GLOBAL DISTRIBUTION OF SPECIES DIVERSITY IN VASCULAR PLANTS: TOWARDS A WORLD MAP OF PHYTODIVERSITY

With 1 figure and 1 supplement (VIII)

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Zusammenfassung: Globale Verteilung der Artenvielfalt Höherer Pflanzen: Vorarbeiten zu einer Weltkarte der Phytodiversität

Als Grundlage einer zukünftigen Weltkarte der Biodiversität wird eine kommentierte farbige Weltkarte der potentiellen Artendiversität von Gefäßpflanzen vorgestellt. Trotz der Vielfalt der Vegetations- und Arealkarten fehlte bis heute – abgesehen von der noch sehr einfachen Karte von MALYSHEV (1975) – eine solche Darstellung. Dies ist um so überraschender, als Biodiversität und die Verteilung Genetischer Ressourcen heute mit im Zentrum einer internationalen und politischen Diskussion stehen.

Der Kenntnisstand der Artenvielfalt Höherer Pflanzen und ihrer Verbreitung ist im Vergleich zu allen anderen großen Organismengruppen (z. B. Arthropoda) extrem gut. Grundlage der Karte ist die Auswertung der Daten aus rund 1400 Florenwerken sowie floristischen, vegetationskundlichen und ökologischen Arbeiten auf regionaler bis kontinentaler Basis. Die Artenzahlen der gegebenen Gebiete (meist politische Einheiten) werden über eine Standardformel auf die Einheitsfläche von 10 000 km² umgerechnet. Es werden zehn Diversitätszonen der Kategorien zwischen < 100 spp. und > 5000 spp. pro 10 000 km² festgelegt und über Farbsignaturen kartographisch erfaßt. Der Verlauf der zonalen Umgrenzungslinien von Flächen gleicher Taxondichte (Isotaxen) muß – da die Datenbasis meist politische und keine naturräumlichen Einheiten umfaßt – durch Klima- und andere Daten extrapoliert werden. Die Weltkarte weicht in erheblichen Details von den bisherigen Vorstellungen zur Verteilung der Diversität ab. Es werden sechs globale Artenmaxima anerkannt: 1. Chocó-Costa Rica-Zentrum, 2. Tropisches Ost-Anden-Zentrum, 3. Atlantisches Brasilien-Zentrum, 4. Ost-Himalaya-Yunnan-Zentrum, 5. Nord-Borneo-Zentrum, 6. Neu Guinea-Zentrum.

Die Ergebnisse werden kommentiert und diskutiert. Notwendigerweise müssen eine Reihe terminologischer Fragen geklärt werden (z. B. Isotaxen-Isoporien, Diversitätsmaxima, Diversitätszentren, Qualitätskriterien zur Erfassung von Diversität, Landschaftsdiversität-Geodiversität-Ökodiversität etc.). Erwartungsgemäß hängt die Biodiversität eines Gebietes nicht nur von seiner Geschichte (Klima- und Florengeschichte, Paläogeographie und evolutive Verfügbarkeit genetischer Vielfalt), seiner Lage (Isolationsgrad und Zonobiom), sondern auch von der Summe der Vielfalt seiner abiotischen Faktoren (Geodiversität) ab. In diesem Zusammenhang zeichnet sich eine Verknüpfung der tropischen Diversitätsmaxima mit den ozeanischen Wasseroberflächentemperaturen von über 27 °C ab.

Es ist zu vermuten, daß mit Bezug auf den ökosystemaren Kontext der detailliert gut kartierbaren Diversität von Primärproduzenten (Gefäßpflanzen) mit den abhängigen Konsumenten- und Destruenten-Ebenen, die hier vorgelegte Karte mit relativ hoher Genauigkeit die globale Verteilung der gesamten terrestrischen Biodiversität widerspiegelt.

1 Introduction

Biodiversity, often oversimplified as "species richness", is a quality of life the significance of which has been recognized only relatively recently. Since the endorsement of the Convention on Biological Diversity in Rio de Janeiro in 1992, biodiversity has been a focal point in economic (bioprospecting and commercial use of genetic resources) and political (environmental problems, extinction rates, sustainability, long-term concepts for the use of genetic resources, and international legal provisions on their accessibility) interests. At the same time, profound scientific knowledge of the material is appallingly limited (MAY 1996, SIMON 1995, STORK 1993 etc.): even the relatively simple question of how many species of organisms exist cannot be answered with any precision. 1.7 million species are known, but it is estimated that there are nearly 20 million species. The estimations, based on differing projections, span a spectrum of between 5 million (STORK 1993) and more than 360 million (ANDRÉ et al. 1994) species. In all probability, we have knowledge of less than 8.5% of all species in existence. This is particularly true for animals, and specifically for the richest and most diverse group, the insects. In contrast, knowledge of the diversity of vascular plants (Tracheophyta), is relatively comprehensive. As producers, and thus fundamental to the entire ecological system, they determine the biodiversity of terrestrial ecosystems. Approximately 300 000 species have been documented (HEYWOOD 1995), whereby the total volume has been estimated at 400 000 species (HAMMOND in GROOMBRIDGE 1992). The geographical distribution of this diversity across our planet is well-known due to many different regional floras (FRODIN, 1984, alone lists nearly 3000 titles). In addition, there

are any number of distribution maps of many taxa (overview INDEX HOLMENSIS 1969) and syntaxonomic maps of vegetation.

In view of these facts, it is duly astonishing that up to the present day, with the possible exception of a few relatively simple predecessors which are now outdated, no new and up-to-date world map exists of the potential species-diversity distribution of vascular plants. The publication of this new and more differentiated preliminary version is an initial effort to close the gap. At the same time, it represents biodiversity with heretofore unequaled accuracy – we again refer to the quantitative ecosystem interdependence between producers, consumers and decomposers (KLAUSNITZER 1995) – as a whole on planet earth.

