

## Altitudinal zonation of montane *Quercus* forests along two transects in Chirripó National Park, Costa Rica

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### Abstract

Abiotic and vegetation data were collected along two altitudinal transects through mature montane *Quercus* forests on the Pacific and Atlantic slopes of Costa Rica's Chirripó Massif. Between 2000 and 3200 m asl twenty-four 0.05 ha forest plots were selected at altitudinal intervals of 100 m, and eight soil profiles were described at intervals of 200 m. A TWINSPLAN classification aided in the determination of eight zonal forest communities on the basis of their floristic composition. They are grouped in two sets of four: (i) the palm-rich lauraceous-fagaceous Lower Montane *Mollinedia-Quercus* Forests (2000–2600 m asl) and (ii) the bamboo-rich myrsinaceous-fagaceous Upper Montane *Schefflera-Quercus* Forests (2500–3200 m asl), respectively. Vegetation changes seem correlated with two major climatic gradients: (i) a temperature gradient (altitude), and (ii) a moisture gradient (wet Atlantic vs. moist Pacific slope). Most soils are Andepts, and residual, colluvial or derived from volcanic material. Humus layers are thicker on the wetter Atlantic slope. A total of 431 vascular plant species consisted of 86 pteridophytes, 1 gymnosperm, 296 dicots and 48 monocots. Species richness, canopy height and stem diameter decrease with increasing altitude, while the canopy surface becomes more flattened. A comparison with other studies shows that Chirripó's montane *Quercus* forests fit within the environmental ranges known from altitudinal zonations elsewhere in the Tropics.

**Abbreviations:** asl – above sea level; dbh – diameter at breast height; LM – Lower Montane; Mt. – Mountain; TWINSPLAN – two way indicator species analysis; UM – Upper Montane; VU – code referring to soil profiles as presented in Van Uffelen (1991).

This paper is dedicated to the memory of Alwyn H. Gentry, an outstanding and inspiring tropical botanist who tragically died in a plane crash in the mountains of Ecuador on August 3 1993, when surveying possible boundaries for a new tropical cloud forest reserve.

### Introduction

During the last fifty years the Chirripó massif in the Costa Rican Cordillera de Talamanca has received increasing attention from scientists (Weber 1958; Kohkemper 1968; Gómez 1986; Boza 1988; Bravo *et al.* 1991). Most authors focussed on specific aspects of

the páramo environment above the upper forest line at ca. 3200 m asl. They carried out diverse studies in such disciplines as geology (Weyl 1980; Calvo 1987), geomorphology (Hastenrath 1973; Bergoing 1977; Barquero & Ellenberg 1986), botany (Süssenguth 1942; Weber 1958; Chaverri *et al.* 1976; Weston 1981; Horn 1989a, 1989b, 1990; Cleef & Chaverri 1992) and

zoology (Stiles 1972; Bravo *et al.* 1991). It was not until recently that researchers, mostly botanical (e.g., Gómez 1986; Kappelle 1991; Richter 1991), took an interest in Talamancan montane forests at altitudes between 2000 and 3200 m asl. However, none of the studies currently available focused on the relationship between climate, geology, soils and vegetation in the montane forest belt. Therefore, an integrated study was carried out, aiming at a better understanding of altitudinal zonation of montane *Quercus* L. forests along the Pacific and Atlantic slopes and of their relation with specific abiotic properties.

## Study area

### *Topography and administrative status*

The 50,150 ha Chirripó National Park was created in 1975 and is located in the central region of the Costa Rican Cordillera de Talamanca (Boza 1988; Bravo *et al.* 1991). It covers parts of San José, Cartago and Limón Provinces, and belongs to the core area of the 612,570 ha binational Amistad Biosphere Reserve (MAB 1990; RBA 1991), which has partially been declared a World Heritage Site (Whitmore 1990; Vernes 1992). The centre of the park is dominated by the 3819 m high Cerro Chirripó, the highest mountain in southern Central America (c. 9° 30' N and 83° 30' W). Small glacial lakes at the foot of Cerro Chirripó's summit form the sources of the main drainages in the park: the Río Chirripó Pacífico, which shapes the Pacific watershed, and the Río Chirripó Duchí, which dominates the Atlantic watershed (Fig. 1).

### *Climate*

Although no continuous climatic record exists for Chirripó National Park, the Costa Rican Electricity Institute (ICE, pers. comm.) estimated on the basis of incidental measurements an average annual rainfall of 2300 mm for the southcentral (Pacific) páramo area in the park (ca. 3600 m asl; 0.5 km SW of Pico Los Crestones along the Río Talari). Richter (1991) presented rainfall data for the same páramo area (3350 m asl) and recorded an average annual precipitation level of 1898 mm. Unfortunately precipitation data for his *Weinmannia* L. *Quercus*-Lauraceae forest site at 2950 m asl were not available. In a UM oakforest at the nearby town of Villa Mills (3000 m), at 25 km WNW of Cerro Chirripó, the average annual tempera-

ture is about 10.9 °C (IMN 1988) with January being the coldest month, while the average annual rainfall is 2812 mm (IMN 1988; Fig. 2). Hall (1985) and Herrera (1986) suppose that average annual precipitation at certain places along Talamanca's Atlantic slopes may reach much higher levels (4000 to 6000 mm), but serious data confirming this assumption are not available. The dry season lasts from December to April, being more pronounced on the Pacific slope. This is explained by the presence of strong tradewinds, which come in from the Caribbean and influence the rainfall regime especially on the Atlantic slope (Coen 1983; Kappelle 1992). However, most precipitation in the Cordillera de Talamanca is of local orographic origin and results from the diurnal formation of condensation belts above ca. 2000 m asl.

### *Geology, geomorphology and soils*

According to different authors (Weyl 1957, 1980; Ballman 1976; Castillo 1984; Calvo 1987; Seyfried *et al.* 1987) the Cordillera de Talamanca is built up of Tertiary (Cretaceous) sediments with a thickness of probably several km, with intercalated volcanic and Upper Miocene plutonic rocks. During the Middle Oligocene and Middle Miocene the region's initial uplift took place (Weyl 1956a), resulting in the gradual transformation of the Meso American Island Arc into the present-day's continental landbridge (Seyfried *et al.* 1987), thus presenting the opportunity for a great biotic interchange between North and South America (Rich & Rich 1983; Stehli & Webb 1985; Kappelle *et al.* 1992). The geomorphology of the Cordillera de Talamanca is dominated by the contrast between steep, deeply fluvially dissected valleys and extensive remains of flattish Pliocene forms at rugged crests. Pleistocene glaciation influenced the Cordillera de Talamanca and glacial erosion shaped the highest regions around Cerro Chirripó (Weyl 1955, 1956a, 1956b; Hastenrath 1973; Bergoeing 1977). Postglacial vegetation at Cerro Chirripó suffered most from fire during the Late Holocene (Horn 1993).

Vásquez (1983) recognized two main soil types in the Cordillera de Talamanca: (i) soils developed from volcanic ash deposits situated on slopes of 30 to 80% on the peaks of the mountain range, which are dark, deep and rich in organic matter, medium-textured, moderately fertile, and excessively drained (mainly Andepts); and (ii): residual soils situated on slopes of 40 to 80%, which have an excessive external drainage, are deep to very shallow, reddish, heavily

