REVIEW

Structure, Function and Floristic Relationships of Plant Communities in Stressful Habitats Marginal to the Brazilian Atlantic Rainforest

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The Brazilian Atlantic rainforest consists of a typical tropical rainforest on mountain slopes, and stands out as a biodiversity hotspot for its high species richness and high level of species endemism. This forest is bordered by plant communities with lower species diversity, due mostly to more extreme environmental conditions than those found in the mesic rainforest. Between the mountain slopes and the sea, the coastal plains have swamp forests, dry semi-deciduous forests and open thicket vegetation on marine sand deposits. At the other extreme, on top of the mountains (>2000 m a.s.l.), the rainforest is substituted by high altitude fields and open thicket vegetation on rocky outcrops. Thus, the plant communities that are marginal to the rainforest are subjected either to flooding, drought, oceanicity or cold winter temperatures. It was found that positive interactions among plants play an important role in the structuring and functioning of a swamp forest, a coastal sandy vegetation and a cold, high altitude vegetation in the state of Rio de Janeiro. Moreover, only a few species seem to adopt this positive role and, therefore, the functioning of these entire systems may rely on them. Curiously, these nurse plants are often epiphytes in the rainforest, and at the study sites are typically terrestrial. Many exhibit crassulacean acid metabolism. Conservation initiatives must treat the Atlantic coastal vegetation as a complex rather than a rainforest alone.   © 2002 Annals of Botany Company

Key words: Review, Atlantic rainforest, biodiversity hotspot, epiphyte, facilitation, nurse plant, high altitude vegetation, marginal habitat, restinga, rocky outcrop, swamp.

INTRODUCTION

The Brazilian Atlantic rainforest once covered most of eastern Brazil. It has now been reduced to only 7·5 % of its original area. Since it stands out as one of the main centres of biodiversity in the world, with high species diversity and high levels of endemism, it is now considered from a global perspective as one of the 25 biodiversity hotspots for conservation priorities (Fonseca, 1985; WCMC, 1992; Myers *et al.*, 2000). The worldwide notoriety of the rainforest at the core of this complex hides the fact that it is only one of several types of plant communities within a much greater vegetation complex. For instance, a recent review of the Atlantic forests defines them as vegetation composed of two forest types: a coastal rainforest and a semi-deciduous forest type (Morellato and Haddad, 2000). Oliveira-Filho and Fontes (2000) proposed that the definition of Atlantic forests should be comprehensive, encompassing rainforests, semi-deciduous forests and also the southern subtropical *Araucaria* forests and the northeastern enclaves of *brejo* forests. My argument is that from evolutionary and conservation viewpoints, the Atlantic coastal vegetation of Brazil, particularly in the case of the state of Rio de Janeiro, should be treated as a mosaic comprising all forest types and also the neighbouring open vegetation. As long ago as 1979, Rizzini noted that the

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Atlantic coastal vegetation should be seen as a complex formed by several plant communities including those at the periphery of the forests.

Plant communities at the periphery of the Atlantic rainforest are subjected to more extreme environmental conditions than plants in the mesic rainforest (Scarano *et al.*, 2001). These communities experience a wide array of adverse environmental conditions, such as high and low (including freezing) temperatures, flooding, drought, constant wind, high salinity and lack of nutrients. Thus, diversity, productivity and structural complexity are lower in these communities. Table 1 lists the main characteristics of the plant communities found within the Atlantic coastal vegetation. Figure 1 illustrates the geographic location of these communities in the state of Rio de Janeiro.