An historical review of published literature on the overall theme of biodiversity mapping is limited to a few essential works: In ALPHONSE DE CANDOLLE's (1855) work on comparative floristics, first estimates of species numbers are made in a table arranged according to geographical regions. A first mapped depiction of African phytodiversity was introduced by LEBRUN (1960), revised in 1976 and later updated for tropical Africa (LEBRUN a. STORK 1991).

A. CAILLEUX (1969) presented calculated data on global species numbers in a modified table. The sole mapped depiction of worldwide phytodiversity was published by MALYSHEV (1975) on the basis of multiple studies conducted by Russian scientists on comparative phytogeography (Fig. 1).

2 *Terminology: diversity of the term "diversity"*

The labels "multiplicity" or "diversity" (Lat. diversitas, French diversité, German Diversität, Spanish diversidad) in colloquial speech were used mainly as a technical term in French scholastic circles. Diversity finds first mention in an encyclopedia by DIDEROT a. D'ALEMBERT in the "Encyclopédie" (Paris 1751–1772) and in subsequent encyclopedias (e.g. LAROUSSE 1929). In contrast, there is no mention of the term (not even the Latin form) in the corresponding German encyclopedias, starting from the monumental, 23 volume, never completed "Deutsche Encyclopedie" (Frankfurt 1778–1804) through MEYER (1909) and almost up to the present in the form of Brockhaus-Encyclopedia (17th edition 1966–1974). The same holds true for English language encyclopedias from the first (Edinburgh 1771) to the fifteenth (Chicago 1979) editions of "Encyclopedia Britannica". This changed dramatically with the introduction of the term "biological diversity" during the 1980's in the English speaking world. In the meantime, the terms "diversity", "biodiversity" and their many combinations have witnessed inflationary application in scientific and political contexts. This necessitates a clear definition of the various terms of "diversity" for the following.

2.1 *Biodiversity*

The term "biological diversity" appeared for the first time in literature at a relatively late date – probably with NORSE a. MCMANUS (1980). It was shortened to "biodiversity" and made popular beyond the realm of biology by E. O. WILSON in his book of the same title, "Biodiversity" (WILSON 1988). Wilson does not define the term "biodiversity". However, his connotation transcends the classical boundaries of systematics, taxonomy and evolutionary research to become a branch of science in its own right, dealing analytically with the special problems of the variety of living organisms principally on the basis of species in a cause and effect context. In most literature, biodiversity means "species variety" or, more simply, "species numbers". Only very few works (approx. 22% according to HENGEVELD 1994) deal with the diversity of syntaxa or ecosystems. Apart from the number of taxa in a certain region, diversity in a biological sense deals with the relative abundance and, where possible, with distributional patterns ("evenness"). Keeping habitat and community in mind, one furthermore still differentiates between alpha-, beta- and gamma-diversity (WHITTAKER 1972). Therefore, in a scientific context, biodiversity can be construed as the sum of genetic diversity among living organisms, their abundance and their "evenness" within a specific study area. Today, the term biodiversity is used not only colloquially and often politically in very simple contexts (species numbers), but also in extremely extended contexts. The important 1992 Convention on Biological Diversity in Rio de Janeiro interprets biological diversity imprecisely as "the variability among living organsims from all sources, including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems" (UN 1992).

The agreement in Rio de Janeiro was reached principally under the aspect of clearly defined utilization, so that potentially useful organisms were emphasized as "genetic resources". In this connection, the "Vavilov centres", world centres of origin of significant cultivated plants, play a major role. Countries with maximum species numbers entered the discussion as "megadiversity countries" and henceforth have received particular consideration in decision taking.

