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Research Article

Tropical Refuges with Exceptionally High Phylogenetic Diversity Reveal Contrasting Phylogenetic Structures

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Loss of phylogenetic diversity (PD) has gained increasing attention in conservation biology. However, PD is not equally distributed in a phylogeny and can be better assessed when species relatedness (phylogenetic structure: PS) is also considered. Here, we investigate PD and PS in two refuges of biodiversity in northeastern Brazil: the Bahia Costal Forest (BCF) in the Atlantic Forest domain and Chapada Diamantina (CD) in the Caatinga domain. We used geographic data of 205 species at two spatial scales and a chronogram of Apocynaceae based on *matK* sequences to estimate PD and PS. Our results show an exceptionally high PD in both refuges, overdispersed in BCF and clustered in CD, although this difference is less evident or absent for recent relationships, especially at a smaller spatial scale. Overall, PS suggests long-term competitive exclusion under climatic stability, currently balanced by habitat filtering, in BCF, and biome conservatism and limited dispersal leading to *in situ* diversification and high density of microendemics in CD. The phylogenetically clustered flora in CD, also threatened by climate changes, are naturally more vulnerable than BCF. Therefore, while *in situ* conservation may ensure protection of biodiversity in BCF, emergency *ex situ* conservation is strongly recommended in CD.

1. Introduction

Currently, the consensus is that biodiversity loss reduces community efficiency, stability, and productiveness [1], and the best strategy for biological conservation is through gains in phylogenetic diversity (PD) [2, 3]. Species do not contribute equally to total PD of an area but with their distinct evolutionary history [4, 5]. Closely related species, sharing a great extent of evolutionary history, are more likely to be redundant, whereas distantly related species are expected to play different ecological functions and provide different goods and services. Therefore, PD, based on the sum of branch length, is an important measure in conservation biology [5–7]. Species loss diminishes PD, but PD loss cannot be directly predicted by species loss, because proportions of PD loss may be higher than proportions of species loss when extinctions are clumped or biased to relictual lineages. Accordingly, communities whose species composition is phylogenetically clustered tend to lose evolutionary diversity more quickly, whereas communities in which species are phylogenetically overdispersed tend to lose less evolutionary diversity during extinctions [8, 9]. Therefore, PD loss depends on how communities are phylogenetically structured (species relatedness).

Phylogenetic structure (PS) represents the overall relatedness in a species assembly (e.g., [10]) and combines community ecology and evolutionary thinking [11] into an interdisciplinary approach, community phylogenetics or ecophylogenetics [12]. PS is obtained by comparing the community phylogenetic distance to a null model, which randomize variants, such as species relationships and distributions [10, 11]. This metric differs from PD, which represents only the sum of phylogenetic distances of a community [5] and does not provide information on how species of this community are phylogenetically related. According to PS, communities may be phylogenetically clustered, which indicates cooccurrence of closely related species and suggests a stronger influence of an environmental filter on the community. In contrast,

phylogenetically overdispersed communities indicate local exclusion of closely related species and suggest a stronger influence of interspecific competition and/or other density-dependent negative interactions [11]. These interpretations are mainly supported by a strong tendency towards phylogenetic niche conservatism (PNC) during diversifications, as shown by Crisp et al. [13] for plants. According to PNC, closely related species tend to share traits and occupy similar habitats [14]. However, PS is scale and context dependent, and alternative interpretations can emerge from similar patterns, often being equivocal when traits are not taken into account. For instance, clustered phylogenies can also result from character displacements among closely related species allowing their coexistence or from limited dispersal and *in situ* speciation. On the other hand, overdispersed phylogenies may also result from convergent ecological traits among distantly related species. Finally, unstructured phylogenies suggest a balance between environmental constraints and biological interactions or a prevalent influence of neutral processes, such as a stochastic dynamic of dispersal, speciation, and extinction, rather than niche-based processes (e.g., [3, 11, 15–19]). Furthermore, null models used for assessing PS can also affect results and eventually confer spurious structures for unstructured phylogenies (e.g., [16, 20–22]).

Ecophylogenetics still lacks a consistent conceptual framework [12] and the use of PD as a proxy for functional diversity has been criticized for lacking empirical evidence [23]. However, PD and PS are complementary measures of biodiversity and can be properly used for biogeography, ecology, and conservation biology. Phylogenetics has been used to assess historical and ecological drivers at different spatial scales [12, 18], from latitudinal gradient of species richness (SR) [24], biogeographic processes during the Cenozoic [25], and coastal dune ecosystem [26] at a global scale to habitat heterogeneity [27, 28], successional pathways [29], and altitudinal gradient [30] at regional or, mainly, local scales. Although Brazil harbours the richest flora in the world, with more than 32,000 species of angiosperms [31], studies applying phylogeny to interpret plant composition (e.g., [32, 33]) are still scarce.

Here, we investigate PD and PS in two centres of biodiversity (rich in species and endemisms), the Chapada Diamantina and the Bahia Costal Forest. Although only ~120 km separates one from the other, these centres are under different environmental conditions and floristic domains and, together, comprise most of the angiosperm diversity in northeastern Brazil (Figure 1).

Chapada Diamantina (CD) is the largest continuous plateau in the northern Espinhaço Range. Above 900 m, particularly in the south and east, the plateau is covered by rocky fields (*Campos Rupestres*), an open vegetation biome associated with quartzite outcrops, rich in plant species and endemisms (e.g., [34]). It is floristically influenced by seasonally dry forests from the surrounding Caatinga but is also home of palaeomicroendemics [35] and was recently postulated as a historical refuge for fire-sensitive lineages [36]. The Bahia Costal Forest (BCF) ecoregion [37] is the largest area of climatic stability in the northern block of the Atlantic Forest [38–40]. Ranging from northern Espirito

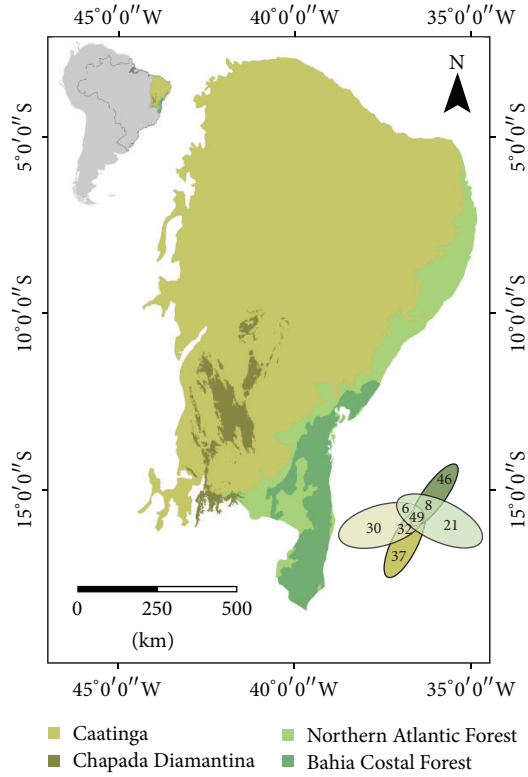


Figure 1: Northeastern Brazil in South America, showing the number of Apocynaceae species per region in a Venn diagram.

Santo to southern Bahia, it is dominated by evergreen forests, harbouring a forest refuge, with high levels of endemism [41] and one of the highest tree species densities in the world [42]. Since CD and BCF are species rich, high PD values are expected for both. However, more species of shrubs and lianas are found in CD whereas BCF is richer in species of trees. This difference probably affected species relatedness and community resilience. Therefore, assessing PS in CD and BCF may provide important basis for phyloconservation policies to protect the high biodiversity found in these areas.