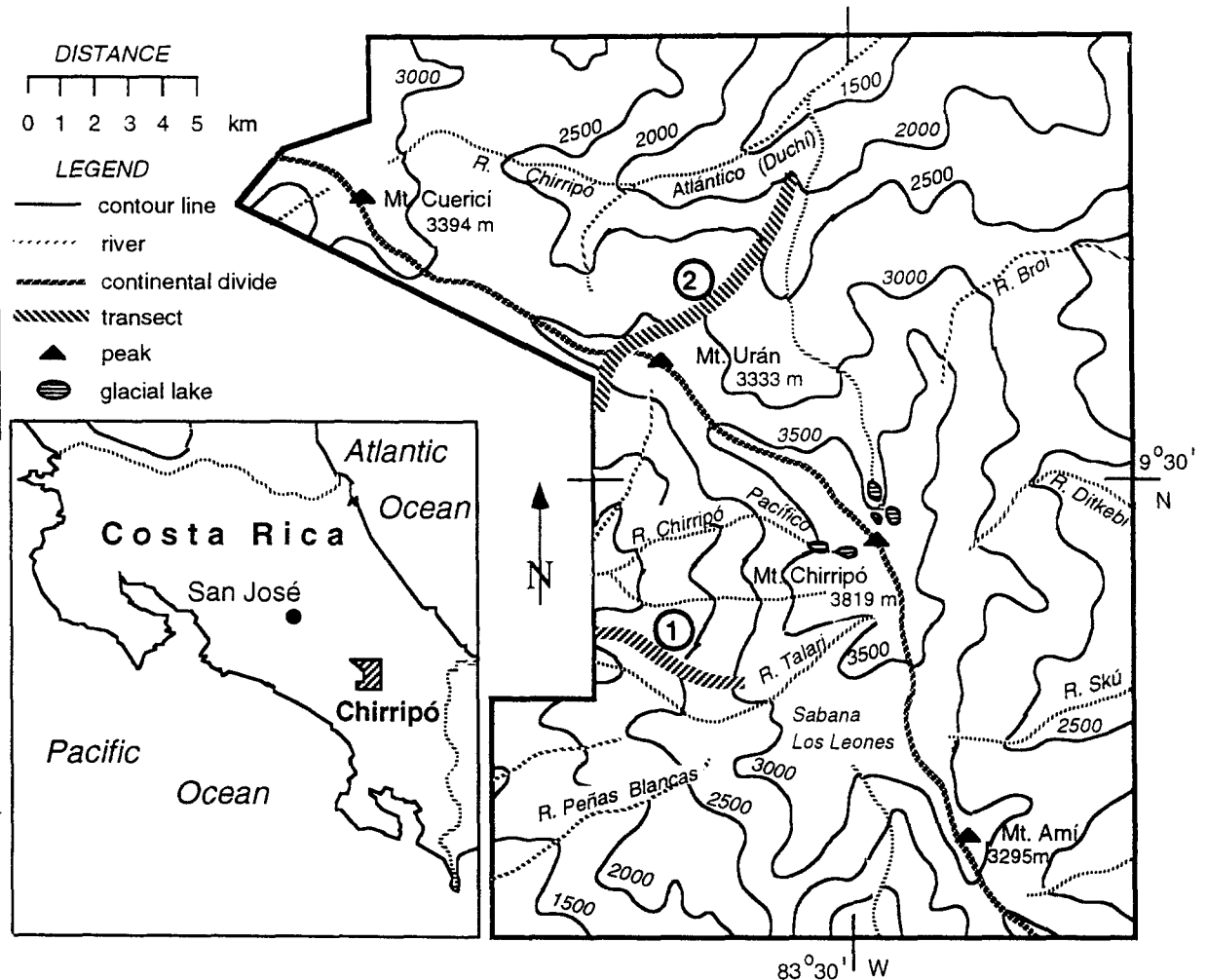


Fig. 1. Physiographic map of Chirripó National Park, Costa Rica. The two altitudinal transects are indicated: (1) The Pacific 'Fila Cementerio de la Máquina' Transect, and (2) the Pacific-Atlantic 'Fila Palmito Morado - Fila Camino de los Indios' Transect. The location of Chirripó park in Costa Rica is given (inset map).

textured and with a low fertility (mainly Tropepts). A more detailed soil study was previously carried out in the montane zone of the 3491 m high Cerro de la Muerte (Buena Vista Massif), which is located at about 30 km WNW of the Cerro Chirripó (Otárola and Alvarado 1976). These authors found Lithic Tropolists at higher elevations, Tropohumods and Dystrandepts at intermediate elevations, and Dystrandepts at lower elevations. Below, detailed descriptions of the soil types found in the present study are given.

For the present study forest plots were located on steep to moderately steep slopes and rugged crests in steeply fluvially dissected terrain, predominantly representing forms of denudational origin. This area shows a dendritic drainage pattern, although river beds

are structurally controlled by faults at some places. Rock types encountered along the slopes are mainly intrusive igneous rocks (granites, diorites and granodiorites). Aerial photo-interpretation learned that landslides are particularly common on the Atlantic slope in the upstream area of the Río Chirripó Duchí. This probably explains the local presence of fine-grained sedimentary rock or fine-grained metamorphic rock of sedimentary origin, which have a low resistance to mass movements.

#### Vegetation zonation

Holdridge *et al.* (1971) described the main ecosystems ('life zones') in Costa Rica on the basis of his climate-

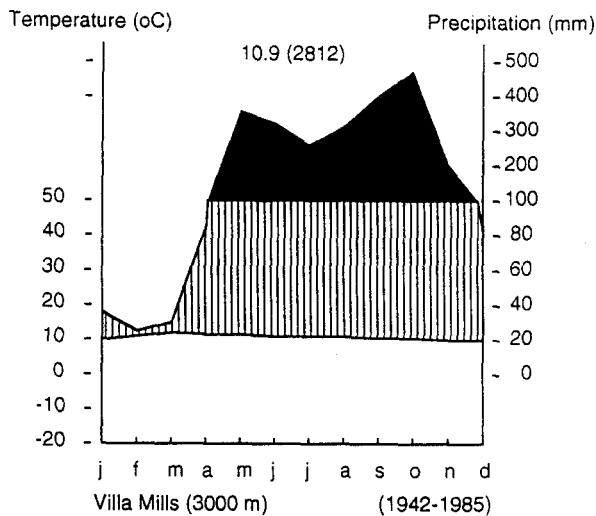


Fig. 2. Walter climate diagram at 3000 m asl in an Upper Montane *Quercus* forest near Villa Mills, Cordillera de Talamanca, Costa Rica.

based Life Zone System (Holdridge 1967). The ecological map of Costa Rica shows that three Holdridge Life Zones occur above 2000 m asl in Chirripó National Park (Tosi 1969): (1) (Sub)alpine Rain Páramo, (2) Montane Rain Forest and (3) Lower Montane Rain Forest. Applying the vegetation-based altitudinal zonation scheme proposed by Grubb (1974, 1977) to the higher parts of the Chirripó Massif, a fourth zone is to be distinguished between (1) and (2): the Subalpine Rain Forest.

In a preliminary study of Chirripó's vegetation zonation, the first author described this characteristic dwarf forest zone, which thrives just below the upper forest line (Kappelle 1991). In that paper the following altitudinal belts were briefly distinguished, described and mapped at a scale of ca. 1 : 200,000: (i) a bamboo páramo belt (3819–3300 m asl; covering 7,250 ha inside the park), (ii) an ericaceous subalpine forest belt (3400–3100 m asl; covering 3,750 ha), (iii) a myrsinaceous-fagaceous UM forest belt (3200–2400 m asl; covering 24,750 ha) and (iv) a lauraceous-fagaceous LM forest belt (2400–1500 m asl; covering 14,250 ha). This paper deals with belts (iii) and (iv), i.e., with montane *Quercus* forest zones as found in the whole UM range (2500–3200 m) as well as in the upper part of the LM belt (2000–2600 m) in Chirripó National Park (Amistad Biosphere Reserve).

### Human impact

In areas adjacent to the park large tracts of montane *Quercus* forests have been cleared for timber production and agriculture, especially during the period 1950–1975 (Schubel 1980; Meza & Bonilla 1990; Kappelle 1993). Extensive pasturelands have replaced the once luxurious vegetation. These forest conversions have resulted in a dramatic increase in landslides. Soil compaction in pasturelands with large numbers of dairy cattle is evident. In general, soil and water resources have been severely depleted, leading to irreversible land degradation (Hartshorn 1982; Ramírez & Maldonado 1988; Sader & Joyce 1988; Gracia 1990). Furthermore, uncontrolled forest fires in and outside the park are repeatedly started by humans. A major fire occurred in 1976, when a large part of the UM Forest, Subalpine Forest and Páramo belts along the 'Fila Cementerio de la Máquina' were burned (Chaverri *et al.* 1976; Horn 1990). Considering these diverse threats, the importance of preservation of still undisturbed mature oak forests thriving within the borders of the park is without doubt (Bravo *et al.* 1991).

### Methods

#### *Transect location and plot selection*

Pre-fieldwork consisted of a preliminary interpretation of aerial photographs (CRIRC; scale 1 : 80,000; April 1984), covering the entire Chirripó National Park, and the subsequent determination of the main physiographic units following Zonneveld (1979), Van Zuidam (1985) and Toubert *et al.* (1989). For that purpose, the topographic map sheets 'Cuericí', 'Dúrika', 'Matama' and 'San Isidro' on a scale 1 : 50,000 were consulted (IGN 1968–1982). In this way a preliminary reconnaissance soil map of the park was derived (Van Uffelen 1991).

On the basis of aerial photo-interpretation and a reconnaissance survey in the area, two SW-NE oriented altitudinal transects were established through the park, following the IUBS (TME)-UNESCO (MAB) manual of mountain transect studies (Van der Hammen *et al.* 1989) and the TROPENBOS guidelines for inventory and evaluation of tropical forests (Toubert *et al.* 1989). Transect 1 ascended the Pacific slope between 2000 and 3000 m asl and followed the trail to Cerro Chirripó along the 'Fila Cementerio de la Máquina' ridge (Fig. 1). Transect 2 ranged from

2900 m on the Pacific slope ('Fila Palmito Morado') up to the 3250 m high continental divide ('Paso de los Indios') just 1 km NW of Cerro Urán (3333 m), and then down to 2000 m on the Atlantic slope, following the 'Fila Camino de los Indios' trail northeastward in the direction of the Cabécar indigenous settlement of Sitio Hilda, just outside the park (Kohkemper 1968; Kappelle 1991). Each transect consisted of a series of 0.05 ha plots (20 × 25 m) laid out in mature *Quercus* forests at altitudinal intervals of ca. 100 m. Plots were established so that the longer axis ran parallel to the contour.

#### *Climate analysis*

Mesoclimatic daily courses of air temperature (°C) and relative humidity (%) were measured at 1.3 m above the forest floor under a closed canopy in a LM forest site (plot 52 at 2000 m asl) and an UM forest site (plot 54 at 2700 m asl) along Transect 1. Measurements were conducted during the dry season ('verano') and wet (or rainy) season ('invierno') of 1989 and 1990, using a monthly Lambrecht thermohygrograph. Weekly climate diagrams showed daily and seasonal differences in air temperature and relative humidity for both altitudes. Averages of hourly recordings (seven days) were plotted in diurnal thermohygrograms following Ellenberg (1975, 1979). Results were compared with data available from Peru/Ecuador (Ellenberg 1979), Colombia (Van der Hammen 1984; Witte, in press; Wolf 1993a, 1993b), Venezuela (Walter 1985) and Borneo (Kitayama 1992).

