

A phytogeographic analysis of cloud forests and other forest subtypes amidst the Atlantic forests in south and southeast Brazil

Ricardo Bertonecello · Kikyo Yamamoto · Leonardo Dias Meireles · George John Shepherd

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Abstract In a previous study near the summit of Mt. Cuscuzeiro (Ubatuba, SP) (820–1270 m), on the SE Brazilian coast, we found two floristically different forests, one above 1120 m, that appears to have a number of features typical of cloud forests, and another on the lower altitude slopes below. Taking these two forests as reference points, we addressed two questions: (1) What are their floristic relationships with other Atlantic forest subtypes in S-SE Brazil?; (2) Do the cloud forests in this region constitute a particular floristic-phytogeographic formation or are they a subset of their surrounding community? Species from 109 surveys (including Mount Cuscuzeiro) of 83 locations in S-SE Brazil were compiled into a binary (presence-absence) floristic matrix. Analyses of similarity among these samples using clustering (UPGMA, TWINSpan) and ordination (DCA, PCO and CA) methods were performed. The surveys were divided into six main groups: (1) Cloud Forests; (2) “Salesópolis” group (3) Coastal Forests, subdivided between (a) Slope Forests and (b) Coastal Plain (“Restinga”) Forests and Mountaintop Forests (not included in the Cloud Forests group); (4) *Araucaria* Forests; (5) Inland Seasonal Forests (from below ca. 700 m); and (6) Inland Montane Forests (from above ca. 700 m). The preferential and indicator species of the Cloud Forest group produced by TWINSpan are presented. The Mount Cuscuzeiro forests from above and from below 1120 m were clustered with the Cloud Forests and the coastal Slope Forests groups, respectively. We concluded that Cloud forests comprise a distinct phytogeographic formation in Brazilian S-SE region.

Keywords Arboreal flora · Atlantic forest · Brazilian coastal forest · Cloud forest · Floristic similarity analysis · Phytogeographic characterization

R. Bertonecello (✉) · L. D. Meireles
Programa de Pós-Graduação em Biologia Vegetal, Departamento de Biologia Vegetal,
Universidade Estadual de Campinas, 6109, Campinas, São Paulo CEP 13083-970, Brazil
e-mail: ricardobertonecello@gmail.com

K. Yamamoto · G. J. Shepherd
Departamento de Biologia Vegetal, Universidade Estadual de Campinas, 6109, Campinas,
São Paulo CEP 13083-970, Brazil

Introduction

With around 31,000 species of Magnoliophyta (Forzza et al. 2010) of an estimated world total of 352,000 (Chapman 2009), Brazil has about 9–10% of the total phanerogamic flora of the world. Covering a total area of 8,514,876,599 km² and about 38° of latitude, this country occupies a major part of South America (IBGE 2008), and includes within its boundaries an enormous diversity of tropical and subtropical habitats and vegetation types, many of them still very poorly known. Since quantitative surveys of Brazilian forests and other vegetation types are relatively recent and are, as yet, very incomplete, classification of the different vegetation types into a phytogeographical system in this country has been and continues to be a major challenge to ecologists, botanists, and phytogeographers. Although the existing national vegetation classification system (Veloso 1992) is widely used in all official publications, it is primarily based on physiognomic criteria and is inadequate to describe variations in floristic composition that occur in many regions and a revised system taking into account floristic data is urgently required.

The Atlantic Forest s.l. comprises one of the largest biomes in Brazil. Including all the forests east of the Andes and south of the Amazon, this biome originally covered an area of nearly 1,300,000,00 km², ranging between the states of Rio Grande do Norte and Rio Grande do Sul, and from the eastern Atlantic coast to the Central Brazilian plateau (“Planalto Central”) and parts of Paraguay and Argentina (Câmara 2005). Nowadays, the Atlantic Forest is among the most threatened biomes on earth, with about 11.4–16% of the original area of vegetation cover (Ribeiro et al. 2009). It is highly fragmented and reduced, with its larger and best preserved remains confined to the high-elevation areas along the Brazilian southern and southeastern coastal regions, mostly on the Serra do Mar mountain ranges. However, this biome still maintains a high level of biodiversity, especially in its larger remnants, and is considered a “super priority Hot Spot” for conservation purposes (Myers et al. 2000). In order to maximise conservation potential, detailed phytogeographic knowledge of this biome is needed, particularly in high-elevation areas, where very few surveys have been made.

The current official Brazilian vegetation classification system (Veloso 1992) is based primarily on physiognomic and altitudinal criteria and follows the guidelines suggested by UNESCO (1973) recognizing three main forest types in the Atlantic Forest biome of southern and southeastern Brazil: (a) the coastal rain forests (Tropical Ombrophilous Dense Forests) that are associated with high temperatures and rainfall, without a biological dry season, and characterized by evergreen trees; (b) the inland “planalto” forests (Tropical or Sub-tropical Semi-deciduous Forests) that are associated with two distinct seasons (summer with high rainfall, and winter with physiological drought and mean temperature below 15°C), and characterized by the presence of 20–50% of the trees shedding leaves during the dry winter; and (c) The Araucaria Forests (Mixed Ombrophilous Forests), with disjunct distribution usually in high-elevation areas, and characterized by the presence of species of the genera *Araucaria* and *Podocarpus*. These three main forest types include Lowland, Sub-montane, Montane and Upper Montane subdivisions according to altitudinal × latitudinal ranges, as well as an Alluvial subtype.

Despite these definitions, there is still an academic debate about the classification and the limits of the forest subtypes of the Atlantic Forest complex (Joly et al. 1999), mainly because the altitudinal/latitudinal ranges suggested by Veloso are not universally applicable throughout the range of the Atlantic Forest and the growing realization that floristically-based subdivisions often do not coincide with the divisions suggested in Veloso’s system. During the last three decades, a considerable body of floristic data has been

gathered by Brazilian workers and analyzed for their floristic similarities using clustering and ordination methods. This has led to a considerable refinement in knowledge about the species that compose the different forest subtypes and how they are geographically and ecologically distributed. For example, two sites close to São Paulo city, on the inland plateau, “Serra da Cantareira” and “Guarulhos”, were classified as Semi-deciduous Forests by Baitello and Aguiar (1982) and Gandolfi et al. (1995), and as Ombrophilous Dense Forest by Gomes (1992), Roizman (1993), and Tomasulo (1995). However, Ivanauskas et al. (2000) after applying a cluster analysis to several surveys from the coastal and the inland plateau, including those two areas, concluded that they would best be described as “transition areas”.

