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Does climate influence spatial variation of tree species alpha diversity in the Brazilian Atlantic rainforest?

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ABSTRACT. We tested the hypothesis that the variation in tree species alpha diversity is driven by climate in the Brazilian Atlantic Rainforest (ARF). Considering 139 samples of trees with DBH ≥ 4.8 cm, we correlated alpha diversity measures (Shannon heterogeneity index H', Chao I richness estimator, and Simpson concentration index C) with climate variables (perhumidity index, mean annual rainfall, and mean annual temperature) and spatial variables (latitude, longitude, and altitude). Using CCA, multiple regression analysis and RDA procedures, we found a positive relationship between latitude, longitude, and altitude with Shannon's diversity index and Chao I richness estimator, and a negative relationship with Simpson concentration index. Over 75% of the variation remained unexplained and were attributed to stochastic processes. These results indicate that climate has a very weak influence on tree species alpha diversity, which is more influenced by spatial variation in the ARF. We propose that the current tree species alpha diversity could be a result of the history of the ARF during the Cenozoic, when geological events and climate oscillations could have triggered biogeographic processes, such as alternating episodes of vicariance and dispersal, which would have lead to the great diversity of species and heterogeneity across the geographic space observed today.

Keywords: diversity indices, latitudinal variation, limited dispersal, spatial variables, biogeographical processes.

O clima influencia a variação espacial da diversidade alfa de espécies arbóreas na floresta pluvial Atlântica do Brasil?

RESUMO. Investigamos a hipótese de que a variação da diversidade alfa de espécies de árvores é determinada pelo clima na Floresta Pluvial Atlântica brasileira (FPA). Considerando 139 amostras de árvores com DAP ≥ 4,8 cm, correlacionamos medidas de diversidade alfa (heterogeneidade de Shannon H', riqueza Chao I e concentração de Simpson C) com variáveis climáticas (índice de perumidade, precipitação total média anual e temperatura anual média) e variáveis espaciais (latitude, longitude e altitude). Aplicando CCA, análise de regressão múltipla e RDA, encontramos correlação positiva da latitude, longitude e altitude com H' e Chao I e uma correlação negativa com a concentração de Simpson. Mais de 75% das variações permaneceram inexplicadas e foram atribuídas a processos estocásticos. Esses resultados indicam que o clima tem uma fraca influência sobre a diversidade alfa de espécies arbóreas, a qual é mais influenciada pela variação do espaço na FPA. Propomos que a atual diversidade de espécies de árvores poderia ser um resultado da história da FPA durante o Cenozoico, quando eventos geológicos e oscilações climáticas poderiam ter desencadeado processos biogeográficos como episódios alternados de vicariância e dispersão, os quais poderiam ter levado à grande diversificação de espécies e sua heterogeneidade no espaço geográfico que se observa atualmente.

Palavras-chave: índices de diversidade, variação latitudinal, limitação da dispersão, variáveis espaciais, processos biogeográfico.

Introduction

Environmental factors, such as rainfall (CLINEBELL II et al., 1995; OLIVEIRA-FILHO; FONTES, 2000), temperature (PAUSAS; AUSTIN, 2001), soil variables (GENTRY, 1991; CÂMARA, 1996; BROCQUE; BUCKNEY, 2003), altitude and latitude (ROSENZWEIG, 1995); COLWELL; LEES, 2000), have been associated with variations in alpha diversity in the Neotropics.

Among them, climatic variables have been identified among the major abiotic factors related to variation in species richness and alpha diversity in tropical forests (GENTRY, 1988). Besides climate, latitudinal variations also play a fundamental role in species richness variation and alpha diversity (OLIVEIRA-FILHO et al., 2005). One of the most species-rich forests in the world is the Brazilian Atlantic Rainforest (ARF), but information on how climate influences alpha diversity in this forest is still lacking.

The Atlantic Forest *sensu stricto* (JOLY et al., 1992), or Atlantic Rain Forest (ARF) (IBGE, 2012), extends from 3° to 30°S, along almost the entire Brazilian coastline. It is considered one of the 35 global biodiversity hotspots, with high species richness and endemism (WERNECK et al., 2011), and is one of the most endangered areas in the world (MYERS et al., 2000; ORME et al., 2005). Although the influence of climate and soil is undeniably important for species diversification, there is no evaluation on the effects on values of alpha diversity across the entire ARF range. Indeed, there are only few studies on the role of climate on the ARF diversity, but most have a local scope, and some controversy has arisen about which factors are the most important to explain the remaining ARF diversity. For instance, Gentry (1988) compared species richness and Shannon diversity index with climate and other environmental variables for several neotropical sites and found a direct relationship with annual rainfall for most areas, but in Linhares, Espírito Santo State, Brazil, an area with average annual rainfall of 1,400 mm, it was higher than expected. Oliveira-Filho and Fontes (2000) and Oliveira-Filho et al. (2005) found a latitudinal correlation between tree species richness and variations in temperature and rainfall.

Although some effort has been made to describe patterns of species distribution in the ARF, many gaps still remain, especially those dealing with species richness distribution along the total area of ARF. Except for Oliveira-Filho and Fontes (2000), there is a general lack of investigations using quantitative analytical tools to associate diversity patterns with climatic variations in the ARF. Considering local tree communities across the entire range of the ARF, this study tested the following predictions: 1) The spatial variation in tree species alpha diversity is associated with one or more abiotic environmental variables; 2) The variation in different diversity indices is related to the same environmental variables across the entire ARF range; 3) The diversity variation, expressed by different indices, has a gradient across the entire ARF range.

Material and methods

Study Area

This study considered the Phytoecological Region of the Atlantic Rainforest (ARF) the area mapped by the Brazilian Institute of Geography and Statistics (IBGE,2012), extending from 3° to 30°S (CÂMARA, 2005) along the coastline. Its elevations range from the sea level to higher than 2,700 m. This area is characterized by a high degree of endemism in plants and animals (MYERS et al., 2000; WERNECK et al., 2011). Its tree formations are classified according to altitude ranges, whose lower and upper limits vary according to latitude (IBGE, 2012): Alluvial (Riparian) Forest, Lowland Forest (5 to 30 or 100 m altitude, depending on latitude), Submontane Forest (30 to 400 or 600 m), Montane Forest (400 to 1000 of 2000 m), and Altimontane Forest (above Montane Forest).

Two predominant climate regimes are found in the ARF: the humid tropical coastal and the subtropical (NETO; NERY, 2005). The humid tropical coastal regime is prevalent in the states of Ceará to São Paulo (approximately from 3° to 22°S), while the subtropical regime, with a subtropical thermal seasonality, prevails from the state of São Paulo to Rio Grande do Sul (approximately from 22° to 30°S). Major landforms found in the ARF are mountain ranges (*serras*), coastal plains (*tabuleiros*), and plateaus (*chapadas*) (BACKES; IRGANG, 2004).

