Plant diversity and biogeography of the Golfo Dulce region, Costa Rica

Diversidad vegetal y biogeografía de la región de Golfo Dulce, Costa Rica

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Abstract: With about 2.700 species of vascular plants, the Golfo Dulce region is one of the most floristically diverse regions of Central America. After a brief historical survey of botanical work in Costa Rica and in the Golfo Dulce region, the paper addresses recent investigations on tree diversity and discusses the reasons for the great botanical richness of the region. A biogeographical analysis of the tree species of the Esquinas forest reveals a close relation to northern South America, especially the Chocó region (parts of Colombia, Ecuador and Peru). The high degree of plant endemism in the Golfo Dulce region is remarkable. An analysis of seven representative families shows that about 18% of the investigated species are endemic. In the herbaceous Marantaceae, even 32% of the species are endemic. The reasons assumed responsible are addressed.

Key words: Costa Rica, Golfo Dulce, flora, biodiversity, biogeography, plant diversity, endemism.

Resumen: Con aproximadamente 2,700 especies de plantas vasculares, la región de Golfo Dulce es una de las áreas vegetacionales más diversas de América Central. Después de una breve investigación histórica sobre el trabajo botánico en Costa Rica y en la región de Golfo Dulce, este documento aborda las recientes investigaciones sobre la diversidad arbórea y discute las razones de la elevada riqueza vegetal de la región. Un análisis biogeográfico de las especies arbóreas del bosque Esquinas, revela una estrecha relación con el norte de América del Sur, especialmente la región de Chocó (parte de Colombia, Ecuador y Perú). Se destaca el alto grado de plantas endémicas en la región de Golfo Dulce. Un análisis de siete familias representativas, muestran que aproximadamente el 18% de las especies estudiadas son endémicas. La familia Marantaceae presenta un 32% de especies endémicas.

Palabras clave: Costa Rica, Golfo Dulce, flora, biodiversidad, biogeografia, diversidad de plantas, endemismo.

Introduction

The present paper presents a brief survey of plant (especially tree) diversity in the Golfo Dulce area and the plants´ biogeographical relations. Starting from a short overview on the botanical work carried out in Costa Rica in the 19th and 20th centuries, recent and current floristic studies and biogeographical analyses are considered. The reasons for the close affinities to the flora of north-western South America and the noticeable endemism are addressed.

Floristic work in Costa Rica – a brief history

Out of all the Central American countries, Costa Rica has received the greatest attention from botanical collectors. While most parts of Central America were explored by Spanish botanists in colonial times, this was not so in Costa Rica. Botanists from various European countries worked in Costa Rica in the 19th century (see Gómez 1986 and Grayum et al. 2004). Among the most prominent were Anders Sandøe Ørsted (1816-1872) from Denmark, Jozef v. Warscewicz (1812-1866) from Lithuania, Karl Hoffmann (1823-1859) from Germany, and Henri Pittier (1857-1950) and Adolphe Tonduz (1862-1921) from Switzerland. Names of many Costa Rican plant genera and species commemorate these scientists, e.g., *Oerstedella*, *Dieffenbachia oerstedii*, *Inga oerstediana*, *Hoffmannia*, *Warscewiczia*, *Cryosophila warscewiczii*, *Annona pittieri*, *Dracontium pittieri*, *Aristolochia tonduzii*, *Ficus tonduzii*, and many others. Significant contributions were also made by local collectors such as Anastasio Alfaro (1865-1951; *Alfaroa*!) and Juan José Cooper (1843-1911; *Ruellia cooperi*). Tonduz collected more than 18.000 specimens in Costa Rica. Durand & Pittier (1891-1901) were the first to publish a Costa Rican flora, the "Primitiae florae costaricensis", which included some 5.000 species. At the end of the 19th century, Central

