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ORIGINAL ARTICLE

Biogeographical relationships among tropical forests in north-eastern Brazil

André M. Melo Santos[1], Deyvson Rodrigues Cavalcanti[1], José Maria Cardoso da Silva[2] and Marcelo Tabarelli[1]*

[1]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco 50670-901, Brazil and [2]Conservation International, Av. Governador José Malcher 652, 2° andar, Belém, Pará 66035-100, Brazil

ABSTRACT

Aim To use parsimony analysis of endemicity and cladistic analysis of distributions and endemism to evaluate two hypotheses addressing biogeographical relationships among Amazonia, the Caatinga forest enclaves, Pernambuco Centre and the southern Atlantic Forest.

Location North-eastern Brazil, South America.

Methods To find the most parsimonious areagram we analysed a matrix composed of the presence (1) or absence (0) of 745 taxa (i.e. 293 genera and 452 species of woody plants) within 16 localities belonging to the four large regions addressed in this study.

Results One most parsimonious areagram was found and it shows a basal separation between the southern Atlantic Forest and all other regions. This break is followed by a separation between all Caatinga forest enclaves (except Baturité) from a cluster composed of Baturité, the Pernambuco Centre and Amazonia. In this cluster, the most basal separation isolates Baturité from the cluster formed by localities from Amazonia and the Pernambuco Centre. The biogeographical relationships among sites could not be explained by either a random distribution of species among sites or by the geographical distance between sites.

Main conclusions We found strong cladistic signal within the raw distribution and phylogenetic data used in our analysis, indicating structured species assemblages in the surveyed localities. They have resulted from the fragmentation of an ancestral biota that was once widely distributed in the region. Our results also support the hypothesis that Atlantic Forest is not a biogeographically natural area, because the Pernambuco Centre is more closely related to Amazonia than to the southern Atlantic Forest. Finally, our data do not support the notion that Caatinga forest enclaves comprise a single biogeographical region, because one Caatinga forest enclave (Baturité) is much more closely related to the cluster formed by Amazonia and the Pernambuco Centre than to other sites. These relationships suggest the occurrence of forest connections between Amazonia and the Atlantic Forests across Caatinga during several periods of the Tertiary and Quaternary. However, palaeoecological data currently available for the Caatinga region are still scarce and do not have either the spatial or temporal resolution required to reconstruct the history of connections among the forests in north-eastern Brazil.

*Correspondence: Marcelo Tabarelli, Departamento de Botânica, Universidade Federal de Pernambuco, Recife-PE, CEP: 50670-901, Brazil.
E-mail: mtrelli@ufpe.br

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Amazonia, areas of endemism, Atlantic Forest, Brazil, Caatinga, CADE, historical biogeography, PAE, plant geography.

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INTRODUCTION

The Atlantic Forest is currently isolated from the two other largest South American forest blocks, Amazonia and the Andean Forest. Caatinga, Cerrado and Pantanal, three regions dominated by open vegetation, separate the Atlantic Forest from Amazonia, while the Chaco, an area of savanna-like vegetation in the southern depressions of South America, separates the Atlantic Forest from the Andean Forest. Such isolation has permitted the evolution of a unique biota which is currently inhabited by a myriad of endemic genera and species (Rizzini, 1997; Silva & Casteletti, 2003).

The Atlantic Forest is one of the largest and most diversified tropical forests on the planet (Mittermeier *et al.*, 2005). It once covered around 1,500,000 km^2 of eastern Brazil, eastern Paraguay and north-eastern Argentina, but currently only 7–8% of the original vegetation remains (Galindo-Leal & Câmara, 2003). At present, the Atlantic Forest is the home of nearly 20,000 species of plants, 263 mammals, 936 birds, 306 reptiles and 475 amphibian species, with endemics ranging from 3% in birds to 44% in plants (Mittermeier *et al.*, 2005).

Outstanding levels of endemism make the Atlantic Forest one of the most distinctive biogeographical units in the entire Neotropical region (Müller, 1973; Rizzini, 1997). However, the Atlantic Forest biota has not always remained in isolation. Phylogenetic studies focusing on endemic species have indicated that the evolution of the biota in the Atlantic Forest has been marked by cycles consisting of periods in which it was connected to other South American forest regions, followed by periods of isolation (Prance, 1987; Prum, 1988; Willis, 1992; Rizzini, 1997). Its biota consequently comprises not only old elements, which differentiated during the Tertiary (Rylands *et al.*, 1996), but also elements that colonized the region more recently during the Quaternary (Marks *et al.*, 2002; Silva & Casteletti, 2003).

