

Coastal plain forests in southern and southeastern Brazil: ecological drivers, floristic patterns and conservation status

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Abstract Coastal Plain Forests (also called Restinga Forests), defined as forest formations that occur in the coastal plain on a recent marine substrate (Quaternary), are primarily distributed in southern and southeastern Brazil. The Coastal Plain Forests represent one of the faces of the Atlantic Forest biome and are one of the most susceptible to degradation, given the high human pressure in coastal plains. In this work, we reviewed nearly 200 studies addressing the flora and vegetation of Restinga Forests over 70 years, aiming to find knowledge gaps and discuss future directions for these ecosystems. We focused on describing the main ecological drivers of the forest, the flora's origin, the forest phenological and reproductive patterns, and on discussing the challenges for the conservation of the Restinga Forests. We found that a relatively large body of knowledge on Restinga Forests was accumulated over the last decades. Studies on flora are relatively well distributed in the region, but some gaps are found in some stretches of coastline (in southern littoral) and for specific forest strata (understory and epiphytic, in southeastern littoral). A total

of 1588 species were listed for Restinga Forests, including trees (754), epiphytes (253), lianas (165), herbs (185), shrubs (68), and others (163). Regarding the flora of the Restinga Forests, 40 % of the species are restricted to the Atlantic Forest region, while 60 % of the species are distributed in other Brazilian ecoregions. These ecosystems are characterized by lower tree diversity when compared to other Atlantic physiognomies; however, studies addressing the processes determining diversity patterns in different scales are still rare. The soil constraints (sandiness, high acidity, low nutrient content, and flooding) strongly limit tree growth but are apparently compensated by a rapid nutrient cycling in the ecosystem and varied morphological and physiological plant adaptations. These forests can be considered seasonal (in reproductive and vegetative phenophases) and apparently depend on animal interactions (seed dispersal). We also found that these systems are highly fragmented and that little attention has been given to ensure the maintenance of its diversity and processes. We suggest that initiatives to ensure integrated and long-term research policies directed toward biodiversity conservation are necessary for these ecosystems.

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Introduction

The vegetation that occurs in the coastal plains in Brazil, collectively called Restingas (see Lacerda et al. 1982 and Souza et al. 2008 for other meanings), is quite heterogeneous, both floristic and structurally, with distinct vegetation forms occurring side by side. The features range from grasslands with predominance of herbaceous plants to

scrubs (shrubby vegetation, traditionally known as Restinga) and forest physiognomies, which feature a “complex” or “mosaic” of vegetation. Thus, these Coastal Plain Forests or Restinga Forests can be understood as forest vegetation that occurs over the coastal plains of the Brazilian coast, formed by marine sediments originated from the Quaternary (CONAMA Resolution 261/1999). In southern and southeastern Brazil, such forests are generally more internalized and often are associated with mangroves (near the mouths of rivers and bays) and forest formations of the Atlantic Forest, especially those that are distributed in the lower portions of the Serra do Mar and the coastal plain itself.

The heterogeneity of vegetation in the coastal plains and the use of regional terms cause some ambiguity in the use of vegetation names. Despite the frequent use of “Restinga Forest” in the literature (Lacerda et al. 1982; Waechter 1990; Araujo 1992; Silva et al. 1994), there are no correspondent terms in the classification of Brazilian vegetation (IBGE 1992). In a direct association, this vegetation can be considered as part of the Edaphic System of First Occupation (over Quaternary sediments) and of the Lowland Dense Rain Forest (over sediments of the Pliopleistocene or Quaternary) in the formal classification (IBGE 1992). Some efforts of standardization and systematization of terms enjoyed some success (e.g., Silva and Brites 2005), but a description of vegetation is inevitable before any comparison among sites can be made.

Restinga Forests are floristically, functionally, and historically associated with other physiognomies in coastal plains. For example, Restinga scrubs and Restinga Forest can share over 50 % of the woody species (Silva 1998). Shifts in the sediment deposition and coast dynamics can result in interchanges among mangroves, dunes, and Restinga Forests (Bartholomeu et al. 2014). The Lowland Forests are the most similar in physiognomy to Restinga Forests in coastal plains, and frequently, they are not clearly distinct (Klein 1978). In contrast to the Restinga Forests, the Lowland Forests are historically older (over Pleistocene sediments), which affects the soil characteristics (higher nutrient availability) and topography (Sztutman & Rodrigues 2002, Scherer et al. 2009; Urbanetz et al. 2010; Assis et al. 2011; Eisenlohr et al. 2013). Therefore, the forest structure and composition can be quite distinctive at small scales (Assis et al. 2011; Joly et al. 2012; Scarnello et al. 2012; Eisenlohr et al. 2013) but less expressive at large and geographical scales (Marques et al. 2011).

In 1982, the researchers Luiz D. Lacerda, Dorothy S. D. Araujo, and Norma C. Maciel published the volume “Brazilian Restingas: a bibliography,” which was the first initiative to build knowledge on the Restingas, including a list of references of studies conducted on the various vegetation types found in the Brazilian coastal plains

(Lacerda et al. 1982). Other successive initiatives (Lacerda et al. 1984; Esteves and Lacerda 2000; and the website www.Restinga.net, organized by D. S. D. Araujo) also organized knowledge about Restingas in more or less defined scales, especially in the Rio de Janeiro State. After more than 30 years from this starting point, the number of researchers and publications in Brazil increased substantially, as well as opportunities for research funding, which resulted in an increasing number of published papers over the years, mainly from 2000 to 2010 (Fig. 1). In parallel, over these last 30 years, the country has increased in human population by 65 % (IBGE 2010), generating more pressure on natural resources and threats to biodiversity. Considering that research can promote the resolution of environmental problems (Sutherland 2008), the organization of knowledge regarding the Restinga Forest can be an important tool to drive future studies and for supporting decision making.

