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Introduction

By Peter M. Jørgensen, David A. Neill, and Susana León-Yánez

The *Catalogue of the Vascular Plants of Ecuador* documents 15,901 plant species known to occur in Ecuador and lists an additional 186 species that are expected to occur. Of the total figure, 595 species are considered to be introduced. Of the 15,306 native species, 4,173 are recorded as endemic to Ecuador. The Catalogue accounts for all plant species included in the published volumes of the *Flora of Ecuador* (Harling & Sparre, 1973–1986; Harling & Andersson, 1986–1998) and all names listed in *Index Kewensis* and *Gray Card Index* as being published on Ecuadorian material. Names used in the *Flora of the Galápagos Islands* (Wiggins & Porter, 1971), *Flora of the Río Palenque Science Center—Los Ríos Province, Ecuador* (Dodson & Gentry, 1978a), *La Flora de Jauneche—Los Ríos, Ecuador* (Dodson et al., 1985), *Flowering Plants of Amazonian Ecuador—a checklist* (Renner et al., 1990), and *Seed Plants of the High Andes of Ecuador—a checklist* (Jørgensen & Ulloa Ulloa, 1994) have likewise been included. It also attempts to account for all names used for specimens in three databases maintained at the Department of Systematic Botany at Aarhus University and Missouri Botanical Garden, and a database of collections of seed plants from the High Andes of Ecuador (Jørgensen & Ulloa Ulloa, 1994). The Catalogue provides a synopsis of the flora of vascular plants found in Ecuador by presenting each species with its synonyms, infraspecific taxa, habit, provenance, and regional, political, and elevational distribution. The number of references cited surpasses 2,500, and more than 13,000 synonyms are listed.

The project, based at the Missouri Botanical Garden, is a cooperative effort between the Herbario QCA at Pontificia Universidad Católica del Ecuador, the Herbario Nacional del Ecuador at the Museo Ecuatoriano de Ciencias Naturales, and the Department of Systematic Botany at Aarhus University in Denmark. A total of 239 specialists have participated as authors and/or served as reviewers of treatments.

The Catalogue was produced along the lines of the *Catalogue of the Flowering Plants and Gymnosperms of Peru* (Brako & Zarucchi, 1993) and will serve as baseline information on Ecuadorian vascular plants. We hope that the Catalogue will stimulate research on the plants of Ecuador by facilitating the gathering of more data on morphology, phylogenetic position, distribution, and useful properties. The number of attributes included in the inventory was purposely limited to produce a comparable dataset, i.e., providing the same amount of information for each accepted species.

A World Wide Web version of the Catalogue will be made available on the Missouri Botanical Garden's website <www.mobot.org>. This web site will house images of plant species or individual specimens, as far as they are available, to facilitate recognition and identification—and it will allow us to update the Catalogue in the future. We would be very grateful to receive new information and updates on the Catalogue web versions.

Geography

By David A. Neill

Ecuador, including the Galápagos Islands, is the smallest of the Andean countries. In South America only Uruguay, Surinam, and French Guiana are smaller. With a land area of approximately 283,000 km², Ecuador is about the size of the state of Colorado, U.S.A., or somewhat larger than Great Britain.

For more than 160 years since its independence from Spain, Ecuador laid claim to a much larger area of upper Amazonia, including territory extending eastwards to the mouths of the Napo and Marañón Rivers. Peru disputed Ecuador's territorial claims, and these disputes led to armed conflict between the two countries in 1941, 1981, and 1995. Peru and Ecuador signed a territorial accord in 1942, the Protocol of Rio de Janeiro, but the wording of this document contained a geographical error because the size and extent of the Cenepa River watershed, east of the Cordillera del Cóndor, was not known at the time of the signing. After aerial photographs of the region became available in the late 1940s and the geographical error became apparent, Ecuador called a halt to the physical demarcation of the boundary and later declared the Rio de Janeiro Protocol inapplicable. The official maps of Ecuador continued to depict a large area of Amazonia as Ecuadorian territory. The Cordillera del Cóndor region continued to be a source of tension and conflict between Peru and Ecuador, and both countries established military posts along the disputed border. Following the armed conflict in 1995, the two countries began diplomatic negotiations, with mediation carried out by Brazil, Argentina, Chile, and the U.S.A. Ecuador and Peru signed a new treaty in Brasilia in October 1998, establishing the precise location of the international border and allowing Ecuador access to the main Amazon River through Peruvian ports. A new set of official maps for Ecuador, showing the border with Peru established by the 1998 treaty, will be published soon.

The name Ecuador is Spanish for equator, and the country straddles the geographic equator, from about 1°30'N to 5°S latitude; mainland Ecuador extends from about 75°20'W to 81°W longitude. An important event in the history of world geography was the 1736 geodesic expedition led by the French geographer C. M. de La Condamine, when the region was part of the Spanish Empire. La Condamine and his colleagues measured arcs of the Earth's curvature on the equator near Quito and near Pedernales on the Pacific coast; these measurements enabled the first accurate determination of the size of the Earth and led to the establishment of the international metric system of measurement. The fame brought to the region by the French geodesic expedition evidently influenced the adoption of the name, Republic of Ecuador, when the country gained independence in 1830.

The Instituto Geográfico Militar (IGM) publishes the official maps of Ecuador. Topographic maps of the country at 1:1,000,000 and 1:500,000 scales are available, and a series of topographic sheets at 1:50,000 scale, published gradually during the past 20 years, now cover most of the country except remote areas of the Amazon basin and parts of the Andean slopes. The IGM has also published thematic maps at 1:1,000,000 scale, including geologic, soils, bioclimatic, and Holdridge life zone maps. A branch of the IGM, the *Centro de Levantamientos Integrados de Recursos Naturales por Sensores Remotos* (CLIRSEN), operates a Landsat and SPOT satellite image receiving station near the Cotopaxi volcano, carries out geographic and natural resource studies using remote sensing data, and sells the satellite imagery to other users.

Ecuador is traditionally divided into four natural regions, a scheme that is followed in this Catalogue: 1) the Pacific Coastal region, in Ecuador called the *Costa*, which includes the lower, western slopes of the Andes below 1,000 m elevation; 2) the Andes Mountains above 1,000 m, which occupy the central portion of the country, known as the *Sierra*; 3) the Amazon lowlands east of the Andes, referred to as the *Oriente*, including the lower, eastern slopes of the Andes up to 1,000 m; and 4) the Galápagos Islands, a volcanic archipelago in the Pacific Ocean 1,000 km west of the mainland.

Ecuador is divided into 21 political provinces (see map on left front endpaper). Each province is largely associated with one of the four geographic regions. The Coastal provinces from north to south are Esmeraldas, Manabí, Los Ríos, Guayas, and El Oro. The Andean provinces are Carchi, Imbabura, Pichincha, Cotopaxi, Tungurahua, Chimborazo, Bolívar, Cañar, Azuay, and Loja. The Amazonian provinces are Sucumbíos, Napo, Pastaza, Morona-Santiago, and Zamora-Chinchipe; the Galápagos Islands are also a province. The correspondence of each province within a particular region is not exact; all Amazonian provinces extend upwards to approximately the summit of the Eastern Cordillera, while several Andean provinces contain considerable areas within the Coastal region.

In 1998 the eastern half of Napo province was recognized as the new province of Orellana, but official maps showing the new province have not yet been produced; we therefore use the pre-1998 boundaries of Napo. The new province of Orellana includes Yasuní National Park, an important area for botanical inventories. Similarly, in 1989 the province of Sucumbíos, which includes the botanically important Cuyabeno Wildlife Reserve, was split off from Napo province. This Catalogue includes the province of Sucumbíos, but herbarium specimens collected prior to 1989 reflect the older boundaries of Napo province.

The coastal region of Ecuador is about 150 km wide from the base of the Andes to the Pacific coastline. A relatively low coastal range of mountains extends parallel to and just inland from the coast, from the city of Esmeraldas in the north to Guayaquil in the south, a distance of about 350 km. The summits of the coastal mountains are mostly between 400 and 600 m elevation, but a few isolated peaks are above 800 m. The coastal range is fairly continuous throughout its length, but is known by different local names: from north to south, the cordilleras of Mache, Chindul, Jama, Colonche, and Chongón.

Between the coastal range and the Andes, south of the equator, is the broad, nearly level Guayas River basin; north of the equator is the valley of the Esmeraldas River. At the mouth of the Guayas River lies Guayaquil, Ecuador's largest city and principal port. The estuary of the Guayas River empties into the Gulf of Guayaquil, the largest embayment of the Pacific Ocean on the South American coast. In the estuary and gulf are a number of low-lying islands, the largest of which is Puná Island. The Santa Elena Peninsula extends west and south of Guayaquil. South of Guayaquil to the Peruvian border there is no coastal range of mountains, and there the coastal region is a narrow lowland strip 25 km wide between the Andes and the Gulf of Guayaquil.

