Species composition and biogeographic relations of the rock outcrop flora on the high plateau of Itatiaia, SE-Brazil

KÁTIA TORRES RIBEIRO1,2,3, BRANCA MARIA OPAZO MEDINA1 and FABIO RUBIO SCARANO1

(received: March 18, 2005; accepted: September 18, 2007)

ABSTRACT – (Species composition and biogeographic relations of the rock outcrop flora on the high plateau of Itatiaia, SE-Brazil). We studied the flora of vegetation islands on rock outcrops on the Itatiaia Plateau (22°21'S and 44°40'W), at 2,400 m.a.s.l. A total of 114 vascular plant species, which correspond to ca. 20%-25% of the currently inventoried flora of the plateau, were sampled in 197 small vegetation islands (total area of 0.034 ha). Xerophytes and hydrophytes were often found side by side due to environmental heterogeneity at a small scale, explaining in part the high species diversity. Rock outcrops may support floras quite distinct from those in neighbouring habitats, due to the action of strong environmental filters, but in Itatiaia the geographic distribution patterns among rupicolous plants appear to mimic those described for the whole flora around it, with 15.1% of narrow endemic species and six strictly rupicolous plants. Underlining the “temperate” nature of the high elevation climate in Itatiaia, the sampled flora was dominated by species of the families Asteraceae and Poaceae, and the number of CAM (crassulacean acid metabolism) species was very low. A few endemic species of tropical origin – Pleurostima gounelleana (Beauv.) Men. (Velloziaceae) and Fernseea itatiaiae (Wawra) Baker (Bromeliaceae) – play a crucial role in this vegetation, as pioneer mat-formers facilitating later establishment of numerous other species. Hemicryptophytes prevail in the sampled flora, while therophytes are exceptionally rare and mainly consist of opportunistic species associated with disturbances. Numerous microhabitats and strong environmental gradients in these high elevation rock outcrops afford opportunities for establishment of a highly diversified flora. These island-like environments may represent an important refuge for grassland species from fire and other disturbances in the surrounding grasslands.

Key words - Atlantic rain forest, biogeography, “campos de altitude”, endemisms, rock outcrops, rupicolous plants

RESUMO – (Composição de espécies e relações biogeográficas da flora sobre afloramentos rochosos no Planalto do Itatiaia, SE do Brasil). O objeto deste estudo foi a flora que se distribui em ilhas de vegetação isoladas sobre a superfície rochosa, no Planalto do Itatiaia (22°21’S e 44°40’W), a 2.400 m de altitude. Foi encontrado um total de 114 espécies vasculares, correspondendo a ca. 20%-25% da flora total atualmente inventariada do Planalto, em 197 pequenas ilhas de vegetação (área total de 0.034 ha). Xerófitas e hidrófitas com freqüência ocorrem lado a lado devido à forte heterogeneidade ambiental em pequena escala espacial, explicando em parte a alta diversidade local. Superfícies rochosas podem abrigar floras muito distintas do entorno em função de fortes filtros ambientais contrastantes, mas no Itatiaia os padrões de distribuição geográfica de plantas rupícolas assemelham-se aos dos campos no entorno, com 15,1% das espécies sendo endêmicas restritas e seis sendo estritamente rupícolas. Destacando a natureza “temperada” do clima de altitude do Itatiaia, a flora estudada foi dominada por espécies de Asteraceae e Poaceae, e o número de espécies CAM (metabolismo ácido das crassuláceas) foi muito baixo. Algumas endêmicas de origem tropical – Fernseea itatiaiae (Wawra) Baker (Bromeliaceae) e Pleurostima gounelleana (Beauv.) Men. (Velloziaceae) – formam tapetes sobre a rocha e são fundamentais para o estabelecimento de ampla gama de espécies. Hemicriptófitas predominam na flora amostrada, enquanto terófitas são excepcionalmente raras e consistem, principalmente, de espécies oportunistas associadas com distúrbios. Os numerosos microhábitats e os marcantes gradientes ambientais nestes afloramentos de altitude elevada criam oportunidades para o estabelecimento de uma flora muito diversificada. Estes ambientes insulares parecem constituir importante refúgio para as espécies dos campos em geral, frente a perturbações como incêndios e outras ações antrópicas.

Palavras-chave - Floresta Pluvial Atlântica, campos de altitude, endemismos, biogeografia, afloramentos rochosos, rupicolous plants

Introduction

Despite their ubiquity, plant communities on rock outcrops have rarely been included in floristic inventories.

This is in part due to the difficulties of access imposed by rocky surfaces, to low economic interest, and possibly to an expectation of low diversity. Partly for these same reasons, rocky sites remain some of the better preserved terrestrial habitats on the planet, protected from grazing, fire and many other economic activities (Debrot & Freitas 1993, Fulls et al. 1993, Larson et al. 2000). From the scientific viewpoint, these habitats are an open avenue for a lot of questions yet underexplored, from ecophysiology (Lüttge 1997, Meirelles et al. 1997) to...

Rocky habitats are inserted within most terrestrial biomes, and their heterogeneity is related to topographic and vegetation patchiness. The floristic composition of vegetation on rock outcrops may vary according to: (1) characteristics of the rock where they grow, such as chemical properties and composition; (2) patterns of erosion and fracturing pattern that are in turn related to rock composition (ultramafic rocks, quartzites, granites, limestones, sandstones) and local environmental conditions; (3) topographic and microclimatic variations; and (4) regional floristic context, paleoclimate and history (Porembski et al. 1994, Escudero 1996, Larson et al. 2000, Seine et al. 2000, Burke 2002a, b). Generally, diversity and vegetation cover on rock outcrops tend to increase according to humidity, rock stability and availability of places for seed germination (Larson et al. 2000), but endemism may be more related to degree of isolation of the rock outcrop in relation to similar habitats and also to how intensely the ecological conditions on the rock surface represent a barrier for establishment of plants from the surrounding (also called ‘matrix’) vegetation (Larson et al. 2000, Burke 2002a, b).

Rock surfaces constitute an ecological barrier to the majority of plant species in surrounding matrix vegetation due to a combination of factors such as low water retention, scarcity of nutrients, difficulties of seed retention and germination, and increased exposure to winds and insolation relative to neighbouring areas (Larson et al. 2000). Thus, rock outcrops frequently support a very specialized vegetation (Sarthou & Villiers 1998, Booth & Larson 1999, Burke 2002a). Some plant groups show clear specialization or pre-adaptations for survival in these environments, such as in the case of the resurrection plants, which are capable of rehydrating desiccated leaves (in South America, mainly Cyperaceae and Velloziaceae; Meirelles et al. 1997), as well as other adaptive characteristics for dry and otherwise poor habitats (e.g., tank-forming leaves, bulbs, and atmospheric roots) common to pioneer species from many families – Orchidaceae, Bromeliaceae, Velloziaceae, Cyperaceae, Cactaceae. Some of these plants, mainly the monocots, spread on the rock surface forming vegetation mats where other plants may grow, in a clear facilitation mechanism (Porembski et al. 1998, Scarano 2002, Medina et al. 2006).