In this review, we temporally score the state of knowledge of Restinga Forests. We performed a search on the published and peer reviewed journals and books (a few theses and dissertations were also included) in the on-line bibliographical sources (ScienceDirect, Google Academic) and physical libraries, considering all of the studies that were performed in the Restinga Forests and in ecotonal areas with Lowland Forests and Restinga scrubs. We considered all studies related to the flora and vegetation of Restinga Forests and the ecological drivers, forest dynamics, and plant species reproduction and adaptations, without time limitation. We restricted our study to the southern and southeastern Brazilian coast because it composes a relatively well-defined florist block of the Brazilian Atlantic Forest (Marques et al. 2011). Thus, we compiled data of nearly 200 references, aiming to answer the following questions: (1) Which are the main ecological

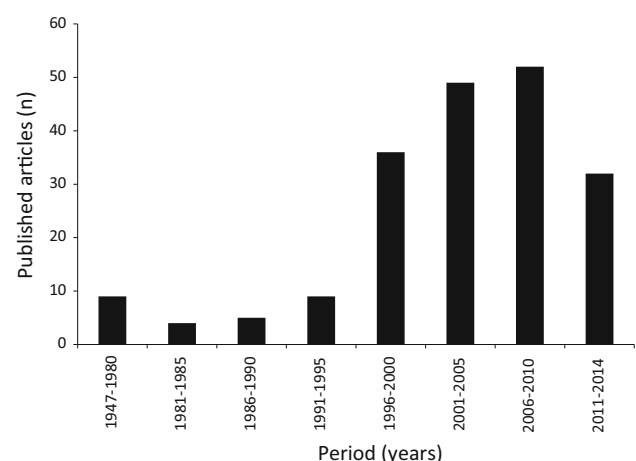


Fig. 1 Distribution of published studies regarding Restinga Forests in southern and southeastern Brazil. Total = 196

drivers for the occurrence of the Restinga Forests? (2) How much is known and what are the possible origins of the Restinga Forest flora? (3) What are the forest phenological and reproductive patterns? (4) What are the challenges for conservation of the Restinga Forests? Finally, we discussed these questions in light of the future of these ecosystems in southern and southeastern Brazil.

Ecological drivers

Geological and historical determinants

In the south and southeast regions of Brazil (states of Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul), the coast exhibits a range of geological, oceanographic, and climatic characteristics that influence the occurrence of distinct landscapes (Silveira 1964). The Espírito Santo littoral is marked by large coastal plains intercalated by outcrops and cliffs from the Barreiras geological formation. From Rio de Janeiro to the middle of the Santa Catarina (Cabo de Santa Marta), the littoral is marked by the presence of the Serra do Mar mountain chain and by an extended and indented coastal plain, defining several bays and lagoons (Silveira 1964). In these two regions, the climate is basically tropical to subtropical, marked by pronounced precipitation caused by the moisture retained in the region of Serra do Mar (Maack 1947). From Cabo de Santa Marta (Santa Catarina) to the southern border between Brazil and Uruguay (Chuí), the climate is subtropical (Maack 1947) and the littoral is characterized by the occurrence of wide sandy sedimentary plains associated with a set of lagoons and small portions of basaltic rocks from the Serra Geral mountain chain in Torres, Rio Grande do Sul (Silveira 1964). In these three regions, the coastal plains are formed by Quaternary sediments deposited in marine and continental environments on which peculiar vegetation has developed (Villwock 1994).

The coastal plains of this regions were formed during the Quaternary (from 2.5 million years BP), when events that occurred mainly at the Late Pleistocene (120,000–10,000 years BP) and the Holocene (from 10,000 years BP) determined the actual conformation of the littoral (Pessenda et al. 2012). Processes determining the actual geomorphology included changes in sea level during the Quaternary, climatic fluctuations, the occurrence of longshore currents (currents essentially parallel to shorelines generated by oblique incidences of waves), the differences in the primary sediment sources (river or continent), and the type of traps for the retention of these sediments (Suguio and Tessler 1984; Suguio and Martin 1990; Ledru et al. 1996; Angulo et al. 2006). As a result of these processes, the actual

coastal plains occur in a climate that is wetter and warmer than in the past (Pessenda et al. 2012) and are characterized by a more or less wavy relief, as reflected in variations of up to three meters in altitude (Rossi and Queiroz-Neto 2001).

Such environmental changes drastically affected the vegetation in the coastal plains. Palynological and archeological studies in different sites of the south and southeast Brazilian littoral reveal successive transitions between sandy and muddy sediments associated with different frequencies of pollen (or charcoal) of specific plant groups. These transitions were interpreted as reflecting the changes among herbaceous physiognomies (marshes), woody physiognomies (scrubs and dry and flooded forests), and mangroves in different regions (Scheel-Ybert 2000; Meyer et al. 2005; Amaral et al. 2006; Bartholomeu et al. 2014). Thus, in addition to the geomorphological changes that occurred with time, the vegetation of the coastal plain was extremely dynamic and interchangeable.

At a small temporal scale (decades), changes in vegetation were historically treated within a successional perspective, with beach vegetation, scrubs, and forests representing various seral stages of a successional process (Dansereau 1947, and later reinforced by Reitz 1961; Velloso and Klein 1961; Joly 1970). This vision of predictable and unidirectional development (*sensu* Clements 1936) is still present in some specific interpretations (Galvão et al. 2002), but no long-term study has empirically demonstrated this process.

Soil and nutritional constraints

In the lowland coastal region, the sequences of sandy marine deposits, continental sediments, and organic material reflect the apparently independent processes of soil formation (Rossi and Queiroz-Neto 2001), resulting in different soil classes (Gomes et al. 1998a, b) in several of its sub-orders and with different degrees of waterlogging (Britez 2005). The most frequent are Spodosols, which are formed by a process that consists of podzolization, i.e., the translocation of organic materials and Al from the soil surface to the soil subsurface, forming the spodic horizon (Gomes et al. 2007; Coelho et al. 2010). These are mainly sandy soils, with low sum and base saturation, acidic, cation exchange capacity and organic matter dependent on Al along with an increase in the content and stability of organic carbon in higher depths (Coelho et al. 2010). These characteristics indicate severe limitations to the plant growth due to low nutrient availability and the high saturation in aluminum.

