REVIEW

BIOGEOGRAPHY OF THE BRAZILIAN ATLANTIC FOREST: EVIDENCE FROM PHYLOGENETIC DATA SETS AND PERSPECTIVES FOR FERN AND LYCOPHYTE STUDIES

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ABSTRACT
Several biogeographic studies on plants and animals have focused on the Brazilian Atlantic Forest, a “hotspot” area for conservation. The majority of these investigations are on animals, and the most recent studies are based on molecular data (phylogeography). Geography of ferns and lycophytes has been a subject of study for a long time and the major papers involving plants from the Neotropics have been based on floristic surveys and taxonomic revisions. These revisions became more numerous about five decades ago. From the floristic surveys, the most important information is presence or absence of taxa in one area; from taxonomic revisions and other kinds of data, like elevational range, substrate preference, and dispersal capacity, additional clues can be found. New data sets from molecular studies, that have suggested hypotheses about fern and lycophyte evolution, have recently become available, but until now they remain largely underutilized. There is an enormous gap in the literature in using these new data to postulate evolution, radiation, and speciation in these groups of plants in South America. Here we present and discuss some of the recent molecular data for fern groups like *Lomariopsis*, *Pellaea viridis*, and *Megalastrum*. They corroborate the primary and secondary centres of diversity and endemism for ferns in tropical America as outlined by Tryon, and indicate that the Brazilian Atlantic Forest (coastal Brazil) and the Andes (from Venezuela to southern Bolivia) are special areas for evolution and speciation for ferns. Additionally, recent data show that the Brazilian Atlantic Forest has 834 species of ferns and lycophytes, of which 321 (approx. 38.5%) are endemics. An integrated evaluation from a phylogeographic perspective remains unexplored.

INTRODUCTION
Phylogeography could be considered a recent subdiscipline derived from traditional biogeography that deals with spatial and temporal dimensions of genealogy (Avise, 2009). The use of molecular data and temporal aspects to understand the origin, history, and evolution of organisms is a new paradigm for natural sciences. For Avise (2009), phylogeography differs from the traditional biogeography by its special focus on conspecific populations and on explicit genealogical information. Phylogeography differs from ecogeography by its special focus on historical causation in addition to the ecological processes.

To investigate phylogeography in animals scientists use mitochondrial DNA
(mtDNA), whereas in plants the principal molecular markers derive from chloroplast DNA (cpDNA). cpDNA occurs in many copies in the cytoplasm of a single cell, and most individuals show a single cpDNA haplotype sequence (i.e., are homoplastic). Individuals within the same species may have detectable differences in cpDNA sequence, which allows the use of plant cpDNA to estimate genealogical histories in plant population (Avise, 2009).

Brazil is one of the largest countries in the world, with an area of ca. 8.5 million km². As such it possesses the world’s richest flora (40,989 species; 18,932 endemics; Forzza et al., 2012) and is home to two biodiversity hotspots: the Cerrado and the Atlantic Forest (Myers et al., 2000). Despite this importance, there is a paucity of biogeographic studies on Brazilian plants (Fiaschi and Pirani, 2009).

The Brazilian Atlantic Forest is considered one of the World’s biodiversity hotspot areas because it contains a high percentage of endemic species and it is highly threatened (Myers et al., 2000). This strip of forest occupies more than 4,000 km along the coast of Brazil (Figure 1), equivalent to the distance from Nova Scotia to Cuba (Thomas, 2008). Also, according to Thomas (2008), it comprises many types of forest, each with its own flora and today with particular conservation problems.

At least three hypothesized areas of endemism for plants have already been postulated for the Brazilian Atlantic forests, two of them located in the northeast and the other in the southeast (Prance, 1987; Thomas et al., 1998). As pointed out by Thomas (2008), in Brazil the northeastern coastal forests can be found in six states (Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, and Bahia) and they differ from most of the forests in the states of Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, that comprise the southeastern portion of the Atlantic Forest. However, part of the forests in the states of Espírito Santo (at the Linhares Reserve) and Rio de Janeiro (Mata do Carvão) are treated as belonging to the northeastern portion of the Atlantic Forest, although they are outside the northeast area, because of their similarities to the forests of southern Bahia. The forests of the northeastern part of the Atlantic Forest are more accessible, more fragmented, and more diverse for flowering plants (Thomas, 2008), but less diverse for ferns and lycophytes (Prado and Sylvestre, 2010).