#### *Geological, geomorphological and soil analyses*

Geological and geomorphological observations were made along both transects. Rock outcrops were examined and samples were taken for a macroscopic classification. A reference collection was stored at OVSI-CORI (Costa Rican Universidad Nacional at Heredia). Following Sevink (1984) soil pits were dug at regular altitudinal intervals of ca. 200 m, under a closed oak forest canopy, and profiles described in accordance with FAO (1977), Klinka *et al.* (1981) and Van der Hammen *et al.* (1989). In each pit soil temperatures were measured at intervals of 10 cm depth (Van der Hammen *et al.* 1989), using a digital Consort T 550 device with a resolution of 0.1 °C. The relationship between soil temperature and altitude was assessed using linear regression analysis. Effective soil depth classes distinguished were: very shallow (< 25 cm),

shallow (25–50 cm), moderately deep (50–100 cm) and deep (> 100 cm), (Soil Survey Staff 1975). Soil colors (moist; hue 10 YR) follow the Munsell Soil Color Charts (1954).

One sample of soil material was taken from each horizon for physical and chemical analyses (Guadalupe Laboratory, Costa Rican Ministry of Agriculture). Soil texture was determined using a hydrometer after the modified method by Bouyoucos (1950). Clay was determined with the hydrometer method after treatment with H<sub>2</sub>O<sub>2</sub> and dispersion with NaOH at pH 10.0. Organic carbon was measured using the Walkley-Black wet combustion method (Van Reeuwijk 1987). Incomplete recovery was compensated for with a multiplication factor of 1.3. The percentage of organic matter is obtained by multiplying the percentage of organic carbon by a factor 1.72. Soil pH (H<sub>2</sub>O) was measured on a solution of fresh soils in deionized water with a soil-to-water weight ratio of 1 : 2.5 (Kitayama 1992). Cation exchange capacity (CEC) was determined by measuring the absorbed Na after saturating with 1 M NaAc at pH 7.0 and leaching with 1 M NH<sub>4</sub>Ac at pH 7.0 (Van Reeuwijk 1987). Exchangeable bases (Ca, Mg, K and Na in m-equiv.·100g<sup>-1</sup>) were determined in the leachate of the soil treated with 1 M NH<sub>4</sub>Ac at pH 7.0. The total of the bases (total CEC) was calculated as the sum of Ca, Mg, K and Na. The Ca/Mg ratio was estimated. Base saturation was determined as the quotient of exchangeable bases and CEC. Phosphorus (ppm) was determined in a modified Olsen extract (Hunter 1974). Dry bulk densities (g·cm<sup>-3</sup>) were determined after drying of soil material at 105 °C for 24 h. On the basis of specific physical and chemical characteristics of each soil horizon, soils were classified using the taxonomic nomenclatures proposed by the FAO (1988) and the U.S. Department of Agriculture (Soil Survey Staff 1975). Soils were classified as andosols whenever they met the requirements for soils with andic properties as given in ICOMAND (1987).

#### *Flora and vegetation analyses*

Over 3000 botanical collections were made, covering the terrestrial vascular flora found in 24 forest plots. In addition, epiphytic vascular plants were collected up to 2.5 m above the forest floor. Plant material was identified using the taxonomic nomenclature by Standley (1937–1938), Woodson & Schery (1943–1980) and Burger (1971–1990) for phanerogams, and Tryon & Tryon (1982) and Lellinger (1989) for pteridophytes. Fertile voucher specimens were stored in herbaria in

Costa Rica (CR), the Netherlands (ASD, U) and the USA (F, MO, NY, US). Epiphytic and epilithic lichens were collected, identified and stored in Costa Rica (CR) and Germany (B) and have been dealt with elsewhere (Kappelle & Sipman 1992). Studies on the bryoflora are in preparation and will be published in the near future.

The growth form of each species was recorded and the aerial crown or shoot cover projection estimated (Braun-Blanquet 1965; Westhof & Van der Maarel 1973). In addition, the average height and cover of the canopy and subcanopy tree, shrub, herb and bryophyte layers were estimated, following Cleef *et al.* (1984). The average height of the tree canopy was estimated using a clinometer. Forest structure data were collected on 0.015 ha subplots (10 × 15 m), in which stems ≥ 10 cm dbh were identified, recorded and mapped (cf. Gentry 1988). Schematic vegetation profile diagrams were drawn for transect areas of 5 × 50 m.

Regression analysis was used to study the relationship between the number of terrestrial vascular plant species per 0.05 ha plot and altitude. In addition, for each plot the Shannon-Wiener diversity index was calculated as follows (Magurran 1988):

Shannon-Wiener's index:

$$H' = -\sum(p_i) \cdot (\log_2 p_i), \quad (1)$$

where  $p_i$  is the proportional cover of the  $i^{\text{th}}$  species in a plot. Significant differences between the outcomes of  $H'$  for each community were searched for, using nonparametric statistics.

A polythetic divisive classification was undertaken with TWINSPAN (Hill 1979) on the data matrix (presence/absence and species-cover data) comprising 24 plots and containing 431 species, each of which occurred in at least two plots (Jongman *et al.* 1987; Kent & Coker 1992). In this way *Quercus* forest communities were distinguished and subsequently described, following the phytosociological procedures developed by Braun-Blanquet (1965) and modified by Westhof & Van der Maarel (1973) and Mueller-Dombois & Ellenberg (1974). Floristic characterization of forest communities was done on the basis of ecological species groups recognized by TWINSPAN. In addition, tree stem density and relative abundance of tree stems were calculated for each plot. Characterizations of soils and vegetation were integrated into geoecological descriptions of montane *Quercus* forest communities. Finally Chirripó's altitudinal oak forest zonation was compared to zonations known from other tropical mountain regions.

## Results

### Climate

Figure 3 shows the daily courses of the air temperature and relative humidity during one week in the dry vs. one week in the wet season for the interior of a LM forest at 2000 m asl (plot 52) and an UM forest at 2700 m asl (plot 54). Data were based on hourly readings, because actual curves generated by the thermohygrographs were even more erratic (J.H.D. Wolf, pers. comm.). Differences between LM and UM as well as between dry and wet seasons are evident. One immediately notes lower relative humidity and higher temperatures at noon, at both altitudes during the dry season in comparison to the wet season. As was expected, temperatures were higher during the dry season in the forest interior of LM (23.2 °C). The lower temperature values occurred in UM forest (10.8 °C), where no significant difference between both seasons was observed. The greatest daily temperature fluctuations were found during the dry season in the forest interior of UM (12.8–19.6 °C). Relative humidity values oscillated greatly during the dry seasons and appeared more stable during the wet seasons. Again, the greatest daily fluctuations were recorded in the forest interior of UM (29 to > 95%). The relative humidity reaches values > 85% during almost every (recorded) day of any season at both altitudes. This is of vital importance to epiphytic bryophytes, which cover the tree trunks and branches of tropical montane 'cloud' forests (Walter 1985; Wolf 1993a), such as these found on the slopes of Cerro Chirripó.

Diurnal climatic trends based on the averages of hourly recordings (seven days) are plotted in Ellenberg's diagrams (Fig. 4). The diurnal climatic rhythm becomes less pronounced in UM forest. This is a well-known phenomenon in tropical montane forests (Walter 1985), recently confirmed by Wolf (1993b) for Andean forests in Colombia. Summarizing, the diurnal climatic course in the LM forest at 2000 m asl is as follows: during the morning and early afternoon the temperature first rises (ca. 6 to 15 h), then drops (15 to 21 h) and finally stabilizes during the night, before the temperature starts to go up again the next morning at sunrise. Simultaneously, the relative humidity drops slowly, having a major dip on mid-afternoon, when temperatures are highest. Then, at ca. 15 to 18 hr air humidity levels rise again, being highest just after midnight. In general, this increase begins around noon by cloud formation in ascending air masses, which cause