The Andes Mountains are the dominant topographic feature of Ecuador and occupy the central third of the country from the northern to southern borders. In northern and central Ecuador, the Andes form two distinct parallel chains: the Western Cordillera and the Eastern Cordillera; the latter is also known as the *Cordillera Real*. Between the Western and Eastern cordilleras are a series of intermontane valleys, which are separated from one another by a series of high, transverse east-west-trending ridges referred to locally as *nudos* (knots). Most of Ecuador's highland cities, including the capital city of Quito, are located in the intermontane valleys. Both the cordilleras are topped by a series of high Quaternary volcanoes; those volcanic peaks that exceed 5,000 m elevation are capped by glaciers. The highest volcano is Chimborazo, at 6,310 m. The major volcanic peaks of the Western Cordillera, from north to south, are: Chiles (along the northern border with Colombia), Cotacachi, Pichincha, Illinizas, and Chimborazo. The major volcanoes of the Eastern Cordillera are Cayambe, Antisana, Cotopaxi, Tungurahua, El Altar, and Sangay.

The Andes of southern Ecuador (Cañar, Azuay, and Loja provinces) are not so clearly differentiated into western and eastern cordilleras, but form a more complex pattern of ridges, some of which trend north-south and some east-west. There are no high, Quaternary volcanoes in southern Ecuador; the highest ridges and peaks are barely above 4,000 m.

Some geographers (e.g., Sauer, 1965) recognize a third cordillera east of the two main chains of the Andes, which is tectonically related to the Cordillera Oriental of Colombia. The third cordillera is not a continuous chain; it forms a series of short ranges, mostly of Cretaceous and Tertiary sediments, including the Cordilleras of Galeras, Cutucú, and Cóndor. The Reventador and Sumaco Volcanoes, in Sucumbíos and Napo provinces, respectively, are part of the third cordillera.

The eastern third of continental Ecuador is part of the upper, westernmost portion of the Amazon River basin. Ecuador occupies only about 2% of the entire Amazon drainage. In Amazonian Ecuador, most of the area of *terra firme* between the major river valleys is not a flat, featureless plain, but rather a *peneplain* with a complex micro-topography of low, but often steep-sided hills. Mostly north of the Napo River, Amazonian Ecuador is a truly flat plain. Areas with poor drainage are occupied by swamps and oligotrophic black-water lakes.

Most of the rivers in Ecuador originate in the Andes and flow either west to the Pacific Ocean or east to the Amazon basin. The intermontane valleys between the Eastern and Western Cordilleras drain either west or east so the continental divide is along the Eastern Cordillera in some parts of the Ecuadorian Andes and along the Western Cordillera in other sections. The major river systems flowing to the Pacific, from north to south, are the Chota/Mira, Santiago/Cayapas, Guayllabamba/Esmeraldas, Daule/Babahoyo/Guayas, Chimbo/Chanchán, Jubones, Puyango, and Catamayo/Calvas river basins. The major river systems flowing to the Amazon basin, from north to south, are the San Miguel/Putumayo, Aguarico, Napo, Curaray, Pastaza, Morona, Upano/Paute/Zamora/Santiago, and Chinchipe river systems. The rivers of northern Amazonian Ecuador (except the Putumayo) flow into the Napo and thence into the main Amazon, just downstream from Iquitos, Peru. The southern rivers flow into the Marañón, a major tributary of the Amazon, within Peruvian territory.

The Galápagos Islands, also known as the Archipiélago de Colón, comprise 12 large islands and numerous smaller islands and exposed rocks; the total land area of the Galápagos is about 8,000 km^2.

Geology

By David A. Neill

The definitive treatise on the geology of Ecuador, and the only modern treatment that covers the whole country, is that of Sauer (1965, in Spanish; the German version of the same work is Sauer, 1971; see a slightly simplified version of Sauer's map on left back endpaper). An earlier work by Wolf (1892; reprinted in 1975 with commentaries by modern authors) contains a wealth of information on Ecuadorian geography as well as geology. More recent geological studies in Ecuador have mostly dealt with Quaternary volcanism (Hall, 1977; Clapperton, 1993) and stratigraphy of the petroleum fields in the Amazonian region (Campbell, 1970). Following is a brief synopsis of the geological history of Ecuador, with emphasis on events and features that bear on present-day distribution of the flora.

During the Jurassic period, about 150 million years before present, South America was still joined to Africa, forming the subcontinent of West Gondwanaland. At that time, coniferous forests were present in Ecuador, with trees related to the modern-day *Araucaria* forests of southern South America; evidence for this are the fossilized tree trunks of the petrified forest in the Puyango valley of Loja and El Oro provinces.

By the mid-Cretaceous period, about 100 million years ago, South America had separated from Africa and begun to drift westward. This period corresponded with the origin and early diversification of the angiosperms on all continents (Raven & Axelrod, 1974). During most of the following 100 million years, South America was an island continent. The angiosperm flora evolved therefore in relative isolation from other land areas. Connections with North America via island chains permitted migration of floristic elements between the two continents long before the final closure of the Panama land bridge in the Pliocene, only about 3 million years ago (Gentry, 1982a) or perhaps as recently as 1.8 million years ago (Keller et al., 1989).

During the mid-Cretaceous, the region that is now Amazonian Ecuador was an embayment of the Pacific Ocean. The core areas of the South American continent, the Guayana and Brazilian Shields, were to the east, and the precursor of today's upper Amazon River flowed westward, eroding the shield areas and depositing sediments in the embayment. Marine deposits in the embayment at this time produced the limestones of the Napo formation, as well as the petroleum deposits that are presently being exploited in Amazonian Ecuador (Campbell, 1970).

Marine deposits of limestone and shale were also made during the Cretaceous and early Tertiary periods in the area that is now western Ecuador. Igneous rocks were also formed in the region during these times, particularly submarine pillow lavas alternating with marine sediments. These formations were later uplifted to form the present-day coastal range.

The westward tectonic movement of the South American plate, and the collision of the leading edge of the South American plate with the Pacific plates, resulted in the upthrust of continental rock that has formed the Andes along the entire western edge of South America. The southern Andes of Bolivia, Chile, and Argentina are the oldest, with considerable uplift during the early Tertiary period about 50 million years ago, but the northern Andes of Colombia and Ecuador are relatively younger, with the major uplift begun in the Miocene, about 25 million years ago.

The base of the Eastern Cordillera of the Ecuadorian Andes is mostly Precambrian metamorphic rock composed of crystalline schists, while the base of the Western Cordillera is mostly Cretaceous volcanic and pyroclastic rock. The inter-Andean corridor between the two cordilleras is a *graben*, a zone where tectonic uplift did not occur. Intense volcanic activity during the Tertiary, on top of the older, uplifted rocks of both cordilleras, began to build up the Andes to greater heights. Intrusions of granitic rock, known as *batholiths*, took place in some zones of both cordilleras.

The third cordillera of the sub-Andean region in eastern Ecuador was also uplifted by tectonic forces. The Cordillera Galeras, in Napo province, is formed mostly of the Cretaceous limestone Napo formation. The Cordillera de Cutucú, farther to the south in Morona-Santiago province, is made partly of the same Napo formation, but also contains older Jurassic sedimentary rocks. The stratigraphy of the Cordillera del Cóndor, along the southeast border of Ecuador with Peru, is poorly known, but includes shales, limestones, and sandstones of Mesozoic and Tertiary age.

The basal Precambrian rock of the Eastern Cordillera is exposed in some areas, such as the Llanganates region east of Ambato. Cerro Hermoso, a peak in the Llanganates over 4,600 m high, is a geological anomaly of the Eastern Cordillera. It is composed of a block of Cretaceous limestone, probably the same Napo formation as the Cordillera Galeras, that was uplifted, faulted, and thrust from the east on top of the basal metamorphic rock (Kennerley & Bromley, 1971). Cerro Hermoso is therefore the only high peak in the main Andean chain in Ecuador that is not of volcanic origin.

During the mid- to late Tertiary (25–2.5 million years ago) intensive volcanic activity on top of the uplifted basal rocks of both the Western and Eastern cordilleras built up the Andes to greater heights. By the end of the Tertiary, volcanic activity ceased in the Andes of southern Ecuador. Along both cordilleras of the northern and central Ecuadorian Andes, however, intensive volcanic activity continued throughout the Quaternary period, during the past 2.5 million years. This activity produced the *avenue of volcanoes* that we see today—the two lines of high peaks along the Western and Eastern cordilleras from Chiles volcano on the Colombian border, south to Chimborazo on the west and Sangay on the east. Quaternary volcanic activity also produced the Reventador and Sumaco volcanoes, east of the main Andes. Throughout the Andes of northern and central Ecuador thick layers of ash from the Quaternary eruptions were deposited. Volcanic ash was also deposited on the Pacific and Amazon plains west and east of the Andes, up to about 50 km from the base of the mountains.

The Galápagos Islands, like other volcanic, oceanic archipelagos such as the Hawaiian Islands, were formed from eruptions of magma issuing through a *hot spot* or weak point in the earth's oceanic crust. The Galápagos are geologically very young, with much of their formation having occurred during the last 1 million years, although some areas of the Galápagos are as old as 3 million years (van der Werff, 1978).