Database

From the literature, we selected published phytosociological tables (quantitative surveys) that sampled trees with DBH (diameter at breast height) ≥ 4.8 cm in the entire ARF range. The phytosociological table represents species lists with the respective species phytosociological descriptors, such as density per area, frequency per sampling unit, and basal area per terrain surface area (CAIAFA; MARTINS, 2007). Since the same study may present results for more than one site, that is, may present more than one phytosociological table, the final total number of phytosociological tables in our dataset was greater than the number of papers we consulted. The tables were then classified and coded according to the IBGE (2012) geographical region and the state in which the survey was conducted.

We took as a starpoint the database FITOGEO (SCUDELLER; MARTINS, 2003), which includes quantitative samplings performed in the ARF from 1946 to early 2005. Then, we surveyed the literature for papers concerning quantitative sampling of trees with DBH ≥ 4.8 cm published from January 2005 to January 2007 in peer-reviewed journals. We added these data to the FITOGEO database to build our own dataset. Afterwards, our final dataset had a total of 139 phytosociological tables from 79 surveys (Figure 1), 2,168 species (six exotic species were removed from the database), 449 genera, 100 families, and 126,238 individuals.

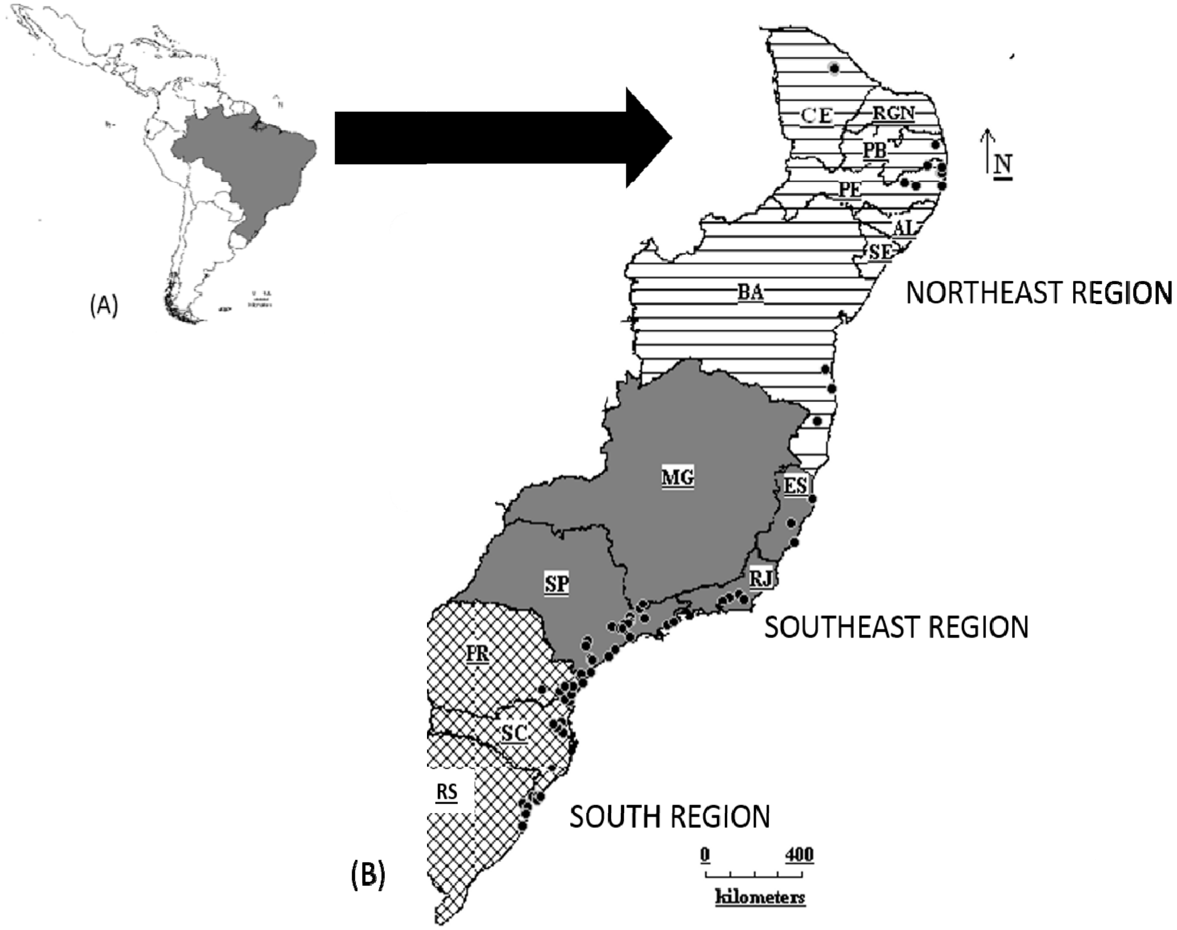

Figure 1. A) Brazil in South America; (B) Map of Brazil indicating the location of the quantitative samplings of trees with DBH ≥ 4.8 cm in the Brazilian Atlantic Rainforest (black dots). Gray and hatched states indicate their geographical region (South, Southeastern, and Northeastern). State acronyms: RS (Rio Grande do Sul), SC (Santa Catarina), PR (Paraná); SP (São Paulo), RJ (Rio de Janeiro), MG (Minas Gerais), ES (Espírito Santo); BA (Bahia), SE (Sergipe), AL (Alagoas), PE (Pernambuco), PB (Paraíba), RGN (Rio Grande do Norte) and CE (Ceará).

We arranged the species in families according to APG III (2009) and checked for updated binomials at http://mobot.mobot.org/W3T/Search/vast.html and http: //www.ipni.org/ipini/ipni.html.

Alpha diversity and climate variables

We used the following three indices to measure alpha diversity of the ARF (Table 1): Shannon's diversity index (H'), Chao I richness estimator (Chao I), and Simpson's concentration index (C). All indices were calculated using the Species Diversity and Richness 4 software (SEABY; HENDERSON, 2006).

Shannon diversity index (H') is a measure of heterogeneity that considers both the relative abundance of individuals and the number of species in a sample. It calculates the best relationship between species richness and evenness (STOCKER et al., 1985). Simpson concentration index (C) is a measure of the concentration of relative abundance on the species (SIMPSON, 1949). It is based on evenness and calculates the probability that two individuals randomly and independently taken from one community belong to the same species. The Chao I richness estimator (CHAO, 1984) uses information on the distribution of rare species in the sample, i.e., those represented by only one or two individuals. The greater the number of rare species in the sample, the greater is the probability that species other than those represented in the sample occur in the area (GOTELLI; COLWELL, 2001).