According to Batalha-Filho and Miyaki (2011), there are only a few publications on phylogeography of the Brazilian biota, and most have focused on animals and insects that occur in the Atlantic Forest, such as bees (Batalha-Filho et al., 2010), frogs (Carnaval et al., 2009; Thomé et al., 2010), reptiles (Pellegrino et al., 2005; Grazziotin et al., 2006), birds (Cabanne et al., 2007), and bats (Martins et al., 2009).

For plant phylogeography, the main focus of the present review, Ribeiro et al. (2010) investigated Dalbergia nigra (Vell.) Allemão ex Benth., an endemic species from the central region of the Brazilian Atlantic Forest (Bahia refugium). They tested two hypotheses: 1) how the historical events of the Pleistocene influenced current genetic diversity and population structure of D. nigra; and 2) how forest fragmentation generated by human actions has affected the genetic diversity of populations. They identified three phylogeographic groups at different latitudes, and obtained evidence that the two northernmost groups maintained larger populations than the southernmost group. Vicariance (i.e., the splitting of one ancestral population into two or more populations, such as by continental drift or the formation of a geographic barrier; Simpson, 2006) plus climatic changes were identified as the main events for diversification of these groups in the Middle Pleistocene (ca. 350,000–780,000 y.a.). Comparisons among populations from large and small areas, as well as disturbed fragments of the same
phylogeographic group, showed anthropogenic effects on genetic diversity. Additionally, the authors concluded that the three phylogenetic groups can be considered three units, all of them needing special attention for preservation; together they represent a relict of the original genetic diversity of *D. nigra*.

Based on the results presented in these papers, Batalha-Filho and Miyaki (2011) compiled a map showing a recurrent result of the phylogeography of organisms along the Atlantic Forest of the Brazilian coast (Figure 1). There are three phylogeographic discontinuities (Figure 1A, B, C) for all studied groups related to glaciations and neo-tectonic activities during the Quaternary. The main hypothesis to explain these discontinuities is based on the Refugia theory (Haffer, 1969; Vanzolini and William, 1970; Brown and Ab’Sáber, 1979). This theory predicts that the wet dense forests, surrounded by dry and open vegetation, are islands (or refugia) for organisms. Also, according to this theory, the size of these forests changed significantly during late Quaternary climatic fluctuations (Pleistocene era). Wet forests retracted during the dry periods (forming the refugia) and expanded during the wet periods (inter-glaciation), whereas the dry vegetation showed an opposite behaviour.

**Figure 1.** Primary (in circles) and secondary (in squares) centres of diversity and endemism for ferns and lycophytes in tropical America (based in Tryon, 1972). The letters A, B, C, represent the areas of refuges of the Quaternary along the Brazilian Atlantic Forest (based in Batalha-Filho and Miyaki, 2011). RN = Rio Grande do Norte State, RS = Rio Grande do Sul State.
Avise (2009) stated that phylogeography as a discipline has grown exponentially during the last 30 years. He commented on the necessity to improve the basic data for phylogeographic analyses, including evidence from the nuclear genome. According to the results by Edwards and Beerli (2000), increasing the number of loci is critical to decreasing the uncertainty in estimates of population time of divergence. The use of a single marker can lead to incorrect phylogeographic hypotheses, because the results may reflect the history of the chosen marker and not the history of the organism itself. The authors also commented that the use of different markers could result in different hypotheses. Brito and Edwards (2009) pointed out that the best way to reduce the coalescent stochasticity effect is to use several genetic markers, from both chloroplasts and nuclei (see details in Brito and Edwards, 2009; Kuhner, 2009).

Moritz et al. (2000), in their studies on diversification of rainforest faunas, stated that phylogeographic interpretation also depends on data about the biology of the species because the presence of a species in a niche is directly related to its ability to tolerate and survive extremes and variations of the environmental conditions during the maximum glacial periods.