In spite of considerable advances in knowledge of floristic composition of lowland and mid-altitude “montane” forests, the information available on the composition and biogeography of Brazilian tropical mountains is still very restricted and fragmented, with very little advance in relation to the state of knowledge that was described by Ab’Saber (1989) as long as two decades ago. Since species diversity in the high-elevation areas is particularly endangered by the prospect of climatic change with increasing temperature, information about floristic variations in these areas is needed, more than ever, to decide on adequate measures to prevent species loss. High-elevation areas contain ecologically different sites related to altitude, declivity, distance from the sea, position (summits, slopes and valleys) and local aspect which largely determines the main direction of the wind, insolation, and presence and persistence of clouds and mist, all of which influence edaphic and microclimatic characteristics. Floristic and structural differences in plant communities related to these different environmental conditions have not yet been well investigated in Brazilian high-elevation areas.

We are particularly concerned with the lack of knowledge about cloud forests in the southern and southeastern regions of Brazil. These are the most densely populated regions in the country, and they also contain the location of the highest, most extensive mountain ranges, especially along the coast, that play determining roles in the regional climate. According to the review of cloud forests in the humid tropics by Stadtmüller (1987), the occurrence of this type of forest is conditioned by frequent cloud and mist cover that gives rise to the entry of additional humidity, besides rainfall. Through the capture and/or condensation of water droplets by plant surfaces, in a process named horizontal precipitation, it “...influences the hydrological regime, radiation balance, and several other climatic, edaphic and ecological parameters”. According to Stadtmüller (1987), cloud forests in the humid tropics add the equivalent of up to 1.5 times of the local rainfall by horizontal precipitation.

The lack of knowledge about cloud forests in Brazil was emphasized by Falkenberg and Voltolini (1995), one of the very few Brazilian workers focusing attention on this type of vegetation, when he observed that we can not even tell whether they form, floristically, a particular vegetation type or a subset of the surrounding formations with similar physiognomies in Atlantic mountain forests.

Information about cloud forests in south and southeast Brazil can be found in floristic and other investigations on high-elevation woody vegetation and other plant communities. Under different denominations, they have been described for different locations of Serra do Mar in the states of São Paulo (Mantovani et al. 1990; Micheletti Neto 2007), Paraná (Roderjan 1994, Rocha 1999, Koehler et al. 2002), Santa Catarina (Klein 1980), and Rio Grande do Sul (Falkenberg 2003), and in the Serra da Mantiqueira on the borders of the states of Minas Gerais and São Paulo (Meiros et al. 2008 and Meireles 2009).

In attempt to investigate how floristic composition and plant community structure change along with altitudinal variation at higher elevations in the vegetation complex covering the Serra do Mar, the most important mountain range along the coast of the Brazilian south and southeast regions, we carried out a study (Bertoncello 2009) on Mount Cuscuzeiro, located in Ubatuba municipality, state of São Paulo, at coordinates 230°18'14''S and 44°47'16''W (SAD'69). At approximately 7 km from the Atlantic coast, this is one of the nearest mountains to the ocean in southeast Brazil. In addition, its summit at 1277 m, is close to the upper altitudinal limit of the Serra do Mar in the border region of the states of São Paulo and Rio de Janeiro, where the most extensive remains of Atlantic rain forests occur. Among many other mountains in the region, we were particularly interested in this particular one because of its frequently clouded summit and because previous modelling studies carried out with the species *Drimys brasiliensis* (Shepherd 2007, unpublished data) suggested the possible occurrence of this species in the upper reaches of this part of the Serra do Mar. There, we found two floristically discrete communities, one between 820 m (the lower elevation level included in the study) and 970 m, where we found typical structure and species from the Slope Forests of the Serra do Mar, and another from 1120 to 1270 m. Since the floristic separation coincided with a great frequency of stagnant clouds above 1120 m, and the structure and species on the upper levels are typical of Cloud Forests described elsewhere (Bertoncello 2009), we considered these two forests in Mount Cuscuzeiro as adequate reference stands for a phytogeographic analysis of cloud forests of the coastal Atlantic forests in south and southeast Brazil.

The present study analyzed the floristic relationships of the two adjacent but floristically distinct forests on Mount Cuscuzeiro with other Atlantic Forest remains that have been previously surveyed in south and southeast Brazil, including lowland to highland and coastal to inland forests representing the three main subtypes of Atlantic forests, the rain forests, the semideciduous forests and the *Araucaria* forests (*sensu* Veloso 1992). Similarity analyses were applied to a set of data compiled from these surveys, aiming to provide a phytogeographic analysis based on floristic relationships of Atlantic Forest subtypes in south and southeast Brazil and, especially, to address two particular questions: (1) What are the floristic relationships of the two Mount Cuscuzeiro forests with the Atlantic forest subtypes in south and southeast Brazil?; (2) Do the cloud forests in this region constitute a distinct floristic-phytogeographic formation, or are they a subset of their surrounding community? We also discuss the wider floristic similarities among the subtypes of Atlantic Forests in the south and southeast regions of Brazil.

Methods

Floristic matrix

A binary floristic matrix from 83 locations from south and southeast Brazil—including the states of Minas Gerais, Rio de Janeiro, São Paulo (including our previous survey from Mount Cuscuzeiro), Paraná, Santa Catarina and Rio Grande do Sul (Fig. 1)—was used for the calculation of similarities. We included data on woody species from floristic lists with at least 70% of the species identified, and excluded those species whose identification was unconfirmed (“cf.”, “aff.”). The completed matrix was then reviewed to remove synonyms and dubious names using recent taxonomic revisions and regional Floras, as well as the websites www.ipni.org, www.mobot.org, and www.nybg.org. Species not found in any of these references were excluded from the analyses. The final matrix contained a total of