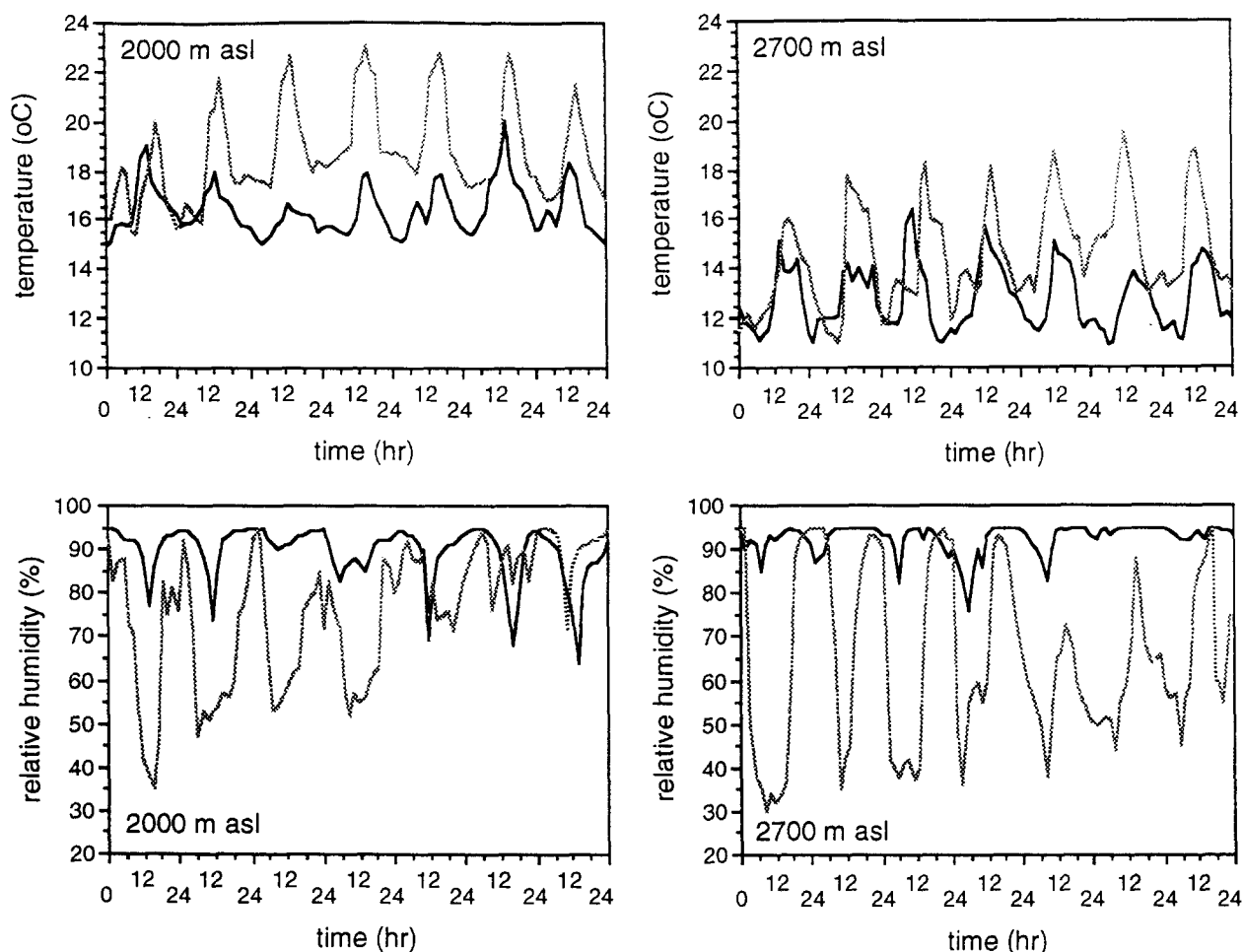


Fig. 3. Daily course of air temperature and relative humidity measured at 1.3 m above the forest floor under closed canopies in two Costa Rican Pacific Montane Forests: Lower Montane Forest at 2000 m asl (plot 52) and Upper Montane Forest at 2700 m asl (plot 54). Data based on hourly readings are presented for one week during the dry season (dotted lines) vs. one week during the wet season (continuous lines). Periods of measurements are: Lower Montane (dry season: March 7–13, 1990; wet season: June 7–13, 1990); Upper Montane (dry season: February 18–24, 1989; wet season: September 18–24, 1989).

mists and drizzle to penetrate the forest interior. This pattern is most clear in the dry season. In UM forest at 2700 m asl the diurnal climate oscillation is rather similar, although the relative humidity may plummet very fast during late morning hours in the dry season when sun radiation is strong and light-intense sunflecks move over the forest floor.

Average temperature values for one week of data recording are for the LM forest at 2000 m asl 18.7 °C during the dry season and 16.4 °C during the wet season, and for the UM forest at 2700 m asl 14.5 °C during the dry season and 12.7 °C during the wet season. Thus, the average air temperature drops ca. 4.0 °C with an altitudinal increase of 700 m (3.7 °C

for wet season and 4.2 °C for dry season data). This means a drop of 0.57 °C per 100 m increase in altitude, a figure which exactly coincides with the value for a Venezuelan montane forest presented by Walter (1985, p. 60). Similar mean temperature drops can be derived from subsoil temperatures (see below).

#### *Geology, geomorphology and soils*

In general, soils along Transect 1 are principally composed of residual and/or colluvial material derived from intrusive igneous rocks, whereas soils along Transect 2 are mainly derived from volcanic rocks (vulcanites: lavas). In addition, along Transect 2 some sed-

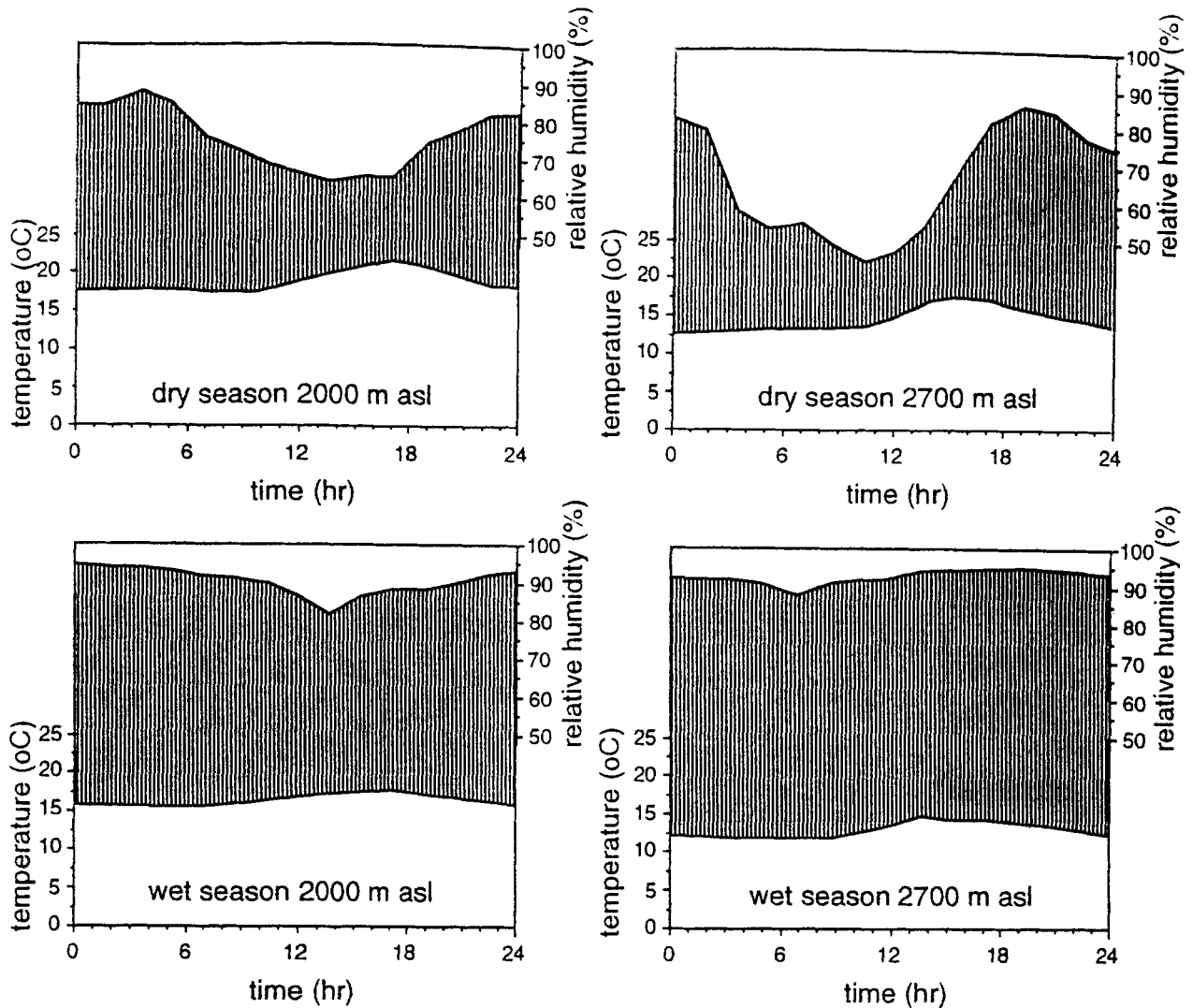


Fig. 4. Diurnal climate diagrams for Chirripó's Lower and Upper Montane Forest following Ellenberg (1975 and 1979). The relative amount of humidity is presented as a hatched area. Data are based on averages of hourly thermohygrograph readings recorded for seven days during the dry and wet season. Original data are given in Fig. 3.

imentary rocks, such as very fine sandstones with a calcareous cement, are locally prominent. At gently-sloping, imperfectly-drained positions on the Atlantic side a thin iron pan has been formed in unconsolidated soil material derived from volcanic rocks (Typic Placidand and Placic Humitropept). Organic matter accumulation is higher on the Atlantic side than on the Pacific (see below). Otherwise, soils are relatively uniform and andic properties are well-developed at most places (Typic, Alic, and Acric Hapludand). Admixture of volcanic ash in these soils is apparent. The influence of parent material as a soil-forming factor is weak from a pedogenetic point of view. Relatively

young soils formed over basic rocks have a relatively high pH ( $H_2O$ ) value of 5.6 to 6.5 in the A-horizon. Soils formed over acid rocks have a low pH ( $H_2O$ ) value ranging from 4.0 to 5.0 throughout the soil depth. In general, soils are extremely acid to strongly acid on both slopes. Base saturation is consistently less than ca. 15%, for soils formed over both basic and acid rock types.