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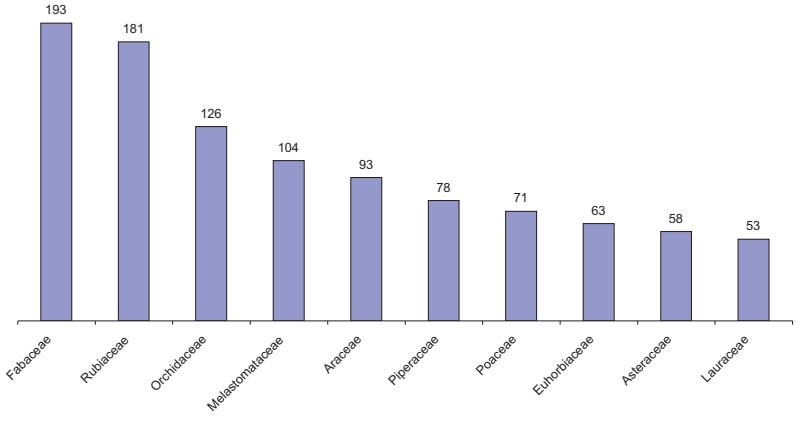

Fig. 1: The ten most species-rich plant families (angiosperms) in the ACOSA region.

America and Costa Rica became politically attractive to the United States, and U.S. botanists started collection work in Costa Rica on a larger scale. John Donnell Smith (1829-1928), Paul C. Standley (1884-1963), Paul H. Allen (1911-1963) and William C. Burger (born 1932), have been among the most active botanists working in Costa Rica in the first half of the 20th century. Paul Standley collected more than 15.000 specimens and produced a four volume flora, the "Flora of Costa Rica" (STANDLEY 1937-1940). This included 6.085 species of higher plants. Standley recognised the country's enormous plant diversity, stating: "Of all Central American countries Costa Rica possesses by far the richest flora". According to GENTRY (1978), William Burger collected about 70.000 specimens for a new flora, the "Flora Costaricensis" (start of publication 1971). In a special paper, he discussed at length the question "Why are there so many kinds of flowering plants in Costa Rica?" (BURGER 1985). In 1985, Gomez-Laurito & Fournier counted about 860 native genera (in 192 families) of woody plants in Costa Rica. Knowledge of the Costa Rican flora has increased rapidly during recent decades. In a joint effort started in 1989, the Missouri Botanical Garden (USA), the Instituto Nacional de Biodiversidad (INBio, CR) and the Museo Nacional de Costa Rica (CR) published the first parts of the "Manual de Plantas de Costa Rica" (I-IV; HAMMEL et al. 2003a,b, 2004, 2007), covering 4.393 species, 817 genera and 104 families. At present, 9.361 species, 2.023 genera and 255 families of higher plants are known in Costa Rica (ZAMORA et al. 2004).

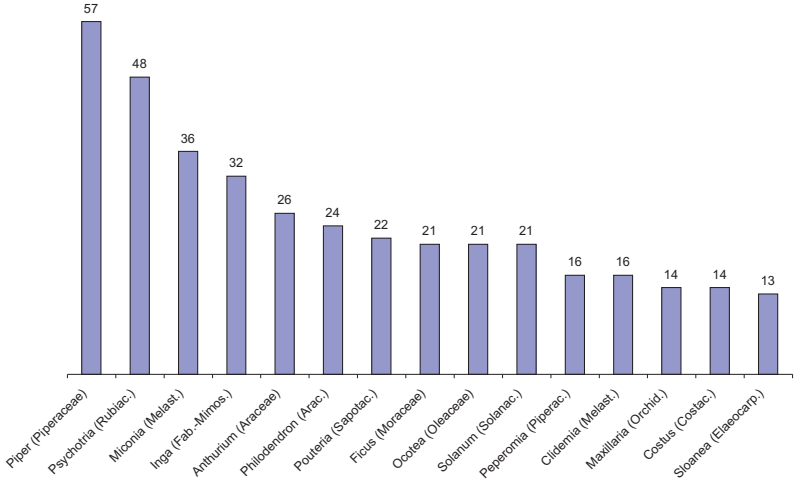

Fig. 2: The 15 most species-rich genera (angiosperms) in the ACOSA region.

