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Foliar elementome and functional traits relationships identify tree species niche in French Guiana rainforests

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Open research: Manuscript data will be available in Dryad data base. Dataset titled "Script and results of the Bayesian analyses of environmental and phylogenetic effects of leaf composition" has been reviewed by our curation team and approved for publication. It is publicly accessible via this link: https://doi.org/doi:10.5061/dryad.2rbnzs7sk.

Abstract. Biogeochemical niche hypothesis (BN) aims to relate species/genotype elemental composition with its niche based on the fact that different elements are involved differentially in distinct plant functions. We here test the BN hypothesis through the analysis of the 10 foliar elemental concentrations and 20 functional-morphological of 60 tree species in a French Guiana tropical forest. We observed strong legacy (phylogenic+species) signals in the species-specific foliar elemental composition (elementome) and, for the first time, provide empirical evidence for a relationship between species-specific foliar elementome and functional traits. Our study thus supports the BN hypothesis and confirms the general niche segregation process through which the species-specific use of bio-elements drives the high levels of α-diversity in this tropical forest. We show that the simple analysis of foliar elementomes may be used to test for BNs of co-occurring species in highly diverse ecosystems, such as tropical rainforests. Although cause and effect mechanisms of leaf functional and morphological traits in species-specific use of bio-elements require confirmation, we posit the hypothesis that divergences in functional-morphological niches and species-specific biogeochemical use are likely to have co-evolved.

Keywords: Diversity; nitrogen; phosphorus; stoichiometry; foliar elementome; tropical forest; phylogeny; sympatric speciation

Introduction

Recent studies have examined species' niche space as a function of the use of bioelements, based on the biogeochemical niche (BN) hypothesis which states that species and/or genotypes, which comprise a unique genetic pool of individuals, are a product of long-term evolutionary processes (Peñuelas et al., 2019; Sardans et al., 2021). BN try to incorporate most, if not all, niche parameters using species-specific elemental composition and stoichiometry. BN is based on the underlying assumptions that each species is a unique genetic pool of individuals product of long-term evolutionary processes, so that each species should have a specific morphological structure and functionality (from gene expression to physiological processes). Moreover, all fundamental biological processes (e.g, growth, secondary metabolism, reproduction and storage) and structures (e.g. wood, leaves, roots,..) have distinct values in different species depending on selection pressures, so different species must differentially allocate elements to various traits of tissues and organs, because each function and structure have their own elemental composition. Thus, each species should tend to have its own elemental composition and stoichiometry (homeostatic component of BN) as a result of the long-term singular evolution (legacy effects). In addition, each species should also have phenotypical plasticity to allow the individuals of each species to adapt their morphology and functionality to environmental and ontogenetic shifts (plasticity component) (Peñuelas et al., 2019; Sardans et al., 2021). Then each singular species can be characterized using specific elemental composition and stoichiometry, as a homeostatic component of a BN, in a species-specific elementome (Peñuelas et al., 2019).

Plant functional diversity is strongly connected with foliar morphological and elemental composition, including foliar concentrations of nitrogen (N) or phosphorous (P) (Zhan et al., 2019; Kamoske et al., 2020), and functional traits, such as photosynthetic carbon (C) assimilation (van ’t Veen et al., 2020). These species-specific functional traits have been related to species-specific niche space at community level (Buzzard et al., 2019; van ’t Veen et al., 2020). Availability of resources, such as soil nutrients, is strongly related to plant species diversity and functional dissimilarity (Gross et al., 2017; Siebenkas et al., 2017), while plant functional traits are linked with important ecosystem traits associated with nutrient cycling, such as soil web structure and composition (Peay et al., 2013; Buzzard et al., 2019). Functional traits such as litter production (Legay et al., 2020) soil microbial community structure and function exert seems to effects and feed-backs on elemental composition of litter mainly during its decomposition (Malik et al., 2020).