Table 1 presents some physical and chemical properties of the upper soil profile in eight forest plots. No clear differences between LM and UM top soils are observed. Atlantic soils, however, appear to be slightly more clayey than Pacific soils. Moreover, on the



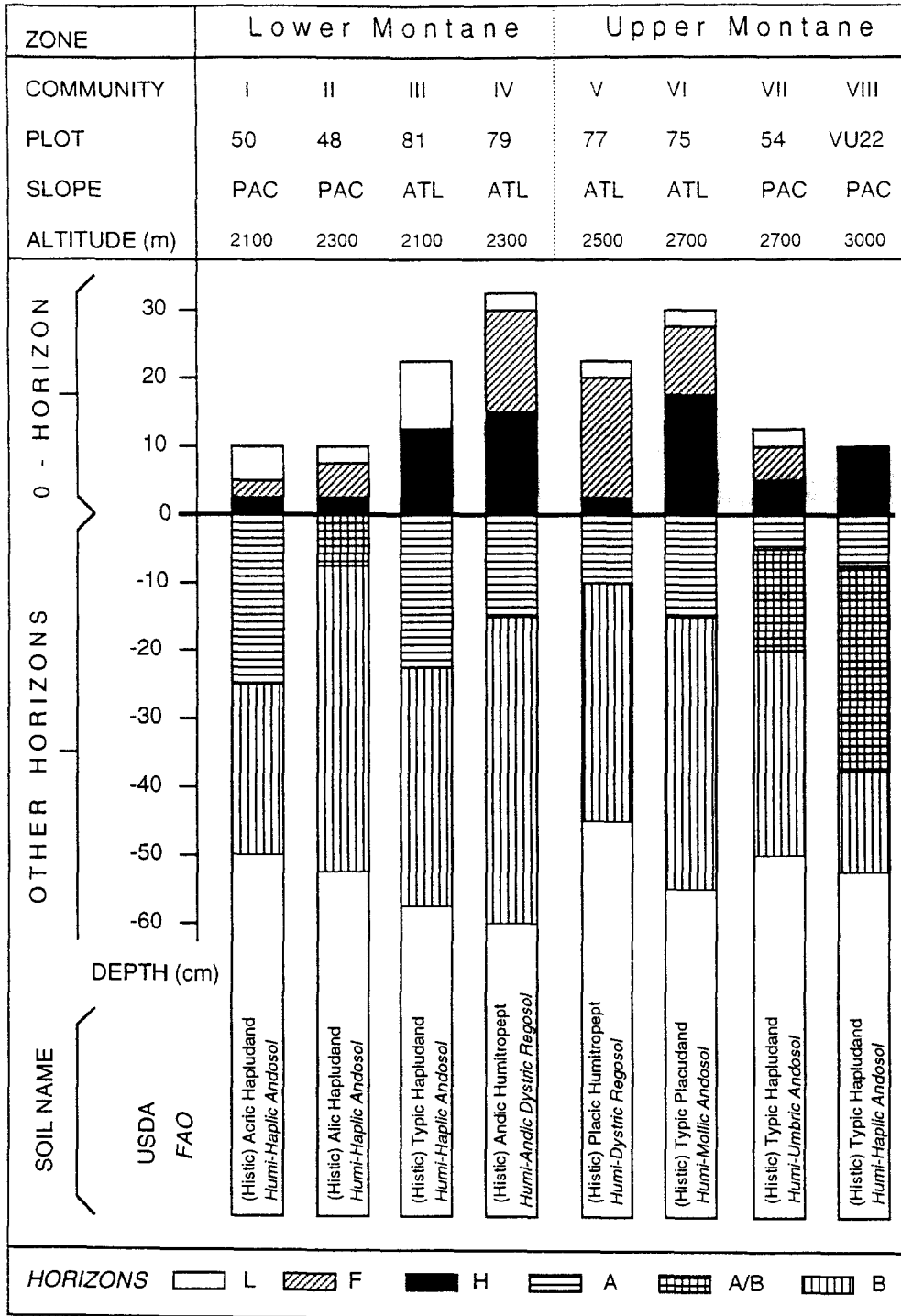


Fig. 5. Sequence of Pacific and Atlantic soil profiles along the transects in Chirripó National Park. Roman numbers refer to *Quercus* forest communities described in the text. Profile VU22 corresponds to a soil pit close to plot 60 (Van Uffelen 1991; see Fig. 3). Slope: PAC = Pacific; ATL = Atlantic. Soil names follow the soil taxonomy by USDA (Soil Survey Staff 1975; plain case) and FAO (1988; italic case). Horizons: L = Litter horizon; F = Fermentation horizon; H = Humus horizon; A = A-horizon; A/B = Transition from A- to B-horizon; B = B-horizon.

Table 1. Physical and chemical properties of upper profiles<sup>1</sup> at selected plots along the transects through montane *Quercus* forests in the Chirripó National Park, Costa Rica (n.d. = not determined).

Zone <sup>2</sup>	Com. <sup>3</sup>	Plot	Alt. (m)	Slope <sup>4</sup>	Soil texture (%)			Org. <sup>5</sup> C (%)	Org. <sup>6</sup> mat. (%)	pH (H <sub>2</sub> O)	Exchangeable elements (m-equiv. 100 g <sup>-1</sup> )						BS <sup>9</sup> (%)	P (ppm)	Ca/Mg
					Sand	Silt	Clay				Ca	Mg	K	Na	Bases <sub>tot</sub> <sup>7</sup>	CEC <sup>8</sup>			
LM	I	50	2100	PAC	61	23	16	11.9	20.4	4.2	0.94	0.75	0.51	0.17	2.37	34.10	7	39	1.25
LM	II	48	2300	PAC	45	37	18	8.5	14.7	4.3	0.50	0.33	0.29	0.15	1.27	41.25	3	25	1.52
LM	III	81	2100	ATL	55	19	26	9.7	16.6	4.3	1.06	0.38	0.26	0.14	1.84	25.85	7	22	2.79
LM	IV	79	2300	ATL	79	7	14	11.4	19.6	4.3	0.88	0.74	0.48	0.18	2.28	n.d.	n.d.	7	1.19
UM	V	77	2500	ATL	45	25	30	8.7	15.0	4.1	0.00	0.60	0.77	0.30	1.67	37.40	n.d.	29	0.00
UM	VI	75	2700	ATL	59	13	28	10.6	18.2	4.6	3.81	0.00	0.39	0.00	4.20	41.80	n.d.	26	—
UM	VII	54	2700	PAC	53	29	18	7.0	12.1	4.3	0.69	0.23	0.19	0.10	1.21	31.90	4	22	3.00
UM	VIII	VU22	3000	PAC	56	34	10	9.0	15.5	4.8	1.00	0.43	0.55	0.12	2.10	40.70	5	11	2.33

<sup>1</sup> Upper profiles refer to soil at 0–5 cm depth, i.e., in the A- or A/B-horizon.

<sup>2</sup> Zone: LM = Lower Montane; UM = Upper Montane.

<sup>3</sup> Com. = Community number (see text).

<sup>4</sup> Slope: PAC = Pacific; ATL = Atlantic.

<sup>5</sup> Org. C = Organic Carbon.

<sup>6</sup> Org. mat. = Organic Matter.

<sup>7</sup> Bases<sub>tot</sub> = Total bases.

<sup>8</sup> CEC = Cation Exchange Capacity.

<sup>9</sup> BS = Base Saturation.

Atlantic slope the O-horizons are much thicker (Fig. 5). In general, the humus profiles are for about half their thickness composed of fine organic material (H layer), which is free of litter fragments and contain some mineral soil material. On the Atlantic slope this well-decomposed organic horizon is overlaid by a less decomposed horizon (F layer) and sometimes by litter (L layer). On the Pacific slope the humus horizon (H) is overlaid by a horizon of about equal amounts of more or less fragmented litter and finely divided organic material (F). This horizon is overlaid by an L layer. In general, humus profiles are very dark-brown. Thickness of the humus profiles ranges from some 10 cm at lower altitudes to some 40 cm at higher altitudes on the Atlantic slope, and from ca. 10 cm at lower altitudes to ca. 20 cm at higher altitudes on the Pacific slope. In the well-decomposed lower parts of the humus profiles thick superficial root mats have developed.

Soil temperatures at 30 cm soil depth between 1900 and 3200 m asl decreased significantly with altitude for both slopes (Fig. 6). The relationship between soil temperature and altitude was assessed through fitting Atlantic slope data to the following linear regression equation:

$$Y = 24.75 - 0.00528X \quad (2)$$

$$(n = 7, r^2 = 0.90, p < 0.001)$$

and through fitting Pacific slope data to the following linear regression equation:

$$Y = 29.19 - 0.00641X \quad (3)$$

$$(n = 7, r^2 = 0.70, p < 0.019),$$

where Y is the soil temperature in degrees Celsius and X is the altitude in m asl. From these equations and Fig. 6 it becomes clear that the soil temperature at a certain elevation on the Atlantic slope may be ca. 0.11 °C lower than on the Pacific slope. However, it has to be taken into account, that  $r^2$  ranges from 0.70 to 0.90 for both equations and that therefore about 10 to 20% of the total variance of Y before these regressions remains unexplained. For the Chirripó Massif as a whole, an average temperature drop of 0.58 °C · 100 m<sup>-1</sup> increase in altitude was calculated.

Each point on the regression lines corresponds to the average annual air temperature for that slope and altitude (Van der Hammen 1984). This means that the average annual air temperature in Chirripó's montane oak forests (2000–3200 m asl) ranges from ca. 15 down to 9 °C. The temperature limit between LM and UM Forests at ca. 2500–2600 m asl lies around 12 °C, which coincides with Holdridge *et al.*'s (1971) biotemperature at the boundary of the lower montane and montane life zones. Holdridge *et al.*'s (1971) critical temperature or frostline (between 16 and 18 °C) is

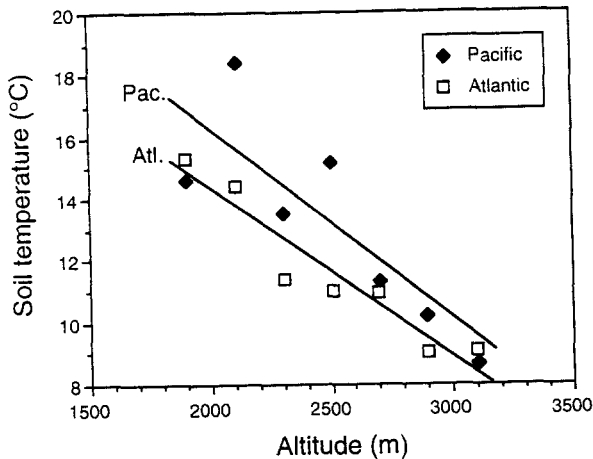


Fig. 6. Relationship between soil temperature at 30 cm soil depth and altitude (m asl) in the montane belt of Chirripó National Park, Costa Rica. The lines are drawn using coefficients from linear regressions of soil temperature and altitude for both slopes. The lines start with a minimum altitude of 1900 m asl and end with a maximum altitude of 3100 m asl.