We focused on the vegetation growing on rock outcrops at the high elevation grasslands on the Itatiaia Plateau, inserted in the Atlantic rain forest domain (Scarano 2002). These grasslands, or “campos de altitude”, occur above 2,000 m a.s.l., along the mountain chains of southeastern Brazil. Montane environments are often spatially heterogeneous (Monasterio & Vuillemier 1986, Safford 1999a), and those in southeastern Brazil have dwarf forests, montane bamboo, marshes, humid slopes and rock outcrops, and each of these habitats has its own physiognomy and floristic composition (Brade 1956). These habitats are all exposed to temperatures below 0 °C on many winter nights, however each has a distinct set of limiting conditions, involving such factors as wind intensity, light radiation, UV and nutrient scarcity (Segadas-Vianna & Dau 1965, Rizzini 1979, Safford 1999a, Scarano et al. 2001). On rock outcrops, however, limiting abiotic conditions are extreme due to plant exposure and absence of soil, causing low water retention and low nutrient availability, as well as reduced buffering of environmental fluctuations (Meirelles et al. 1997, Larson et al. 2000).

We report on the floristic composition of rupicolous vegetation of the Itatiaia Plateau, and present data about biogeographic relations, life-form distribution and association with different micro-habitats. We also discuss the implications of variation in area of vegetation islands, investigating in details the general trends outlined by Safford & Martinelli (2000) for the rock outcrop vegetation in elevated places, in southeastern Brazil.

Material and methods

Study site – The Itatiaia Plateau (22°21’S and 44°40’W) is located at the central portion of the “Serra da Mantiqueira”, which runs parallel to “Serra do Mar” and to the southeastern and southern Brazilian coast. The grasslands occur above 2,000 m a.s.l., above the cloud forest belt (Brade 1956). The study site is within the limits of the “Parque Nacional do Itatiaia” . Many other high altitude grasslands are found on mountain peaks in the “Serra da Mantiqueira” and “Serra do Mar”, totalling ca. 350 km² (Safford 1999a). The climate is mesothermic, markedly seasonal, with cold and dry winters and very wet summers. Mean annual temperature is about 14 °C and lower temperatures sometimes fall below -10 °C among the ca. 56 nights of freezing temperatures per year. Annual rainfall is ca. 2,400 mm, concentrated in the summer months. Although there is no clear lack of rainfall during the winter, the reduced cloudiness and the high evaporation rates (mean about 90 mm in August; Segadas-Vianna & Dau 1965) in this season result in strong desiccation of the vegetation, specially on shallow soils.
Above 2,000 m a.s.l., the plateau has an area of ca. 50 km² and from 415 (Martinelli et al. 1989) to 550 (Safford 1999a) species described. The former authors claim that 11% of the total number of species are restricted endemics to high elevation habitats on the Itatiaia Plateau, and a further 21% are more widespread habitat endemics to southeast Brazilian high-elevation grasslands in general. Shrubs appear only rarely in these grasslands, and woody vegetation often forms clumps protected by boulders, which is probably related to the previous fire regime (Brade 1956, Daubenmire 1968, Safford 2001, Medina et al. 2006). A recent review of climatic and physical characteristics of Brazilian high altitudinal grasslands based on climatic data from Segadas-Vianna & Dau (1965) is found in Safford (1999a, b). No other study focused specifically the rupicolous vegetation of Itatiaia.

In Itatiaia, the predominant rock is nepheline-syenite, an alkaline plutonic rock not very common in Brazil, where it occurs only in Poços de Caldas (state of Minas Gerais), the island of São Sebastião (state of São Paulo), and the mid-Atlantic island of Trindade, 1,167 km west of the state of Espírito Santo (Almeida 1961, Leinz & Amaral 1989). Nepheline-syenite has small crystals and high dissolution rates, frequently forming channels and holes (Leinz & Amaral 1989). However, narrow fissures, which are common in granite and allow for rooting of vascular plants, are rare. In Itatiaia, the proto-soils associated with rock surfaces are extremely rich in aluminium, as discussed by Benites et al. (2003). Like heavy metals, high aluminium concentration may be avoided, tolerated or even required, as showed by Haridasan (2000) for some “cerrado” species, and may be another important causal factor in the genesis of endemisms (Major 1988).

The rupicolous vegetation is often distributed as isolated patches with relatively well delimited borders, and may be treated as vegetation islands, with the theoretical and methodological approach set by the island biogeography studies (Michelangeli 2000, Rosenzweig 1995).

Sampling – We sampled a total of 337.1 m² of vegetation studies (Michelangeli 2000, Rosenzweig 1995). A methodological approach set by the island biogeography treated as vegetation islands, with the theoretical and patches with relatively well delimited borders, and may be avoided, tolerated or even required, as showed by Haridasan (2000) for some “cerrado” species, and may be another important causal factor in the genesis of endemisms (Major 1988).

The following geographic distribution patterns were recognised: E = species endemic to the “Itatiaia” Plateau; SE = restricted to southeastern Brazil; SE+S = southeastern and southern Brazil; SE+NE = southeastern and northeastern Brazil; B = Brazil; A = South America or Americas; C = cosmopolitan. Few species also occur in Central Brazil (CB: states of Goiás, Mato Grosso and/or Mato Grosso do Sul) and/or on southern countries (ConeS: Paraguay, Uruguay and/or Argentina). H = restricted to mountains, irrespective of distribution, also included plants that occur in low altitude places only in high latitudes (Brazilian state of Rio Grande do Sul, Argentina, Uruguay). We also noted cases of disjunction between the Andes and southeastern Brazil at both the genus and species level (table 1).