We obtained climate variables from DIVA-GIS 5.2 (HIJMANS et al., 2005) and used rainfall data to calculate the Perhumidity Index according to WALSH (1996). Monthly Perhumidity Indices may vary from -24 to +24, depending on the average rainfall. A very wet month ($p > 200$ mm) receives a score +2, a humid month ($100 \leq p \leq 200$ mm) receives a score of +1, a dry month ($50 \leq p \leq 99$ mm) has a score of -1, and a very dry month ($p < 50$ mm) a score of -2.

Table 1. Phytosociological tables, with coded geographical divisions (SE: southeast, S: south, NE: northeast) and States (BA: Bahia; CE: Ceará; ES: Espírito Santo; MG: Minas Gerais; PR: Paraná; PE: Pernambuco; SP: São Paulo; RN: Rio Grande do Norte; RS: Rio Grande do Sul; RJ: Rio de Janeiro; SC: Santa Catarina). Values for diversity indices and environmental variables: H ': Shannon's diversity index (nats/ind.); CHAO I: Chao I richness estimator; C: Simpson's concentration index. Environmental variables: ALT: altitude (meters); LAT: latitude (decimal degrees); LONG: longitude (decimal degrees); PER: perhumidity index; TMA: mean annual temperature (ºC); PMA: mean annual rainfall (mm).

LOCATION	H'	CHAO I	C	ALT	TMA	PMA	LAT	LONG	PER
SE-SP(1)	4.0264	170.4	0.028313	25.000	22.525	2536.000	23.450	45.067	35.000
SE-SP(2)	3.9612	140.6	0.034928	181.000	22.250	2324.000	23.367	44.800	31.500
SE-SP(3)	3.7289	141.2	0.041051	753.000	18.354	1405.000	23.425	46.481	18.500
SE-SP(4)	4.3146	179.6	0.022143	20.000	22.042	2639.000	23.900	46.417	36.500
SE-SP(5)	4.1607	227.0	0.038432	191.000	20.854	2050.000	24.547	47.242	29.500
SE-SP(6)	3.4799	83.8	0.049875	181.000	22.250	2324.000	23.367	44.800	31.500
SE-ES(7)	5.5058	482.5	0.009579	719.000	20.754	1294.000	19.951	40.525	18.000
SE-SP(8)	3.3884	95.67	0.054142	30.000	22.513	2001.000	24.283	47.000	29.500
SE-SP(9)	4.2212	204.0	0.017937	782.000	18.083	1401.000	23.650	46.617	16.500
SE-SP(10)	4.1067	194.6	0.026717	782.000	18.083	1401.000	23.650	46.617	18.500
SE-SP(11)	3.7829	81.63	0.028555	588.000	19.342	1267.000	23.200	45.867	16.500
SE-SP(12)	3.4732	117.5	0.060569	588.000	19.342	1267.000	23.200	45.867	16.500
SE-SP(13)	3.3241	102	0.085837	588.000	19.342	1267.000	23.200	45.867	16.500
SE-SP(14)	3.1488	111	0.127243	588.000	19.342	1267.000	23.200	45.867	16.500
SE-SP(15)	3.9305	88.67	0.022795	588.000	19.342	1267.000	23.200	45.867	16.500
SE-SP(16)	3.5026	102.3	0.036603	588.000	19.342	1267.000	23.200	45.867	16.500
SE-SP(17)	4.0226	117.4	0.022635	588.000	19.342	1267.000	23.200	45.867	16.500
SE-SP(18)	3.4648	110.3	0.058173	782.000	18.083	1401.000	23.636	46.614	18.500
SE-SP(19)	3.6845	90.18	0.033311	747.000	18.571	1400.000	23.562	46.727	19.500
SE-ES(20)	5.0000	364.4	0.011077	4.000	24.142	1261.000	19.100	39.750	20.000
S-RS(21)	3.0667	55	0.071839	10.000	18.846	1442.000	29.479	49.834	29.500
S-RS(22)	3.2384	66.25	0.056915	10.000	18.846	1442.000	29.479	49.834	29.500
S-RS(23)	3.6737	141.6	0.046339	375.000	17.338	1620.000	29.358	49.976	31.000
SE-RJ(24)	4.1917	224.4	0.025183	254.000	21.988	1500.000	22.450	42.833	17.500
SE-RJ(25)	4.1000	143.3	0.018911	94.000	22.642	1560.000	22.578	43.028	21.500
NE-BA(26)	3.6519	97.08	0.034118	41.000	24.250	1621.000	15.283	39.050	31.000
SE-SP(27)	4.1766	167.2	0.028225	934.000	17.242	1424.000	23.367	46.433	19.500
SE-SP(28)	3.2655	106.5	0.074349	782.000	18.083	1401.000	23.636	46.614	18.500
SE-SP(29)	3.1122	50	0.06502	621.000	18.629	1461.000	24.200	48.050	21.500
S-RS(30)	1.9754	19.5	0.201939	12.000	18.825	1500.000	29.967	50.233	31.000
SE-SP(31)	4.2044	198.7	0.028802	30.000	22.513	2001.000	24.283	47.000	29.500
SE-SP(32)	4.2110	278.7	0.033956	46.000	21.975	1639.000	24.668	47.877	24.500
SE-SP(33)	3.7870	149.1	0.059488	23.000	22.150	1613.000	24.608	47.885	24.500
S-PR(34)	3.1800	61	0.05872	539.000	20.700	1287.000	22.483	48.288	17.500
SE-SP(35)	3.7588	129.9	0.037793	759.000	18.542	1372.000	23.583	46.700	18.500
SE-RJ(36)	4.0345	276	0.041051	1109.000	17.225	1461.000	22.350	42.450	18.500
SE-RJ(37)	3.6732	207.4	0.051894	1109.000	17.225	1461.000	22.350	42.450	18.500
S-SC(38)	2.7906	66	0.204415	108.000	19.625	1665.000	27.083	48.933	28.500
S-SC(39)	2.0947	16	0.16592	4.000	18.858	1399.000	29.333	49.733	28.000
S-SC(40)	2.4427	53	0.151814	4.000	18.858	1399.000	29.333	49.733	28.000
S-SC(41)	2.7111	0.0000	0.136874	89.000	19.638	1678.000	27.117	48.900	29.500
S-SC(42)	2.6906	40.25	0.11558	55.000	20.946	1779.000	26.017	48.850	28.500
S-SC(43)	2.1759	25.5	0.211104	205.000	19.892	1598.000	26.817	49.217	29.500
S-SC(44)	2.5701	35.13	0.123213	175.000	19.733	1609.000	26.917	49.117	29.500
SE-SP(45)	3.6642	97.25	0.043497	930.000	17.154	1423.000	23.524	47.113	20.500
SE-SP(46)	3.5993	77.57	0.036832	930.000	17.154	1423.000	23.524	47.113	20.500
SE-SP(47)	3.6189	80.8	0.037608	930.000	17.154	1423.000	23.524	47.100	20.500
SE-SP(48)	2.5204	30.13	0.114903	181.000	22.250	2324.000	23.367	44.800	31.500
SE-SP(49)	3.4595	55.8	0.037538	181.000	22.250	2324.000	23.367	44.800	31.500
SE-SP(50)	3.1975	63	0.060132	181.000	22.250	2324.000	23.367	44.800	29.500
SE-SP(51)	3.3836	75.45	0.052383	181.000	22.250	2324.000	23.367	44.800	31.500
SE-SP(52)	3.4093	76.18	0.048473	181.000	22.250	2324.000	23.367	44.800	31.500
SE-SP(53)	4.3438	155.1	0.017532	815.000	18.021	1376.000	23.167	46.417	19.500
S-PR(54)	2.3455	46	0.22604	17.000	20.804	2016.000	25.783	48.558	30.500
S-PR(55)	2.0098	34	0.300391	8.000	20.842	2116.000	25.594	48.389	30.500
S-PR(56)	1.1941	13.17	0.490196	157.000	21.742	2149.000	25.102	48.209	31.500
S-PR(57)	1.6931	34.17	0.390778	54.000	20.725	2002.000	25.839	48.574	28.500
S-PR(58)	1.9031	26	0.318979	15.000	20.767	2027.000	25.733	48.583	30.500
S-PR(59)	3.7448	88.89	0.036062	15.000	20.767	2027.000	25.733	48.583	30.500
S-PR(60)	0.7111	14.13	0.725689	30.000	21.150	1997.000	25.525	48.803	29.500
S-SC(61)	2.9352	152.1	0.189286	82.000	20.054	1579.000	26.917	49.083	29.500
SE-SP(62)	3.3690	107.2	0.065274	782.000	18.083	1401.000	23.636	46.614	18.500
SE-SP(63)	3.7805	116	0.022821	759.000	18.542	1372.000	23.583	46.700	18.500
SE-SP(64)	3.8338	172.7	0.046707	929.000	17.571	1407.000	23.417	46.638	19.500
SE-SP(65)	1.8415	67.4	0.384025	30.000	22.513	2001.000	24.283	47.000	29.500
SE-SP(66)	3.5308	157.9	0.1	6.000	22.633	2469.000	25.051	47.897	32.500
S-RS(67)	3.3400	108	0.057937	87.000	18.571	1532.000	29.708	50.150	31.000
S-RS(68)	3.4084	91.22	0.059453	557.000	16.604	1836.000	29.606	50.375	31.000
S-SC(69)	3.7488	132.5	0.050378	171.000	19.421	1452.000	28.359	49.291	25.500