The characteristics of soils under Restinga Forests have profound effects on the distribution of vegetation (Hay and Lacerda 1980). As the soil fertility is restricted to the first layer (0–10 cm), it has been estimated that 70–80 % of the

root system of the plants is in the first 10 cm of the surface and more than 90 % between 0 and 20 cm (Bonilha et al. 2012). Physiological and anatomical mechanisms explain the survival of species in this situation. For example, *Tapirira guianensis* (Anacardiaceae) has a high tolerance to aluminum because aluminum toxicity is avoided by a mechanism of chelation in the soil around the root (through the secretion of organic substances) or by accumulation of the element at the root, preventing translocation to shoots (Britez et al. 2002a). *Faramea marginata* (Rubiaceae) has a unique mechanism of tolerance, which consists of aluminum accumulation in plant tissues in the form of silicate (i.e., reacting with silicon), which is less toxic to plants (Britez et al. 2002b). Other anatomical characteristics of the leaves of tree species also appear to facilitate adaptation to low nutrients in areas of the Restinga Forests (Boeger and Wisniewski 2003; Boeger et al. 2004, 2005; Santos et al. 2010).

Optimization of nutrient cycling

Although the soil fertility of the Restinga Forests is considered very low, nutrient cycling of indigenous biomass tends to compensate for this restriction to plant development. The input of nutrients in the system occurs via recycling of plant biomass and via marine salinity in areas close to the sea (Britez et al. 2005). The leaves, the most abundant elements in the composition of litter (Boeger et al. 2000; Britez et al. 2005; Paula et al. 2009), fall at the beginning of the wet season (Ramos and Pellens 1994; Marques and Oliveira 2004; Britez et al. 2005; Paula et al. 2009). The leaching of nutrients (K, Ca, Mg and Na) occurs, especially in the early period of high rainfall and contributes greatly to the decomposition of litter (Dickow et al. 2009a). Microbial decomposition occurs in late spring, especially in the layer of leaf litter (Peña et al. 2005).

The tree species of the Restinga Forests generally have lower nutrient content in the leaves compared to the species of lowland forests (Moraes and Domingos 1997), despite the demonstrated large variation among the Restinga species (Boeger and Wisniewski 2002; Pinto and Marques 2003; Dickow et al. 2009a, b). However, such low concentrations are compensated for by endogenous mechanisms of nutrient economy (Moraes et al. 1999). For example, the translocation rate (measured as the difference between the concentration of a nutrient in the living leaf and litter) is much greater in the Restinga Forest species compared with species from the Lowland and the Lower Montane Atlantic Forest: 14 % higher for Mg, 21 % for N, 57 % for P, and up to 166 % for S (Moraes and Domingos 1997). There is a negative correlation between the amount of litter produced and the nutrient concentration in leaves,

which seems to be related to the degree of scleromorphism: species with rigid leaves (larger amount of lignin) produce high amounts of litter but have lower nutrient contents (Pinto and Marques 2003; Prottil et al. 2009).

In general, the litter deposition in the Restinga Forests is lower when compared to other tropical forests. In undisturbed forests, the annual litter is from 3,900 to 11,300 kg ha⁻¹ (Moraes et al. 1999; Britez et al. 2005; Paula et al. 2009; Assis et al. 2011; Pereira et al. 2012). These values are slightly lower than expected for tropical forests (Jordan 1985). From this range, higher values of litter input were observed in flooded forests (Britez et al. 2005; Paula et al. 2009; Pereira et al. 2012), which also encompass the higher species richness. The litter decomposition occurs slowly in Restinga Forests (between 0.0015 and 0.0031 g g⁻¹ day⁻¹), which allows for estimation of a half-life (time for 50 % of the leaf material to decompose) of between 217 and 462 days (Paula et al. 2009; Pereira et al. 2012). It has been verified that any disruption caused by deforestation can dramatically reduce litter production, affecting the ecosystem balance (Boeger et al. 2000; Pinto and Marques 2003).

Despite this efficient nutrient cycling mechanism, the biomass of Restinga Forests is apparently much lower than other associated forests. Estimates of the above-ground live biomass (considering trees, palms and ferns) reaches 166.3 ton ha⁻¹ in the Restinga Forest, a lower value than that found in the adjacent Lowland (218.08 t ha⁻¹), Lower Montane (253.8) and Montane Forests (283.2 t ha⁻¹) (Alves et al. 2010; Assis et al. 2011). Nevertheless, considering that biomass estimates can be forest-specific (Chave et al. 2005), the elaboration of predictive models specifically for the Restinga Forest is still rare (Scaranello et al. 2012; Moreira-Burger and Delitti 2010) but necessary for better estimates of the ecosystem process in these forests.

Flooding and forest structure

Several situations determine the soil moisture gradient in the coastal plains. One of the conditions is the configuration of the coastal ridges that define subtle differences in relief (1–3 m), changing the depth of the water table, which can substantially influence the vegetation (Britez et al. 1997, but see Dorneles and Waechter 2004 and Guedes et al. 2006). In addition, the forest proximity to the rivers promotes a water horizontal gradient, reflecting in soil humidity and forest structure (Silva et al. 1994; Magnago et al. 2012). In regions of lake occurrences (mainly in Rio de Janeiro and Rio Grande do Sul coasts), possibly historical changes in drainage and water accumulation in the lower regions created situations of soil moisture (Waechter and Jarenkow 1998; Dorneles and Waechter 2004).

Additionally, the areas of marine depression and alluvial lowlands favor the occurrence of these wetlands, influencing vegetation (Lima et al. 2006).

In all of these situations, the soil conditions change substantially. In flooded areas, organic matter is less mineralized, bases are more leached, the pH is higher and the C:N ratio higher, which suggests a slower process of decomposition of organic matter (Paula et al. 2013). In non-flooded soils, there are higher levels of P, cation exchange capacity and the sum of bases (Paula et al. 2013). Although these differences can determine different chemical constraints for the plants in both situations, the water saturation itself appears to be the major limiting factor for plant establishment in some situations (Magnago et al. 2012).