Life form characterization – Species were classified into life-forms following the widely used scheme of Raunkiaer (1934, apud Cain 1950), allowing comparisons with other published accounts (Cain 1950, Pavón et al. 2000). The following grouped categories were used: Ph – phanerophytes (including the bambuses); H – hemicryptophytes, distinguishing here those with rosetted leaves (H (R)); C – Cryptophytes (including geophytes and hydrophytes), and Th – Therophytes. Classification followed mainly field observations. The spectrum obtained was compared to those described by other studies about rupicolous vegetation (table 2).
Figures 1-8. View of the Prateleiras massif from the “Pico das Agulhas Negras”. 1. The arrow indicates the study area. 2. Illustration of the main habitats within the study area – A. open shield area; B. boulder on the talus slope. 3, 4. The pioneer mat-forming hemicriptophyte *Fernseea itatiaiae* (Bromeliaceae) respectively in the boulder area, in a well-drained shallow depression, and within a flooded rock pool, associated to the moss *Campylops pilifer*, forming horseshoe shaped islands. 5. The geophyte *Hippeastrum morelianum* common in all island types, associated to the endemic *Chusquea microphylla*, that occurs only in the open shield area. 6. An island formed basically by *Pleurostima gounelleana* that was in a clear splitting process, with plant parts surviving better in the shallow depressions. 7. Abundance of rock pools devoided of vascular plantas in the Agulhas Negras massif. 8. An individual of the pioneer shrub *Baccharis stylosa* exposed to the strong winds of September 2000 – the showed shoots were dead in the following month, with reduction in plant height due to wind action.
Table 1. Checklist of the species sampled on rock outcrops of Itatiaia Plateau and patterns of geographic distribution: E = endemic to the Itatiaia plateau and neighbouring peaks; SE = occurrence across southeastern Brazil; SE+S = Southeastern and Southern Brazil; SE+NE = Southeastern and Northeastern Brazil; B = Brazil; A = South America or Americas; C = cosmopolitan. ConeS = occurring also in southern countries of South America (Argentina, Uruguay and/or Paraguay); CB = found also in states of Central Brazil (Mato Grosso do Sul, Mato Grosso and/or Goiás). R = restricted to mountain ranges whatever the distribution, including those species restricted to mountains when in the tropics, but with generalized distribution at higher latitudes (RS, Argentina, Uruguay). See text for details. The following notations were also included: Andes – Southeast Brazil disjunction at the genus level (†), on species level $. Life-forms: G = geophyte; H = hemicryptophyte of graminoid habit; Hros = hemicryptophyte with leaf rosette; Ch = chamaephyte; Ph = phanerophyte; Th = therophyte; S = succulent; and bambuses.

<table>
<thead>
<tr>
<th>Families / Species</th>
<th>Life-form</th>
<th>Geogr. distribution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ANGIOSPERMS</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ALSTROEMERIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>AMARYLIDACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hippeastrum morelianum Lem.</td>
<td>G</td>
<td>SE, R</td>
<td>J. Dutilh (unpublished data)</td>
</tr>
<tr>
<td><strong>APIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eryngium eurycephalum Malme</td>
<td>Hros</td>
<td>SE, R *</td>
<td></td>
</tr>
<tr>
<td><strong>AQUIFOLIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilex amara (Vell.) Loes.</td>
<td>Ph</td>
<td>SE+S*</td>
<td></td>
</tr>
<tr>
<td><strong>ASTERACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Achyrocline satureoides (Lam.) DC.</td>
<td>Ch</td>
<td>A</td>
<td>Barroso (1957)</td>
</tr>
<tr>
<td>Baccharis glaziowii Baker</td>
<td>Ph</td>
<td>SE, R *</td>
<td></td>
</tr>
<tr>
<td>Baccharis lateralis Baker</td>
<td>Ph</td>
<td>SE+S, R</td>
<td>Barroso (1957)</td>
</tr>
<tr>
<td>Baccharis uncinella DC.</td>
<td>Ph</td>
<td>SE+S, R *</td>
<td></td>
</tr>
<tr>
<td>Chinolaena capitata (Baker) Freire</td>
<td>Ph</td>
<td>SE+S, R</td>
<td>Freire (1993)</td>
</tr>
<tr>
<td>Gamochaeta pensylvanica (Will.) Cabrera</td>
<td>Hros</td>
<td>C</td>
<td>W3 Tropicos</td>
</tr>
<tr>
<td>Senecio argyrotrichus Dusén</td>
<td>Ph</td>
<td>E</td>
<td>Barroso (1957)</td>
</tr>
<tr>
<td>Stevia camporum Baker</td>
<td>G</td>
<td>SE, R</td>
<td>Barroso (1957)</td>
</tr>
<tr>
<td>Symphyopappus itatiayensis (Hieron.)</td>
<td>Ph</td>
<td>SE+S</td>
<td>Cabrera &amp; Klein (1989)</td>
</tr>
<tr>
<td>Verbesina glabrata Hook. &amp; Arn.</td>
<td>Ph</td>
<td>B</td>
<td>Barroso (1957)</td>
</tr>
<tr>
<td><strong>BEGONIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Begonia lanstakii Brade</td>
<td>G</td>
<td>E</td>
<td>Brade (1959-61)</td>
</tr>
<tr>
<td><strong>BROMELIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fernseea itatiaiae (Wawra) Baker</td>
<td>Hros</td>
<td>E</td>
<td>Smith &amp; Downs (1979)</td>
</tr>
<tr>
<td>Vriesea itatiaiae Wawra</td>
<td>Hros</td>
<td>SE, R</td>
<td>Smith &amp; Downs (1977)</td>
</tr>
<tr>
<td><strong>CACTACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Schlumbergera microsphaerica (K. Schum.) Hoovel</td>
<td>S</td>
<td>SE, R</td>
<td>Hunt (1968)</td>
</tr>
<tr>
<td><strong>CAMPANULACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lobelia camporum Pohl</td>
<td>Ch</td>
<td>SE+S, R</td>
<td>Trinta &amp; Santos (1989)</td>
</tr>
<tr>
<td>Siphocampylus westianus (Billb.) Pohl</td>
<td>G</td>
<td>SE, R *</td>
<td>Trinta &amp; Santos (1989)</td>
</tr>
<tr>
<td>Siphocampylus longopedunculatus Pohl</td>
<td>Ch (liana)</td>
<td>SE+S</td>
<td></td>
</tr>
<tr>
<td><strong>CARYOPHYLLACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paronychia chilensis DC.</td>
<td>Ch</td>
<td>A, R</td>
<td>Duke (1961)</td>
</tr>
<tr>
<td><strong>CUNONIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weinmannia humilis Engler</td>
<td>Ph</td>
<td>SE+S, R</td>
<td>Cuatrecasas &amp; Smith (1971)</td>
</tr>
</tbody>
</table>

