Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate[1]

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ABSTRACT

The tree flora of southeastern Brazilian Atlantic forests was investigated according to two main aspects: (a) the variations in floristic composition of both rain and semi-deciduous forests were analyzed in terms of geographic and climatic variables by performing multivariate analyses on 125 existing floristic checklists; and (b) the links of both rain and semi-deciduous forests to Amazonian forests and Cerrados (woody savanna) were assessed. All analyses were performed at the species, genus, and family levels. The information obtained for the 125 forest areas was organized into an environmental database containing geographic and climatic records, and a floristic database containing binary presence records for 2532 species, 520 genera, and 106 families. Canonical correspondence analyses (CCA) were utilized to assess the relationship between geographic and climatic variables, and tree flora composition. Venn diagrams and cluster analyses were used to assess the floristic links to Amazonian forests and Cerrados. The following patterns were detected at all three taxonomic levels: (a) the differentiation between rain and semi-deciduous forests is floristically consistent and strongly correlated with rainfall regime, although transitions may be abrupt to gradual; (b) a north–south differentiation exists for both rain and semi-deciduous forests, probably caused by variations in both temperature and rainfall regime; (c) The flora of semi-deciduous forests also changes with increasing distance from the ocean and the associated increasing rainfall seasonality; and (d) elevation and associated temperatures are strongly correlated with the internal differentiation of both rain and semi-deciduous forests. To a considerable extent, the tree flora of semi-deciduous forests is a subset of the rain forest flora, probably extracting species that are able to cope with a longer dry season. There is greater floristic similarity at the species level between Atlantic rain and semi-deciduous forests than between any of these and either Amazonian rain forests or Cerrados. Nevertheless, semi-deciduous forests and Cerrados show stronger links, particularly at the generic and familial levels. Therefore, there is little floristic ground for viewing Atlantic rain forests as being closer to their Amazonian counterparts than to the adjacent semi-deciduous forests. The most appropriate view of rain and semi-deciduous forests in southeastern Brazil is that of a continuum in tree species distribution. We suggest that the definition of Atlantic forests should be as comprehensive as that of Amazonian forests.

RESUMO

A flora arbórea das florestas Atlânticas do sudeste do Brasil é investigada sob dois aspectos principais: (a) as variações em composição florística de florestas ombrófilas e semidecíduas são analisadas sob a ótica de variáveis geográficas e climáticas por meio de análises multivariadas de 125 listagens florísticas existentes na literatura; e (b) os laços das florestas ombrófilas e semidecíduas com as florestas Amazônicas e cerrados são avaliados. Todas análises foram feitas nos níveis de espécie, gênero e família. A informação obtida para as 125 áreas de floresta foi organizada em um banco de dados ambientais, contendo registros geográficos e climáticos, e um banco de dados florísticos, contendo registros binários de presença para 2532 espécies, 520 gêneros e 106 famílias. Análises de correspondência canônica (ACC) foram utilizadas para avaliar as relações entre variáveis geográficas e climáticas e a composição da flora arbórea. Diagramas de Venn e análises de agrupamento foram utilizados para avaliar os laços florísticos com florestas Amazônicas e cerrados. Os seguintes padrões foram detectados para todos os níveis taxonômicos: (a) A diferenciação entre florestas ombrófilas e semidecíduas é floristicamente consistente e fortemente correlacionada com o regime de chuvas, embora as transições possam ser abruptas a graduais; (b) Há uma diferenciação norte-sul tanto para florestas ombrófilas como semidecíduas, provavelmente causada por variações em temperatura e regime de chuvas; (c) A flora das florestas semidecíduas também muda com a distância do oceano e o correspondente aumento da duração da estação seca; e (d) Altitude e suas correspondentes variações de temperatura são fortemente correlacionadas com a diferenciação interna tanto das florestas ombrófilas como semidecíduas. A flora arbórea das florestas semidecíduas é, em boa medida, um sub-conjunto da flora das florestas ombrófilas, provavelmente extraindo espécies capazes de enfrentar uma estação seca mais prolongada. Há mais similaridade florística, no nível de espécies, entre florestas Atlânticas ombrófilas e semidecíduas do que entre qualquer destas e as florestas Amazônicas, ou mesmo os cerrados. No entanto, florestas semidecíduas e cerrados mostram laços florísticos mais fortes, particularmente nos níveis de gênero e família. Portanto, há pouco fundamento florístico para se pensar nas florestas ombrófilas Atlânticas como mais próximas de suas correspondentes Amazônicas do que de suas vizinhas semidecíduas. A abordagem mais correta para florestas ombrófilas e semidecíduas do sudeste brasileiro é de um contínuo de distribuição de espécies. Sugerimos, portanto, que a definição de florestas Atlânticas deve ser tão abrangente quanto a das florestas Amazônicas.

Key words: Atlantic forests; Brazil; climate; multivariate analysis; phytogeography; tree flora; tropical rain forests, tropical seasonal forests.

THE BRAZILIAN ATLANTIC FORESTS ORIGINALLY COV-
ERED an area of *ca* 1.1 million km², corresponding
to 12 percent of the land surface of the country,
stretching for > 3300 km along the eastern Brazilian
coast between the latitudes of 6 and 30°S (SOS
Mata Atlântica & INPE 1993). Atlantic forests
make up the second largest tropical moist forest area
of South America, after the vast Amazonian domain.
The two forests are separated by the so-called "di-
agonal of open formations," a corridor of seasonal
and open formations that includes the semiarid Caa-
tingas of northeastern Brazil, the Cerrado (woody
savanna) of central Brazil, and the Chaco of Para-
guay–Argentina–Bolivia (Prado & Gibbs 1993). At-
lantic forests are among the most threatened tropical
forests in the world, because their range largely co-
incides with the most populated areas of Brazil
where the settlement of European pioneers and Af-
rican slaves started four centuries ago. They now are
reduced to only *ca* 5 percent of their original cover
and most remnants are either small and disturbed
fragments or wider areas sheltered on steep moun-
tain slopes (Viana & Tabanez 1996, SOS Mata At-
lântica 1998).

As might be expected for a vast and diversified
vegetation province, the Atlantic forests have been
labeled with several names and their classification
and geographic distribution are still controversial
(Leitão Filho 1987, 1993; Camara 1990). The ac-
ademic discord about the inland extent of Atlantic
forests became a bitter political dispute after they
were granted strict legal protection by the 1988 Bra-
zilian Constitution and declared a Biosphere Reserve
by UNESCO. Fixing inland limits to the Atlantic
forests, however, is no easy task, since their transition
to the hinterland open formations is very complex
and more or less gradual. This transition can be
classified into three regions according to the adjacent
open formation.

A relatively abrupt transition to the semiarid
Caatingas occurs in northeastern Brazil where a nar-
row strip (<50 km) of coastal rain forests is bor-
dered by an equally narrow inland belt of seasonal
semi-deciduous forests, which also occurs as hinter-
land montane forest enclaves, the brejos (Andrade-
Lima 1982). The transition between coastal rain for-
ests and Cerrados in southeastern Brazil involves a
much larger extent of semi-deciduous forests that
becomes increasingly wider toward the south and
forms complex mosaics with Cerrado vegetation to
the west (Fig. 1). These semi-deciduous forests also
stretch southward along the Paraná River basin into
eastern Paraguay and northeastern Argentina where
they are transitional to the Chaco. In this subtropical

region, large extents of *Araucaria* mixed forests sep-
arate the coastal rain forests and the western semi-
deciduous forests.

The many definitions of Atlantic forests found
in the literature can be classified into two main views
that we call here *sensu stricto* (ss) and *sensu lato* (sl).
Strictly speaking, Atlantic forests (ss) comprise only
the coastal rain forests up to 300 km inland, where
rainfall is locally boosted by oceanic winds and sea-
side mountain ranges, particularly in the south. This
is the most traditional and widespread definition of
Atlantic forests since Azevedo (1950) coined the
term Mata Atlântica. For instance, the IBGE clas-
sification system for Brazilian vegetation (Veloso *et
al.* 1991) includes all Atlantic forests in the category
"dense rain forest," along with most Amazonian for-
ests. Some authors have suggested that the physi-
ognomic similarity between Amazonian and Atlantic
rain forests would show corresponding strong floris-
tic links reinforced by numerous disjunct species
(Rizzini 1963, Andrade-Lima 1964, Mori *et al.*
1981).

For Atlantic forests (ss) supporters, the neigh-
boring semi-deciduous forests are a distinct vegeta-
tion formation, often called matas de planalto (pla-
teau forests), due to their distribution on the hin-
terland highlands. Cabrera and Willink (1973)
raised this differentiation to the biogeographic level,
merging the semi-deciduous forests of the Paraná
River basin with the *Araucaria* mixed forests to con-
stitute the Paranense Biogeographic Province. The
flora of semi-deciduous forests is considered as either
transitional between that of rain forests and Cerra-
dos (*e.g.*, Leitão Filho 1987) or part of a continuum
of forest species distribution that includes central
Brazilian gallery forests that eventually links Atlantic
to Amazonian forests (Oliveira-Filho & Ratter
1995).