This paper synthesizes a decade of research on the plant communities at the periphery of the Atlantic forest in the state of Rio de Janeiro. It covers aspects related to plant community structure, community function and phytogeography. It focuses on three vegetation types: the open scrub vegetation of the sandy coastal plains, the swamp forests and the vegetation growing on rocky outcrops at high altitude. Despite the extreme environmental differences between these habitats, I propose that community structure and function among these habitats is strikingly similar. On the basis of evidence presented in this paper and also the floristic and evolutionary links between marginal habitats and the Atlantic rainforest (Rizzini, 1979; Araujo, 2000;

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TABLE 1. *Some of the main plant communities of the Atlantic forest complex in the state of Rio de Janeiro, south-eastern Brazil*

Habitat	Location	Limiting factors	References
High altitude	Includes *Araucaria* forest, marshes and rocky outcrops; >2000 m a.s.l.	Frost, drought, shallow or absent soil, high light irradiation	Safford (1999*a, b*)
Rainforest	Sea level to approx. 1500 m a.s.l.	Deep shade	Rizzini (1979)
Rocky outcrops	Coast and inland; elevations from 0–1400 m a.s.l.	Drought, shallow or absent soil, salinity (coast)	Meirelles *et al.* (1999)
Swamp forest	Coastal lowlands	Flooding	Scarano *et al.* (1997)
Dry forests	Coastal lowlands (mainly at Búzios-Cabo Frio region, north of Rio de Janeiro)	Drought, salinity, low in nutrients	Araujo (1997)
Restingas	Along the coast, includes marshes, dry and swamp forests and open clumped vegetation	Drought, salinity, low in nutrients	Lacerda *et al.* (1993)

The rainforest is the predominant formation in area and diversity, whereas the associated formations have fewer species.
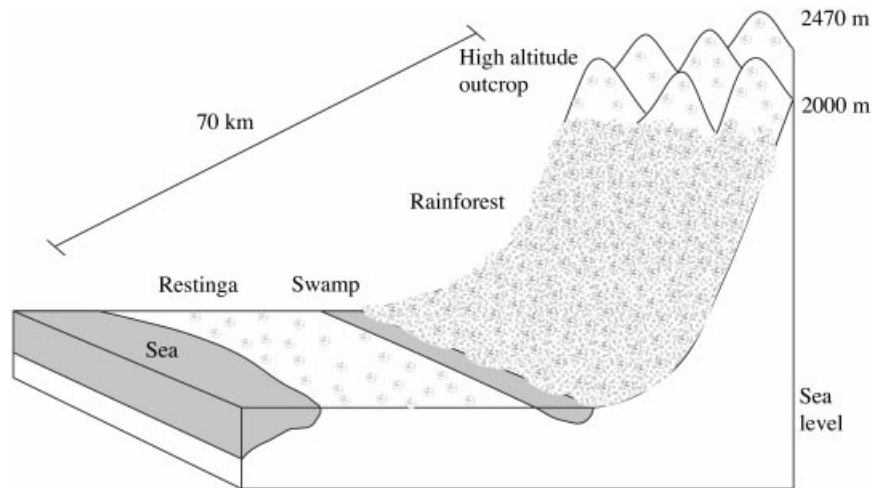

FIG. 1. Schematic representation of the Atlantic forest complex in the state of Rio de Janeiro. Note that the distance between the lowland and the high altitude vegetation is only approx. 70 km as the crow flies.

Lima, 2000), I also propose that conservation initiatives must treat the Atlantic forest as a vegetation complex rather than as a single entity, i.e. the forest formations.

STUDY SITES

This paper reviews studies conducted in three vegetation types: (*a*) swamp forests growing on periodically or permanently flooded terrain at the foot of the coastal mountain; (*b*) a mosaic of plant communities collectively known as the *restinga*, which occupies the sandy plains formed by marine deposits in the late Quaternary that stand between the sea and the Atlantic forest mountain chain; and (*c*) high altitude vegetation, on the mountain highlands above the treeline and ranging from 2000 to 2470 m a.s.l., consisting of fields covered by grasslands, marshes and vegetation on rocky outcrops. This review compares data collected for specific plant communities within each of these three vegetation types, in the state of Rio de Janeiro.

The information in Table 2 briefly describes the sites where most of the research for this review was conducted.