One of the best regions for studying the dynamics of connections between Amazonia and the Atlantic Forest is north-eastern Brazil, north of the São Francisco River. This region is mostly dominated by Caatinga – a semi-arid biome which is dominated by scrub vegetation as well as by tropical dry forests and lies between Cerrado, Amazonia and the Atlantic Forest (Prado, 2003) – but contains two subregions covered by tropical rain forests (Fig. 1).

The first subregion is known as the Pernambuco Centre (Prance, 1982). It once comprised a continuous block of forest (56,000 km^2) along the coast and covered the region from sea level to the scarps of the Borborema Plateau (Silva *et al.*, 2004). This subregion has been identified as one important centre of endemism for plants (Prance, 1982), forest butterflies (Brown, 1979; Tyler *et al.*, 1994) and birds (Silva *et al.*, 2004).

The second subregion is composed of a collection of small-to-medium patches of tropical rain forest enclaves that cover the slopes of some isolated plateaus within the large Caatinga depression. These Caatinga forest enclaves are locally known as *brejos* and the complete set of enclaves in north-eastern Brazil was termed *Brejos Nordestinos* by Silva & Casteletti (2003). Caatinga forest enclaves are located along the slopes of plateaus with altitude ranging from 600 to 1100 m, and because of this receive rainfall of more than 1200 mm year^{-1} (Tabarelli & Santos, 2004). These forest enclaves harbour endemic species of several groups of organisms (Andrade-Lima, 1982; Borges-Nojosa & Caramaschi, 2003; Silva *et al.*, 2003), but their biota has not been properly analysed from an evolutionary viewpoint.

The floristic biogeographical relationships between Amazonia, the Pernambuco Centre and the southern Atlantic Forest (we used this name to refer all the Atlantic Forests south of the São Francisco River) have not been evaluated by any modern biogeographical methods, although three major hypotheses have been proposed to date. The first hypothesis states that the

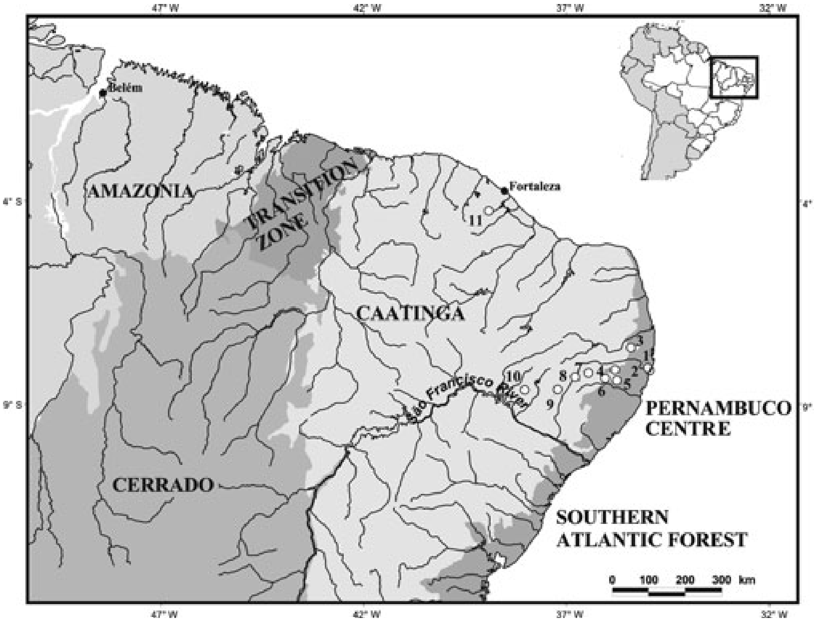

Figure 1 The localities of the Pernambuco Centre and Caatinga forest enclaves according to their position in relation to Amazonia, the southern Atlantic Forest, Cerrado and Caatinga. Pernambuco Centre: 1, Dois Irmãos; 2, Curado. Caatinga forest enclaves: 3, São Vicente Ferrer; 4, Bezerros; 5, Bonito; 6, Caruaru; 7, Brejo da Madre de Deus; 8, Pesqueira; 9, Buíque; 10, Floresta; 11, Baturité.