The botanical work that has been carried out around the Golfo Dulce must be considered in particular depth. Among the first botanists collecting extensively in the region was the Austrian botanist Georg Cufodontis (1896-1974) (see papers of DÍAZ and WEBER, this volume). In the 1950s, the US botanist Paul Allen, who lived in Palmar Sur, published the "The Rain Forests of Golfo Dulce" (ALLEN 1956), which remains a classic. At the end of the 1980s, INBio started to collect plants and to establish forest plots on the Osa Peninsula. The great amount of data is largely unpublished so far. Only a semi-popular field guide to the trees of the Osa Peninsula has appeared (QUESADA et al. 1997). In 1993, HUBER (1996a, 1996b, 2005) and WEISSENHOFER (1996, 1997, 2005) started botanical investigations in the Esquinas Forest (now Piedras Blancas National Park), establishing plots which have been monitored continuously ever since. In 2001 the "Introductory field guide to the flowering plants of the Golfo Dulce Rainforests, Costa Rica" (WEBER et al. 2001) was published.

Flora

The Golfo Dulce region is one of those rare places on earth where an enormous biological diversity can be found within a relatively small geographical area (VAUGHAN 1981). By any measure, it is one of the botanically most diverse regions of Central America. This is partly because of Costa Rica's role as a "corridor" which enables migration of plants and animals from North to South America and vice versa. In 2001, 2.369 species of vascular plants – roughly a quarter of all Costa Rican plant species – were recorded from the Golfo Dulce area (WEISSENHOFER et al. 2001). At present, 2.662 species are recorded in the INBio database for the ACOSA region (see map, Fig. 3). At the family level, the flora contains 23 families of pteridophytes, two families of gymnosperms (with one species each), and 162 families of angiosperms. It is also notable that the region harbours over 700 tree species. This is the greatest tree species diversity known from Central America, and represents one quarter of all tree species found in Costa Rica (QUESADA et al. 1997).

The families with the highest species richness in the ACOSA region are shown in Fig. 1. The two largest families are Fabaceae (sensu lato; 193 spp.) and Rubia-

ceae (181 spp.), numbering almost 200 species each, followed by Orchidaceae and Melastomataceae, each with more than 100 species. These are followed by Araceae (93), Piperaceae (78), Poaceae (71), Euphorbiaceae (63), Asteraceae (58) Lauraceae (53), Moraceae (49), Solanaceae (45) and Arecaceae (44).

With regard to the generic level, the most diverse genera are shown in Fig. 2. The most speciose genera are *Piper* (Piperaceae) and *Psychotria* (Rubiaceae), with nearly 60 and 50 species, respectively.

In the recent past, about 62 species from the Golfo Dulce area have been described as new to science. Significant and conspicuous new species include *Porina pilifera* (Lichenes), *Costus osaensis* (Costaceae), *Ruptiliocarpon caracolito* (Lepidobotryaceae), *Justicia peninsularis* (Acanthaceae), *Lycaste bruncana* (Orchidaceae), *Pleurothyrium golfodulcensis* (Lauraceae), *Aiouea obscura* (Lauraceae), *Ocotea patula* (Lauraceae), *Inga golfodulcensis* (Fabaceae/Mimosoideae), and *Stemmadenia paulii* (Apocynaceae). More than 50 species were recorded as new for the flora of Costa Rica, including *Ziziphus chloroxylon* (Rhamnaceae), *Oecopetalum greenmanii* (Icacinaceae), *Recchia simplicifolia* (Simaroubaceae), *Micropholis venulosa* (Sapotaceae) and *Buchenavia tetraphylla* (Combretaceae). This shows that knowledge of plant diversity is still increasing and, more generally, that the tropical flora is badly known and under-collected (WEISSENHOFER et al. 2001). Ironically, most of the new discoveries were made along paths or near clearings.

Plant diversity and reasons assumed responsible

One of the most distinctive features of tropical forests worldwide, and neotropical lowland forests in particular, is the high diversity of plants and animals. The species richness tends to be highest in the wet lowlands, including the Golfo Dulce region. The Golfo Dulce area has an important climatic peculiarity; it experiences 1-3 months of low precipitation (WEISSENHOFER & HUBER, this volume). The slight seasonality seems to have a significant effect on species diversity. Moreover, there are special climatic conditions related to the position of the area: this is protected from north winds and drought effects by the presence and position of the Cordillera Talamanca. Rainfall is mostly due to southern pacific winds (HERRERA 1985). In addition, the area is geologically and geomorphologically unique with regard to its tectonic origin, hilly terrain, and peninsular situation, with the Osa Peninsula almost entirely surrounded by the sea.