There is still little detailed and uncontroversial information about the palaeo-ecological, geological and recent environmental history of the study sites and of the Atlantic complex in Rio de Janeiro as a whole. The rainforests in the state of Rio de Janeiro date from the Tertiary and cover areas with annual rainfall as low as 1173 mm; rainfall is, however, well-distributed (Oliveira-Filho and Fontes, 2000). In the north of Rio de Janeiro state the mountains are further from the coast than they are in the south (Oliveira-Filho and Fontes, 2000), and the north therefore has more extensive and wider lowland plains (see Fig. 1). The swamps stand on a substrate that is composed mainly of Quaternary alluviums, and are punctuated by rounded hills ranging from 30 to 205 m. Vegetation on the hills is typically a sub-montane rainforest. Forest cover of swamps in Rio de Janeiro has been reduced to a minimum since the mid-20th century due to river dam construction and

Table 2. *Characteristics of the Brazilian Atlantic Rainforest and associated habitats referred to in the text*

Habitat	Location	Climate	Nurse plant species	References
High altitude rocky outcrops	Itatiaia National Park (20°25′S, 44°50′W; 2400 m a.s.l.)	Markedly seasonal. Annual rainfall of 2273 mm, concentrated in the summer (November to February). Winter (May to August): cold, dry, and less cloudy than the summer. Summer daytime maximum temperature of 23 °C and winter night-time minimum of –10 °C.	*Fernseea itatiaiae**, *Pleurostima gounelleana**, *Campylopus pilifer**, *Polytrichum commune**	Scarano *et al*. (2001); Ribeiro (2002)
Swamp forest	Poço das Antas Biological Reserve (22°30′S, 42°15′W; sea level)	2260 mm rainfall well distributed throughout the year, with a discrete dry season from May to August. Annual temperatures: mean = 25 °C, max = 38 °C, min = 14 °C.	*Nidularium procerum*[†]	Scarano *et al*. (1997); Rôças *et al*. (2001)
Open restingas	Environmental Protection Area of Massambaba (22°56′S, 42°13′W; sea level)	Markedly seasonal. Annual rainfall of 800 mm concentrated in the summer (November to February). Annual temperatures: mean = 25 °C, max = 36 °C, min = 12 °C.	*Allagoptera arenaria**, *Neoregelia cruenta*[†], *Clusia fluminensis*[†]	Zaluar and Scarano (2000); Scarano *et al*. (2001)
	Restinga de Jurubatiba National Park (22°23′S, 41°45′W; sea level)	Markedly seasonal. Annual rainfall of 1164 mm concentrated in the summer (November to February). Annual temperatures: mean = 23 °C, max = 30 °C, min = 20 °C.	*Allagoptera arenaria**, *Aechmea nudicaulis*[†], *Clusia hilariana*[†]	Zaluar and Scarano (2000); Liebig *et al*. (2001)

* Both pioneer and nurse plants.
[†] Nurse plants only.

wood extraction. The data discussed here were obtained at the Poço das Antas Biological Reserve, where only 50 % of the total area consists of well-preserved remnants (Lima, 2000).

Most sandy coastal plains in the state of Rio de Janeiro consist of two beach ridges dating from the Holocene [5000 to 3000 years before the present (BP)]. The oldest sandy plains established in the state date from the Pleistocene (120 000 years BP; see Martin *et al*., 1993). Araujo (2000) classified the restingas of the state of Rio de Janeiro into ten zones according to their flora, which is related to local variation in climate and geological history. The data reviewed here were obtained in two of these zones, both located on the northern coast of the state. The climate here is drier due to the cold oceanic upwelling of the Cabo Frio region (Araujo, 1997). One of the sites examined is within the Cabo Frio region (Environmental Protection Area of Massambaba), and the other (Restinga de Jurubatiba National Park) is approx. 100 km further north (see also Table 2).

The Massambaba sandy plains stretch between the ocean and the pleistocenic lagoon called Araruama, which is Brazil's second largest salt lake. They are composed of two parallel beach ridges of different ages, separated by a low area, where holocenic lagoons showing different sedimentation stages are situated (Muehe, 1994). On its east side, where most of the data reviewed here were collected, the pleistocenic, innermost beach ridge (Martin and Suguio, 1989) was covered by a dune system approx. 2000 years BP (FEEMA, 1988). Here, the distance between the ocean and the Araruama lagoon is approx. 1·5 km (Scarano *et al*., 2001).

