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# Global Centers of Vascular Plant Diversity

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With 2 Figures and 1 Table

## *Abstract*

The diversity of vascular plants is very unevenly distributed across the globe. The five centres that reach species richness of more than 5,000 spp./10,000 km$^2$ (Costa Rica-Chocó, Atlantic Brazil, Tropical Eastern Andes, Northern Borneo, New Guinea) cover only 0.2 % of the terrestrial surface. On the other hand approximately 18,500 spp. are endemic to these centres which represent 6.2 % of all vascular plant species. A world map of vascular plant richness is presented based on an extensively expanded data base (more than 3,300 species richness figures for different regions of the world) and a refined methodology. Most of the global centres are located in mountainous regions within the humid tropics, where suitable climatic conditions and high levels of geodiversity, i.e., the diversity of abiotic conditions, coincide. A complete review of most prominent climatic, geologic, and floristic features of the 20 centres of phytodiversity with more than 3,000 spp. / 10,000 km$^2$ is presented.

## *Zusammenfassung*

Die Vielfalt der Gefäßpflanzen ist äußerst ungleichmäßig auf der Erde verteilt. Die fünf Zentren mit mehr als 5000 spp./10000 km$^2$ (Costa Rica-Chocó, Atlantisches Brasilien, Tropische Ost-Anden, Nord-Borneo, Neu-Guinea) bedecken zwar lediglich nur 0,2 % der gesamten Erdoberfläche, jedoch sind ungefähr 18500 spp. endemisch für diese Zentren (6,2 % der Gefäßpflanzenarten weltweit). Eine Weltkarte der Pflanzenvielfalt wird vorgestellt, welche auf einer erweiterten Datengrundlage (weltweit mehr als 3300 Artenzahlen für verschiedene Regionen) und einem verfeinerten methodischen Ansatz basiert. Die meisten Zentren der Artenvielfalt liegen innerhalb gebirgiger Regionen der immerfeuchten Tropen, wo geeignete klimatische Verhältnisse und ein hohes Maß an Geodiversität (Vielfalt abiotischer Faktoren) aufeinander treffen. Ein Überblick über die wichtigsten klimatischen, geologischen und floristischen Charakteristika der 20 globalen Phytodiversitätszentren mit mehr als 3000 Gefäßpflanzenarten pro 10000 km$^2$ wird präsentiert.

## 1. Introduction

The exploration of large-scale patterns of biodiversity has attracted massive scientific interest at least since the first European botanists, zoologists, and biogeographers set out to the tropics to discover and describe the plenty of life. Despite the long tradition of the scientific exploration of the spatial variation of diversity, patterns, and processes are still poorly understood. The knowledge on the distribution of life on earth and its underlying causes is not merely of academic interest for ecologists and biogeographers, but has rather become a crucial need in the context of conservation planning, international politics, and sustainable use of genetic resources. Vascular plants play an important role as primary producers in most terrestrial ecosystems; they are comparatively well known and are thus extraordinarily suitable for global mapping and monitoring approaches. The United Nations Earth Summit 1992 held in Rio de Janeiro highlighted the general lack of knowledge regarding the magnitude and distribution of biological diversity and stressed the need to develop scientific strategies to provide a basic understanding of processes that determine and maintain diversity (*UNCED* 1992). At the conference of the parties to the United Nation's Convention on Biological Diversity (CBD) held 2002 in The Hague (COP VI) the Global Strategy on Plant Conservation (GSPC) was adopted. Among others, the GSPC includes two targets: to protect 50 % of the most important centers of plant diversity and to conserve 60 % of the world's most threatened species *in situ* by the year 2010 (decision of the COP VI/9). To fulfill these targets, detailed information about spatial patterns of phytodiversity is a central prerequisite.

In this contribution we briefly outline the history of the exploration of large-scale patterns of biodiversity which started in the early 19th century. Different mapping approaches are presented and discussed. We then review the present knowledge on patterns of plant diversity on continental to global scale and discuss possible hypotheses about the underlying causes. In the last part, we summarize the prominent physical, climatic, floristic, and biogeographic features of the most important global centers of vascular plants.

## 2. A Short Historical Sketch of the Exploration of Diversity Patterns of Vascular Plants

The beginning of the scientific exploration of global patterns of plant diversity dates back to the very beginning of ecology and biogeography (HUMBOLDT 1806, WALLACE 1878, and HAWKINS 2001). Alexander VON HUMBOLDT (1806) was the first who described the increase of species richness from the poles towards the equator – a nowadays well documented pattern and perhaps one of the most general ecological phenomena known as the 'latitudinal gradient of diversity' (ROSENZWEIG 1995). Even 200 years after its first description and after numerous examples from different groups of organisms and at different spatial scales have been described, the explanation for the latitudinal gradient is still subject of a lively scientific debate (see RHODE 1992, WILLIG et al. 2003, HAWKINS and DINIZ-FILHO 2004, and HILLEBRAND 2004 for extensive reviews). Even 200 years after its discovery, an explanation for the 'latitudinal gradient' still remains the 'holy grail of ecology' (HUSTON 1994).

Inspired by his journey through the New World, the richest of all floristic kingdoms, HUMBOLDT (1845–1858) was also the first person who predicted the Chocó region and nearby Andean forests as one of the mega-centers of phytodiversity: '*Die dem Äquator nahe Gebirgsgegend … von Neugranada* [today: Columbia] … *ist der Teil der Oberfläche unseres Planeten, wo im engsten Raum die Mannigfaltigkeit der Natureindrücke* [today: biodiversity] *ihr Maximum erreicht*' (HUMBOLDT 1845, p. 12) (English translation by OTTÉ (1860, p. 10): '… *The countries bordering on the equator* [meant is the present-day country of Colombia] *posses another advantage … This portion of the surface of the globe affords in the smallest space the greatest possible variety of impressions from the contemplation of nature* [today: biodiversity]'. Moreover, he hypothesized possible explanations for the extraordinary diversity like the complex topography and the variety of suitable climatic conditions for plant life in the region (HUMBOLDT 1808, 1845), which we today term 'geodiversity' (BARTHLOTT et al. 1996, 1999), 'environmental heterogeneity' (RICKLEFS 1977), or 'environmental diversity' (FAITH and WALKER 1996): '*Die Mannigfaltigkeit erreicht ihr Maximum …* (wenn wie) … *in den tiefgefurchten Andenketten die Klimate und die durch sie bestimmten Pflanzen-Zonen schichtweise übereinander gelagert* (sind) …' (HUMBOLDT 1845) (English translation by OTTÉ (1860, p. 11–12)): '*The greatest variety of nature …* (in) … *the colossal mountains of Cundinamarca, of Quito, and of Peru, furrowed by deep ravines,* … (if) … *the different climates are ranged the one above the other, stage by stage, like the vegetable zones …*').

Early approaches of mapping large-scale spatial patterns of phytodiversity include Dr. Heinrich Berghaus' Physikalischer Atlas (BERGHAUS 1837–1847) and the Kosmos Atlas (BROMME 1851/1852) which simply bring known species numbers for different regions of the world on a map, based on figures elaborated by Alexander VON HUMBOLDT (1815, 1817). Hence, these maps rather reflect the state of knowledge of the mid 19th century than real patterns. For instance, a figure of 3,880 known species is given for Tropical America, which is contrasted by a modern estimate of 90,000 spp. (GENTRY 1982b). Nevertheless, HUMBOLDT (1849) estimated that there is a total of 213,000 plant species worldwide based on the 'Nomenclator Botanicus Hortensis' (HEYNHOLD 1840). His estimate is astonishingly close to most recent estimates (compare PRANCE 2001).