Differences in topography and water availability are reflected in the forest structure. In the coastal plains of the south and southeastern coasts, it is possible to observe shifting between unflooded forests (also called sandy, psammophilous, or dry forests) and partially or permanently flooded forests (hydrophilous, peat, or swampy forests) (Klein 1979; Silva et al. 1994; Dorneles and Wachter 2004; Scarano 2006). The responses of vegetation to the flooding are variable, but it is known that environmental heterogeneity is an essential factor for the maintenance of the diversity in this forest type (Oliveira et al. 2014). Differences between forests growing in ridges (flooded) and those growing over the ridges (unflooded) include increased species richness, diversity, and basal area and decreased individual density in flooded forests than in the unflooded forests (Silva 1998, Marques et al. 2009). The species composition also differs, although ~50 % of species are shared between them. In these situations, the flooded forest also boasts a faster species turnover than the unflooded forest (Marques et al. 2009). However, the gradient related to distance from the river exhibited a higher richness and diversity in better drained soils (Magnago et al. 2010, 2011, 2012).

In these flooded forests, there is a strong specialization in occupying habitats, apparently limited by phylogenetic relations among species, where more related species tend to occupy contrasting habitats (Oliveira et al. 2014). For example, very often, permanently flooded areas exhibit a dominance of *Tabebuia cassinoides* and *Calophyllum brasiliense*, both highly specialized and tolerant to soil water saturation (Kolb and Joly 2009, 2010; Oliveira and Joly 2010). These forests, called “caxetais” and “guanandizais” in some regions, are restricted to small areas and, in most cases, have suffered from drainage activities for road construction (Galvão et al. 2002). These forests are very fragile and dependent on the fine tuning of some inter-specific interactions (Scarano et al. 1997; Scarano 2006).

Floristic and phytogeographical patterns

Flora of Restinga Forests

For an overview of the state of knowledge of the Restinga Forest flora, we compiled all studies of inventories and phytosociological surveys of canopy (trees and shrubs), and understory (ground herbs and shrubs) strata of Restinga Forests in south-southeast Brazil (see details in Box S1). Inventories of plants not belonging to a specific stratum, i.e., lianas and vines, were also included. A total of 64 studies (80 sites) were performed in this region (Fig. 2; Tables 1, S1). These studies varied regarding the survey methods, sample area, and sample criteria (Table 1), but most of the studies surveyed small areas (<1 ha, Table S1). There was a large number of surveys in the states of São Paulo, Espírito Santo, Rio Grande do Sul and Rio de Janeiro, where the littoral is larger, and fewer in Paraná, the state with the shortest coast (Fig. 2). In Santa Catarina State, there were few surveys despite the large coastal plain (Fig. 2), but some descriptive studies were historically published (Klein 1979; Reitz 1961; Veloso and Klein 1961; Falkenberg 1999) and new inventories have been recently performed (Korte et al. 2013). Very little has been sampled regarding lianas and only one study sampled bryophytes (Santos et al. 2011). Thus, there are apparently still some gaps to fully understand the variations of Restinga Forest flora.

The checklist generated from these studies resulted in 1588 species and 154 families, including Angiosperms (1466 species), Ferns (121) and Gymnosperms (1) (Tables 2, S2). From the total of species (1588), 47 % were trees, 16 % epiphytes, 12 % herbs, 10 % lianas, 4 % shrubs, and 10 % species occurring in more than one life-form (Table S2). The canopy of Restinga Forests concentrates the higher species richness (859) and is characterized by the presence of tree species of Myrtaceae, in addition to other widely distributed species such as *Guapira opposita*, *Pera glabrata*, *Alchornea triplinervia*, and *Tapirira guianensis* (Table 2). The understory is also highly species rich (424) but highly variable in species composition, considering that even the most frequent species were present in less than 50 % of sites (Table S2). Such differences in species composition are possibly explained by large variations in topography, soil characteristics and light incidence in these forests (Citadini-Zanette 1984). Nevertheless, it is also possible that this pattern is an effect of the low sampling of this forest strata, or even the concentration of some inventories in one plant group (Orchids: Fraga and Peixoto 2004; Ferns: Santos et al. 2004, Athayde-Filho and Windisch 2006) (Table 3).

The epiphytic stratum (total 310 species, Table 2) is relatively marked in Restinga Forests (Kersten et al. 2009;

Table 1 Characteristics of all published floristic/phytosociological studies on Restinga Forests in south and southeast Brazil, according to forest strata

Characteristics	Sampled stratum		Understory	Epiphytic	Lianas ^a
	Canopy and sub-canopy				
Published studies (<i>n</i>)	44	16		10	3
Sites (<i>n</i>)	47	16		11	7
Survey method	Floristic and phytosociological (plot, point-centered quarter)	Floristic and phytosociological (plot)	Floristic and phytosociological (plot)	Floristic and phytosociological (phorophyte used as a plot)	Floristic
Sample area	0.056–2.5 ha	100–1,200 m ²		3,000–10,000 m ² (8–800 phorophytes)	na
Sample criteria	1.5 ≥ minimum DBH ≥ 10 cm, or BD ≥ 2.5 cm and <i>h</i> ≥ 1 m	150 ≥ <i>h</i> ≥ 5 cm, or life form		Phorophyte BD ≥ 5 cm, or DBH ≥ 30 cm	Life-form
Sites codes and references					
ES	Cob (Pereira and Gomes 1993), Gui (Fabrís and Cesar 1996), Vve (Pereira and Zambom 1998), Lin (Pereira et al. 1998), Vit (Pereira and Assis 2000), Ser (Pereira et al. 2000), Gua (Assis et al. 2004a, b), Phe (Braz et al. 2013), Con (Giaretta et al. 2013)	Vio (Pereira and Assis 2000), Gup (Assis et al. 2004a), Esa (Fraga and Peixoto 2004), Lih (Rodrigues and Simonelli 2007), Prk (Braz et al. 2013)			Pre (Braz et al. 2013)
RJ	Saq (Sá 1992); Igr (Araujo and Oliveira 1998), Arm (Lobão and Kurtz 2000), Sjb (Assumpção and Nascimento 2000), Sal (Sá and Araujo 2009), Mar (Menezes et al. 2010), Car (Kurtz et al. 2013)	Mai (Silva and Oliveira 1989), Qui (Santos et al. 2004), Sae (Araujo et al. 2009)		Sar (Fontoura et al. 2009)	
SP	Pic (Cesar and Monteiro 1995), Igu (Carvalhoes 1997), Ica (Sugiyama 1998a), Ier (Sugiyama 1998b), Jur (Melo et al. 2000), Bei, Ber (Guedes et al. 2006), Ubu (Assis 1999), Ian (Reis-Duarte 2004), Ico (Silva 2006), Bea, Bem (Martins et al. 2008), Uba (Assis et al. 2011), Pia (Sanchez et al. 2013)	Can (Salino and Almeida 2008), Uta (Nóbrega et al. 2011)		Ubt (Mania and Monteiro 2010)	Beg, Icd, Per, Uaa (Moraes et al. 2014), Beo, Bet (Martins et al. 2008)
PR	Par (Rotta et al. 1997), Ime (Silva et al. 1994), Gub (Galvão et al. 2002), Sup (Jaster 1995), Imm, Iml (Silva 1998)				
SC	Ita (Negrelle 2006); Ger (Citadini-Zanette et al. 2001), Ara (Martins et al. 2013)	Itp (Negrelle 2006)		Ipo (Labiak and Prado 1998)	
RS	Ars (Rossoni and Baptista 1995), Tai (Waechter and Jarenkow 1998), Via (Waechter et al. 2000), Pal (Moraes and Mondini 2001), Mos (Dorneles and Waechter 2004), Vib (Scherer et al. 2005), Tor (Santos et al. 2012), Pel (Venzke et al. 2012)	Tos (Citadini-Zanette 1984), Vim (Muller and Waechter 2001), Xan (Athayde-Filho and Windisch 2006), Mot (Záchia and Waechter 2011), Arl (Rossoni and Baptista 1995)		Toe (Waechter 1986), Tea (Gonçalves and Waechter 2003), Arr (Staudt et al. 2012), Aro (Becker et al. 2013)	