Unlike most sandy coastal plains in Rio de Janeiro, the Jurubatiba plains consist of a series of parallel pleistocenic beach ridges (120 000 years BP) formed by the silting of marine sediments, which formed several lagoons due to the obstruction of ancient river deltas (Henriques *et al*., 1986). The series of beach ridges reach a maximum width of 10 km. Along the Brazilian coast, three successive transgression movements of the sea took place during the Holocene (approx. 5100 years BP, 3900–3600 years BP and 2700–2500 years BP) followed by regressions (Martin *et al*., 1989). However, the length of transgression was progressively smaller here and apparently did not destroy the Pleistocene ridges completely.

The high altitude vegetation in Rio de Janeiro state has recently been reviewed with regard to climatic, physical and biotic characteristics (Safford, 1999*a, b*). The data described here refer mostly to the rocky outcrops within the high altitude fields of the Itatiaia Plateau, at the Itatiaia National Park (see also Table 2). Whether or not glaciers occurred in this region during glaciation peaks is still the subject of debate (Ebert, 1960; Segadas-Vianna, 1965). However, a temperature regime similar to the current one in the plateau (Table 2) may have occurred at altitudes 1000 m lower, while peri-glacial conditions reigned in the plateau itself (Behling, 1998). Rocky outcrops dominate the landscape of the plateau and the predominant rock is nepheline-sienite, an alkaline pluton not very common in Brazil. It has a high dissolution rate, and channels and holes form frequently (Leinz and Amaral, 1989). However, narrow fissures, which are common in granite and favour the fixation of plant species, are rare. The occurrence of soil on the rocks is also rare, patchy and shallow.

PHYTOGEOGRAPHY AND FLORISTIC RELATIONSHIPS

Restingas, swamps and high altitude vegetation have distinct floristic links with the neighbouring Atlantic rainforest. While most of the flora of the restinga (Rizzini, 1979) and the swamp forest (Lima, 2000) originated from the Atlantic rainforest, the flora of the high altitude rocky outcrop vegetation bears less resemblance to it (Safford, 1999*a*, *b*; Ribeiro, 2002). Araujo (2000) showed that approx. 60 % of the species listed for the restinga of coastal Rio de Janeiro occur in the Atlantic rainforest; the remainder originated in other vegetation of Rio de Janeiro (coastal inselbergs and semi-deciduous dry forests) and elsewhere in Brazil (cerrado, caatinga and the Amazon). Oliveira-Filho and Ratter (1995) showed that many rainforest species have expanded their distribution into markedly seasonal habitats via riverside forests; this may also apply to the restingas. Very few plant species seem to be endemic to this vegetation. The same is true for birds and mammals: 98 % of restinga birds are found in the rainforest (Reis, 1998) and restinga mammals are a mere sub-group of the same fauna from the rainforest (Cerqueira *et al.*, 1990).

To date, the swamps have not been subjected to a thorough phytogeographic study (but see Lima, 2000), but some of the species lists available indicate that the flora is mixed, being mostly composed of: (*a*) a few typically flood-tolerant trees broadly distributed in other parts of Brazil, such as *Calophyllum brasiliense* Cambess and *Symphonia globulifera* L.f. (both Clusiaceae); (*b*) a few flood-tolerant trees restricted to the southeast of the country, e.g. *Tabebuia cassinoides* (Lam.) D.C. (Bignoniaceae); and (*c*) many less abundant tree species that also have their origins in the Atlantic rainforest (Scarano *et al.*, 1998).