In 1926 the Russian botanist, agronomist, geneticist, and phytogeographer Nikolay Ivanovich VAVILOV published his famous *Centers of Cultivated Plant Origins* (VAVILOV 1926) and thereby founded a Russian tradition of diversity mapping. On his map, India, China, the Indo-Malayan, Central Asia, the Mediterranean, the Near East, Ethiopia, South Mexico/Central America, and South America are highlighted as centers of the origin of useful and economically important plants. Eugenii Wladimirovich WULFF (1935), a Russian botanist and plant geographer at the herbarium of the Department of Geography of Cultivated Plants of the U.S.S.R., was the first who published a map that gives species numbers with a nearly worldwide coverage. General patterns and important trends of plant diversity become already visible on this map. However, the comparison of different regions is difficult because the approximately 140 species numbers presented do not refer to a standard area. Based on species richness figures for c. 400 regions world-wide, MALYSHEV (1975) published a world map of species richness where, for the first time, species richness of vascular plants was calculated for a standard area of 100,000 km$^2$. In 1996, we published a first version of a world map on a 10,000 km$^2$ resolution which was based upon species richness figures for some 1,800 geographic units from which 1,030 suitable units were included in the mapping approach (BARTHLOTT et al. 1996). The map we present here is based upon an extensively expanded data set which includes more than 3,300 species richness figures. Furthermore, a refined methodology has been applied (see below and compare MUTKE 2002, KIER et al. 2005a,b).

The most commonly used measure of diversity of different mapping approaches is species richness. In general, there are two methodological approaches to produce diversity maps (for a detailed review see KIER et al. 2005a). In the taxon-based approach distributional information for single species, i.e. data from herbarium records, taxonomic revisions, or range maps delineated by an expert's knowledge, is overlaid in order to generate maps of species richness or endemism (e.g. LOVETT et al. 2000, CRISP et al. 2001, LINDER 2001, KREFT et al. submitted). On the other hand, the inventory-based approach uses summary data for geographic units such as species numbers of different countries, national parks, biogeographic regions, or mountain ranges (BARTHLOTT et al. 1996, 1999, MUTKE et al. 2002). Since geographic units differ in size, species numbers have to be converted to a standard area using, e.g., the power model of the species-area relationship of ARRHENIUS (1920, 1921). Data gaps are filled by interpolation using additional information on, e.g., climate, vegetation, or geodiversity (compare Mutke 2002, Mutke et al. 2002).

Both approaches have certain advantages and disadvantages in their applicability and in the way they reduce information. The taxon-based approach requires huge amounts of distribution data for the analyzed taxa. Here, the easiest way to generate species richness maps is to use pre-processed range maps of the analyzed taxa. Other data sources might be, e.g., herbarium records or distributional information from taxonomic revisions. Generally, the distributional information is projected to a grid system and species occurrences per grid are counted resulting in a map of species density per grid cell. Since most regions of the world are not equally sampled (Frodin 2001b), one has to manage the problem of sampling artifacts, because the imbalance of sampling activity and knowledge might result in artificial gaps and peaks of diversity. A commonly applied technique to tackle these shortcomings is range modeling (e.g. Skov and Borchsenius 1997, Guisan and Zimmermann 2000, Skov 2000, Raxworthy et al. 2003, Sommer et al. 2003, Leimbeck et al. 2004, Vargas et al. 2004). The potential distribution range of a species is estimated with the aid of modeling algorithms and abiotic data (e.g. climate, geology, topography) that might represent the physical requirements of species. Nonetheless, for many groups of organisms the knowledge of their distribution is still very fragmentary and taxon-based mapping approaches do not produce reliable results (Müller et al. 2003). Furthermore, species distributions are not only a function of environmental conditions but of many other factors which are difficult to model, such as competition and historical processes. When compared with inventory-based mapping, the two main disadvantages of the taxon-based approach are probably the very labor-intense data collection and the fact that for many regions of the world, very little taxon-based data of adequate quality are available, whereas the main advantages are high repeatability of methods, good compatibility with widespread geographic mapping standards, and the wide set of applications for further analyses in research and conservation (Kier et al. in press).

The inventory-based approach takes advantage of the bulk of available information compiled in thousands of floras, local checklists, and regional species accounts (Frodin 1984, 2001a). The world map of species richness of vascular plants presented in Figure 1 is the complete revision of an earlier version (Barthlott et al. 1996, 1999) using the inventory-based mapping approach. Whereas for the earlier version of the map c. 1,800 geographic units were used, the new data base for the raw data has been extensively expanded and currently includes more than 3,300 species richness figures. Species richness refers to an area of 10,000 km$^2$ standardized by the species-area relationship of Arrhenius (1920, 1921). This standard area offers a sufficient spatial resolution and is regarded as suitable for large scale conservation approaches. Furthermore, the resolution matches most grid-based mapping schemes which use a one degree resolution (~12,300 km$^2$ at the equator and below 10,000 km$^2$ in temperate regions). Although the inventory-based approach reduces information about the identity of species, it is the only applicable method at the moment to map groups of organisms as large as vascular plants at a global scale.

## 3. Plant Diversity: Patterns and Causes of an Uneven Distribution

The world map of plant diversity shows a general increase of species richness towards the equator (Fig. 1). Most global centers of species richness are located within the humid tropics (e.g. Tropical Andes, Central American Cordillera, Borneo, and central range of New Guinea). However, not all tropical regions show high species richness. For instance, vast parts of the Congo basin have only moderate levels of species richness which is comparable to many parts of Central Europe. Moreover, also some extratropical regions like the Cape of South Africa, the Alpes Maritime of Southern France, or the Caucasus reach very high diversity.

Absolute minima of species richness are found in the Arctic tundra, in the driest parts of deserts (e.g. Rub' al-Khali or parts of the Sahara) or in extensive high alpine deserts (e.g. Tibetan upland). These minima coincide with either a lack of available ambient energy or humidity which limits plant growth. The hot sandy desert Rub' al-Khali on the Arabian Peninsula for instance houses only 37 spp. of vascular plants on approx. 500,000 km$^2$ (Davis et al. 1994), an area comparable with that of mainland Spain. The Namib Desert is one of the exceptions to the rule. With an estimated 4,500–7,000 spp. and a portion of 35–50 % endemics the unique flora of this coastal desert is extraordinarily rich (White 1983b, Davis et al. 1994). The old age and the associated long evolutionary history, in combination with a high topographic and edaphic complexity as well as highly predictable rainfalls (which result from constantly developed fog layers especially in the winter), favor high species richness and endemism (Shmida 1985).

In general, patterns of species richness on a continental to global scale are statistically well correlated with different climatic factors related to ambient energy, water availability, or productivity. Factors like annual precipitation, actual and potential evapotranspiration, and net primary productivity are good predictors of species richness of plants (O'Brien 1993, 1998, Mutke 2002, Mutke et al. 2002, Francis and Currie 2003, Mutke and Barthlott 2005). However, the predictive value of different factors varies between continents and between climatic and vegetation zones (Mutke and Barthlott 2005). In the temperate zone factors like mean annual temperature, length of the vegetation period, or number of frost days show high correlations with species richness. On the other hand, in high energy regions like the tropics and subtropics the influence of water availability gains a stronger influence resulting in higher correlation coefficients with factors like actual evapotranspiration, annual precipitation, or the number of dry months. In many regions, high plant diversity can not exclusively be explained by contemporary climate. Historical factors like, e.g., long term climatic stability or geologic history also have to be considered. It has been demonstrated for vascular plants and different groups of vertebrates that long term climatic stability explains high degrees of endemism (Dynesius and Jansson 2000, Jansson and Dynesius 2002, Jansson 2003).

Another important factor which favors species richness of vascular plants is geodiversity, the diversity of abiotic factors (Barthlott et al. 1996, Faith and Walker 1996, Barthlott et al. 1999, 2000, Jedicke 2001, Braun et al. 2002). Especially mountainous regions are characterized by steep climatic gradients within short distances, heterogeneous geology and a diversity of different soil conditions. In fact, most of the global centers of vascular plant diversity are located in mountainous regions of the humid tropics and subtropics or otherwise highly geodiverse areas (Fig. 2). The diversity of the physical environment favors ecological specialization and complex landscapes offer a greater potential for allopatric speciation.