For assessing PS in CD and BCF, we used Apocynaceae and ecophylogenetics in a macroecological approach. The Apocynaceae are one of the ten largest families of angiosperms and their SR distribution shows the highest correlation with angiosperm SR distribution in Brazil, when the five richest angiosperm families in the country are taken into account (Figure 2). This high correlation strongly confirms the Apocynaceae to be a good indicator for plant diversity across the Brazilian territory. The Apocynaceae consist of approximately 5,000 species [43] and 360 genera [44] and are also well represented in Brazil, with 770 species and 73 genera [45]. They are latescent plants with pentamerous, gamopetalous, isostemonous, bicarpelar flowers and comprise a broad range of habits (trees, shrubs, herbs, and lianas) and have pollen transferred as monads, tetrads, or in pollinia, berry-like or bifollicular fruits and seeds with or without coma. The family is widespread over the world, especially in tropical and subtropical regions, and occurs

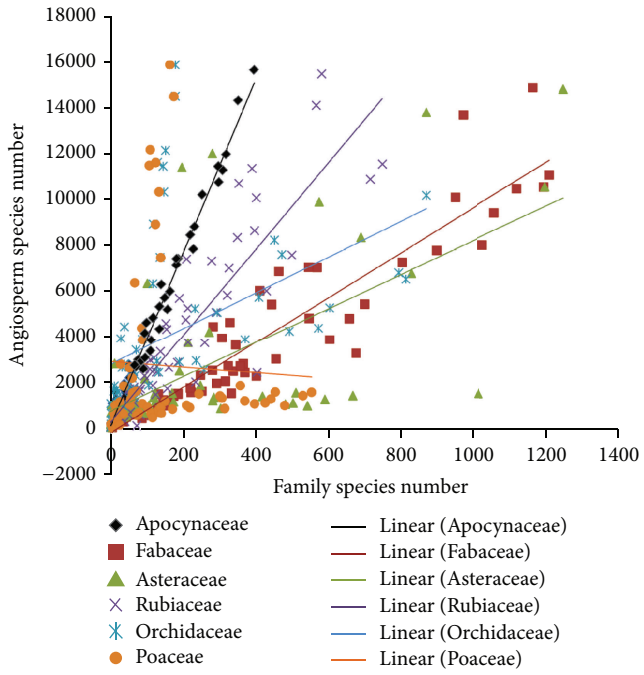


FIGURE 2: Family species number × angiosperm species number per vegetation, states, and regions of Brazil. Spearman's correlation values for Apocynaceae and the five richest families of angiosperm in Brazil [31]: Apocynaceae, $r_s = 0.98$ ($P < 2.2e-16$); Fabaceae, $r_s = 0.95$ ($P < 2.2e-16$); Rubiaceae, $r_s = 0.88$ ($P < 2.2e-16$); Orchidaceae, $r_s = 0.81$ ($P = 5.47e-15$); Asteraceae, $r_s = 0.71$ ($P = 3.29e-10$); and Poaceae, $r_s = 0.28$ ($P = 0.03$).

in almost any habitat, from lowland wet forests to deserts and grasslands in high altitudes [46, 47]. In Brazil, such diversity is classified in three subfamilies: Apocynoideae, Asclepiadoideae, and Rauvolfioideae [47]. Asclepiadoideae comprises a clade that consists mainly of shrubs and lianas, and CD is an important centre of diversity of the subfamily. Together, Apocynoideae and Rauvolfioideae comprise the early diverging lineages of Apocynaceae; the former consists mainly of shrubs and lianas, whereas trees are prevalent in the latter subfamily. Apocynoideae and Rauvolfioideae form a basal grade in Apocynaceae and their species are usually broadly distributed or inhabit predominantly tropical forests such as BCF.

In this study, we map the Apocynaceae PD in northeastern Brazil to evaluate whether CD and BCF present exceptionally high PD and compare the Apocynaceae PS in the two areas. Taking into account the ecological specificities across the Apocynaceae phylogeny, we would expect to find clustered communities in both CD and BCF but concentrated in different lineages. The most derived Asclepiadoideae would be concentrated in CD whereas lineages of the Rauvolfioideae-Apocynoideae basal grade would be mainly concentrated in BCF. We then try to identify ecological and evolutionary factors that may have affected plant community in the two areas and suggest general perspectives for conserving the biodiversity in both.

2. Material and Methods

We built a database with approximately 7,000 specimens, representing 205 species and 47 genera of Apocynaceae native to the Caatinga and Atlantic Forest domains in northeast Brazil (Table 1) based on exsiccates from the main herbaria in Brazil, Europe, and the United States. GPS coordinates were extracted from labels and confirmed or recovered with the help of Google Earth. Specimens without locality were treated at the municipal headquarter.

A calibrated phylogeny was constructed with *matK* sequences of 142 species of Apocynaceae and five from the Loganiaceae (outgroup) from Genbank (the appendix). We sampled 95 genera, representing the five subfamilies and most tribes of Apocynaceae. Sequences were initially aligned in Muscle [48] and subsequently manually adjusted in mesquite [49]. Age estimates were obtained using BEAST 1.8 [50] as implemented in CIPRES [51], using a GTR substitution model, gamma distribution, and relaxed molecular clock. The analysis was conducted from a random starting tree, with a Yule speciation model. Dating was calibrated using two fossils: a comose seed (*Apocynospermum*) from the Eocene (mean = 1.5, Std.Dev. = 1, and Offset = 47, Lognormal prior) assigned to the APSA clade stem node (Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae) [52] and a tetrad (*Polyporotetradites laevigatus*) from the Oligocene/Miocene boundary (mean = 1.5, Std.Dev. = 1, and Offset = 23, Lognormal prior) assigned to *Tacazzea* (Periplocoideae stem node) [53]. A Monte Carlo-Markov chain was run for 5×10^7 generations, saving a tree every 2,000 generations. The log file was analysed in TRACER 1.6 [54] to assess whether the effective sample size reached 200 for all parameters. The maximum credibility tree was recovered in TreeAnnotator 1.8.0 [54], after deleting the first 10% of saved trees (*burn-in*).

We assessed Apocynaceae PD and PS using a pseudochronogram constructed from the calibrated tree, in which species branch length was treated as an average of total lineage branch length. We estimated the total branch length of a lineage assuming half-aged, successive, and balanced dichotomies. Accordingly, species were added regularly at the middistance of the longest branch of that lineage and the sum of lineage branch lengths was divided by the number of species of the lineage in northeastern Brazil (Figure 3). Eight genera lacking molecular data were included based on their taxonomic position and/or other molecular markers [47].

Since biodiversity metrics may be strongly affected by scales, we calculated SR, PD, and PS for $0.5^\circ \times 0.5^\circ$ and $0.08^\circ \times 0.08^\circ$ grids to test the consistence of observed patterns under different spatial scales. PD, after standardization of species branch length, and SR were calculated using Biodiverse v. 0.19 [55]. We estimated PS through net relatedness index (NRI) and nearest taxon index (NTI) for CD and BCF based on cells with exceptionally high PD (higher than 95% of cells for $05^\circ \times 05^\circ$ grid and higher than 97.5% for $0.08^\circ \times 0.08^\circ$ grid) using Phylocom 4.2 [56]. Null communities were generated adopting a model that randomizes species relationships keeping their original species richness [22, 57]. Species abundance was not considered because our data is based on herbarium

Table 1: Native species of Apocynaceae from northeastern Brazil (Caatinga and Atlantic Forest domains in the Northeast Brazil), indicating species occurring in the Caatinga and Atlantic forest. CD denotes species occurring in Chapada Diamantina and BCF in Bahia Costal Forest, in bold when they are endemic to these regions and with an asterisk when they appear in $0.08^{\circ} \times 0.08^{\circ}$ cells with exceptionally high phylogenetic diversity, considering one neighborhood cell.

Species	Floristic domains	
	Caatinga	Atlantic Forest
Allamanda blanchetii A.DC.	CD*	
Allamanda calcicola Souza-Silva & Rapini	x	
Allamanda cathartica L.		BCF*
Allamanda doniana Müll.Arg.	x	BCF*
Allamanda martii Müll.Arg.		BCF*
Allamanda puberula A.DC.	CD*	BCF
Allamanda thevetifolia Müll.Arg.	x	
Araujia sericifera Brot.		x
Asclepias candida Vell.	CD*	
Asclepias curassavica L.	CD*	BCF*
Asclepias mellodora A.St.-Hil.	CD*	BCF*
Aspidosperma cuspa S.F.Blake ex Pittier	CD	
Aspidosperma cylindrocarpon Müll.Arg.		x
Aspidosperma discolor A.DC.	CD*	BCF*
Aspidosperma illustre (Vell.) Kuhlm. & Pirajá	x	BCF
Aspidosperma limae Woodson		x
Aspidosperma macrocarpon Mart.	CD	
Aspidosperma multiflorum A.DC.	x	x
Aspidosperma parvifolium A.DC.	CD*	BCF*
Aspidosperma polyneuron Müll.Arg.	CD*	BCF
Aspidosperma pyricollum Müll.Arg.		x
Aspidosperma pyrifolium Mart.	CD*	BCF*
Aspidosperma ramiflorum Müll.Arg.		BCF
Aspidosperma schultesii Woodson		BCF
Aspidosperma spruceanum Benth. ex Müll.Arg.	CD*	BCF*
Aspidosperma subincanum Mart.	x	
Aspidosperma thomasii Marc.-Ferr.		**BCF***
Aspidosperma tomentosum Mart.	CD*	x
Aspidosperma ulei Markgr.	x	
Bahiella blanchetii (A.DC.) J.F.Morales		**BCF***
Bahiella infundibuliflora J.F.Morales		**BCF**
Barjonia chlorifolia Decne.	CD*	
Barjonia erecta (Vell.) K.Schum.	CD*	
Barjonia glazioui Marquete	CD*	
Blepharodon ampliflorum E.Fourn.	CD*	x
Blepharodon bicolor Decne.	CD	
Blepharodon costae Fontella & Morillo		BCF*
Blepharodon manicatum (Decne.) Fontella	CD*	
Blepharodon pictum (Vahl) W.D.Stevens	CD*	BCF*
Condylocarpon intermedium Müll.Arg.		BCF*
Condylocarpon isthmicum (Vell.) A.DC.	CD*	BCF*
Couma rigida Müll.Arg.	CD*	BCF*
Cynanchum montevidense Spreng.	x	x
Cynanchum roulinioides (E.Fourn.) Rapini	CD*	

Table 1: Continued.