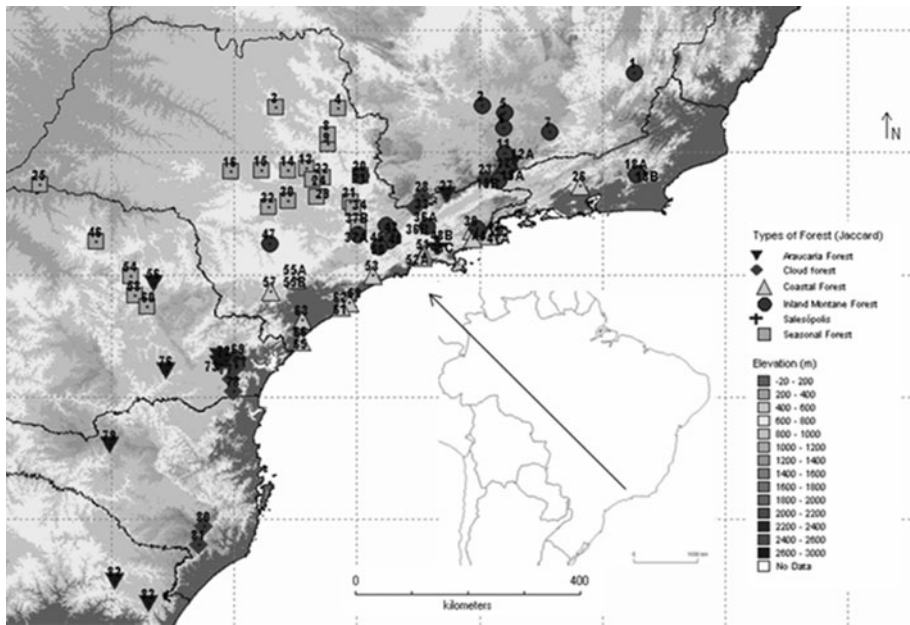


Fig. 1 Topographical map of south and southeastern Brazil with the sites of the surveys used in this article. The *symbols* represent the groups established by the UPGMA analysis and the numerical codes of the surveys are presented in Table 1

1,564 species from 109 surveys (some locations had multiple surveys). The locations, the numerical codes for the surveys, elevations, and bibliographic references for the surveys are summarized in Table 1. In this table, the surveys are numbered and displayed in sequence from lower to higher latitudes. Surveys from the same study but from different elevations or formations were subdivided and analyzed separately. Multiple surveys made by a same author in a single location were given the same number, but distinguished by letters—for instance, the Mount Cuscuzeiro survey from 820 to 970 m is called 40A, and from 1120 to 1270 m, 40B.

Data analysis

Similarity between surveys was estimated using the Jaccard index, and the resulting matrix was analyzed using standard clustering techniques such as Group Average (UPGMA) in order to define the floristic groups formed by the surveys. Groups were also obtained from a divisive method, the Two Way Indicator Species Analysis (TWINSPAN), and the results compared. The latter also provided a list of preferential and indicator species for each division.

The relationships between surveys and species were investigated using ordination methods, including Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA), and Principal Coordinates Analysis (PCO) of the Jaccard matrix. Three dimensional representations of the data (using VRML) were generated to help visualize the relationships between the samples (data not shown). The software FITOPAC 1.6.4 (Shepherd 2007) was used to perform all the analyses.

Table 1 General information on surveys included in the current study. NP: Not provided by the author

State	Locality	Numerical code	Elevation (m)	References
MG	Serra do Brigadeiro	1	1410	Ribeiro (2003)
MG	Lavras	2	925	Oliveira-Filho et al. (1994)
SP	Jaboticabal	3	595	Pinto (1989)
SP	Cajuru	4	550	Meira-Neto and Bernacci (1986)
MG	Itutinga	5	920	Berg and Oliveira-Filho (2000)
MG	Carrancas	6	1500	Oliveira-Filho et al. (2004)
MG	Serra do Ibitipoca	7	1390–1490	Carvalho et al. (2000)
SP	Santa Rita do Passa Quatro	8	700	Martins (1991)
SP	Santa Rita do Passa Quatro	9	600	Bertoni et al. (1988)
SP	Porto Ferreira	10	550	Bertoni and Martins (1987)
MG	Airuoca	11	1100	Pereira et al. (2006)
MG	Bocaina de Minas	12A	1135	Pereira et al. (2006)
MG	Bocaina de Minas	12B	1300	Pereira et al. (2006)
MG	Bocaina de Minas	12C	1450	Pereira et al. (2006)
SP	Itirapina	13	750	Kotchetkoff-Henriques and Joly (1994)
SP	Brotas	14	530	Salis et al. (1994)
SP	Jaú	15	556	Nicolini (1990)
SP	Bauru	16	570	Cavassan et al. (1984)
RJ	Visconde de Mauá	17	1200	Pereira et al. (2006)
RJ	Macaé de Cima	18A	1100	Guedes-Bruni (1998)
RJ	Macaé de Cima	18B	1100	Guedes-Bruni (1998)
RJ	Serra do Itatiaia	19A	NP	Schumm (2006)
RJ	Serra do Itatiaia	19B	NP	Guedes-Bruni (1998)
SP	Mogi Guaçu	20	600	Gibbs and Leitão-Filho (1978)
SP	Mogi Guaçu	21	600	Mantovani et al. (1989)
SP	Rio Claro	22	630	Pagano and Leitão-Filho (1987)
MG	Serra Fina	23	2300	Meirele and Shepherd (2009)
SP	Ipeúna	24	600	Mantovani et al. (1986) apud Salis (1990)
SP	Teodoro Sampaio	25	600	Baitello et al. (1988)
RJ	Nova Iguaçu (Tinguá)	26	650–900	Rodrigues (1996)
SP	Campos do Jordão	27	1500	Los (2004)
MG	Camanducaia	28	1900	França and Stehmann (2004)
SP	Piracicaba	29	600	Catharino (1989)
SP	Anhembi	30	500	Cesar O Leitão-Filho (1990)
SP	Campinas	31	700	Tamashiro et al. (1986)
SP	Botucatu	32	600	Gabriel (1990)
MG	Camanducaia (Monte Verde)	33	1840–1920	Meireles et al. (2008)
SP	Campinas	34	700	Matthes et al. (1988)
SP	Atibaia	35	1150	Grombone et al. (1990)