continue
<table>
<thead>
<tr>
<th>Families / Species</th>
<th>Life-form</th>
<th>Geogr. distribution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CYPERACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Rhynchospora cf. pallae</em> Kuek.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cladium ensifolium</em> Benth.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lagenocarpus cf. triquetrus</em> (Boeck.) Kuntze</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carex aff. fuscula</em> d’Urv.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carex</em> sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyperaceae</em> sp. 1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>DIOCOREACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dioscorea perdicum</em> Taubert</td>
<td>G</td>
<td>SE+NE</td>
<td>G. Pedralli (unpublished data)</td>
</tr>
<tr>
<td><em>Dioscorea demourae</em> R. Knuth</td>
<td>G</td>
<td>A</td>
<td>G. Pedralli (unpublished data)</td>
</tr>
<tr>
<td><strong>ERICACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gouvêa</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ERIOCAULACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leiothrix argyroderma</em> Ruhl.</td>
<td>Hros</td>
<td>E</td>
<td>Brade (1956)</td>
</tr>
<tr>
<td><em>Leiothrix beckii</em> (Szysz.) Ruhl.</td>
<td>Hros</td>
<td>E</td>
<td>Brade (1956)</td>
</tr>
<tr>
<td><em>Paepalanthus itatiaiensis</em> Ruhl.</td>
<td>Hros</td>
<td>E</td>
<td>Brade (1956)</td>
</tr>
<tr>
<td><strong>EUPHORBIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>GESNERIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sinningia gigantifolia</em> Chautems</td>
<td>Ch</td>
<td>SE, R *</td>
<td></td>
</tr>
<tr>
<td><strong>IRIDACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sisyrinchium</em> sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sphenostigma sellowiana</em> Klatt.</td>
<td>G</td>
<td>SE, R</td>
<td>Brade (1956)</td>
</tr>
<tr>
<td><em>Trimezia</em> sp.</td>
<td>G</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Iridaceae</em> sp. 1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>JUNCACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Juncus microcephalus</em> Kunth</td>
<td>G</td>
<td>A, R 5</td>
<td>Balslev (1996)</td>
</tr>
<tr>
<td><strong>LAMIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Salvia itatiaiensis</em> Dusén</td>
<td>Ph</td>
<td>E</td>
<td>Pereira (1957)</td>
</tr>
<tr>
<td><em>Lepechinnea speciosa</em> (A. St.-Hil.) Epling</td>
<td>Ph</td>
<td>SE, R (5)</td>
<td>Pereira (1957)</td>
</tr>
<tr>
<td><strong>LENTIBULARIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Utricularia reniformis</em> A. St.-Hil.</td>
<td>G</td>
<td>SE+S, R</td>
<td>Taylor (1980)</td>
</tr>
<tr>
<td><em>Utricularia globulariaefolia</em> Mart. ex Benj.</td>
<td>G</td>
<td>SE, R *</td>
<td></td>
</tr>
<tr>
<td><strong>MELASTOMATACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tibouchina hospita</em> Cogn.</td>
<td>Ph</td>
<td>SE+S, R</td>
<td>Brade (1956)</td>
</tr>
<tr>
<td><em>Leandra sulfurea</em> (Naud.) Cogn.</td>
<td>Ph</td>
<td>SE, R</td>
<td>Brade (1956)</td>
</tr>
<tr>
<td><em>Chaetostoma glaziovii</em> Cogn.</td>
<td>Ch</td>
<td>SE, R *</td>
<td></td>
</tr>
<tr>
<td><em>Tibouchina</em> sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Melastomataceae</em> sp. 1</td>
<td>Ph</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Melastomataceae</em> sp. 2</td>
<td>Ph</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>MYRISINACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Myrsine gardneriana</em> A. DC.</td>
<td>Ph</td>
<td>SE+S, R</td>
<td></td>
</tr>
<tr>
<td><strong>MYRTACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Myrtaceae</em> sp. 1</td>
<td>Ph</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Myrtaceae</em> sp. 2</td>
<td>Ph</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ONAGRACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fuchsia regia</em> (Vell.) Munz subsp. regia</td>
<td>Ch</td>
<td>SE, R</td>
<td>Grillo &amp; Giulietti (1998)</td>
</tr>
</tbody>
</table>

continue
<table>
<thead>
<tr>
<th>Families / Species</th>
<th>Life-form</th>
<th>Geogr. distribution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ORCHIDACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Prescottia montana</em> Barb. Rodr.</td>
<td>G</td>
<td>SE, R</td>
<td></td>
</tr>
<tr>
<td><em>Habenaria rolfeana</em> Schltr.</td>
<td>G</td>
<td>SE, R</td>
<td></td>
</tr>
<tr>
<td><em>Pelexia itatiayae</em> Schltr.</td>
<td>G</td>
<td>SE, R</td>
<td></td>
</tr>
<tr>
<td><em>Habenaria parviflora</em> Lindl.</td>
<td></td>
<td>SE*</td>
<td></td>
</tr>
<tr>
<td><strong>OXALIDACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Oxalis rupestris</em> A. St.-Hil.</td>
<td>G</td>
<td>SE+R</td>
<td>Loureig (1983)</td>
</tr>
<tr>
<td><strong>PIPERACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Peperomia galioides</em> Kunth</td>
<td>Ch</td>
<td>C</td>
<td>Yuncker (1974)</td>
</tr>
<tr>
<td><strong>PLANTAGINACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Plantago</em> sp.</td>
<td>Hros</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>POACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chusquea heterophylla</em> Nees</td>
<td>Bambu</td>
<td>SE, R</td>
<td>Clark (1992)</td>
</tr>
<tr>
<td><em>Chusquea microphylla</em> (Döll) L. G. Clark</td>
<td>Bambu</td>
<td>E</td>
<td>Clark (1992)</td>
</tr>
<tr>
<td><em>Agrostis aff. lenis</em> B. R. Arill. &amp; Izag.</td>
<td>H</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Briza itatiae</em> Ekman</td>
<td>H</td>
<td>E</td>
<td>Longhi-Wagner (2001)</td>
</tr>
<tr>
<td><em>Cortaderia modesta</em> (Döll) Hack. ex Dusén</td>
<td>H</td>
<td>SE, R</td>
<td>Longhi-Wagner (2001)</td>
</tr>
<tr>
<td><em>Danthonia montana</em> Döll</td>
<td>H</td>
<td>SE+S, R</td>
<td>Longhi-Wagner (2001)</td>
</tr>
<tr>
<td><em>Danthonia</em> sp.</td>
<td>H</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Panicum</em> sp.</td>
<td>H</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poaceae sp. 1</td>
<td>H</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poaceae sp. 2</td>
<td>H</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poaceae sp. 3</td>
<td>H</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>POLYGALACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Polygala pulchella</em> A. St.-Hil. &amp; Moq.</td>
<td>Ch</td>
<td>SE+S, R</td>
<td>Marques (1988)</td>
</tr>
<tr>
<td><strong>POLYGONACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>PROTEACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Roupala impressiuscula</em> Mez</td>
<td>Ph</td>
<td>SE, R*</td>
<td></td>
</tr>
<tr>
<td><strong>ROSACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Prunus</em> sp.</td>
<td>Ph</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>RUBIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Relbunium hypocarpium</em> (L.) Humsl.</td>
<td>Ch</td>
<td>SE+CB*</td>
<td></td>
</tr>
<tr>
<td><em>Coccospermum lyman-smithii</em> Standley</td>
<td>Ch</td>
<td>B, R*</td>
<td></td>
</tr>
<tr>
<td>Rubiaceae sp. 1</td>
<td>Ch</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SAXIFRAGACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Escallonia</em> sp.</td>
<td>Ph</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>SCROPHULARIACEAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Esterhazya eitenorum</em> Barringer</td>
<td>Ph</td>
<td>SE, R</td>
<td>Moura &amp; Alves (1999)</td>
</tr>
</tbody>
</table>
Results and discussion