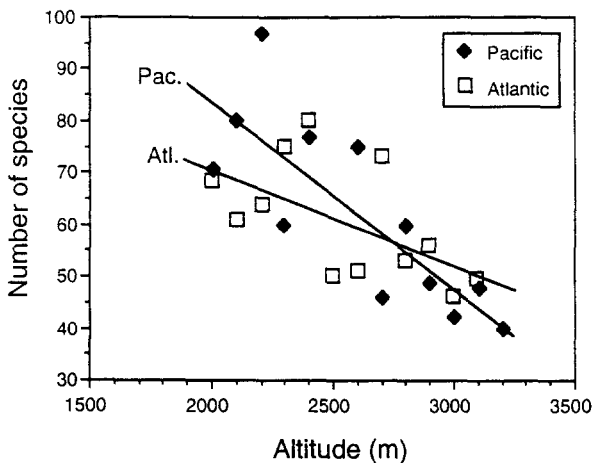


Fig. 7. Relationship between number of vascular plant species per 0.05 ha plot and altitude (m asl) in the montane belt of Chirripó National Park, Costa Rica. The lines are drawn using coefficients from linear regressions of number of vascular plant species and altitude for both slopes. The lines start with a minimum altitude of 2000 m asl and end with a maximum altitude of 3200 m asl.

found at even lower elevations in the area (ca. 1500–1800 m asl), separating the premontane from the lower montane forest zone (Van Uffelen 1991).

#### Floristics

Identification of the plant material resulted in 431 species of – mainly terrestrial – vascular plants: 86 pteridophytes, 1 gymnosperm, 296 dicots and 48

Table 2. Most diverse vascular plant families (>10 spp.) and genera (>5 spp.) in the montane *Quercus* forests of the Chirripó Massif, Costa Rica. Number of species in brackets.

Families	Genera
RUBIACEAE (26)	<i>Peperomia</i> (17)
PIPERACEAE (21)	<i>Elaphoglossum</i> (16)
ASTERACEAE (20)	<i>Miconia</i> (12)
MELASTOMATACEAE (20)	<i>Grammitis</i> (11)
POLYPODIACEAE (20)	<i>Solanum</i> (9)
ERICACEAE (17)	<i>Ocotea</i> (8)
LOMARIOPSIDACEAE (17)	<i>Palicourea</i> (8)
SOLANACEAE (16)	<i>Asplenium</i> (8)
LAURACEAE (15)	<i>Anthurium</i> (6)
MYRSINACEAE (13)	
ARACEAE (11)	

monocots. Table 2 presents the more speciose families and genera. Five families were represented by 20 or more species, while four genera were found with 10 or more congeners. Altitudinal ranges and vernacular names of trees, shrubs, bamboos, lianas and ferns, as well as changes in woody species diversity along the altitudinal gradient have been treated in detail on earlier occasions (Kappelle *et al.* 1991; Kappelle & Gómez 1992; Kappelle & Zamora, in press).

The number of terrestrial vascular plant species per 0.05 ha plot between 2000 and 3200 m asl decreased significantly with altitude for both slopes, from an average species richness of 73 in LM to 51 in UM forests (Fig. 7). Pacific plot 49 at 2200 m asl was most species-rich (97 spp.) and Pacific plot 57 at 3000 m asl most species-poor (42 spp.). The relationship between the number of terrestrial vascular plant species per 0.05 ha plot and altitude was assessed through fitting Atlantic slope data to the following linear regression equation:

$$Y = 108.82 - 0.01892X \quad (4)$$

$$(n = 12, r^2 = 0.35, p < 0.042)$$

and through fitting Pacific slope data to the following linear regression equation:

$$Y = 153.74 - 0.03520X \quad (5)$$

$$(n = 12, r^2 = 0.64, p < 0.002),$$

where Y is the number of terrestrial vascular plant species per 0.05 ha plot and X is the altitude in m asl.

Table 3. Mean maximum height and aerial cover of forest structure layers for eight montane *Quercus* forest communities in the Chirripó National Park, Costa Rica. Roman numbers refer to the communities described in the text. A Kruskal-Wallis nonparametric ANOVA of all ten structural parameters showed significant differences among communities only for the cover of the bryophyte layer ( $P = 0.027$ ).

Zone	Lower montane				Upper montane			
	Pac	Pac	Atl	Atl	Atl	Atl	Pac	Pac/Atl
Community	I	II	III	IV	V	VI	VII	VIII
Mean maximum height (m)								
Canopy tree layer <sup>a</sup>	40	35	35	35	35	35	30	25
Subcanopy tree layer	20	20	15	18	20	16	15	12
Shrub layer <sup>a</sup>	5	5	3	3	5	6	6	6
Herb layer	1	1	0.5	1	1	1	1	1
Bryophyte layer	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Mean cover (%)								
Canopy tree layer <sup>a</sup>	70	70	90	80	80	80	65	60
Subcanopy tree layer	60	55	60	60	50	45	50	65
Shrub layer <sup>a</sup>	60	75	85	75	40	90	90	70
Herb layer	35	20	85	70	60	65	40	25
Bryophyte layer	10	5	5	12	8	60	35	50

<sup>a</sup> The canopy tree layer corresponds to the *Quercus* tree layer and the shrub layer to the *Chusquea* bamboo layer as defined by other authors (e.g., Blaser 1987).

It has to be taken into account, that  $r^2$  ranges from ca. 0.35 to 0.65 for both equations and that therefore about 35 to 70% of the total variance of Y before these regressions remains unexplained. For the Chirripó Massif as a whole, an average drop of 2.7 species per 0.05 ha was calculated for every 100 mincrease in altitude.

The Shannon-Wiener diversity index  $H'$  ranged from 4.02 to 4.93 in LM forest plots ( $n = 11$ ; mean  $\pm 1$  S.E. =  $4.48 \pm 0.10$ ) and from 3.24 to 4.39 in UM forest plots ( $n = 13$ ; mean  $\pm 1$  S.E. =  $3.24 \pm 0.09$ ). However, the Shannon-Wiener values did not differ significantly between both altitudinal forest belts (nonparametric Mann-Whitney  $U$  test,  $p = 0.41$ ). The average Shannon-Wiener index (mean  $\pm 1$  S.E.) was  $4.03 \pm 0.13$  on the Pacific slope ( $n = 12$ ),  $4.19 \pm 0.14$  on the Atlantic slope ( $n = 12$ ), and did not differ significantly between both slopes. However, differences for Shannon-Wiener index values among the communities described below were clearly significant (Kruskal-Wallis nonparametric ANOVA,  $p = 0.015$ ). Linear regression analysis of Shannon-Wiener index values on altitude was significant along both slopes (Atlantic slope:  $n = 12$ ,  $r^2 = 0.80$ ,  $p < 0.001$ ; Pacific slope:  $n = 12$ ,  $r^2 = 0.49$ ,  $p < 0.01$ ) and very similar to the linear regression analysis between the number of terrestrial vascular plant species per 0.05 ha plot and

altitude, as calculated above for both the Pacific and Atlantic slope (Fig. 7).

#### Forest structure

Observations show that the average height of the canopy and subcanopy layers decreases from LM to UM forest, while the stature of the shrub, herb and bryophyte layers remains relatively equal (Table 3). This suggests a telescope-like compaction and lowering of forest structure layers at higher elevations. Average cover values fluctuate between 60 and 90% for the oak-dominated canopy tree layers, and between 45 and 65% for the more open (lauraceous or myrsinaceous) subcanopy tree layers. The shrub layers are dense and reach high cover percentages due to the presence of 5 to 6 m tall *Chusquea* Kunth bamboos. The cover of the herb layer has the greatest range (20 to 85%), as a consequence of locally abundant species like *Besleria formosa* Morton and *Hansteinia ventricosa* (J.D. Smith) D. Gibson in community III (plot 81), or Rubiaceae (*Palicourea* Aublet and *Psychotria* L.) in community IV (Table 4). The terrestrial bryophyte cover is also very variable, which is probably caused by local differences in light regimes at the forest floor, e.g., canopy openings. In general, the bryophyte lay-



Table 4 b.