The distribution of plant species in relation to different geologic substrates is a topic that has not received much attention by botanists in Ecuador. There appears to be some evidence for floristic differences associated with substrates in areas where calcareous limestone and more acidic volcanic rocks occur together (D. Neill, pers. obs.). For example, in the deciduous forests of the Cordillera de Chongón near Guayaquil, stands dominated by *Ceiba trichistandra* are common on limestone substrate, while *Cavanillesia platanifolia* is more common on adjacent substrates of volcanic cherts. In Napo province, the lower montane rain forest atop the limestone massif of the Cordillera Galeras at 1,500 m elevation is floristically distinct from nearby forest at the same elevation on the slopes of the Sumaco volcano. In the same sub-Andean region of Napo, rheophytes such as *Matelea rivularis* and *Phragmipedium pearcei* are found along streams with calcareous rocks but not with volcanic lavas.

Paleoclimates

By David A. Neill

During the past 30 years, much scientific attention has focused on study of climatic fluctuations during the Pleistocene and their effects on plant distributions. Debate among scientists has centered on the question of whether lowland Amazonia was significantly drier during Pleistocene glacial maxima (Ab'Sáber, 1982) or colder (Colinvaux, 1987; Bush et al., 1990; Colinvaux et al., 1997) or both (Piperno & Pearsall, 1998), and whether or not the Amazon forest was reduced to a few *Pleistocene refuges* (Prance, 1982) with consequent effects on present-day diversity and endemism patterns of plants and animals in the Neotropical lowlands.

In the high Andes, temperatures were about 6–7°C lower than at present during the last Pleistocene glacial maximum (18,000–13,000 years ago), and the lower limits of glaciers in the northern Andes were at 3,100–3,800 m (van der Hammen, 1974, 1982). At present, the lower limits of glaciers on the Ecuadorian volcanoes are about 4,700–5,100 m (Jørgensen & Ulloa Ulloa, 1994). The upper limit of forest in the Andes during the Pleistocene glacial maxima was at about 2,000 m, i.e., about 1,500 m lower than the present-day upper limit of forest at about 3,500 m (van der Hammen, 1982). Therefore, most of the areas in the high Andes that are today covered with páramo, were beneath glacial ice during the Pleistocene maxima, and páramo vegetation then covered a much larger area than at present, on the slopes and the inter-Andean valleys above 2,000 m. Regional and world temperatures fluctuated up and down a number of times during the 2.5-million-year history of the Pleistocene, so the altitudinal belts of glacial ice, páramo, and montane forests also shifted up and down the slopes of the northern Andes a number of times (Hooghiemstra & Cleef, 1995).

Climatic shifts during the Pleistocene in the Neotropical lowlands certainly occurred, but the nature and magnitude of the changes, and their effect on vegetation patterns, are still being debated. The original *Pleistocene refuge* theory (Haffer, 1969)—which postulated that most of the Amazon basin was so dry during the Pleistocene glacial periods that the Amazon forest was replaced by savanna except for a few wetter *refuges* where forest remained—was popular during the 1970s and early 1980s (Prance, 1982), but has now been discredited because much more paleoecological evidence is available for the lowland Neotropics (summarized in Piperno & Pearsall, 1998). The Pleistocene climate was cooler in the Amazon lowlands than it is today, probably 5–7°C cooler, and also somewhat drier, with perhaps 25–40% less rainfall than at present. Central and western Amazonia, including the Ecuadorian portion of the basin, remained forested throughout the Pleistocene, but the floristic composition was different, with taxa that are now restricted to the montane forests of the Andes above 1,200 m, such as *Podocarpus* and *Hedyosmum* (Colinvaux et al., 1997; Athens, 1997), growing in the lowlands. Lowland Amazonian forests evidently had a different mix of species during the Pleistocene than is present there today, with montane species growing together with some of the lowland taxa that make up modern Amazonian forests.

Climates

By David A. Neill and Peter M. Jørgensen

A large variety and range of climatic regimes are found in Ecuador, and this variety has a major effect on the extension of the vegetation types and on the diverse flora of the country. The climatic regimes found in Ecuador are influenced by its geographical position astride the equator, the general circulation of the atmosphere, the position and movements of the ocean currents, and by orographic effects produced by the abrupt topography of the Andes as well as the smaller coastal ranges.

Descriptions of climatic patterns in Ecuador are found in Naranjo (1981), Porrut (1983), and Cañadas (1983); each of these works includes tables and diagrams of precipitation and temperature records for a number of sites in the country, and together provide the basis for the following summary of Ecuador's climates. Another useful source is a discussion of climate in the tropical Andes by Sarmiento (1986). The study of climate in Ecuador is hampered by a shortage of long-term records and, particularly, by complete lack of records from many remote, sparsely populated areas where climatic extremes such as very high rainfall are presumed to occur but have not been measured. Only a few sites in the country have meteorological records of 50 years or more—mostly larger cities such as Quito, Guayaquil, and Cuenca. A network of more than 125 meteorological stations throughout Ecuador was established in the early 1960s.

Due to Ecuador's position on the equator, the day length changes very little throughout the year—every day has about 12 hours of sunlight, varying no more than about 30 minutes at any point in the country. On the equator, the total amount of solar radiation reaches a maximum at the equinoxes; this is only 13% higher than the minimum amount of radiation intercepted at the solstices. A consequence of this relative annual constancy in solar radiation is the low seasonal variation in mean air temperature at equatorial latitudes. From month to month, the mean temperatures at all sites in Ecuador are relatively constant; monthly means do not vary more than 3°C at any site, and at many sites vary less than 1°C. In contrast, the daily fluctuations in temperature over 24-hour periods are much more pronounced; the circadian cycle of temperature change is therefore much more important than the annual change in mean temperature. Daily temperature fluctuation at mid- to upper elevations in the Andes is often 20°C or more. In the lowlands, the daily fluctuation in temperature is generally much less, closer to about 10°C. The daily maxima and minima do have significant annual variation at some sites, for example, at high elevations where freezing temperatures are more prevalent during the dry season with clear skies.

Temperature in Ecuador varies rather predictably with altitude. At sea level in coastal Ecuador, the mean annual temperature is about 25°C. On moist tropical mountains, following the adiabatic lapse rate, temperature decreases at about 0.5°C for each increase of 100 m in altitude. The lapse rate, as determined from climatic records at various elevations, is slightly different for the western slopes versus the eastern slopes of the Andes (Cañadas, 1983), and sites in the inter-Andean valleys are somewhat warmer than sites at equivalent elevations on the outer slopes of the cordilleras (Naranjo, 1981). Nevertheless, the relative constancy of the adiabatic lapse rate allows us to approximate the mean temperature at different altitudes in Ecuador (the values at a particular site may differ by as much as 1.5°C from the approximate mean temperatures in Table 1).

Freezing temperatures occur at about 3,000 m elevation in the Andes and are increasingly frequent at greater elevations. Frosts are rare below the 3,000-m line and have never been recorded, for example, in the center of Quito at 2,800 m elevation, the only site in Ecuador with a 100-year meteorological record. The lowest temperature recorded in Quito is 2°C.

In contrast to the constancy of temperature regimes in Ecuador, rainfall regimes vary enormously from place to place, in both the annual amount of precipitation and in the patterns of seasonal distribution of rainfall. Different patterns of rainfall are found in the Coastal, Andean, and Amazonian regions of continental Ecuador, and in the Galápagos Islands; variation also occurs from north to south in each main geographical region, and on a local scale according to topography and other factors. Figure 1 is a generalized climatic map of Ecuador, showing elevation contours (which correspond approximately to the mean temperature values indicated in Table 1), annual precipitation isohyets, and Walter climate diagrams (Walter, 1979) for 23 sites throughout the country, selected to represent the range of climatic patterns in Ecuador.

Annual patterns of rainfall in the Andean region of Ecuador are profoundly influenced by the oscillations of the Intertropical Convergence Zone (ITCZ), the trough of low pressure between the large currents of continental air masses north and south of the equator, that is associated with cloudiness and heavy precipitation. The ITCZ shifts from a position at about 10°N latitude at the June solstice, to about 5°S latitude at the December solstice. Therefore, the ITCZ passes over Ecuador twice during the year on its northward and southward oscillations. The shifts in the ITCZ produce a bimodal distribution of rainfall at Andean localities in Ecuador, with two rainy periods and two drier periods during the year. This bimodal pattern is illustrated by the climate diagrams for Tulcán, Mira, Ibarra, Quito, Tumbaco, Cotopaxi, Riobamba, and Cuenca (Figure 1). In the Ecuadorian Andes, the major dry season is during July–August and, in some cases, extending to September. A less pronounced dry period is discernible at most sites during January. Periods of high rainfall for most Andean sites are during March–April and again in October. Precipitation frequently occurs as violent afternoon thunderstorms, sometimes with hail at sites above 2,500 m. The mean annual precipitation for the sites indicated varies from about 1,250 mm for Quito, to just 400 mm for Riobamba.