Table 1 continued

State	Locality	Numerical code	Elevation (m)	References
SP	São José do Campos	36A	740	Silva (1989)
SP	São José do Campos	36B	790	Silva (1989)
SP	São José do Campos	36C	840	Silva (1989)
SP	São José do Campos	36D	890	Silva (1989)
SP	São José do Campos	36E	1040	Silva (1989)
SP	Serra do Japi	37A	1170	Rodrigues et al. (1989)
SP	Serra do Japi	37B	870	Rodrigues et al. (1989)
SP	Cunha	38	1300	Aguiar et al. (2001)
SP	Santa Virgínia	39	870–1100	Tabarelli (1997)
SP	Ubatuba (Picinguaba)	40A	820–970	Bertoncello (2009)
SP	Ubatuba (Picinguaba)	40B	1120–1270	Bertoncello (2009)
SP	Ubatuba (Picinguaba)	41A	Plain	Sanchez (2001)
SP	Ubatuba (Picinguaba)	41B	100	Sanchez (2001)
SP	Ubatuba (Picinguaba)	41C	300	Sanchez (2001)
SP	Ubatuba (Picinguaba)	41D	600	Sanchez (2001)
SP	Ubatuba (Picinguaba)	41E	1000	Sanchez (2001)
SP	Ubatuba (Picinguaba)	42	Plain	Micheletti Neto (2007)
SP	Serra da Cantareira	43	850–1200	Baitello et al. (1992)
SP	Ubatuba (IAC)	44	160–190	Silva and Leitão-Filho (1982)
SP	Guarulhos	45	900	Gandolfi (1991)
PR	Londrina	46	700	Soares-Silva and Barroso (1992)
SP	Angatuba	47	600	Torres (1989)
SP	Salesópolis	48A	800–1200 (top)	Mantovani et al. (1990)
SP	Salesópolis	48B	800–1200	Mantovani et al. (1990)
SP	Salesópolis	48C	800–1200	Mantovani et al. (1990)
SP	Salesópolis	48D	800–1200	Mantovani et al. (1990)
SP	São Paulo	49	700	Struffaldi-de-Vuono (1985)
SP	São Paulo	50	700	Rossi (1987)
SP	Boracéia	51	850 (top)	Micheletti Neto (2007)
SP	Bertioga	52A	Plain	Martins et al. (2008)
SP	Bertioga	52B	Plain	Martins et al. (2008)
SP	Curucutu	53	800–850 (top)	Micheletti Neto (2007)
PR	Sapopema	54	780	Silva et al. (1995)
SP	Carlos Botelho	55A	50	Custódio-Filho (2002)
SP	Carlos Botelho	55B	200	Custódio-Filho (2002)
SP	Carlos Botelho	55C	400	Custódio-Filho (2002)
SP	Carlos Botelho	55D	600	Custódio-Filho (2002)
SP	Carlos Botelho	55E	800	Custódio-Filho (2002)
SP	Carlos Botelho	55F	1000	Custódio-Filho (2002)
PR	Ventania	56	1000	Estevan (2006)
SP	Intervales	57	1000 (top)	Micheletti Neto (2007)

Table 1 continued

State	Locality	Numerical code	Elevation (m)	References
PR	Telêmaco Borba	58	600	Nakajima et al. (1996)
SP	Iguape (Juréia)	59	Plain	Carvalhoes (1997)
PR	Tibagi	60	700	Dias et al. (1989)
SP	Iguape (Juréia)	61	Plain	Micheletti Neto (2007)
SP	Iguape (Juréia)	62	50–300	Mantovani (1993)
SP	Pariquera-Açu	63	25–30	Ivanauskas (1997)
SP	Pariquera-Açu	64A	Plain (hill)	Sztutman and Rodrigues (2002)
SP	Pariquera-Açu	64B	Plain	Sztutman and Rodrigues (2002)
SP	Cananéia (Ilha do Cardoso)	65	Plain	Sampaio et al. (2005)
SP	Cananéia (Ilha do Cardoso)	66	100–150	Melo (2000)
SP	Cananéia (Ilha do Cardoso)	67	Plain	Micheletti Neto (2007)
PR	Colombo	68	920	Silva and Marconi (1990)
PR	Mãe Catira	69	1590	Koehler et al. (2002)
PR	Morro do Anhangava	70A	1000–1200	Roderjan (1994)
PR	Morro do Anhangava	70B	1200–1300	Roderjan (1994)
PR	Morro do Anhangava	70C	1300–1400	Roderjan (1994)
PR	Morro do Anhangava	71	1460	Koehler et al. (2002)
PR	Pinhais	72	900	Seeger et al. (2005)
PR	Curitiba	73	900	Neto et al. (2002a)
PR	Marumbi	74	1385	Rocha (1999)
PR	Morro do Vigia	75	1545	Koehler et al. (2002)
PR	São João do Triunfo	76	780	Sanquetta et al. (2002)
PR	Serra do Salto	77	1390	Koehler et al. (2002)
PR	Morro Araçatuba	78	1610	Koehler et al. (2002)
SC	Caçador	79	1100	Negrelle and Silva (1992)
SC	Morro da Igreja	80	1710	Falkenberg (2003)
SC	Serra do Rio do Rastro	81	1400	Falkenberg (2003)
RS	Criúva	82	860	Neto et al. (2002b)
RS	São Francisco de Paula	83	930	Narvaes et al. (2005)

Due to the high number of “rare” species that appear only in very few surveys, before starting the analyses we tested the effect of removal of species occurring in less than 5 surveys [<5 survey] to verify if their absence would affect adversely the subsequent analyses. Initial clustering, followed by ordination analyses, was performed with both matrices (with and without the rare species). The resulting pairs of dendrograms generated by cluster analysis were almost identical. The results of the ordinations were also very similar but the DCA without the rare species showed a higher proportion of explained variance. Tests were also made excluding species that occurred in less than 10 surveys and in less than 20 surveys (data not shown) resulting in similar patterns, showing that the major patterns observed in the filtered and in non filtered matrices were very robust and

that the rarer species add little useful information. However, to avoid loss of finer details of composition, the [<5 survey] species exclusion limit was considered more adequate and we therefore excluded these [<5 survey] species and used a “final” matrix of 567 species (from 109 surveys) in all subsequent analyses.

Results

The UPGMA analysis (Fig. 2) created a well established group of Cloud Forests of south and southeast Brazil, including the Mount Cuscuzeiro 1120–1270 m forest (40B). This group of Cloud Forests consisted of three main subdivisions: (1) sites from Rio de Janeiro and Minas Gerais; (2) sites from Paraná, to which the Mount Cuscuzeiro sample 40B was attached; and (3) sites from Santa Catarina. The second major group detected by the UPGMA clustering method was a Coastal Forest group composed of two main subdivisions, one of Slope Forests including the Mount Cuscuzeiro 820–970 m survey (sample 40A), and the other containing two further subdivisions, of Mountaintop forests and Coastal Plain “restinga” forests. At a similar branching level to the Coastal Forest group, another distinct group was formed by four samples from different locations in Salesópolis municipality (São Paulo State), within Serra do Mar (Salesópolis group): on the top of a mountain (48A), on a valley (48B), on a high slope facing the Atlantic Ocean (48C) and on another high slope facing the inland plateau (48D). The remaining groups consisted of inland forests, generally occurring at some distance from the coast. The first was an *Araucaria* Forests group while the remainder was divided between an Inland Seasonal Forest group that included samples from below elevations of ca. 700 m, and an Inland Montane Forest group with samples from above elevations of ca. 700 m.