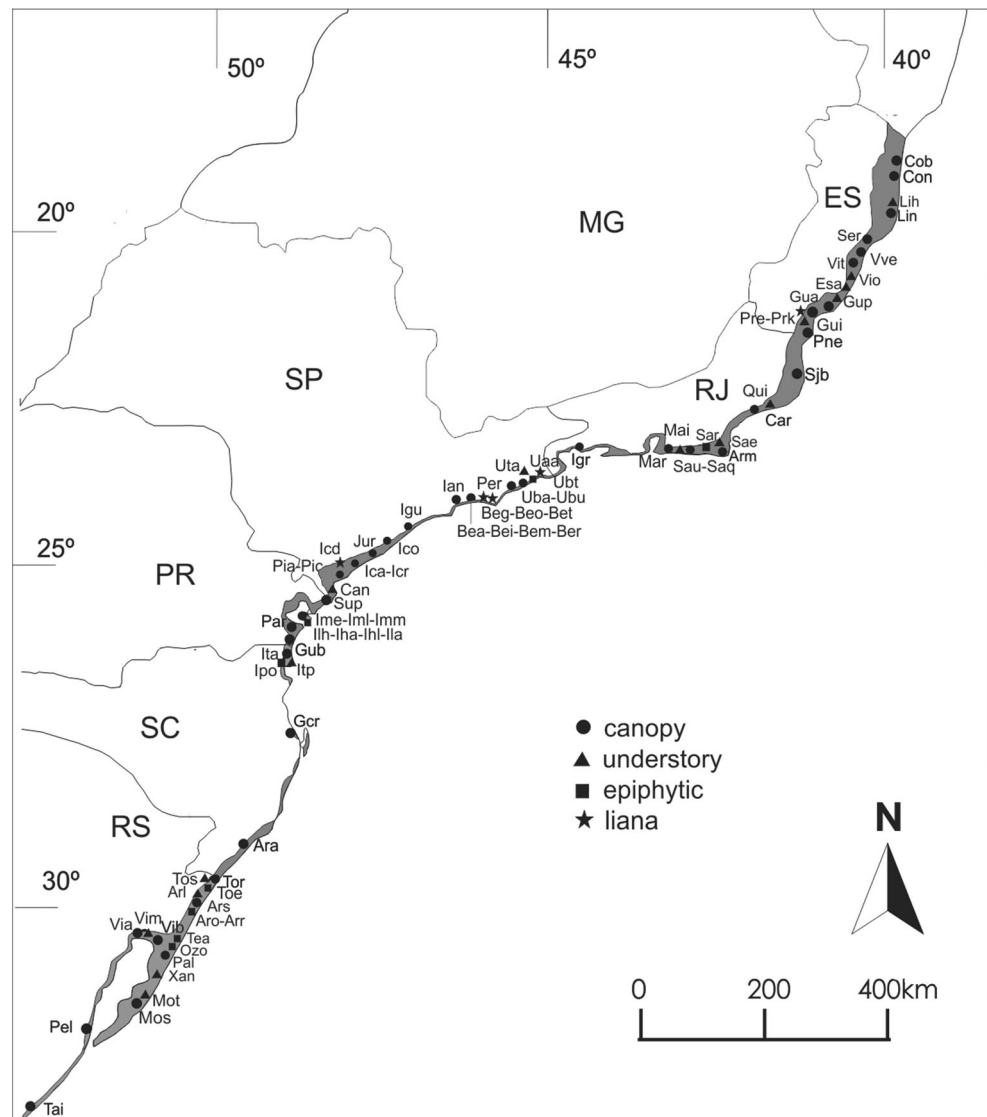
The complete lists of studies and species are found in Tables S1 and S2, respectively

DBH diameter at breast height, BD base diameter, *h* total height

na not applicable

^a Lianas are not considered a defined stratum

Fig. 2 Distribution of floristic and phytosociological studies in Coastal Plain Forests in southern and southeastern Brazil. In gray is the distribution of the coastal plains in Brazil. Sites and references, according to Tables 1 and S1



Kersten 2010), probably because of a combination of factors including high atmospheric humidity (due to the proximity of the sea) and the high incidence of solar radiation. Some widely distributed species are also very common to Restinga Forests, such as *Aechmea nudicaulis*, *Microgramma vacciniifolia* and *Tillandsia geminiflora* (Table 2). Although not a defined stratum and despite the small number of surveys, a total of 171 species of lianas were found. The most frequent species include the *Condylocarpon isthmicum*, *Mandevilla funiformi*, *Ipomoea cairica* and *Chiococca alba* (Table 2).