The almost total absence of endemic plant species in the lowlands suggests that, despite the differences in terms of selective pressures between these peripheral habitats and the rainforest, there has been insufficient time for plant speciation. Perhaps even more surprising is the fact that species richness in the lowlands is quite high. This implies that a large number of rainforest plant species were able to adjust to extreme conditions in order to colonize the geologically younger lowlands. Since new species could not have evolved during this time, it is likely that the successful migrating plant species from the Atlantic rainforest had a broad ecological plasticity. Recent studies have indicated wide inter- and intrapopulation phenotypic variation for some of these species, both locally and across habitats, with regard to architecture, leaf and wood morphology and anatomy, physiology and growth patterns (Freitas *et al.*, 1998; Herzog *et al.*, 1999; Callado *et al.*, 2001*a*, *b*; Cirne and Scarano, 2001; Rôças *et al.*, 2001; Scarano *et al.*, 2001), which is evidence of such ecological plasticity.

Historically, the high altitude vegetation has offered several opportunities for the fixation and differentiation of forest, cerrado (the neotropical savanna) and temperate species (Brade, 1956). For instance, during the Pleistocene glaciations, the high altitude areas were probably nearer to distinct kinds of open vegetation, while forests were retracting (Ribeiro, 2002). Climatic oscillations could also explain its floristic disjunctions regarding the Andes (Brade, 1956; Safford, 1999*a*), and the grassland vegetation of southern Brazil (Brade, 1956). On the other hand, the current border with the Atlantic forest is a possible port of entry for tropical species in a temperate environment (Ribeiro, 2002). However, the high altitude flora in the state of Rio de Janeiro currently differs floristically from the rainforest at lower altitudes in physiognomy and floristics, mostly due to soil scarcity and patchiness (see Study Sites) and climate (Safford, 1999*a*, *b*; Ribeiro, 2002). Temperatures below 0 °C are common on winter nights on the Itatiaia Plateau, where an average of 56 frosts occur per year (Segadas-Vianna, 1965; Segadas-Vianna and Dau, 1965). These low temperatures provide a strong barrier for establishment of most taxa from the rainforest, which are predominantly tropical (Gentry, 1982). Temperatures between 6 and 10 °C are sufficient to cause chilling injury, whereas those below 0 °C cause freezing injury in most tropical plants (Crawford, 1989). Thus, low temperatures have led to selection for a high proportion of local endemics and species endemic to mountain peaks (Safford, 1999*a*; Ribeiro, 2002). Despite the high level of endemism, Scarano *et al.* (2001) have shown that some of these species are apparently quite plastic in terms of carbon, water and nitrogen use. For instance, *Fernseea itatiaiae* (Wawra) Baker, a local endemic to the high altitude rocky outcrops, showed the highest variation of $\delta^{15}N$ values among the approx. 30 species investigated from restingas, dry forests and high altitudes. Values ranged from –2·52 to +1·81 ‰ (4·3 ‰ variation). This might be related to variation in root system functioning in response to soil depth, before reaching bare rock.

COMMUNITY STRUCTURE AND FUNCTION

Other than the obvious structural difference between swamp forests and open, scrub vegetation of restingas and high altitude rocky outcrops, these three marginal vegetation types are strikingly similar in structure and function. They are species-rich but are dominated by one (swamp) or a few (open vegetation types) species. Monodominance and oligarchy are common features in habitats subjected to extreme environmental conditions. Additionally, the functioning of these vegetation types appears to rely on a few species that provide appropriate environmental conditions for germination and growth of other species, the so-called 'nurse plants' (Franco and Nobel, 1989; Young *et al.*, 1995). An overview of studies conducted on the swamp forests (Scarano *et al.*, 1997, 1998, 1999; Freitas *et al.*, 1998) suggests that it can be divided into three functional groups related to characteristic plant interactions: (*a*) the mono-dominant, emergent, deciduous tree, *Tabebuia cassinoides* DC (Bignoniaceae), which does not provide year-round shade to understorey plants; (*b*) 59 tree species represented by a small number of individuals (approx. 30 % of the total, on 0·5 ha) that are mostly evergreen, and provide shade to the understorey throughout the year; and (*c*) the monodominant understorey herb, the light-sensitive tank-bromeliad *Nidularium procerum* Lindm., which provides safe germination sites (wide leaf tanks that trap litter and