In the coastal region of Ecuador, annual rainfall patterns

Table 1. Approximate mean temperature at different elevations. / Tabla 1. Temperatura promedio a diferentes altitudes.

Elevation	Temperature in °C
Sea level	25.0
500 m	22.5
1000 m	20.0
1500 m	17.5
2000 m	15.0
2500 m	12.5
3000 m	10.0
3500 m	7.5
4000 m	5.0

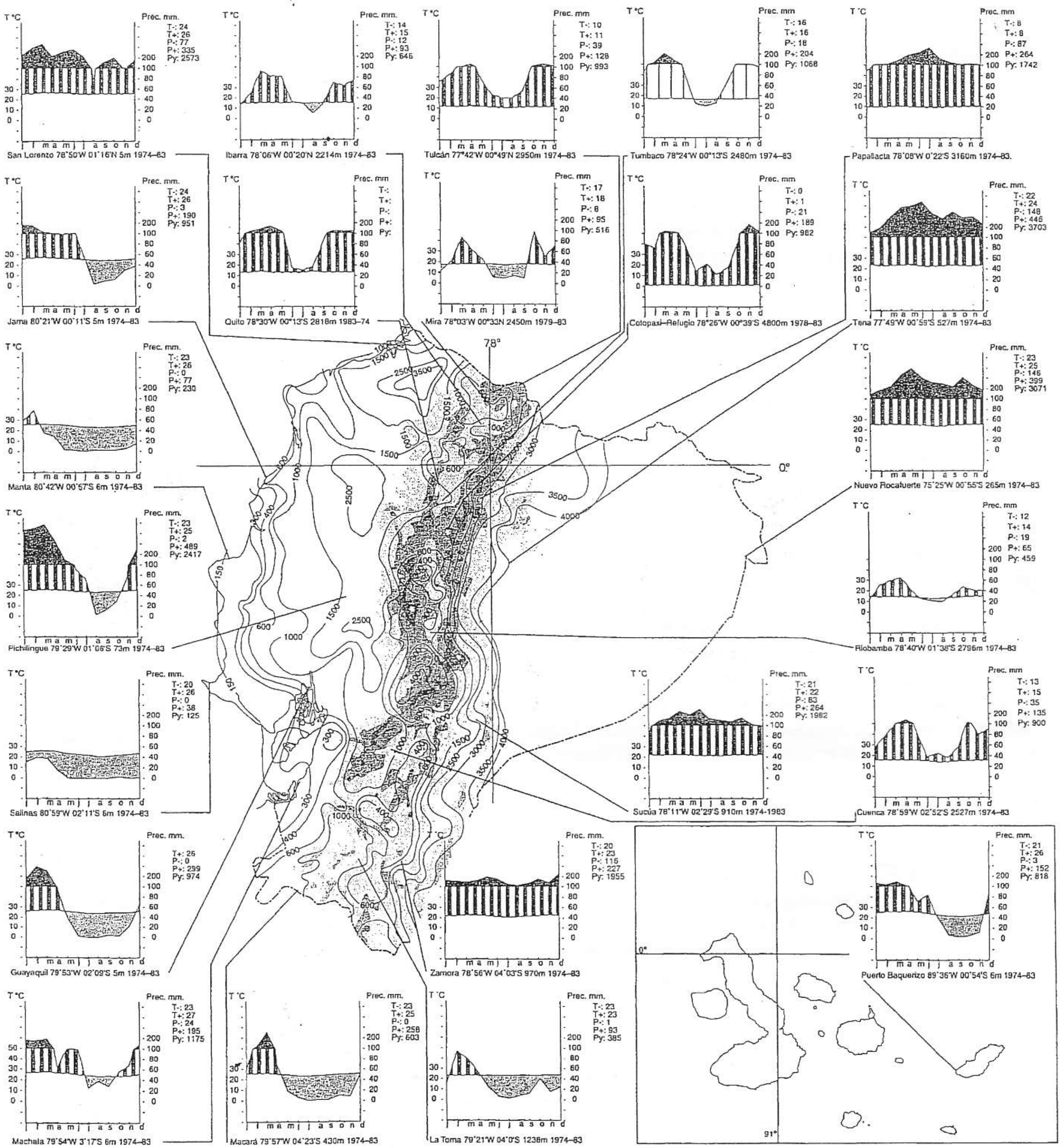

Figure 1. Climate map of Ecuador showing elevation, annual precipitation ishohyets, and Walter climate diagrams for 23 selected sites throughout the country. For each climate diagram, the left scale is mean monthly temperature in degrees Celsius; right scale is mean monthly precipitation in millimeters; months of year from January to December indicated at bottom. Symbols to right of diagram for mean values: (T-), monthly minimum temperature; (T+), monthly maximum temperature; (P-), monthly minimum precipitation; (P+), monthly maximum precipitation; (Py), annual precipitation. Humid months are indicated by vertical lines, and months with more than 100 mm precipitation are indicated by the black area above the vertical lines. Dry months are indicated by a gray area.

Figura 1. Mapa climatológico del Ecuador con elevación, precipitación anual y diagramas climáticos de Walter para 23 sitios seleccionados a lo largo del país. Para cada diagrama climático, la escala de la izquierda es la temperatura promedio mensual en grados Celsius; la escala de la derecha es la precipitación promedio mensual en milímetros, los meses del año de enero a diciembre se indican abajo. Los símbolos a la derecha del diagrama para valores promedio: (T-), temperatura mínima mensual; (T+), temperatura máxima mensual; (P-), precipitación mínima mensual; (P+), precipitación máxima mensual; (Py), precipitación anual. Los meses húmedos se indican con líneas verticales y los meses con más de 100 milímetros de precipitación se indican con sombra negra sobre las líneas verticales. Los meses más secos se indican con sombra gris.

are under the influence of the two principal ocean currents in the Pacific, near the shore of northwestern South America. These include the cold Humboldt Current, which flows northward along the coast of Chile, Peru, and southern Ecuador, and turns eastward at about the equator and flows past the Galápagos Islands. The second is the warm equatorial current that flows southward from the Gulf of Panama, along the Pacific coast of Colombia, and meets the Humboldt Current near the equator along the north-central coast of Ecuador.

The Humboldt Current brings arid conditions to the adjacent coast, as the cool oceanic air passes over the relatively warmer landmass. Another effect of the Humboldt Current is the overcast skies—the low clouds, known locally as *garúa*—that form a layer about 600 m above sea level and cover most of western Ecuador throughout the dry season.

The warm equatorial current that bathes the northwest coast of Ecuador brings with it moist air and rainfall. During most years, the warm equatorial current pushes farther to the south of the equator for a few months, December to April generally, bringing rainfall and warm, moist air to the areas of the central and southern Ecuadorian coast that are under the influence of the dry, cool Humboldt Current the remainder of the year. This phenomenon is known locally as *El Niño* (the Christ Child) because the annual rains usually begin in mid- to late December, around Christmas.

Due to the annual southward incursion of the warm equatorial current, most of coastal Ecuador, as well as the Galápagos Islands, has a unimodal pattern of precipitation, with one rainy season extending from December to April or May, and a long dry season from May to December. The length and intensity of the dry season vary at different sites in the coastal region. Salinas, for example, at the western tip of the Santa Elena peninsula, is most strongly affected by the Humboldt Current flowing just offshore, and receives only about 125 mm of rain annually, mostly during February and March. Guayaquil, at the mouth of the Guayas River, and farther from the influence of the Humboldt Current, receives nearly 1,000 mm of rain, with a 7-month dry season. Pichilingue, in the inland Guayas valley and farther north, receives over 2,400 mm but experiences a significant 4-month dry season from August to November. San Lorenzo, in the northwest corner of the country, has a climate influenced by the warm equatorial current and has only a short dry period around November. Inland areas on the coastal plain, near the northern border with Colombia, probably receive more than 5,000 mm of rain annually, but meteorological records are lacking.

At irregular intervals, but averaging about every seven years, the *El Niño* phenomenon is much stronger than normal along the Pacific coast of South America. During *El Niño* years, the warm equatorial waters push much farther south into coastal Peruvian waters, displacing the cold Humboldt Current, bringing heavy rains to the Peruvian desert as well as coastal Ecuador. The warm water conditions may last for more than a year before the Humboldt Current again brings dry weather to the coast. The heavy rains associated with *El Niño* cause flooding in coastal Ecuador and destroy roads, bridges, houses, and crops. The last two major *El Niño* events were during 1982–1983 and 1997–1998.

In Amazonian Ecuador, rainfall is relatively constant throughout the year. The extensive forests of the Amazon basin recirculate moisture through evapotranspiration, and the relative humidity of the atmosphere above the Amazonian forests remains high throughout the year. Convective and orographic effects produce rainfall, sometimes as afternoon and evening thunderstorms, and sometimes as steady drizzles that may last several days. Amazonian sites in Ecuador, exemplified in Figure 1 by the climate diagrams for Tena, Nuevo Rocafuerte, Papallacta (on the eastern slopes of the Andes, with an Amazonian rainfall regime), Sucúa, and Zamora, receive rain throughout the year; no month shows a moisture deficit for these sites. The Amazonian sites do, however, have periods of somewhat lower rainfall, generally during August and again in January, the months that correspond to the dry season in the Andes associated with the movements of the ICTZ.