Species richness – In a discontinuous sample area of 0.034 ha, we found 114 species of vascular plants – of which nine were ferns – belonging to 47 families (table 1). This is more than 25% of the total of species reported for the whole plateau (n = 415) by Martinelli et al. (1989), and reveals the importance of these rock surfaces for overall diversity. All but one species (Solanum aff. macrotonum) had already been registered for the plateau, mainly by Brade (1956). This Solanum is a new species or a new disjunction “Andes-Itatiaia”, still to be confirmed (L. Freire unpublished data). The fact that in our small sampling area we found a large proportion of known species suggests that accounts of species richness for the entire plateau ranging from ca. 400-500 species (Martinelli et al. 1989) are probably underestimates, which might result from the fact that the Prateleiras microregion is the most intensely studied in the plateau. Alternatively, it may also mean that the Prateleiras, due to the high diversity of habitat types it comprises, might indeed maintain in its vegetation islands a considerable proportion of the species found in the whole region.

* Geographic distributions described directly from herbaria surveys.
Table 2. Life-form spectra of rupicolous communities from different sites and also the spectrum for the whole vegetation of the Itatiaia Plateau, accompanied by the Normal Spectrum built by Raunkier (1934 *apud* Cain 1950) for a sample of 1,000 species worldwide. Life-forms (%): H = hemicyryptophyte, Ch = chamaephyte; Ph = phanerophyte; Th = therophyte; G = geophyte. The prevalent life-form in each community is indicated in bold.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Altitude</th>
<th>Geographic coordinates</th>
<th>Mean Precipitation/temperature</th>
<th>Species number</th>
<th>Number of families</th>
<th>Dominant families</th>
<th>Ph</th>
<th>Ch</th>
<th>H</th>
<th>G</th>
<th>Th</th>
</tr>
</thead>
<tbody>
<tr>
<td>Itatiaia – rupicolous vegetation</td>
<td>2,400 m</td>
<td>22°25' S / 44°40' W</td>
<td>2,273 mm / 17°C</td>
<td>114</td>
<td>48</td>
<td>Poaceae, Asteraceae</td>
<td>29.8</td>
<td>15.8</td>
<td>36.8</td>
<td>15.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Vegetation on inselbergs in French Guiana&lt;sup&gt;1&lt;/sup&gt;</td>
<td>200-400 m</td>
<td>3°28'-4°03' N / 52°13'-44' W</td>
<td>2,750 mm / 36.5°C</td>
<td>81</td>
<td>37</td>
<td>Cyperaceae, Poaceae, Lentibulariaceae</td>
<td>16</td>
<td>21</td>
<td>41</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Rupicolous vegetation from “super páramos” – Venezuela&lt;sup&gt;2&lt;/sup&gt;</td>
<td>4,000 m</td>
<td>8°30'-40' N / 69°55'-71°07' W</td>
<td>1,553 mm / 0.3°C</td>
<td>58</td>
<td>17</td>
<td>Asteraceae, Poaceae Rosaceae</td>
<td>6.3</td>
<td>25.3</td>
<td>51.9</td>
<td>6.3</td>
<td>3.8</td>
</tr>
<tr>
<td>“Serra das Cabeças”&lt;sup&gt;3&lt;/sup&gt;</td>
<td>1,722 m</td>
<td></td>
<td>1,300 mm / 18°C</td>
<td>81</td>
<td>31</td>
<td>Orchidaceae, Asteraceae, Melastomataceae</td>
<td>28.3</td>
<td>28.4</td>
<td>32.1</td>
<td>7.4</td>
<td>8.6</td>
</tr>
<tr>
<td>Atibaia&lt;sup&gt;4&lt;/sup&gt;</td>
<td>1,400 m</td>
<td>23°08'S / 46°35' W</td>
<td>1,500 mm / 18°C</td>
<td>101</td>
<td>43</td>
<td>Asteraceae, Bromeliaceae, Orchidaceae</td>
<td>22.7</td>
<td>7.9</td>
<td>29.7</td>
<td>11.8</td>
<td>16.8</td>
</tr>
<tr>
<td>“Serra do Mar”&lt;sup&gt;5&lt;/sup&gt;</td>
<td>1,000-1,600 m</td>
<td>22.5’S / 43° W</td>
<td>Not given</td>
<td>127</td>
<td>51</td>
<td>Asteraceae, Bromeliaceae, Orchidaceae</td>
<td>33.8</td>
<td>38.1</td>
<td>16.9</td>
<td>10.6</td>
<td>0.6</td>
</tr>
<tr>
<td>“Pão de Açúcar”&lt;sup&gt;5&lt;/sup&gt;</td>
<td>50-398 m</td>
<td>22°57’S / 43°09’ W</td>
<td>1,299 mm / 22.7°C</td>
<td>57</td>
<td>24</td>
<td>Bromeliaceae, Orchidaceae, Velloziaceae</td>
<td>38.9</td>
<td>42.1</td>
<td>8.4</td>
<td>5.3</td>
<td>5.3</td>
</tr>
<tr>
<td>Rio de Janeiro’s coastline&lt;sup&gt;6&lt;/sup&gt;</td>
<td>50-400 m</td>
<td>22°57’S / 43°09’ W</td>
<td>1,299 mm / 22.7°C</td>
<td>97</td>
<td>49</td>
<td>Bromeliaceae, Orchidaceae, Cactaceae</td>
<td>31.8</td>
<td>2.3</td>
<td>43.5</td>
<td>4.7</td>
<td>2.3</td>
</tr>
<tr>
<td>Ivory Coast&lt;sup&gt;7&lt;/sup&gt;</td>
<td>180-220 m</td>
<td>5°52’ N / 7°20’ W</td>
<td>1,829 mm / 26.0°C</td>
<td>66</td>
<td>26</td>
<td>Cyperaceae, Poaceae, Malvaceae</td>
<td>18.3</td>
<td>21.7</td>
<td>6.7</td>
<td>8.3</td>
<td>45.0</td>
</tr>
</tbody>
</table>