seeds) for plants that would not germinate on the permanently flooded soil below them. Although there is a lack of long-term monitoring of water-level fluctuations in the swamp, it is possible that in drier years massive seed germination might take place in the soil since the water layer is only superficial. In spite of this, the tank-bromeliad plays a vital role for the locally rare trees by providing year-round germination sites, while the rare trees provide year-round shade for the light-sensitive bromeliads. The monodominant tree *T. cassinoides* does not seem to have any positive interaction with the locally rare trees or with the bromeliads. Although seeds of *T. cassinoides* may germinate in the 'suspended soil' provided by the bromeliads, it does not rely on this exclusively since it is able to reproduce vegetatively. Scarano *et al.* (1998) proposed that this functional organization is the reason why degraded swamp forests often turn into exclusive stands of *T. cassinoides*: removal of the shade-providing locally rare trees results in the disappearance of bromeliads and *vice versa*, whereas the *T. cassinoides* population remains unaffected. It remains to be seen how these bromeliads are capable of withstanding long-term flooding. The very small rhizomes of these plants may rule out the possibility of tolerance mechanisms. Freitas *et al.* (1998) proposed that these plants behave as 'epiphytes on mud'. Shoot autonomy for foraging and the formation of tank roots, i.e. geotropically negative roots that forage into the leaf rosette above them (see Pittendrigh, 1948; Medina, 1974), probably constitute an efficient escape mechanism on the flooded ground, as they do in epiphytic habitats for these bromeliads.

Positive plant–plant interactions, such as those described for the swamp forest, are also seen in the open vegetation types. Zaluar and Scarano (2000) reviewed colonization and vegetation dynamics in the open scrub vegetation of the restingas. There has been much debate as to why this vegetation is open and there is a lack of palaeo-ecological evidence in this respect. However, it is known that human occupation of the sandy plains of Rio de Janeiro dates from 8000 years BP (Kneip and Pallestrini, 1984), but more dramatic changes in the landscape have probably taken place since the country was discovered by the Portuguese in the year 1500. Today, some restingas still suffer man-made impact through fire (Cirne and Scarano, 2001) or cattle, but even apparently pristine areas display an open physiognomy.

In the restingas, formation of vegetation islands and succession are triggered by the colonization of pioneer herbs and/or woody plants, which may favour the entry of other species into this community. The ability to colonize bare sand (which may reach temperatures as high as 70 °C during mid-summer at the peak of radiation) via seeds is restricted to a few species such as the geophyte palm *Allagoptera arenaria* (Gomes) Kuntze. Seeds of drought-resistant plants such as cacti and bromeliads require shade provided by shrubs to germinate. Small vegetation islands formed by the palm, cacti [e.g. *Pilosocereus arrabidae* (Lem.) Byles & G.D. Rowley and *Cereus fernambucensis* Lem.] and bromeliads [e.g. *Aechmea nudicaulis* (L.) Griseb and *Neoregelia cruenta* (Graham) L.B. Sm.] favour the entry

of woody species. Among the woody species, those belonging to the genus *Clusia* (e.g. *C. hilariana* Schlecht. and *C. fluminensis* Planch & Triana) seem to be the main nurse plants under which many plant species become established (Zaluar and Scarano, 2000). However, other woody species may form vegetation islands where few or no other species become established [e.g. *Protium icicariba* (DC.) Marchand]. In some cases, such as in the Restinga de Jurubatiba National Park, *P. icicariba* and *C. hilariana* share community dominance. Thus, neighbouring vegetation islands of a given restinga may have totally different species richness, diversity and structure depending on the dominant woody species of the vegetation island. They may also be in different trajectories along the successional process. Small islands can be either newly formed or simply an old fragment of a larger island, which retracted due to the death of its nurse tree. Large islands can also result from fusion of several smaller islands. In the future, analyses of time series of aerial photographs, along with species addition and removal experiments, will allow a better understanding of the dynamics and succession of vegetation islands in the restingas.