Vegetation

By David A. Neill

Studies of the vegetation of Ecuador were initiated nearly 200 years ago. Indeed, it may be said that Alexander von Humboldt (1807) founded the scientific disciplines of vegetation ecology and phytogeography following his travels in Ecuador and other regions of tropical America with Aimé Bonpland during 1799–1804. Humboldt's famous illustration of the vegetation zones in the equatorial Andes, from the tropical lowlands to the páramos and glaciated peak of Chimborazo Volcano, is reproduced on the cover. His descriptions of the changes in vegetation as one ascends a tropical mountain, and his comparisons with the similar vegetation changes observed as one travels from the equator to the poles, were seminal concepts in the history of biogeography (Botting, 1973).

Since the time of Humboldt, a number of botanists have published descriptions of the vegetation and phytogeography of continental Ecuador, including L. Sodiro (1874), Diels (1937), Acosta-Solís (1969b, 1976), Harling (1979), and Cañadas (1983). A discussion of the vegetation and phytogeographical patterns in the high Andes above 2,400 m elevation is found in Ulloa Ulloa and Jørgensen (1993) and Jørgensen and Ulloa Ulloa (1994). Wiggins and Porter (1971) and van der Werff (1978) described the vegetation of the Galápagos Islands. Recently, a collaborative group, including geographer R. Sierra and botanists C. Cerón, W. Palacios, and R. Valencia, devised a new classification system for the vegetation of mainland Ecuador, using floristic and climatic information that has become available in the past 20 years, as well as remote-sensing (Landsat) images and Geographic Information Systems (GIS) technology. The Ecuadorian group has produced a draft version of the vegetation system, including a vegetation map (Sierra, 1997) currently being revised for publication. The classification system is hierarchical and generally follows the terminology for vegetation units, as well as the hierarchical concepts, used by Huber and Alarcón (1988) for a vegetation map of Venezuela, and by Huber (1995) for the vegetation of the Venezuelan Guayana.

The new vegetation classification system and map for Ecuador by Sierra and collaborators are being adopted by the Ministry of the Environment for purposes of conservation planning, gap analysis, and management of national parks and reserves. For such purposes, the new system is an improvement over earlier vegetation studies in Ecuador because at the lowest hierarchical level, it recognizes differences in regional floristic composition among vegetation types of similar physiognomy and structure. Once published, the system will provide a new framework for studies on the vegetation of Ecuador, and the vegetation map will be widely used. Since it is a work in progress, we cannot use the vegetation system of Sierra and collaborators in this Catalogue.

For purposes of this Catalogue, we use Harling's (1979) account of vegetation formations of Ecuador and reproduce his map on the right back endpaper. Harling's scheme is simple, with 16 main vegetation types, and is sufficient as a framework for the brief discussion of vegetation types in Ecuador that follows.

Vegetation types

Mangrove

Mangrove formations occur in the salt- and brackish-water tidal zone of river estuaries and bays along coasts. The largest extent of mangrove is found in northern Esmeraldas, in the area around San Lorenzo, in the large estuary of the Santiago and Cayapas Rivers; another large area of mangrove is in the Gulf of Guayaquil. The mangrove stands are dominated by *Rhizophora harrisonii* and *R. mangle*; on the landward edge of the stands the other common species of neotropical mangroves are found: *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus*. *Pelliciera rhizophorae* is found in the northern mangroves, but not in the Guayas-area stands. The Esmeraldas mangroves are among the tallest and best developed in the Neotropics, with *Rhizophora* trees over 30 m in some stands (Acosta-Solís, 1959; Little & Dixon, 1969).

In the Esmeraldas area, landward from the true mangroves, are fresh-water swamps dominated by a few tree species such as *Campnosperma panamense* and *Otoba gracilipes*; also present are *Pterocarpus officinalis* and *Mora megistosperma*.

In the past 25 years, large areas of mangroves have been destroyed and converted to diked ponds for production of shrimp, most of which is exported. The mangroves in the Gulf of Guayaquil were the first to suffer extensive destruction, but in recent years the shrimp aquaculture industry has spread to the Esmeraldas mangroves, despite Ecuadorian laws that prohibit clearing of mangroves.

Coastal desert and semi-desert

Arid scrub vegetation occurs on the Peninsula of Santa Elena and adjacent areas of southwest Ecuador, where annual precipitation is generally less than 300 mm and the dry season lasts for nine months (see climate diagram, Figure 1). The vegetation is composed of scattered columnar cacti, mostly *Armatocereus cartwrightianus*, and low shrubs and treelets including *Capparis crotonoides*, *Loxopterygium huasango*, *Maytenus octogona*, *Bursera graveolens*, and *Vallesia glabra*.

A similar arid scrub vegetation occurs in the lowland areas of the Galápagos Islands, with some of the same species that are found on the mainland of Ecuador, such as *Bursera graveolens* and *Maytenus octogona*, and also tall cacti including *Jasminocereus thouarsii* and *Opuntia echios* (van der Werff, 1978).

Savanna and deciduous forest

Savanna and deciduous forest occur in extensive areas of lowland coastal Ecuador where the annual precipitation ranges from about 800 to 1,200 mm and the dry season is about seven months long (Figure 1). The vegetation of these areas has been modified by human activities for so long that it is difficult to discern what the potential natural vegetation would be in the absence of human intervention, and the boundary between savanna and deciduous forest is not readily apparent. True savanna, in the sense of open grassland with scattered trees, is probably confined mostly to the alluvial plains with deep soils. Such areas were undoubtedly affected by human-induced fires, which helped to suppress woody vegetation and maintain the dominance of grasses, since the late Pleistocene. Deciduous forest with a relatively closed canopy and near absence of grasses is prevalent in the same region on the shallow, stony soils of the hillsides. These two vegetation types, therefore, occurred together as a mosaic, corresponding to the different edaphic types, in large areas of western Ecuador.

Historical records suggest that the lower Guayas River basin, between Babahoyo and Guayaquil, was originally a seasonally inundated grassland savanna, with forest on the flood-free hills that dot the plain (Hidalgo, 1998).

In the deciduous forest, virtually all of the trees and understory shrubs shed their leaves during the long dry season. Occasional individuals of *Ficus* with thick coriaceous leaves, usually found near watercourses, remain evergreen. The most conspicuous floristic element of the deciduous forest is the Bombacaceae tree *Ceiba trichistandra* with its grotesque, thick twisted limbs and trunk and green bark, which is photosynthetic through the dry season when the tree lacks leaves; the species is common throughout the dry forest zone from northern Manabí to Loja. Other Bombacaceae trees are also common, including *Eriotheca ruizii*, *Pseudobombax guayasense*, and west of Guayaquil, *Cavanillesia platanifolia*. *Machaerium millei* and *Pradosia montana* are other dominant trees of the deciduous forest. In the areas of savanna on the alluvial plains, scattered Mimosaceae trees are most common, including *Samanea saman* with its broad umbrella-shaped crown, and *Pseudosamanea guachapele*.

Descriptions of deciduous forest vegetation in western Ecuador are found in Kessler (1992) and Parker and Carr (1992). Josse and Balslev (1994) carried out quantitative forest inventories in this vegetation type, in one-hectare sample plots in Machalilla National Park.

Semi-deciduous forest

Semi-deciduous forest formerly covered extensive areas of the central coastal plain in western Ecuador. This vegetation type has an annual rainfall ranging from about 1,500 to 2,500 mm (Figure 1), with a dry season of about three months; it is therefore intermediate in the moisture gradient between deciduous forest, which occurs mostly in southwestern Ecuador, and lowland rain forest in the northwest. This vegetation type corresponds approximately to "Tropical Moist Forest" in the Holdridge system (Holdridge, 1967; Cañadas, 1983).

In the Guayas River basin, with its fertile soils, the original forest was almost entirely cleared for agriculture, a process that was essentially completed during the 1950s and 1960s (Dodson & Gentry, 1991). A small remnant (about 130 ha) of semi-deciduous forest in the Guayas basin was preserved at the Jauneche Biological Station; a floristic study of Jauneche was published by Dodson et al. (1985). The largest remaining fragment of this vegetation type is probably a narrow strip, comprising several thousand hectares of undisturbed forest, along the coast between Jama and Pedernales in northern Manabí province (D. Neill, pers. obs.).

As the name of this vegetation type implies, some of the canopy tree species shed their leaves during the dry season while others retain them; among common species of the former group are *Centrolobium ochroxylum, Erythrina poeppigiana, Gallesia integrifolia, Castilla elastica,* and *Pseudobombax millei*; among the latter group of canopy trees are *Brosimum alicastrum, Poulsenia armata*, and species of *Ficus*. The canopy palm *Attalea colenda* and the understory palm *Phytelephas aequatorialis* are ubiquitous in the semi-deciduous forest. Both these palms are economically important, and in large areas of coastal Ecuador where this forest type has been cleared, they are virtually the only tree species left standing in pastures and agricultural plots.