The broad view of Atlantic forests (sl) attaches
semi-deciduous forests and *Araucaria* mixed forests
to coastal rain forests, pushing the limits of the do-
main up to 700 km inward from the coast (Fernan-
des & Bezerra 1990). This definition largely corre-
sponds to the first attempt to classify Brazilian veg-
etation (von Martius 1840), which named all eastern
extra-Amazonian forests Dryads. To avoid misun-
derstandings caused by the long-term association be-
tween rain forests and Atlantic forests, authors
adopting the broad view usually added the adjective
"moist" to encompass both rain and semi-deciduous
forests (*e.g.*, Viana *et al.* 1997). This definition of
Atlantic forests has recently become widespread in
the literature, although it was caused less by a chang-
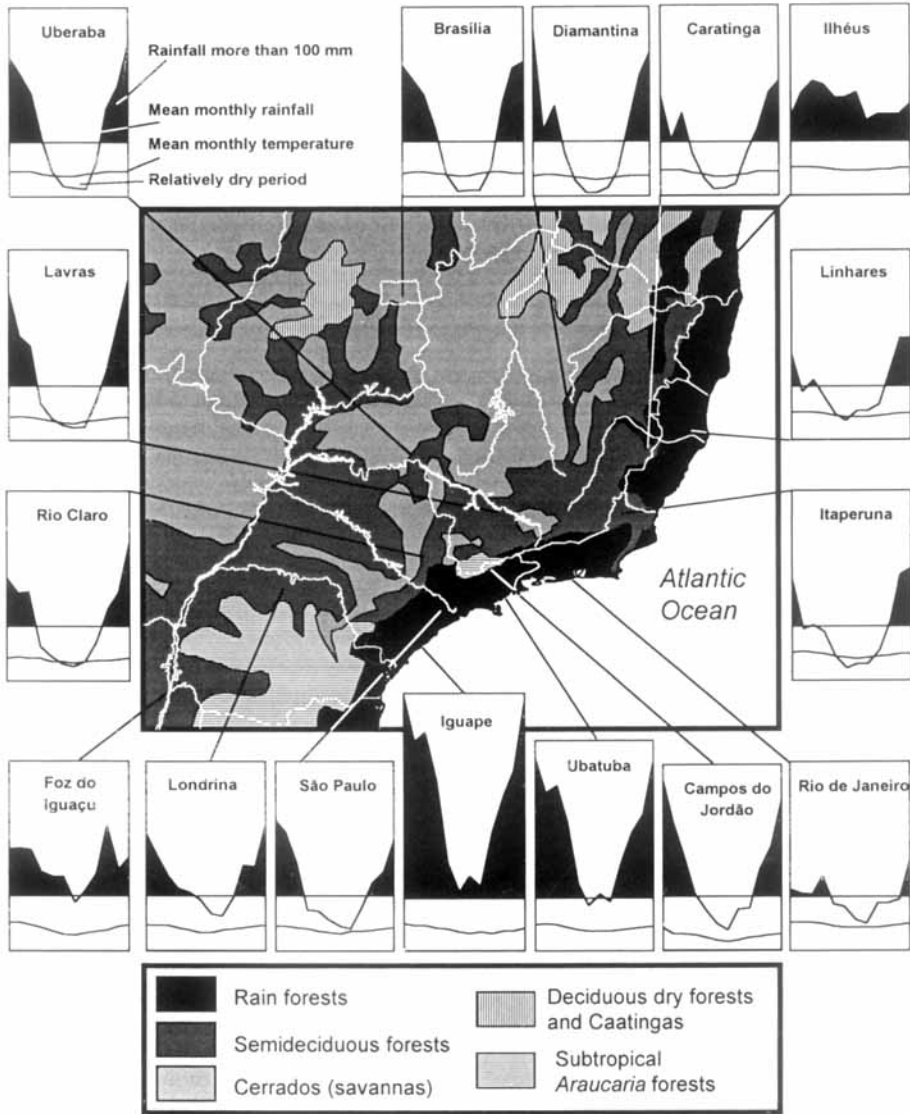ing scientific approach than by the current policies

FIGURE 1.   Map of southeastern Brazil showing the predominant vegetation formations, adapted from IBGE (1993), and Walter climatic diagrams for selected localities.

of both environmental conservation and research funding. Sound quantitative assessments of floristic variation in Atlantic forests (sl), in association with underlying environmental factors, are important to understanding the geographic patterns of these forests for both scientific and conservation purposes.

We sought patterns of floristic differentiation among Atlantic forests (sl) that could be associated with geographic and climatic variables, and assessed the floristic links among Atlantic forests (both rain and semi-deciduous), Amazonian forests, and Cer-

rados. We chose the arboreal component and focused on southeastern Brazil (transition to Cerrados) due to data availability, and because we believed that the three scenarios of transition to open formations required separate analyses. We addressed the following questions: (a) is the traditional treatment of coastal Atlantic rain forests as the only Atlantic forests consistent in terms of floristic composition; *i.e.,* how strongly differentiated are semi-deciduous and rain forests?; (b) to what extent is the tree species composition of semi-deciduous forests transitional

between those of rain forests and Cerrados?; (c) are coastal Atlantic rain forests closer to Amazonian rain forests in terms of floristic composition than they are to neighboring semi-deciduous forests?; (d) do both rain and semi-deciduous forests change their floristic composition with the climatic variations occurring within their range?; are rainfall regime and elevation as important for floristic patterns as they are for traditional physiognomic classification systems?; and (e) how are the above questions answered at the species, genus and family levels?

The major patterns emerging from our analyses add an important contribution to discussion of the floristic composition of Atlantic forests. In addition, the results also contribute information on the patterns of plant species diversity and distribution in the region, which is important for planning research and conservation policies.

METHODS

FLORISTIC, GEOGRAPHIC, AND CLIMATIC DATA.—We selected from the literature a total of 144 floristic checklists produced by surveys of the tree flora in 125 areas of the Atlantic Forest (sl) in southeastern Brazil (contact authors for data). The geographic range was defined between the eastern Brazilian coast and 55° longitude, and between 14°00′ and 26°30′S latitude (Fig. 2). Vegetation physiognomies included coastal rain forests and semi-deciduous forests, both coastal and hinterland. Forest areas of edaphic climax were not included (e.g., those on coastal sand dunes, swamps, and calcareous outcrops). Survey methods varied widely: most authors used plot or plotless (PCQ) sampling; only six surveys were based on intensive collecting of plant specimens; and many combined both procedures. Forest areas were defined arbitrarily within a maximum range of 20 km width and 150 m elevation, including sections of large continuous forest tracts (e.g., Uba, Prd), assemblages of forest fragments (e.g., Viç, Ter), and areas separated by altitude (e.g., P1-P2-P3, Itt-Vma). A few areas with greater elevational range (e.g., Mci) required consulting the authors about the predominant altitude of plant collecting activities. We obtained the following geographic information for each area: latitude and longitude at the center of the area, median altitude, and shortest distance from the ocean. We also extracted from the literature the annual and monthly means for the temperature and rainfall of each forest area or the nearest meteorological stations. When the same source of the checklist did not provide the climatic records, they were

obtained from DNMet (1992). Most areas required interpolation and/or standard correction for altitude (Thorntwaite 1948). We obtained the "mean duration of the dry season" for each area from the number of days of water shortage given by Walter diagrams (Walter 1985). We also calculated a "rainfall distribution ratio" from the proportion between the mean precipitation of the dry (June–August) and rainy (December–February) seasons. Summarized information for the 125 areas is available from author upon request.

CLASSIFICATION OF THE FOREST AREAS.—Traditional classification systems for Brazilian vegetation (e.g., IBGE System; Veloso et al. 1991) usually classify forest physiognomies based essentially on rainfall regime and temperature, the latter inferred from latitude and altitude. To assess this approach from the floristic perspective, we classified the 125 forest areas as either rain forests or semi-deciduous forests, and divided them into four elevational classes, resulting in eight main forest formations (Fig. 2). Areas north of 23°20′S (tropical climates) or above 700 m (mountain climates) were classified as rain forests in which the dry season lasts for 30 days or less; others (40–160 days) were semi-deciduous forests, following Borhidi (1991). Areas situated south of 23°20′S and below 700 m (non-montane subtropical climates) were classified as semi-deciduous and rain forests with total annual rainfall between 1500 and 2000 mm and 2000 and 3600 mm, respectively (moist and wet subtropical forests of Holdridge et al. [1971]). The elevational categories were: lowland, <300 m; submontane, 300–700 m; lower montane, 700–1100 m; and upper montane, >1100 m. The classification criteria were arbitrary and not intended to represent any objective limit between forest formations; however, the geographic distribution of the classified areas coincided almost perfectly with the vegetation units of the map produced by IBGE (1993; compare Figs. 1 and 2).