Carnaval et al. (2009) published a good example of a study using molecular genetic data of three particular species of frogs, from distinct populations distributed along the Brazilian Atlantic Forest, to test hypotheses of how these different species populations responded to late Quaternary climate changes in South America and how these fluctuations helped to model present-day diversity. Besides traditional data for biogeographic approaches, they used a mitochondrial marker (mtDNA). The results revealed a hotspot within the Brazilian Atlantic Forest (the Bahian area). This place was a probable refugium for biodiversity during climatic extremes of the Late Pleistocene. The authors also commented that the genetic diversity and narrow endemisms in the central corridor of the biome (exactly in this area) have been greatly underestimated, because the collection efforts, molecular studies, and conservation priorities have been concentrated toward southern and southeastern Brazil. It is problematic since this part of the country has higher deforestation rates than in São Paulo State and southern Brazil (Carnaval et al., 2009). At the end of this paper the authors presented a model to investigate biodiversity prediction. This model might be tested for some fern genera that speciated in this biome, like Megalastrum, various grammitid genera, Serpocaulon, Campyloneurum, Pecluma, Pteris, and others.

In addition to the molecular data and historical aspects to formulate phylogeographic hypotheses for ferns and lycophytes, two other important aspects need to be considered, the level of ploidy of the organisms and long-distance dispersal.

Haufler (2007) has commented on the importance of ideas published by Klekowski (1979) on polyploidy in ferns. He noted that for Klekowski: “… homosporous ferns could store variation among the several to many sets of chromosomes contained within single polyploid individuals. In effect, individuals could act as small populations, each containing considerable genetic variability, … even though individual sporophytes might originate through fertilization of genetically identical eggs and sperms (rendering them 100% homologously homozygous in a single generation) the variation introduced via the chromosome sets obtained through interspecific hybridization and subsequent polyploidy would perpetuate homoeologous heterozygosity”. This mechanism has provided support for changes over time for homosporous ferns (Klekowski, 1979). Unfortunately, there are no data available of ploidy levels for ferns and lycophytes from Atlantic Forest.
Long-distance dispersal is a process that has been regularly investigated in the papers cited above, based on fern morphology, but has not been very well explored in recent phylogenetic papers that included plants from the Brazilian Atlantic Forest (e.g., Labiak et al., 2010; Prado et al., 2013), because they demand more population studies of each taxon to explain the current and previous pattern of geographic distribution.

Although Haufler (2007) summarized in a table the changes of perspectives about the studies of genetics, diversification, and biogeography of ferns, until now, only a few sets of data including these aspects on ferns and lycophytes are available and, consequently, only a few approaches can be used.

**BIOGEOGRAPHY OF FERNS: A SHORT OVERVIEW**

Several authors have discussed ideas about fern biogeography and speciation in tropical America, but there are no recent approaches using the available molecular data sets. According to Moran (2008), the earliest published works on fern and lycophyte biogeography (by d’Urrville, 1835; Baker, 1868; Lyell, 1879; all cited by Moran, 2008) were based on numerical data only and involved percentages and/or occurrences of species in floristic regions around the world. These observations were amplified in subsequent publications by Christ (1910) and Winkler (1938), who detailed the floras by regions (see discussion in Moran, 2008). Copeland (1939) also published on biogeography, and the main focus of his views derived from the idea that ferns and lycophytes were ancestral in the Southern Hemisphere. Copeland concluded that most fern genera were of Antarctic origin (Moran, 2008), but his paper has been ignored by most recent pteridologists, because his assessment was too dogmatic (Moran, 2008).

Since Copeland’s work, several articles have been published by R. Tryon and others on fern biogeography.

Although his first ideas about biogeography dealt with the dynamic phytogeography of *Doryopteris* (R. Tryon, 1944), a representative group of ferns from the Brazilian Atlantic Forest, Tryon later published a series of papers dealing with speciation and biogeography of ferns and lycophytes (R. Tryon, 1970, 1971, 1972, 1985, 1986). Tryon’s ideas about fern biogeography were based on data sets from several taxonomic revisions available. Some of these were published by him or his students (e.g., R. Tryon, 1941, 1942, 1956, 1976; Gastony, 1973; Windisch, 1977, 1978; Barrington, 1978), but some were by other authors (Alston et al., 1981; Bishop, 1977, 1978; Copeland, 1952; Evans, 1969; Hauke, 1963, 1978; Kramer, 1957; Lellinger, 1972; Mickel, 1962, 1981; Morton, 1947; Murillo, 1968; Smith, 1971, 1974, 1980; Stolze, 1974); A. Tryon, 1957, 1962, 1970.