Lowland rain forest

Lowland rain forest, in Harling's vegetation classification, covers the northern Pacific coastal lowlands below about 700 m elevation, including most of Esmeraldas and adjacent parts of Pichincha provinces, and small areas of northern Manabí and Los Ríos. This vegetation type also includes virtually all of the Amazonian lowlands east of the Andes. Climatically, lowland rain forest is characterized by annual rainfall in excess of 3,000 mm (Figure 1) and lack of a distinct dry season (i.e., generally, no more than one month with less than 100 mm precipitation). This is the most extensive vegetation type in the country, covering more than one-third of continental Ecuador.

The lowland rain forest is tall, dense, and evergreen, with a canopy height usually 30 m or taller, and high species diversity. Alpha diversity of trees, as sampled in one-hectare forest plots, is much higher in Amazonian Ecuador than in the rain forest area of the northern Pacific coast (Valencia et al., 1998). In lowland Esmeraldas, 110–120 tree species (with a minimum sampling diameter of 10 cm DBH) are typically found in one-hectare forest plots (Palacios et al., 1997). In lowland Amazonian Ecuador, upwards of 200–240 tree species (Balslev et al., 1987; Korning et al., 1991; Cerón & Montalvo, 1997; Palacios, 1997) and in one case over 300 species (Valencia et al., 1994, 1997; Balslev et al., 1998) are found in equivalent one-hectare samples. Density and diversity of epiphytes, however, are probably equally as high or even higher in the forests of northwestern Ecuador, as compared with lowland Amazonia; Gentry and Dodson (1987) recorded exceptionally high epiphyte diversity at Río Palenque in western Ecuador, with 127 epiphyte species in an area of only 0.1 hectare. In Amazonian Ecuador, Balslev et al. (1998) recorded a total of 172 epiphyte species in one hectare.

The lowland rain forest of northwestern Ecuador is coterminous with that of the Colombian Chocó region of the Pacific coast and shares many species with the Chocó, but there is also a significant element of endemic species that are not known north of the Colombian border. Many species are also shared with the rain forests of Amazonia and/or those of Central America. Floristic studies in this region include Dodson and Gentry's (1978a) flora of the Río Palenque Science Center, near the southernmost extent of this vegetation type, and Little and Dixon's (1969) work on the common trees of Esmeraldas province. An earlier forestry survey (Holdridge et al., 1947) described the lowland rain forest in the northwest as well as the other forest types in western Ecuador and the Andes; another early general description of forest vegetation and flora is found in Rimbach (1932). The flora, vegetation, and conservation status of the region are summarized in Neill (1997). Common canopy tree species in the region include *Brosimum utile, Humiriastrum procerum, Dacryodes cupularis, Nectandra guadaripo, Virola dixonii,* and *Otoba novogranatensis*; the palm *Wettinia quinaria* is abundant in the subcanopy.

Intensive floristic inventories in lowland Amazonian Ecuador during the past 20 years have greatly increased our knowledge of that region; much of the inventory work has been associated with petroleum development activities. Checklists of the trees of the region (Neill & Palacios, 1989) and of all flowering plants (Renner et al., 1990; see also Balslev & Renner, 1989) have been published, but are far from complete; species new to science and new records for Ecuador continue to accumulate each year for lowland Amazonian Ecuador as well as for other regions of the country. Vegetation studies in the region, besides the one-hectare forest plot samples cited above, include ecophysiological studies by Grubb et al. (1963) and Grubb and Whitmore (1966a, 1966b); inventory of ground vegetation beneath the forest canopy (Poulsen & Balslev, 1991); and forest dynamics (growth and mortality of trees) in permanent sample plots and transects (Korning & Balslev, 1994). A pilot study on mapping palm species distributions correlated with climatic parameters, using GIS technology, was carried out by Skov and Borchsenius (1997).

Several large-scale vegetation studies are currently being conducted in the Yasuní National Park region: a 50-hectare permanent plot in mature-phase forest (preliminary data on a two-hectare subsample in Romoleroux et al., 1997); meso-scale patterns of tree species diversity on different substrates (J. F. Duivenvoorden & collaborators) and a large series of one-hectare forest sample plots (N. Pitman). A general overview of the flora and vegetation of the Yasuní Park region is found in Herrera-MacBryde and Neill (1997).

Cedrelinga cateniformis is a common canopy emergent tree throughout lowland Amazonian Ecuador on well-drained sites; *Ceiba pentandra* is a frequently observed emergent on richer alluvial soils. Common tree species of the forest canopy in the region include *Parkia multijuga, Hymenaea oblongifolia, Schizolobium parahyba, Dussia tesssmannii, Sterculia colombiana, Otoba parvifolia, Pseudolmedia laevis, Pouteria multiflora*, and *Erisma uncinatum*. Subcanopy palms, especially *Iriartea deltoidea* and *Oenocarpus bataua*, are abundant. Extensive areas of swamps are dominated by nearly monospecific stands of the palm *Mauritia flexuosa*. Black-water inundated areas in the Cuyabeno region and the lower Yasuní River are dominated by a distinctive suite of tree species including *Macrolobium acaciifolium, Astrocaryum jauari*, and *Coussapoa trinervia*. The "white sand" podzolic soil type that is characteristic of parts of the Guayana and Brazilian Shield areas does not occur in Amazonian Ecuador, as far as is known, so the distinctive, oligotrophic Amazonian "white sand" vegetation (Pires & Prance, 1985) and its component taxa are not recorded from Ecuador. Extensive deforestation of the lowland rain forest has taken place in both western and eastern Ecuador, especially during the past several decades. Rudel and Horowitz (1993) carried out a sociological study of forest clearing by small farmers in Amazonian Ecuador. Sierra (1996) described and quantified deforestation in the northwestern lowlands using remote sensing data.

Lower montane rain forest

In Harling's vegetation classification, lower montane rain forest occurs on the western and eastern Andean slopes between about 700 and 2,500 m elevation. Following common usage of the term "cloud forest" elsewhere in the Neotropics, this zone as well as the forest above 2,500 m elevation may appropriately be termed "cloud forest" along with the upper montane rain forest (see discussion in Webster, 1995). The climatic and physiognomic hallmarks of cloud forest are present in this vegetation type: nearly constant high atmospheric humidity, frequent fog- and mist-associated precipitation, and dense loads of vascular epiphytes as well as bryophytes on tree branches and trunks. On the summits of the Pacific coastal range in western Ecuador, physiognomically typical cloud forest vegetation occurs as low as 400 m (Parker & Carr, 1992).

In general, alpha diversity of tree species, as well as general height of the forest canopy, decreases with increasing elevation on both sides of the Andes. On the eastern slopes, 132 tree species (DBH≥10 cm) were recorded in a one-hectare plot at 1,200 m near the Sumaco volcano, and 45 species in a comparative sample at 2,000 m near Baeza (Valencia, 1996; Valencia et al., 1998). Density and diversity of vascular epiphytes in the lower montane rain forest zone are undoubtedly higher than in the lowland rain forest, but quantitative data are lacking.

Floristic studies of lower montane rain forest on the western Andean slopes have been carried out most thoroughly at the Maquipucuna forest reserve in Pichincha province (Webster & Rhode, in press). Common canopy tree species on the western slopes include *Ruagea glabra, R. pubescens, Dussia lehmannii, Meriania tomentosa, Cinchona pubescens, Roupala obovata*, and *Nectandra acutifolia*.

For the eastern Andean slopes, an overview of the flora and vegetation in the Sumaco volcano region of Napo province is described in Neill and Palacios (1997). Common canopy tree species in this vegetation type include the tall palm *Dictyocarym lamarckianum* as well as *Erythrina edulis, Clethra fagifolia, Hyeronima macrocarpa, Ruagea glabra, Dacryodes cupularis, Metteniusa tessmannii, Meriania hexamera*, and *Ocotea javitensis*.

Floristically distinct facies of lower montane rain forest occur on the non-volcanic substrates of the "third cordillera," east of the main Andean chain. These areas include the limestone massifs of the Cordillera de Galeras and Cordillera de Cutucú, and the mosaic of shale, limestone, and sandstone substrates of the Cordillera del Cóndor. All three ranges are, as yet, poorly known botanically, but each supports some endemic taxa. The Cordillera del Cóndor on the Ecuador-Peru border is probably the most diverse and probably has the most local endemics (Schulenberg & Awbrey, 1997); the Cordillera del Cóndor flora also includes several genera, including *Pterozonium, Stenopadus, Phainantha*, and *Bonnetia*, that are essentially disjunct from the "tepuis" of the Guyana Shield (Berry et al., 1995).