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LOCATION	H'	CHAO I	C	ALT	TMA	PMA	LAT	LONG	PER
S-SC(70)	3.9265	142.7	0.035881	14.000	21.154	1882.000	26.067	48.633	28.500
NE-CE(71)	2.7830	37	0.091491	828.000	21.067	1551.000	4.250	38.917	19.500
NE-CE(72)	2.5665	0	0.091575	828.000	21.067	1551.000	4.250	38.917	19.500
S-RS(73)	3.5320	112	0.064061	9.000	18.850	1426.000	29.383	49.833	29.500
S-RS(74)	3.4442	123.6	0.056689	114.000	18.529	1555.000	29.659	50.213	31.000
S-SC(75)	4.1103	231.6	0.044267	370.000	18.717	1656.000	26.786	48.926	30.500
SE-MG(76)	3.3331	74.8	0.052854	1607.000	13.825	1874.000	22.894	46.043	22.500
SE-SP(77)	4.2329	167.7	0.020016	181.000	22.250	2324.000	23.367	44.800	31.500
SE-SP(78)	4.0420	137	0.037495	181.000	22.250	2324.000	23.367	44.800	31.500
SE-SP(79)	3.9714	141	0.029833	181.000	22.250	2324.000	23.367	44.800	31.500
NE-BA(80)	3.9436	138.1	0.031387	179.000	23.879	1169.000	16.367	39.567	17.500
SE-ES(81)	3.2871	91.06	0.067295	4.000	24.146	1262.000	19.083	39.750	20.000
SE-RJ(82)	2.3450	172	0.144134	80.000	22.871	1166.000	22.500	42.250	16.500
SE-RJ(83)	3.5470	120.1	0.040064	80.000	22.871	1166.000	22.500	42.250	16.500
SE-SP(84)	2.0056	45.13	0.284657	30.000	22.513	2001.000	24.283	47.000	29.500
SE-SP(85)	4.0584	135	0.027152	19.000	21.913	1734.000	24.667	47.800	26.500
SE-SP(86)	0.8179	5	0.481232	19.000	21.913	1734.000	24.667	47.800	26.500
SE-SP(87)	2.9840	61.13	0.093633	19.000	21.913	1734.000	24.667	47.800	26.500
SE-SP(88)	4.5864	267	0.023089	779.000	17.608	1374.000	24.054	47.983	17.500
SE-RJ(89)	3.9783	120.8	0.025426	80.000	22.871	1166.000	22.500	42.250	16.500
SE-RJ(90)	4.5494	296.5	0.015865	80.000	22.871	1166.000	22.500	42.250	16.500
SE-RJ(91)	4.4117	172.1	0.015679	254.000	21.988	1500.000	22.450	42.833	18.500
SE-RJ(92)	4.0508	172	0.034106	1109.000	17.225	1461.000	22.350	42.450	18.500
SE-RJ(93)	3.5791	120.1	0.051706	1109.000	17.225	1461.000	22.350	42.450	18.500
SE-RJ(94)	3.8428	242.2	0.090009	80.000	22.871	1166.000	22.500	42.250	16.500
SE-SP(95)	3.8913	103.3	0.022252	779.000	17.608	1374.000	24.054	47.983	17.500
SE-SP(96)	4.0371	92.52	0.020773	779.000	17.608	1374.000	24.054	47.983	17.500
SE-SP(97)	4.1435	146.8	0.017737	680.000	18.367	1258.000	24.000	48.000	16.000
SE-SP(98)	4.2588	124.6	0.013592	680.000	18.367	1258.000	24.000	48.000	16.000
SE-SP(99)	4.2278	150.8	0.015221	680.000	18.367	1258.000	24.000	48.000	16.000
SE-SP(100)	3.1300	84.8	0.092336	680.000	18.367	1258.000	24.000	48.000	16.000
S-SC(101)	3.3268	81.33	0.062344	14.000	21.154	1882.000	26.067	48.633	28.500
S-PR(102)	2.2430	57.5	0.158253	74.000	21.950	2163.000	25.177	48.296	31.500
S-PR(103)	1.6800	54.25	0.309502	12.000	20.779	2067.000	25.500	48.500	31.500
S-PR(104)	2.9772	56.08	0.078125	12.000	20.779	2067.000	25.500	48.500	31.500
S-PR(105)	3.4665	87.58	0.059102	12.000	20.779	2067.000	25.500	48.500	31.500
S-PR(106)	3.5740	79	0.041563	782.000	17.246	1630.000	25.728	48.975	25.500
S-PR(107)	3.3424	61.55	0.053248	782.000	17.246	1630.000	25.728	48.975	25.500
S-PR(108)	3.6031	66.5	0.036403	782.000	17.246	1630.000	25.728	48.975	25.500
S-PR(109)	1.1592	16.25	0.416667	11.000	21.829	2332.000	25.382	48.184	32.500
S-PR(110)	3.9750	106.2	0.028074	11.000	21.829	2332.000	25.382	48.185	32.500
S-PR(111)	3.8812	98.78	0.02624	11.000	21.829	2332.000	25.382	48.184	32.500
NE-PE(112)	3.4548	133.1	0.052521	72.000	25.008	1764.000	7.821	34.991	22.500
NE-PE(113)	2.6620	83.5	0.133976	81.000	24.771	1792.000	7.691	34.960	23.500
NE-PE(114)	4.0093	172.8	0.031466	402.000	23.563	1122.000	7.633	35.500	13.500
NE-PE(115)	3.5544	115.9	0.059312	98.000	24.821	1618.000	7.839	35.003	19.500
NE-PE(116)	2.8947	65.33	0.114863	970.000	19.908	701.000	8.187	36.404	5.500
NE-PE(117)	3.4370	88.45	0.049334	31.000	25.083	2029.000	8.308	34.978	29.500
NE-PE(118)	3.7068	116	0.037651	586.000	21.604	550.000	8.300	36.000	1.000
SE-SP(119)	2.3520	36.25	0.14497	6.000	22.633	2469.000	25.051	47.897	32.500
S-RS(120)	3.3566	81.67	0.044563	243.000	17.817	1619.000	29.864	50.258	31.000
S-PR(121)	3.6926	85.53	0.034048	920.000	16.704	1344.000	25.650	49.650	24.000
NE-RN(122)	3.2170	50.79	0.057504	98.000	25.213	1178.000	6.917	35.200	13.500
S-RS(123)	2.1338	24.13	0.170882	12.000	18.708	1479.000	30.363	50.351	29.500
SE-SP(124)	4.5743	309.4	0.022497	680.000	18.367	1258.000	24.000	48.000	16.000
SE-SP(125)	3.0430	72.05	0.096993	747.000	18.571	1400.000	23.562	46.727	19.500
NE-BA(126)	3.3542	50.8	0.040519	103.000	24.142	1596.000	14.615	39.265	29.500
SE-MG(127)	2.9050	87	0.078003	1721.000	13.450	1916.000	22.711	45.932	22.500
SE-ES(128)	3.7339	120.2	0.036711	5.000	24.575	1105.000	20.559	40.383	14.500
SE-ES(129)	5.0244	422.1	0.014465	4.000	24.142	1261.000	19.100	39.750	20.000
NE-CE(130)	3.6547	122	0.055866	828.000	21.067	1551.000	4.218	38.932	19.500
NE-CE(131)	3.8359	171.4	0.050378	460.000	23.342	1227.000	4.206	38.971	12.500
NE-CE(132)	3.6098	102.1	0.040274	762.000	21.592	1535.000	4.297	38.933	18.500
NE-CE(133)	3.8304	107	0.031017	762.000	21.592	1535.000	4.298	38.920	18.500
SE-SP(134)	3.5584	106.7	0.050454	803.000	18.042	1458.000	23.597	46.833	19.500
SE-SP(135)	3.8850	176.1	0.03251	803.000	18.042	1458.000	23.597	46.833	19.500
SE-SP(136)	3.9794	164.1	0.024697	803.000	18.042	1458.000	23.597	46.833	19.500
SE-SP(137)	4.0805	135.8	0.027732	803.000	18.042	1458.000	23.597	46.833	19.500
SE-SP(138)	4.1510	169.4	0.021753	803.000	18.042	1458.000	23.597	46.833	19.500
SE-SP(139)	4.2411	141.1	0.018212	803.000	18.042	1458.000	23.597	46.833	19.500