Tryon was especially interested in ferns and lycophytes occurring on isolated islands (R. Tryon, 1970). In this paper, he gave special attention to the processes of dispersal and migration of species to islands. He stated that these are complementary processes. The establishment of a species on an island is an individual event and it is closely related to the genetic variability of the species itself, because dispersal events cannot bring the entire genetic variability of a source population.

In his second paper, Tryon (1972) focused on plants growing on continents. He concluded that tropical American ferns are concentrated in three primary geographic areas: Mexico, the Andes, and Brazil (mainly Atlantic Forest). Two other secondary areas, Central America and the Guianas, were also discussed (Figure 1). Also according to Tryon, these regions contain 90% of the continental fern flora, of which ca. 60% are endemic to one particular region.
Smith (1972) also discussed several factors influencing fern distributions and categorized them as biotic (with a biological base) or as abiotic (with physical or chemical basis). He discussed the influence of each one and presented some cases of species distribution. Smith called attention to the distribution pattern between the Americas and Africa, and recorded a list of “species pairs” or species complexes occurring in both continents. In some cases, e.g., *Adiantum poiretii* Wikstr.*, Asplenium auritum* Sw.*, *A. formosum* Willd.*, *A. lividum* Mett. ex Kuhn, *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf.*, and *Trichomanes reptans* Sw.*, the species occur in both areas. Examples of species pairs are: *Asplenium feei* Kunze ex Fée*–A. anisophyllum* Kunze, *A. serra* Sw.*–A. friesiorum* C.Chr., *Blechnum schomburgkii* (Koltzsch) C.Chr.*–B. tabulare* (Thunb.) Kuhn, *Elaphoglossum erinaceum* (Fée) T.Moore*–*E. hybridum* (Bory) Brack., *Microgramma lycopodioides* (L.) Copel.*–*M. mauritiana* (Willd.) Tard., and *Trichomanes radicans* Sw.–*T. giganteum* Bory ex Willd. The species marked with an asterisk occur in the Brazilian Atlantic Forest.

Moran and Smith (2001) amplified this list of species/species pairs in the Neotropics and Africa and presented more details about the species themselves, as well as the floristic affinities between both areas. To explain floristic affinities between the areas, they invoked long-distance dispersal, but at that time phylogenetic studies to support these examples were virtually non-existent. There were only a few groups for which molecular data existed (e.g., *rbcL*, for Vittariaceae; Crane et al., 1995).

Furthering their studies, Tryon and Tryon (1982) identified four regions of the Neotropics with high species diversity and endemism: Greater Antilles, southern Mexico and Central America, Andean region, and southeastern Brazil. In each region ca. 40% of the species are endemics. The region of southeastern Brazil from the states of Minas Gerais and Espírito Santo south to Rio Grande do Sul contains about 600 species, mostly in the wet montane regions of the “Serra do Mar” (Tryon and Tryon, 1982). Some genera are especially diverse in this region and have several endemic species: *Doryopteris* (with 19 species) and *Anemia* subg. *Coptophyllum* (with 11 spp.) (Tryon and Tryon, l.c.). The Brazilian Atlantic Forest is considered to be one of the most important sites for conservation of biodiversity, and within this domain there are subregions with different levels of species composition, species richness, and endemism.

Salino and Almeida (2009) recorded 840 species to the Brazilian Atlantic Forest, and 269 of them are endemic (approx. 32%). The area included in this account, from the states of Rio Grande do Norte to Rio Grande do Sul (Figure 1), is larger than the area considered by Tryon and Tryon (1982) and that, in part, explains the different number of species.