Species	Floristic domains	
	Caatinga	Atlantic Forest
Ditassa arianeae Fontella & E.A.Schwarz	x	BCF*
Ditassa blanchetii Decne.		BCF*
Ditassa capillaris E.Fourn.	CD*	BCF*
Ditassa congesta E.Fourn.	x	
Ditassa crassifolia Decne.	CD	BCF*
Ditassa dardanoi T.U.P.Konno & Wand.	CD	
Ditassa dolichoglossa Schltr.	x	
Ditassa glazioui E.Fourn.	CD*	x
Ditassa grandiflora E.Fourn.	CD*	
Ditassa hastata Decne.	CD*	x
Ditassa hispida (Vell.) Fontella	CD	BCF*
Ditassa lenheirensis Silveira	CD*	x
Ditassa melantha Silveira	CD*	
Ditassa obcordata Mart.	CD*	
Ditassa oxyphylla Turcz.	CD*	BCF
Ditassa pohliana E.Fourn.	CD*	BCF
Ditassa retusa Mart.	CD*	x
Ditassa rotundifolia (Decne.) Baill. ex K.Schum.	CD*	x
Ditassa succedanea Rapini	CD*	
Fischeria stellata (Vell.) E.Fourn.	CD	BCF
Forsteronia australis Müll.Arg.	CD*	BCF
Forsteronia glabrescens Müll.Arg.	x	
Forsteronia leptocarpa (Hook. & Arn.) A.DC.	CD	BCF*
Forsteronia montana Müll.Arg.		BCF*
Forsteronia pubescens A.DC.	CD*	x
Forsteronia rufa Müll.Arg.	CD*	BCF
Forsteronia thyrsoidea Müll.Arg.	CD*	BCF
Funastrum clausum (Jacq.) Schltr.	CD*	BCF*
Geissospermum laeve (Vell.) Miers		BCF*
Gonolobus parviflorus Decne.	x	BCF*
Gonolobus rostratus (Vahl) R.Br. ex Shult.	x	
Hancornia speciosa Gomes	CD*	BCF*
Hemipogon carassensis (Malme) Rapini	CD*	
Himatanthus bracteatus (A. DC.) Woodson	CD*	BCF*
Himatanthus drasticus (Mart.) Plumel	CD*	BCF
Himatanthus obovatus (Müll. Arg.) Woodson	CD	BCF*
Himatanthus phagedaenicus (Mart.) Woodson		x
Jobinia connivens (Hook. & Arn.) Malme	CD*	
Jobinia lindbergii E.Fourn.	CD*	
Lacmellea bahiensis J.F.Morales		**BCF***
Lacmellea pauciflora (Kuhlm.) Markgr.		**BCF**
Macoubea guianensis Aubl.		BCF*
Macroditassa laurifolia (Decne.) Fontella	CD*	BCF*
Malouetia cestroides (Nees ex Mart.) Müll.Arg.		BCF*
Mandevilla alexicaca (Mart. ex Stadelm.) M.F.Sales	**CD***	

Table 1: Continued.

Species	Floristic domains	
	Caatinga	Atlantic Forest
Mandevilla bahiensis (Woodson) M.F.Sales & Kin.-Gouv.	CD*	**BCF***
Mandevilla catimbauensis-Silva et al.	x	
Mandevilla dardanoi M.F.Sales et al.	x	x
Mandevilla emarginata (Vell.) C.Ezcurra	CD*	
Mandevilla fistulosa M.F.Sales et al.		BCF
Mandevilla guanabarica Casar. ex M.F.Sales, Kin.-Gouv. & A.O.Simões		BCF
Mandevilla hatschbachii M.F.Sales et al.	**CD**	
Mandevilla hirsuta (A.Rich.) K.Schum.	CD*	BCF
Mandevilla illustris (Vell.) Woodson	CD*	x
Mandevilla leptophylla (A.DC.) K.Schum.	CD*	
Mandevilla longiflora (Desf.) Pichon	CD*	
Mandevilla luetzelburgii Woodson	CD	BCF
Mandevilla martiana (Stadelm.) Woodson	CD*	
Mandevilla martii (Müll.Arg.) Pichon	CD	
Mandevilla microphylla (Stadelm.) M.F.Sales & Kin.-Gouv.	**CD***	**BCF***
Mandevilla moricandiana (A.DC.) Woodson	CD*	BCF*
Mandevilla myriophylla (Taub. ex Ule) Woodson	CD	
Mandevilla permixta Woodson		**BCF***
Mandevilla sancta (Stadelm.) Woodson	**CD***	x
Mandevilla scabra (Hoffmanns. ex Roem. & Schult.) K.Schum.	CD*	BCF*
Mandevilla tenuifolia (J.C.Mikan) Woodson	CD*	x
Marsdenia altissima (Jacq.) Dugand	CD*	BCF
Marsdenia caatingae Morillo	x	BCF*
Marsdenia carvalhoi Morillo & Carnevali		**BCF**
Marsdenia dorothyae Fontella & Morillo		BCF*
Marsdenia heringeri Fontella	x	
Marsdenia hilariana E.Fourn.	CD*	BCF
Marsdenia loniceroides E.Fourn.	x	x
Marsdenia macrophylla (Humb. & Bonpl. ex Schult.) E.Fourn.	x	
Marsdenia megalantha Goyder & Morillo	x	
Marsdenia pickelii Fontella & Morillo	x	
Marsdenia queirozii Fontella	x	
Marsdenia suberosa (E.Fourn.) Malme	CD*	BCF
Marsdenia zehntneri Fontella	CD	
Matelea bahiensis Morillo & Fontella		**BCF***
Matelea denticulata (Vahl) Fontella & E.A.Schwarz	x	BCF*
Matelea endressiae Fontella & Goes	CD	
Matelea ganglinosa (Vell.) Rapini	CD*	BCF*
Matelea harleyi Fontella & Morillo	CD	
Matelea morilloana Fontella	**CD***	
Matelea nigra (Decne.) Morillo & Fontella	CD*	
Matelea orthosioides (E.Fourn.) Fontella	CD*	BCF*
Matelea pedalis (E.Fourn.) Fontella & E.A.Schwarz	CD*	

Table 1: Continued.

Species	Floristic domains	
	Caatinga	Atlantic Forest
Matelea riparia Morillo		BCF
Matelea roulinioides Agra & W.D.Stevens	x	
Matelea santosii Morillo & Fontella		**BCF**
Metastelma giuliettianum Fontella	**CD***	
Metastelma harleyi Fontella	**CD***	
Metastelma myrtifolium Decne.	**CD***	
Minaria acerosa (Mart.) T.U.P.Konno & Rapini	CD*	
Minaria cordata (Turcz.) T.U.P.Konno & Rapini	CD*	x
Minaria decussata (Mart.) T.U.P.Konno & Rapini	CD	
Minaria harleyi (Fontella & Marquete) Rapini & U.C.S.Silva	**CD***	
Minaria volubilis Rapini & U.C.S.Silva	**CD***	
Monsanima morrenioides (Goyder) Liede & Meve	**CD***	
Nephradenia asparagoides (Decne.) E.Fourn.	CD*	
Odontadenia hypoglauca Müll.Arg.	x	
Odontadenia lutea (Vell.) Markgr.	CD*	BCF*
Orthosia parviflora (E.Fourn.) Liede & Meve		BCF*
Orthosia scoparia (Nutt.) Liede & Meve	x	
Oxypetalum arachnoideum E.Fourn.	CD*	
Oxypetalum banksii R.Br. ex Schult.	CD	BCF*
Oxypetalum capitatum Mart.	CD*	
Oxypetalum erostre E.Fourn.	CD*	
Oxypetalum harleyi (Fontella & Goyder) Farinaccio	CD*	BCF
Oxypetalum jacobinae Decne.	CD*	BCF
Oxypetalum laciniatum Rapini & Farinaccio		**BCF**
Oxypetalum montanum Mart.	CD*	
Oxypetalum pachyglossum Decne.		BCF*
Oxypetalum strictum Mart.	CD*	
Oxypetalum warmingii (E.Fourn.) Fontella & Marquete	x	
Peltastes peltatus (Vell.) Woodson		BCF*
Peltastes pulcher (Miers) J.F.Morales		BCF*
Peplonia adnata (E.Fourn.) U.C.S.Silva & Rapini	CD*	BCF
Peplonia asteria (Vell.) Fontella & E.A.Schwarz		BCF*
Peplonia axillaris (Vell.) Fontella & Rapini		BCF
Peplonia bradeana (Fontella & E.A.Schwarz) Fontella & Rapini		BCF*
Peplonia macrophylla (Malme) U.C.S.Silva & Rapini	CD*	
Petalostelma cearense Malme	x	
Petalostelma dardanoi Fontella	x	
Petalostelma martianum (Decne.) E.Fourn.	x	
Prestonia annularis G.Don		BCF
Prestonia bahiensis Müll.Arg.	CD*	BCF*
Prestonia calycina Müll.Arg.	x	BCF
Prestonia coalita (Vell.) Woodson	CD*	BCF*
Prestonia didyma (Vell.) Woodson		BCF*

Table 1: Continued.