There are other important reasons for the high diversity of plants. The region shows a very wide range of different habitats, with natural habitats ranging from lowland rainforests to lower montane forest, and the inclusion of azonal vegetation such as mangroves, swamps, ponds, riverine vegetation etc.

As to altitude, three principal vegetation patterns can be distinguished:

(1) Vegetation on alluvial soils. This is mainly found in flat areas near or along the coast (Osa Peninsula) and includes the mangroves. The temperatures are distinctly higher than in the other types. Several floristic elements are restricted to this area.

(2) Vegetation on hilly terrain, located mainly between 40 and 500 m above sea level (a.s.l.). This covers most of the area, including the whole Esquinas forest. Here the highest species diversity is found.

(3) Vegetation over 500 m a.s.l. (up to 745 m a.s.l.: Cerro Rincon). This area experiences cloudy conditions. The occurrence of montane elements is characteristic, some belonging to temperate families and genera (Fagaceae: *Quercus insignis*, *Q. rapurahuensis;* Juglandaceae: *Oreomunnea pterocarpa*, *Alfaroa guanacastensis*; see ZAMORA et al. 2004 and SINAC 2007).

Generally, the forests around the Golfo Dulce have a strong spatial structure at the landscape scale and thus provide a great variety of ecosystems, microhabitats and ecological niches (see WEISSENHOFER et al., this volume). Rapid forest dynamics contribute to the maintenance of high diversity on a geographical gradient. Furthermore, the high edaphic heterogeneity and diversity of soils support a high plant-diversity (CONDIT et al. 2002). PAMPERL (2001) documented a high degree of soil heterogeneity in the research plots in the Esquinas forest. Today, man-made habitats such as pastures and agriculture land, found at all altitude levels, play a significant role.

A recent study (CASTILLO et al. 2007), analysing 76 one-hectare plots in order to determine the distribution and abundance of canopy trees species in the Osa Peninsula, reached the conclusion that in the western Golfo Dulce area five centres of tree diversity can be distinguished: (1) Mogos, (2) Bahía de Chal-Alto San Juan, (2) Rincón-Rancho Quemado, (3) La Palma, (4) Fila Carbonera, and (5) Corcovado National Park. The study recorded 5.227 individuals of 65 selected tree species (≥ 5 cm diameter at breast height) in the whole area. Among the most abundant species were *Symphonia globulifera* (759 individuals), *Carapa guianensis* (625), *Brosimum utile* (456), *Vochysia ferruginea* (373), *Peltogyne purpurea* (259), *Pouteria laevigata* (203), *Qualea polychroma* (208), *Aspidosperma spruceanum* (176), *Vantanea barbourii* (117), *Vochysia allenii* (144), *Tachigali versicolor*

Table 1: Diversity of plant species in one-hectare plots in the Golfo Dulce rainforest.

Site in the Golfo Dulce region	d.b.h.	Number of indiv./ha	No. of spp./ha	Literature
Corcovado - Punta Llorona	≥ 10 cm	354	48	Hartshorn (1983)
Esquinas – ravine forest	≥ 10 cm	482	121	Huber (2005), Weissenhofer (2005)
Esquinas – slope forest (inland)	≥ 10 cm	527	133	Huber (2005), Weissenhofer (2005)
Esquinas – slope forest (coastal)	≥ 10 cm	588	108	Huber (2005), Weissenhofer (2005)
Esquinas –ridge forest	≥ 10 cm	847	179	Huber (2005), Weissenhofer (2005)
Bahia de Chal	≥ 5 cm	1161	201	Zamora (unpubl).
Agujas	≥ 5 cm	1098	189	Zamora (unpubl.)
Corcovado- near Sirena	≥ 5 cm	881	149	Zamora (unpubl.)
Esquinas - near ranger station	≥ 5 cm	871	188	Zamora (unpubl.)