More recently, Prado and Sylvestre (2010) published a full account of the Brazilian fern and lycophyte diversity. They recorded 1,176 species in the country, 123 spp. of lycophytes and 1,053 spp. of ferns. Among them, 450 spp. (38.2%) are endemic to Brazil (Figure 2). Most of the endemic species are distributed along the Brazilian Atlantic Forest (321 endemics of 834 spp.; 38.5%, Figure 2) (Forzza et al., 2012). A full data set of the Brazilian diversity of plants and fungi can be found at the following website; these data are continually updated:

http://floradobrasil.jbrj.gov.br/jabot/listaBrasil/ConsultaPublicaUC/ConsultaPublicaUC.do

The most diverse Brazilian genera, with the number of endemic species, are summarized in Table 1 (based on Prado and Sylvestre, 2010). Genera with the highest percentage (> 55%) of endemic species in Brazil are: *Megalastrum*, with 18 species, 13 of which (72.2%) are endemic (Moran et al., 2009a); *Huperzia s.l.*, with 38 species, 25
Figure 2. Diversity and endemism of ferns and lycophytes in Brazil and in their different types of vegetation. Source: Prado and Sylvestre (2010). (A.F.= Atlantic Forest; Am=Amazon; Ce=Cerrado; Ca=Caatinga; Pt=Pantanal; Pm=Pampa).
of which (65.8%) are endemic (Windisch, 1996); and *Doryopteris*, with 27 species, 16 of which (59.5%) are endemic (R. Tryon, 1942).

Despite these interesting numerical data of endemism and fern and lycophyte distribution, there are no publications on phylogeography of these groups of plants for South America in general, or for Brazil in particular. Does the endemism in these genera represent a radiation within the Atlantic Forest region, or does it represent many separate migrations of species into the region? In the next section we present some cases where the molecular data have helped to clarify taxonomic decisions about species delimitation or show interesting trends of speciation processes in the Brazilian Atlantic Forest.

**RECENT MOLECULAR PHYLOGENETIC STUDIES INVOLVING BRAZILIAN FERNS**

For the last two decades, phylogenetic papers involving ferns and lycophytes, based on DNA markers and morphology, have helped to elucidate the evolution and relationships among the major lineages of the ferns and lycophytes (e.g., Hasebe *et al.*, 1994, 1995; Pryer *et al.*, 1995, 2001; Korall and Kenrick, 2002, 2004; Schneider *et al.*, 2004; Schuettpelez *et al.*, 2007; Schuettpelez and Pryer, 2007; Rai and Graham, 2010). These general syntheses, as well as others, have stimulated the publication of new classification systems (Smith *et al.*, 2006, 2008; Christenhusz *et al.*, 2011a, b), and helped to address many long-standing questions about the taxonomic position for some groups, like the tree ferns, *Psilotum*, *Equisetum*, and the aquatic ferns. Concomitantly, new inferences about fern biogeography can be made, e.g., on origin of genera (Schneider *et al.*, 2007), origin of floras (Geiger *et al.*, 2007), and on diversification of a particular group in a given area (Polypodiaceae in Africa: Janssen *et al.*, 2007; cheilanthoid ferns in Cape region: Eiserhardt *et al.*, 2011).

More specifically for South America, there are no general papers dealing with origin of genera or floras, diversification of fern groups, or species radiations. However, there are a few examples that can be extracted from recently published phylogenies for a few genera or species that can serve as a first step for further investigations.

*Lomariopsis* is an example of a pantropical genus with species occurring in America and Africa/Madagascar (Moran, 2000; Rouhan *et al.*, 2007). According to the phylogeny of this genus, based on chloroplast intergenic spacer trnL-trnF, the *Lomariopsis sorbifolia*-group is entirely neotropical and another small group within this group, the *Japurensis*-group, occurs in the Neotropics and Paleotropics, forming monophyletic lineages in both regions. Within the *Japurensis*-group, the neotropical clade, formed by *L. marginata* (Schrad.) Kuhn, *L. prieuriana* Fée, *L. latipinna* Stolze, *L. nigropaleata* Holttum, and *L. guineensis* (Underw.) Alston, nests within a subclade formed by two African species, *L. guineensis* (Underw.) Alston and *L. palustris* (Hook.) Mett. ex Kuhn. The authors considered this nested relationship as a probable result of long-distance spore dispersal from the Neotropics to Africa, rather than as a result of continental drift (Moran and Smith, 2001). Morphological evidence of this relationship is the presence of long-spined spores in both African species. This kind of spore ornamentation is not found in other African species of *Lomariopsis*, but is present in *L. prieuriana*, a neotropical species. *Lomariopsis* shows evidence of local diversification in both New and Old Worlds (Haufler, 2007), and the combined data suggests that some African species have an ancestor in the Neotropics. Unfortunately, until now, this hypothesis has not been investigated in detail since publication of the first data set. This genus has one endemic species in the Brazilian Atlantic forest (*L. marginata*) that could be postulated as the
Table 1. Most diverse genera in Brazil and number of endemic species. 