Species	Floristic domains	
	Caatinga	Atlantic Forest
Prestonia erecta (Malme) J.F.Morales	CD	
Prestonia lagoensis (Müll.Arg.) Woodson	CD*	
Prestonia quinquangularis (Jacq.) Spreng.		BCF*
Rauvolfia atlantica Emygdio		**BCF***
Rauvolfia bahiensis A.DC.		**BCF***
Rauvolfia grandiflora Mart.	x	BCF
Rauvolfia ligustrina Willd.	x	x*
Rauvolfia mattfeldiana Markgr.	CD	
Rauvolfia moricandii A.DC.		BCF*
Rauvolfia paucifolia A.DC.	CD	
Schubertia grandiflora Mart.	CD*	
Schubertia morilloana Fontella	CD*	
Schubertia multiflora Mart.	CD*	BCF
Secondatia densiflora A.DC.	CD*	x
Secondatia floribunda A.DC.	CD*	BCF*
Skytanthus hancorniifolius (A.DC.) Miers	CD*	x
Stenomeria decalepis Turcz.		BCF*
Stipecoma peltigera (Stadelm.) Müll.Arg.	CD*	x
Tabernaemontana catharinensis A.DC.	x	x
Tabernaemontana flavicans Willd. ex Roem. & Schult.		BCF*
Tabernaemontana grandiflora L.		BCF
Tabernaemontana hystrix Steud.		BCF
Tabernaemontana laeta Mart.	x	BCF
Tabernaemontana salzmannii A.DC.		BCF*
Tabernaemontana solanifolia A.DC.	CD*	BCF
Tassadia burchellii E.Fourn.	CD*	
Tassadia obovata Decne.		BCF*
Tassadia propinqua Decne.		BCF*
Temnadenia odorifera (Vell.) J.F.Morales		BCF*
Temnadenia violacea (Vell.) Miers	CD*	BCF

material and analysed at relatively large scales. Ten thousand random (phylogenetically unstructured) communities were generated using the Apocynaceae pseudochronogram and a species pool from northeastern Brazil. This region is much larger than both CD and BCF, but only approximately one-quarter of the species in northeastern Brazil are not represented in either CD or BCF (Figure 1). To assess statistical differences in SR, PD, NRI, and NTI between CD and BCF, we used Kruskal-Wallis test and pairwise correlations between measures of diversity using Spearman's index, both in R statistical software [58]. To ensure that results of statistical tests are not overestimated due to spatial autocorrelation of analysis [59, 60], we also performed Kruskal-Wallis tests for SR, PD, and PS values without neighborhood cells at both spatial scales.

3. Results

Apocynaceae chronogram from *matK* sequences (Figure S1; see Supplementary Material available online at http://dx.doi.org/10.1155/2015/758019) mostly agree with the topology summarized in Rapini [47], based on several phylogenetic studies, and also with the most recent classification of the family [44]. The few hard conflicts (posterior probability = 100%) were (1) *Tylophora* sister to Asclepiadinae-Cynanchinae clade, rather than within Cynanchinae; (2) *Macropharynx*, *Peltastes*, and *Temnadenia* forming a clade without *Prestonia*, but agreeing with Peltastinae circumscription [44]; and (3) *Ambelania* sister to *Tabernaemontana*, making Ambelaniinae paraphyletic. The origin of Apocynaceae (stem group) was estimated at 68.56 million years

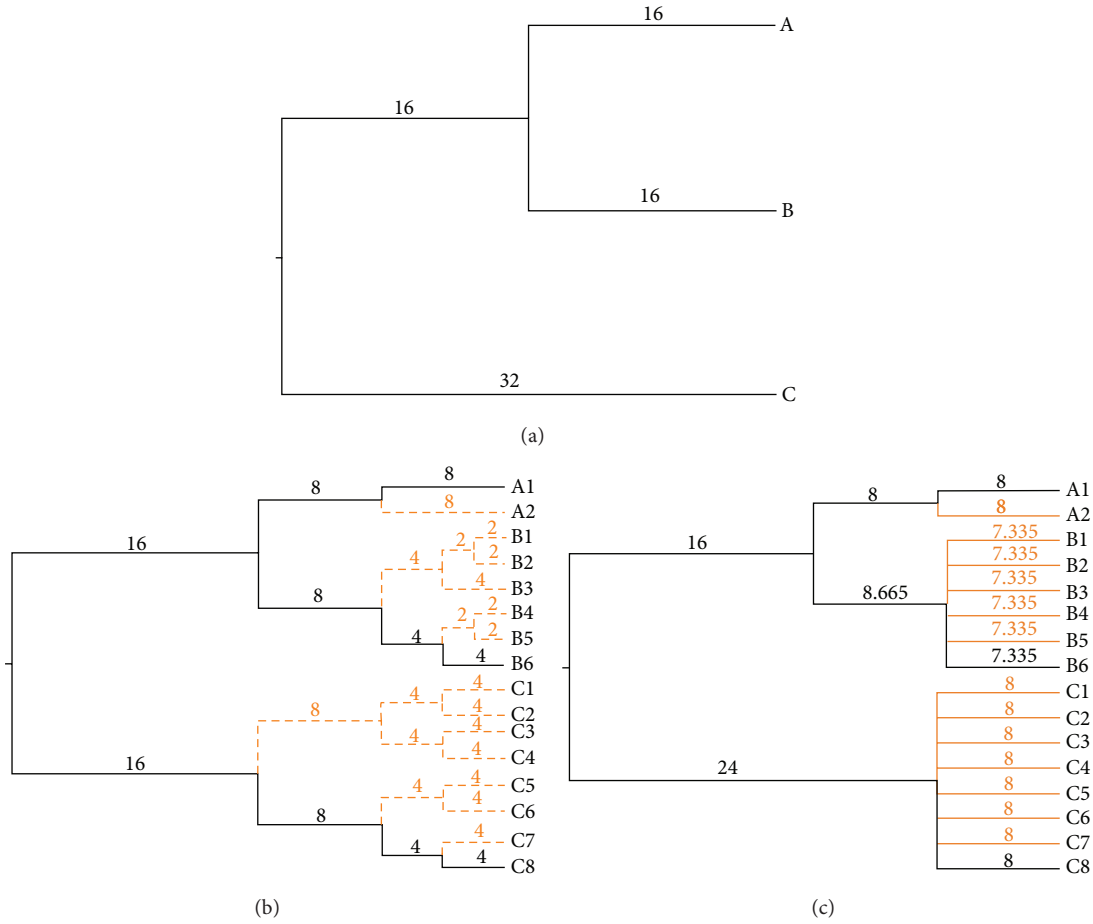


FIGURE 3: Procedure for calculating species' branch lengths. (a) Chronogram from Bayesian analysis. (b) Estimating lineage branch length: species lacking molecular data are inserted sequentially at the half length of the longest branches (dashed, orange branches). (c) Total branch length of the clade is standardized and species polytomized at the stem, which corresponds to the original age of lineage minus the species standardized branch length.