(123), *Hyeronima alchorneoides* (118), *Ruptiliocarpon caracolito* (118), and *Vochysia megalophylla* (108).

Particular studies on the tree diversity revealed 98 species (≥ 10 cm d.b.h.) per hectare (Holdridge et al. 1971) in the Corcovado National Park, and 108 to 179 species (≥ 10 cm d.b.h.) per hectare in the Piedras Blancal National Park (Esquinas forest)(Huber 2005, Weissenhofer 2005). An unpublished analysis of Zamora et al. shows that 149 to 201 species of woody plants (≥ 5 cm d.b.h.) per hectare are growing at four different sites in the rainforests around the Golfo Dulce rainforests (Table 1).

During the early evolutionary history of angiosperms, North and South America were separated. The isthmus between them formed in the Late Tertiary (c. 5 Million years ago). Though little is known about the of the geographical history of plants in Central and South America (Croat & Busey 1975), it can be assumed that plants – like animals – migrated in both directions during the Late Tertiary.

Biogeography and floristic affinities

Central America belongs to the most diverse floristic regions in the world (Gentry 1978) and forms part of the neotropical floristic kingdom (Takhtajan 1986). About 32 angiosperm families are restricted to the neotropics (Borhidi 1991), including Bromeliaceae, Cactaceae (except *Rhipsalis* in Africa and Madagascar), Caryocaraceae, Cyclanthaceae, Heliconiaceae, Humiriaceae, Marcgraviaceae, Quiinaceae, Theophrastaceae, Vochysiaceae, and others. Nonetheless, it is clear that the neotropical flora shares a common origin with the Palaeotropical flora and it may be assumed, at least for the flowering plants, that its roots are in the Palaeotropical kingdom. Many families have a pan-tropical distribution, e.g., Annonaceae, Bignoniaceae, Bombacaceae (now Malvaceae-Bombacoideae), Chrysobalanaceae, Clusiaceae, Lauraceae, Malpighiaceae, Moraceae, Myristicaceae, Proteaceae, Sapindaceae, Sapotaceae, and many others.

The neotropical plant kingdom can be subdivided into five floristic regions (Takhtajan 1986). Costa Rica belongs to the Caribbean Region and is part of the Central American Province. This reaches from Mexico to the northern parts of South America, including the highly diverse region of the Chocó (Pacific lowlands of Colombia, Ecuador and northern Peru). A general comparison of the flora (vascular plants) of the ACOSA area (2.662 species counted so far) with the flora of Panama (Correa et al. 2004), Chocó (Forero & Gentry 1989), Ecuador (Jørgensen et al. 1999), and Perú (Brako & Zarucchi 1993) shows that the percentage of shared species with those countries is: Panama: 79-80%, Chocó: 36%, Ecuador: 47%, and Peru: 35.6% (here, only seed plants have been considered).

A biogeographical analysis of the 312 tree species occurring in four 1 ha plots of the Esquinas forest (Hu-

Table 2: Geographical distribution of seven selected plant families.

	Life form	No. of species in the Golfo Dulce region	No. of species endemic to the Golfo Dulce region	No. of species. restricted to Central America	No. of species restricted to Central and South America	Neophytic
Chrysobalanaceae	tree	22	6	3	12	
Clusiaceae	tree	30	2	8	20	
Costaceae	herb	15	3	2	9	1
Lauraceae	tree	55	10	23	22	
Lecythidaceae	tree	10	2	2	6	
Marantaceae	herb	25	8	4	13	
Sapotaceae	tree	40	4	11	24	1

BER 2005) showed that about half (161 species, 51%) are widespread in both South and Central America. More species have ranges extending to the east and south (to Panama: 251, Colombia: 197, Ecuador 166 and Amazon forest: 141) than to the west and north (Nicaragua: 186; Honduras; 109). The explanation is simple: the climatic situation is similar in north-western South America and the Golfo Dulce and leads one to expect a certain amount of floristic similarity. Apparently, these tree species originated in Amazonia, which is the main centre of tree diversity in the neotropics, and invaded Central America from there. This was enabled by the formation of the Central American land bridge and by the appropriate palaeoclimatic conditions for migration and establishment. In conclusion, the data clearly support the view that the Golfo Dulce area has strong floristic affinities to the forests of South America (GENTRY 1978, 1982a) and, in particular, to the Chocó region of north-western South America (STANDLEY 1937, HARTSHORN 1983, HARTSHORN & HAMMEL 1994, HUBER 1996, 2005).