<table>
<thead>
<tr>
<th>Genera</th>
<th>Total of species</th>
<th>Number of Endemic species (and %)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thelypteris</td>
<td>87</td>
<td>47 (54.0)</td>
</tr>
<tr>
<td>Elaphoglossum</td>
<td>82</td>
<td>37 (45.1)</td>
</tr>
<tr>
<td>Asplenium</td>
<td>74</td>
<td>23 (55.4)</td>
</tr>
<tr>
<td>Anemia</td>
<td>70</td>
<td>41 (58.5)</td>
</tr>
<tr>
<td>Adiantum</td>
<td>63</td>
<td>19 (30.1)</td>
</tr>
<tr>
<td>Selaginella</td>
<td>55</td>
<td>15 (27.2)</td>
</tr>
<tr>
<td>Phlegmariurus</td>
<td>39</td>
<td>25 (64.1)</td>
</tr>
<tr>
<td>Cyathea</td>
<td>35</td>
<td>20 (57.1)</td>
</tr>
<tr>
<td>Trichomanes</td>
<td>33</td>
<td>2 (6.1)</td>
</tr>
<tr>
<td>Hymenophyllum</td>
<td>29</td>
<td>8 (27.6)</td>
</tr>
<tr>
<td>Blechnum</td>
<td>29</td>
<td>8 (27.6)</td>
</tr>
<tr>
<td>Doryopteris</td>
<td>28</td>
<td>16 (57.1)</td>
</tr>
<tr>
<td>Lindsaea</td>
<td>27</td>
<td>5 (18.5)</td>
</tr>
<tr>
<td>Diplazium</td>
<td>23</td>
<td>9 (39.1)</td>
</tr>
<tr>
<td>Pteris</td>
<td>22</td>
<td>6 (27.3)</td>
</tr>
<tr>
<td>Campyloneurum</td>
<td>21</td>
<td>5 (23.8)</td>
</tr>
<tr>
<td>Isoetes</td>
<td>21</td>
<td>16 (76.2)</td>
</tr>
<tr>
<td>Pecluma</td>
<td>19</td>
<td>8 (44.4)</td>
</tr>
<tr>
<td>Megalastrum</td>
<td>18</td>
<td>13 (72.2)</td>
</tr>
<tr>
<td>Microgramma</td>
<td>18</td>
<td>1 (5.5)</td>
</tr>
<tr>
<td>Ctenitis</td>
<td>17</td>
<td>10 (58.8)</td>
</tr>
</tbody>
</table>
putative ancestor of the radiation of the genus to Africa by vicariance or long-distance spore dispersal. Or the ancestor could be another species that belongs to the *Lomariopsis sorbifolia*-group.

For species with a disjunct distribution between America and Africa, Prado *et al.* (2013) studied a species pair, mentioned previously by Moran and Smith (2001): *Pellaea flavescens* Fée–*P. viridis* (Forssk.) Prantl. Moran and Smith had concluded that these two species are very similar but distinct, based on slight morphological differences. Prado *et al.* (l.c.), based on the analysis of plastid *rbcL* sequences, showed that *P. flavescens* from eastern Brazil is nested within the Old World species *P. viridis*, and the latter is the correct name for this taxon. However, its distributional history remains unsolved. Prado *et al.* considered two possibilities: 1) *P. viridis* may have been introduced in Brazil and subsequently naturalized; or 2) its occurrence in America is a natural result of long-distance dispersal, probably from Africa to Brazil.