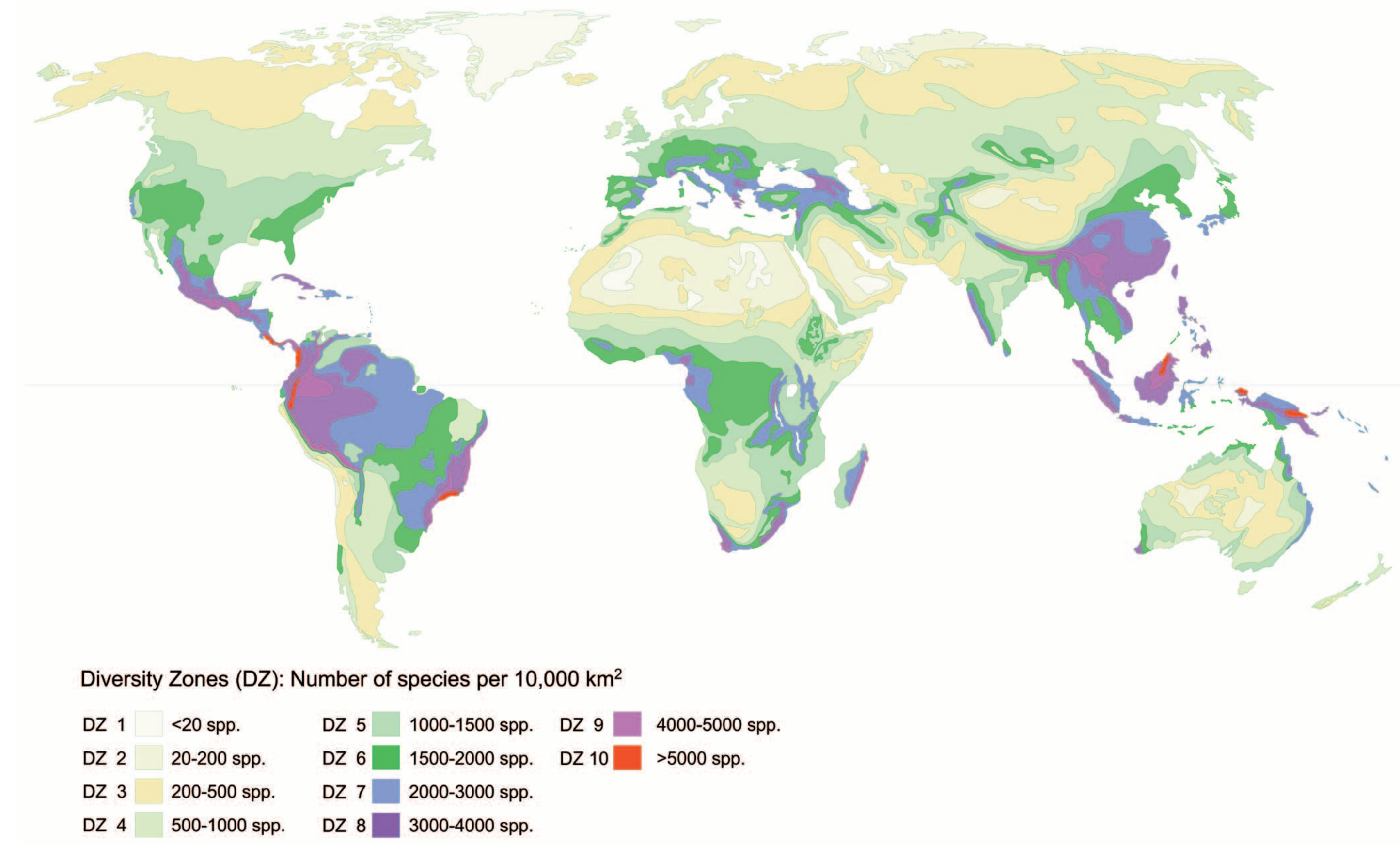

Fig. 1 Global Biodiversity: Species numbers of vascular plants. W. BARTHLOTT, G. KIER, H. KREFT, W. KÜPER, D. RAFIQPOOR and J. MUTKE 2005 revised after BARTHLOTT et al. 1996, Nees Institute for Biodiversity of Plants, University of Bonn. Robinson Projection, Standard Parallels 38 °N and 38 °S

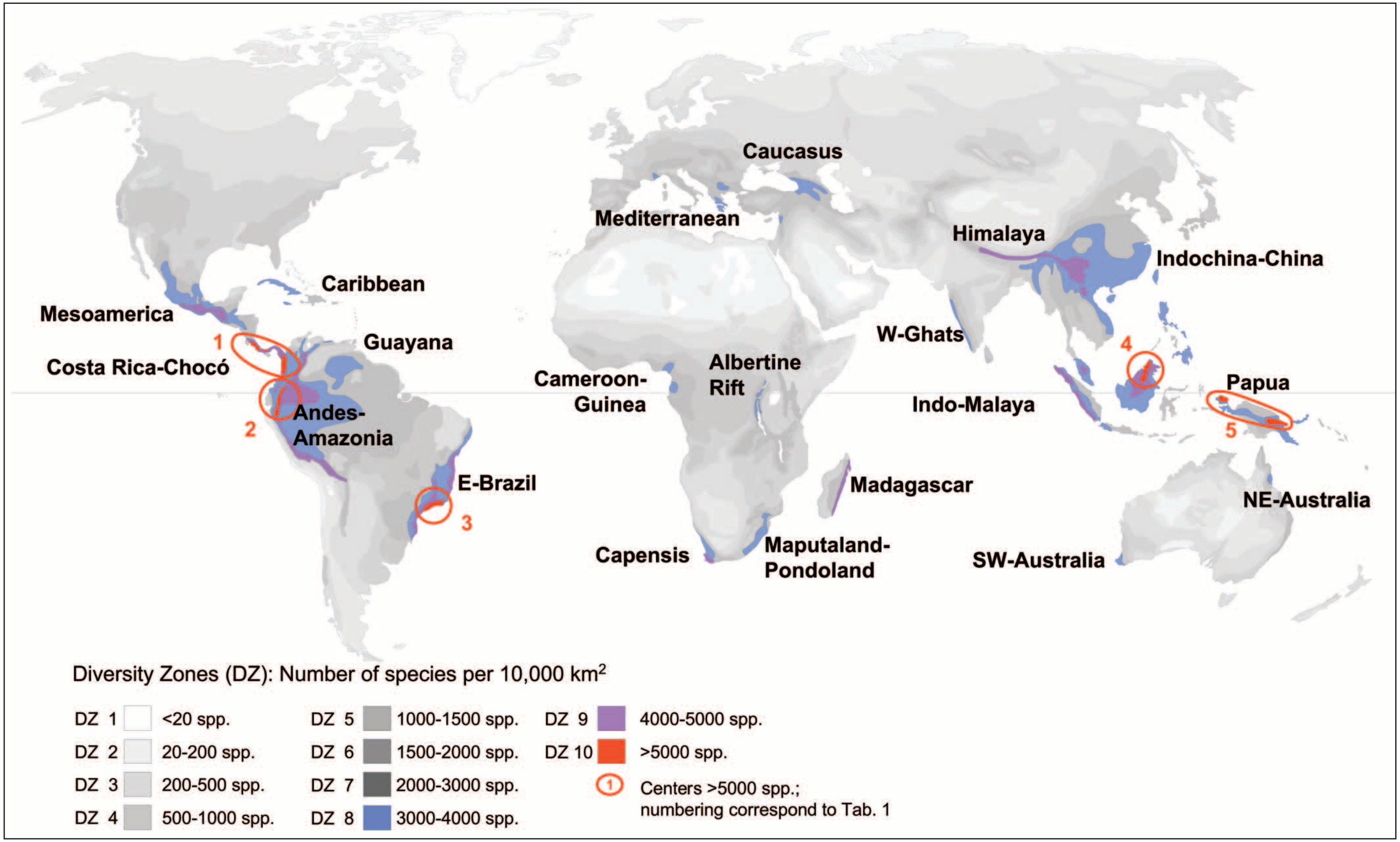

Fig. 2 Global Biodiversity: Centers of vascular plant diversity. W. BARTHLOTT, G. KIER, H. KREFT, W. KÜPER, D. RAFIQPOOR and J. MUTKE 2005 revised after BARTHLOTT et al. 1996, Nees Institute for Biodiversity of Plants, University of Bonn. Robinson Projection, Standard Parallels 38 °N and 38 °S

## 4. The Centers of Plant Diversity

In Figure 2 all global centers with a species density of more than 3,000 species per 10,000 $km^2$ are highlighted (this corresponds to Diversity Zones (DZ) 8–10). This classification results in 20 global centers characterized by high to highest values of species richness. Five centers fall into the highest category of more than 5,000 species per 10,000 $km^2$ (DZ 10): Costa Rica-Chocó, Tropical Eastern Andes, Atlantic Brazil, Northern Borneo, and New Guinea (see Tab. 1 and compare Fig. 2). Interestingly, all five centers with maximum species richness represent mountainous regions in the humid tropics. According to the ecoregion scheme of WWF (Olson et al. 2001), all of these centers fall within the biome of 'Tropical moist broadleaf forests'. Together they comprise an area of only 0.2 % of the earth's terrestrial surface which is roughly equal to the size of Germany. In Table 1 we give conservative estimates of total species numbers and numbers of endemic plants for each center which were derived from various sources. Unfortunately, it is not possible to give a reliable estimate of the total species number of vascular plants that are native in all five centers, because there are no reliable data on the floristic overlap available. However, the different sources about endemism in these centers allow an educated guess that probably more than 18,500 spp. are endemic to these centers (~6.2 % of all global plant species, compare Tab. 1).