Oettli (1904, apud Larson et al. 2000) observed that on rocks, many distinct habitats can occur close together and/or in mosaic, so that, e.g., marsh plants may grow next to desiccation-tolerant plants. This is also true for Itatiaia. Vegetation islands dominated by Pleurostima gounelleana or Fernseea itatiaiae, plants with xerophytic morphological and physiological traits (Scarano et al. 2001), were often neighbours of wetland plants such as Juncus microcephalus, Xyris teres and Utricularia reniformis, or of mesic woody plants like Baccharis stylosa and Eupatorium alpestre. This spatial heterogeneity explains the high diversity and the high proportion of species on the plateau that are able to establish on rocks. However, there was a clear repetition of species associations that were related to microhabitat variation. For example, P. gounelleana was often associated with the moss Campylopus pilifer, each one occurring in more than 50% of the vegetation islands on exposed rock outcrops, in any microtopography (figure 9). Nevertheless, these species were nearly absent from the talus slope area, where the tank bromeliad Vriesea itatiaiae was common (figure 9). Locally high diversity and the repetition of communities/associations on a broader spatial scale is a common trend on mountain slopes and peaks (Escudero 1996, Alves 2000, Larson et al. 2000, but see Porembski et al. 1998).

Three moss species were particularly abundant and seemed to play an important ecological role in the formation and expansion of vegetation islands on rocks: Campylopus pilifer, Polytrichum commune and Hedwigium integrifolium (figure 4). The latter grows mainly in water flushes, and C. pilifer is a pantropical pioneer species occupying mainly poorly drained sites in “Itatiaia”. Other moss species occurred on rocks but at lower densities and played a less clear role in rugicolous vegetation dynamics. More than a hundred moss species have been described for the plateau as a whole (D.P. Costa unpublished data.).

The dominant families of vascular plants were Poaceae and Asteraceae (14.9% and 10.5% of the species total, respectively), followed by Melastomataceae, Cyperaceae, Orchidaceae and Rubiaceae (table 1). This pattern conforms to the grasslands in general, but is in clear contrast with data from other rock outcrops in southeastern Brazil at lower elevations, where Orchidaceae and Bromeliaceae are often among the most species-rich families (table 1). Legume species are dramatically reduced in richness and abundance in the high altitude grasslands: only nine species are reported, of which five are Lupinus, a genus associated with temperate climates (Brade 1956). This is relevant, since Fabaceae is a dominant family in many other rock outcrops (Seine et al. 2000), as well as in the adjacent Atlantic forest (Oliveira Filho & Fontes 2000).

Some other absences are noteworthy, such as species from the genera Epidendrum, Laelia and Pleurothallis (Orchidaceae), Tillandsia and Dickya (Bromeliaceae), Trilepis (Cyperaceae), Cereus and Rhipsalis (Cactaceae), that are highly diversified and abundant in most other surveyed sites within the Atlantic forest domain (Safford & Martinelli 2000, Caiafa 2002). Nevertheless, all these genera were found in Pedra Branca (K.T. Ribeiro unpublished data), a syenite rock outcrop 170 km from Itatiaia, in the municipality of Caldas (Minas Gerais State), which reaches 1,850 m a.s.l.. At this site the dominant species in Itatiaia were absent – for example, the narrow endemics P. gounelleana and F. itatiaiae, showing the effects of climate upon rocky type. Among available studies, the most useful for comparison with Itatiaia due to altitude is the survey of Caiafa (2002) in the “Serra das Cabeças”, also part of the “Serra da Mantiqueira” (Municipality of Vioçosa, MG), a mountain top at 1,722 m a.s.l covered with grasslands and rugicolous mats, 270 km from “Itatiaia”. Just six species were common to both sites, and the profile of dominant families and genera was also very different. Further, in the “Serra das Cabeças” the dominant species were Pleurothallis teres and Trilepis lhotzkiana, which represent genera absent from “Itatiaia”, as already mentioned. This may be explained in part due to the effects of distance upon the differentiation of the rugicolous flora, as clearly stated by Seine et al. (2000), who proposed that comparisons between rugicolous florulae should be made at higher taxonomic levels. Another aspect is, however, the unequivocal influence of the temperate climate on the vegetation profile of Itatiaia.

We avoided comparisons of richness with other studies, since these variables are strongly affected by sampling effort (both in time and space), by the criteria used for including each habitat type in the analyses, and by the structure of the habitat, including species area relationships and the successional stage of each island, according to size and age. There is still a large avenue for discussion about standardizing sampling methods in rugicolous vegetation in order to allow adequate comparisons.

Geographic distribution patterns – The distribution patterns of the rugicolous species we sampled also pointed to the isolation of this vegetation in relation to the adjacent tropical rain forest. There were no species with a generalized distribution in the neighbouring Atlantic forest, unlike other ecosystems found adjacent to the rainforest, such as “restingas” (Araujo et al. 1998, Scarano 2002). More widespread distribution patterns...
Figure 9. Ranked frequency of species in the rupicolous vegetation islands in Itatiaia. The frequency of each species in islands from the open shields is represented by solid bars and frequency in islands from the boulder area is represented by open bars. The first column indicate the proportion of islands sampled in each habitat. Brackets indicate the mat-forming species.
are reported for the ruderal *Gamochaeta pensylvanica*, for the rupicolous or epiphytic Piperaceae *Peperomia galioides*, and the temperate or tropical montane *Rumex acetosella* (a cosmopolitan species); and for eight species widely distributed in high and/or temperate localities in the Americas (table 1). A high proportion of the species found were restricted to southeastern Brazil or to southeastern and southern Brazil (*n* = 63, 72.4%). Of this group, 13 were narrow endemics, found only on the Itatiaia plateau and on the peaks of some adjacent mountain chains (“Serra Negra”, “Serra Fina” and “Pico do Itaguaré”; see Brade 1956); 26 species were restricted to the southeastern mountains in general (“Serra da Mantiqueira” and “Cadeia do Espinhaço”); and 19 occurred also in decreasing altitudes towards southern Brazil. The rupicolous vegetation sampled showed a higher proportion of endemics than the flora of the plateau as a whole (14.4% vs. 11%), from which two were nearly confined to the rock surfaces – *Fernseea itatiaiae* and *Pleurostima gounelleana*. These two species and the montane *Vriesea itatiaiae* were dominant in the landscape, and were responsible for the formation and/or expansion of most vegetation mats (figures 1-9). Additionally, they all belong to typically tropical families with low species richness in cold places (Smith & Downs 1979).