Unlike the restingas, the openness of the vegetation on rocky outcrops of Itatiaia has not been attributed to long-term human intervention, but rather to the inherent difficulties related to plant fixation on rocks or shallow soil, as discussed previously. However, the study area is not totally free from current human intervention, since predatory tourism (on a more regular basis) and man-made fires (less frequent) occur. Similarly to the open restinga vegetation, it has been determined that plants which form mats on the rocky surfaces of the high altitude outcrops are nurse plants that provide the substrate upon which other plants establish (Ribeiro, 2002). Common pioneer mat species at altitude in Itatiaia are *Fernseea itatiaiae* (Bromeliaceae), *Pleurostima gounelleana* (Beauv) N.L.de Menezes (Velloziaceae), *Campylopus pilifer* Brid. and *Polytrichum commune* Hedw. (both Musci). Geophytes such as *Stevia camporum* Baker (Asteraceae) and *Alstroemeria foliosa* Mart. (Alstroemeriaceae) grow on mat species and not on the bare rock. The former is more frequent on islands of mosses, whereas the latter is more abundant on islands of *Pleurostima*. Although variations in relief on the rocky outcrops provide a myriad of microhabitats, habitat preference of these geophytes is dependent upon the mat species. Successional mechanisms on the high altitude rocky outcrops are therefore more decisively triggered by species–species relationships than by topography.

RAINFOREST CANOPY PLANTS AS TERRESTRIAL NURSE PLANTS IN THE MARGINAL HABITATS OF THE FOREST

Table 2 summarizes the species that play a role as nurse plants in the plant communities studied. Typically, most of the nurse plants are epiphytes in the Atlantic rainforest, whereas in the marginal habitats they are terrestrial plants playing a role as nurse plants. This is true of the bromeliads in the swamp forests (*Nidularium procerum*), in the restingas (*Neoregelia cruenta* and *Aechmea nudicaulis*)

and in the high altitude rocky outcrops (*Fernseea itatiaiae*). Similarly, the *Clusia* plants in the restinga are hemiepiphytic stranglers in the rainforest. These species, with the apparent exception of *Fernseea* (Scarano *et al.*, 2001), are CAM (crassulacean acid metabolism) plants (Franco *et al.*, 1996; Reinert *et al.*, 1997; Lüttge, 1999; Scarano *et al.*, 1999).

CAM is characteristically a stress-resistance mechanism that maximizes water-use efficiency. Although, it is not surprising that stress-resistant plants may nurse less resistant ones, the fact that these terrestrial clusias and bromeliads have CAM metabolism and originate in the montane Atlantic rainforest is of great interest. Their migration to the geologically younger lowlands of the restingas and swamp forests was seemingly followed by the expression of a new habit (from epiphytic in the rainforest to terrestrial plants in the lowlands) and a new ecological function (nursing seeds and seedlings of other plant species). Thus, the rainforest strangler *Clusia* is the most dominant nurse shrub of the open restingas, and the epiphytic bromeliads of the rainforest provide safe germination sites as terrestrial plants in inhospitable substrates such as the hot sandy soil of the restingas and the flooded soil of the swamps. Although CAM is not a common feature of plants on the high altitude rocky outcrops (see Scarano *et al.*, 2001), the main nurse plants (bromeliads, Velloziaceae and musci) are either epiphytic in forests or linked to phylogenetic groups where epiphytism is common. Porembski *et al.* (1998) proposed that the high plant species diversity found in inselbergs within the Atlantic forest domain is partially due to exchange of species between the rocky habitats and the canopy of neighbouring forests.

Medina (1974) discussed the question of whether forest epiphytes originated from terrestrial parents in open, sun-exposed vegetation or if epiphytes migrated from the forest floor to the canopy, and then subsequently colonized open vegetation. The latter possibility seems more plausible for the geologically younger lowlands and sandy plains, whereas the former possibility may have occurred at high altitude. In the case of the Atlantic forest complex, then, both trajectories seem likely.