Tab. 1 Summary information about the five global centers of plant diversity which surpass 5,000 spp. per 10,000 $km^2$.

| Center | Area ($km^2$) | Total spp.[1] | Endemism[1] spp. | | Elevation % | Latitude (m a.s.l.) | WWF-Biomes[2] | Percent protected[3] |
|---|---|---|---|---|---|---|---|---|
| 1. Costa Rica-Chocó | 78,000 | ≥ 12,500[a] | 5,500[a] | 44 % | 0–3,800 | 4°N–10°N | 1; 2; 14 | 18.8 % |
| 2. Tropical Eastern Andes | 62,000 | 10,000[b] | 3,000[b] | 30 % | 250–3,500 | 1.5°N–5°S | 1; 10 | 19.1 % |
| 3. Atlantic Brazil | 50,000 | ≥ 6,000[c] | 4,500[c] | 75 % | 0–2,800 | 21.5S°–24°S | 1; 7 | 6.3 % |
| 4. Northern Borneo | 57,000 | 9,000[d] | 3,500[d] | 39 % | 0–4,100 | 2°N–7°N | 1; 10; 14 | 7.7 % |
| 5. New Guinea | 87,000 | ≥ 6,000[e] | 2,000[e] | 33 % | 0–4,500 | 0.5°S–6.5°S | 1; 10 | 1.8 % |
| total | 334,000 | | 18,500 | | | | | |
| % of world's total[4] | 0.2 % | | 6.2 % | | | | | |

[1] Figures for total species number and endemism represent conservative estimates after various sources (Myers 1988, Groombridge 1992, Jørgensen and León-Yánez 1999, Davis et al. 1997):
[a] La Amistad Biosphere Reserve = 10,000 spp., 3,000 end. spp. (Davis et al. 1997), plus endemic species of the Chocó Department: 2,500 spp. (Myers 1988). [b] baseline Ecuadorian Andes >1,000 m = 9,865 spp. (Jørgensen and León-Yánez 1999); 3,040 national endemic plants in the Ecuadorian Andes (Valencia et al. 2000): minus W-Andes endemics, plus narrow endemics of Peru and Colombia. [c] Mountain ranges of Rio de Janeiro: 5,000–6,000 spp., 75 % endemism (Davis et al. 1997). [d] Northern Borneo 9,000 spp., 3,510 end. spp. (Myers 1988). [e] Bismarck Falls, Ramu, Mt. Otto, Mt. Wilhelm: 5,000–6,000 spp. (Groombridge 1992), 30 % endemism estimated (considering that estimated endemism for whole New Guinea ranges between 55 and 90 % (Groombridge 1992, Myers 1988).

[2] WWF-Biomes after Olson et al. 2001: (1) Tropical moist broadleaf forest; (2) Tropical and subtropical dry broadleaf forest; (7) Tropical and Subtropical Grasslands, Savannas and Shrublands; (10) Montane Grasslands and Savannas; (14) Mangroves.

[3] Portion of the centre which is protected according to IUCN categories I–IV (after *World database on protected areas* (*UNEP* and *IUCN* 2003).

[4] Baselines for world's total: terrestrial earth's surface = $144.5 * 10^6$ $km^2$; global species number of vascular plants = 300,000 spp.

There are no centers that reach DZ 10 in Africa, Australia, or Europe. Asia and the Americas show the highest number of centers of the categories DZ 8–10 with six centers each. Like in many other biogeographic features, Africa stands as the 'odd man out' (RICHARDS 1973) with lower overall diversity than in the Neotropics and Asia and achieving high species numbers only in quite restricted regions like, e.g., in the Cape region, the Cameroon-Guinea region, and in some areas of the East African mountains.

In the following section we give a brief synopsis about the geologic, climatic, and physical setting of the centers of plant diversity. We summarize important factors which are responsible for the high diversity and discuss most important biogeographic and floristic features.

### *4.1 The Americas*

The **Mesoamerica Center** (DZ 8–9; 737,000 km$^2$) ranges from 27° to 13° N and encompasses two sub-centers: the **Mexican Highland Sub-center** (DZ 8; 362,000 km$^2$) and the **Sierra Madre del Sur Sub-center** (DZ 8–9; 375,000 km$^2$). The center is characterized by a very complex geologic history. Alongside Central America stretch topographical and geological diverse highlands, ranging from sea level up to 5,700 m (Pico de Orizaba). Recent volcanic activity has led to a broken topography and volcanic material has produced fertile soils as a basis for high phytodiversity (LAUER et al. 2003). Whereas the northern parts are under stronger influence of extra-tropical climate and frequent break-ins of cold air masses from the North ('Northers'; KLAUS 1973), the southern parts are characterized by more evenly tropical climate, where precipitation may exceed 3,500 mm and dry season is shorter than two months in most of the area. Furthermore, there is a strong climatic differentiation between the Pacific and Caribbean sides of the mountain ranges. Whereas the Pacific side shows a pronounced dry season, the effects of a dry season are alleviated by luv effects of the trade wind on the Caribbean side. This leads to a highly asymmetrical arrangement of vegetation types with dry forest on the Pacific and wet broadleaf forests on the Caribbean side. After the closing of the Isthmus of Panama (2–3 million years ago [mya]), mountain ranges acted as immigration routes of Holarctic plants into the tropical parts of Central and South America (BADER 1960, TROLL 1968, STEHLI and WEBB 1985). Classical examples are the tree genera *Alnus* (distributed South as far as Argentina), *Quercus* (Colombia), and *Pinus* (Guatemala). The mixture of Neotropical and Holarctic elements to some extent explains the remarkably high diversity in Mesoamerica. In addition, the rise of geologically young mountain chains has led to allopatric speciation and high levels of local endemism (GENTRY 1982a, b). More than 10,000 plants are considered to occur in the **Mesoamerica Center** of which about 30 % are endemic (DAVIS et al. 1994). The figure of more than 8,200 documented species for the Mexican state of Chiapas by BREEDLOVE (1986) even suggests much higher total species numbers.

The **Costa Rica-Chocó Center** (DZ 8–10; 224,000 km$^2$) includes the two sub-centers: **Central Cordillera of Costa Rica and Panama** (DZ 9–10; 106,000 km$^2$) and the **Chocó-Center** (DZ 8–10; 118,000 km$^2$). The **Central Cordillera of Costa Rica and Panama Sub-center** includes the diverse tropical lowland and montane rainforests of the Isthmus region. The Cordillera de Talamanca is the most prominent topographic feature with the Chiriquí as its highest peak and a flora of estimated 10,000 spp. (DAVIS et al. 1997). The adjoining **Chocó Sub-center** comprises parts of the Pacific coast between Panama (9° N) and Central Ecuador (2° S). The sub-center ranges from the lowlands of Pacific coast with low coastal mountain ranges up to humid montane forests of the western flank of the Andes to an elevation of c. 2,000 m. Climate is characterized by very high annual rainfall in most parts. Under the influence of the inner tropical convergence zone (ITCZ) a low-pressure trough on the continent is produced which is responsible for the inflow of very humid monsoon type winds. The consequence are the highest rainfalls world-wide in the inner tropics (>8,000 mm). The perhumid climate in combination with high annual temperatures and a geologic heterogeneous underground is the basis for an extraordinarily rich flora with a high degree of endemism (8,000–9,000 spp., 56 % endemism; GENTRY 1982b, c, 1992). Most important families in terms of species numbers are the Orchidaceae, Leguminosae, Asteraceae and Polypodiaceae (GENTRY 1986). Furthermore, the Chocó has the richest palm flora of the entire Neotropics (KREFT et al. submitted). GALEANO et al. (1998) report very high levels of alpha diversity for the Chocó region. In a plot with an area of just 0.1 ha in the Colombian Chocó the authors recorded a total of 442 vascular plant species.