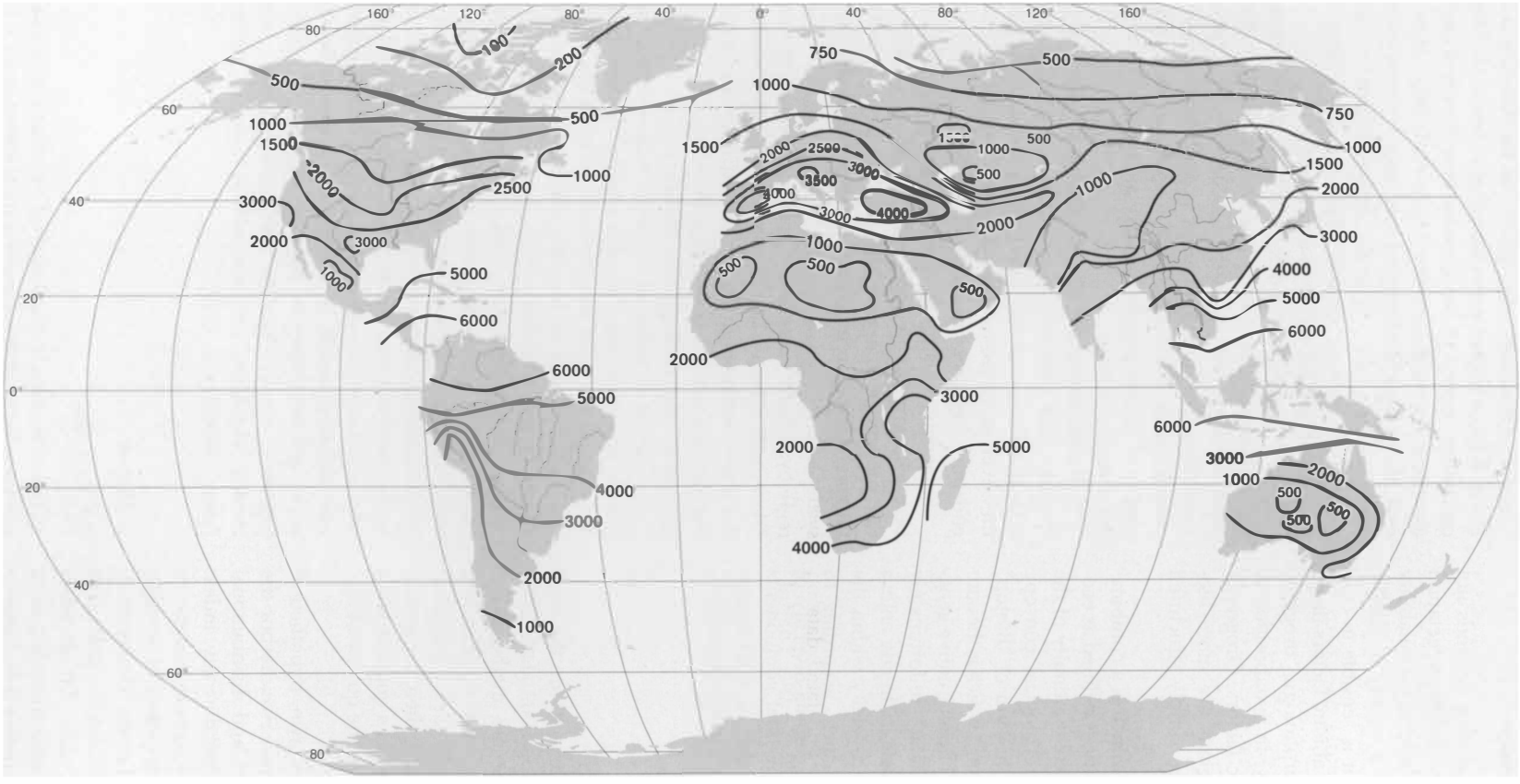

Fig. 1: The map by MALYSHEV (1975) was the first and only cartographical depiction of global diversity (species numbers per 100 000 sq. km.) of vascular plants until now

Die Karte von MALYSHEV (1975) war bisher die einzige kartographische Darstellung der globalen Diversität (Artenzahlen pro 100 000 km²) von Gefäßpflanzen

2.2 *Biodiversity, geodiversity, ecodiversity*

The biodiversity of a particular area depends not only on historical factors such as climate, vegetation history, paleogeography and evolutionary availability of genetic resources, but also on a variety of abiotic factors, as well. For this reason, it is sensible to consider geodiversity, i. e. the sum of abiotic factors (from the sectors climatology, geomorphology, orogeny, geology, pedology and hydrology) in juxtaposition to biodiversity, or the sum of biotic factors. Orographically or climatically diverse regions are more biodiverse than corresponding, more simply structured regions.

The total diversity of a region, which is a combination of biodiversity and geodiversity, is defined as ecodiversity. This represents the logical continuity of the idea, derived from a landscape-ecological concept, which also defines "Ökotop" as the sum of "Biotop" and "Geotop" as well as "Ökosystem", which is the sum of "Biosystem" and "Geosystem". The alternative geographical term "Landschaftsdiversität" unfortunately cannot be used in this sense because it already enjoys general application as landscape diversity within the biodiversity research sector in which, according to WHITTAKER (1972), it means the gamma-diversity of a region. This is comprised of the dual components of alpha-diversity (species numbers in a particular region) and beta-diversity (heterogeneity of communities along a habitat gradient).

2.3 *Quality of biodiversity*

Biodiversity can be quantified exactly on the basis of diversity indices (PIELOU 1975, HAEUPLER 1982, MAGURRAN 1988). These indices are mathematical formulas which take into account the number and abundance of taxa (e.g. Jaccard-Index, Sørensen-Index). Apart from the fact that, when measuring diversity the number of taxa per se as a quantity has a quality, these indices say little about the quality of biodiversity in a particular area.

In illustration, let us consider two hypothetical islands, A and B. Both are of equal size, harbor the same species number, abundance and distributional patterns and thus share the same diversity index. Island A, situated on the coast of western Europe, is home to 100 species out of 20 genera and 10 families. All species are widely distributed in the Holarctis, so that none is endemic to island A. Island B is isolated in the Atlantic ocean, the spectrum of its 100 species is much more diverse: they belong to 40 different genera out of 20 families. Half of all the species is endemic to island B. Obviously, the quality of biodiversity on island B has a higher status than that of island A. The qualitative aspects of biodiversity have hardly found an echo in scientific literature (DAVIS et al. 1994). However, they play a fundamental role where diversity is a criterium for quality e.g. in the designation of natural reserves or "genetic centres". Five criteria designate the quality of biodiversity in a given area:

1) The biodiversity index, which takes taxa numbers, abundance and evenness into account, is the basis for deliberations on the quality of biodiversity. Population sizes and numbers of sexually mature individuals, which the IUCN (1994) uses in evaluating the vitality of species populations, are already elements in the diversity indices.

2) Range size of the occurring taxa: are they widespread – with reference to population size and range, is their main occurrence within the study area – or are they even restricted to the study area? The existence of endemics increases quality significantly.

3) Genetic separation of the taxa: are we dealing here with groups of closely related taxa which are in the process of adaptive radiation or perhaps with members of different genera or even different families?

4) Systematic scattering of occurring taxa: a certain "systematic evenness" can be seen in conjunction with the above mentioned third criterium: the more even the distribution of the organisms over the entire system, the higher the quality of diversity.

5) Current or potential economic values of taxa as genetic resources (e.g. "Vavilov centres") constitute a major criterium from an anthropocentric viewpoint.

The uniqueness of habitats, often determined by abiotic factors (e. g. hot springs, wadden sea), constitutes a criterium for quality that, in the end, is encompassed in the preceeding five criteria. Quantitative extremes in numbers of taxa per unit of area are labeled neutrally in the following as diversity-maxima or diversity-minima. The term "diversity centre" must take qualitative aspects into account. In connection with the designation of nature reserves or national parks and according to MYERS (1988), endangered regions – mostly through man's interference – are termed "Hot Spots" and in a political context "Priority Areas" (BIBBY et al. 1992).