Almost all grasses occurring in the study area (e.g., *Chusquea* – Bambuseae, *Cortaderia* – Arundinaceae, *Agrostis* – Agrostidaceae, and *Danthonia* – Danthoniaceae) are mesothermic, according to Burkart (1975), since they occur only in mild temperate climates (mean temperatures: 10 to 20 °C), unlike megathermic (means over 20 °C) and microthermic (below 10 °C) grasses. In the Andes, at correspondent latitudes, mesothermic conditions occur from 1,500 to 3,500 m a.s.l., and in Brazil, between 28° and 40° latitude S (Burkart 1975), and at decreasing altitudes southward.

The characteristics of a temperate climate are also suggested when photosynthetic mechanisms are considered. Although very common in rocky surfaces at lower elevations, CAM (crassulacean acid metabolism) plants are nearly absent in Itatiaia (Scarano et al. 2001). For example, the bromeliad *Nidularium itatiaiae* was one of few CAM species, as detected by 13C discrimination analysis (carbon isotope ratio) of leaf tissues, and was found in places protected from the wind and temperature extremes, which are possibly places where nocturnal stomata opening is possible. The other bromeliad, *Fernseea itatiaiae*, a narrow endemic but common in a large range of habitat types on the plateau, showed all the characteristics of C3 metabolism (Scarano et al. 2001). The authors remark that this species belongs to a sub-family (Bromelioideae) where all other species have been reported as CAM. The cactus *Schlumbergera obtusangula* also demonstrated C3 behaviour, which is another curious exception since its family is almost entirely CAM. The prevalence of the C3 pathway on the Itatiaia Plateau may reflect the very low nocturnal temperatures. However, since other other high altitude zones in South America have CAM plants (Medina & Delgado 1976, Keeley & Keeley 1989), the shortage of CAM species in this vegetation deserves further investigation.

Life forms – Understanding why rupicolous vegetation from different places can show such different life-form spectra is a difficult task since two factors have strong effects upon the plants – the climate itself, which originated the rationale supporting the proposition of life-forms by Raunkiaer (the phytoclimates; Cain 1950) and the edaphic conditions, in that differences in substrate, topography and drainage can completely change the dominance of contrasting life-forms.

The distribution of life forms in the rupicolous vegetation was in harmony with the local characteristics of temperate climate (Cain 1950). There was a predominance of hemicryptophytes, which were either graminoids (32 species) or rosettes (10 species), and belonged to various families (table 1). The dominance of this life form was also observed in five other studies on rupicolous vegetation (see table 2). There were also many phanerophytes, mostly small-sized, due probably to wind action (figure 8). In areas protected by boulders, shrubs and trees may reach heights of 3-4 m. Cain (1950) showed a trend of increasing proportions of chamaephytes with elevation, accompanied by an increasing proportion of hemicryptophytes on many mountain slopes. Pavón et al. (2000) also found the same pattern for chamaephytes, but the opposite for cacti and phanerophytes in a semiarid valley in Mexico. Among those studies about rupicolous vegetation within the Atlantic forest domain, no obvious pattern is readily apparent (table 2).

In the “Serra Fina”, a mountain massif just 20 km far from the “Itatiaia” massif and at the same average altitude, the rock surface covered with fissures and cracks harboured a much larger proportion of phanerophytes (B.M.O. Medina, unpublished data) than the prevalent convex surface of Itatiaia, where hemicryptophytes are able to grow forming mats. In our Itatiaia site, phanerophytes were under-represented in part due to scarcity of cracks. Further, differences in sampling methods and in criteria for inclusion of each one of the many vegetation types found on rock outcrops (from monocot mats to thickets on deeper soils) may result in larger or lesser inclusion of phanerophytes.

Cryptophytes were an important component of rupicolous vegetation in Itatiaia, as already indicated by
Brade (1956). We found 18 species (15.8% of the total), mostly geophytes, a similar proportion found in the rupicolous flora of Atibaia (state of São Paulo), at 1,600 m a.s.l. (11.8%; Meirelles 1996). Caiafa (2002), in “Serra do Brigadeiro” (state of Minas Gerais), found just 8.6% geophytes in rupicolous vegetation patches. In a rock outcrop in the “superpáramos” (Sierra Nevada, Venezuela, elevation ca. 4,000 m), geophytes were only 0.04% of the flora (Berg 1998) and in inselbergs in French Guiana they were completely absent (Sarthou & Villiers 1998).

The relative abundance of this life form in Atibaia and Itatiaia, as opposed to its scarcity in the “superpáramos” or absence in equatorial inselbergs, may result from the marked seasonality of temperature and humidity in the Brazilian sites. The “páramos”, conversely, have almost constant monthly mean temperatures and near 0 °C temperatures almost every night. Thus, in the latter, and mainly in the colder “superpáramos”, the investment in underground reserves may be less favoured than strategies that allow for shoot maintenance throughout the year, such as in the case of caulescent rosette plants, cushion plants (Monasterio 1986, Berg 1998) or even small phanerophytes (Sarthou & Villiers 1998).

The low proportion of therophytes in Itatiaia (1.8%) and in many nearby sites deserves further investigation, as stated by Safford & Martinelli (2000), mainly if compared with data from Taï forest in Ivory Coast, West Africa, where Porembski et al. (1996) found 45% of therophytes (table 2). Therophytes may be rare on Itatiaia rocks due to a combination of short growing seasons and low nutrient budgets on rock surfaces (Larson et al. 2000, Benites et al. 2003) that preclude rapid establishment and growth. Low temperatures alone do not explain the absence of therophytes in Itatiaia, since this life strategy is very common in many temperate regions (Cain 1950).

This is reinforced by the observation that after an extensive wildfire in July 2001, many therophytes like Gamochaeta pennsylvanica and Rumex acetosella established and flowered in large numbers, even in unburnt islands (Ribeiro 2002). This was possibly due to an input of usually limiting nutrients, mainly phosphorous, triggering the germination, establishment and growth of these ruderal species (Whelan 1995, Enright et al. 1997, Verboom et al. 2002). This pattern is paralleled by Yates et al. (2003), who showed that in a frequently burnt rock outcrop in Australia, most species were therophytes (45%) and only 7% were geophytes.