Tropical forests have high levels of biodiversity, including at local spatial scales, with high number of different species at levels of ha (Vitousek and Sanford, 1986; da Silva et al., 2011; Chisholm et al., 2013) associated to environmental factors including climate (Vitousek, 2004), topography (Ferry et al., 2010), and seasonality (Girardin et al., 2016), among several others (Wright, 2002; John et al., 2007; Becerra, 2015; Soong et al., 2020; Pennington et al., 2009). All these variables make tropical forests an unique scenario to test the relationships of foliar elementome and functional traits in the frame of the BN hypothesis. As a representation of species niche based on elemental composition, BN should, at some extend, be related with species functional differences. Thus, despite the difficulty of controlling all the functions of a plant, we aim, for first time, to analyze the relationships of BN with species-specific set of functions based on leaves of several coexisting tree species in a tropical rain-forest.

To improve understanding of the relationship between tree species-specific elementomes and species-specific functional traits in the identification of species-specific BN in the n-dimensional space of multivariate analyses formed by the concentrations of the different elements within a semi-pristine tropical rainforest, we tested the hypotheses that (i) species-specific use of bio-elements is linked, at least in part, to phylogenetic species legacy effects, confirming the the important role of evolutionary processes in the existence of species-specific BN; (ii) diverse tropical forest tree BNs are associated to species-specific functional traits characteristics linked with contrasting use of bio-elements; and, (iii) tropical tree species elementomes and BNs are a product of legacy effects and prevailing variability in environmental conditions.

Material and Methods

Study sites

The study was conducted in a semi-pristine lowland wet tropical forest at the Nouragues (4°05′N, 52°40′W) and Paracou (5°18′N, 52°53′W) research stations in French Guiana (Van Langenhove et al., 2020), where mean annual rainfall is 2990 and 3160 mm, respectively (Van Langenhove et al., 2020). A pronounced dry season, from September to November, is associated with the displacement of the inter-tropical convergence zone, while a wet period of high daily rainfall is most prominent between March and July.

Experimental design

At each forest site we established 12 plots of 0.25 ha at each site stratified by three topographic positions to account for this heterogeneity: at the top, slope, and bottom of hills. We set a central 20-m quadrat in each plot, where we marked and geolocated five evenly spaced sampling points around which we focused our measurements. Thus, this design contained between 72 and 120 sampling points (2 sites x 3 topographic positions x 4 replicate plots per position x 3–5 sampling points in each plot). Plots at each location were separated by 10–200 m. At both study sites, soil sand content was greater at the bottom plots than at top and slope plots, whereas clay content was lower (Courtois et al., 2018).

Leaf sample collection

Leaf samples were collected from all tree species present within each study plot for bio-element and functional trait analysis (Table S1). The sampling took place twice in 2015 during the rainy season from May to the end of June and during the dry season from the beginning of October until late November. For details, see Appendix S1: Material and Methods.

Bio-element analysis

Verdant and senescent leaves from 60 tree species (Urbina et al., 2021) were oven-dried at 70°C to a constant weight and then ground using a ball mill (MM400, Restch GmbH); dry biomass was measured using a precision balance A(B204 Mettler Toledo). We determined leaf C, N, P, potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), manganese (Mn), strontium (Sr), and iron (Fe) concentrations. For details, see Appendix S1: Material and Methods.

Functional traits

Leaf gas exchange, reflectance, and morphological variables were analyzed from samples collected from the 60 tree species. Although a species accumulation curve suggests that the complete regional pool must contain up to 250 tree species (see Appendix S1: Fig S1), these 60 species were those with the highest abundance and occurrence in the studied plots, therefore, this subset should be representative of the evolutionary and functional diversity of the tree species present in the area. We measured leaf maximum carboxylation rate (Vcmax), maximum rate of electron transport (Jmax), proportion of leaf to ambient CO_2 concentrations (CiCa), leaf transpiration (Trmmol), maximum quantum efficiency of photosystem II (PSII; Fv/Fm), nonphotochemical chlorophyll fluorescence quenching (NPQ), solar radiation intensity (R; wm^{-2}), and electron transport rate (ETR), leaf reflectance, normalized difference vegetation index (NDVI), photochemical reflectance index (PRI), water index (WI), structure independent pigment index (SIPI), normalized difference pigment index (NDPI), simple ratio pigment index (SPRI), leaf chlorophyll content and leaf thickness. See Appendix S1: Material and Methods**.**

Statistical analyses

Species elementome and functional traits

We conducted permutational multivariate analyses of variance (PERMANOVA) (Anderson et al., 2008) using Euclidean distance, with research station location (Nouragues, N; Paracou, O), season (dry and wet), topography (top, slope and bottom), canopy (top and bottom leaves), and species as independent factors to test the importance of species in foliar elemental and functional trait composition. For details, see Appendix S1: Material and Methods.