Amazonia, the Caatinga forest enclaves, the Pernambuco Centre and the southern Atlantic Forest were once connected and that the current patterns of plant species distribution and differentiation resulted from the fragmentation of this ancestral biota (Andrade-Lima, 1982; Bigarella & Andrade-Lima, 1982). If so, then one could expect that species assemblages are historically structured, i.e. they have been formed mostly by: (1) speciation involving vicariance of widespread ancestral populations and (2) biotic interchange by diffusion or secular dispersion rather than being historically unstructured, i.e. they have been formed mostly by non-vicariant modes of speciation and by long-distance dispersal (Cracraft, 1994). The second hypothesis, based on the analysis of the geographical distribution of woody plant species in north-eastern Brazil, states that Atlantic Forest is not a single natural region because the Pernambuco Centre is more closely related to Amazonia than to the southern Atlantic Forest (Andrade-Lima, 1953, 1982). Finally, the third hypothesis suggests that Caatinga forest enclaves form a natural biogeographical region because the species assemblages of these isolated patches share a common history that is not shared with any other region (Silva & Casteletti, 2003). In this paper, we evaluate these three hypotheses by analysing the distribution of woody plant species in Amazonia, the Caatinga forest enclaves, the Pernambuco Centre and the southern Atlantic Forest.

MATERIALS AND METHODS

Floristic analyses are usually based on raw comparisons of the number of shared species among localities or regions by using a suite of phenetic methods, and rely on the intuitive assumption that similarities in the species assemblages can be, at least partially, the consequence of shared geographical history (e.g. Oliveira-Filho & Ratter, 1995). However, the results of these techniques are limited by the fact that they are neutral, and therefore their strict biogeographical meaning can be enigmatic (Rosen, 1992; Ron, 2000). In addition: (1) the data sets are frequently used to provide a variety of classifications without any objective criterion in order to favour any particular phenogram (Lambshead & Paterson, 1986), (2) the same similarity matrix of distances can be obtained from very different data sets of characters (Penny, 1982), and (3) such methods completely ignore the original state of the character as they are replaced by distances (Nel *et al.*, 1998).

The most appropriate methods for recovering historical relationships among areas are those generically known as cladistic or vicariance biogeographical methods (for reviews see Humphries & Parenti, 1999). The basic assumption of this group of methods is that the history of the distribution of taxa co-varies with their history of speciation (Wiley, 1988). However, cladistic methods require information about the phylogeny of taxa distributed allopatrically in the target regions and there are few well-supported phylogenetic hypotheses for most plants and animals inhabiting the Neotropical region (Ron, 2000).

Two alternative yet closely related methods use raw distribution data to make inferences about historical relationships among areas: parsimony analysis of endemicity (PAE) and cladistic analysis of distributions and endemism (CADE). These two methods are analogous to phylogenetic analyses by using cladistic procedures to classify a set of objects [operational geographical units (OGUs), that can be localities, regions or centres of endemism] based on a hierarchical system of shared characters (presence or absence of taxa), which result from their states compared to states present in a reference object, the outgroup. Both methods generate areagrams defined by synendemics, i.e. taxa that are found at more than one OGU (Rosen, 1992). Hierarchical subgroupings are determined by the most parsimonious allocation of progressively narrower-ranging synendemics to the locality set. Consequently, member areas within the smallest subgroup will share taxa not found in any other area in the data set (Rosen, 1992).

Both PAE and CADE contain two underlying assumptions: (1) the absence of a taxon is 'primitive' and its presence is 'derived' and (2) the hypothetical 'ancestral' or 'outgroup' area is one in which none of the sample set of the current taxa exist (Rosen & Smith, 1988). Rosen (1988) states that the logic underlying the use of PAE is the assumption that sites sharing taxa are closely related because they share a more recent history of faunistic exchange. Cracraft (1991) offered a more elaborate interpretation to justify the use of CADE. He suggested that shared taxa among areas of endemism serve as evidence of historical relatedness and they result from the failure of speciation during the period for which areas remained separated. According to Cracraft (1994), if biotic dispersion is historically constrained, it should be expected that the distribution of natural taxa will exhibit hierarchical congruence when examined cladistically.