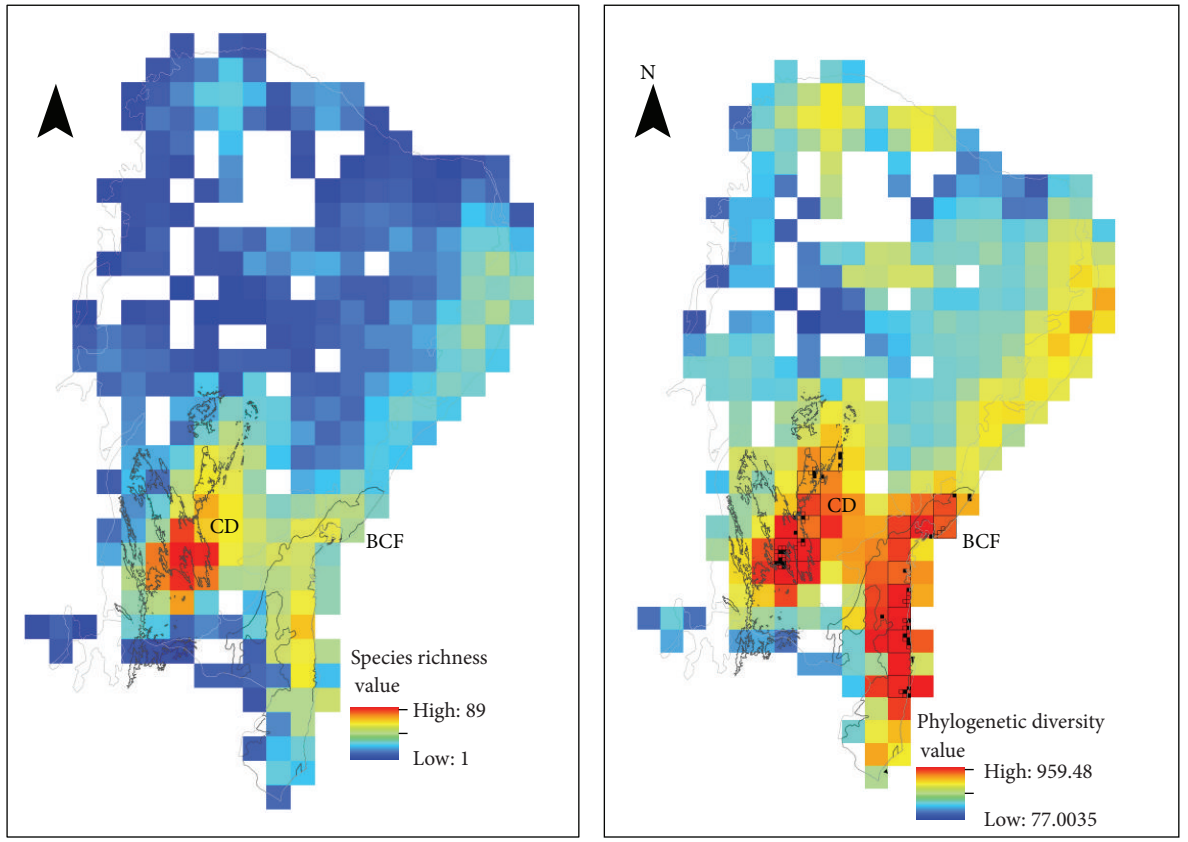
ago (Ma; HPD 95% = 55.92–84.4 Ma), of APSA clade at 50.52 Ma (47.19–56.38), and of Asclepiadoideae at 27.35 Ma (21.57–33.48). Genera estimates ranged from 36.83 Ma (22.6–52.9) for *Rauvolfia* to 4.8 Ma (1.2–9.4) for the monotypic *Hancornia* (*H. speciosa*).

The Atlantic Forest domain shelters 130 species of Apocynaceae in northeastern Brazil and the Caatinga domain 154; 79 of these species occur in both domains. PD, estimated from the pseudochronogram (Figure S2), and SR were strongly correlated ($P \leq 2.2e - 16$, $r_s = 0.945$) and showed similar distributions in northeastern Brazil, with exceptionally high values concentrated in the CD and BCF (Figure 4). CD corresponds to only 4.5% of Caatinga in northeastern Brazil but shelters 77% of its SR (118 of 154 species) and 78% of its PD; 22% (37 species) of SR from CD was not found elsewhere in Caatinga, representing 8% of a restricted PD. BCF corresponds to 41% of the northeastern Atlantic Forest and comprises 80% of its SR (103 of 130 species) and 88% of its PD; 44% (46 species) of SR from BCF is not found anywhere else in the northern Atlantic Forest, representing 21% of a restricted PD (Figure 1).

PDs in CD and BCF are not statistically different, but their SR and NRIs are (Table 2). Overall, the Apocynaceae are phylogenetically clustered (NRI > 0) in CD and overdispersed (NRI < 0) in BCF. Recent relationships are not evidently structured in either region and the difference between them is not significant at small spatial scale (0.08° × 0.08°) when neighbour cells are not considered; otherwise, the difference is significant (Table 2), with CD appearing to be clustered (NTI > 0) only at a large spatial scale (0.5° × 0.5°) when neighbour cells are not considered and BCF tending toward overdispersion (NTI < 0) (Figure 5). SR correlates to PD but only correlates to NRI when 0.08° cells is used in CD. SR is not statistically correlated to NTI and PD is not correlated to NRI or NTI in most cases (Table 3).

4. Discussion

The Apocynaceae have been phylogenetically investigated using several molecular regions (summarized in [47]) and, more recently, plastome analyses were also employed to resolve major relationships in the APSA clade [61]. Advances



(a) (b)

Figure 4: Distribution of species richness (a) and phylogenetic diversity (b) of Apocynaceae in northeastern Brazil, using 0.5° × 0.5° cells with one neighborhood cell; 0.5° cells with black margins present exceptionally high (5% highest) phylogenetic diversity without neighborhood in Chapada Diamantina (CD) and Bahia Costal Forest (BCF); 0.08° cells present exceptionally high (2.5% highest) phylogenetic diversity with (black margins) and without neighborhood cells (black squares) in CD and BCF.

Table 2: Kruskal-Wallis test for species richness (SR), phylogenetic diversity (PD), net relatedness index (NRI), and nearest taxon index (NTI) in cells with exceptionally high PD in Chapada Diamantina and Bahia Costal Forest, using 0.5° × 0.5° and 0.08° × 0.08° cells, with (Nc) and without (wNc) one neighborhood cell.

	0.5° Nc		0.5° wNc		0.08° Nc		0.08° wNc	
	P	x^2	P	x^2	P	x^2	P	x^2
PD	0.6256	0.2381	0.2976	1.0848	0.5311	0.3923	0.2744	1.1946
SR	0.001	10.7407	0.03136	4.6333	$3.49E-05$	17.1326	0.0002	13.3278
NRI	0.0006	11.6667	0.001194	10.5	$7.43E-07$	24.5	$2.96E-05$	17.4414
NTI	0.005	7.8107	0.007774	7.0848	0.005194	7.8107	0.08184	3.028

in Apocynaceae systematics is incorporated into an updated classification at the tribal and subtribal levels [44], but many genera are not monophyletic (e.g., [62, 63]) or still need a thorough phylogenetic investigation [47]. So far, dated phylogenies in Apocynaceae focused only on less inclusive groups, such as Asclepiadoideae [64], Tylophorinae [65], and *Minaria* [66], and used *trnL* intron and *trnL-F* intergenic space (*trnL-F*) for the Apocynaceae big picture. Therefore, this is the first Apocynaceae dated phylogeny using *matK*. Our results consistently recovered relationships obtained in previous studies and age estimates overlap those with *trnL-F* [66] when confidence intervals are taken into account. However, the small sampling in major groups of Apocynaceae prevents a comprehensive biogeographic discussion.

Most of the Apocynaceae diversity in northeastern Brazil is concentrated in the *Campos Rupestres* of Chapada Diamantina (CD) and in the Bahia Costal Forest (BCF). CD and BCF are historical refuges for plants in two different floristic domains. CD is considered a refuge for grasslands during interglacial periods (e.g., [34, 67, 68]) or for fire-sensitive lineages after the expansion of the fire-prone Cerrado in Central Brazil [36, 66], whereas BCF is a refuge for forest associated lineages [40]. These plant refuges shelter an exceptionally high PD, which is phylogenetically clustered