Phylogenetic signature

We prepared a phylogenetic tree of the sampled species (Figure S2) by testing for phylogenetic signals (Blomberg's K) in the studied variables and using R statistical software (R Development Core Team 2011) from the Guyafor phylogeny (Baraloto et al., 2012). For details, see Appendix S1: Material and Methods.

Drivers of species elementomes

We tested for effects of site, season and topography on foliar concentrations and stoichiometry of bio-elements, functional traits, and canonical scores derived from the GDA described below, using Bayesian phylogenetic linear mixed models and the MCMCglmm package (Halfield, 2010) in R. We included season, topography, and research station as fixed effects and phylogeny and species as random factors. Phylogeny accounted for variability in shared ancestry, while species accounted for species-specific traits independent of shared ancestry; thus, the two random factors together accounted for variance explained by heritability. We used the phylogenetic tree based on Baraloto et al. (2012).

Tree species leaf elementomes and functional traits

We conducted general discriminant analyses (GDA) using Statistica 8.0 (StatSoft, Inc., Tulsa, USA) to determine overall differences in foliar elemental composition and functional traits with species as grouping Factor. For details, see Appendix S1: Material and Methods.

Results

Species elementome and functional traits

Topographical (top, slope and bottom), geographical (research station) location, canopy (top and bottom leaves) and season (wet, dry) as independent spatio-temporal variables in PERMANOVA analyses explained a low proportion of the total variance in tree species elementome (R^2=0.011, 0.026, 0.023 and 0.07, respectively), whereas legacy (species) effects explained a greater proportion (R^2=0.46) when included in the mixed model or as a single independent factor (Table 1). Topographical and geographical location, canopy and season explained a moderate proportion of the total variance in tree species functional traits (R^2=0.041, 0.20, 0.064 and 0.08, respectively), while species, when included in the mixed model, explained a greater proportion (R^2=0.39); species explained even a slightly greater proportion of variance when included as a single independent factor (R^2=0.40) (Table 1). There were phylogenetic signals in leaf C, N, P, Ca, and Cu concentrations, in 14 of the 20 tested functional variables, and in the GDA canonical scores of leaf elementome roots 1, 2, and 4 and the first four roots of the leaf functional variables (Appendix S1: Table S2).

Bayesian GLMM

Topographic and geographic location and season explained a 14.6 ± 5(SE) on average of the total variation in foliar bio-element content and stoichiometry, functional traits, and GDA canonical scores, whereas legacy effects explained 24.6 ± 8 on average of total variance (To be deposited in Dryad upon acceptance). For example, legacy effects accounted for 75.4, 62.8, and 28.6% of the total variance in leaf concentration of C, N, and P, respectively, while topographic + geographic location + season accounted for 3.75, 22.5, and 2.35%, respectively, and legacy effects accounted for 77.5% of the variance in canonical scores for root 1 (To be deposited in Dryad upon acceptance).

Tree species leaf elementomes and functional traits

We found that foliar elementomes and functional traits were associated with 78 and 73% of tree species pairwise comparisons significantly separated by euclidean distances (Squared Mahalanobis distances) respectively ($P<0.05$, n=306; Appendix S1: Fig. S3). There were negative relationships between canonical scores for tree species functional traits (root 1) and elementomes (roots 1 and 2) (R=-0.35, *P*=0.004 and R=-0.40, *P*<0.0001, respectively; Fig. 1). The phylogenetic diagram of canonical scores of GDA root 1 and root 2 of elemental foliar composition is depicted in Figs. 2A and 2B, and the diagram for functional traits in Figs. 2C and 2D. These diagrams show that the values of variables (represented by a color scale) are significantly more similar between/among species the more proxime in the phylogenetic diagram they are.