Nonetheless, the high degree of endemism is remarkable. Of the 312 tree species analysed, 86 species are found exclusively in Central America. 99 species (c. 31%) occur only in the Pacific region (and not in the Caribbean region) of Costa Rica. This shows again that the Golfo Dulce forests reveal strong floristic differences to their counterparts on the Caribbean slope of Costa Rica. The reason for this is the presence of high mountain ranges separating the Pacific from the Carribean slope. They are the result of strong tectonic movements in the region's eventful geological history.

In the frame of the present study, the geographical distribution of five selected tropical families of trees (Chrysobalanaceae, Clusiaceae, Lauraceae, Lecythidaceae, and Sapotaceae) and two families of herbs (Costaceae, Marantaceae) was analysed – with a total of 197 species (157 trees, 45 herbs). About 15% of the trees, and 27% of the herbaceous species proved endemic to southern Costa Rica (Table 2). In the Marantaceae, 8 out of 25 species (that is 32%) are endemic in the Golfo Dulce area.

Another (rough) analysis, relating to the whole flora of the ACOSA region (with 2.662 species counted so far) (ZAMORA, unpubl.), showed that about 150 species are endemic (c. 6%).

The considerable degree of endemism can be seen in context with the idea that the Golfo Dulce region was a natural refuge, cut off from the neighbouring forests during the Pleistocene (STILES 1983, HEPPNER 1991). Due to its isolated position, speciation occurred at an accelerated rate and many new species evolved in the fragmented forests. This resulted in "hot-spots" of biodiver-

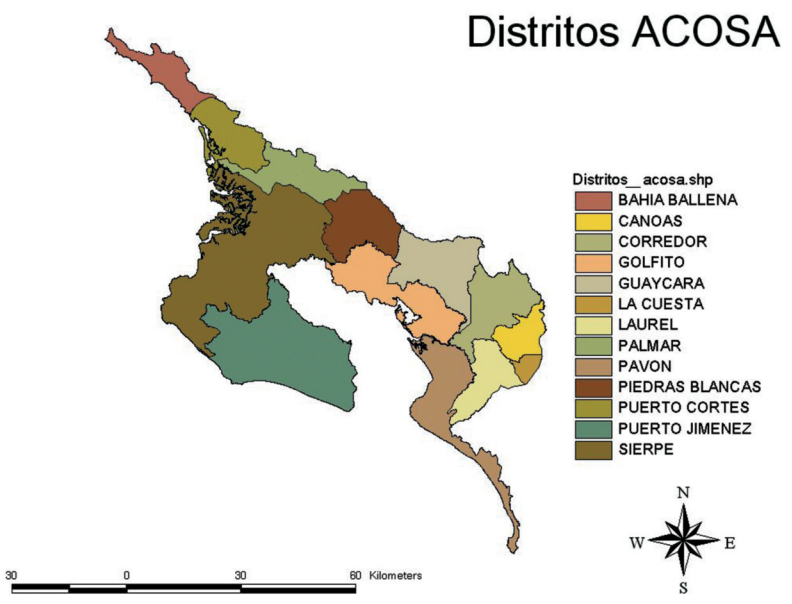

Fig. 3: Map of the ACOSA region.

Fig. 4: *Costus osae* (Costaceae) is a herbaceous plant endemic to the Golfo Dulce region and is often found along small streams.

Fig. 5: *Calliandra grandifolia* (Fabaceae-Mimosoideae) is a beautiful tree endemic to the Golfo Dulce region.

sity, containing high numbers of endemic species. The MINAE (Ministerio de Natural, Ambiente y Energia de Costa Rica) qualifies the region around the Golfo Dulce as one of those areas of Costa Rica that are richest in endemic plants.

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