The differences between PAE and CADE have been recently reviewed by Porzecanski & Cracraft (2005). Basically, they pointed out two major differences: (1) PAE use localities as preferential OGUs whereas CADE uses as OGUs only predetermined areas of endemism, which were previously identified by evaluating the congruence of distributions across target taxa and (2) CADE requires the incorporation of cladistic information into the data matrix by coding distribution for more inclusive hierarchical levels (e.g. species and their subspecies, genera and their species, to the extent that systematic data are available).

In this paper we used a hybrid method because we used localities as OGUs, but we incorporated cladistic information into the data matrix by coding distributions of genera and their species across the localities. This second procedure has been used in PAE studies as well (see Rosen, 1988; Myers, 1991; Morrone, 1998). We used localities for two main reasons. First, except for the two localities in Amazonia, for which the boundaries within a large-scale landscape are not easily defined, all other localities are currently isolated from other forest patches either by natural processes (forest patches representing the Caatinga forest enclaves) or by human intervention in the landscape (localities within the Pernambuco Centre and the southern Atlantic Forest). Second, we used localities to maintain the comparison among them at an appropriate spatial scale, because number of species increases with size of the sampling area (e.g. Brown & Lomolino, 1998), and large differences in the number of species between OGUs can influence the topology of the areagram, placing poorer OGUs at basal positions in the areagram (Trejo-Torres & Ackerman, 2001).

We assembled information about the geographical distribution of all woody plant species recorded at the 16 sites that were selected – first to represent the four major regions addressed in our study and second because their floras have been intensively and properly sampled over the last three decades. These localities were grouped into four categories (Fig. 1; Table 1): (1) Amazonia (Reserva Ducke and Caxiuanã), (2) Caatinga forest enclaves (Baturité, São Vicente Ferrer, Bezerros, Bonito, Caruaru, Brejo da Madre de Deus, Pesqueira, Buíque and Floresta), (3) the Pernambuco Centre (Dois Irmãos and Curado) and (4) the southern Atlantic Forest (Santa Genebra, Capivari and São Pedro).

The species distributional data were obtained by checking: (1) plant monographs and checklists (e.g. issues of Flora Neotropica; Gomes, 1992; Matthes, 1992; Correia, 1996; Sales *et al.*, 1998; Ribeiro *et al.*, 1999; Cavalcante *et al.*, 2000; Ferraz, 2002), (2) plant records stored in eight regional herbaria: Herbário da Universidade Federal de Pernambuco – PE (UFP), Herbário do Instituto de Pesquisas Agropecuárias – PE (IPA), Herbário Vasconcelos Sobrinho – PE (PEUFR), Herbário Prisco Bezerra – CE (UFC), Herbário Alexandre Costa Leal – BA (ALCB) (see Holmgren *et al.*, 1990), Herbário Jayme Coelho de Moraes – PB (EAN), Herbário do Instituto de Meio Ambiente – AL (MAC), Herbário Honório Monteiro (MUFAL) and Herbário Sergio Tavares – PE (HST) (see Barbosa & Barbosa, 1996), and (3) data bases from scientific institutions available on the world wide web [e.g. Base de Dados Tropical (BDT); Centro Nordestino de Informações Sobre Plantas (CNIP); Royal Botanical Garden (KEW); The International Plant Names Index (IPNI), the Missouri Botanical Garden (MBOT)].

A data matrix was built in which the columns represent taxa (genera or species) and the rows represent the localities. In the matrix, the absence of species is codified as '0' and the presence as '1'. A hypothetical locality coded '0' was added for all columns to root the final areagram. We found the most parsimonious areagram by performing the 'ie*' (implicit enumeration) option in the computer program Hennig86 (Farris, 1988). To determine branch support, we performed a bootstrap procedure (10,000 replications) through the program Winclada 0.9.99m24 (Nixon, 1999). The bootstrap value for each node represents the frequency in which the branches occur in a set of randomly generated trees. The data matrices are available from the authors by request or they can be downloaded from http://www.cepan.org.br.

Table 1 Sites from Amazonia, Caatinga forest enclaves, the Pernambuco Centre and the southern Atlantic Forest.