PREPARATION AND REVISION OF THE DATABASES.—We entered the information from the 125 checklists onto spreadsheets using Microsoft Excel 97 in order to produce two databases. The first consisted of basic information about each area—forest formation, geographic coordinates, median altitude, distance from the ocean, annual and monthly means for temperature and rainfall, mean duration of dry season, rainfall distribution ratio, and literature source. The second database was essentially a matrix of tree species presence in the 125 forest areas. Before reaching its final form, the information contained in this da-
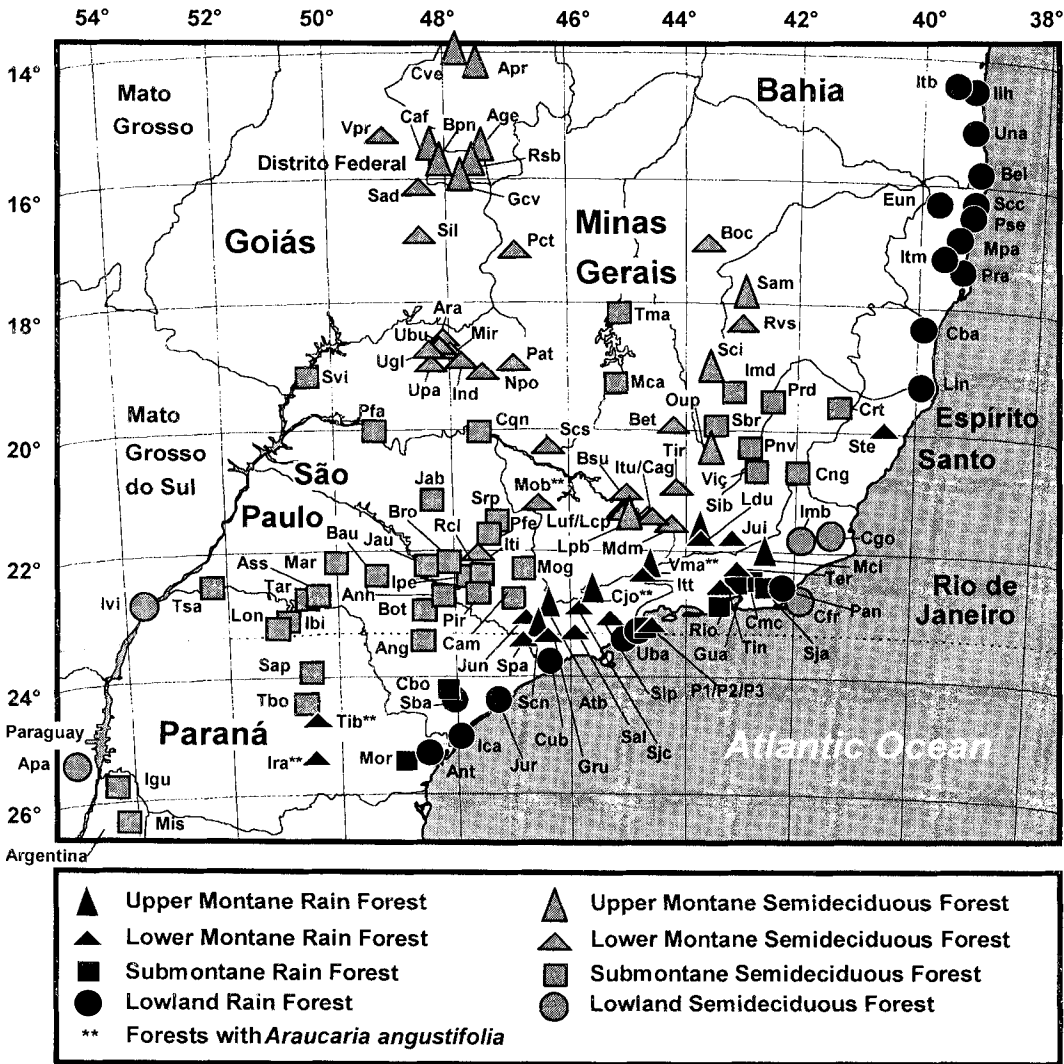
FIGURE 2.   Map of southeastern Brazil showing the location of the 125 areas of Atlantic Forest used in the floristic analyses. The forest areas are identified by three-letter codes (contact authors for details), and classified as either rain or semi-deciduous forest, and into four elevational categories: lowland, <300 m; submontane, 300–700 m; lower montane, 700–1100 m; and upper montane, >1100 m.

tabase underwent a detailed revision to check all species names cited in the checklists for synonymy and geographic distribution. This task required consulting 337 monographs and revisions, as well as specialists from the Universities of São Paulo, Campinas, Rio de Janeiro, Belo Horizonte, and Brasília, and the Botanical Gardens of Rio de Janeiro, São Paulo, Kew, New York, and Missouri. When the monographs referred to herbarium specimens unequivocally collected in any of the 125 areas, the species was added to the database. The final database contained 2532 species, 520 genera, and 106 fami-

lies. To compare the tree flora of southeastern Brazilian Atlantic forests to that of Amazonian rain forests and Cerrados, we analyzed two additional databases. The first was extracted from Oliveira-Filho and Ratter (1994) and consisted of 22 areas of terra firme (upland) Amazonian rain forests that contained 1530 species. The second consisted of 98 areas of Cerrado (Ratter et al. 1996) that included 528 species. We also derived databases containing the number of species per genus and family in each of the 125 forest areas, as well as in the Amazonian forests and Cerrado checklists.

MULTIVARIATE ANALYSES.—We used canonical corre-
spondence analysis, CCA (ter Braak 1987, 1995)
processed by the program PC-ORD 3.0 (McCune
& Mefford 1997) to investigate the relationships be-
tween tree flora and geographic and climatic (here-
after geo-climatic) variables of the 125 forest areas.
CCA seeks patterns of data structure from a matrix
of floristic records correlated to a set of variables
provided by an environmental matrix. We prepared
floristic matrices at three taxonomic levels—species,
genus, and family. The species matrix consisted of
binary data of species presence per forest area and
included the 1002 species present on five or more
areas. The generic matrix was comprised of the
number of species per genus in the 125 forest areas
and contained all 520 genera. The familial matrix
consisted of the number of species per family in the
125 forest areas and incorporated all 106 families.
The patterns emerging from each of these floristic
matrices were related by CCA to 13 variables con-
tained in a geo-climatic matrix. These were the geo-
graphic variables: (a) latitude; (b) longitude; (c) me-
dian altitude; (d) distance from the ocean and the
climatic variables (e) mean annual temperature and
mean monthly temperatures in (f) July and (g) Jan-
uary; (h) mean temperature range (January–July); (i)
mean annual rainfall and mean monthly rainfall of
the (j) dry (June–August) and (k) rainy (December–
February) seasons; (l) rainfall distribution ratio; and
(m) mean duration of the dry season. After prelim-
inary analyses, six variables were eliminated due to
either high redundancy (variance inflation factor
>20) or poor correlation (intra-set correlations with
axes 1, 2, or 3 <0.4). The eliminated variables were:
(a) longitude, highly redundant with distance from
the ocean; (b) latitude, poorly correlated with the
axes; and the monthly temperatures (f, g) and season
rainfall (j, k), all redundant with the respective an-
nual means. The Monte Carlo permutation test was
performed to assess the significance of the correla-
tions found.

CONDENSED FLORISTIC DATA.—Because the CCAs
demonstrated that the forest classification system
adopted was highly consistent, we eventually con-
densed the floristic information contained in the da-
tabases by clustering the records within main forest
formations; however, as the CCAs also detected an
additional north–south differentiation for rain and
semi-deciduous forests of lower altitudes and an
east–west pattern for semi-deciduous forests, the re-
spective subcategories were split accordingly. A con-
secutive upper level clustering operation, with both
rain and semi-deciduous forests, merged lowland

and submontane forests as "low altitude forests,"
and lower and upper montane forests as simply
"high altitude forests." We used the condensed data
to perform a direct quantitative assessment of the
floristic links between the forest formations by plot-
ting the number of shared and exclusive species in
Venn diagrams. We also performed hierarchical clas-
sifications (Kent & Coker 1992) of the condensed
matrices using the program PC-ORD 3.0. Cluster
analyses used Sorensen distances for species presence
data and euclidian distances for genera and families
(number of species as abundance data); the linkage
method was group average. A TWINSPAN analysis
of the condensed species matrix was performed to
identify indicator species for the forest formations.
The genera and families with the highest number of
species in each forest formation were extracted from
the matrices.

RESULTS

MULTIVARIATE ANALYSES.—CCA results for the three
taxonomic levels are summarized in Table 1. Eigen-
values were relatively high for species (>0.3), indi-
cating considerable species turnover along the gra-
dients summarized in axes 1 and 2. On the other
hand, they were increasingly small for genera and
families (<0.2), indicating "short" gradients (i.e,
there were large proportions of genera and families
occurring throughout the gradients, varying essen-
tially in abundance; ter Braak 1995). The cumula-
tive percentage variances accounted for by CCA axes
were also small, indicating that considerable "noise"
remained unexplained. As might be expected for
higher and more widely distributed taxa, the per-
centage variance was higher for families (i.e., the
"noise" was lower). Small eigenvalues and low ex-
plained variances are normal in vegetation data and
do not impair the significance of taxa–environment
relations (ter Braak 1988). In fact, Pearson's corre-
lations for taxa–environment were consistently high.
In addition, Monte Carlo permutation tests indicat-
ed that taxa data and geo-climatic variables were sig-
nificantly correlated for the first three canonical axes
of all ordinations.

    The first canonical axis in the species ordination
was correlated best with distance from the ocean,
followed by rainfall distribution ratio, altitude and
duration of the dry season (Table 2). Also, duration
of the dry season was highly correlated with distance
from the ocean (positively) and rainfall distribution
ratio (negatively). This indicates that the data struc-
ture summarized by the first axis primarily reflected
a geographic gradient based on penetration into the

TABLE 1.   *Summary of canonical correspondence analyses (CCAs) and Monte Carlo permutation test of the tree flora and geo-climatic variables for 125 areas of the Atlantic Forest performed for binary data of species presence, and for genera and families using the number of species as abundance data.*

	Axis 1	Axis 2	Axis 3
Eigenvalue (species)	0.405	0.290	0.180
Cumulative percentage variance of species presence data	6.4	10.9	13.7
Pearson's correlation for species–environment	0.954	0.934	0.829
Significance of species–environment correlation (Monte Carlo test)	0.01	0.01	0.01
Eigenvalue (genera)	0.200	0.138	0.092
Cumulative percentage variance of genera abundance data	6.4	10.9	13.8
Pearson's correlation for genera–environment	0.933	0.917	0.784
Significance of genera–environment correlation (Monte Carlo test)	0.01	0.01	0.05
Eigenvalue (families)	0.081	0.046	0.028
Cumulative percentage variance of families abundance data	10.5	16.4	20.0
Pearson's correlation for families–environment	0.886	0.822	0.741
Significance of families–environment correlation (Monte Carlo test)	0.01	0.01	0.01

continent's interior which corresponded to a major climatic gradient (*i.e.,* an increasingly longer dry season). Altitude, another important geographic gradient in the first canonical axis, was highly and negatively correlated with both annual temperature and rainfall seasonality. The second canonical axis had stronger correlations with annual temperature and temperature range. The CCA for genera showed correlation patterns very similar to those found for species, although inverting the relative weight of some variables on the first two axes. Unlike the former ordinations, the CCA for families related the distance from the ocean and rainfall variables to axis 2, and altitude and temperature variables to axis 1.