However, when a dry or very dry month follows a humid or very wet month, its score is increased by -0.5 and -1.5, respectively, since the availability of water in the soil may still be high. Therefore, the smaller the Perhumidity Index, the drier and more seasonal the climate is. Then, we checked for multicollinearity among all variables available in DIVA-GIS plus the Perhumidity Index by means of a Principal Component Analysis. Among the 19 climate variables analysed, only four (Altitude, Perhumidity, Average Annual Rainfall, and Mean Annual Temperature) showed no collinearity and were thus selected for our analyses. In addition to those four variables, we included Latitude (LAT), Longitude (LONG), and the Perhumidity Index (PER).

Data analysis

To test our hypotheses, Canonical Correspondence Analysis (CCA), (TER BRAAK, 1995), multiple regressions and partial redundancy analysis (BORCARD et al., 1992) were run. A matrix of the localities per diversity values (columns) and another with the localities per environmental variables were used for the CCA. The CCA was used to identify environmental variables associated with diversity indices. Because of large differences in scale among the variables, the data were normalized using a ranging transformation. To test the significance of CCA correlations, a Monte Carlo permutation test (999 permutations) was performed. All the analyses and transformations were performed in Fitopac Shell 2 (SHEPHERD; URBANETZ, 2010).

Using multiple regression analysis, minimal models were obtained by the stepwise method in Systat 10, permitting the removal of the non significant variables ($p > 0.05$). Samples generating high levels of residuals and representing outliers (Stantard Deviation > 2.0) were removed from the analysis. Analysis of values for T_g1 and T_g2 showed the need to transform H', C, and Chao I variables to base 10 logarithm. With the transformation of the dependent variables, all explanatory variables were also transformed. Since some samples showed negative values, we added 19 to all results, thus obtaining positive values for all samples.