The moist woods on the volcanic slopes of the Galápagos Islands, for purposes of this review, are included in the lower montane rain forest vegetation type. The "*Scalesia* zone" and "*Miconia* zone" vegetation of the Galápagos (Wiggins & Porter, 1971; van der Werff, 1978) are certainly not "rain forests" like the lower slopes of the Andes, but the vegetation is equally influenced by fog-associated precipitation; the trees support mostly epiphytic bryophytes. The evolutionary radiation of the endemic tree genus *Scalesia* on different islands is one of the remarkable features of the flora of Galápagos.

It is ironic that *Cinchona pubescens*, a common tree of the western Andean slopes that was exploited in past centuries to the point of depletion in its native range for the extraction of quinine to treat malaria (Acosta-Solís, 1961), was introduced to the equivalent vegetation zone of the Galágapos and has become an aggressively invasive threat to the native Galápagos flora (MacDonald et al., 1988). Several papers on introduced plant species in Galápagos and their impact on the native vegetation are included in a volume edited by Lawesson et al. (1990).

Cloud forest

Harling also uses the term "upper montane rain forest" for this vegetation type, which is in agreement with the terminology for Neotropical montane forests suggested by Webster (1995). Upper montane rain forest occurs on the high Andean slopes from 2,500 m elevation to the upper limit of closed forest, which is variable but frequently at 3,400–3,600 m elevation. The Spanish term *ceja andina* ("eyebrows of the mountains") is often used for the "elfin forest" near the upper limit of forest. With increase in altitude, the height of the tree canopy becomes lower, the trees are more twisted and gnarled and tend to be multiple-stemmed, and alpha diversity of trees also decreases (Valencia et al., 1998).

Quantitative vegetation studies of high-altitude Andean forests were carried out in a series of four one-hectare plots at sites ranging from 2,700 to 3,300 m elevation: two sites in northern Ecuador (Valencia & Jørgensen, 1992) and two in southern Ecuador (Madsen & Øllgaard, 1994; the four plots compared in Jørgensen et al., 1995). Tree species richness was much higher in the two southern plots (75 and 90 species) than in the northern plots (32 and 39 species); the northern sites may have been subjected to more recent disturbance. Structural characteristics, including density, canopy height, and basal area, differed considerably among the four study sites.

Characterization of forest types above 2,800 m elevation was carried out at 140 sites throughout the Ecuadorian Andes, with multivariate analysis of tree species composition and frequency (Fehse et al., 1998). Four main forest types were recognized, with 8 subtypes: 1) Forests in the central and southern Andes of Ecuador between 2,800 and 3,200 m, dominated by: 1a) *Myrcianthes* in Loja province; 1b) *Myrsine*, *Ilex*, and *Weinmannia glabra*; 1c) *Clusia flaviflora*, *Weinmannia glabra*, and *Ruagea hirsuta*; 2) forests throughout the Ecuadorian Andes at 2,800–3,600 m elevation dominated by: 2a) *Weinmannia pinnata*, *Schefflera sodiroi*, and *Myrcianthes rhopaloides;* 2b) *Hedyosmum cumbalense*, *H. luteynii*, and *Oreopanax ecuadoriensis*; 3) forests at intermediate altitudes (3,200–3,700 m) dominated by *Hesperomeles ferruginea* and *Weinmannia fagaroides*; 4) high-altitude forests (3,600–4,300 m) dominated by: 4a) *Gynoxys acostae*, *Escallonia myrtilloides*, and *Buddleja*; 4b) forests dominated by *Polylepis*.

A description of the montane forests and páramos of the Sangay National Park region in the eastern cordillera is found in Mena et al. (1997); montane forests of the "Huancabamba region" in extreme southern Ecuador and northern Peru are described in Young and Reynel (1997).

Montane forests in many areas of the tropical Andes occur on very steep slopes that are geologically unstable, being subjected to frequent landslides caused by earthquakes and other natural disturbances. Stern (1996) described vegetation succession on earthquake-triggered landslide sites in the eastern Ecuadorian Andes.

North Ecuadorian grassland and quebrada vegetation

This vegetation type occurs in the densely populated inter-Andean valleys, where the original vegetation was almost entirely removed during past centuries and replaced by agricultural plots and pastures. Remnants of the original vegetation are now found only in steep ravines (*quebradas* in Spanish) and other agriculturally marginal sites. These remnants are composed mostly of shrubs and small trees, often spiny, such as *Barnadesia arborea*, *Mimosa quitensis*, *Hesperomeles obtusifolia*, and *Duranta triacantha*.

The landscapes of the inter-Andean valleys today are dominated visually by stands of *Eucalyptus globulus*, introduced from Australia in the 1860s, which line roadsides and field borders and are also grown in silvicultural plots for timber production. In some areas there are large stands of *Pinus radiata* and *Pinus patula*, introduced from California and Mexico, respectively, around the turn of the 20th century. A study of the ecologial impact of the pine plantations indicated that on moister sites, in the northern valleys, the planting of pines results in reduced soil organic matter and moisture, but in drier sites, in valleys of the central Ecuadorian Andes, where pines were planted on eroded soils, the plantations protect the sites from further degradation (Hofstede, 1997). Large areas of the inter-Andean valleys are dedicated to grazing by dairy cattle, and the introduced African grass *Pennisetum clandestinum*, among other introduced grasses, predominates in most of the pastures.

Historical information, including municipal records and traveler's descriptions, allows a partial reconstruction of the original vegetation of the inter-Andean valleys at the time of European contact during the 16th century, and the changes that have occurred since then (Hidalgo, 1998). For example, the upper Guayllabamba River basin south and southeast of Quito (present-day Machachi area and Valle de los Chillos) was covered with a tall, dense montane forest at least until the 18th century. The floristic composition of these forests is not known, but probably included such canopy tree species as *Cedrela montana*, *Juglans neotropica*, *Symplocos quitensis*, *Myrcianthes rhopaloides*, and *Inga insignis*, which are still found in the area as isolated trees. The protected forest of Pasochoa volcano, south of Quito, is one of few remnants of inter-Andean forests. The valley floor of the upper basin of the Mira river in Carchi province was densely forested well into the 20th century; a remnant forest patch near San Gabriel, dominated by *Myrcianthes rhopaloides*, is still standing.

The Patate River basin—the region of Latacunga and Ambato—was not forested at the time of European contact, according to the historical records of Hidalgo (1998), but rather was characterized by low, open scrub vegetation, due to frequent disturbance from mudslides resulting from eruptions of the Cotopaxi volcano.

South Ecuadorian shrub vegetation

This vegetation type, like the previous one, has been profoundly altered by human activities. This montane scrub occurs in the inter-Andean valleys of southern Ecuador between 2,000 and 3,000 m elevation. The climate is generally drier than in the northern valleys, and the soil, derived from Tertiary volcanic substrate rather than Quaternary volcanic ash as in the north, is more highly weathered, poorer in nutrients, and in many areas has been heavily eroded. The vegetation is characterized by a discontinuous cover of shrubs and small trees, generally with bare ground between the woody plants. Common species include *Oreocallis grandiflora*, *Lomatia hirsuta*, *Hypericum laricifolium*, *Bejaria aestuans*, and *Cantua quercifolia*. Some species that are endemic to this vegetation type, especially *Streptosolen jamesonii* and *Chionanthus pubescens*, are frequently cultivated in the cities of northern

Ecuador as ornamentals. Quantitative ecological studies of this vegetation type do not exist. It is not clear, from the information available, whether the original vegetation of the southern valleys and slopes was a closed-canopy forest as in the northern valleys, or if the open shrubby vegetation is in fact the "climatic climax" for these areas.

Dry scrub vegetation of southernmost Ecuador

This vegetation type is confined to the arid intermontane valley of the Chinchipe river, in southern Loja and Zamora-Chinchipe provinces. The vegetation is dominated by scattered low, thorny shrubs or small trees such as *Acacia macracantha, Anadenanthera colubrina, Cercidium praecox,* and *Prosopis juliflora*, as well as some columnar cacti and *Opuntia*.

Inter-Andean desert and semi-desert

This vegetation type occurs in the lower portions of most inter-Andean valleys, where precipitation is reduced due to the "rain shadow" effects of the surrounding high cordilleras. Annual rainfall in these deep, arid valleys is generally less than 300 mm (Figure 1). Among the valleys that have this type of vegetation are those of the Chota, Guayllabamba, Patate, Chanchán, and León rivers, and the Catamayo valley. In most sites, the vegetation is dominated by scattered low shrubs of *Acacia macracantha*. Other shrubs include *Croton wagneri, Dodonaea viscosa*, and *Caesalpinia spinosa*. The rosette-plant *Agave americana* is common on some slopes, as well as the introduced *Aloe vera*. Cacti are frequent on some sites, including *Opuntia soederstromiana, O. pubescens*, and *O. tunicata*. Species of epiphytic Bromeliaceae that are adapted to long periods of drought, including *Tillandsia recurvata* and *T. secunda*, occur frequently on the branches of the *Acacia macracantha* shrubs. On more humid sites, such as along watercourses, are small trees of *Salix humboldtiana* and *Schinus molle*.