Forest canopy plants have apparently played a major role in increasing species richness in these marginal habitats. In the high altitude outcrops, the nurse plants are also pioneers, capable of germinating and growing on almost bare rock; this does not seem to be the case in the lowlands: clusias and bromeliads are unable to germinate on bare sand or on flooded soil. The pioneer plant in the restingas is predominantly the geophyte palm *Allagoptera arenaria*. Establishment is therefore a major hurdle to be overcome by plants in such habitats, and only a few can do so without the aid of another species. Thus, stress-resistance through mechanisms such as CAM (Herzog *et al.*, 1999; Scarano *et al.*, 2001) or flood-tolerance (Scarano *et al.*, 1997) are not sufficient to ensure establishment in restingas and swamps.

small number of nurse plants. This small number of nurse plants, in an otherwise species-rich community, often results in a smaller degree of functional redundancy and in higher community fragility (see Shrader-Frechette and McCoy, 1993). The eventual loss of nurse plants in such communities may result in dramatic changes in species composition and diversity, as shown by Scarano *et al.* (1998) for the swamp forest. Experimental removal of nurse plants in similarly structured communities often results in major changes in species composition (e.g. Holzapfel and Mahall, 1999).

The functional ecology of plant communities is often not a part of conservation initiatives, which are mostly based on numerical diversity, levels of community endemism and rates of habitat destruction. In the Atlantic forest complex, an apparent dualism exists between the rainforest, which fits these criteria, and its marginal habitats, which are less diverse and show less endemism (although the high altitude rocky outcrops are a notable exception). For instance, the classification of biodiversity hotspots provided by Myers *et al.* (2000) does not include these marginal habitats. Unfortunately, the distribution of federal conservation units in Brazil is also more concentrated on 'hotspots', e.g. only 14 000 ha of restingas are protected as the single federal conservation unit for restinga in the country (Restinga de Jurubatiba National Park).

Smith *et al.* (2001) pointed out that bias might arise from the biodiversity hotspot classification, resulting in a disregard for important evolutionary and adaptive processes taking place in low diversity communities and/or ecotones. Thus, the eventual establishment of conservation goals or research priorities as guided by such a classification could be misleading. This could be the case for the Atlantic rainforest complex, if viewed solely as the rainforest and not inclusively as the rainforest plus its marginal habitats. This is also true with regards to animal conservation. Although fragmentation has often removed connections between the rainforest and its marginal habitats, many bird species from the rainforest are reported to use the restingas as a buffer zone and as a geographic extension of their distribution (Gonzaga *et al.*, 2000). In the case of mammals, the only two studies on large-scale movements in the landscape (Pires and Fernandez, 1999; Pires *et al.*, 2002) report movements of marsupials and rodents between isolated forest fragments in the Atlantic forest lowlands where the swamps are located.

Perhaps more importantly than endemism, the rainforest has a pool of highly environmentally plastic species which have the capacity to colonize habitats distinctly different from their own, such as restingas and swamps. This ecological plasticity expressed in plants at these marginal habitats may be of key relevance in a global change scenario and must not be treated as a lower conservation priority.

CONSERVATION

The plant communities marginal to the Atlantic rainforest are structurally and functionally dependent on a

FINAL REMARKS

This overview has presented an evolutionary hypothesis about the origins, structure and functioning of some plant

communities that are marginal to the Atlantic rainforest of Rio de Janeiro, and a viewpoint regarding conservation of this vegetation complex. To further advance this hypothesis and to provide more subsidies for conservation, some key aspects must be addressed in the future: (*a*) palaeoecological studies, particularly of the Quaternary (e.g. Behling, 1998; Ledru *et al*., 1998), are required to provide further insights into floristic and ecological links between the distinct plant communities; (*b*) DNA phylogenetic studies (Vaasen *et al*., 2002) are needed to provide a molecular basis for the understanding of processes such as migration, speciation, vicariance and phenotypic plasticity; (*c*) studies on population genetics (e.g. Cardoso *et al*., 1998) coupled with reproductive biology (e.g. Wendt *et al*., 2001, 2002) are essential to assess genetic diversity and mating systems of nurse plants; and finally (*d*) experimental transplantation of species between habitats (e.g. Freitas *et al*., 1998) and addition and removal of species within habitats will allow a more accurate assessment of the functional role of nurse plants and also of species plasticity.

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