Discussion

In this study, we identified distinct foliar elementomes for 60 coexisting tree species, resulting from different evolutionary legacies, including recent evolution convergence and divergence (see Sardans et al., 2021). We further found that the elementomes were associated with leaf functional traits, such as indicators of photosynthesis and morphology. Thus, our study of tree leaf elemental composition supports the BN hypothesis (Peñuelas et al., 2019) and confirms that foliar BNs are linked to overall leaf functionality, akin to a functional niche (Smith et al., 2013). Most species with high levels of foliar N along root 1 of the GDA conducted with elementome variables of *Agondra silvatica*, *Lecythis poiteaui*, *Lecythis zabucajo*, *Eperua falcata*, *Inga nouraguensis*, *Oxandra asbeckii*, and *Vauacapoua americana* are characterized by high levels of photosynthetic performance, as indicated by V_{cmax} and J_{max} along root 2 of the GDA conducted with functional variables (Fig. 1; Appendix S1: Fig. S2). *Anacardium spruceanum, Eperua falcata,* and *Inga nouraguensis* are the species that have at the same time the highest loadings in Root 1 and 2 in the direction to higher N and Mg concentrations at once coinciding with the higher loadings towards higher Jmax and Vcmax along root 1 in the GDA conducted with functional variables. This higher photosynthetic activity also coincided with low leaf thickness and higher solar radiation along the root 1. Moreover, species such as *Chrysophyllum sanguinolentum*, *Licania alba*, *Sterculia speciosa*, *Tapura capitulifera*, and *Vochysia tomentosa* with high values of Root 2 scores of BN GDA also had low values of Root 1 scores of functional variables GDA (Fig. 1; Appendix 1: Fig. S2). This relationship is mainly supported by lower values of foliar N concentration associated with higher leaf thickness (Appendix S1: Fig. S2).

Indeed, we found that functional variables that may account directly for differences in soil temperature, water content, and fertility (topographical and geographical location, season) explained only 1.4% and 1.7% of the roots 1 and 2 variance of the GDA of all sampled elementomes (when species were taken as grouping factor), whereas legacy effects explain more than 70% of these roots 1 and 2 variance (Figure 1b, To be deposited in Dryad upon acceptance) and also consistently with the PERMANOVA analyses (Table 1). These results are consistent with several findings showing that soil heterogeneity at micro-scale level reporting for instance changes in soil nutrient availability have all been cited as drivers of biodiversity in tropical forests (John et al., 2007; van Breugel et al., 2018).

We have demonstrated that the BN hypothesis, based on the elementome identity of species/genotypes, is valid. BN differences among species reflected by the foliar elementome differences are also related with overall functional traits. This contrasting use of bio-elements by tree species may avoid direct competition among sympatric species, thus facilitating species coexistence and biodiversity. The evolutionary drivers of functional and morphological divergences that have led to high levels of biodiversity of rainforest ecosystems are likely to have been a complex set of synergistic and antagonistic feedback mechanisms based on differential use of basic resources, such as light, water, and bio-elements. This, together with a range of biotic interactions, including symbiotic, mutualistic, and plant-herbivore relationships has led to species-specific strategies in the use, uptake, and allocation of bio-elements. However, whether these divergences in functional and morphological traits are causes or effects of species-specific use of bio-elements remains unresolved. Further studies are warranted to figure it out.

Overall, our study also supports previous work reporting that high levels of plant community diversity, from local to landscape scales, leads to heterogeneity of chemical, structural, and functional traits known to affect biogeochemical processes (Townsend et al., 2008). Summarizing, this study has directly demonstrated the link of foliar elemental composition with species evolutionary legacy and species functionality in tropical forest, consistently with previous studies that have observed relationships of plant species elemental composition with species evolutionary legacy and/or with determined function and ecological strategies in tropical (Pennington et al., 2015; Uriarte et al., 2015; Gargallo-Garriga et al., 2020a) but also in extratropical ecosystems such as European forests (Sardans et al., 2015), boreal forests (Reiman et al., 2018), temperate shrublands (Urbina et al., 2017), Chinese forests (Wu et al., 2017; Zhao et al., 2018), Mediterranean woodlands (Rivas-Ubach et al., 2012; de la Riva et al., 2017) and arid lands (Castellanos et al., 2018). Global studies of tree species have also detected that different habitats, ecological strategies, and sympatric competence are related to different BN (Sardans et al., 2015;2021; Peñuelas et al., 2019; Vallicrosa et al., 2021). Niche concrete characterization is a difficult task but BN should be considered as a tool to concretely identify of different niches in plant communities (Peñuelas et al. 2019). This study demonstrates the suitability of BN as a proxy for species niche identification based on the use of the bio-elements that each species has due to its particular morphology and functioning in the occupation of its ecological niche.