The TWINSpan analysis (see dendrogram on Fig. 3, and the preferential and indicator species of the Cloud Forest group in Table 2) largely corroborates the UPGMA results, with some minor differences. To avoid confusion with UPGMA groups, the clusters formed by TWINSpan are numbered. A group of Cloud Forests (Group 1) was formed with exactly the same surveys as the UPGMA group, but in this case Mount Cuscuzeiro sample 40B was clustered with a subgroup containing samples from Santa Catarina, Rio de Janeiro, and Minas Gerais, rather than with the Paraná forests. The Mount Cuscuzeiro 40A sample was once again included with a group of Coastal Forests (Group 2). Group 2 is very similar to the Coastal Forests group formed by UPGMA, the only differences being the inclusion of two samples from Salesópolis [48B (valley) and 48C (high slope facing the Atlantic Ocean)], that UPGMA clustered together with the other two Salesópolis surveys. The Serra da Cantareira sample (43) that UPGMA clustered with the Inland Montane Forests group was included by TWINSpan in its Coastal Forests group (Group 2). TWINSpan further subdivided Group 2 into two subgroups, (2a) containing samples from coastal plain and mountaintop forests (again, as in UPGMA), and (2b) with samples from slope forests. TWINSpan’s Group 3 corresponds to the Inland Montane Forest group formed in the UPGMA analysis, but it includes some samples of the UPGMA *Araucaria* forests group (27, 72, 83, and 12A), and two samples from Salesópolis located on the top of the mountain (48A) and on the high slope facing the inland plateau (48D). TWINSpan’s group 4 was further subdivided into 4a and 4b, the first corresponding exactly to the UPGMA Inland Seasonal Forests group, with the exclusion of a sample from Paraná (60) and the latter formed by a number of samples from São Paulo and Minas Gerais belonging to the UPGMA Inland Montane Forests group (samples 2, 5, 11, 35, 45, 47, and 50). As happened in the UPGMA clustering, TWINSpan formed a group of *Araucaria* forests

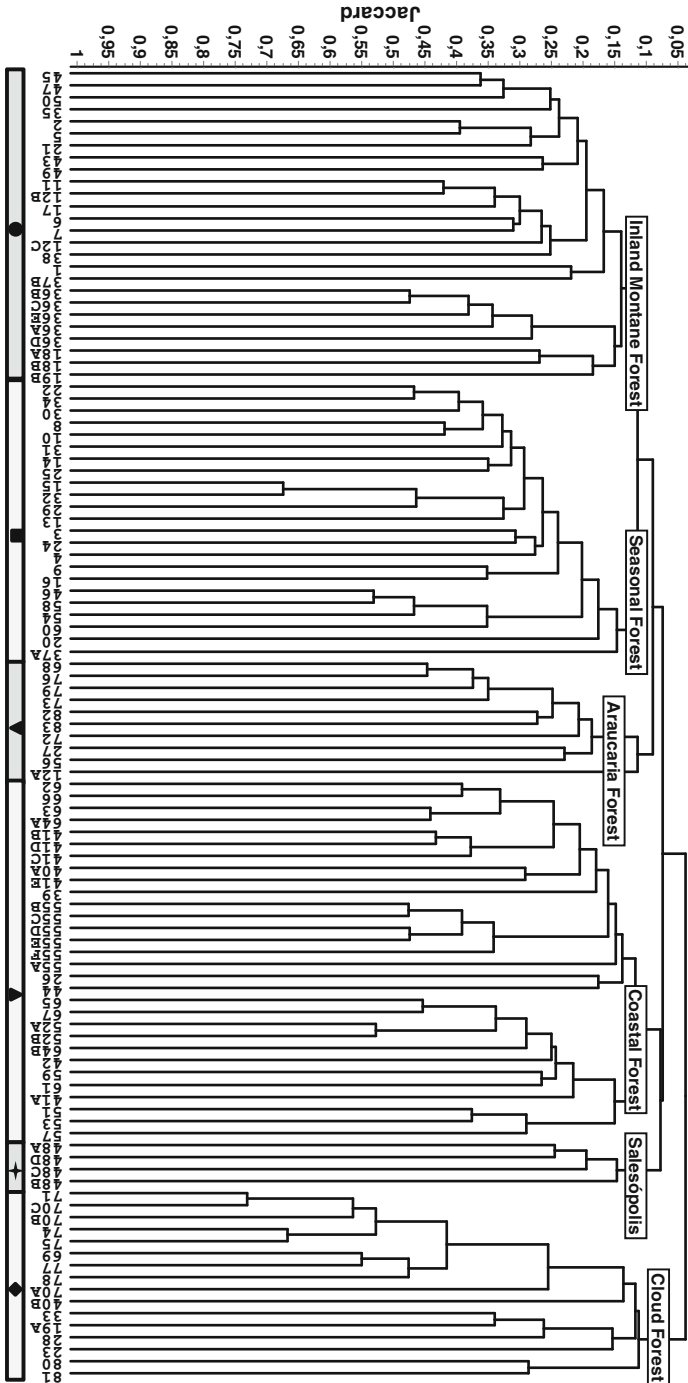


Fig. 2 Similarity analysis using Jaccard index with Group Average Clustering (UPGMA) using surveys from south and southeastern Brazil. The *symbols* used for each group are explained in Fig. 3

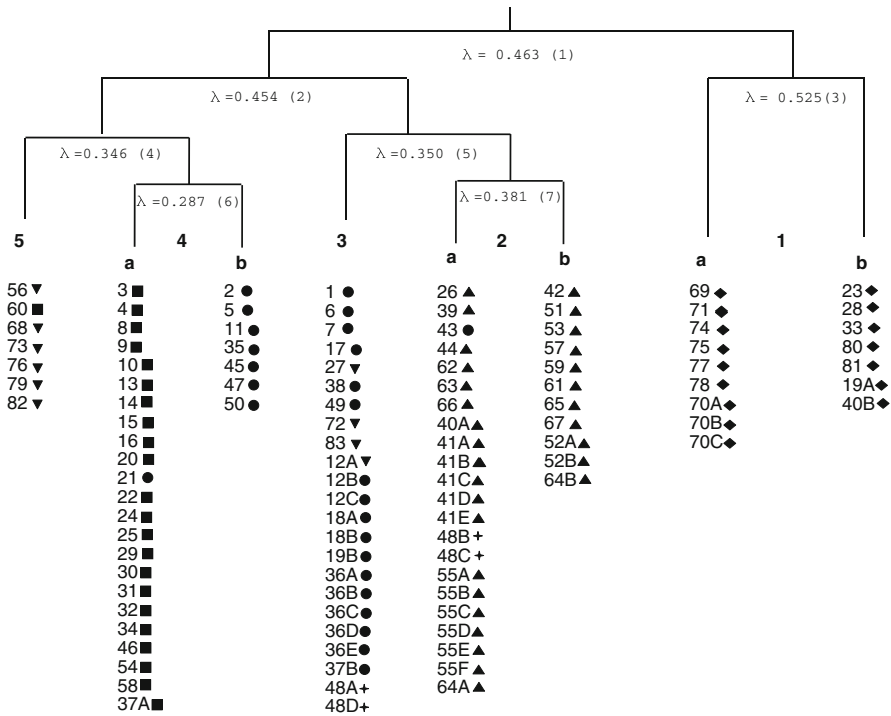


Fig. 3 Dendrogram showing groups formed by TWINSpan divisions using samples from south and southeastern Brazil. The eigenvalues are represented by λ . The numbers of each division are represented in parentheses. The symbols correspond to the groups formed by UPGMA in Fig. 2: inverted triangle Araucaria Forest; square Seasonal Forest; circle Inland Montane Forest; triangle Coastal Forest; plus Salesópolis samples; and diamond Cloud Forest

(Group 5) but included one survey from Paraná (60) that UPGMA clustered with the Inland Seasonal Forests group and excluding surveys 27, 72, 83 and 12A.