The **Andes-Amazonia Center** (DZ 8–10; 2,812,000 km$^2$) comprises two distinct sub-centers: the **Western Amazonia Sub-center** (DZ 8–9; 2,166,000 km$^2$) which includes parts of Ecuador, Colombia, Brazil, and Peru and the **East Andean Sub-center** (DZ 8–10; 646,000 km$^2$) ranging from Colombia into the northern part of Bolivia. The highly structured landscape of the **East Andean Sub-center** ranges from premontane forests over mist engulfed montane forests to the snow covered volcanoes (>6,000 m) of the Eastern Andean cordillera. The heterogeneous geology with Precambrian to Cretaceous-Tertiary rocks has produced a variety of different soils. The influence of the ITCZ and additional luv effects at the eastern flank of the Andes result in high amounts of rainfall and largely aseasonal wet conditions. In the zone of maximum cloud formation and precipitation, annual precipitation may exceed 4,000 mm. Highest species richness on a regional scale is reached in an elevation zone between 1,000 and 2,000 m (JØRGENSEN and LEÓN-YÁNEZ 1999, VAN DER WERFF and CONSIGLIO 2004), whereas the upper montane forests (2,500–3,500 m) and the páramo vegetation above 4,500 m show the highest levels of endemism (LAUER et al. 2001, KESSLER 2002b). For instance, 76 % of the 4,011 spp. of vascular plants endemic to Ecuador occur in the Andean region (VALENCIA et al. 2000). The relatively recent uplift of the northern Andes and the topographic and climatic diversity have led to an explosive radiation within many taxonomic groups (GENTRY 1982a, GENTRY and DODSON 1987, LUTEYN 2002, YOUNG et al. 2002). Vascular epiphytes are the most speciose life-form in Andean montane forests (KESSLER 2002a, KÜPER et al. 2004, VAN DER WERFF and CONSIGLIO 2004). In Ecuador they contribute 30 % to the country's flora, and 35 % of the endemic plants of Ecuador are epiphytes (JØRGENSEN and LEÓN-YÁNEZ 1999, VALENCIA et al. 2000, KÜPER et al. 2004). The elevation belt of the páramo is dominated by tussock grasses of the genera *Festuca* and *Calamagrostis* and numerous species of the Asteraceae, Ericaceae, Polygalaceae, Polygonaceae, Gentianaceae, Caryophyllaceae and Scrophulariaceae (LAUER et al. 2001). Probably among the most conspicuous plants of the Andean páramos are the giant rosette plants of the genera *Espeletia* and *Puya*. During the glacial periods of the Quaternary, the forest line was lowered by about 1,000 m (VAN DER HAMMEN and CLEEF 1986). Consequently, páramo vegetation has repeatedly spread during colder periods and retreated during the warmer interglacials which has led to a highly complex biogeographic history (HOOGHIEMSTRA and VAN DER HAMMEN 2004).

The adjacent **Western Amazonia Sub-center** is characterized by relatively high and principally aseasonal rainfall (3,000–4,000 mm/a) as well as richer soils compared to the central and eastern parts of Amazonia. Furthermore, parts of the region comprise the Napo refuge, the largest of the Pleistocene forest refugia proposed for the Neotropics (Haffer 1969, 1982, 1987, Prance 1982, Haffer and Prance 2001, but see as well Colinvaux et al. 2001, Knapp and Mallet 2003). This might have contributed to higher species richness and higher levels of endemism. Additionally, Kreft et al. (2004) have shown that high epiphyte diversity in Western Amazonia is partially due to an influence of Andean species which are able to descend into the lowlands because of the proximity to the Andes and suitable perhumid climate conditions. Furthermore, the region of the Upper Napo in the Ecuadorian Amazon exhibits the world's highest alpha diversity for trees (Valencia et al. 1994, Pitman et al. 1999) and lianas (Nabe-Nielsen 2001) that has been recorded so far. On the other hand, compared to Andean forests, beta diversity seems to be comparatively low in the Amazonian lowlands (Pitman et al. 2002), although there can be a high diversity of different forest types and ecological specialization on the local scale (Tuomisto et al. 1995, Tuomisto and Dalberg Poulson 1996).

The **Guayana Center** (DZ 8) is part of the Precambrian Guayana Shield and covers an area of 379,000 km$^2$. The scattered tabletop mountains or tepuis which are characteristic for the region reach elevations of up to 2,800 m (Mt. Roraima). The tepuis are parts of a horizontally aligned, approx. 3,000 m thick packet of Proterozoic sandstone. Annual precipitation in the region varies locally between 2,000 and 4,000 mm with a slight decrease from January to March. The typical vegetation in the lowlands is a mosaic of lowland rainforests and savannas. The slopes and bases of the tepuis, on the other hand, are covered with different montane forest communities, whereas the summits are mainly covered by floristically and physiognomically distinct scrub and herbaceous formations (Berry et al. 1995b). So far, it is estimated that more than 9,000 spp. of vascular plants natively occur in the Guayanas, 3,000 of them are found in the Pantepui region above 1,500 m (Berry et al. 1995a, Davis et al. 1997). The flora has been described as 'biogeographically unique' (Maguire 1970, Berry et al. 1995b, Kelloff and Funk 2004) and endemism is regarded to be high: 40 % of the species covered by the 'Flora of the Venezuelan Guayana' are endemic to the Guayana Shield (Steyermark et al. 1995). The fern family Hymenophyllopsidaceae and the monotypic angiosperm family Saccifoliaceae are endemic to the Pantepui region (Berry et al. 1995b). Additionally, there are 39 endemic genera restricted to the unique habitats of the summits of the tepuis (Berry et al. 1995a). Numerically, the most important families are Orchidaceae, Bromeliaceae, Melastomataceae, and Rubiaceae, whereas the familial composition on the summits of the tepuis differs considerably (e.g. Theaceae, Xyridaceae, Rapateaceae, and Ericaceae) (Steyermark et al. 1995).

The **Eastern Brazil Center** (DZ 8–10) stretches as a long band along the Atlantic coast from Salvador de Bahia (8° S) to Porto Alegre (28° S) on an area of 754,000 km$^2$. Favored by the warm Brazil current, this center reaches far South into the subtropics. The topography is dominated by the mosaic-like dissected Sierra da Mantiqueira (sea level up to 2,767 m). The Archaic and Proterozoic rocks of the Brazilian Shield as well as Mesozoic and Cainozoic deposits have produced different tropical red clay soils (Ferrasole and Luvisole). The center is characterized by strong climatic gradients. Whereas the north-eastern parts receive only little amounts of rainfall (~500 mm), the Atlantic flank of the mountain ranges profits from a luv effect of the trade winds and the natural vegetation are luxuriant evergreen tropical broadleaf forests (Mata Atlântica). In the southern part the vegetation changes gradually into species rich subtropical wet forests of the Serra do Mar. The latter have comparably high species diversity. 5,000–6,000 spp. are reported from the surroundings of Rio de Janeiro of which 70–80 % are endemic (Davis et al. 1997). Among the tree species, especially Myrtaceae, Leguminosae, Sapotaceae, Lauraceae, and Rubiaceae play an important role, whereas palms are only represented with low species numbers (Mutke 2002, Kreft et al. submitted). The natural vegetation is heavily depleted because of deforestation and agricultural conversion. It is estimated that primary vegetation remains on only 5 to 7.5 % of its original extent (Fonseca 1985, Myers et al. 2000).