3 *Methods*

3.1 *Data base*

The systematic compilation of vascular plants and our knowledge of their geographical distribution i. e.

the basis of our data, are excellent in comparison to all other large groups (e. g. insects), as already mentioned in the introduction. For the map under presentation, roughly 1400 floras, floristic studies, biogeographical essays and vegetation studies were evaluated; a complete bibliography would go beyond the limitations of this essay and will be published elsewhere (BARTHLOTT a. LAUER 1997). A preliminary version of this phytodiversity map has already been published (BARTHLOTT et al. 1995). From the comprehensive literature available, we refer to only a very few overviews: the fundamental summary by FRODIN (1984), the compendium "Plants in Danger" by IUCN (DAVIS et al. 1986), "Global Biodiversity" by WCMC (GROOMBRIDGE 1992), "Global Biodiversity Assessment" by UNEP (HEYWOOD 1995) as well as the three volumes "Centres of Plant Diversity" (DAVIS et al. 1994–1996).

3.2 Calculation of species numbers per standard unit of area

The data presented allow statements about species numbers within divergent areas: in most cases, they are political units (e. g. floras of countries), less frequently areas naturally delimited by geographical characteristics (e. g. floras of the Sahara or of the Alps). In order to create comparable diversity categories (i. e. in this case, species numbers per unit of area), the given species numbers had to be calculated to units of area of equal size. ARRHENIUS (1920, 1921) was the first to calculate species numbers on the basis of differing unit sizes in connection with plant-sociological aspects.

Apart from the basic premise that species numbers increase with area increment, he also included the floristic spatial diversity of the study region in his formula. Predictably, this led to problems of method. For this reason, today (e. g. LEBRUN 1960, 1976) a formula to calculate relative species richness according to EVANS et al. (1955) is commonly used. This formula is based only on area size and species numbers:

$A = S/\log(x + 1)\log(X + 1)$

A is the species number sought in a standard unit of area (e. g. per 10 000 sq. km.), S is the given species number in a given unit of area (e. g. of a country), x is the size of the given unit of area and X is the size of the chosen standard unit of area.

We have followed modern authors in choosing a standard unit of area of 10 000 sq. km. (LEBRUN a. STORK 1991). As already stated by EVANS et al. (1955), it is necessary to consider that data derived from areas that are smaller than the sought standard unit of area cannot be superimposed on larger units of area. This is the reason why units of area under 10 000 sq. km. were adopted without alteration.

3.3 Definition of categories of diversity

The species numbers calculated cover a spectrum of less than 100 species up to approximately 17000 species per 10000 sq. km. For this mapped presentation, this range was purposely divided into ten diversity zones (DZ 1 to DZ 10), which are marked by corresponding colour labels. The higher the species number in a particular region, the smaller the populations and generally on average also the ranges of the species. For that reason, the span of the zones with higher diversity increases. The ten diversity zones (DZ) with species numbers per 10000 sq. km. are:

DZ 1	<100 spp.	DZ 6	1500–2000 spp.
DZ 2	100–200 spp.	DZ 7	2000–3000 spp.
DZ 3	200–500 spp.	DZ 8	3000–4000 spp.
DZ 4	500–1000 spp.	DZ 9	4000–5000 spp.
DZ 5	1000–1500 spp.	DZ 10	>5000 spp.

3.4 Cartographic depiction

A world map of the "Robinson-Projection" recommended by the American Geographical Society (overview see BRETTERBAUER 1994) was chosen as the basis for our cartographic depiction. The ten diversity zones are each distinguished by a different colour. The boundaries between diversity zones are marked by continuous lines. According to ROTHMALER (1950), lines of identical species numbers are termed "Isoporien". More correctly they should be labeled "Pseudoisoporien" (compare WITT 1970), because on this map lines demarcate diversity zones. Unfortunately, the term "Isoporien", which has hardly found acceptance in scientific literature, is applicable by its definition only on the level of species. For purposes of further cartographical work, a term for lines which encompass equal numbers of taxa does not exist: we herewith introduce the term "Isotaxas".

The assignment of a region to one of the ten diversity zones labeled by colour is undertaken on the basis of the calculated number according to EVANS et al. (1955). The methodical cartographical difficulty lies in drawing the isotaxas. The data base allows the calculation of species numbers for political and geographical units, which neither in relation to geodiversity nor to biodiversity represent homogeneous regions. The linear course of the isotaxas has been imputed on the basis of other gradient lines (vegetation zones, climate zones). It was necessary to refer to additional maps on vegetation or climate (e. g. SCHMITHÜSEN 1976), espe-

cially for countries which show distinct gradients in their geodiversity (e. g. climate zones within USA). At the same time, corrections were necessary in species numbers per area in different sub-regions. They were implemented with the aid of regional and local floras.

Mountains, elements which increase geodiversity, have a special status: in mountain ranges, a rapid succession of diversity zones occurs, the calculation of which can only be touched upon in this essay. Larger ranges as e.g. the Andes or the Himalayas are easily portrayable, whereby smaller ranges are represented as a unit and not in detail, for reasons of scale.

3.5 Methodical limitations

An assignment to the given ten diversity zones is difficult for some tropical and subtropical regions because only fragmentary, outdated or incompleted floras exist (e.g. Brazil, Madagascar). A second uncertainty lies in the extrapolation of the detailed demarcation of the isotaxas.

4 Spatial distribution of species diversity of vascular plants

In supplement to the enclosed cartographic representation of potential species richness in plants (Supp. VIII), there is a short characterization of the diversity listed according to continents. Islands or island groups are assigned, where possible, to corresponding continents.