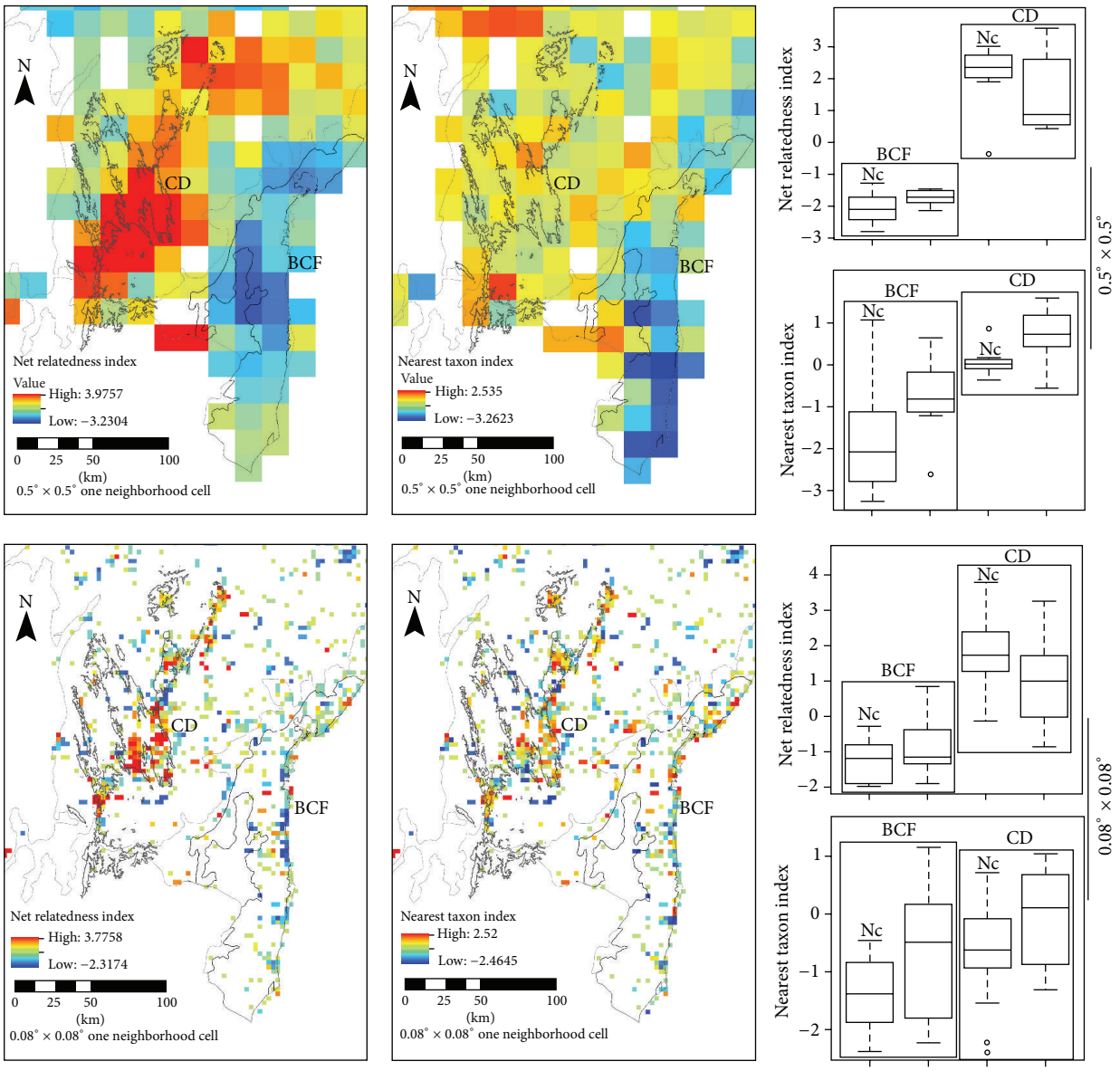


Figure 5: Distribution of net relatedness index (NRI) and nearest taxon index (NTI) in northeastern Brazil with bloxplots comparing 32 cells with exceptionally high phylogenetic diversity (Figure 4) in Chapada Diamantina (CD) and Bahia Costal Forest (BCF), using different scales (0.5° × 0.5° and 0.08° × 0.08° cells), with (Nc) and without one neighborhood cell.

Table 3: Spearman's correlation values for species richness (SR), phylogenetic diversity (PD), net relatedness index (NRI), and nearest taxon index (NTI) in cells with exceptionally high PD in the Bahia Costal Forest (BCF) and Chapada Diamantina (CD), using 0.5° × 0.5° and 0.08° × 0.08° cells, with (Nc) and without (wNc) one neighborhood cell; asterisks indicate the significance values ($P < 0.05$).

	Scales	SR-PD		SR-NRI		SR-NTI		PD-NRI		PD-NTI	
		P value	r_s	P value	r_s	P value	r_s	P value	r_s	P value	r_s
BCF	0.5° Nc	0.0003*	0.9	0.91	0.03	0.47	0.25	0.82	−0.07	0.72	0.12
	0.5° wNc	0.005*	0.86	0.79	−0.1	0.12	−0.59	0.38	−0.35	0.028*	−0.76
	0.08° Nc	0.01*	0.62	0.15	0.4	0.7	−0.11	0.28	−0.3	0.74	0.09
	0.08° wNc	0.019*	0.57	0.37	0.23	0.17	0.35	0.31	−0.26	0.38	−0.23
CD	0.5° Nc	0.002519*	0.92	0.7599	0.14	0.75	−0.14	0.87	−0.07	0.75	−0.14
	0.°5 wNc	0.01*	0.85	0.21	0.53	0.75	−0.14	0.38	0.39	0.39	−0.39
	0.08° Nc	$3.50E-09$*	0.92	0.0007	0.67	0.64	−0.1	$5.89E-05$*	0.76	0.07	−0.39
	0.08° wNc	0.0002*	0.78	0.002	0.7	0.74	0.09	0.18	0.35	0.12	−0.39

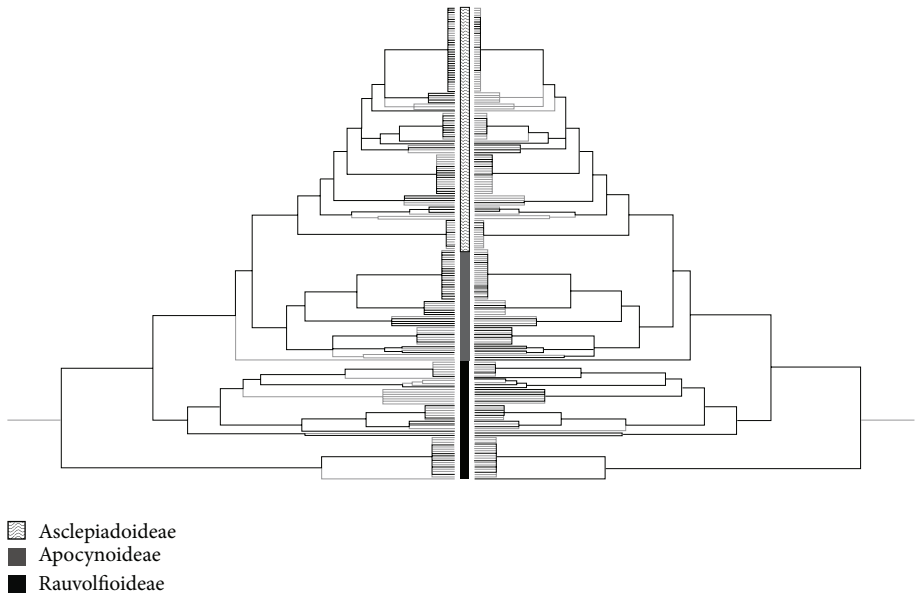


Figure 6: Backbone of Apocynaceae pseudochronogram (modified from Figure S2) showing the lineages represented in the exceptionally high PD cells of the Chapada Diamantina (left) and Bahia Costal Forest (right) in bold.

in CD but overdispersed in BCF. This difference is mirrored in SR, which is higher and spatially concentrated in CD. The Asclepiadoideae and the upper Apocynoideae grade are better represented in CD, contributing to a high number of young lineages, while the Apocynaceae basal grade, including Rauvolfioideae and the early Apocynoideae, is better represented in BCF, contributing to fewer but older lineages (Figure 6).

Plants in tropical forests have usually presented clustered phylogenies (e.g., [10, 20, 69–71]), contrasting with BCF. There are several potential explanations for this difference. First, most studies in tropical forests considered only tree communities, which tend to be phylogenetically clustered [30]. Second, their phylogenetic scale often comprises the whole angiosperms, and scales that are phylogenetically more inclusive are more likely to produce clustered PS [15–17] and also lose the power for predicting ecological processes as convergent traits increase to deeper relationships [3]. Third, such analyses are usually produced from poorly resolved phylogenies, in which species are unresolved within genera and genera within families. A lack of phylogenetic resolution also limits the analysis power and results can be incorrect, particularly near the tips, because many families are still awaiting phylogenetic analyses at the genus level.

In BCF, the overdispersed phylogeny at family scale is possibly produced by phenotypic repulsion caused by long-term competitive exclusion in a climatically stable region, rather than by phylogenetic attraction because of convergent traits, which is more likely at higher phylogenetic scales. When species are phylogenetically evenly distributed, as in BCF, niche overlap is expected to be reduced, and species probably have complementary fluctuations, responding differently to environmental changes and replacing one another in dominance, while maintaining ecosystem function. Because of that, diverse communities are more robust to species invasion, more productive and more resilient to environmental changes [12]. Under climatic changes, estimates are that in 50 years, neotropical ever-wet zones will be one-third smaller because of increasing seasonal variability in rainfall [72]. As such, refuges of biodiversity like BCF—stable climatic region that is home of a high and phylogenetically evenly distributed evolutionary diversity—deserve high priority for *in situ* conservation.

The Apocynaceae are spatially and phylogenetically compact in CD, a pattern different from that in BFC. The overall clustering in CD reflects the heterogeneity and fragmented distribution of *Campos Rupestres*. At mountaintops, this biome consists of a mosaic of microhabitats at a small scale with an insular distribution at a large scale, resulting in high β diversity [73]. Accordingly, the same spatial scales used in BCF tend to comprise more heterogeneous areas in CD and, therefore, are more likely to support species with different ecological traits in larger clades (e.g., Metastelmatinae) and also a higher number of allopatric, closely-related, microendemic species with similar ecological traits. This biogeographic pattern is reflected by the overall clustered PS in CD. For recent relationships, the phylogeny is not evidently structured, suggesting a stronger influence of neutral processes. Therefore, at a biogeographic context, deeper and narrower phylogenetic structures together suggest a stronger influence of niche conservatism, limited dispersal and *in situ* diversification in CD, which can explain the high density of microendemic species in the *Campos Rupestres* as a result of nonadaptive, geographic radiations, as postulated by Ribeiro et al. ([36]; see also [66]).