Important factors causing the high diversity in the **Caribbean Center** (DZ 8; 103,000 km$^2$) are the heterogeneous topography (ranging up to 2,005 m; Turquino), the isolation of the different islands within the archipelago and the highly differentiated geologic bedrock. Depending on the geology (serpentinite, gabbro, diorite, granite, basalt, dolomite, lime- and sandstone) a diversity of different soils has developed (Vertisols, Cambisols, Ferrasols, Luvisols, and Histisols). Climate in the Caribbean is under steady influence of the trade winds which cause sharp differences in precipitation between leeward and luvward sides of mountain ranges (600–5,000 mm). Whereas the lowland vegetation mainly consists of seasonal dry to moist forest, the northern flanks of mountains are covered with lush and evergreen tropical broadleaf vegetation. It is estimated that 13,000 spp. of vascular plants are native to the Caribbean Islands (Davis et al. 1997). With 6,498 native species Cuba exhibits both the richest flora and the highest level of endemism (50 %) among the Caribbean Islands (Borhidi 1991), followed by Hispaniola (5,135 spp., 28 %), Jamaica (3,304 spp., 28 %), Puerto Rico (2,492 spp., 10 %), and Trinidad and Tobago (2,259 spp., 11 %) (Davis et al. 1997).

### *4.2 Africa*

The **Cameroon-Guinea Center** (DZ 8; 88,000 km$^2$) includes the **Mount Cameroon Sub-center** and the **Guinea Sub-center** (44,000 km$^2$ each). Mount Cameroon (4,100 m) is the prominent topographic structure and represents the northernmost outlier of a band of volcanic activity from São Tomé, Príncipe, and Bioko (Fernando Po) in the Gulf of Guinea. The Crystal Mountains (1,525 m) in Equatorial Guinea, on the other hand, are of crystalline origin. Ancient crystalline rocks of the African Shield and relatively recent volcanic material provide a variety of pedologically diverse habitats. The climate is markedly influenced by the monsoon as a consequence of the atmospheric circulations and land-water antagonism in the region. This causes comparatively high annual rainfalls at the SW flank of Mt. Cameroon (more than 10,000 mm), in Equatorial Guinea, and in Gabon (Libreville: 2,592 mm). The moist evergreen lowland forests are the richest of the whole Guinea-Congolian region. The montane and in particular the alpine vegetation of Mt. Cameroon, on the other hand, shows a close relationship to that of the East African Mountains. Various authors (Hamilton 1976, Mayr and O'Hara 1986, Hamilton and Taylor 1991) have postulated that the high diversity in the Gulf of Guinea regions corresponds to one of the most important Pleistocene rain forest refugia in Africa. Evidence comes from the fact that the region shows the highest number of vascular plant families in Africa and a high number of palaeoendemics. Although they state that the flora is comparatively poorly known, Davis et al. (1994) estimate that there are 3,500 spp. on Mt. Cameroon. Taking into account that the most recent checklist for the region includes 2,435 spp. (Cable and Cheek 1998), this seems to be a reasonable estimate. 49 taxa are known to be strictly endemic to the massif (Cable and Cheek 1998).

Highest species richness in East Africa is reached in the **Albertine Rift Center** (DZ 8; 55,000 km$^2$). The center extends from Lake Albert in the North down to Lake Tanganyika in the South and encompasses parts of the Democratic Republic of Congo, Uganda, Rwanda, Burundi, and Tanzania. The three disjunct parts of the center include the Rwenzori Mts., Mitumba Mts., and the Virunga volcanoes along the Western Rift Valley. With an altitude of 5,118 m, Mt. Stanley in the Rwenzori Mts. is the highest peak of this center. Natural vegetation types incorporate the very eastern portion of the Guinea-Congolian rainforest in the lowlands below 600 m, luxuriant montane forests, ericaceous, and afroalpine vegetation. The altitudinal belt of the afromontane forests shows the highest species richness and highest concentration of endemic species. Above 3,500 m tropical alpine vegetation is found which is remarkably poor in species compared to other tropical alpine plant communities in the South American and Indo-Malayan tropics. About 300–350 spp. are considered to be genuine afroalpine elements (HEDBERG 1986, 1992). Morphologically similar adaptations to harsh environmental conditions of afroalpine giant rosette plants *Dendrosenecio* and *Lobelia* to South American (e.g. *Espeletia*, *Puya*), Hawaiian (*Argyroxiphium sandwichsense*), or New Guinean (*Cyathea*) species are striking examples of convergent evolution (MONASTERIO and VUILLEUMIER 1986, RAMSAY and OXLEY 1997). A most recent update by PLUMPTRE et al. (2003) gives a number of 5,793 spp. for the flora of the Albertine Rift which is nearly a quarter of the whole flora of tropical Africa (compare GROOMBRIDGE 1992, LEBRUN and STORK 1998). Furthermore, the center is considered as one of the most important centers of local endemism in Africa (LINDER 1998).

The **Maputaland-Pondoland Center** (DZ 8; 150,000 km$^2$) forms an approx. 150 km broad band along the coast of the Indian Ocean and ranges from the southern tip of Mozambique down South to the Eastern Cape Province. The region is characterized by a highly diverse topography which corresponds to partial overlap with the Drakensberg region and the margin of the Great Escarpment, with altitudes ranging from sea level up to 1,800 m. Due to the influence of the warm Agulhas current, the **Maputaland-Pondoland Center** receives most of its annual precipitation during the summer. Annual rainfall ranges regionally between 400 and 1,200 mm, and in most parts along the coast there is a relatively high humidity with frequent occurrence of fog (VAN WYK and SMITH 2001). The natural vegetation represents a mosaic of different grassland, thicket, and forest communities. VAN WYK and SMITH (2001) estimate that the indigenous flora of the center consists of about 7,000 spp. of which more than 1,800 spp. are endemic. The highest concentration of endemic species can be found in grassland communities. Especially rich in endemic species are the Asclepiadaceae (103 endemic spp.), Asteraceae (102), Fabaceae (90), Liliaceae (71), and Orchidaceae (60). Furthermore, there is a remarkably high number of endemic species in succulent genera like *Aloe* (30 endemic spp.), *Brachystelma* (20), and *Euphorbia* (20).

The **Capensis Center** (DZ 8–9; 87,000 km$^2$) comprises the Cape Floristic Region at the southern tip of the African continent forming a narrow strip from the Namib coastal desert to the vicinity of Cap Agulhas. The eastern parts of the Capensis reaching Port Elizabeth have lower species richness and are not included in this center. Most of the region falls into the climatic zone of subtropical winter rainfall. The warm Agulhas current in the East and the cold Benguela current in the West are the decisive factors for the regional climate. The cold Benguela current causes fog which has impact on a 200 km wide coastal strip and on parts of the Great Escarpment. The mainly leaf-succulent vegetation may profit from water condensation caused by fog. With greater distance from the Atlantic coast the subtropical regime prevails with summer rains resulting in a greater importance of plants with succulent stems. Especially in the transition zone between both rainfall regimes there is a complex mosaic of different vegetation types (LAUER and RAFIQPOOR 2002). At the eastern coast air masses carry moisture laden air masses from the sea which raise and condensate at the Great Escarpment and which provide high humidity throughout the year. GOLDBLATT and MANNING (2002) state that there are more than 9,000 spp. of vascular plants in the Cape, of which 69 % are endemic. Continental analyses show that the southern African Cape is the most important diversity center for plant diversity in Continental Africa (Lovett et al. 2000, Kier and Barthlott 2001, Linder 2001, Mutke et al. 2002, Kier et al. 2005, Küper et al. 2004). The Cape flora exhibits more species than can be expected from its latitude, and its diversity is comparable with many areas within the humid tropics (Linder 2003). The numerically most important families in the Cape flora are Asteraceae (1,036 spp., 63 % endemic), Fabaceae (761 spp., 83 %), Iridaceae (677 spp., 80 %), Aizoaceae (659 spp., 80 %), Ericaceae (657 spp., 97 %), Scrophulariaceae (414 spp., 72 %), Proteaceae (329 spp., 97 %), and Restionaceae (294 spp., 93 %) (Goldblatt and Manning 2002). According to the classification of the *Angiosperm Phylogeny Group* (*APG* 1998) there are five endemic families (Penaeaceae, Stilbaceae s. str., Grubbiaceae, Roridulaceae, Geissolomataceae) within the Cape flora (Goldblatt and Manning 2002). Furthermore, Linder (2003) recognizes 33 'Cape floral clades' which have diversified extensively within the **Capensis Center** and which account for almost half of the outstanding diversity of the Cape flora. The diversification within these clades started between 18 and 8 mya and was associated with climatic changes since the Cenozoic. Further factors that are closely linked with the diversification within these taxa might be limited gene flow caused by the heavily dissected landscape, pollinator specialization, and high levels of geodiversity (e.g. soils, climate, altitudinal changes, and fire regimes) (Goldblatt and Manning 2002, Cowling and Proches 2005).