We conducted a partial redundancy analysis (RDA) (LEGENDRE; LEGENDRE, 1998) to investigate which factors (environmental, spatial or stochastic) most determine the variation of alpha diversity values across the ARF. As factor-variables, we used a matrix of localities per environmental data (Altitude, Perhumidity, mean annual rainfall and mean annual temperature) and a matrix of localities per spatial data (latitude and longitude). As response-variable, we used a matrix with localities per alpha diversity indices (H ', Chao and C). Analyses were performed using the Varpart function of the Vegan package in R (R DEVELOPMENT CORE TEAM, 2010).

Results

The highest values of heterogeneity (Shannon H'), richness estimate (Chao I) and the lowest values of abundance concentration (Simpson C) occur unevenly at latitudes corresponding to the middle range of the ARF (Table 1). Since the ARF ranges from 3° to 30° south latitude, the greatest diversity values are found around 19° S. These latitudes correspond to the Doce River valley.

The canonical eigenvalues for all axes of the CCA were low (less than 18%), indicating a weak relationship between diversity indices and environmental variables (Figure 2). The Monte Carlo permutation test showed a correlation between diversity indices and environmental variables for the first two canonical axes (Axis 1. eigenvalue = 0.0259, p = 0.0010; Axis 2. eigenvalue = 0.0025, p = 0.0350). Percentage of the explained variance for the first axis was 16.17% and for the second axis, 1.59%. The sum of the eigenvalues for axes 1 and 2 explained only 17.76% of the correlation between environmental variables and diversity indices. The sum of the non-canonical eigenvalues accounted for 83% of the explanatory power of the results, i.e., 83% of the results could not be explained by the correlation model of species diversity and climatic variables.

We performed the CCA in two modes, one considering the diversity indices, and the other considering the environmental variables. Both types of ordination provided similar results (Figure 2). Spatial variables (latitude, longitude, altitude) were opposed to climatic variables (mean annual temperature, mean total annual rainfall and perhumidity index). This means that as latitude, longitude and altitude increase, the mean annual temperature, the mean annual total rainfall and the perhumidity index decrease, indicating that drier, colder and more seasonal climates prevail at greater latitudes, longitudes and altitudes. In both ordinations, Shannon H' and Chao I were positively correlated with the spatial variables, whereas Simpson C was positively correlated with the climatic variables. This means that richness (Chao I) and heterogeneity (Shannon H') vary with latitude, longitude and altitude, whereas the abundance concentration in few species (Simpson C) varies as climate varies.

For the Shannon's diversity index (H'), the model obtained by multiple regression retained only variables of altitude, latitude, and longitude ($R = 0.462$; $R^2 = 0.214$; $SD = 0.088$, $\hat{y} = 2.335 + 0.049\ ALT + 0.236\ LAT - 1.341\ LONG$).

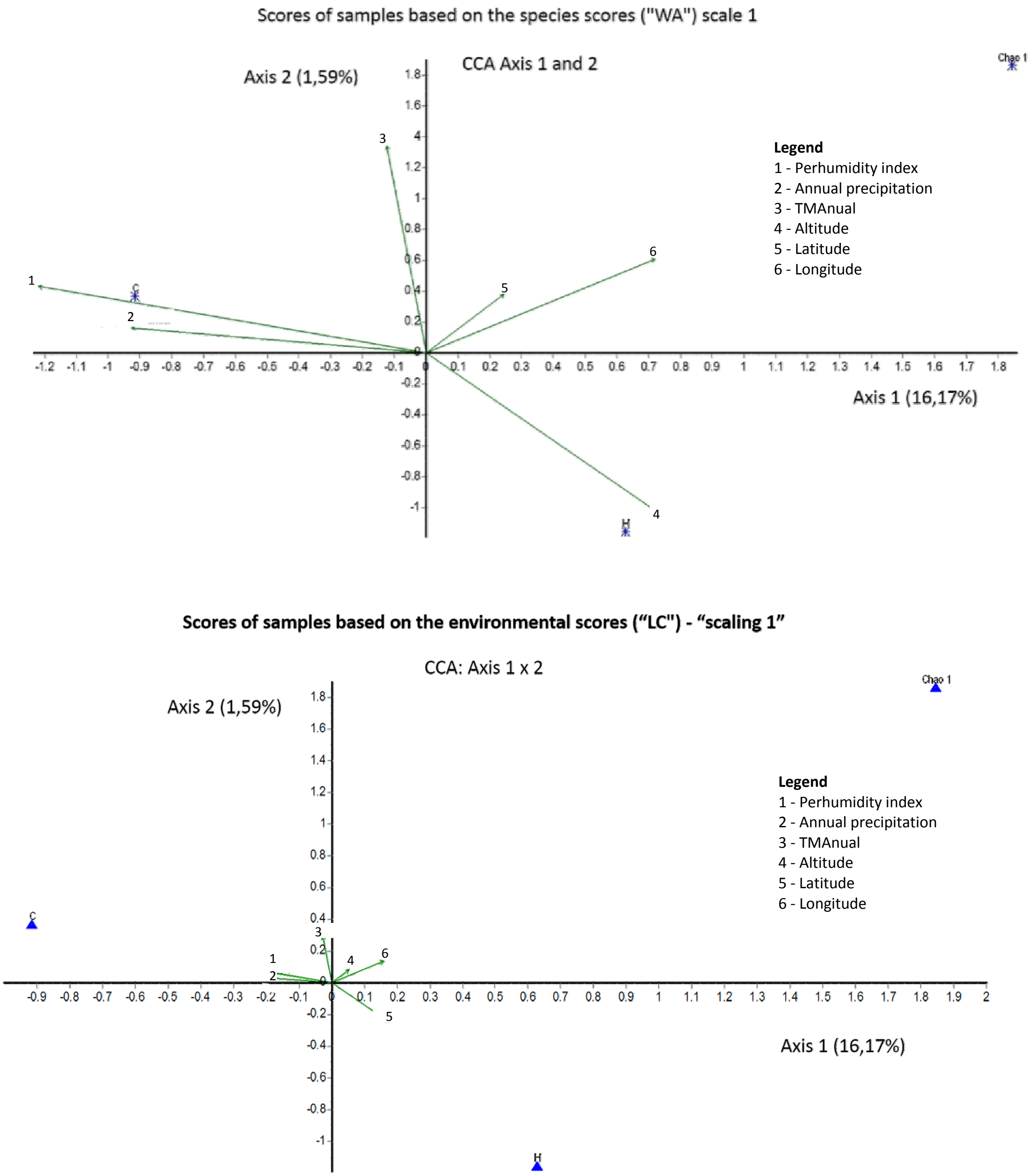

Figure 2. CCA ordination diagram for axes 1 and 2, based on scores for the diversity indices (WA) and environmental variables (LC). H': Shannon diversity index; CHAO: Chao I richness estimator; C: Simpson concentration index. Environmental variables: ALT: altitude; LAT: latitude; LONG: longitude; TMAnual: mean annual temperature, Perhumidity index and Mean Annual rainfall.