Community	I I I	II II II	III III	IV IV IV	V V	VI VI VI	VII VII VII VII	VIII VIII VIII VIII
Altitude (x 100 m asl)	20 21 22	23 24 26	20 21	22 23 24	25 26	27 28 29	27 28 29 31	30 32 31 30
Plot Number	52 50 49	48 47 53	82 81	80 79 78	77 76	75 74 73	54 55 56 58	57 60 71 72
Pacific - Atlantic Lower Montane Species								
<i>Anthurium pallens</i>	<1 - <1	<1 - <1	<1 <1	- - -	- - -	- - -	- - -	- - -
<i>Bellucia costaricensis</i>	2 - <1	1 - -	3 2	- - -	- - -	- - -	- - -	- - -
<i>Begonia vestita</i>	- <1 <1	- - -	<1 -	- - -	- - -	- - -	- - -	- - -
<i>Elaeagia auriculata</i>	3 - -	- - -	20 -	- - -	- - -	- - -	- - -	- - -
<i>Polybotrya alfredii</i>	<1 - -	- - -	<1 -	- - -	- - -	- - -	- - -	- - -
<i>Psychotria dichroa</i>	- - -	- - 2	10 7	- - -	- - -	- - -	- - -	- - -
<i>Persaea caerulea</i>	- - -	1 - -	6 2	- - -	- - -	- - -	- - -	- - -
<i>Asplenium auritum</i>	- - -	<1 - -	<1 -	- - -	- - -	- - -	- - -	- - -
<i>Grammitis asplenifolia</i>	- - -	- <1 -	<1 -	- - -	- - -	- - -	- - -	- - -
<i>Oreopanax oerstedianus</i>	- <1 <1	1 <1 1	- -	<1 <1	- - -	- - -	- - -	- - -
<i>Iresine diffusa</i>	<1 <1 -	- 1 <1	- -	1 <1	- - -	- - -	- - -	- - -
<i>Phoebe cinnamomifolia</i>	3 - 1	<1 - -	- - -	- - 6	- - -	3 - -	- - -	- - -
<i>Cyclanthera langaei</i>	- - <1	- <1 -	- - -	<1 <1	- - -	- - -	- - -	- - -
<i>Quercus copeyensis</i>	20 - -	75 70 60	20 25	15 20 40	80 60	- - -	- - -	- - -
<i>Geonoma hoffmanniana</i>	3 3 20	60 5 10	15 5	20 40 65	4 -	- - -	- - -	- - -
<i>Mollinedia pinchotiana</i>	2 1 3	2 3 4	8 12	6 5 -	- - -	- - -	<1 - -	- - -
<i>Chamaedorea warszewiczii</i>	<1 3 <1	<1 4 1	1 1	<1 <1 <1	- - -	- - -	- - -	- - -
<i>Prestoea allenii</i>	- - <1	1 2 1	3 6	10 15 5	1 -	- - -	- - -	- - -
<i>Asplenium harpeodes</i>	<1 <1 -	- - <1 <1	<1 <1	1 <1 <1	- - -	- - -	- - -	- - -
<i>Trichilia havanensis</i>	3 3 -	1 <1 6	- 7	- 4 <1	- - -	- - -	- - -	- - -
<i>Monstera deliciosa</i>	<1 <1 <1	<1 <1 <1	- <1	1 - -	- - -	- - -	- - -	- - -
<i>Cissus martiniana</i>	<1 - <1	<1 <1 <1	<1 <1	- - <1	- - -	- - -	- - -	- - -
<i>Arcisia glandulosomarginata</i>	- - 1	- - 1	2 5	8 <1 1	- - -	- - -	1 - -	- - -
<i>Vittaria graminifolia</i>	- - <1	<1 <1 <1	- <1	<1 - <1	- - -	- - -	- - -	- - -
<i>Peperomia palmata</i>	- - <1	<1 <1 <1	- <1	<1 <1 -	- - -	- - -	<1 - -	- - -
<i>Tovomitopsis allenii</i>	2 - 4	2 - -	35 5	3 - -	- - -	- - -	- - -	- - -
<i>Billia hippocastanum</i>	5 - 3	1 - -	- 8	- 15 5	- - -	- - -	- - -	- - -
<i>Nectandra salicina</i>	2 10 2	1 - -	3 -	- - <1	- - -	- - -	1 - <1	- - -
<i>Tradescantia commelinoides</i>	- - <1	- <1 -	1 <1	- <1 <1	- - -	- - -	- - -	- - -
<i>Microtropis occidentalis</i>	- - 2	- 3 4	- 2	- 3 -	- - -	- - -	<1 - -	- - -
<i>Centronia phlomidoides</i>	- - 2	- 4 -	- <1	4 - -	- - -	- - -	- - -	- - -
<i>Guarea tonduzii</i>	3 - 1	- - -	- 6	25 30 10	- - -	- - -	- - -	- - -
<i>Alchornea latifolia</i>	- 1 5	- - -	1 -	30 - 8	1 -	- - -	- - -	- - -
<i>Besleria formosa</i>	- - 3	- - -	5 20	- 1 <1	- - -	- - -	- - -	- - -
<i>Meliosma glabrata</i>	5 - -	- - -	<1 2	- 6 2	- - -	- - -	- - -	- - -
<i>Miconia platyphylla</i>	2 <1 1	- - -	5 -	- <1 -	- - -	- - -	- - -	- - -
<i>Campyloneurum xalapense</i>	<1 - <1	- - -	- <1	<1 <1 -	- - -	- - -	- - -	- - -
<i>Begonia sp. (MK 3085)</i>	- - <1	- - -	<1 -	<1 <1 -	- - -	- - -	- - -	- - -
<i>Aulonemia viscosa</i>	10 75 -	- - -	- -	- - 25	- - -	- - -	- - -	- - -
<i>Lozania mutsiiana</i>	<1 - 2	- - -	- -	18 - -	- - -	- - -	- - -	- - -
<i>Piper imperiale</i>	- <1 1	- - -	- -	3 - -	- - -	- - -	- - -	- - -
<i>Cyperaceae sp. 2 (MK 3069)</i>	<1 - <1	- - -	- -	- <1 -	- - -	- - -	- - -	- - -
<i>Pteris altissima</i>	<1 - <1	- - -	- -	- - <1	- - -	- - -	- - -	- - -
<i>Blechnum divergens</i>	- - <1	- - -	- -	- <1 <1	- - -	- - -	- - -	- - -
<i>Croton schiedeianus</i>	- - 2	- - -	- -	- - 1	- - -	- - -	- - -	- - -
<i>Picramnia quaternaria</i>	- 1 -	- - -	- -	<1 - -	- - -	- - -	- - -	- - -
<i>Clematis haenckeana</i>	<1 -	- - -	- -	<1 - -	- - -	- - -	- - -	- - -
<i>Ocotea austinii</i>	- - -	- - 5	2 -	1 8 2	- - -	- - -	<1 - -	- - -
<i>Ocotea holdridgeana</i>	- - -	- - 2	- 3	2 1 2	- - -	- - -	- - -	- - -
<i>Peperomia syringifolia</i>	- - -	- - <1	- <1	- <1 <1	- - -	- - -	- - -	- - -
<i>Peperomia elata</i>	- - -	- <1 <1	- -	- - <1	- - -	- - -	- - -	- - -
<i>Passiflora membranacea</i>	- - -	- - <1	- -	- <1 <1	- - -	- - -	- - -	- - -
Atlantic Lower Montane Species								
<i>Heliconia tortuosa</i>	- - -	- - -	1 <1	- - -	- - -	- - -	- - -	- - -
<i>Philodendron sp. 1 (MK 5386)</i>	- - -	- - -	<1 <1	- - -	- - -	- - -	- - -	- - -
<i>Phoebe hammeliana</i>	- - <1	1 - -	5 8	7 5 2	- - -	- - -	- - -	- - -
<i>Hansteinia ventricosa</i>	- - -	- - -	7 15	4 <1 <1	- - -	- - -	- - -	- - -
<i>Miconia cremadena</i>	- - -	- - -	1 3	2 2 6	- - -	<1 - -	- - -	- - -
<i>Anthurium mickelii</i>	- - -	- - -	<1 <1	<1 <1 <1	- - -	- - -	- - -	- - -

Table 4 c.