Because of its long isolation from mainland Africa, the **Madagascar Center** (DZ 9; 91,000 km$^2$) has a very special biogeographic history. On a length of 1,600 km, the coastal mountain ranges in the eastern part of the island are the center of species richness of vascular plants. Single mountain tops reach elevations of more than 2,800 m. There are two general climatic gradients: decreasing precipitation from the North to the South and from the East to the West. The SE trade winds that come from the Indian Ocean bring high precipitation all year round to the luvward mountain ranges of the eastern highlands (2,000–3,500 mm). The leeward sides, on the other hand, are much drier. The moist tropical broadleaf and montane forests contain the highest species richness. Typical families within these forests are Anacardiaceae, Araliaceae, Myrtaceae, Rubiaceae, Euphorbiaceae, Flacourtiaceae, Loganiaceae, Malpighiaceae, and Sapindaceae. Because Madagascar has been isolated for more than 270 million years, endemism is high on all taxonomic levels. Four families (Didieraceae, Didymelaceae, Sarcolaenaceae, Sphaerosepalaceae; following Cronquist 1981) and 350 genera are restricted to Madagascar. According to Grubb (2003) two most notable features distinguish the flora of Madagascar from the flora of continental Africa: its high species richness and its endemicity. 81 % of the 9,345 described species of vascular plants are endemic to Madagascar (Davis et al. 1994), more than 6,000 spp. occur in the rainforests of East Madagascar (White 1983a, Myers 1988). Furthermore, Madagascar has one of the richest and most endemic palm floras of the world (167 spp., 99 % endemism), many of them have only recently been described (Dransfield and Beentje 1995). Other taxa that are much more speciose in Madagascar than on continental Africa include pandans, tree ferns and bamboos. Grubb (2003) evaluated 28 families of vascular plants occurring in East Africa and Madagascar and found that all analyzed families have much more representatives in Madagascar than in the adjacent parts of East Africa. A reasonable explanation could be that, compared to continental Africa, the Madagascan flora suffered less from extinction during drier periods in the Pliocene and Pleistocene (Leroy 1978, Grubb 2003).

### *4.3 Europe*

The **Mediterranean Center** houses four relatively small, disjunct sub-centers which reach DZ 8: the **Alpes Maritimes-,** the **Balkans-,** the **Rhodope-,** and the **Phoenici Sub-center**. Together they cover an area of 97,000 km$^2$. High species richness is reached in regions of the alpidic mountain ranges. A decisive factor for plant life is the regime of winter rainfalls with mild, humid winters and hot, dry summers. Thermal conditions are favorable throughout the year with little probability of frosts in most circum-Mediterranean regions. Hence, the seasonal rhythm of plant life is mainly determined by hygric factors (LAUER and RAFIQPOOR 2002). Terra rossa and terra fusca (sub-fossil clay soils) based on Mesozoic limestone are the dominant soil types. For the whole Mediterranean, the number of species is estimated at 24,000 with about 50 % endemism (GREUTER 1991). There are more than 3,000 spp. in the **Rhodope Sub-center** alone with many local and regional endemics. Although many elements show floristic affinities to Asia and arctic-alpine regions, a considerable portion of the Mediterranean flora is regarded to be Tertiary relicts. The closest relatives of many species show disjunct distributions in East Asia and the Himalaya (TAKHTAJAN 1986).

### *4.4 Asia*

The **Caucasus Center** (DZ 8) covers an area of 170,000 km$^2$ between the Black Sea and the Caspian Sea. The highest peaks of the central part of the Greater Caucasus reach higher than 5,000 m: Elbrus 5,642 m; Kazbek 5,043 m. The **Caucasus Center** lies at the transition zone from the subtropics to the temperate zone. Although the region receives most of the precipitation during the winter, convectional rainfall during the summertime is common for the higher altitudes of the mountain ranges. The altitudinal zonation of vegetation types ranges from the wet and subtropical-like lowland vegetation of the Colchis over species-rich coniferous forests up to alpine meadows. The total flora comprises c. 6,000 spp. of flowering plants. 1,200 spp. (20 %) are considered to be endemic (DAVIS et al. 1995). Among these there are a considerable number of Tertiary relicts like, e.g., *Zelkova* spp. or *Parrotia persica*. Furthermore, there are many different phytogeographic influences noticeable within the Caucasian flora and the region shows floristic affinities to the European, Himalayan, Far East, Mediterranean, Hyrcanian, and Irano-Turanian flora.

The **Himalaya Center** (DZ 9; 125,000 km$^2$) represents a narrow band at the southern flank of the eastern Himalaya. The Himalaya is the world's largest and highest massif ranging from the plain of the Ganges up to the numerous summits which frequently exceed 8,000 m. Climate is pronouncedly influenced by monsoonal rain bringing most of the annual precipitation in summer. Locally, mean annual precipitation may exceed 10,000 mm (Cherrapunji: 10,798 mm), though highly complex regional rainfall patterns exist due to, e.g., rain shadow effects. Shillong, which is located 50 km north of Cherrapunji, receives only 2,300 mm. The western limit of this centre is determined by a distinct climatic and floristic gradient; the westwards decrease of precipitation goes along with a decline of species richness. On the other hand, the eastern limits are much harder to define and the region is inseparably connected to the Indochina-China Center. The Himalaya exhibits the world's greatest altitudinal range with a zonation from tropical lowland and swamp forest in the valleys of the Ganges and the Brahmaputra up to the timberline at about 4,800 m and alpine meadows which reach as high as 5,500 m (RAO 1993). Whereas the lowland forests (100–1,200 m) are dominated by *Diptero-*

*carpus*, *Shorea,* and *Terminalia*, in the zone between 1,800–3,000 m many temperate genera like *Quercus*, *Acer*, *Alnus*, *Castanopsis*, and *Rhododendron* are found. The eastern Himalaya is also claimed to be a 'cradle of flowering plants' and a sanctuary of ancient groups of angiosperms (Rao 1993). The number of plants in this centre is far beyond 6,000 (Davis et al. 1995). Myers (1988) even estimates a number of 9,000 spp. for the Eastern Himalaya, of which 39 % are endemic. The most diverse elevation zone in terms of species richness probably lies between 1,500 and 2,500 m, whereas the maximum concentration of endemic species is found between 3,800 and 4,200 m (Vetaas and Grytnes 2002, Bhattarai and Vetaas 2003).

The **Indochina-China Center** (DZ 8–9; 2,592,000 km$^2$) comprises parts of the southern Chinese highlands in the South of the Sichuan basin, the plateau of Yunnan and the adjacent mountainous regions of NE Burma, N Laos, and N Vietnam. Monsoonal precipitation (1,100–1,600 mm) in combination with favorable temperatures in all seasons produces suitable conditions for plant life. The **Yunnan Sub-center** (DZ 9; 290,000 km$^2$) shows the highest species richness within the **Indochina-China Center**, with a conservative estimate of 7,000 plant species occurring in this province alone (Davis et al. 1986). Yang et al. (2004) even estimate that a total of 16,600 spp. of vascular plants are native for Yunnan. The flora represents a very complex mixture of tropical and temperate elements reflecting its position at the transition from the tropics to the subtropics (Xiwen and Walker 1986). Furthermore, the region contains by far the richest gymnosperm flora of the world (Hostert 2002, Mutke and Barthlott 2005).