Thus, despite Restinga Forest being generally considered a physiognomy with low floristic diversity compared to Lowland and Montane Atlantic Forest (Assis et al. 2011; Marques et al. 2011), it is a habitat of a large number of plant species that should be considered in future conservation strategies. Future inventories of undersampled life

forms (herbs, shrubs, epiphytes and lianas) and regions (as shown in Fig. 2) can improve the actual floristic knowledge of Restinga Forests.

Phytogeographical patterns

For many botanists and phytogeographers, the flora of Restingas is a subset of species from the Atlantic Forest complex (see Fiaschi and Pirani 2009 and references therein). These species could have colonized the coastal plain during the last 10,000 years, after the last glaciations, resulting in flora that is relatively less diverse and with little endemism (Araujo 2000). To estimate these relative contributions of different floras on Restinga Forests, we used the checklist compiled from all floristic and phytosociologic studies (Table S2) and classified all species according to their geographical distribution patterns

Table 2 Richness and composition of Restinga Forests in south and southeast Brazil, according to forest stratum

	Forest stratum			
	Canopy/sub-canopy	Understory	Epiphytic	Lianas ^a
Families	89	98	26	34
Richer families (<i>n</i> species)	Myrtaceae (137) Fabaceae (86) Rubiaceae (47) Lauraceae (45) Melastomataceae (30)	Orchidaceae (35) Bromeliaceae (34) Poaceae (23) Rubiaceae (22) Asteraceae (20)	Orchidaceae (125) Bromeliaceae (50) Polypodiaceae (28) Cactaceae (20) Araceae (13)	Asteraceae (25) Apocynaceae (17) Fabaceae (17) Sapindaceae (14) Bignoniaceae (12)
Species	859	424	310	171
Species range	12–181	6–146	25–120	19–97
Angiosperms	857	350	234	170
Gymnosperms	1	0	0	0
Ferns	1	74	76	1
Frequent species (% sites)	<i>Guapira opposita</i> (77) <i>Pera glabrata</i> (72) <i>Psidium cattleianum</i> (66) <i>Tapirira guianensis</i> (53) <i>Alchornea triplinervia</i> (53) <i>Calophyllum brasiliense</i> (51) <i>Myrcia multiflora</i> (51)	<i>Bromelia antiacantha</i> (44) <i>Rumohra adiantiformis</i> (37) <i>Blechnum serrulatum</i> (31) <i>Cynophalla flexuosa</i> (31) <i>Lindsaea quadrangularis</i> (31) <i>Mesadenella cuspidata</i> (31) <i>Peperomia pereskiaefolia</i> (31)	<i>Aechmea nudicaulis</i> (91) <i>Microgramma vacciniifolia</i> (82) <i>Tillandsia geminiflora</i> (73) <i>Virola gigantea</i> (73) <i>Codonanthe devosiana</i> (73) <i>Epidendrum rigidum</i> (73) <i>Pleopeltis pleopeltifolia</i> (73)	<i>Condylocarpon isthmicum</i> (86) <i>Mandevilla funiformis</i> (86) <i>Ipomoea cairica</i> (86) <i>Chiococca alba</i> (86) <i>Cissus verticillata</i> (86) <i>Oxypetalum banksii</i> (71) <i>Mikania biformis</i> (71)

^a Lianas are not considered a defined stratum

Table 3 Biogeographical patterns of woody species found in Restinga Forests of south and southern Brazil. Adapted from Araujo 2000

Biogeographical pattern	Description
Atlantic coast	Species occupying the Brazilian coast between Paraíba and Rio Grande do Sul and the inland areas of Minas Gerais, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul (north). Species also occur in northeastern Argentina and eastern Paraguay. Such regions include Dense Rain Forest, Araucaria Forest and Deciduous and Semi-deciduous Seasonal Forests (IBGE 1992)
Southern and eastern Brazil (and neighboring countries)	Species occurring in the eastern part of Brazil, mainly in the Atlantic Forest but also penetrating the Central Plateau (Cerrado). To the south, the region may exceed the limits of the country and penetrate Uruguay, Paraguay, and northern Argentina but not the Chaco (Paraguay)
Widely distributed	Species with distributions that exceed the boundaries of the South American continent or occur in almost any area of this tropical continent
Peri–Amazonian	Species occurring in the vicinity of the central Amazon basin, overplain terrains, and almost completely surrounding this region
Disjunctive Amazon–Atlantic coast	Species found in these two rain forests and absent in the open formations (Cerrado, Caatinga) that separate them
Atlantic Coast–Restinga Forest	Species potentially restricted to Restinga Forests

(Table 2), based on the species descriptions of regional floras (see methodological details in Box S2). We found that the geographical pattern of species of Restinga Forests are mainly the “Atlantic Coast” (40 %) and the “Southern and Eastern Brazil” (30 %), accounting for 70 % of the

total species (Fig. 3). Interestingly, for epiphytes and lianas these percentages are bit contrasting, with epiphytes mainly with Atlantic Coast pattern and lianas with Southern and Eastern Brazil pattern (Fig. 3). This observation is possible evidence that the flora of Restinga Forests is formed mainly

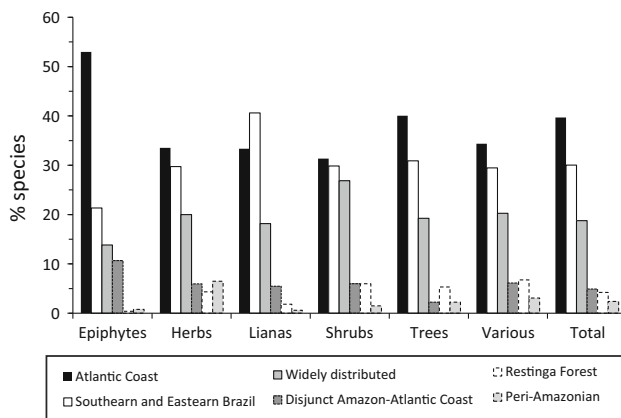


Fig. 3 Biogeographical patterns of tree species occurring in Coastal Plain Forests in southern and southeastern Brazil

by species from Dense Rain Forest, Araucaria Forest and Deciduous and Semi-deciduous Seasonal Forests (IBGE 1992), in addition to species from gallery forests (inset Cerrado) and the forests from the Parana River Basin. Therefore, these interior forests have contributed as an important source of species for the Atlantic flora (Oliveira-Filho and Ratter 1995).