The DCA, CA and PCO analyses resulted in rather similar ordinations that largely corroborate the major groups formed by UPGMA and TWINSpan, so we opted to show only the DCA figure here because this was the one that gave the best spread of the groups, providing the best visualization (Fig. 4). The ordination analyses showed the Mount Cuscuzeiro 40B survey close to the border of the cloud forest cluster, but with some affinity with mountaintop forests of the Serra do Mar (e.g., 48A, 51 and 57), and even with samples from the coastal plain (64B, 65 and 67). Depending on the viewing angle in three dimensional images (data not shown), sample 40B appears closer to one or to another of these aggregations, which illustrates its intermediate nature and a dual floristic influence of the “core” cloud forests and the Serra do Mar mountaintop forests, but in both the UPGMA and Twinspan analyses, sample 40B, showed a higher average similarity with the cloud forest group.

Also in DCA analysis (Fig. 4), the Coastal Forest samples form a conspicuous group containing the Mount Cuscuzeiro 40A survey. However, there is some internal differentiation in this aggregation, with the mountaintop and coastal plain samples located mostly to the right of the group and closer to the Cloud Forest group. Three-dimensional representations of the DCA (not shown) made this gradient very clear, clustering all samples

Table 2 Preferential species for the Cloud Forest group formed by TWINSPAN

<i>Blepharocalyx salicifolius</i>
<i>Citronella paniculata</i>
<i>Clethra uleana</i>
<i>Drimys brasiliensis</i>
<i>Eugenia neomyrtifolia</i>
<i>Gomidesia sellowiana</i>
<i>Gordonia fruticosa</i>
<i>Ilex dumosa</i>
<i>Ilex microdonta</i>
<i>Ilex taubertiana</i>
<i>Myrceugenia alpigena</i>
<i>Myrceugenia ovata</i>
<i>Myrcia obtecta</i>
<i>Myrcia richardiana</i>
<i>Myrsine altomontana</i>
<i>Ocotea catharinensis</i>
<i>Ocotea daphnifolia</i>
<i>Persea pyrifolia</i>
<i>Pimenta pseudocaryophyllus</i>
<i>Podocarpus sellowii</i>
<i>Rhamnus sphaerosperma</i>
<i>Siphoneugena reitzii</i>
<i>Solanum sanctae-katharinae</i>
<i>Symplocos corymboclados</i>
<i>Symplocos falcata</i>
<i>Tabebuia catarinensis</i>
<i>Tibouchina reitzii</i>
<i>Weinmannia humilis</i>
<i>Weinmannia paulliniifolia</i>

The indicator species are represented in bold

from “Carlos Botelho”, a location within Serra do Mar in the state of São Paulo (55A, 55B, 55C, 55D, 55E, and 55F), on the extreme of this gradient and forming a “Carlos Botelho” subgroup.

In ordination analyses, the UPGMA Inland Seasonal Forests group also appears as a very conspicuous group (4a), but beside it, there is a small aggregation of samples (2, 5, 11, 35, 45, 47, and 50) included in the UPGMA inland Montane Forest group and in TWINSPAN subgroup 4b (Fig. 3) (forests from São Paulo and Minas Gerais), that appears midway between these two groups of forests that typically occur below and above ca. 700 m elevation, respectively.

TWINSPAN analysis excluded samples 12A, 27, 72, and 83 from the UPGMA *Araucaria* Forests group. The DCA places samples 72 (Pinhais, PR) and 83 (São Francisco de Paula, RS) close to the core of the *Araucaria* Forests aggregation, but samples 12A (Bocaina, MG) and 27 (Campos de Jordão, SP) are closer to samples of the inland Montane Forests aggregation.

The Salesópolis samples are scattered in DCA analysis. Sample 48A (mountain top) is in an intermediate position between the aggregations formed by the other mountaintop

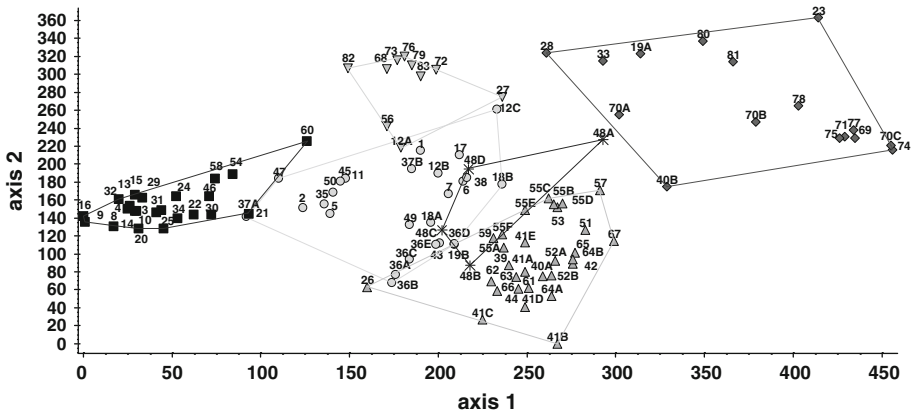


Fig. 4 Axis 1 and 2 of the DCA analysis using samples from south and southeastern Brazil. The symbols correspond to the groups formed by UPGMA in Fig. 2: inverted triangle Araucaria Forest; square Seasonal Forest; circle Inland Montane Forest; triangle Coastal Forest; plus Salesópolis samples; and diamond Cloud Forest

forests and the cloud forests; sample 48B (valley) is close to the coastal slope forests; and samples 48C (slope facing ocean) and 48D (inland facing slope) are close to the inland Montane forest samples.

In ordination analyses, the inland Montane forests did not form a tight group and were scattered near the aggregations of coastal forests, seasonal forests, and *Araucaria* forests.