Grass páramos

This vegetation type, which occurs throughout the Ecuadorian Andes from about 3,400 to over 4,000 m elevation, is dominated by bunch- or tussock-forming grasses, mostly species of *Calamagrostis* as well as *Festuca* and, in the drier páramos of southern Ecuador, *Stipa*. Taller tussocks of *Cortaderia* are frequent at the edges of páramo, where it borders with patches of forest or shrubs, and in disturbed areas such as along roadsides. In between the grass tussocks grow a diverse assemblage of herbaceous plants, some prostrate and some erect, including species of *Halenia, Gentiana, Gentianella, Ranunculus, Geranium, Castilleja, Lupinus,* and *Valeriana*. Scattered small shrubs such as *Chuquiraga jussieui, Baccharis caespitosa*, and *Lupinus pubescens* also occur amid the bunch-grasses.

The giant stem-rosette plant *Espeletia pycnophylla* forms extensive populations covering thousands of hectares that dominate the bunchgrass páramos of Carchi province in northern Ecuador near the Colombian border, on both the western and eastern cordilleras. Very small disjunct populations of *Espeletia pycnophylla*, not more than 5 hectares in extent, occur 200 km to the south, in the Llanganates region of the Eastern Cordillera. Rosette plants of the genus *Puya* are more widespread throughout the bunchgrass páramos, especially on moister sites. The vegetation of the Chiles volcano, on the Ecuador-Colombia border, and nearby volcanoes in southern Colombia, is described by Rangel and Garzón (1997).

In very wet areas of the Eastern Cordillera, instead of *Calamagrostis* bunchgrass páramos are dense thickets of the erect dwarf bamboo *Neurolepis aristata*. Such thickets most notably cover extensive areas in the Llanganates region.

Most grass páramo areas are burned annually, or at least every few years, by fires set deliberately by the local inhabitants in order to maintain pasture for beef cattle and sheep. All of the páramo plant taxa, therefore, possess adaptations that enable them to survive the frequent fires (Lægaard, 1992); such adaptations include the ability to resprout from fleshy roots or rhizomes, seeds that germinate after fires, and in the case of rosette plants, protection of the apical bud. As Lægaard (1992) pointed out, these adaptations must have evolved long before anthropogenic fires began to have an impact on páramos, within the past 10,000 years or so. The morphological and physiological characteristics that enable páramo plants to survive frequent fires probably evolved as adaptations to other factors such as drought and diurnal temperature fluctuations.

In many areas, the grass páramo is interspersed with copses of small trees up to 4,100 m elevation. These fragments of upper montane forest are composed mostly of *Polylepis* and also include a few other tree taxa such as *Oreopanax, Buddleja, Clethra, Baccharis,* and *Gynoxys*. These copses occur generally on microsites that appear to be protected from fires, such as on scree and boulder slopes and in small hollows. The occurrence of tree patches does not appear to be related to any differences in soil structure or topography from the areas of grass páramo (Lægaard, 1992).

The ecological dynamics of the lower altitudinal limit of grass páramo and the upper limit of montane forest is a matter of great interest that has not been entirely resolved as yet. Most authors agree that the grass páramo is highly influenced by human activities, particularly by the frequent human-caused fires. Lægaard (1992) argued that since copses of trees occur up to about 4,100 m elevation, the "true timberline," i.e., the physiological upper limit of continuous tree cover, is at that elevation, and virtually all of the grass páramo below about 4,100 m is a fire-induced disclimax. If fires were suppressed, woody vegetation would invade the grass páramo and replace it with a continuous upper montane woodland of *Polylepis* and other small trees. This hypothesis appears reasonable but has not yet been put to a rigorous experimental test in Ecuador. Circumstantial evidence for a lower natural limit of grass páramo may be found in Løjtnant and Molau (1982) who surveyed a "virgin" páramo on the isolated summit of Sumaco volcano. This remote site has never been subjected to human intervention—

burning or grazing. The páramo community on Sumaco extends from the upper limit of elfin forest at 3,300 m, to the summit above 3,700 m. The flora of the Sumaco páramo is depauperate, dominated by *Cortaderia nitida* and *Blechnum loxense*. Although this site has not been subjected to human-caused disturbance, lightning-induced fires may affect its vegetation dynamics.

Shrub and cushion páramos

Shrub and cushion páramos occur at elevations above the grass páramo, generally at 4,000–4,500 m. Bunch-grasses begin to decrease in density at about 4,000 m and are replaced by cushion plants, acaulescent rosette plants, and low shrubs. These sites are mostly on the slopes of the Quaternary strato-volcanoes of northern and central Ecuador. The vegetation cover is generally not continuous; bare sandy soil is exposed between the individual plants.

The cushion plant life-form is a very notable feature of this vegetation type. Cushion plants have very small sclerophyllous leaves, and are densely branching with short internodes, so that a dense, pillow-like mound is formed. The cushion plant form is evidently an adaptation to the nightly frosts; the surface of cushion plants is less exposed to temperature extremes than adjacent bare soil (Hedberg, 1992). A number of genera form cushion plants; among the most common taxa in the Ecuadorian Andes are *Azorella aretioides, A. corymbosa, A. pedunculata, Plantago rigida, Draba aretioides, Distichia muscoides,* and *Xenophyllum humile.*

Scattered small shrubs of a number of taxa including *Chuquiraga jussieui, Pernettya prostrata, Baccharis latifolia,* and *Gynoxys buxifolia* occur in this type of páramo, and also rosette plants including *Lupinus alopecuroides* and *L. nubigenus*.

Desert páramos

This type of páramo is found at the highest elevations of vascular plant growth on the slopes of the major volcanoes, from about 4,500 to 4,900 m, nearly up to the lower limit of glacial ice. Plant growth at this elevation is probably not limited so much by arid conditions, as the name of the vegetation type implies, but rather by the nightly freezing temperatures. Plant cover is sparse, and most plants have rather deep tap roots that anchor them in the loose sandy soil. High winds frequently blow the soil about. Most plants are prostrate or nearly so, and are either herbaceous or woody at base. Some cushion-forming species are present. Characteristic species include *Nototriche phyllanthos, Astragalus geminiflorus, Azorella pedunculata, Culcitium nivale, Calandrinia acaulis, Ephedra americana,* and *Xenophyllum rigidum.*

The glaciers of the Andean volcanoes have been steadily retreating during the 20th century, leaving newly exposed areas available for colonization by plants (Clapperton, 1993). A study of primary succession was carried out on Cotopaxi volcano by Stern and Guerrero (1997), which included an area newly exposed by glacial retreat at 4,600–4,800 m, and a lava flow at 4,100 m.

Seasonally inundated areas

This vegetation type, as mapped by Harling, occurs in the lower portion of the Guayas River basin. This low-lying region, mostly between Babahoyo and Guayaquil, is subject to flooding during the rainy season. Historical records (Hidalgo, 1998) indicate that the original vegetation of this region was a seasonally inundated savanna, dominated by tall grasses, with deciduous forest on the scattered non-inundated hills. Most of the region has now been partially drained and is dedicated to cultivation of rice and sugar cane.

History of collecting

By Peter M. Jørgensen

The following overview of the history of collecting in Ecuador, while not exhaustive, does highlight the most important collectors and collecting expeditions. It also provides some data that are not readily accessible. The sources for this account are Diels (1937), Acosta-Solís (1969b), Holm-Nielsen (1986a), Molau (1986), Wiggins and Porter (1971), Jørgensen et al. (1992), and Renner (1993), as well as several biographies and general references (Stafleu & Cowan, 1976–1988; Stafleu & Mennega, 1992–1997; and Barnhart, 1965). The author's observations from personal knowledge are also included. Herbarium acronyms follow Holmgren et al. (1990).

The 18th century—The first botanist to collect plants in Ecuador for scientific purposes was **Joseph de Jussieu** (1704–1779), from France, a participant in the French Geodesic expedition to Ecuador from 1735 to 1743 (Zúñiga, 1977). The primary objective of the expedition was to measure the length of a degree close to the equator. The length of a degree would be constant if the earth was a perfect sphere, so a similar expedition was simultaneously making measurements in Lapland, Sweden, for comparison. This seems a trivial question today, but it was very important to cartography and navigation in the 18th century. Jussieu's first collections were made in Panama, and he continued collecting in Ecuador for the duration of the eight-year expedition. After the successful completion of the expedition, he continued to collect in Peru and Bolivia and remained in South America until 1771. However, Jussieu went insane while working in Ecuador (von Hagen, 1945). A shortage of money kept him from returning to Paris at the end of the expedition; later, his medical abilities may have kept him in Quito where his services were needed during a smallpox outbreak (Steele, 1964). Linné (see Steele, 1964) wrote, "Those who have been with him say that he has done almost nothing [of a botanical nature], he has only practiced [medicine]." A contributing factor to Jussieu's insanity may be found in the fact that he lost most of the documentation for his work; he had entrusted a trunk full of notebooks and dried plant specimens to a servant who ran away with the "treasure" across the border to Brazil. A minor portion of his collections survived and