Vegetation structure – Some characteristics of the dominant rock in Itatiaia – the nepheline-syenite – seem to also have a role in the promotion of plant diversity. The erosion by dissolution creates many holes and shallow depressions with variable flooding regimes. Additionally, the scarcity of cracks and fissures favours the establishment of mat-forming species, mainly rosetted hemicyrptophytes, upon which a large array of other species may establish. Vegetation islands seem to correspond to different successional stages, according in part to their area, as suggested by a strong species-area relationship, where the slope coefficient is above 0.30 in the logarithmic space (Ribeiro 2002). Small islands bear a few (usually 2 to 4) species, many of them specialized rupicolous plants, either epilithic or saxicolous. But high species richness is associated with this group of small islands, since the composition of low abundance species associated with the mat forming plants is highly variable and sorted from a large pool of species.

Nearly all islands are dominated by hemicyrptophytes, such as bromeliads or Velloziaceae, and sometimes ferns like Doryopteris itatiaiae and mosses, with the periodic appearance of graminoids and cryptophytes. These species provide different establishment conditions for other plants, according to their growth forms and to microhabitat conditions where each different species prevails (Ribeiro 2002, Medina et al. 2006).

There is a clear segregation in species composition between the two habitats – the rock shields and the talus slope (figure 9). Campylopus pilifer, Pleurostima gounelleana and Baccharis stylosa, frequent in the rock shield, were absent from the talus slope, whereas Vriesea itatiaiae has just two individuals in the former, but was found in 15.5% of the islands of the latter. The geophytes Stevia camporum, Alstroemeria foliosa and Hippeastrum morelianum and the bromeliad Fernseea itatiaiae were the most widespread species, found in high frequencies in all microhabitat types (present in 51.9%; 41.1%; 27.1% and 25.6% of the total group of islands, respectively).

On the rock shields there was a large number of rocky pools, most of them devoid of vascular species (figure 7). Islands with a horseshoe shape were common in pools flooded for a longer time, since pioneer species occupy only their borders, avoiding flooding (figure 4). Conversely, the steep surfaces at these exposed sites were rarely occupied by vascular plants or even mosses, due to humidity deficit and lack of fissures. More islands were found in flatter areas, associated with depressions and under contrasting drainage regimes. Depending on the relative position of a given depression in the landscape, it may continuously receive a large amount of water drained from neighbouring vegetation or, conversely, be dry most of the time, supporting very different species.

A different picture was found along the boulders at the talus slope. These boulders are more protected from
wind and direct sunlight, and the islands formed on them do not receive any water drained from upper sites. So, they represent more mesic and homogeneous places, in contrast with the rocky shield, where plants may be flooded and/or highly desiccated. In the main vegetated microhabitat types there were smooth surfaces of variable inclinations and shallow depressions. Species that preferably occupy each of such topographies are listed in Ribeiro & Medina (2002).

Since there was a direct relationship between island area and species richness in this system (Ribeiro 2002) and in similar cases (Michelangeli 2000), it is relevant to ask which are the limits for increase in island size. In Itatiaia, plants are often confined to concavities (figures 3, 4, 6), and most of the vegetation on exposed places show high patchiness, associated either with well-drained shallow depressions or rock pools. This is probably caused by a combination of harsh climatic conditions (strong winds, dryness and freezing temperatures) and the scarcity of safe sites for seed establishment (see Jumpponen et al. 1999), namely lack of soil and associated nutrients and available water. The only exceptions are the steep and smooth surfaces of protected boulders where V. itatiaiae clumps are abundant. There, the plume seeds of this species are able to adhere to the rock surface in these constantly humid places, together with many moss species. But the weight of these tank-forming bromeliads may impair the continuous growth of the clumps in very steep surfaces.

In Itatiaia, the very smooth rock surfaces and the desiccating wind impair plant establishment. The amount of water that a rocky surface may hold is proportional to its fracturing pattern and to the size of the crystals (Larson et al. 2000). The limitations to growth may hinder fusion between islands and the successional process. Islands are often poorly attached to the rocks, given the scarcity of fissures and large crystals, and therefore many are uprooted by extreme weather, or trampled by tourists and livestock. Thus, even extensive flat surfaces are occupied by small islands, and fusion between these islands is rare.

Final remarks – High altitude tropical ecosystems occurring near the equatorial line, within ca. 11°N and 8°S, have been collectively named “páramos” – a term originated in Peru, Venezuela and Colombia – in various studies (e.g., Lauer 1981, Rundel 1994, Hofstede et al. 2003). We argue that Safford’s (1999 a, b) use of the expression “Brazilian páramos”, in reference to Brazilian high altitudinal grasslands or “campos de altitude”, should be seen with caution, although we agree that establishing broad taxonomic categories for vegetation types is a necessary step toward the understanding of continental or worldwide biogeographic patterns. From the several factors discussed in this paper that confer a strong individuality to the “campos de altitude”, we highlight the following: (1) exposure to a stronger seasonality as compared to mountain vegetation from north Peru up to Costa Rica; (2) proximity to the species-rich Atlantic rain forest and distance from the Andean region, conferring floristic individuality to the “campos de altitude”, despite the presence of some genera and a few species in common with the latter.

Irrespective of this terminological debate, it is clear that the rupicolous vegetation is of exceptional importance to the ecological and botanical diversity of the Itatiaia Plateau. The sensitivity of this vegetation to disturbance such as trampling (by both livestock and tourists) and fire demands special attention regarding its protection (Ribeiro et al. 2004). This is particularly necessary in the face of increasing pressure on “Itatiaia” by those practicing outdoor recreation (Tierney 2002).

Acknowledgements – We thank Léo Nascimento and his staff at “Parque Nacional do Itatiaia” (Ibama) for accommodation facilities and support; Brazilian Research (CNPq) and Graduate Education Councils (Capes) for research grants to all authors; Fundação Botânica Margaret Mee for a fellowship to KTR that supported her work in Kew Botanical Gardens (UK); and Pronex-Finep (0877) for funding. We are particularly thankful to the specialists who identified most of the botanical material (Daniela Zappi (K), Elsie Guimarães (RB), Gilberto Pedrall (Cetec), Henrik Balslev (AAU), Hilda Longhi-Wagner (UFRGS), João Marcelo Braga (RB), José Baumgratz (RB), Julie Dutill (Unicamp), Lana Sylvestre (RB), Lúcia Freire (RB), Maria das Graças Wanderley (IB), Maria de Fátima Freitas (USP), Ana Maria Giulietti (UFFS), Paulo Labiak (UFPR), Roberto Esteves (R), Ruy Alves (R) and Tânia Wendt (SFA).

References