Sites	Location (S; W)	NT (NIF)	Ref.*(herb)†
Amazonia			
Reserva Ducke – AM	03°04′00″; 59°54′20″	1072 (323)	9
Caxiuanã – PA	01°47′57″; 51°42′11″	393 (239)	12
Caatinga forest enclaves			
Baturité–CE	04°15′00″; 38°54′36″	74 (65)	8
Pesqueira – PE	8°19′37″; 36°47′27″	159 (133)	2,10 (2,3,4)
Buíque – PE	8°38′18″; 37°13′08″	216 (155)	10 (1,2,3,4)
Floresta – PE	8°38′59″; 38°01′49″	217 (162)	10 (1,2,3,4)
Brejo da Madre de Deus – PE	8°13′40″; 36°27′34″	173 (145)	6,10 (1,2,3,4)
Bezerros – PE	8°09′03″; 35°48′12″	120 (105)	10 (2,3)
Bonito – PE	8°24′58″; 35°45′32″	135 (114)	10 (1,2,3,4)
Caruaru – PE	8°21′47″; 36°2′47″	306 (261)	10,11 (2,3,4,5)
São Vicente Ferrer – PE	7°36′21″; 35°24′43″	194 (181)	3,10
Pernambuco Centre			
Dois Irmãos – PE	8°10′00″; 34°56′53″	264 (198)	5
Curado – PE	8°6′24″; 34°59′48″	205 (175)	1 (1,2,3,4)
Southern Atlantic Forest			
Santa Genebra – SP	22°48′37″; 47°05′25″	150 (108)	7
Capivari – MG	20°10′59″; 44°19′36″	280 (160)	4
São Pedro – RJ	21°24′28″; 41°06′01″	111 (65)	13

NT, number of taxa (species + genus) analysed; NIF, number of biogeographically informative taxa used in the parsimony analysis of endemicity; Ref., reference (herb = herbaria).

*1, Andrade & Brito (1993); 2, Correia (1996); 3, Ferraz (2002); 4, Souza *et al.* (2003); 5, Guedes (1992); 6, Lyra (1982); 7, Matthes (1992); 8, Cavalcante *et al.* (2000); 9, Ribeiro *et al.* (1999); 10, Sales *et al.* (1998); 11, Tavares (1998); 12, Almeida *et al.* (2003); 13, Silva & Nascimento (2001).

†Herbaria (see text for key to full names of herbaria): 1, HST; 2, IPA; 3, PEUFR; 4, UFP; 5, ASE (see Holmgren *et al.*, 1990).

We used the g1 statistic (Sokal & Rohlf, 1996) to test the hypothesis that the final arrangement of sites within the areagram cannot be explained by a random distribution of species among sites (i.e. cladistically structured data). Precisely, we evaluated the skewness of the tree length of 10,000 randomly generated trees through the program RandomCladistic 4.0.3 (Siddall, 1997), using 'mh,bb' as the method for tree construction (Farris, 1988). A significant left skew indicates that the length of the original tree is shorter than the randomly generated ones, and thereby accepted as resulting from a cladistically structured data set.

Finally, to make sure that the relationships depicted by the areagram are not simply a consequence of the geographical distance between the sites, we evaluated the greatest agreement subtree dissimilarity (d_{GAS}) (Finden & Gordon, 1985) using Component software 2.00 (Page, 1993), which allows us to assess the congruence between the topologies of the PAE areagram and the topology of the geographical distance dendrogram as measured by ArcView GIS 3.2a (ESRI, 1998). The 'd_{GAS}' represents the smallest number of leaves (i.e. terminal nodes) removed to obtain the greatest agreement subtree. We used the Euclidean distance option to generate the matrix of geographical distance, and the weighted arithmetic average (WPGMA; weighted pair group method using arithmetic averaging) option to connect clusters. We used NTSYSpc 2.01t software (Rohlf, 2000) to execute both procedures.