The relationship between the geo-climatic variables and the species composition of the 125 forest areas is illustrated by the CCA biplot in Figure 3. The application of the forest classification categories to the ordinated areas helped the interpretation of the biplot. The dichotomy between rain and semi-deciduous forests appears as a diagonal perpendicular to the arrow of distance from the ocean. Toward the right side of the diagram, the pattern summarized for rain forests (closed symbols) involves decreasing altitude and temperature range, and increasing annual temperature and rainfall distribution uniformity. Lower and upper montane rain forests are clearly discriminated at the top of the diagram. The areas of low altitude rain forests are found in two distinct groups: the northern group (bottom-right) composed of the areas in Bahia and Espírito Santo, and the southern group (top right), which includes the areas in Rio de Janeiro, São Paulo, and Paraná. The rainiest areas of coastal São Paulo and Paraná, all with annual rainfall > 2000 mm, are more clear-

ly discriminated in axis 3 (not shown), which is strongly correlated with annual rainfall.

Three main patterns are summarized for semi-deciduous forests (open symbols) on the CCA biplot (Fig. 3). The areas of coastal lowland semi-deciduous forests of northern Rio de Janeiro (Cfr, Cgo, Imb) appear on the bottom right, not far from the northern lowland rain forests, and are highly correlated with elevated temperatures. They are followed toward the center left by the submontane semi-deciduous forests of the Rio Doce basin in eastern Minas Gerais (Prd, Crt, Cng, Viç, Pnv, Imd, Sbr), all of northern distribution. Most submontane semi-deciduous forests of southern distribution (São Paulo and Paraná) appear on the center-left of the diagram and are followed toward the left by lower and upper montane semi-deciduous forests. The strongly seasonal areas of western distribution (Goiás, Distrito Federal, northern São Paulo, and western Minas Gerais) are accommodated on the bottom left of the diagram and also show an altitudinal gradient.

As happened with the CCA for species, the same forest groups are distinguished in the biplots yielded by the CCAs for genera and families (Fig. 4). This made clear that the same geographic and climatic variables underlie the floristic patterns at all three taxonomic levels. The ordination of species, genera, and families by CCA is not shown in Figures 3 and 4 because the biplots would be crowded by countless taxa dots.

ANALYSES OF CONDENSED FLORISTIC INFORMATION.— As they were extracted from floristic checklists for particular forest areas, the condensed information must be regarded as a means of quantitatively as-

TABLE 2. Canonical correspondence analyses (CCAs) of the tree flora and geo-climatic variables for 125 areas of the Atlantic Forest performed for binary data of species presence, and for genera and families using the number of species as abundance data: intra-set and inter-set correlations for the first two ordination axes, and weighted correlation matrix for the geo-climatic variables supplied. Correlations with absolute values ≥0.5 are enhanced in bold.

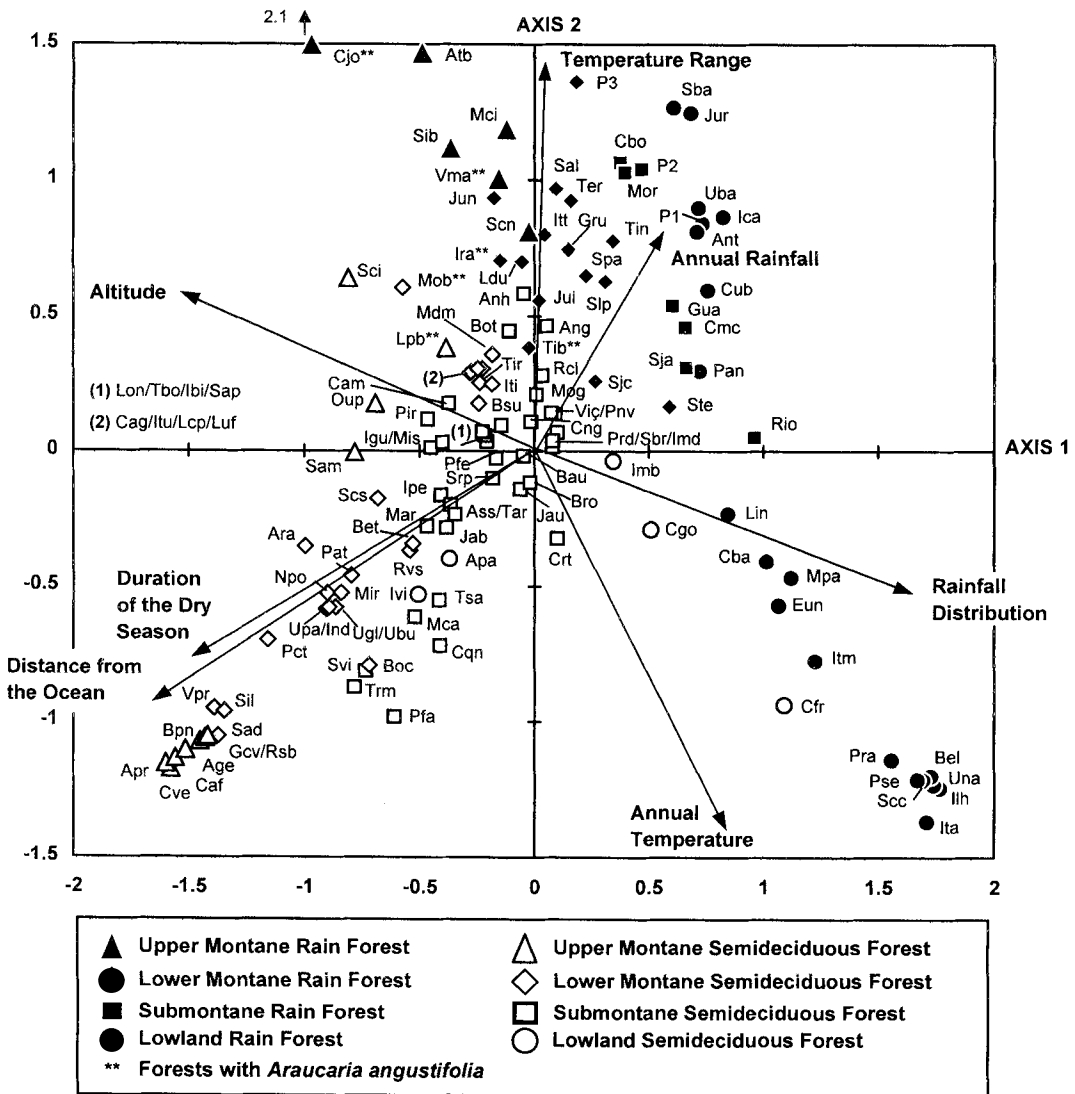| Geo-climatic variables	Intra-set correlations Axis 1	Intra-set correlations Axis 2	Inter-set correlations Axis 1	Inter-set correlations Axis 2	Geo-climatic variables Altit.	Dist. ocean	Ann. temp.	Temp. range	Ann. rainf.	Rainf. distr.
CCA for species:										
Altitude	**-0.76**	0.31	**-0.72**	0.29	—					
Distance from the ocean	**-0.82**	**-0.50**	**-0.78**	-0.47	0.41	—				
Annual temperature	0.42	**-0.75**	0.40	**-0.70**	**-0.77**	0.06	—			
Temperature range	0.06	**0.75**	0.06	**0.71**	0.08	-0.35	-0.49	—		
Annual rainfall	0.28	0.43	0.27	0.40	-0.17	-0.27	-0.11	0.26	—	
Rainfall distribution ratio	**0.81**	-0.29	**0.78**	-0.27	**-0.62**	-0.47	0.40	-0.03	0.18	—
Duration of dry season	**-0.73**	-0.41	**-0.70**	-0.38	0.35	**0.72**	0.07	-0.39	-0.44	**-0.65**
CCA for genera:										
Altitude	**-0.88**	0.16	**-0.82**	0.15	—					
Distance from the ocean	**-0.53**	**-0.74**	**-0.50**	**-0.68**	0.42	—				
Annual temperature	**0.76**	**-0.57**	**0.71**	**-0.52**	**-0.80**	0.02	—			
Temperature range	-0.34	0.44	-0.32	0.40	0.13	-0.31	**-0.51**	—		
Annual rainfall	0.09	**0.56**	0.08	**0.51**	-0.15	-0.27	-0.11	0.26	—	
Rainfall distribution ratio	**0.83**	0.18	**0.77**	0.16	**-0.63**	-0.48	0.44	-0.10	0.17	—
Duration of dry season	-0.46	**-0.68**	-0.43	**-0.62**	0.35	**0.73**	0.04	-0.35	-0.44	**-0.63**
CCA for families:										
Altitude	**0.82**	-0.49	**0.72**	-0.40	—					
Distance from the ocean	-0.10	**-0.78**	-0.09	**-0.66**	0.42	—				
Annual temperature	**-0.95**	0.17	**-0.84**	0.14	**-0.80**	0.02	—			
Temperature range	0.41	-0.03	0.37	-0.03	0.13	-0.31	**-0.51**	—		
Annual rainfall	0.26	**0.58**	0.23	0.48	-0.15	-0.27	-0.11	0.26	—	
Rainfall distribution ratio	-0.39	**0.71**	-0.35	**0.59**	**-0.63**	-0.48	0.44	-0.10	0.17	—
Duration of dry season	-0.12	**-0.78**	-0.11	**-0.64**	0.35	**0.73**	0.04	-0.35	-0.44	**-0.63**

FIGURE 3. Biplot yielded by canonical correspondence analysis showing the ordination of 125 areas of Atlantic Forest on the first two axes, based on the presence of 1002 tree species, and their correlation with geo-climatic variables, shown as arrows (scaled 2.5 × for clarity). Forest areas are identified by their three-letter codes (Fig. 2) and forest formations are indicated by symbols.

sessing the floristic links between the main forest formations and not as actual figures for number of species, either total or in common.