4.1 Europe

In accordance with the geodiversity, the isotaxas in central Europe run in a west-east direction with increasing values between DZ 2–5. Minimal species numbers are reached in the Arctic (DZ 1) and maxima are reached in the Mediterranean and Near Eastern mountain ranges (DZ 6–7).

4.2 Africa

Continental Africa: Northwestern Africa encompasses the Mediterranean zones (DZ 4–5). The isotaxas run closely parallel to the Atlas Range up to Cyrenaica. In the central Sahara (DZ 2) three absolute minima are found (DZ 1: Majabat al Koubra, Ténéré, Djourab). Species-poor is the Kalahari, while the Mediterranean region of the Capensis is distinguished by surprisingly high diversity (DZ 7–9). Embedded in the wide belt of the savannas and dry forests (DZ 3–5), diversity increases in the rain forests DZ 6–9, climaxing in the Cameroon-Gaboon Centre (DZ 9) and reaching high species numbers along the East African Rift Valley (DZ 8). In the relatively species-poor west African rain forests (DZ 6), only the Nimba and the Loma mountains reach DZ 7.

Madagascar: There is high diversity in the relatively dry west (DZ 7), which increases in the rainy east (DZ 8), with a north-south-isotaxa along the central plateau.

Islands in the Atlantic Ocean: The Cape Verde Islands are in DZ 4, the islands Sao Tomé and Príncipe in the Gulf of Guinea are similarly species-rich (DZ 3–4). St. Helena is species-poor (DZ 1) but extremely rich in endemics (approx. 83%).

Islands in the Indian Ocean: Socotra with DZ 4 corresponds to the diversity of the neighbouring African continent, with a high portion of endemics. The tropical Seychelles, Comoro Islands, Réunion and Mauritius are divergently species-rich (DZ 3–4), and rich in endemics.

4.3 Asia

Continental Asia: Similar to Europe, the isotaxas run in an west-east direction within extra-tropical Asia with diversity minima in the Arctic (Nowaja Semlja, Taimyr Peninsula, New Siberian Islands). The extratropical maxima lie in the Mediterranean regions of the Irano-Turanian zone and, because of the high geodiversity, in the high mountain ranges of central Asia (Tien Shan, Pamiro-Alai, Pamir) as well. The eastern Asian deciduous forests reach DZ 7. Greater species numbers are encountered in the coastal regions (e. g. Kamchatka).

Bordered by the continental system of mountain ranges are the species-poor deserts (e. g. Gobi, DZ 2–3) with a minimum in the Tarim Basin (DZ 1). Striking is the diversity leap between the minimum in the arctic desert of the Tibetan plateau (DZ 1) to the maximum in the subtropical-tropical eastern Himalaya Range (DZ 8–10): the highest species numbers are reached in the Yunnan Province (DZ 10). Tropical eastern Asia is likewise highly species-rich (DZ 8–9).

The monsoon forests and the dry regions of the Indian subcontinent are relatively species-poor (DZ 3–5). The maximum in India, apart from the Himalaya region, is reached in the geodiverse southern portion of the Western Ghats (DZ 8).

Sri Lanka: Sri Lanka possesses a higher diversity (DZ 6–7) than neighbouring continental India. The southern lowland rain forests are more species-rich (DZ 7) than the northeastern portion of the island (DZ 6).

Arabian Peninsula: The deserts and semi-arid deserts are, as can be expected, species-poor (DZ 2–3), reaching a minimum in the central Arabian desert (Rub'al Khali, DZ 1). Alone the geodiverse ranges of Saudi Arabia and Yemen (e.g. Jebel Bura', Jebel Mehan) reach DZ 5. In addition, the climatically favoured Dhofar Fog Oasis in the southeast of the peninsula reaches higher species numbers (DZ 4).

Malesian Archipelago, Malay Peninsula: The entire southeast Asian region possesses high diversity (DZ 7–10). The Philippines lie in DZ 8. The Malay Peninsula reaches DZ 9, due to its high geodiversity. Borneo is the most species-rich of the Sunda islands with a maximum in the region around Mount Kinabalu (DZ 10). Relatively species-poor are Java, the Moluccas and Sulawesi (DZ 7). New Guinea (East Malesia) possesses high species numbers (DZ 8-10) and reaches a maximum in the eastern mountain range (e.g. Mount Wilhelm) with DZ 10.

4.4 Australia and New Zealand

Due to its aridity, great parts of Australia are species-poor (DZ 1–3), with two minima in the semideserts (Lake Eyre region, Nullarbor Plain). The humid central Australian mountain ranges (e. g. Macdonell Range) reach higher species numbers (DZ 4). The humid Eucalyptus forests span DZ 4-7. A climax is reached in the northeastern coastal rain forests of Queensland (DZ 8). Similarly species-rich is the Mediterranean region of southwestern Australia (DZ 8).

New Zealand possesses the greatest diversity in the mountainous northwest of South Island (DZ 4). In the direction of the drier regions, the species numbers decrease (DZ 3). Both Australia and New Zealand are rich in endemics (approx. 90% and 81% resp., DAVIS et al. 1995).

4.5 Islands in the Pacific

For paleogeographic reasons, New Caledonia distinguishes itself through great species numbers (DZ 7) and a high percentage of endemics (approx. 80%). The more northerly Solomon Islands also reach DZ 7. The Fiji Islands are species-poor (DZ 5). Hawaii (DZ 5) possesses a high portion of endemics (approx. 83%, DAVIS et al. 1995). The small coral islands in the Pacific Ocean are generally poor in both species and endemics.