Final remarks and conclusions

We found there were phylogenetic and species signals in leaf elemental composition and functional traits of 60 coexisting tropical rainforest tree species, where foliar elemental composition was related to functional traits. Thus, we conclude that 1) leaf elemental composition is an indicator of biogeochemical niches at small spatial scales in this tropical forest; 2) species-specific foliar elemental composition and functional traits are related; and 3) the observed high species-specific use of bio-elements confirms the existence of a BN that reflects general niche segregation. Our hypothesis, that functional-morphological traits and biogeochemical niche differentiation co-evolve in parallel among species, requires testing through further research. Overall, our study provides empirical evidence for an association between species-specific use of key bio-elements and leaf functional traits in this high diverse Guiana rainforest as a result of legacy effects.

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Table 1. Analysis of effects (PERMANOVA) of topographic (slope position) and geographic (research station) location, season, and species on tropical tree elementomes (A) and on tropical tree leaf function (B).

(A)Model including main effects of topographical location, season, geographical location, and species on tropical tree elementomes					
Variable	Df	Sum of Squares	*F* (Model)	R^2	*P*
Topography	2	0.349	3.08	0.011	0.009
Season	1	2.12	37.4	0.07	0.001
Canopy	1	0.104	1.89	0.023	0.0045
Geography	1	0.80	14.04	0.026	0.001
Species	59	13.6	4.83	0.46	0.001
Residuals	260	12.4		0.41	
Total	324	29.3		1	
Model including main effect of species					
Species	59	13.9	3.93	0.46	0.001
Residuals	265	15.9		0.54	
Total	324	29.7		1	
(B)Model including main effects of topographical location, season, geographical location, and species on tropical tree leaf function					
Variable	Df	Sum of Squares	*F* (Model)	R^2	*Pr(>F)*
Topography	2	0.180	7.85	0.041	0.001
Season	1	0.92	159.4	0.200	0.001
Canopy	1	0.201	7.12	0.064	0.001
Geography	1	0.35	60.4	0.080	0.001
Species	59	0.931	3.99	0.390	0.001
Residuals	260	1.23		0.225	
Total	324	3.71		1	
Model including main effect of species					
Species	59	0.921	2.94	0.396	0.001
Residuals	265	1.41		0.604	
Total	324	2.33		1	

Figure captions

Figure 1. Regression analysis of the relationship between GDA canonical scores of root 1 foliar functional traits and GDA canonical scores of roots 1 (A) and 2 (B) of foliar bio-elements grouped by species. Numbers in the figure refer to species listed in Table 1.

Figure 2. Phylogenetic diagram of canonical scores of GDA root 1 and root 2 of elemental foliar composition (A and B) and functional traits (C and D). This diagram was obtained using the contMap function of the phytools package in R, representing the value structure used to estimate phylogenetic signals in variables. The contMap function estimates the ancestral characters at internal nodes using maximum likelihood and assuming Brownian motion as a model for trait evolution (Münkemüller et al. 2012), and then interpolates the ancestral condition along the branches of the tree (Pagel, 1999).