The Venn diagrams in Figure 5 give a direct assessment of the composition and patterns for the tree flora in some main Atlantic Forest formations. It is evident from the first diagram that the flora of rain forests is much richer in tree species than that of semi-deciduous forests. Rain forests had 31 percent more species than semi-deciduous forests, although they were represented by a smaller number

of surveyed areas. It is also clear that rain and semi-deciduous forests shared a high proportion of tree species: 50 and 66 percent, respectively. Furthermore, the proportion is higher on the semi-deciduous side, suggesting that their arboreal flora is, to a great extent, a fraction of the much richer rain forest flora.

The second and third Venn diagrams in Figure 5 show the distribution of the number of species on two altitudinal classes of both rain and semi-deciduous forests, the latter also showing the relationship
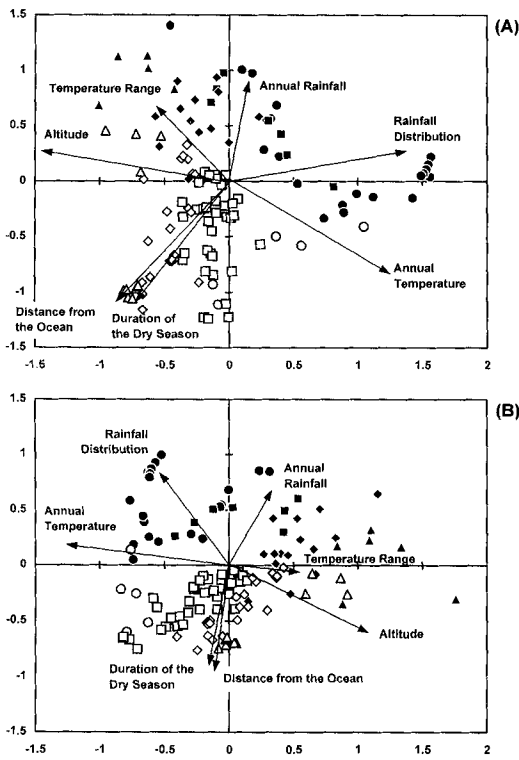
FIGURE 4. Biplots yielded by canonical correspondence analyses showing the ordination of 125 areas of Atlantic Forest on the first two axes based on the number of tree species per genus (A) and family (B), and their correlation with geo-climatic variables, shown as arrows (scaled 2.5 × for clarity). Forest areas are identified by their three-letter codes (Fig. 2) and forest formations are indicated by symbols (see Fig. 3).

FIGURE 5. Venn diagrams showing the number of tree species shared by 125 areas of Atlantic forest, merged into main Atlantic Forest formations, 22 areas of Amazonian Rain Forests, and 98 areas of Cerrado. N = number of checklists; S = number of species.

to the western forests. Although the total number of species decreased with altitude in both cases, the number of surveyed areas also decreased, and this may have accentuated the decline. The proportion of species shared by the two altitudinal classes was similar: 37 and 35 percent for rain and semi-deciduous forests, respectively. Western semi-deciduous forests shared 63 and 59 percent of species with low and high altitude semi-deciduous forests.

The fourth and fifth Venn diagrams strongly reinforce the differentiation between the northern (Bahia, Espírito Santo, and eastern Minas Gerais) and southern (Rio de Janeiro, São Paulo and Paraná) sections of both low altitude rain and semi-deciduous forests. They shared only 26 and 33 percent of the species, while northern rain and semi-deciduous forests shared 29 percent (sixth diagram) and southern rain and semi-deciduous forests shared 24 per-

cent (seventh diagram) of the species. Therefore, the differentiation between northern and southern groups of the same forest formation were apparently of a similar magnitude in terms of the differentiation between different formations within the same geographic region.

Cerrados shared a much larger proportion (55%) of their flora with Atlantic forests than did Amazonian forests (20%; eighth and ninth diagrams). Also, the Cerrado flora was much more closely related to Atlantic semi-deciduous forests than to the Atlantic rain forests, while the species shared with Amazonian forests were distributed more evenly.

The classification dendrograms (Fig. 6) show some common patterns for the three taxonomic levels. Most rain and semi-deciduous Atlantic forests tend to cluster together. The flora of both Cerrado and Amazonian forests were highly differentiated
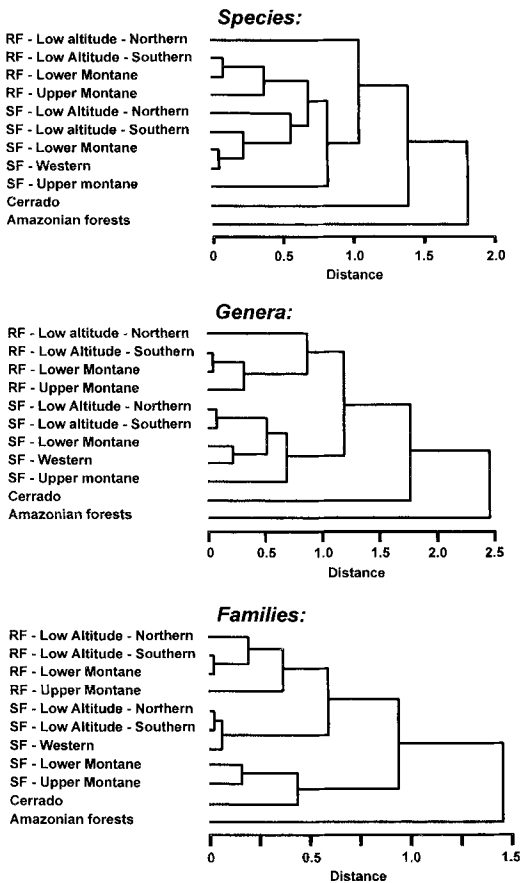
FIGURE 6. Dendrograms from group averaging of Sørensen's floristic similarity for species and squared euclidian distances for genera and families of the arboreal flora of 125 areas of Atlantic Forests, merged into nine main forest formations, 23 areas of Amazonian Forests, and 98 areas of Cerrado. RF = rain forests; SF = Semi-deciduous Forests. Distance on the dendrogram scale is Wishart's objective function, not a raw dissimilarity measure.

from the Atlantic forests at the species and generic levels. At the familial level, however, Cerrado merged at a low level with montane semi-deciduous forests, while Amazonian forests remained drastically separated.

The most important genera and families of each main forest formation are given in Tables 3 and 4, and a selection of indicator species given by TWIN-SPAN for some formations is provided in Table 5. The frequency of these species or the relative abundance of some genera and families in a survey may help classify the forest area and allow inferences about the local climate. Some interesting trends can be observed with increasing altitude in the five main Atlantic Forest formations (Table 3). The relative

importance decreased for some genera such as *Marlierea, Pouteria, Trichilia, Erythroxylum, Swartzia, Ficus,* and *Machaerium,* and increased for others such as *Miconia, Mollinedia, Nectandra, Myrsine, Tibouchina, Solanum, Ilex,* and *Gomidesia.* The same happened with some families: the relative importance of Sapotaceae, Chrysobalanaceae, Rutaceae, and Moraceae decreased, while that of Melastomataceae, Compositae, Solanaceae, and Myrsinaceae increased with increasing altitude. Western semi-deciduous forests apparently combine elements of both low and high altitude.

The rank of genera and families with the highest number of species given in Table 4 reinforces the patterns shown in the dendrograms. A few genera and families showed marked differences in their rank position between Atlantic rain and semi-deciduous forests (*e.g., Pouteria, Gomidesia, Ilex, Machaerium,* Sapotaceae, and Chrysobalanaceae). Many genera ranked high in both Atlantic forests were less important either in Cerrado (*e.g., Ocotea, Inga, Ficus,* and *Trichilia*) or Amazonian rain forests (*e.g., Myrcia, Inga, Machaerium,* and *Solanum*). Likewise, important families in Atlantic forests were ranked in a lower position in Cerrados (*e.g.,* Lauraceae and Euphorbiaceae) and Amazonian rain forests (*e.g.,* Melastomataceae and Myrtaceae). In addition, Cerrado had particularly important genera (*e.g., Byrsonima, Kielmeyera, Vochysia,* and *Alibertia*) and families (*e.g.,* Malpiphiaceae and Vochysiaceae). The same is observed in Amazonian forests for some genera (*e.g., Licania, Protium, Eschweilera, Virola,* and *Mouriri*) and families (*e.g.,* Sapotaceae, Chrysobalanaceae, Burseraceae, and Lecythidaceae). An important link between Amazonian and Atlantic rain forests, however, lies in the numerous species of Sapotaceae and Chrysobalanaceae, and in the higher diversity of Lecythidaceae, compared to semi-deciduous forests.