Discussion

The results obtained from the analyses suggest that the two forest types encountered on Mt. Cuscuzeiro belong to two distinct groups of forests. A conspicuous group of Cloud Forests was formed in all the clustering and ordination analyses, supporting the idea of a distinct floristic and phytogeographic unit. The indicator species that separated the Cloud Forests Group from all other forest subtypes in south and southeast Brazil in the TWINSPAN analysis were *Drimys brasiliensis*, *Ilex microdonta* and *Weinmannia paulliniifolia*.

Apparently, the Paraná cloud forests form a well-defined group while another is formed by the cloud forests of Serra da Mantiqueira (MG), Aparados da Serra (SC) and Itatiaia (RJ). The position of Mount Cuscuzeiro survey 40B is not well defined between these two Cloud Forest subgroups (UPGMA and TWINSPAN point to different clusterings). Besides, survey 40B shows a moderate relationship with the non cloud forests from the top of the Serra do Mar, which may be due to their occurrence on the same geological base and to geographic and climatic proximity.

This result suggests that the higher levels of Mount Cuscuzeiro (from 1120 to the top at 1270 m) represent a distinctive formation from a biogeographic perspective. Its marked differentiation from the surrounding community (survey 40A, and also surveys 41B, 41C, 41D, and 41E from the nearby Mount Corisco, which were clustered with the Coastal Slope Forest Group) may be a consequence of historical factors responsible for the disjunct distribution of species of high-elevation areas of southern and southeastern Brazil, as suggested by Meireles (2003). Palinological records from central and southeastern Brazil

indicate that climatic changes during the Pleistocene may have had a strong impact on the distribution of species and on forest physiognomies (Joly et al. 1999). According to Ledru et al. (1998), the climate was cold and dry at the beginning of Holocene (10,000–7,000 years BP), but became humid, though still cold, at about 4,000 years BP. This fact may have led to the expansion of the *Araucaria* forests ca. 2,500 years BP in areas like Campos de Jordão in the state of São Paulo (Behling and Lichte 1997). Likewise, the cloud forests may have attained larger areas of southern and southeastern Brazil at this time, which was later diminished and restricted to higher and colder regions with particular cloud stagnation conditions, characterizing their archipelagic distribution in Neotropical region (Luna-Vega et al. 2001).

Elevation plays a major role in the distribution of tree species on Mount Cuscuzeiro. The elevation level around 1120 m that floristically separates the surveys 40A and 40B may be the critical altitude in this particular mountain for the presence of stagnant clouds, not only because this area is higher than most of the other forests sampled along the top of Serra do Mar, but also because of its closeness to the sea. But amongst the other cloud forests, the Mount Cuscuzeiro '40B' forest has the lowest elevation. The presence of a cloud forest at such a low elevation on Cuscuzeiro can be explained by the mountain mass elevation effect ('Massenerhebung effect'), according to which physiognomically and sometimes floristically similar vegetation types may occur at high elevations on large mountain masses and at lower elevations in small and isolated peaks, especially those that are in or near the sea (Flenley 1995), which is the case of Mount Cuscuzeiro. This effect may also explain why some forests from high elevation areas in the far inland state of Minas Gerais were not clustered with the cloud forests. To our knowledge, the only other study carried out on Serra do Mar in São Paulo state, at similar elevations to Mount Cuscuzeiro, is the survey made by Mantovani et al. (1990) on a mountaintop forest in Salesópolis (1200 m) (23°33'S, 45°50'W) (sample 48A), that was not grouped with the Cloud Forests groups in the clustering analyses (UPGMA and TWINSpan). But in the DCA analysis, the 48A sample sits just outside the Cloud Forests group, showing their floristic affinity. In sample 48A, we note the presence of two of the three indicator species of the TWINSpan Cloud Forest Group (*Drimys brasiliensis* and *Ilex microdonta*), which is probably why it sits close to the Cloud Forest Group. The absence of the third indicator species (*Weinmannia pauliniifolia*) and of all the preferential species (Table 2) of this group may explain why 48A is not clustered within it. This may be related to historical factors (e.g., the species never arrived there) and to the present conditions such as the local topography, the position in relation to the sea coast and/or to the main direction of winds, or to all these features together, that does not favor frequent cloud cover as much as in Mount Cuscuzeiro.

The UPGMA analysis separated the inland from the coastal forests, and this latter group into two subgroups, basically, one with the slope forests, and another with the mountaintop forests together with the coastal plain forests. This pattern is very similar to that encountered by Ivanauskas et al. (2000). Applying multivariate analyses to floristic and Phytosociological data, Scudeller et al. (2001) also discriminated the coastal forests and the Atlantic (inland) plateau forests but Oliveira-Filho and Fontes (2000), in a wide-ranging study of forests in SE Brazil, found a phylogeographic gradient, with change in floristic composition correlated with increasing penetration into the interior of the continent. This gradient corresponds to a major climatic variation in seasonality, with an increasingly long and more severe dry season further inland, responsible for the distinction between the coastal and the inland plateau forests. According to these authors, this transition is abrupt in São Paulo due to the proximity to the sea of the mountain range and the strikingly steep

descent from summit to sea level in a very short (horizontal) distance. The mountains in São Paulo are closer to the sea coast and higher when compared to other sites containing Atlantic Forests north of this state, where the transition is more gradual. A similar situation also occurs in the state of Paraná, where a block of high peaks appear close to sea coast, contrasting with the quite extensive low-lying landscape of the coast in the south of São Paulo state. It is on these high peaks that the “Paraná group” of cloud forests discriminated by the UPGMA analysis occurs.

Leitão-Filho (1982) suggested that the coastal forests from the northern and the southern halves of the coast of São Paulo state are different due to climatic differences, especially the occurrence of frost in the southern half. In contrast, Scudeller et al. (2001) indicated that there is no such a distinct north–south separation in the Atlantic Ombrophilic Dense Forest in São Paulo state, but a segregation of the arboreal flora of the coastal forests into altitudinal classes, and Ivanauskas et al. (2000) reached a similar conclusion. Our results indicate that the main floristic changes are in the transition from the coastal plain to the slope forests and from the slope forests to the top of the Serra do Mar, with North/South differentiation leading to relatively minor differences in composition of the slope forests alone.