According to the most popular hypothesis of diversification in the Espinhaço Range, the *Campos Rupestres* is cold associated, contracting to highlands during warmer periods

and expanding to lowlands during cooler periods. Diversification resulted from successive contraction-expansion cycles caused by Pleistocene climatic fluctuations (e.g., [34, 67, 68]), as also suggested by refugial sites in different continents (e.g., [74, 75]). Alternatively, highlands represent refuges for fire-sensitive lineages and diversification was driven by the expansion of fire-prone Cerrado and fragmentation of *Campos Rupestres* since the late Miocene-Pliocene [36]. According to this hypothesis, milder weather and a high concentration of rocky outcrops in the highlands have helped to prevent frequent, intense fires, and diversification is result of a long-term contraction of the *Campos Rupestres*. Both scenarios consider mountaintops along the Espinhaço Range ecologically stable areas buffering biome conservative lineages during environmental changes and fit the PS recovered for Apocynaceae here.

Phylogenetic diversity and species relatedness reflect important properties for community function and stability [12, 76]. The high PD in CD resulted from high SR of closely related species, in clustered structured communities; therefore, communities in CD are probably more vulnerable than in BCF. Past and future distribution models estimated a smaller distribution of *Campos Rupestres* today compared to in the Last Maximum Glacial and even smaller distributions in the future, almost disappearing in CD by the end of this century because of increasing seasonality [77]. Under this scenario, the reduction of the *Campos Rupestres* range is a natural process and loss of biodiversity in CD is probably inevitable. However, this process has been greatly accelerated by anthropogenic changes and CD may not represent a biodiversity refuge in the short future. Therefore, *ex situ* conservation is probably an important strategy to retain the biodiversity from the *Campos Rupestres* of the CD available in the future.

5. Conclusion

Ecology and phylogeny have been used independently from each other in biogeography [24]. Ecophylogenetics fills part of this gap and its use for investigating community structure has been increasing quickly [78]. However, ecophylogenetics and macroecology are still somewhat separate from each other, and few authors (e.g., [25, 79]) dared to analyse PS at large geographical scales. Although attention has been given more recently to species evolutionary distinctiveness, different components of a multifaceted biodiversity cannot be confidently used as surrogate of others (e.g., [80–82]).

The use of phylogenies through PD (*sensu* Faith [5]) in conservation goes beyond the traditional SR because it also includes evolutionary information. However, PD does not take into account species relationships and therefore misses an important aspect from which processes and factors that have driven community diversity can be inferred and functional diversity can be estimated [80]. PS emerges as a key concept in this context because it distributes PD across SR, shaping the evolutionary trace of a community, and, at the same time, provides indirect access for functional diversity, in particular when traits show a high phylogenetic signal. Thus, PS becomes an important measure to assess the vulnerability of communities against climatic changes or ecological and anthropogenic disturbances, providing information for conservation, and can be used for both understanding the past and anticipating the future.

SR, PD, and PS represent different aspects of biodiversity, and, together, they provide a more complete framework for conservation assessments. Our study shows that individual extinctions are probably more influent phylogenetically in BCF than in CD because PD/SR ratio is higher in BCF. However, communities in BCF are usually overdispersed and, therefore, probably more resilient against invasive species, climatic changes, and anthropogenic disturbances than communities in CD, which are phylogenetically unstructured or more often clustered. Based on PS pattern, different general conservation strategies can be designed; while *in situ* conservation may fit well for communities in BCF, an *ex situ* conservation is also recommended for protecting biodiversity in CD.

Appendix

Taxa (Genbank Accession Number of *matK* Sequence)

These include the following: *Allamanda cathartica* L. (Z70190); *Acokanthera oblongifolia* Benth. & Hook.f. (Z70182); *Allamanda schottii* Pohl (DQ660495); *Alstonia boonei* De Wild. (KC627675); *Alstonia scholaris* (L.) R.Br. (AJ429321); *Alyxia reinwardtii* Blume (DQ660496); *Alyxia oblongata* Domin (EF456370); *Ambelania acida* Aubl. (DQ660497); *Apocynum cannabinum* L. (DQ660500); *Apocynum androsaemifolium* L. (Z70183); *Araujia sericifera* Brot. (Z98194); *Asclepias syriaca* L. (DQ660501); *Asclepias curassavica* L. (DQ026716); *Aspidosperma cylindrocarpon* Müll.Arg. (DQ660503); *Aspidosperma australe* Müll.Arg. (DQ660502); *Baissea multiflora* A.DC. (EF456319); *Baissea zygodioides* Stapf (DQ221120); *Barjonia laxa* Malme (JN805851); *Barjonia cymosa* E.Fourn. (JN805848); *Barjonia erecta* (Vell.) K.Schum. (JN805849); *Blepharodon lineare* (Decne.) Decne. (DQ026718); *Blepharodon ampliflorum* E.Fourn. (JN805852); *Blepharodon nitidum* (Vell.) J.F.Macbr. (DQ026720); *Calotropis gigantea* (L.) W.T.Aiton (JN228932); *Carissa ovata* R.Br. (DQ660506); *Carissa macrocarpa* A.DC. (DQ660505); *Condylocarpon isthmicum* (Vell.) A.DC. (DQ660511); *Condylocarpon amazonicum* (Markgr.) Ducke (DQ837537); *Couma guianensis* Aubl. (DQ660512); *Cryptolepis sinensis* Merr. (EF456374); *Cryptostegia grandiflora* R.Br. (Z98176); *Cynanchum acutum* L. (AY899939); *Cynanchum auriculatum* Buch.-Ham. ex Wight (GU373529); *Ditassa banksii* R.Br. ex Schult. (DQ026719); *Ditassa auriflora* Rapini (JN805856); *Ditassa retusa* Mart. (DQ026728); *Dregea sinensis* Hemsl. (Z98188); *Dyera costulata* Hook.f. (DQ660515); *Farquharia elliptica* Stapf (EF456357); *Fockea capensis* Endl. (Z98187); *Fockea edulis* K.Schum. (EF456383); *Forsteronia velloziana* (A.DC.) Woodson (DQ522596); *Forsteronia acouci* A.DC. (DQ522594); *Funastrum clausum* Schltr. (DQ026730); *Galactophora schomburgkiana* Woodson (EF456300); *Geissospermum laeve* Miers (DQ660517);