DISCUSSION

Most floristic patterns and their correlation with geo-climatic variables, particularly rainfall seasonality and temperature, were consistent at all three taxonomic levels, suggesting that these factors have had a long time influence on the evolution and speciation of tree taxa in southeastern Brazil. This was not a surprise because rainfall and temperature are the chief factors determining the distribution of the world's vegetation formations, and the history of vegetation and climate in southeastern Brazil during the Quaternary shows dramatic shifts in both temperature and rainfall regime (Ledru 1993, Ledru et al. 1998).

TABLE 3. *Genera and families with the highest number of species (S) on the tree flora for 102 areas of the Atlantic Forest classified into five main forest formations. N = number of areas.*

	Rain forests (N = 48)				Semi-deciduous forests (N = 77)					
	Low altitude (N = 27)	S 1475	High altitude (N = 21)	S 1280	Low altitude (N = 36)	S 1124	High altitude (N = 16)	S 709	Western (N = 25)	S 699
	Eugenia	70	Eugenia	73	Eugenia	44	Miconia	26	Miconia	25
	Myrcia	37	Miconia	48	Ocotea	32	Myrcia	24	Eugenia	19
	Ocotea	36	Ocotea	40	Myrcia	26	Ocotea	22	Ficus	14
	Miconia	35	Myrcia	32	Miconia	25	Eugenia	16	Myrcia	14
	Pouteria	26	Mollinedia	27	Machaerium	21	Inga	11	Machaerium	12
	Marlierea	22	Inga	24	Ficus	19	Ilex	10	Aspidosperma	11
	Erythroxylum	21	Solanum	21	Inga	15	Nectandra	10	Inga	10
	Inga	20	Gomidesia	17	Casearia	14	Tabebuia	9	Erythroxylum	9
	Licania	19	Tibouchina	16	Maytenus	12	Tibouchina	9	Casearia	9
	Ficus	19	Psychotria	16	Erythroxylum	12	Trichilia	9	Nectandra	9
	Tibouchina	18	Maytenus	15	Trichilia	12	Solanum	9	Ocotea	9
	Psychotria	17	Marlierea	15	Mollinedia	12	Machaerium	8	Trichilia	8
	Tabebuia	16	Myrsine	13	Solanum	11	Ficus	8	Symplocos	8
	Trichilia	16	Myrceugenia	13	Guatteria	11	Psychotria	8	Ilex	7
	Gomidesia	16	Pouteria	13	Tabebuia	10	Guatteria	7	Maytenus	7
	Machaerium	15	Casearia	12	Swartzia	10	Aspidosperma	7	Byrsonima	7
	Casearia	14	Machaerium	12	Pouteria	9	Maytenus	7	Guapira	7
	Guatteria	13	Trichilia	12	Cordia	9	Erythroxylum	7	Hirtella	6
	Cordia	13	Rudgea	12	Rudgea	9	Casearia	7	Campomanesia	6
	Mollinedia	13	Symplocos	11	Nectandra	9	Senna	7	Pouteria	6
	Nectandra	12	Ficus	11	Campomanesia	9	Mollinedia	6	Vochysia	6
	Myrtaceae	203	Myrtaceae	203	Myrtaceae	129	Myrtaceae	83	Myrtaceae	61
	Fabaceae	91	Melastomataceae	82	Fabaceae	83	Lauraceae	44	Fabaceae	52
	Rubiaceae	84	Lauraceae	81	Rubiaceae	66	Melastomataceae	38	Rubiaceae	35
	Lauraceae	78	Rubiaceae	76	Lauraceae	61	Fabaceae	31	Melastomataceae	30
	Melastomataceae	76	Fabaceae	58	Euphorbiaceae	47	Rubiaceae	31	Mimosaceae	27
	Caesalpiniaceae	58	Mimosaceae	49	Mimosaceae	46	Mimosaceae	28	Euphorbiaceae	26
	Mimosaceae	49	Euphorbiaceae	35	Caesalpiniaceae	40	Euphorbiaceae	25	Lauraceae	25
	Sapotaceae	49	Caesalpiniaceae	35	Moraceae	35	Caesalpiniaceae	23	Caesalpiniaceae	24
	Chrysobalanaceae	43	Monimiaceae	35	Melastomataceae	34	Asteraceae	22	Moraceae	19
	Euphorbiaceae	42	Solanaceae	31	Annonaceae	30	Annonaceae	19	Annonaceae	16

TABLE 3. Continued.

	Rain forests (N = 48)				Semi-deciduous forests (N = 77)					
	Low altitude (N = 27)	S 1475	High altitude (N = 21)	S 1280	Low altitude (N = 36)	S 1124	High altitude (N = 16)	S 709	Western (N = 25)	S 699
	Moraceae	41	Asteraceae	30	Rutaceae	28	Bignoniaceae	14	Apocynaceae	15
	Annonaceae	38	Sapotaceae	29	Flacourtiaceae	24	Clusiaceae	14	Flacourtiaceae	15
	Clusiaceae	27	Annonaceae	25	Sapotaceae	23	Meliaceae	14	Vochysiaceae	15
	Meliaceae	26	Clusiaceae	23	Sapindaceae	21	Rutaceae	14	Meliaceae	14
	Apocynaceae	25	Sapindaceae	23	Bignoniaceae	19	Sapindaceae	13	Arecaceae	13
	Sapindaceae	25	Flacourtiaceae	19	Meliaceae	18	Flacourtiaceae	13	Bignoniaceae	13
	Bignoniaceae	24	Meliaceae	19	Solanaceae	18	Moraceae	13	Asteraceae	12
	Rutaceae	23	Myrsinaceae	19	Clusiaceae	17	Solanaceae	13	Chrysobalanaceae	12
	Flacourtiaceae	22	Moraceae	18	Monimiaceae	18	Monimiaceae	11	Clusiaceae	11
	Erythroxylaceae	21	Vochysiaceae	18	Nyctaginaceae	18	Verbenaceae	11	Rutaceae	11
	Arecaceae	20	Bignoniaceae	17	Apocynaceae	17	Aquifoliaceae	10	Sapindaceae	11
	Monimiaceae	17	Chrysobalanaceae	17	Myrsinaceae	17	Vochysiaceae	10	Anacardiaceae	10

The tree species composition of both rain and semi-deciduous forests also was highly influenced by altitude and associated temperatures at all three taxonomic levels, a well-known fact for mountain vegetation worldwide (Hugget 1995). Some floristic patterns found with increasing altitude also coincided with those cited by Gentry (1995) for Andean and Central American forests (i.e., the increasing contribution of Asteraceae, Melastomataceae, and Solanaceae to the tree flora and the decrease of Leguminosae, with the exception of *Inga* species). Many genera strongly correlated with high altitudes in southeastern Brazil such as *Drymis, Hedyosmum, Weinmannia, Clethra, Podocarpus, Meliosma, Meriania, Ilex, Clusia, Myrsine, Miconia, Prunus, Roupala,* and *Trichipteris,* are also considered diagnostic of Neotropical cloud forests (Webster 1995). At the species level, many listed as high altitude indicators such as *Drymis brasiliensis, Weinmannia discolor, W. paullinifolia, Podocarpus lambertii, P. sellowii,* and *Hedyosmum brasiliense,* are already known to follow an upper montane distribution pattern along Brazilian mountain ranges (Giulietti & Pirani 1988).

The importance of altitude in the floristic differentiation of semi-deciduous forests has been documented for the state of São Paulo (Salis et al. 1995, Torres et al. 1997), and southeastern Brazil in general (Oliveira-Filho et al. 1994). Occasional frosts have been mentioned by Oliveira-Filho et al. (1994) as an important factor limiting species distribution toward both higher elevations and latitudes. Resistance to frosts is a key factor determining tree species distribution in Australian forests (Read & Hill 1989, Read & Hope 1989). The influence of altitude on climate, however, is far more complex than creating temperature gradients and frost events. Rising elevation also decreases atmospheric pressure, increases solar radiation, accelerates air masses, promotes higher cloudiness, and boosts rainfall (Jones 1992).