Among the total, 67 species (4 %, Fig. 3) were cited only for the Restinga Forests, which suggests some degree of endemism in this vegetation. Although these areas of the coastal plain are recent, there is evidence that speciation occurred in the Holocene for animal groups (e.g., rodents, Gava and Freitas 2003, Freygang et al. 2004). As a result, it is likely that some plant species have advanced from neighboring areas to the newly formed Quaternary sediments and had conditions for differentiation, resulting in new species. A total of 19 % of the species exhibited a pattern of wide distribution. This value is higher than expected for the Atlantic Forest (11 %, Lima et al. 1997). Other less frequent geographical patterns include the “Peri-Amazonian” and “Disjunctive Amazon-Atlantic Coast” patterns. These species generally have occasional occurrence at lower altitudes or permanence as relicts from the past connection between the Atlantic Forest and Amazonia and the subsequent separation between the end of the Tertiary and Quaternary (Oliveira Filho and Ratter 1995).

Some authors have also suggested that Restinga species have a floristic connection to other physiognomies. For example, herbarium observations showed a disjunctive distribution pattern between the extra zonal formations of the *campos rupestres* (rocky grasslands) in the Espinhaço mountain range and the Restingas (including scrubs) for 16 % of the investigated species (Alves et al. 2007). The possible historical association among these vegetation types is not clearly explained, but ecological factors such

as soil nutritional limitations and soil rapid drainage (Alves et al. 2007) could have favored the permanence of some tolerant species in this disjunctive distribution.

Phenological and reproductive patterns

Climate and phenology

While there is evident latitudinal variations and local determinants (Dau 1960; Brites and Marques 2005), the climate in the region of occurrence of Restinga Forests of southern and southeastern Brazil is strongly influenced by the proximity to the sea. The gradient formed from the beach line toward the interior of the continent is characterized by a continuous decrease in temperature and humidity, associated with lower salinity. Despite small variations in monthly temperatures, the average annual rainfall is high (mean 2,369 mm) due to the frequent accumulation of warm and moist air masses (Marques et al. 2011).

Even in this situation of low water restriction but seasonality in temperature (and photoperiod), several events of the life cycle of plants and ecosystem processes may exhibit seasonality. Litter deposition peaks on some of the wettest months of the year (November, December, January) in forests of Paraná (Marques and Oliveira 2004; Brites et al. 2005) and other sites associated with Restinga Forests (Jackson 1978; Delitti 1987). However, in Rio Grande do Sul, the leaf fall occurs in drier winter months (Marchioretto et al. 2007), which is a pattern that is closer to the standard pattern of tropical forests occurring in greater seasonality (Jordan 1985).

The other phenological phases, i.e., leaf flushing, flowering and fruiting, follow the subsequent months of spring and summer. For example, peaks of leaf flushing in November-January, of flowering in December-January, and of fruiting in March–May were observed in Paraná (Marques and Oliveira 2004, 2008). A similar pattern was observed in the coastal plain forests in São Paulo (Morellato et al. 2000; Staggemeier and Morellato 2011), but in Rio Grande do Sul, these phenological phases seem to occur earlier (Marchioretto et al. 2007). The seedling emergence also shows strong seasonality, with a peak of species germinating in the wet season (January–February) (Marques and Oliveira 2008).

Therefore, the occurrence of rhythms indicates that plants of Restinga Forests respond to even small changes in temperature, daylength and rainfall along the years (Marques and Oliveira 2004). Furthermore, the rapid drainage of water on sandy soil may promote some degree of water stress and seasonality, mainly for herbaceous plants (Marques and Oliveira 2004).

Pollination and seed dispersal

Some estimates of more general mechanisms of reproduction, pollination and seed dispersal at the level of plant communities were held in areas of Restinga Forests. Reproductive systems vary according to forest physiognomy (permanently flooded forests, seasonally flooded and non-flooded). In general, in the three situations, there is a predominance of hermaphroditic species (63, 59 and 68 % for permanently flooded, seasonally flooded, and non-flooded forests, respectively) and minor proportions of monoecious (27, 19, and 13 % for permanently flooded, seasonally flooded and non-flooded forests, respectively) and dioecious species (10, 21, and 19 % for permanently flooded, seasonally flooded and non-flooded forests, respectively) (Matallana et al. 2005). If the abundances of species are considered, the percentage of dioecy can reach 42 % of individuals, which is a high value for tropical forests (Vamosi 2006).

Little has been discussed about the pollination of species of these forests at a community level, but estimates indicate that 95 % of species are entomophilous (Negrelle 2002), and among these, specialized insect pollination can occur in over 60 % of the tree species (Matallana et al. 2005). Other approaches of reproductive studies at the population level are rare (Fischer and Santos 2001; Cesário and Gaglianone 2008)

Seed dispersal in Restinga Forests is, for 74 % of the species, mediated by animals; a lower proportion of anemochory (22 %) and autocory (4 %) is present (Marques and Oliveira 2005). If only the trees are considered, the frequency of animal-dispersed species is even higher (>89 %) (Negrelle 2002; Marques and Oliveira 2005). Tree species with typical zoochorous fruits may also present secondary dispersal by ants, which plays an important role in structuring plant populations (Passos and Oliveira 2003; Pizo 2008). Mutualistic interaction networks between frugivorous birds and forest species exhibit a relatively small number of interactions, low connectance and a general seed dispersal system (Scherer et al. 2007), which seems to be related to the low richness of Restinga Forests.

Disturbance, resilience and biodiversity conservation

Causes and consequences of disturbance

The history of disturbance of Restinga Forests coincides with the history of Brazil. The arrival of Portuguese colonists and the consequent exploitation of plant resources and the setting of towns and cities (Dean 1996) included mandatory disruption to areas of the coastal plain. In the

southern and southeastern coasts of Brazil, where the areas of the coastal plain are relatively large, the relief allowed the use of land for agriculture and livestock. In the early twentieth century, when the industrial revolution encouraged the growth of large cities, coastal areas were gradually occupied by buildings for dwellings, leisure, and fabrics, constituting the most crowded area in the Brazilian territory.