Gomphocarpus fruticosus R.Br. (HM850833); *Gonolobus xanthotrichus* Brandegee (Z98195); *Gymnanthera oblonga* (Burm.f.) P.S.Green (EF456376); *Hancornia speciosa* Gomes (DQ660519); *Hemipogon abietoides* E.Fourn. (JN805868); *Hemipogon luteus* E.Fourn. (JN805874); *Himatanthus bracteatus* (A.DC.) Woodson (EF456366); *Hunteria eburnea* Pichon (DQ660521); *Hunteria umbellata* Hallier f. (KC627769); *Hunteria zeylanica* Gardner ex Thwaites (JX517717); *Lacmellea aculeata* (Ducke) Monach. (DQ660523); *Lacmellea panamensis* (Woodson) Markgr. (GQ982028); *Logania vaginalis* (Labill.) F.Muell. (AJ429324); *Macoubea guianensis* Aubl. (GU973901); *Macroditassa grandiflora* (E.Fourn.) Malme (JN805877); *Macroditassa adnata* Malme (JN805876); *Macroditassa melantha* (Silveira) Rapini (JN805879); *Macropharynx renteriae* A.H.Gentry (JQ586549); *Macroscepis hirsuta* (Vahl) Schltr. (JQ586771); *Malouetia tamaquarina* A.DC. (EF456346); *Malouetia bequaertiana* Woodson (EF456358); *Mandevilla hirsuta* (Rich.) K.Schum. (DQ522614); *Mandevilla syrinx* Woodson (DQ522637); *Marsdenia engleriana* W.Rothe (JQ586772); *Melodinus australis* (F.Muell.) Pierre (DQ660524); *Melodinus cochinchinensis* (Lour.) Merr. (DQ660525); *Mesechites mansoanus* (A.DC.) Woodson (DQ522644); *Mesechites roseus* (A.DC.) Miers (DQ522646); *Metastelma schaffneri* A.Gray (JN805884); *Metastelma parviflorum* (Sw.) Schult. (JN805883); *Minaria harleyi* (Fontella & Marquete) Rapini & U.C.S.Silva (JN805850); *Minaria volubilis* Rapini & U.C.S.Silva (JN805871); *Minaria grazielae* (Fontella & Marquete) T.U.P.Konno & Rapini (DQ026724); *Mitreola petiolata* (J.F.Gmel.) Torr. & A.Gray (JQ588153); *Molongum laxum* (Benth.) Pichon (Z70185); *Mondia ecornuta* (N.E.Br.) Bullock (AY899941); *Motandra guineensis* A.DC. (DQ221121); *Mucoa duckei* (Markgr.) Zarucchi (GU973902); *Nautonia nummularia* Decne. (JN805886); *Neocouma ternstroemiacea* (Müll.Arg.) Pierre (GU973903); *Nephradenia filipes* Malme (JN805889); *Nephradenia asparagoides* E.Fourn (JN805888); *Nephradenia acerosa* Decne. (JN805887); *Nerium oleander* L. (Z98173); *Odontadenia lutea* (Vell.) Markgr. (DQ522648); *Odontadenia perrottetii* (A.DC.) Woodson (EF456272); *Oncinotis tenuiloba* Stapf (DQ660529); *Orthosia scoparia* (Nutt.) Liede & Meve (KF539851); *Oxypetalum sublanatum* Malme (DQ026738); *Oxypetalum banksii* Schult. (DQ026735); *Parahancornia fasciculata* (Poir.) Benoist (DQ660530); *Peltastes isthmicus* Woodson (EF456301); *Peltastes peltatus* (Vell.) Woodson (DQ660532); *Pentopetia grevei* (Baill.) Venter (AY899943); *Peplonia macrophylla* (Malme) U.C.S.Silva & Rapini (JN805878); *Peplonia organensis* (E.Fourn.) Fontella & Rapini (JN805891); *Peplonia asteria* (Vell.) Fontella & E.A.Schwarz (JN805890); *Periploca graeca* L. (Z98178); *Pervillaea phillipsonii* Klack. (AJ312408); *Pervillaea venenata* (Baill.) Klack. (Z98181); *Petalostelma martianum* E.Fourn. (JN805892); *Petalostelma sarcostemma* (Lillo) Liede & Meve (JN805893); *Petopentia natalensis* (Schltr.) Bullock (DQ660533); *Philibertia discolor* (Schltr.) Goyder (DQ026732); *Philibertia lysimachioides* (Wedd.) T.Mey. (DQ026741); *Phyllanthera grayi* (P.I.Forst.) Venter (DQ660534); *Pleiocarpa pycnantha* Stapf (JX517964); *Pleiocarpa mutica* Benth. (DQ660535); *Pleiocarpa rostrata* Benth. (KC627551); *Prestonia lagoensis* Woodson (EF456329); *Prestonia mexicana* A.DC. (EF456345); *Raphionacme flanaganii* Schltr. (EF456377); *Raphionacme welwitschii* Schltr. & Rendle (Z98179); *Rauvolfia vomitoria* Wennberg (DQ660538); *Rauvolfia mannii* Stapf (Z70181); *Rhabdadenia biflora* Müll.Arg. (EF456277); *Rhabdadenia macrostoma* Müll.Arg. (EF456349); *Rhigospira quadrangularis* (Müll.Arg.) Miers (GU973904); *Secamone elliptica* R.Br. (DQ660541); *Secamone bosseri* Klack. (Z98182); *Secamone geayi* Costantin & Gallaud (Z98184); *Secamonopsis madagascariensis* Jum. (Z98185); *Secondatia densiflora* A.DC. (DQ522653); *Spigelia anthelmia* L. (JQ588156); *Spongiosperma macrophyllum* (Müll.Arg.) Zarucchi (GU973905); *Stapelia gigantea* N.E.Br. (JQ025000); *Stephanostema stenocarpum* K.Schum. (DQ660543); *Stipecoma peltigera* Müll.Arg. (EF456314); *Strychnos axillaris* Colebr. (AB636276); *Tabernaemontana cuspidata* Rusby (GU973931); *Tabernaemontana hystrix* Steud. (GU973942); *Tacazzea apiculata* Oliv. (AY899945); *Temnadenia violacea* (Vell.) Miers (EF456341); *Temnadenia odorifera* (Vell.) J.F.Morales (EF456353); *Thevetia peruviana* K.Schum. (Z70188); *Thevetia ahouai* A.DC. (GQ982112); *Toxocarpus villosus* Decne. (EF456379); *Tylophora indica* Merr. (Z98193); *Vallesia antillana* Woodson (AM295075); *Wrightia dubia* Spreng. (EF456257); *Wrightia lanceolata* Kerr (EF456291).

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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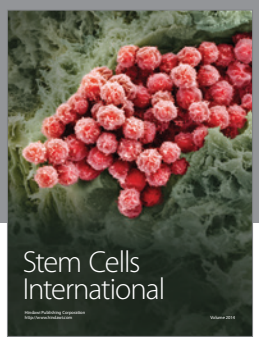

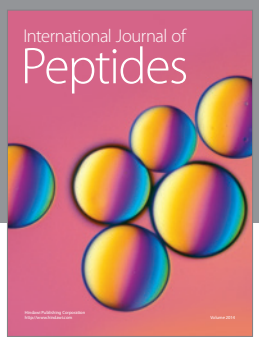

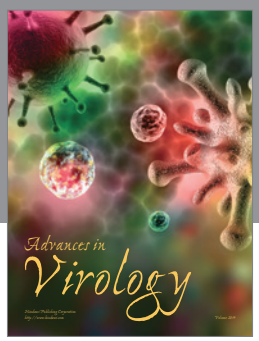

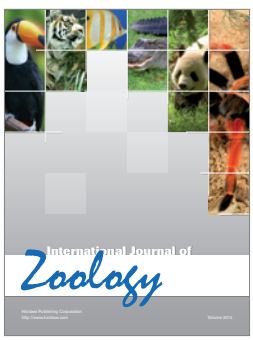

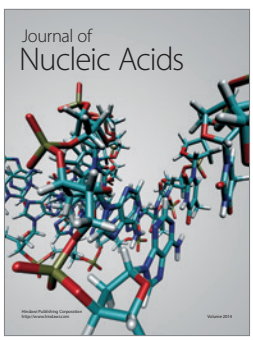

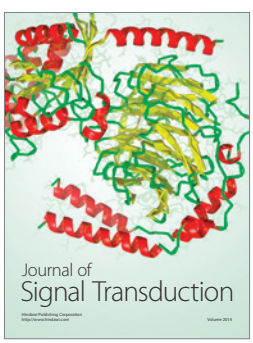

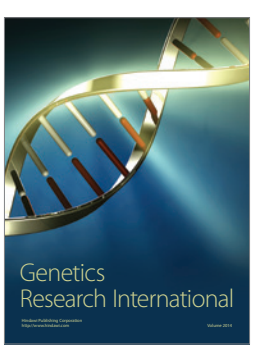

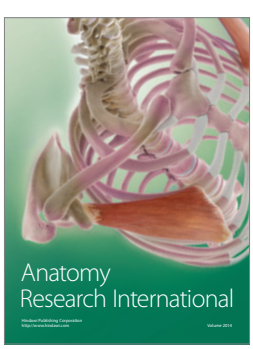

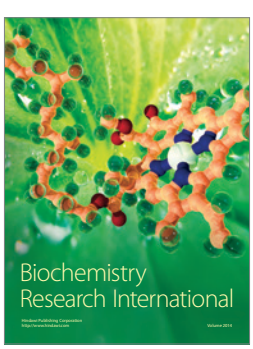

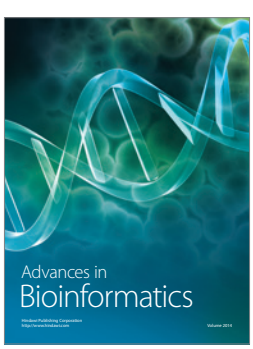

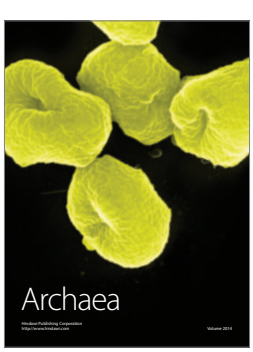

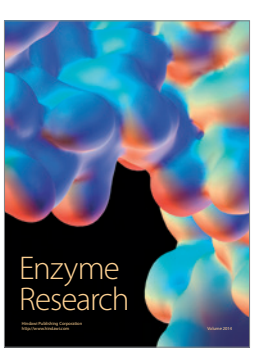

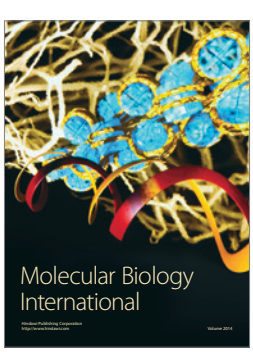

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