4.6 North America and Mexico

Similar to Europe, the isotaxas take a west-east direction. The minimum (DZ 1) lies in the arctic regions (Greenland, islands in the Arctic Ocean). In the prairies and arid regions in the Great Basin, species numbers increase to DZ 4. The deciduous forests of North America possess DZ 5–6 and reach a maximum in subtropical Florida with DZ 7. A second climax is reached in Mediterranean California (DZ 7). The geodiverse Rocky Mountains reach, in the southern portion, DZ 6. In the mild oceanic climates on the east coast of North America, greater species numbers are reached.

The Sonora and the Chihuahua deserts are extremely species-rich (DZ 5). The species-rich Mexican highlands possess a maximum in the Sierras at Oaxaca and Chiapas (DZ 9).

4.7 Central and South America

Continental Central and South America: The rain forests of the Amazons correspond to DZ 7–8, as does perhumid eastern Brazil with a maximum in the Mata Atlantica (DZ 10). The semi-humid Campos Cerrados and the Pampas lie in DZ 5, the arid Caatinga and the Gran Chaco in DZ 4. Surprising is the diversity minimum of the Llanos (DZ 3) in the Guyana Shield, which is probably caused by edaphic factors. The Guyana Highlands reach DZ 8. The dispersal of plants across the Central American isthmus and high geodiversity provided the basis for the continued maximal diversity through Costa Rica and Panama along the Columbian West Andes in the Chocó region (DZ 10) to end in Ecuador. The tropical East Andean Centre (DZ 10) stretches along the Amazonian side of the folded mountains from southern Columbia through Ecuador and Peru to Bolivia. There is a diversity minimum in the Atacama desert (DZ 1). Mediterranean Chile lies in DZ 6. In the cold southern regions, the species numbers are predictably low and reach only DZ 5 in the temperate Valdivian rain forests.

Caribbean Islands: Cuba (DZ 8) is the largest and most species-rich island in the Greater Antilles. Hispaniola and Puerto Rico lie in DZ 7, as do the Lesser Antilles (seen as a whole).

4.8 Antarctic and Antarctic Islands

Predictably, this region is species-poor (DZ 1). Only the Falkland Islands reach DZ 2.

5 Distribution of global diversity

The world map under presentation encompasses regions of extremely varying diversity. It spans species

minima in the Arctic and in deserts with less than 100 species per 10000 sq. km. (= DZ 1) to species maxima in the geodiverse tropics (orographically highly structured) with more than 5000 species per 10000 sq. km. (DZ 10). As a fundamental tendency, the distributional patterns correspond roughly to the prevailing data and to the few maps which have been published. However, it diverges often in details and, most important, it presents a cartographic portrayal of diversity zones for the first time ever.

This becomes clearly apparent when looking at the first meritorious map of global phytodiversity (Fig. 1) by LEONID MALYSHEV (1975). MALYSHEV employed the same method and extrapolated the Arrhenius formula but took a larger standard area of 100 000 sq. km. The map was thus less precise and obviously based on a much smaller data base in 1975 (MALYSHEV assessed 459 floras). As a result, the map as well as the demarcation of the isotaxas is much simpler. The global geodiverse, tropical centres of phytodiversity are less differentiated.

For Africa, however, an excellent map of diversity by JEAN LEBRUN (1960) and the revised version by JEAN-PIERRE LEBRUN (1976) are in existence. The latter was refined (LEBRUN a. STORK 1991) for tropical Africa and corresponds fundamentally with the map now presented, which is distinguished by the detailed demarcation of the isotaxas. The Cameroon-Gaboon-Centre was not taken into account on earlier maps, due most likely to the lack of literature and data for this region. Current data indicate the region unequivocally as a centre of diversity (DAVIS et al. 1994).

5.1 Geodiversity and biodiversity

Geodiversity, the variety of the abiotic geofactors, exerts great influence on the degree of biodiversity of all regions on earth: The map clearly shows the close interaction between biodiversity and geodiversity. The latter is clearly not only the result of climatic influences, but also of the relative configuration of the continents to each other, their relief, their accidental position in the oceans as well as geologic development.

A look at the map reveals that the tundras and the boreal coniferous forest bioms belong to the species-poor diversity zones (DZ 2-3). This is the result of entirely unfavourable abiotic conditions such as thermic minima (frost) in connection with shortened vegetation periods. The same is true for deserts. They also belong to diversity zones 1-3, because of the extremely adverse climatic parameters. On the one hand, they are subject to extreme daily and yearly temperature fluctuations as well as intensive global radiation and, on the other hand, to an entirely negative radiation balance as well as extreme aridity.

High phytodiversity, dependent on favourable, tropical temperatures and high amounts of annual precipitation, occurs in forest bioms in the perhumid, lower latitudes in America, Africa and Asia in the region of the Malesian Archipelago. Maxima of biodiversity (DZ 9–10) are reached through geodiversity maxima within the tropical zonobioms. This is the result of several geodiversity factors, e. g. orographic parameters or daily mesoclimatic phenomena such as slope winds, the stratification of condensation levels at the slopes of the mountains (montane cloud forests (Wolkenwald) and upper montane fog-forests (Nebelwald)), as well as the morphological faciting of the mountain environments.

The interaction of the geodiverse characteristics mentioned above enhance phytodiversity, especially in regions of orobioms (e. g. in the centres of Chocó, Costa Rica, tropical eastern Andes, eastern Himalaya-Yunnan, northern Borneo, New Guinea). Under optimal conditions, an additional element which increases diversity appears: spatial heterogeneity is augmented by the bios itself (e. g. architecture of a rain forest, which is a factor particularly stressed by HUSTON 1994).

The monsoon-like character of the innertropical Westwind circulation, with utmost evaporation over the warmest ocean basins in the Malesian Archipelago as well as on the Columbian coast and in the Cameroon-Guinea Bay, contributes to the highest diversity zones (DZ 9–10). The moisture-laden Trade Winds, as a factor of geodiversity in the region of the tropical-subtropical east coast climates, are connected to a high phytodiversity in coastal mountain ranges e. g. eastern Brazil, Central America, northeastern Australia and Madagascar.