Molecular evidence for *Megalastrum* (with 91 species, Moran *et al.* in prep.) is an excellent example of a genus with wide distribution and speciation processes in the Neotropics (Moran *et al*., 2009a, b; Moran and Prado, 2010; Moran *et al*., submitted), Africa/Madagascar (Rouhan and Moran, 2011), and circumaustral regions (Sundue *et al*., 2010) (Figure 3). The Andean region contains the highest number of species in the genus (46 spp.) and the highest level of endemism (38 spp.; 83%) (Moran *et al*., submitted). The Andean and the coastal Brazilian regions represent the primary centres of diversity and endemisms for *Megalastrum*. According to Moran *et al.* (2009a), *Megalastrum* in Brazil is represented by 18 species and 13 (72%) of them are confined

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**Figure 3.** Diversity and distribution of *Megalastrum* in the world. Note the proportion of endemism in Brazil and the Andes (the number at left is the total number of species; the number at right side is the number of endemic species in the area).
to the Brazilian Atlantic Forest (the genus is absent from the Amazon Forest). Within this forest, some species show narrow endemism, such as *M. littorale* R.C. Moran *et al.*, *M. indusiatum* R.C. Moran *et al.*, *M. organense* R.C. Moran *et al.*, *M. substrigosum* R.C. Moran *et al.*, and *M. retrorsum* R.C. Moran *et al.* All of these Brazilian species appear in the same clade in multiple analyses. These species represent a lineage that diversified in the Brazilian Atlantic Forest.

Despite the importance of the South American flora, and the available data sets from literature and herbarium collections, none of the molecular papers here cited have postulated new ideas about the origin or diversification of the studied groups in the Neotropics; however, the data suggest an important process of diversification in the Brazilian Atlantic Forest.

**FURTHER INVESTIGATION**

Phylogeographic studies involving ferns and lycophytes are potentially important to show that these groups can be used as confident indicators to prioritize areas for protection and conservation of the Brazilian Atlantic Forest, a relictual biota and a hotspot area of biodiversity. Such studies are now feasible because there are several data sets already available for the groups such as, e.g., the high percentage of endemic species and their distribution (Forzza *et al.*, 2010 plus subsequent updates), recent molecular data for some genera and species, as well as biogeographic data that can be taken from taxonomic revisions of the genera or groups of species.

However, to improve the data sets we need the following: further phylogenetic monographs of genera to identify common or putatively ancestral lineages within genera or group of species; studies of groups known or thought to comprise elements in both Africa and South America, or other areas; more studies of older lineages like filmy ferns; better integration of climatic/paleobotanical data with phylogenetic data; more populational studies of particular groups to understand the current and previous geographic distribution, and determination of ploidy level in the Brazilian plants.

For the Brazilian Atlantic Forest several groups (with many endemic and/or widely distributed species) can be investigated following this new paradigm, and among them we suggest: *Asplenium*, *Ctenitis*, *Cyathea*, *Doryopteris*, *Elaphoglossum*, and *Thelypteris* (ferns), *Isoetes* and *Phlegmariurus* (lycophytes) (see Table 1).

As already commented by Moran (2007), recently several new sources of information about fern phylogeny have accumulated, and this set of data affects interpretations of distance dispersal versus continental drift in explaining intercontinental relationships. The intercontinental disjunctions between Brazil and Africa are particularly interesting, but the absence of data from the Brazilian ferns and lycophytes imposes barriers for new interpretations about these distributions. Most of the taxa involved in these kinds of disjunctions between Brazil and Africa are from different regions of the Brazilian Atlantic Forest (see examples given above). Molecular studies based on DNA samples from different populations of these species, allied to the molecular clock methods, are necessary for better understanding and clarification of these patterns of species distribution. Unfortunately, phylogeographic studies on ferns and lycophytes from Brazilian Atlantic Forest are not in progress and this field of research remains unexplored.

Another interesting aspect to be investigated relates to the particular patterns of distribution of fern and lycophyte species along the Brazilian Atlantic Forest. Further examination of these lineages in a phylogenetic context will help to clarify the micro-endemism found in some genera, the high percentage of endemism in general for
these groups as well as whether the actual scenario is the result of isolated speciation events or species radiations processes. However, the last two points need to be studied using temporal information and robust phylogenetic hypotheses (Schneider et al., 2010).

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