Longitude showed a negative relationship with increasing H' values. To obtain the minimal model for the Chao I richness estimator, four phytosociological tables [SE-SP(2), S-SC(41), NE-CE(72), and SE-SP(86)] were removed from the analysis due to high levels of residuals, and because they represented outliers. The minimal model retained the same variables, showing a negative relationship with the increase in the Chao I estimator richness values ($R = 0.437$; $R2 = 0.191$; SD. $= 0.265$; $\hat{y} = 8.5751 + 0.117ALT + 0.802\ LAT - 4.767\ LONG$). The minimal model obtained for the Simpson concentration index (C) retained the same variables, and showed a negative correlation with latitude and altitude and a positive correlation with longitude ($R = 0.476$;

R2 = 0.227; SD. = 0.333; ŷ = -8.096 - 0.195 ALT – 0.882 LAT + 5.08 LONG). By applying the partial redundancy analysis (RDA), we found that the variation of alpha diversity in the ARF was not significantly explained by pure environmental variables and spatial components, or by the spatially structured environmental variation (Figure 3). The greatest explanatory power came from the stochastic processes, presented as residual in our results.

Discussion

Studies conducted in tropical forests showed close relationships between climatic variables and variations in species richness and diversity (PAUSAS; AUSTIN, 2001). Although these relationships are well established in the literature and are important to predict species richness in a site, some issues have been raised on which environmental variables best explain species distribution.

Comparative studies have associated the increase in species richness with average annual total rainfall, number of dry days in the year, altitude, mean annual temperature, and latitudinal variation (SCUDELLER et al. 2001, OLIVEIRA-FILHO et al., 2005). Average annual rainfall is considered one of the most important environmental factors in determining species diversity in tropical forests (GENTRY, 1982; 1988; CLINEBELL II et al., 1995, OLIVEIRA-FILHO; FONTES, 2000; LINDER, 2001 SCUDELLER et al, 2001). Nevertheless, our results showed no direct relationship of this variable with the increase or reduction in alpha diversity in the ARF. Walsh (1996) considered annual rainfall values of at least 1700 mm, with a dry season either absent or short, as requirements for a tropical rain forest with its expected high species diversity. Nevertheless, our findings showed that the degree of variation in the mean annual rainfall may not be such a significant factor in determining species alpha diversity in the ARF.

Altitude had a positive relationship with the Shannon diversity index and the Chao I richness estimator. Influence of altitude on the distribution of tree species in the ARF is already well known (OLIVEIRA-FILHO et al., 2005).

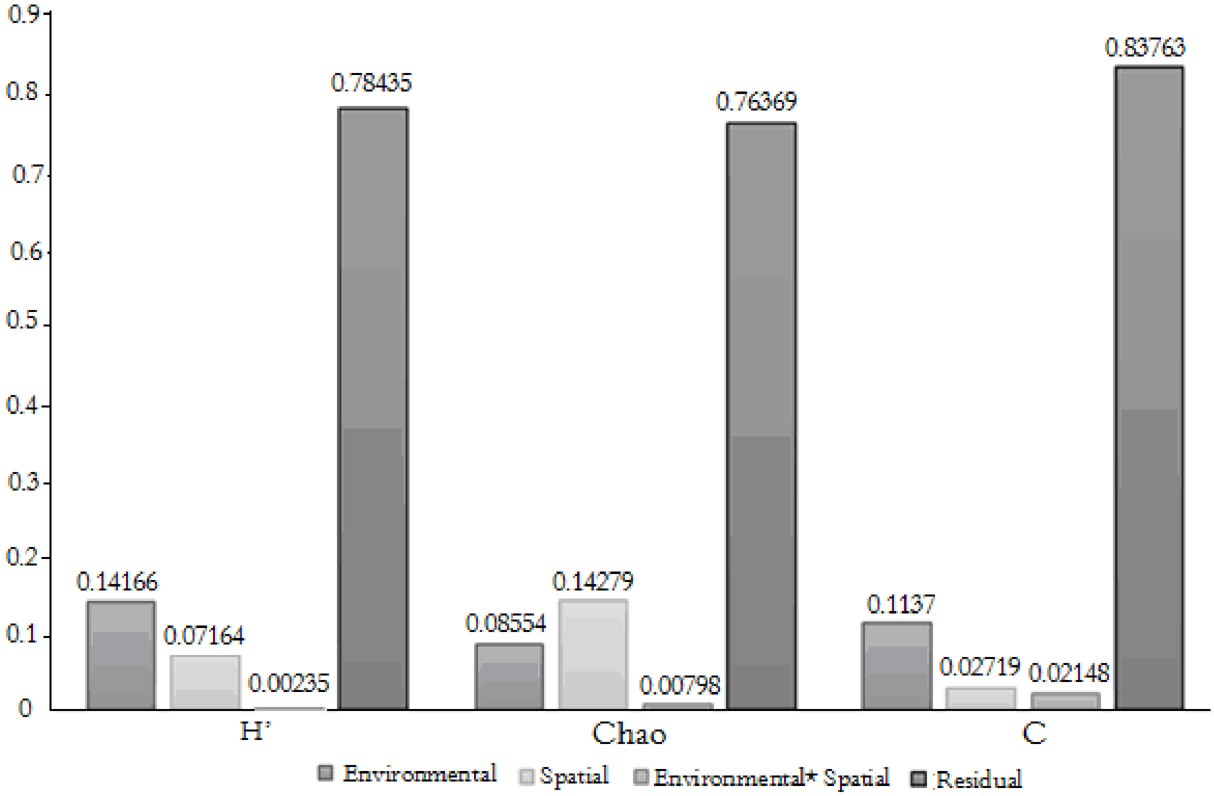

Figure 3. Variation partitioning by RDA for different indices of alpha diversity (Shannon H', Chao I, and Simpson C) in the Atlantic Rainforest. The numbers over the bars indicate the variation explained by pure environmental factors, by pure spatial variables, by spatially structured environmental variation, and the residue. Most variation (over 75%) remained unexplained.