The occupation of the coastal plain areas over the past five decades has involved a series of procedures that significantly changed the environment. Degradation factors include introduction of exotic species (Bechara et al. 2014), vegetation removal for the construction of roads, sand removal and selective extraction of economically important plants, especially ornamentals (Rocha et al. 2007). Other factors directly affecting the coastal plains of the coastal zone of southeastern and southern Brazil include agricultural activities, mainly crops on the small and medium scales of manioc, sugar cane, banana, ginger, pineapple and rice, with the latter mainly in the lowland areas. However, due to the high nutrient deficiency of the soils, agricultural areas were abandoned after some annual production cycles. This abandonment has caused fragmentation, in addition to the accelerated process of degradation by soil and water pollution in urbanized areas (Rocha et al. 2007).

When disturbed, the Restinga Forests have some potential for natural regeneration, depending on the level of the disturbance and the availability of propagule sources. In general, the seed bank appears to be unrepresentative of the regeneration of undisturbed forests (Guedes et al. 2005), although it may be of importance in the restoration of areas through the implementation of soil surrounding forests (Vieira 2004). Seed rain is apparently the main source of new individuals for tree species populations (Simões and Marques 2007; Marques and Oliveira 2008; Rodrigues et al. 2010). Some tree species germinate immediately after dispersal, while others have some degree of dormancy (Marques and Oliveira 2008; Pires et al. 2009a, b). Interestingly, even as forest species, some trees are distributed across a large gradient of light availability (Pires et al. 2009a, b, 2012), which also allows for their establishment in open areas and scrubs. The vegetative propagation is restricted to only 20 % of species (Simões and Marques 2007), or for some species after fire events (Cirne and Scarano 2001; Cirne et al. 2003; Menezes and Araujo 2004).

Deforestation and stump removal (Sá 1996, 2002; Gonçalves and Sá 1998), high temperatures of exposed soil (Araujo et al. 1997; Gonçalves and Sá 1998), low soil fertility (Araujo et al. 1997), the impacts of pasture (Vieira and Pessoa 2001) and the oxygen deficit in flooded soils (Scarano et al. 1998; Scarano 2006) reduce the recruitment of forest species, interfere with successional trajectory and

An overview of the federal-protected areas that include Restinga Forests in southeastern and southern Brazil (see Box S3) indicates that a total of 70 protected areas (1,766,350 ha) were established in this region (Fig. 4). However, 66 % of this total area (25 protected areas, 1,098,818 ha; Table S2) is included in the “sustainable use” category (mainly Environmental Protection Areas), a Brazilian-protected area category that allows for the partial use of biological resources (SNUC 2000). In contrast, only 34 % of the total protected area (45 protected areas, 569,411 ha; Table S2) is of the “integral protection” type, guaranteeing a higher protection of biodiversity (SNUC 2000). Despite the presence of other small state- and municipality-protected areas in the region, this limitation of integral protection areas (Rocha et al. 2007), the possible social conflicts arising from the creation of protected areas (Milano 2002; Diegues 2004), the external pressures of various social groups, and even the ignorance about the existence of these protected areas (Vitali and Uhlig 2010) are factors that directly affect conservation efforts of Restinga Forests. These factors can cause future species extinctions; estimates suggest that there are 33 threatened plant species occurring in the Restingas (Fundação Biodiversitas 2005; Leão et al. 2014).

Conclusions

The Restinga Forests are certainly one of the Brazilian vegetation types that exhibits some of the more contrasting characteristics. The geographical localization at the edges of the Atlantic Forest, limited by the Atlantic Ocean on one side and by urban centers on the other, naturally exposes the Restinga Forest fragments to the pressures that are projected to intensify in the future as the effects of sea level elevation (resulting from global warming) and the disordered development of cities (resulting from population growth) continue (Goudie 2013). Its physiognomy, characterized by discontinuous stretches of low and high forests with low diversity interspersed with areas of exposed sandy soil and open formations, contributed to the lower level attention to these ecosystems over the years. However, we argue that these remaining fragments preserve a large part of the ecosystem processes and services (MEA 2005) in the Atlantic region, such as sediment retention, nutrient cycling, soil formation, protection of water bodies, carbon sequestration, and pollination, among others. Thus, although spatially limited, Restinga Forests play an important role in the conservation of the Atlantic Forest Biome.

In this review, we demonstrated that a relatively large body of studies was performed over the last decades that allowed for identification of the flora of Restinga Forests in most regions (but some gaps apparently exist) and suggest that it is typical sub-formation of the Atlantic Forest, but

with some floristic specificity. The studies have also suggested that the forest diversity is supported by fine adjustments involving the maintenance of nutrients in the ecosystem and the interaction with the flora and fauna of the neighboring vegetation types. Possibly, some of these processes are temporal- and spatial-scale dependent, which reinforces the importance of long-term and coordinating studies, which are still rare in these systems (Lima et al. 2011; Joly et al. 2012). Future approaches on Restinga Forests should fill some gaps in the knowledge of these systems. For example, studies on the phylogeography and phylogeny of the species occurring in Restinga Forests (provided in the Online Resource) could help to explain the processes of species dispersal and colonization of the plain coasts and to more precisely determine the vegetation formation. The comparative study of the ecological processes occurring among Restinga Forests and other ecosystems of the Atlantic Forest Biome (Lowland and Montane Forests, Restinga scrubs, mangroves, marshes, etc.) could help to understand how the diversity of such highly diverse systems is maintained. Additionally, studies on the physiological and morphological variations in species occurring in Restinga Forests, Restinga scrubs and Lowland Forests could explain the differences in the physiognomies in the coastal plains in south and southern Brazil.

Finally, despite the considerable number of protected areas and other legal instruments for biodiversity conservation, Restinga Forests are still permeable to various law subterfuges, which place them in a situation of extreme vulnerability. Restinga Forests have been considered as less important and “impoverished” in relation to the neighboring forests that compose the Atlantic Forest ecosystems, but the maintenance of the biodiversity of the biome depends on the conservation of these associated ecosystems, with which it has strong ecological interactions (Scarano 2002, 2009). Thus, future conservation actions for Atlantic Forest should improve the effectiveness of the existing protected areas and guarantee the connection between fragments of Restinga Forests and the other ecosystems of the littoral.

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