The well established differentiation between rain and semi-deciduous Atlantic forests based on physiognomy was floristically consistent at all three taxonomic levels, and to some extent correlates with the coastland–hinterland dichotomy. This has been demonstrated for the state of São Paulo (Torres et al. 1997) where there is a strong floristic separation between coastal "hygrophyllous forests" (annual rainfall >2000 mm and no dry season) and hinterland "mesophyllous forests" (annual rainfall ca 1400 mm and a dry season). São Paulo and Paraná are where this dichotomy is most pronounced in southeastern Brazil due to the relatively abrupt vegetational transition at the Serra do Mar, the coastal mountain range that helps create two sharply dis-

TABLE 4. *Genera and families with the highest number of species (S) on the tree flora of Atlantic rain forests, semi-deciduous forests, Amazonian rain forests, and Cerrados.* N = *number of areas.*

Atlantic rain forests (N = 48)	S 2012	Atlantic semi-deciduous forests (N = 77)	S 1533	Amazonian rain forests (N = 22)	S 1530	Cerrado (N = 98)	S 528
Eugenia	108	Eugenia	59	Pouteria	44	Myrcia	24
Miconia	59	Miconia	46	Licania	38	Miconia	20
Myrcia	57	Myrcia	46	Inga	37	Byrsonima	18
Ocotea	49	Ocotea	37	Protium	35	Eugenia	12
Mollinedia	30	Machaerium	24	Miconia	26	Aspidosperma	11
Inga	28	Ficus	22	Swartzia	25	Psidium	9
Tibouchina	28	Ilex	20	Ocotea	24	Kielmeyera	8
Erythroxylum	27	Erythroxylum	19	Eschweilera	19	Vochysia	8
Marlierea	27	Inga	19	Sloanea	18	Cordia	7
Pouteria	27	Casearia	15	Casearia	18	Bauhinia	7
Gomidesia	25	Solanum	15	Eugenia	18	Machaerium	7
Solanum	25	Guatteria	14	Ficus	17	Alibertia	7
Psychotria	23	Maytenus	14	Virola	17	Symplocos	7
Licania	21	Senna	14	Duguetia	15	Licania	6
Ficus	21	Tibouchina	14	Mouriri	15	Erythroxylum	6
Machaerium	20	Mollinedia	14	Cordia	14	Casearia	6
Trichilia	19	Aspidosperma	13	Pourouma	14	Vernonia	5
Maytenus	18	Nectandra	13	Hirtella	14	Ocotea	5
Rudgea	18	Trichilia	13	Aniba	14	Qualea	5
Tabebuia	17	Campomanesia	12	Micropholis	14	Myrsine	5
Casearia	16	Pouteria	12	Iryanthera	13	Solanum	5
Myrtaceae	308	Myrtaceae	187	Fabaceae	93	Myrtaceae	51
Melastomataceae	117	Fabaceae	100	Sapotaceae	88	Rubiaceae	30
Rubiaceae	116	Rubiaceae	84	Lauraceae	79	Melastomataceae	27
Fabaceae	111	Lauraceae	76	Mimosaceae	76	Caesalpiniaceae	25
Lauraceae	106	Melastomataceae	67	Annonaceae	74	Asteraceae	24
Caesalpiniaceae	68	Mimosaceae	57	Caesalpiniaceae	73	Fabaceae	24
Mimosaceae	67	Caesalpiniaceae	55	Chrysobalanaceae	68	Malpighiaceae	22
Euphorbiaceae	53	Euphorbiaceae	54	Moraceae	62	Vochysiaceae	18
Sapotaceae	50	Moraceae	38	Rubiaceae	52	Apocynaceae	17
Chrysobalanaceae	49	Annonaceae	37	Burseraceae	51	Annonaceae	16
Annonaceae	48	Rutaceae	30	Euphorbiaceae	49	Mimosaceae	16
Moraceae	43	Asteraceae	29	Lecythidaceae	47	Clusiaceae	13
Monimiaceae	40	Sapindaceae	29	Apocynaceae	46	Euphorbiaceae	12
Clusiaceae	39	Flacourtiaceae	26	Myrtaceae	40	Anacardiaceae	10
Solanaceae	38	Sapotaceae	26	Arecaceae	36	Arecaceae	10
Asteraceae	37	Clusiaceae	25	Melastomataceae	35	Chrysobalanaceae	10
Sapindaceae	33	Solanaceae	24	Myristicaceae	33	Verbenaceae	9
Rutaceae	31	Apocynaceae	23	Clusiaceae	32	Bignoniaceae	8
Meliaceae	29	Bignoniaceae	23	Flacourtiaceae	32	Lauraceae	8
Bignoniaceae	28	Nyctaginaceae	22	Meliaceae	30	Boraginaceae	7
Erythroxylaceae	27	Monimiaceae	21	Sapindaceae	29	Combretaceae	7
Flacourtiaceae	27	Myrsinaceae	21	Bombacaceae	27	Myrsinaceae	7

tinct climates. The seaward side of the Serra do Mar has the highest mean annual rainfall (up to 3600 mm) of the entire Atlantic Forest range, while the inland side has typical seasonal climates with annual rainfall between 1300 and 1600 mm. This reinforces the inaccurate image of two sharply distinct forest formations.

The transition from rain to semi-deciduous forests may be gradual and complex, and not necessar-

ily linked to the coastal–hinterland climatic gradients. Coastal climates vary dramatically in southeastern Brazil. Annual rainfall declines from southern São Paulo toward the north of Rio de Janeiro state where semi-deciduous forests reach the coast near Campos dos Goitacazes and give rise to a gap in rain forest distribution (Fig. 1). The drier coastal climate of this region is caused by the cold oceanic upwelling of Cabo Frio (Araujo 1997). Coastal rain

TABLE 5. *Selection of tree species associated with major groups of Atlantic Forest formations based on TWINSPAN classification of 125 forest areas and 1002 species.*

Northern low altitude rain forests: *Bactris setosa, Bathysa nicholsonii, Brosimum guianensis, Byrsonima sericea, Campomanesia guaviroba, Carpotroche brasiliensis, Caryocar edule, Casearia ulmifolia, Cedrela odorata, Chrysophyllum lucentifolium, Cupania emarginata, Dalbergia nigra, Diplotropis incexis, Ecclinusa ramiflora, Esenbeckia leiocarpa, Eugenia brasiliensis, E. moraviana, E. stictosepala, E. sulcata, E. umbelliflora, E. verrucosa, Ficus organensis, Gallesia integrifolia, Geissospermum laeve, Heliocarpus americanus, Himatanthus lancifolius, Hortia arborea, Hydrogaster trinervis, Hymenolobium janeirense, Inga edulis, I. flagelliformis, I. striata, Ixora gardneriana, Jacaranda puberula, Jacaratia heptaphylla, Joannesia princeps, Lecythis pisonis, Lonchocarpus campestris, Machaerium scleroxylum, Marlierea obscura, M. sylvatica, Maytenus robusta, Melanoxylon brauna, Metrodorea nigra, Micropholis gardnerianum, Mouriri chamissoana, Myrocarpus frondosus, Ocotea elegans, O. indecora, O. puberula, O. velutina, Paratecoma peroba, Platymiscium floribundum, Pogonophora schomburgkiana, Pourouma guianensis, Protium warmingianum, Pseudobombax grandiflorum, Pseudopiptadenia contorta, P. leptostachya, Pterocarpus rohrii, Pterygota brasiliensis, Rinorea bahiensis, Rustia formosa, Schizolobium parahyba, Simarouba amara, Sloanea guianensis, Solanum swartzianum, Sparattosperma leucanthum, Stryphnodendron pulcherrimum, Swartzia acutifolia, S. flaemingii, Tabebuia roseo-alba, Tetrastylidium grandifolium, Thyrsodium spruceanum, Trichilia casaretti, T. elegans, T. lepidota, Vataireopsis araroba, Virola gardneri, V. officinalis, V. oleifera, Vismia baccifera, Vitex megapotamica, Zanthoxylum monogynum, Zollernia ilicifolia.*

Southern low altitude rain forests: *Allophylus petiolulatus, Alseis floribunda, Aniba firmula, Astrocaryum aculeatissimum, Attalea dubia, Balizia pedicellaris, Bathysa meridionalis, Brosimum glazioui, Calyptranthes grandifolia, Chrysophyllum flexuosum, Citronella megaphylla, Coussapoa microcarpa, Cryptocarya moschata, Cupania racemosa, Ecclinusa ramiflora, Eriotheca pentaphylla, Eugenia cerasiflora, Euterpe edulis, Ficus organensis, Galipea multiflora, Gomidesia anacardiaefolia, G. spectabilis, Guatteria australis, Heisteria silvianii, Hymenolobium janeirense, Ilex dumosa, Inga capitata, I. edulis, Jacaranda puberula, Licaria armeniaca, Lonchocarpus muehlbergianus, Malouetia arborea, Marlierea suaveolens, M. tomentosa, Micropholis crassipedicellata, Mollinedia schottiana, M. uleana, Myrcia pubipetala, Nectandra membranacea, Neomytranthes glomerata, Nephelea sternbergii, Ocotea brachybotra, O. dispersa, O. divaricata, O. puberula, Parinari excelsa, Pilocarpus pauciflorus, Posoqueria acutifolia, Pouteria caimito, P. venosa, Psychotria carthagenensis, Pterocarpus rohrri, Quiina glaziovii, Ruprechtia laxiflora, Sclerolobium denudatum, Sebastiania brasiliensis, Stylogyne ambigua, Sweetia fruticosa, Tabebuia heptaphylla, Talauma ovata, Tetrastylidium grandifolium, Tetrorchidium rubrivenium, Virola gardneri, V. oleifera.*

High altitude rain and semi-deciduous forests: *Bathysa meridionalis, Byrsonima laxiflora, Calyptranthes clusiaefolia, Casearia obliqua, Cecropia glazioui, Cinnamomum glazioui, Clethra scabra, Clusia criuva, Connarus regnellii, Cryptocarya saligna, Daphnopsis fasciculata, Drimys brasiliensis, Eremanthus incanus, Eugenia blastantha, Euplassa incana, Ficus luschnatiana, F. mexiae, Geonoma schottiana, Gomidesia eriocalyx, G. spectabilis, Gordonia fruticosa, Guatteria nigrescens, Hedyosmum brasiliensis, Heisteria silvianii, Hieronyma ferruginea, Leucochlorum incuriale, Maytenus glazioviana, M. salicifolia, Meliosma sellowii, Miconia brunnea, M. chartacea, M. cinnamomifolia, M. pepericarpa, M. theaezans, Mollinedia argyrogyna, Myrcia laruotteana, Myrsine lancifolia, Nectandra grandiflora, N. lanceolata, N. nitidula, N. puberula, Ocotea brachybotra, O. silvestris, Ouratea semiserrata, Picramnia glazioviana, Pimenta pseudocaryophyllus, Protium widgrenii, Psychotria suterella, Qualea jundiahy, Quiina glaziovii, Schefflera angustissima, S. calva, Salacia elliptica, Siphoneugena widgreniana, Solanum bullatum, Symplocos celastrinea, Tabebuia chrysotricha, Tibouchina stenocarpa, Trembleya parviflora, Trichilia emarginata, Trichipteris corcovadensis, Vanillosmopsis erythropappa, Vismia brasiliensis, Weinmania pauliniaefolia, Xylosma ciliatifolium.*