The **Western Ghats Center** (DZ 8; 75,000 km$^2$) is restricted to the coastal mountain ranges between Bombay and Trivandrum which form a barrier for the SW monsoon. In the northern region of the Precambrian Shield the Western Ghats have mainly the nature of highlands and consist of quartz-sericite (Joshi and Janarthanam 2004). Only in the southern parts mountain tops reach considerable elevations (Nilgiri: 2,633 m; Anaimudi: 2,698 m). Rainfall is almost exclusively restricted to the monsoonal period from about April to November with highest rainfalls from June to July and an average of 3,500 mm (Joshi and Janarthanam 2004). On the leeward side of the mountain ranges the amount of rainfall decreases constantly with greater distance from the sea. Dominant vegetation types are evergreen forests in the southern part, moist deciduous forests and plateau vegetation. Davis et al. (1995) estimate that there are more than 4,000 spp. and as many as 1,500–1,600 spp. might be endemic to the center (Nayar 1996). About one quarter of India's flora occurs in this center. Joshi and Janarthanam (2004) have shown that the ephemeral plant communities of the plateaus are exceptionally rich in both species and endemics. During the dry periods the plateau vegetation has a dried up and barren appearance due to the low water holding capacity of the lateritic rock, but during the monsoons a species rich vegetation of annual herbs awakes.

The **Indo-Malaya Center** (DZ 8–10; 1,343,000 km$^2$) contains four sub-centers: the **Malaya Sub-center** (DZ 8–9; 138,000 km$^2$), the **Philippines Sub-center** (DZ 8; 181,000 km$^2$), the **Sumatra Sub-center** (DZ 8–9; 302,000 km$^2$), and the **Borneo Sub-center** (DZ 8–10; 722,000 km$^2$). Some of the islands of the Indo-Malayan archipelago consist of ancient Palaeozoic parts with a recent volcanic cover which causes a great heterogeneity in topography, geology, and soils. On some of the islands there is a considerable altitudinal range (e.g. Mt. Kinabalu 4,100 m). The equatorial setting and high sea surface temperatures promote perhumid climatic conditions (2,500 to 4,000 mm). The most diverse sub-center is Borneo with a complex altitudinal zonation at Mt. Kinabalu, where so far more than 5,000 spp. have been documented on an area of only 1,200 km$^2$ (Beaman 2005). Highest concentration of species on Mt. Kinabalu is found in an altitudinal belt at about 1,500 m (Beaman 2005). The relatively recent uplift during the late Pliocene-Pleistocene and its isolation from other high-elevation tropical regions have produced a speciose and highly endemic flora. Important families in the surrounding lowland rainforests are especially Dipterocarpaceae, Sapindaceae, Sterculiaceae, Leguminosae, Anacardiaceae, and Ebenaceae. In the montane forests (1,400–3,400 m), temperate elements such as oaks and stone oaks (*Quercus*/*Lithocarpus*) and other Fagaceae show up. Other important tree families in this altitudinal zone include Lauraceae, Moraceae, Myrtaceae, Rubiaceae, and various gymnosperms. Moreover, a unique assemblage of species at high elevations can be found on ultramafic rock, a class of rock which crystallized from silicate minerals under highest temperatures (Beaman 2005). Wood and Cribb (1994) estimate that there is a total of 20,000 and 25,000 spp. on Borneo. Whitten et al. (1987) give an estimate of 10,000 spp. for Sumatra alone. The most speciose family of Borneo are the Orchidaceae with ~1,500 spp. and 149 genera (Wood and Cribb 1994), among these 40 % are endemic (Lamb 1991).

The island of New Guinea which houses the **Papua Center** (DZ 8–10; 416,000 km$^2$) represents the largest tropical islands. The geology and topography of New Guinea is very complex (Mount Jaya: 4,860 m; Mount Wilhelm: 4,509 m). The island is made up of three geologic provinces: the continental or craton part in the SW, the central collision zone, and the NE volcanic islands. The craton belongs to the Australian plate and consists of Palaeozoic metamorphic and granitic rocks. Geologic facies vary from Cretaceous-Tertiary rocks of the Irian Jaya to Precambrian rocks at Mt. Wilhelm resulting in a variety of different soils. The isothermal, equatorial climate brings high amounts of rainfall (2,500 to >5,000 mm). The complex topography and geology, the equatorial wet climate, and the island setting synergistically produced a species rich and highly endemic flora. Davis et al. (1995) estimate that New Guinea contains between 15,000 and 20,000 spp. of which about 70–80 % are endemic. It is even estimated that the surroundings of Mt. Wilhelm have 5,000 to 6,000 spp. on an area of only 9,000 km$^2$ (Davis et al. 1995). Thus, New Guinea is one of the most outstanding regions in terms of species richness and endemism in the whole Indo-Malayan archipelago. Furthermore, the flora of the tropical alpine belt is the richest of the whole Malayan archipelago (Johns 2001). Although the **Papua Center** is in great proximity to the Australian outliers of the Australasian tropical rainforest, the floristic affinities are much closer to the Indo-Malayan flora. 465 genera indicate a relationship to the Indo-Malayan archipelago, whereas only 60 genera occur in Australia (van Balgooy 1976). Furthermore, with 145 spp. New Guinea contains one of the richest palm floras of the world (Bachman et al. 2004).

### *4.5 Australia*

The forests in the **Northeast Australia Center** (DZ 8) are the southernmost outlier of the Australasian rainforests. The center comprises an area of 21,000 km$^2$ at the eastern flank of the Atherton Plateau in NE Queensland. Three major geomorphic units converge in the region: the tablelands of the Great Dividing Range, the Great Eastern Escarpments, and the lowland coastal belt (Davis et al. 1995). Mt. Bartle Frere is the highest peak with an altitude of 1,622 m. The geologic underground consists of metamorphic, schistous rocks of Precambric origin. The seasonality of the tropical circulation in the region is buffered by the effects of the SE trade winds which cause locally aseaonal wet conditions and provide a basis for tropical wet broadleaf forests in the vicinity of Cairns. Locally, mean annual rainfall may even exceed 8,000 mm. Furthermore, frequently occurring tropical cyclones play an important role in the region. The heterogeneous relief and soil conditions, the spatial variation in rainfall together with a complex evolutionary history have led to a high diversity of floristically distinct forest types. TRACEY (1982) gives an overview of the forest vegetation of NE Queensland. Although there are noticeable floristic affinities, the species richness in these forests is inferior to most rain forests of other Australasian regions. The flora of the **Northeast Australia Center** is estimated to exceed 3,850 spp. (DAVIS et al. 1995). There is considerable endemism on the level of genera (43 genera are restricted to the region) and species (43 % endemism) (DAVIS et al. 1995). Remarkably, there is a great portion of members of basal clades within the flora like, e.g., Annonaceae, Eupomatiaceae, Winteraceae, or the monotypic, endemic families Austrobaileyaceae and Idiospermaceae (DAVIS et al. 1995).

The **Southwest Australia Center** (DZ 9; 27,000 km$^2$) represents a very distinct biogeographical province and is the floristically richest part of the Australian continent. Metamorphic and volcanic rocks of the Precambrian and Palaeozoic era are superimposed by Mesozoic sedimentary rock. Thus, soils are extraordinarily poor in nutrients. In contrast to other regions with winter rainfall, the SW part of Australia receives respectable annual precipitation (1,000–1,400 mm). The typical vegetation types are *Eucalyptus*-dominated ‘mallee’ formations. These formations are physiognomically similar to other Mediterranean scrub vegetation, e.g. mattoral (Chile), chaparral (California), or the Southern African fynbos (MORCOM and WESTBROOKE 1990). Most important families are Myrtaceae, followed by Proteaceae, Fabaceae, Asteraceae, and Epacridaceae (BEARD et al. 2000). There are also four endemic families (Cephalotaceae, Eremosynaceae, Stylobasiaceae, and Emblingiaceae) and more than 125 endemic genera (GOOD 1974). Like in other Mediterranean diversity centers a few single genera have undergone an extensive radiation. The five most speciose genera of the **Southwest Australia Center** (*Acacia*, *Eucalyptus*, *Grevillea*, *Stylidium*, *Melaleuca*) constitute about 20 % of all 5,710 native species of vascular plants (BEARD et al. 2000). Interestingly, especially shrubby and sclerophyllous groups show highest species numbers and levels of endemism. BEARD et al. (2000) argue that this coincides with adaptations to the extreme poverty of the soils which might favor sclerophylly and habitat specialization. The explosive adaptive radiation within these taxa has resulted in very high endemism (79 %) at the species level (BEARD et al. 2000).

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