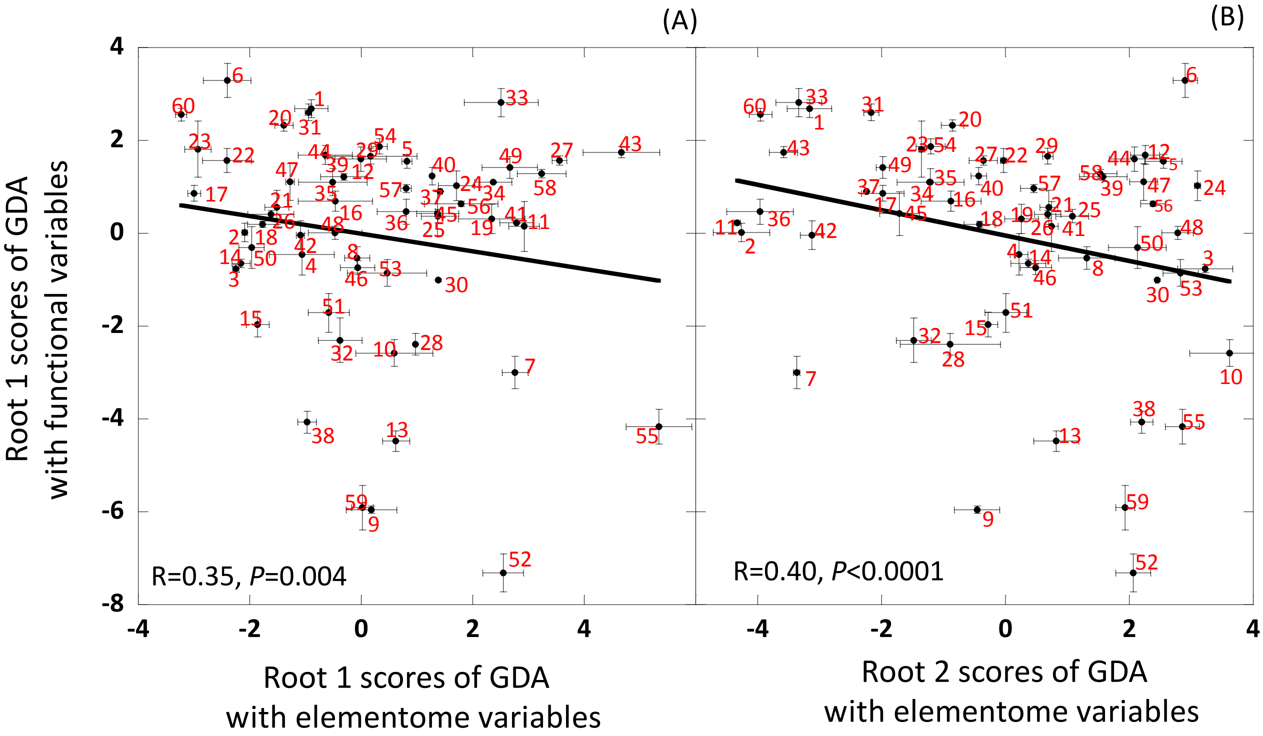
(A)
(B)
Root 1 scores of GDA with functional variables
Root 1 scores of GDA with elementome variables
Root 2 scores of GDA with elementome variables
R=0.35, P=0.004
R=0.40, P<0.0001
4
2
0
-2
-4
-6
-8
-4
-2
0
2
4
-4
-2
0
2
4

Figure 1.