Eastern low altitude semi-deciduous forests: *Acacia glomerosa, A. polyphylla, Albizia niopoides, Aloysia virgata, Apuleia leiocarpa, Aspidosperma polyneuron, Astronium fraxinifolium, Balfourodendron riedelianum, Bastardiopsis densiflora, Chrysophyllum gononocarpum, Copaifera langsdorffii, Cordia trichotoma, Cupania oblongifolia, Duguetia lanceolata, Enterolobium contortisiliquum, Esenbeckia leiocarpa, Eugenia involucrata, E. moraviana, E. sulcata, Ficus guaranitica, F. insipida, F. obtusifolia, Guarea guidonea, G. kunthiana, Himatanthus lanceifolius, Holocalyx balansae, Lonchocarpus cultratus, Machaerium paraguariensis, Maytenus aquifolia, Metrodorea stipularis, Myrcia multiflora, M. rostrata, M. tomentosa, Nectandra cissiflora, Ocotea puberula, Ouratea castaneifolia, Parapiptadenia rigida, Patagonula americana, Picramnia sellowii, Pisonia ambigua, Prockia crucis, Prunus sellowii, Pterogyne nitens, Siparuna guianensis, Solanum granuloso-leprosum, Swartzia apetala, Sweetia fruticosa, Tabernaemontana hystrix, Trichilia casaretti, T. catigua, T. claussenii, T. elegans, T. hirta, Xylopia sericea, Zanthoxylum caribaeum, Z. riedelianum, Zeyheria tuberculosa.*

Western montane and submontane semi-deciduous forests: *Acosmium dasycarpum, Acrocomia aculeata, Aegiphila lhotzkiana, Agonandra brasiliensis, Albizia niopoides, Alibertia concolor, A. macrophylla, Anadenanthera peregrina, Apeiba tibourbou, Astronium fraxinifolium, Bastardiopsis densiflora, Callisthene major, Dalbergia miscolobium, Diospyros hispida, Eugenia punicifolia, Faramea cyanea, Genipa americana, Gomidesia lindeniana, Guatteria sellowiana, Hedyosmum brasiliense, Inga alba, Ixora warmingii, Luehea paniculata, Machaerium acutifolium, Margaritaria nobilis, Miconia chamissois, M. sellowiana, Myrcia tomentosa, Nectandra cissiflora, Platypodium elegans, Pouteria gardnerii, Protium spruceanum, Pseudobombax tomentosum, Pseudolmedia guaranitica, Pterogyne nitens, Qualea dichotoma, Rudgea viburnoides, Salacia elliptica, Siparuna guianensis, Siphoneugena densiflora, Styrax camporum, Sweetia fruticosa, Symplocus nitens, Terminalia argentea, Tibouchina candolleana, Virola sebifera, Vismia guianensis, Xylopia aromatica.*

TABLE 5.   *Continued.*

"Supertramp" species: *Aegiphila sellowiana, Alchornea glandulosa, A. triplinervea, Amaioua guianensis, Andira fraxinifolia, Aspidosperma parvifolium, Cabralea canjerana, Calophyllum brasiliense, Cariniana estrellensis, Casearia decandra, C. sylvestris, Cecropia pachystachya, Cedrella fissilis, Celtis iguanaea, Copaifera langsdorffii, Cordia sellowiana, Croton floribundus, Cupania vernalis, Dendropanax cuneatum, Endlicheria paniculata, Erythroxylum citrifolium, Eugenia florida, Guapira opposita, Guarea guidonia, G. macrophylla, Guazuma ulmifolia, Hymenaea courbaril, Inga vera, Jacaratia spinosa, Luehea divaricata, Mabea fistulifera, Maclura tinctoria, Matayba elaeagnoides, M. guianensis, Maytenus communis, Myrcia rostrata, Myrciaria floribunda, Myrsine umbellata, Nectandra oppositifolia, Ocotea corymbosa, Pera glabrata, Piptadenia gonoacantha, Protium heptaphyllum, Roupala brasiliensis, Sapium glandulatum, Sorocea bonplandii, Tabebuia serratifolia, Tapirira guianensis, Trema micrantha, Trichilia catigua, Zanthoxylum rhoifolium.*

forests reappear in Espírito Santo state, as annual rainfall increases and seasonality decreases, until reaching the warm and hyper-humid "hylaea" of southern Bahia state. As demonstrated by the floristic analyses, these climatic variations correlated with a strong floristic differentiation between northern and southern coastal rain forests, a fact already detected by Siqueira (1994) and Oliveira-Filho and Ratter (1995). These two forest blocks represent different and gradual floristic transitions from rain to semi-deciduous forests as rainfall amounts decrease, both ending at the Campos dos Goitacazes gap. The northern transition occurs in warmer climate and includes declining mean temperatures toward the south. The southern transition starts in cooler subtropical climate and includes rising temperatures toward the north. Mean temperature is probably the chief factor determining the north–south floristic differentiation of coastal rain forests, while both temperature and rainfall regime account for much of the internal variation within the two forest blocks.

Another important change toward the north is that the mountain ranges are progressively farther from the coast and become lower in altitude, particularly north of Rio Doce. This opens space for a wider band of coastal lowlands known as tabuleiros that extend from northern Rio de Janeiro to northeastern Brazil. Changes in rainfall regime toward the interior are more gradual and have a smaller range in Espírito Santo, eastern Minas Gerais, and southern Bahia than in São Paulo and neighboring states. Likewise, the transition between rain and semi-deciduous forests is relatively gentler in the north. Additionally, low altitudes penetrate deep into the continent along the valleys of the Rio Doce, Mucuri, and Jequitinhonha, allowing typical lowland rain forest species to expand their distribution toward the interior. This is known for many rain forest species, both Amazonian and Atlantic, that are able to expand their distribution into areas of strongly seasonal climates via riverine forests (Oliveira-Filho & Ratter 1995). This may explain why the areas of semi-

deciduous forest in the Rio Doce River basin show strong floristic links with the tabuleiro rain forests of Espírito Santo and southern Bahia.

Rainfall seasonality was apparently more important than annual rainfall in distinguishing rain and semi-deciduous forests, and the 30-day duration of the dry season was an effective limiting criterion that produced a geographic distribution largely coincident with that of IBGE (1993). Rain forests are found in areas with annual rainfall as low as 1173 mm (Rio de Janeiro), provided that the rains are well distributed. Only among subtropical forests of low altitudes does annual rainfall prevail over seasonality in separating rain and semi-deciduous forests, probably because low winter temperatures play an additional role in forest deciduousness as suggested by Holdridge *et al.* (1971). Increasing rainfall seasonality with increasing distance from the ocean also was a leading factor determining floristic differentiation among hinterland semi-deciduous forests. The forest enclaves occurring within the Cerrado domain (*e.g.*, Brasília), where dry seasons may last for up to 160 days, were the most differentiated semi-deciduous forests; they also had greater floristic links with the Cerrado tree flora. These facts may reinforce the view of rain and semi-deciduous forests in southeastern Brazil as a continuum of tree species distribution determined basically by rainfall regime that also leads to the Cerrado tree flora, as suggested by Leitão Filho (1987); however, one must bear in mind that other important factors also intervene in forest–savanna transitions, particularly fire and soil fertility (Furley *et al.* 1992).

To a considerable extent, the tree flora of semi-deciduous forests is a fraction of the much richer rain forest flora, and probably is composed of species able to cope with relatively longer dry seasons. Tree species diversity is highly correlated with water consumption and energy uptake, resources that are partitioned among species and limit their number in forest communities (Hugget 1995). Water shortage probably plays the chief role in reducing species rich-

ness of semi-deciduous forests compared to rain forests. The simpler structure of semi-deciduous forests also favors a comparatively reduced number of understory species (Gentry & Emmons 1987). There was greater floristic similarity at all taxonomic levels between Atlantic rain and semi-deciduous forests than between any of the latter and Amazonian rain forests. Therefore, there is little floristic ground for viewing Atlantic rain forests as being closer to Amazonian rain forests than to their adjacent semi-deciduous forests. Amazonian and Atlantic rain forests are more similar in physiognomic characteristics than floristic aspects (Silva & Shepherd 1986). It is not incorrect to describe rain and semi-deciduous forests as physiognomic and floristic expressions of a single great Atlantic Forest domain if the concept of the Amazonian forest domain includes closed rain forests (both upland and floodplain), open rain forests (monsoon forests), heath forests (campinarana), and incidentally, semi-deciduous forests (Veloso *et al.* 1991). The definition of Atlantic forests should be as comprehensive as that of Amazonian forests in order to encompass all forest physiognomies east of the dry corridor, from northeastern Brazil to southern Brazil, eastern Paraguay, and northeastern Argentina. This adds not only the semi-deciduous forests but also the southern subtropical *Araucaria* forests and the northeastern enclaves of brejo forests to the South American Atlantic forests.

ACKNOWLEDGMENTS

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