In addition, plant dispersal from the Holarctic or Antarctic regions resp. to tropical mountain ranges, triggered by frequent climatic changes within the late Tertiary or Quaternary, produces biodiversity maxima. This is especially true for the Malesian Archipelago and the Andean mountain chains including the Central American isthmus.

The subtropical winter-rain regions play a prominent role in phytodiversity. The inverse climatic cycle (cool winter rainy season and warm summer dry periods) provides for greater phytodiversity in humid orobioms, as in the European Mediterranean, California, central Chile, the Cape region and southwestern Australia. Additional geodiverse characteristics enhance biodiversity in the floristic region of the Cape (DZ 9) in several ways. First of all, the influence

of a foggy atmosphere in the environs of the cool Benguela current, the continous, relatively short-term mild climatic oscillations (evolutionary "calculable" disturbances) and the long-term weak climatic change during the last historical eras were favourable for the long evolutionary process of the smallest floristic region.

5.2 Global maxima, minima and centres of diversity

One of the main goals in mapping phytodiversity is locating and delimiting global "diversity centres" as precisely as possible through isotaxas: the latter could play an essential role in the designation of threatened areas ("Priority Areas", BIBBY et al. 1992) and especially of "Hot Spots" where endangered by man. A further purpose is to aid in decision taking on conservation measures and the sustainable use of high diversity (bioprospecting, genetic resources). The map depicts above all maximum species numbers of vascular plants. As already discussed (chap. 2.3), "diversity centres" must additionally fulfill qualitative prerequisites. When viewing the relationship between consumers and producers, we can assume that plant maxima correspond to maxima of total biodiversity. Furthermore, we can expect that those maxima also fulfill the other most significant qualitative criteria (high endemic rate, high genetic separation, high taxonomic scattering i.e. "systematic evenness").

Thus, we may equate the maxima described above with "diversity centres". Qualitative characteristics also played only a minor role in the centres of diversity described until now (e.g. IUCN 1990, DAVIS et al. 1994) and simple calculations of species numbers were used for methodical reasons.

All global diversity maxima with more than 5000 species per 10000 sq. km. (DZ 10) are situated in the humid tropics and subtropics, regions which are richly structured orographically with high geodiversity. The six global diversity centres are listed according to their species numbers:

1. Chocó-Costa Rica Centre
2. Tropical Eastern Andes Centre
3. Atlantic Brazil Centre
4. Eastern Himalaya-Yunnan Centre
5. Northern Borneo Centre
6. New Guinea Centre

Regions of maximum species numbers

Because also all lower species numbers maxima (≥ DZ 7) are of great significance for all floristic regions, they are summarized below in the following list in geographical order. They are defined as the global centres of maximum species richness of plants and are listed according to continents. In some cases, there are within those diversity centres certain regions of particular species richness which can be differentiated more precisely (listed in brackets behind the centres).

Europe: Mediterranean Centre (Sierra Nevada, Pyrenees, Alpes-Maritimes, Balkan Mountains, Mountains of South and Central Greece, Caucasus) DZ 7

Africa: Liberia-Ivory Coast Centre (Nimba and Loma Mountains) DZ 7; Cameroon-Gaboon Centre DZ 8–9; East African Rift Valley Centre DZ 8; Cape region Centre DZ 9; Madagascar Centre DZ 7–8

Asia: Tien Shan-Pamir Alai Centre DZ 7; Eastern Himalaya-Yunnan Centre DZ 8–10; Western-Ghats-Ceylon Centre DZ 7–8; Indomalesian Archipelago Centre DZ 8-10 (Malay Peninsula Centre DZ 9, Northern Borneo Centre DZ 9–10 [Mount Kinabalu DZ 10], New Guinea Centre DZ 8–10 [Eastern mountain chain DZ 10])

Australia and New Zealand: Northeastern Australia Centre DZ 8; Southwestern Australia Centre DZ 8

Pazific Islands: New Caledonia Centre DZ 7

North America and Mexico: Califonia Centre DZ 7; Florida-Appalaches Centre DZ 7; Chiapas-Guatemala Centre DZ 8–9 (Sierras of Oaxaca and Chiapas DZ 9)

Central and South America: Cuba Centre DZ 8; Chocó-Costa Rica Centre DZ 10; Tropical Eastern Andes Centre DZ 10; Amazonian Centre DZ 7–8 (Guyana Highlands Centre DZ 8); Atlantic Brazil Centre DZ 8–10 (Mata Atlantica Centre DZ 10)

In conclusion, note that the map reflects species numbers minima which were not expected. That minimal species numbers (less than 100 species per 10000 sq. km.) are found in the polar regions and desert centres does not come as a surprise. However, the occurrence of a minimum e.g. in the neotropical Llanos in Venezuela is unexpected. Presumably it is caused by certain edaphic conditions such as nutrient deficiencies.

5.3 Phytodiversity and total biodiversity

The map presented depicts global terrestrial distribution of the diversity of vascular plant species (Tracheophyta). The question arises whether the map also reflects the total terrestrial distribution of biodiversity. The following arguments underline this assumption:

1) Our knowledge of approx. 75% of the species diversity of the Tracheophyta is the best of all major groups of organisms (known to science are 300 000 spp., estimated total number 400 000 spp.). Of the estimated 20 million species in the other groups of

organisms (such as consumers like insects or decomposers like fungi), less than 8.5% (approx. 1.7 million species) are known to science.