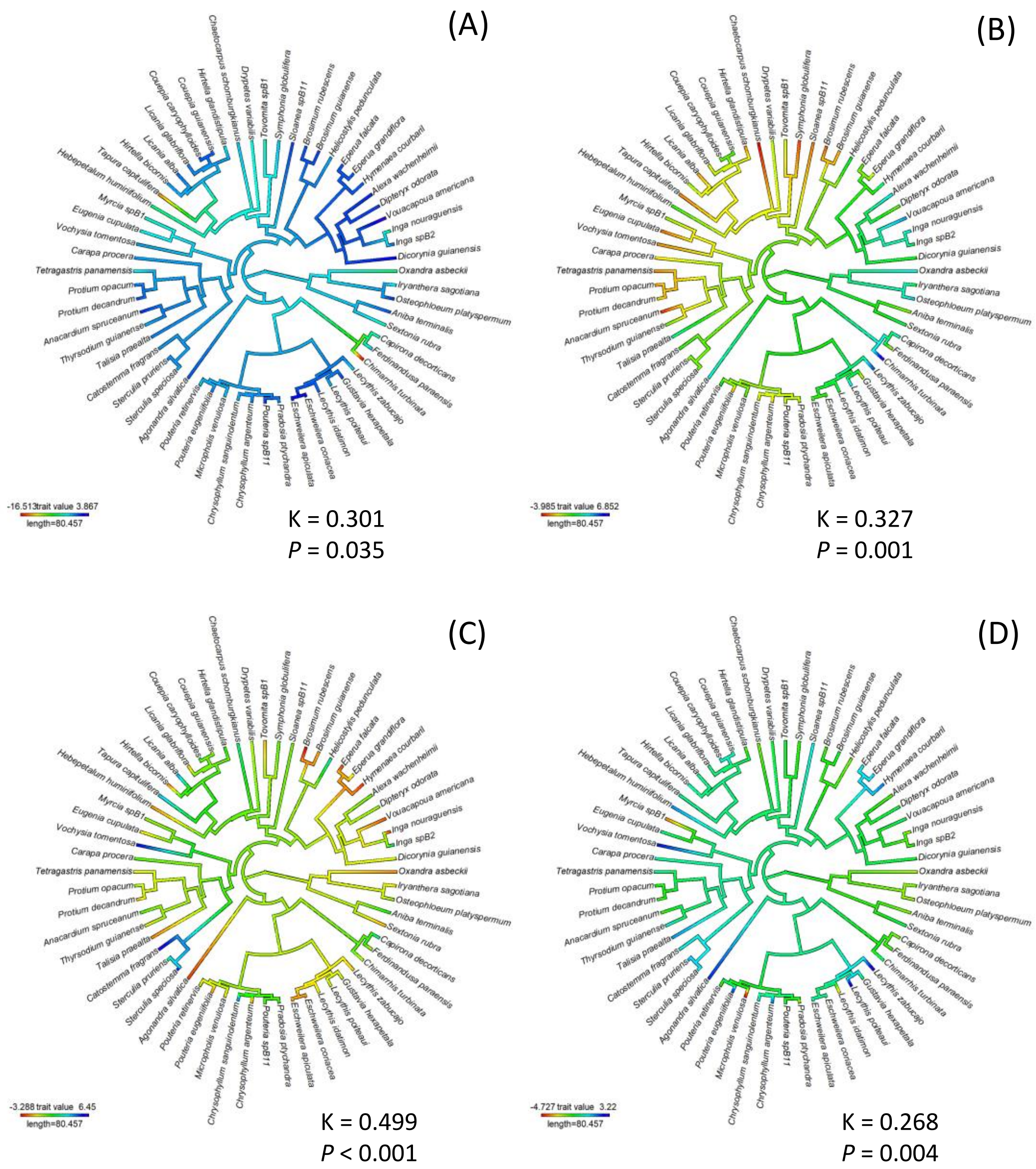
(A)
(B)
(C)
(D)
Chaetocarpus schomburgkianus
Drypetes variabilis
Tovomita spB1
Symphonia globulifera
Sloanea spB11
Brosimum rubescens
Helicostylis pedunculata
Brosimum guianense
Eperua falcata
Eperua grandiflora
Hymenaea courbaril
Alexa wachenheimii
Dipteryx odorata
Vouacapoua americana
Inga nouraguensis
Inga spB2
Dicorynia guianensis
Oxandra asbeckii
Iryanthera sagotiana
Osteophloeum platyspermum
Aniba terminalis
Sextonia rubra
Capirona decorticans
Ferdinandusa paraensis
Chimarrhis turbinata
Lecythis poiteaui
Gustavia hexapetala
Lecythis zabucajo
Lecythis idatimon
Eschweilera coriacea
Eschweilera apiculata
Pradosia ptychandra
Pouteria spB11
Chrysophyllum argenteum
Chrysophyllum sanguinolentum
Micropholis venulosa
Pouteria eugeniifolia
Pouteria retinervis
Agonandra silvatica
Sterculia speciosa
Sterculia pruriens
Catostemma fragrans
Talisia praealta
Thyrsodium guianense
Anacardium spruceanum
Protium decandrum
Protium opacum
Tetragastris panamensis
Carapa procera
Vochysia tomentosa
Eugenia cupulata
Myrcia spB1
Hebepetalum humiriifolium
Tapura capitulifera
Hirtella bicornis
Licania alba
Licania glabriflora
Couepia caryophylloides
Couepia guianensis
Hirtella glandulistipula
-16.513 trait value 3.867
length=80.457
K = 0.301
P = 0.035
-3.985 trait value 6.852
length=80.457
K = 0.327
P = 0.001
-3.288 trait value 6.45
length=80.457
K = 0.499
P < 0.001
-4.727 trait value 3.22
length=80.457
K = 0.268
P = 0.004

Figure 2