RESULTS

We characterized the distribution of 293 genera and 452 woody plant species, and all of them were phylogenetically informative because we excluded from the data matrix all taxa that occur either in all localities or in only one area. When analysed cladistically, a single most parsimonious tree (Fig. 2) was found (tree length = 1729; consistency index = 0.43; retention index = 0.42). In this tree, the most basal separation is between the southern Atlantic Forest (Santa Genebra, Capivari and São Pedro) and all other regions. Then, there is another basal separation between localities representing Caatinga forest enclaves (São Vicente Ferrer, Bezerros, Bonito, Caruaru, Brejo da Madre de Deus, Pesqueira, Buíque and Floresta) and the cluster formed by Baturité, localities of the Pernambuco Centre (Dois Irmãos and Curado) and localities of Amazonia (Reserva Ducke and Caxiuanã).

Within the cluster of localities that comprised the Caatinga forest enclaves, there is a basal separation between the group formed by Brejo da Madre de Deus, Pesqueira, Buíque, Floresta and Bezerros and the group formed by São Vicente Ferrer, Bonito and Caruaru. Within the cluster formed by Baturité, the Pernambuco Centre and Amazonia, the most basal separation is Baturité from the other localities, followed by a separation between the localities of Pernambuco Centre and Amazonia.

Bootstrap indices show that the strength of support for nodes in this areagram varies considerably. The weakest support value among critical nodes is for the relationships between Caatinga forest enclave localities and the cluster formed by Baturité, the Pernambuco Centre and Amazonia, but this node is supported by four synendemic taxa. Strong support (indices ranging from 99 to 100) was found for: (1) the basal division between the southern Atlantic Forest and all remaining localities, (2) the division between the Pernambuco Centre and Amazonia localities, (3) the division between localities within the southern Atlantic Forest, and (4) the division within Amazonia (Fig. 2).

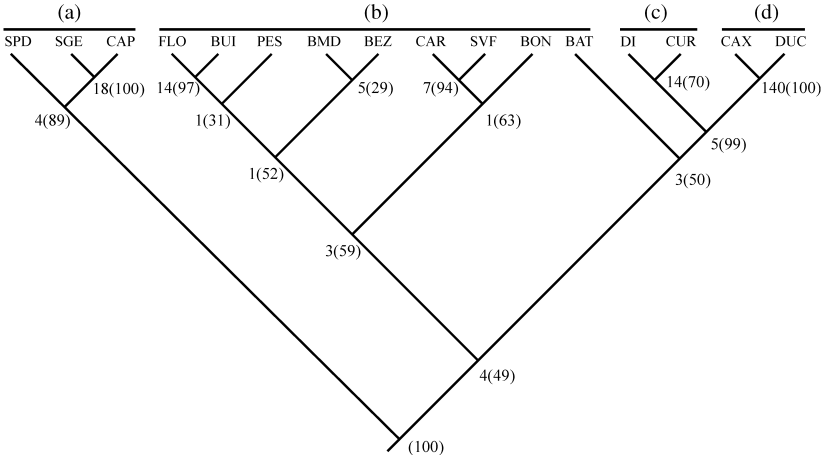

Figure 2 The most parsimonious areagram (tree length = 1729; consistency index = 43; retention index = 42) obtained through a parsimony analysis of endemicity, which was based on the distribution of 452 woody plant species plus 293 genera (745 taxa) within 16 sites from (a) the southern Atlantic Forest (SPD, Fazenda São Pedro; SGE, Santa Genebra; CAP, Capivari), (b) Caatinga forest enclaves (BAT, Baturité; PES, Pesqueira; BUI, Buíque; FLO, Floresta; BMD, Brejo da Madre de Deus; BEZ, Bezerros; BON, Bonito; CAR, Caruaru; SVF, São Vicente Ferrer), (c) Pernambuco Centre (CUR, Curado; DI, Dois Irmãos) and (d) Amazonia (CAX, Caxiuanã; DUC, Reserva Ducke). The values shown in each node refer to the number of species exclusively found in all sites of the branch and, in parenthesis, the results of a bootstrap analysis (10,000 replications).

The length distribution of a randomly generated areagram was skewed to the left ($g_1 = -1.314$; $P < 0.001$; 10,000 replications). This result indicated that the data matrix of sites contains cladistically structured data and, therefore, the presence/absence of taxa among sites was non-random (Fig. 3). The topology of the geographical distance dendrogram (Fig. 4) was incompatible with the topology of the PAE areagram. For the most parsimonious areagram, the smallest number of leaves moved out to obtain the greatest agreement subtrees was eight, generating a subtree with only eight (50%) congruent sites.