The results of Gentry (1988) diverge from ours, since this author registered that the site diversity in tropical regions tends to decrease with increasing altitude, though that pattern is not necessarily valid for all forests. Oliveira-Filho and Fontes (2000) reported a gradient of species, genera, and families in the ARF, regulated by variations in altitude, and distinguishing the ARF of the Northeast and Southeast Brazil (Espírito Santo and Bahia) from the ARF of the Southeastern and Southern Brazil (Rio de Janeiro, São Paulo, and Paraná). Scudeller et al. (2001) verified that altitude represents a strong environmental variable determining tree species distribution in the São Paulo State. Oliveira-Filho et al. (2005) registered that variations in altitude are strongly correlated with the internal differentiation of both the ARF and the Seasonal Semidecidious Forests.

According to these findings, physiognomic variations in the Phyto-ecological Region of the ARF would be a result of environmental conditions associated with altitudinal and latitudinal variations and that higher species diversity at high altitudes is due to the altitudinal gradient of diversity, with the montane and altimontane forests presenting greater species diversity than the lowland and lower-montane forests. Another important factor to consider in the distribution of the ARF is the type of relief. In Southeastern Brazil, the diversity center of the ARF (R.M.CERQUEIRA, unpublished data), the main form of relief is mountain ranges (*serras*), whereas in the Northeast prevail coastal plains (*tabuleiros*) and plateaus (*chapadas*). Areas with predominance of mountain ranges, usually located at higher altitudes, have sites with better preserved vegetation probably because of difficulties of access and mechanization for land use. Therefore, altitude, an important variable in determining species diversity in the ARF, should be considered within the context of variations in landforms.

Both Shannon diversity index (H') and Chao I richness estimator (Chao I) were positively correlated with increasing latitude. Our results contrast with the general trend of increasing biodiversity with reducing latitude. Fischer (1960), Pianka (1966), Gentry (1988), Rosenzweig (1995), among others, associated increasing biodiversity of the sites with decreasing latitude. Although we registered a positive correlation of diversity indices with latitude in the ARF, we believe that this correlation is because the richness center of the ARF is located in the Southeastern Region, as firstly indicated by Smith (1962) and confirmed by R.M. Cerqueira (unpublished data). According to R.M. Cerqueira (unpublished data), the higher alpha diversity in the central portion of ARF could be the outcome of historical factors (climatic fluctuations of the Quaternary) and associated biogeographical processes (alternating vicariance and dispersal) that occurred in this phytoecological region, which caused alternating retraction and expansion of forest areas in the ARF. The higher values of the Shannon's diversity index (H') in the ARF middle range could have biased the results of the canonical correlation and regression, without necessarily implying that areas of higher latitudes have greater biodiversity.

The negative correlation between longitude and species richness was analyzed in different countries and in different geographic regions of Brazil, but no investigation of this correlation had been carried out so far for the total extension of the ARF in Brazil. By analyzing samples from the ARF and from the Seasonal Semidecidious Forests in the São Paulo State, R.J. Oliveira (unpublished data) found a negative correlation of tree species richness with distance from the Atlantic. The author concluded that the direct correlation of species richness with latitude and annual thermal amplitude may be a consequence of the correlation of these variables with the distance from the Atlantic. Thus, the author found an indirect effect of the distance from the Atlantic and its associated humidity gradient. O'Brien (1993) described a pattern of longitudinal variation for the woody flora richness in South Africa, with climate accounting for the 78% of that variation. Although all these authors investigated directly the variation in the number of species, not the composite indices that we used, our findings of the longitudinal pattern of decreasing tree species diversity, with a gradual replacement of species along the coastal-inland gradient, corroborated other studies performed in tropical forests.

The Simpson concentration index (C) was negatively correlated with latitude and altitude, the opposite to that found for Shannon heterogeneity H' and the Chao I richness estimator. Communities with high diversity tend to show great evenness (MARTINS; SANTOS, 1999) and species richness. Our findings show that more diverse areas tend to have higher species evenness, with less concentration of abundance; whereas those with lower species diversity tend to have lower evenness and greater abundance concentration. Also, our results show that high H' and Chao I and small C vary in this way as latitude, longitude and altitude vary in the ARF.

Spatial variables alone (latitude, longitude, and altitude) were retained for our minimum models of multiple regression, indicating that the space has a greater explanatory power than environmental factors for species diversity variation in the ARF. However, in the partial redundancy analysis (RDA), the space had little power to explain the variation of alpha diversity values. Stochastic processes were determinants and explained more than 75% of the variation of the alpha diversity. It is more likely that the current distribution patterns of tree species in the ARF are a result of vicariance and dispersal events caused by climatic oscillations and geological events in the Cenozoic (ANDRADE-LIMA, 1982; BIGARELLA; ANDRADE-LIMA, 1982) than resulting from limitations imposed by variations in climatic factors. Scudeller et al. (2001) showed a significant negative relationship between floristic similarity and geographical distance in samples from the ARF: the farther two communities are, the less similar they are. This pattern may be indicative of dispersal limitation, a basic process in stochastic models for community assembly (HUBBELL, 2001).

Species of wide distribution may have great ability for dispersal and tolerance to different types of environments, whereas species of restricted distribution tend to have limited dispersal ability (BOULANGEAT et al., 2012). The dispersal ability may influence species replacement rate and is directly associated with distance, being independent from local weather conditions (SVENNING; SKOV, 2004). Plants with limited dispersal range are called stenotopic, almost 54% of the tree species in the ARF are characterized as such (CAIAFA; MARTINS, 2010). R.M. Cerqueira (unpublished data) have shown that most of the analyzed tree taxa (families, genera, and species) in the ARF have low relative constancy (occurrence in less than 20% of the total number of samples). Altogether, these findings suggest that ARF tree species have reduced dispersal ability and tend to remain in the place of origin.

Conclusion

Regardless of which diversity index (Shannon H', Chao I, or Simpson C) or community attribute (species richness, or species richness and abundance) were used in our analyses, we found similar results, indicating that our findings are consistent. The Atlantic Rainforest is characterized by high diversity of tree species. A very small fraction of the tree species diversity in the ARF is conditioned by climate, a greater portion (but still small) is conditioned by the spatial variables of altitude, latitude and longitude, and most part (over 75%) is conditioned by stochastic factors. These results indicate that climate has a weak influence on the values of diversity indices, which vary with spatial variation, but are mostly explained by historical events and biogeographic processes that are manifestations of stochasticity. We found a positive correlation between alpha diversity and latitude, probably due to the location of a richness center in the middle range of the ARF. The current status of the ARF diversity could be a result of regional biogeographic processes triggered by stochastic geological events and climate oscillation occurring over time and resulting in alternating processes of vicariance and dispersal, which have influenced the present patterns in tree species diversity. Environmental variables, such as mean annual rainfall, perhumidity, and mean annual temperature, although considered important in studies performed so far in tropical forests, showed a very weak influence on the values of alpha diversity in the ARF.

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