2) Within terrestrial ecosystems, vascular plants are the dominant group of producers (400 000 species) in the context of biomass and diversity. An estimated 20 million species of consumers and decomposers depend on them. In this way, a basic relationship exists between one single vascular plant species and nearly 66 species of animals, fungi, bacteria and other organisms. If this basic relationship is independent of geography, meaning that this is valid for the diverse tropics as well as for all extra tropical regions, the map would reflect the total diversity of life with high accuracy. There are no data that contradict this assumption. All mentions of maxima of global diversity in the domain of consumers (e.g. insects) point to the phytodiversity species maxima on our map, which are most probably identical with global centres of diversity.

We note that for the moment we cannot visualize any method for mapping global biodiversity other than by mapping terrestrial primary producers, which is the best known group in comparison. Every attempt to map global biodiversity on the basis of e. g. the most species-rich and, therefore, most relevant group of organisms, the insects (estimated are 2–200 million species, GROOMBRIDGE 1992) would be questionable if not absurd because of our extremely insufficient knowledge (known are 0.9–1 million species, SIMON 1995) in this domain.

The only possible alternative would be the creation of total inventories on a local scale, such as the currently proposed INBITTA project (Inventario de la Biodiversidad de todos los Taxones) in Costa Rica. However, this exemplary total inventorying must be implemented in all zonobioms of the earth. Unfortunately, there are no efforts in this direction at the present time.

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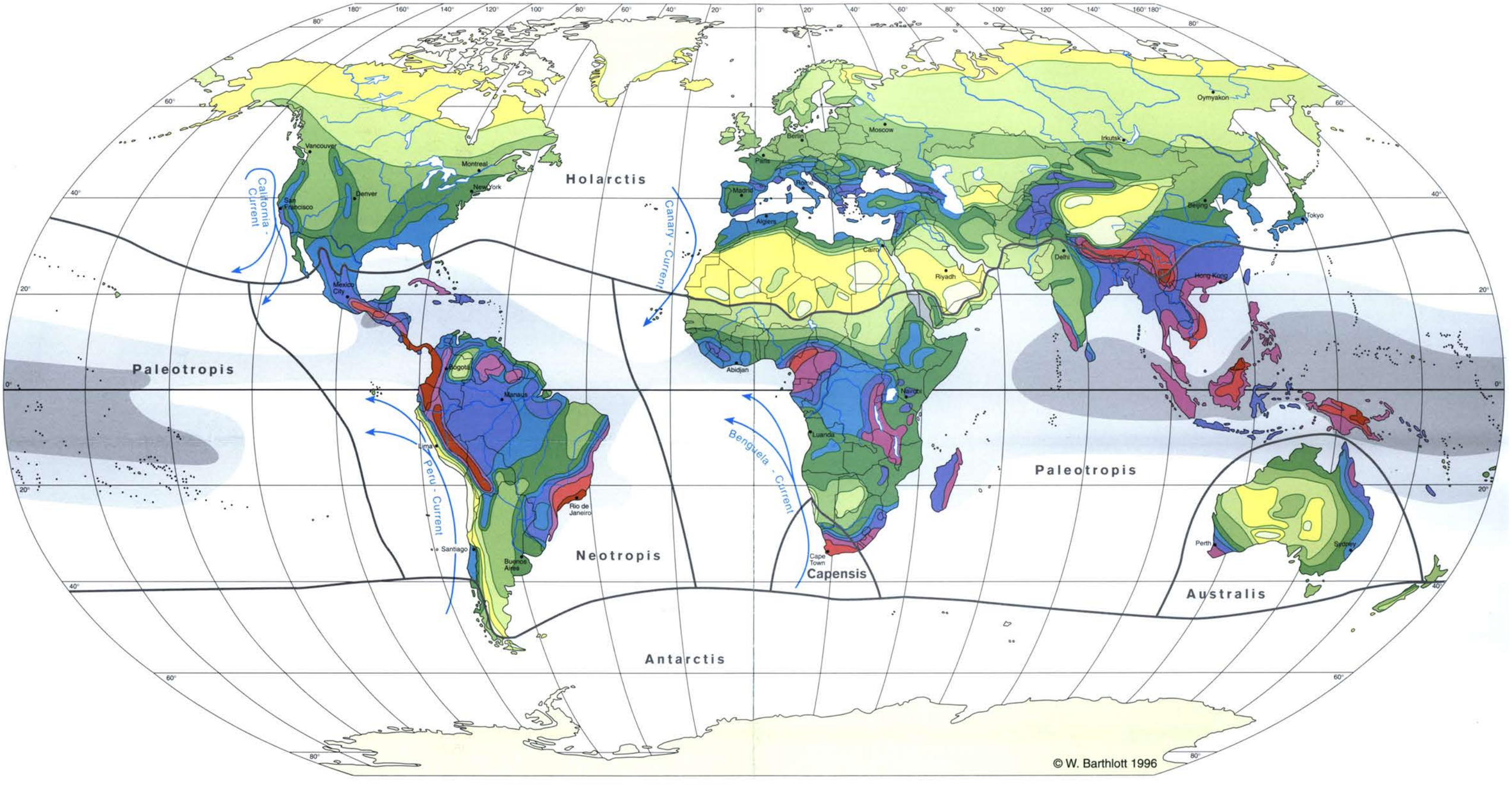
GLOBAL BIODIVERSITY: SPECIES NUMBERS OF VASCULAR PLANTS



Robinson Projection
Standard Parallels 38°N und 38°S
Scale 1: 85000000

Diversity Zones (DZ): Number of species per 10.000km^2

- DZ 1 (<100)
- DZ 2 (100 - 200)
- DZ 3 (200 - 500)
- DZ 4 (500 - 1000)
- DZ 5 (1000 - 1500)
- DZ 6 (1500 - 2000)
- DZ 7 (2000 - 3000)
- DZ 8 (3000 - 4000)
- DZ 9 (4000 - 5000)
- DZ 10 (≥5000)

Capensis floristic regions

sea surface temperature

- >29°C
- >27°C

cold currents

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