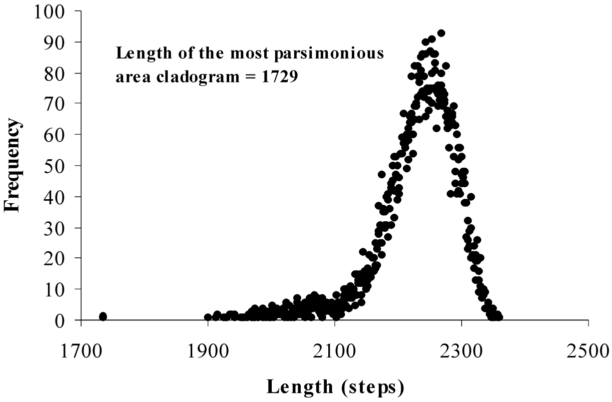

Figure 3 Length distribution of a randomly generated areagram compared with the length of the most parsimonious areagram, which was obtained through a parsimony analysis of endemicity. The average length of the randomly generated trees was larger than the length of the most parsimonious areagram. The left skew ($g_1 = -1.314$; $P < 0.001$; 10,000 replications) indicates that the presence/absence of taxa is not random.

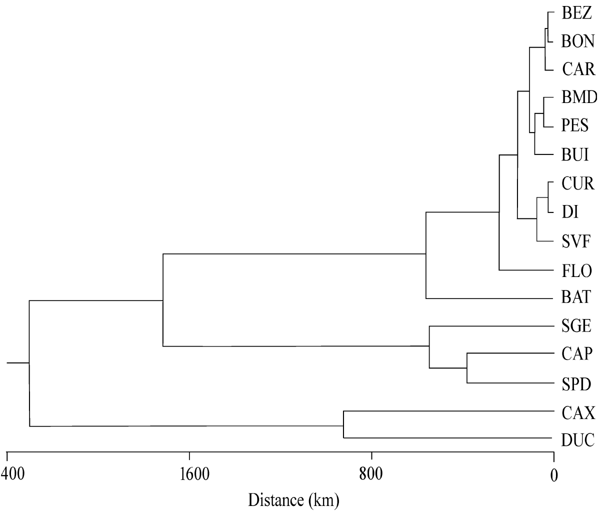

Figure 4 Dendrogram indicating the distance among the 16 localities that were surveyed in this study: southern Atlantic Forest (SPD, Fazenda São Pedro; SGE, Santa Genebra; CAP, Capivari), Caatinga forest enclaves (BAT, Baturité; PES, Pesqueira; BUI, Buíque; FLO, Floresta; BMD, Brejo da Madre de Deus; BEZ, Bezerros; BON, Bonito; CAR, Caruaru; SVF, São Vicente Ferrer), Pernambuco Centre (CUR, Curado; DI, Dois Irmãos) and Amazonia (CAX, Caxiuanã; DUC, Reserva Ducke).

DISCUSSION

We found a strong cladistic signal within the raw distribution and phylogenetic data used in our analysis, indicating that species assemblages in the localities surveyed are not a product of random long-distance dispersal but that they were possibly formed as a consequence of the fragmentation of an ancestral biota that was once widely distributed in the region, such as suggested by Andrade-Lima (1964, 1982) and Bigarella *et al.* (1975). This supports our first hypothesis and also the statement by Cracraft (1991) in which long-distance dispersal has a minor role in structuring intracontinental species assemblages and that biotic dispersion is also historically constrained. Because the relationships depicted in the areagram were not correlated with the geographical distance between the localities, we can exclude the hypothesis that the resulting areagram simply reflects shared ecological conditions among localities rather than a signal of a historical sequence of floristic exchange (Rosen, 1988).

The areagram supports Andrade-Lima's hypotheses that the Atlantic Forest is not a biogeographically natural area, as the Pernambuco Centre is closer to Amazonian localities than to any other localities in this study. This relationship is strongly supported by both bootstrap indices and the number of synendemic species supporting this node. The strong biogeographical connection between the Pernambuco Centre and Amazonia is also supported by Prance (1979, 1989), who pointed out that most of the Chrysobalanaceae species (e.g. *Couepia rufa* Ducke, *Couepia pernambucencis* Prance) occurring in the Pernambuco Centre have their closest relatives in Amazonia rather than in the southern Atlantic Forest, as well as by Teixeira *et al.* (1986), who indicated that lowland sites in the Pernambuco Centre have avifauna more closely related to Amazonian avifauna than to the fauna of the southern Atlantic Forest.

