−0.1848	0.5792	0.5498	0.3932

Table A1. Continued.

Code	TAXON	N	MCS A1	MCS A2	VSC A1	VSC A2
69	*Micropholis obscura* Pennington	13	1.4093	1.0604	0.1067	0.3415
70	*Minquartia guianensis* Aubl.	13	−0.0949	0.3931	0.1579	0.13
71	*Moronobea coccinea* Aubl.	17	0.1437	−0.4859	0.1626	0.2965
72	*Mouriri crassifolia* Sagot	12	−0.0589	−1.1154	0.1461	0.3303
73	*Myrcia decorticans* DC.	12	−2.5896	1.9611	1.1069	0.4517
74	*Ocotea ceanothifolia* (Nees) Mez	11	0.7036	0.8004	0.1651	0.2184
75	*Ocotea rubra* Mez	12	0.998	1.2187	0.1975	0.174
76	*Ocotea schomburgkiana* (Nees) Mez	13	0.0502	0.8483	0.5503	0.378
77	*Oenocarpus bacaba* Mart.	14	1.285	1.5072	0.1153	0.1479
78	*Ouratea melinonii* (Tiegh.) Lemee	17	−0.411	−0.7922	0.124	0.1782
79	*Oxandra asbeckii* (Pulle) R.E. Fries	74	0.4117	−0.8328	0.1085	0.2997
80	*Pachira dolichocalyx* Robyns	19	0.6676	−0.3246	0.1816	0.2743
81	*Poraqueiba guianensis* Aubl.	34	−0.3321	−0.5275	0.2239	0.2326
82	*Posoqueria latifolia* (Rudge) Roem. & Schult.	32	0.3529	0.6891	0.465	0.3644
83	*Pourouma laevis* Benoist	12	1.0929	1.1599	0.1537	0.2753
84	*Pouteria egregia* Sandw.	28	0.5952	0.8534	0.2274	0.1868
85	*Pouteria eugeniifolia* (Pierre) Baehni	10	0.5691	−0.9587	0.1002	0.5428
86	*Pouteria gongrijpii* Eyma	37	−0.5279	−0.5926	0.3401	0.3218
87	*Pouteria grandis* Eyma	28	−0.1204	−1.6575	0.0998	0.3641
88	*Pouteria guianensis* Aubl.	20	0.1555	0.1292	0.2315	0.2449
89	*Pouteria sp.21*	33	1.2488	1.7653	0.1671	0.0877
90	*Pouteria torta* (Mart.) Radlk.	17	1.3031	0.6088	0.0942	0.4091
91	*Pradosia cochlearia* (Lecomte) Pennington	13	0.1538	−0.6711	0.1421	0.2914
92	*Pradosia ptychandra* (Eyma) Pennington	28	0.1021	−0.3139	0.1679	0.303
93	*Protium opacum* Swart *var. rabelianum* Daly	16	−1.0798	0.7437	0.6481	0.3195
94	*Protium sp.1*	52	0.5097	0.2932	0.2506	0.3309
95	*Protium subserratum* (Engl.) Engl.	12	1.2143	0.6701	0.1409	0.3512
96	*Rinorea pectino-squamata* Hekking	40	0.1077	−1.0985	0.0907	0.4066
97	*Ruitzerania albiflora*	11	−0.4369	1.0719	0.5959	0.2557
98	*Sandwithia guianensis* Lanj.	144	0.2453	−0.0023	0.3061	0.3979
99	*Schefflera decaphylla* (Seem.) Harms	11	0.6669	0.6381	0.2001	0.2294
100	*Sclerolobium melinonii* Harms	11	−2.8188	1.5674	1.1654	0.7025
101	*Siparuna decipiens* (Tul.) A. DC.	17	0.4281	1.243	0.5552	0.2832
102	*Sloanea sp.*	11	1.5096	1.7528	0.0967	0.132
103	*Sterculia pruriens* (Aubl.) K. Schum.	10	−0.3754	1.0007	0.7028	0.3452
104	*Swartzia polyphylla* DC.	25	−0.0613	−0.0007	0.3296	0.3473
105	*Symphonia sp.1*	35	0.4622	0.1007	0.1592	0.2608
106	*Talisia microphylla* Uittien	14	0.5773	−0.8122	0.1351	0.5362
107	*Tetragastris panamensis* (Engl.) Kuntze	12	1.3911	0.987	0.1037	0.3565
108	*Theobroma subincanum* Mart.	14	0.2117	0.3581	0.5753	0.5964
109	*Thyrsodium guianense* Sagot ex March.	16	1.4483	1.0734	0.0945	0.3737
110	*Tovomita sp.*	40	0.5553	1.0308	0.413	0.3362
111	*Tovomita sp.1*	20	0.3177	0.4549	0.1799	0.2714
112	*Tovomita sp.5*	11	−0.1304	−0.2706	0.5713	0.5698
113	*Trymatococcus oligandrus* (Benoist) Lanj.	11	0.441	−1.2573	0.1331	0.4481
114	*Unonopsis rufescens* (Baill.) R.E. Fries	45	1.1686	0.8153	0.1445	0.3242
115	*Virola michelii* Heckel	46	0.4965	0.2048	0.1502	0.3101
116	*Vouacapoua americana* Aubl.	71	0.1087	0.5539	0.4773	0.3887
117	*Xylopia nitida* Dunal	17	−0.1858	−0.618	0.1234	0.1469
118	*Zygia racemosa* (Ducke) Barneby & Grimes	14	0.3417	−0.3473	0.1303	0.3565

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