Ivanauskas et al. (2000) found that samples from Carlos Botelho, a slope forest in the south of São Paulo state, are transitional from the coastal forests to the inland Montane (“planalto”) forests groups. Our results showed them as part of the coastal forest, but with some floristic differences from the other samples of this group, as they form a well-defined subgroup. These samples were taken within the Serra do Mar but, at their location, at about latitude 24°S, the mountain range bends inland, far from the coast, so, that the flora of this area is probably influenced by climatic conditions that are more similar to those of the “planalto” forests. The Serra da Cantareira, a forest-covered mountain range close to São Paulo city (sample 43), was also classified as a transition area by Ivanauskas et al. (2000), coinciding with our results; this was the only sample clustered by UPGMA with the Inland Montane Forests group (from above 700 m) that was included in TWINSpan group 2a (coastal Slope Forests).

It is noteworthy that sample 64A, from Pariquera-açú, state of São Paulo, south of Carlos Botelho and Intervales (Sztutman and Rodrigues 2002), was the only survey from the coastal plain that clustered with the Slope Forest samples in the UPGMA and in TWINSpan analyses. This may be explained by the fact that the sample 64A was surveyed on an isolated hill of igneous rock on the coastal plain, so that clustering with the slope forests would be expected. In fact, Sztutman and Rodrigues (2002) found this forest to be more similar to some slope forests than to other coastal plain (“restinga”) forests measured by the Jaccard Index.

Another branch of the UPGMA dendrogram that corresponds to group 2b of TWINSpan division was formed by two subgroups, one with samples from the coastal plain and the other with samples from the top of the Serra do Mar (excluding Salesópolis, which formed another cluster). Although these subgroups are distinct, as pointed out by Micheletti Neto (2007), they are related at a higher clustering level, as shown in Fig. 2 (dendrogram of UPGMA) and in Fig. 3 (TWINSpan), at least from the viewpoint of qualitative floristic data. Moreover, these groups have similar physiognomies (Micheletti Neto 2007). Otherwise, our results show that the coastal plain (“restinga”) forest is different from the nearby slope forest, as Ivanauskas et al. (2000) had already suggested. What approximates the “restinga” and the mountaintop forests remains unexplained.

The group composed of Salesópolis samples is very intriguing. Although the surveys of this group were made in the Serra do Mar, not far from the ocean, they formed a group by

themselves, located close to the Coastal Forest group in UPGMA. Scudeller et al. (2001) found these samples to be in the Atlantic (inland) plateau group (composed of inland forests from both, below and above 700 m) rather than in Coastal Forest group, as would be expected, at least for samples 48A (mountaintop), 48B (valley), and 48C (ocean facing slope). In the present study, TWINSPAN clustered samples 48B and 48C with the Coastal Forest group, while UPGMA and Complete Linkage clustering did likewise, probably due to its local moist conditions. From their location and the survey's authors' description (Mantovani et al. 1990), these samples should be in, or close to, the core Coastal Forest group. The somewhat ambiguous position of these samples and their relative isolation from what appear to be similar forests, however, remain puzzling.

Our results confirmed the floristic separation of the inland forests at elevations above about 700 m, as Torres (1989) and Salis et al. (1995) had previously found in analyses comprehending much fewer forest samples than in this study. Samples from distinct locations tend to cluster as elevation increases, explaining the patchy distribution of the inland Montane forests (from above ca. 700 m) shown by DCA (Fig. 4). Samples from the same location but from different elevation levels (above or below ca. 700 m) were separated. For instance, two samples from different elevations in the Itatiaia region, 19A and 19B, were separated between the Cloud Forests group and the inland Montane Forest; also, two samples from Serra do Japí, 37A (870 m) and 37B (1170 m) were separated between the Inland Seasonal and the Inland Montane Forests groups, as were the Cuzcuzeiro samples (40A and 40B) that showed considerable dissimilarity between geographically close sites over a short vertical distance and became separated between the Cloud Forests and the Coastal Slope Forests groups. These cases suggest that the transitions between these forest types are relatively abrupt and occur over quite limited distances and altitudinal ranges, but the nature of these transitions has not yet been investigated in detail.

The results of the multivariate analyses presented here may have been somewhat influenced by unidentified species (especially of Myrtaceae), occasional misidentification, different inclusion criteria used in the surveys, and different successional stages (often not reported by the authors of the surveys). However, the patterns presented here are very consistent and robust as they show quite similar and compatible results among the different methods applied. Our results show that cloud forests comprise a distinct phytogeographic formation from other high-elevation forests in south and southeast Brazil. This study also contributes to clarifying the broad outlines for a classification system for eastern Brazilian forests, in place of the Brazilian official classification system (Veloso 1992), which increasingly seems to be inadequate to describe the actual vegetation types found in SE Brazil (having been proposed at a time when very few quantitative vegetation studies were available in Brazil), and reinforces concepts that have already been pointed out by previous, more limited studies on the same matter. However, we feel that a proposal for a new classification system seems to be premature at this point, since some of the forest types recognized here are still inadequately sampled and details of transitional zones in many cases have not yet been investigated. We have therefore opted to use a set of informal names, until it becomes possible to construct a more adequate classification based on the greatly increased knowledge of composition and structure of forest vegetation in SE Brazil that has become available in recent years.

The proportions of the different forest subtypes and the percentage of these forests inside Protected Areas are still unclear. This is because it is not yet possible to take into account floristic and even some structural differentiations through satellite images. Besides, the limited and uneven geographic distribution of the surveys hinders extrapolations that could help discriminating the different forest subtypes.

Considering only the Cloud Forest surveys, we found that 46.1% (6 surveys) are actually in Full Protection Protected Areas (i.e., Parks or Reserves, where the vegetation is fully protected), while another 46.1% (6 surveys) are in Sustainable Use Protected Areas (i.e., Environmental Protected Area or “APA” from Área de Proteção Ambiental) and 7.7% (1 survey) is out of Protected Areas. One must take into account that the “Environmental Protected Areas” (APA) in Brazil are areas of sustainable use, meaning that no restriction exists to clear cut, other than those determined by the Atlantic Forest Law, unless it is discriminated in the management plan.

In any case, regardless of the actual protection status of the remaining patches of Cloud Forest, global warming will, or already is leading to the elevation of orographic clouds and/or increasing the rates of evapotranspiration, thus causing a double disturbance in Cloud Forests, related to both microclimatic change and the possibility of local invasion by species from lower elevation areas (Still et al. 1999). Due to the alteration of the dynamics of cloud forests, most of the species of the summits of the mountains are at risk of disappearing (Colwell et al. 2008), including many endemic species together with the forest itself (Foster 2001). The disturbance in the hydrological regime will affect a larger area than that occupied by this type of forest, reducing the amount of water in the system and changing the distribution pattern of species. In the case of the Serra do Mar forest, these changes may increase water flow on the steep slopes, causing erosion and flooding. The delimitation and mapping of different forest subtypes by floristic and structural features make it possible to monitor environmental change more accurately, which is the first step to any possible conservation action.

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