The hypothesis that Caatinga forest enclaves comprise a single biogeographical entity, as proposed by Silva & Casteletti (2003), is not supported, because Baturité is more closely related to the Pernambuco Centre and Amazonia in the areagram than to any other Caatinga forest enclaves. Borges-Nojosa & Caramaschi (2003) analysed the distribution of lizards and amphisbaenids in some Caatinga forest enclaves and indicated that those located along the coast of the State of Ceará, such as Baturité, are distinct from a biogeographical viewpoint from all other forest enclaves in the region. The relationships among the remaining localities representing Caatinga forest enclaves need to be assessed with more information from woody plant species as well as from other groups of organisms. These relationships were weakly supported by bootstrap indices, suggesting that random biogeographical or ecological processes may have played an important role in shaping the nature of their woody plant species assemblages. Tabarelli & Santos (2004) have pointed out that local extirpations driven by human interventions in the landscape have been one of the major ecological forces shaping the current species composition in these forest enclaves.

The areagram proposed here indicates one sequence of vicariant events to explain the current patterns of distribution and endemism in the forests of north-eastern Brazil. To our knowledge, this is the first time that a hypothesis of this kind has been proposed for this region and it opens the way for more refined studies. Further testing requires biogeographical studies of several taxa as well as comparisons based on geological and palaeoecological information. Andrade-Lima (1953) used geological information presented by Katzer (1933) to propose that connections between Amazonia and the Pernambuco Centre are old and have occurred at least since the Tertiary. Later, Rizzini (1963), Andrade-Lima (1964) and Bigarella *et al.* (1975) proposed two historical connections between the Pernambuco Centre and Amazonia: one coastal route that follows basically the Tertiary sedimentary lowlands bordering the Atlantic coast and another route across the ancient inlands that are currently covered by the Caatinga semi-arid vegetation. Bigarella *et al.* (1975) stated that such connections resulted from events of expansion and retraction of both Amazonia and the Atlantic Forest in response to global changes in climate.

Oliveira *et al.* (2000) presented the first palynological data for Caatinga and identified five main changes in vegetation and climate during the last 11,000 years in dune fields found along the São Francisco River. They indicated that during the late Pleistocene (10,990–10,000 yr BP) the pollen zone contained pollen of taxa currently recorded in both Amazonia and the Atlantic Forest, as well as in montane forests, thus suggesting very humid climatic conditions parallel to more reduced temperatures. Behling *et al.* (2000) studied pollen found in marine sediments (core GeoB 3104-1; c. 150 km distant from Baturité) and indicated that semi-arid Caatinga vegetation predominated in the region from 42,000 to 8500 yr BP, except during the interval between 15,500 and 11,800 yr BP that was the wettest period recorded for the region. This period was marked by the expansion of mountain, floodplain and gallery forests across the region. Evidence so far suggests that climate within Caatinga fluctuates from dry and hot to wet and cold along the Quaternary.

In synthesis, the few palynological studies carried out in the Caatinga region indicate that there were suitable environmental conditions during the late Pleistocene to allow floristic exchanges between Amazonia and the Atlantic Forest. However, the duration of these periods (a few thousand years) seems not to be long enough to generate the complex sequence of events and evolutionary changes synthesized in the areagram proposed here. An integrated research agenda combining biological inventories in critical areas, molecular phylogenies of targeted taxa, comparative phylogeography, vicariance biogeography and generation of geoscientific information is needed to improve our knowledge about the evolution and dynamics of the humid forests across north-eastern Brazil.

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BIOSKETCHES

André Maurício Melo Santos and **Devyson Rodrigues Cavalcanti** are ecologists interested in plant biogeography and landscape ecology in north-eastern Brazil.

José Maria Cardoso da Silva works on systematics, evolution, ecology, biogeography and conservation of Neotropical birds.

Marcelo Tabarelli is an ecologist who currently works on plant population and community ecology, biogeography and conservation of Atlantic Forest woody plant species.

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