Community	I I I	II II II	III III	IV IV IV	V V	VI VI VI	VII VII VII VII	VIII VIII VIII VIII
Altitude (x 100 m asl)	20 21 22	23 24 26	20 21	22 23 24	25 26	27 28 29	27 28 29 31	30 32 31 30
Plot Number	52 50 49	48 47 53	82 81	80 79 78	77 76	75 74 73	54 55 56 58	57 60 71 72
Atlantic Lower Montane Species (continued)								
<i>Psychotria panamensis</i>	- - -	- - -	- 10	8 3 4	- -	- - -	- - -	- - -
<i>Pilea costaricensis</i>	- - -	- - -	<1 1	<1 <1 -	- -	- - -	- - -	- - -
<i>Hymenophyllum consanguineum</i>	- - -	- - -	<1 <1	- <1 <1	- -	- - -	- - -	- - -
<i>Pilea auriculata</i>	- - -	- - -	- <1	<1 <1 <1	- -	- - -	- - -	- - -
<i>Asplundia microphylla</i>	- - -	- - -	2 2	3 - -	- -	- - -	- - -	- - -
<i>Danaea cuspidata</i>	- - -	- - -	1 <1	<1 - -	- -	- - -	- - -	- - -
<i>Cestrum racemosum</i>	- - -	- - -	- 1	<1 <1 -	- -	- - -	- - -	- - -
<i>Peperomia omnicola</i>	- - -	- - -	<1 <1	- <1 -	- -	- - -	- - -	- - -
<i>Mikania leiostachya</i>	- - -	- - -	- <1	<1 <1 -	- -	- - -	- - -	- - -
<i>Diplazium lindbergii</i>	- - -	- - -	- <1	- <1 <1	- -	- - -	- - -	- - -
<i>Palicourea padifolia</i>	- - -	- - -	- 6	8 - -	- -	- - -	- - -	- - -
<i>Nectandra cufodontsii</i>	- - -	- - -	- 1	8 2 20	- -	- - -	- - -	- - -
<i>Cyathea sp. 1 (MK 5210)</i>	- - -	- - -	- -	5 3 -	- -	- - -	- - -	- - -
<i>Besleria barbensis</i>	- - -	- - -	- -	5 <1 -	- -	- - -	- - -	- - -
<i>Parathesis calophylla</i>	- - -	- - -	1 - -	- <1 -	- -	- - -	- - -	- - -
<i>Solanum incomptum</i>	- - -	- - -	- -	<1 1 -	- -	- - -	- - -	- - -
<i>Columnea anisophylla</i>	- - -	- - -	<1 -	<1 - -	- -	- - -	- - -	- - -
<i>Grammadenia rufa</i>	- - -	- - -	- -	- <1 <1	- -	- - -	- - -	- - -
Wide-ranging Species								
<i>Sphaeradenia irazuensis</i>	- - 1	5 40 -	- - -	1 4 3	5 15	- - -	- - -	- - -
<i>Hydrangea asterolasia</i>	- 1 <1	<1 <1 <1	<1 - -	- <1 1	- -	1 <1 6	- - -	- - -
<i>Saurauia veraguasensis</i>	<1 5 2	- - -	- - -	- - -	- -	8 5 6	- - -	- - -
<i>Prunus annularis</i>	- 3 -	- - 5	3 - -	- - -	3 4	6 - -	- - -	- - -
<i>Piper hispidum</i>	- - 1	- - -	- 2	- <1 1	- <1	<1 - -	- - -	- - -
<i>Spiranthes sp. (MK 5190)</i>	<1 - -	- - -	- - -	<1 <1 -	- -	<1 - -	- - -	- - -
<i>Elaphoglossum firmum</i>	<1 <1 <1	1 <1 -	2 - -	- 2 <1	30 10	8 5 -	3 - -	- - -
<i>Asplenium serra</i>	- <1 <1	<1 <1 -	<1 <1	- <1 <1	- -	<1 <1 <1	<1 - -	- - -
<i>Styrax argenteus</i>	- 3 -	1 2 3	- - -	- - -	6 3	- - -	1 5 4 4	- - -
<i>Quercus seemannii</i>	50 75 70	- - -	- - -	- - -	- -	35 - -	50 60 50 80	- - -
<i>Elaphoglossum eximium</i>	- <1 -	- - -	1 3	2 <1 1	- -	5 - -	- - <1	- - -
<i>Smilax kunthii</i>	- <1 <1	- - <1	- - -	- - -	- <1	<1 <1 -	<1 - -	- - -
<i>Miconia sp. 2 (MK 3118)</i>	- 2 1	- - <1	- - -	- - -	- -	- - -	- 2 1 -	- - -
<i>Asteraceae sp. (MK 3156)</i>	- <1 <1	- - -	- - -	1 - -	- -	<1 - -	- 1 <1	- - -
<i>Pilea gracilipes</i>	- <1 <1	<1 <1 -	- - -	- - -	- -	- - -	- <1 <1	- - -
<i>Phytolacca rugosa</i>	- 1 -	- <1 -	- - -	1 - -	- -	- - <1	- 1 -	- - -
<i>Polypodium loriceum</i>	- <1 -	- - <1	- - -	- - -	- -	- - -	30 - -	- - -
<i>Anthurium concinatum</i>	- <1 <1	<1 1 1	- - -	<1 <1 <1	2 1	1 1 <1	30 2 5 3	3 - <1 <1
<i>Clusia stenophylla</i>	1 25 10	10 10 5	1 - -	- 2 1	1 2	2 20 6	40 3 10 -	5 - - 10
<i>Bomarea acutifolia</i>	- <1 <1	- <1 <1	<1 - -	- - <1	- -	<1 <1 -	- <1 <1 <1	- <1 <1 -
<i>Mikania cordifolia</i>	- <1 <1	<1 <1 -	<1 - -	- - -	- <1	- - <1	- <1 <1 <1	- - 2 1
<i>Viburnum costaricanum</i>	<1 <1 1	2 2 -	- - -	- - -	- -	- <1 -	<1 3 2 4	- 4 - -
<i>Symplocos serrulata</i>	- - 3	- - -	- - -	- 2	5 -	- - -	- - -	- 2 1
<i>Alloplectus ichtyoderma</i>	- - -	<1 <1 <1	- - -	<1 <1 <1	<1 <1	<1 <1 <1	<1 <1 <1	- - -
<i>Dicksonia gigantea</i>	- - -	- 2	5 - -	- 4	2 -	- - -	2 - -	- - -
<i>Topobea storkii</i>	- - -	3 2 -	- - -	1 - -	- -	- - <1	- - -	- - -
<i>Elaphoglossum erinaceum</i>	- - -	- - <1	- - -	- - <1	3 -	- - -	- - -	- - -
<i>Fuchsia arborescens</i>	- - -	- 1 -	- - -	- - -	- -	2 - -	- - -	- - -
<i>Elaphoglossum biolleyi</i>	- - -	<1 - -	- - -	- - -	- <1	- - -	- - -	- - -
<i>Goodyera erosa</i>	- - -	- <1 -	- - -	- - -	- <1	- - -	- - -	- - -
<i>Plantago australis</i>	- - -	- <1 -	- - -	- - -	- -	- <1 -	- - -	- - -
<i>Aegiphila odontophylla</i>	- - -	- - <1	- - -	- - -	- -	- <1 -	- - -	- - -
<i>Senecio megaphyllus</i>	- - -	- - <1	- - -	- - -	- -	- - -	- <1 1 <1	- - -
<i>Alnus acuminata</i>	- - -	- 2 10	- - -	- - -	- -	- - -	3 - -	- - -
<i>Peperomia quadrifolia</i>	- - -	- - <1	- - -	- - -	- -	- - -	<1 <1 -	- - -
<i>Palicourea elempalmensis</i>	- - -	- - 5	- - -	- - -	- -	- - -	1 - -	- - -
<i>Psammisia sp. (MK3719)</i>	- - -	- - 1	- - -	- - -	- -	- - -	2 - -	- - -
<i>Jungia ferruginea</i>	- - -	- - 1	- - -	- - -	- -	- - -	- - <1	- - -
<i>Hedyosmum mexicanum</i>	- - -	- - <1	- - -	- - -	- -	- - -	<1 - -	- - -
<i>Arenaria lanuginosa</i>	- - -	- - <1	- - -	- - -	- -	- - -	- <1 - -	- - -

Table 4 d.

Community	I I I	II II II	III III	IV IV IV	V V	VI VI VI	VII VII VII	VIII VIII VIII
Altitude (x 100 m asl)	20 21 22	23 24 26	20 21	22 23 24	25 26	27 28 29	27 28 29 31	30 32 31 30
Plot Number	52 50 49	48 47 53	82 81	80 79 78	77 76	75 74 73	54 55 56 58	57 60 71 72
Wide-ranging Species (continued)								
<i>Cyathea fulva</i>	- - -	- - -	3 5	3 2 -	- <1	2 5 -	- - - -	- - - -
<i>Cestrum</i> sp. 2 (MK 5397)	- - -	- - -	1 <1	- <1 <1	1 -	<1 - -	- - - -	- - - -
<i>Burmeistera silencioensis</i>	- - -	- - -	- <1	<1 - <1	<1 1	- - -	- - - -	- - - -
<i>Witheringia coccoloboides</i>	- - -	- - -	<1 <1	- 2 -	- - -	- <1 -	- - - -	- - - -
<i>Smilax vanilliodora</i>	- - -	- - -	1 <1	<1 - -	- 1 -	- - -	- - - -	- - - -
<i>Oligactis volubilis</i>	- - -	- - -	1 -	- - -	<1 -	- - -	- - - -	- - - -
<i>Ardisia palmana</i>	- - -	- 1 -	- - -	2 1 2	12 25	12 - -	- - - -	- - - -
<i>Palicourea lasiorrhachis</i>	- - -	- - -	- - -	- 3 1	3 1 -	- - -	- - - -	- - - -
<i>Miconia</i> sp. 3 (MK 4994)	- - -	- - -	- - -	- <1 -	2 3 -	- - -	- - - -	- - - -
<i>Dysoxylum glechomoides</i>	- - -	- - -	- - -	<1 - <1	- - -	<1 - -	- - - -	- - - -
<i>Miconia</i> sp. 1 (MK 4995)	- - -	- - -	- - -	- 1 -	- <1 -	- - -	- - - -	- - - -
<i>Anthurium camosum</i>	- - -	- - -	- - -	- - <1	<1 -	- - -	- - - -	- - - -
<i>Blechnum fragile</i>	- - -	- - -	- - -	- - <1	<1 -	- - -	- - - -	- - - -
<i>Weinmannia pinnata</i>	- - -	10 2 30	8 8	1 4 5	3 15	10 15 4	6 8 3 <1	3 4 - -
<i>Oreopanax capitatus</i>	- - -	- 2 <1	- - -	- - -	- - -	3 1 2	- <1 1 1	1 1 2 3
<i>Piper pittieri</i>	- - -	- - <1	3 -	1 1 <1	- <1	3 2 <1	- <1 - -	- - 1 <1
<i>Begonia udisilvestris</i>	- - -	- <1 <1	- - -	<1 <1 <1	<1 1	1 <1 <1	- <1 - -	- - <1
<i>Symplocos austinsmithii</i>	- - -	2 1 -	- - -	10 3 4	<1 <1	- - -	- - 3 <1	- <1 - -
<i>Arachniodes denticulata</i>	- - -	<1 <1 -	- - -	- - -	<1 <1	<1 - -	<1 <1 - -	- - <1 <1
<i>Pitcairnia werckleana</i>	- - -	- - <1	- - -	- <1 2	10 2	<1 <1 2	- - - -	- - 5 -
<i>Polypodium ptilorhizon</i>	- - -	- - <1	- <1	- - -	- - -	- - -	- 5 - -	- - 1 1
<i>Polystichum muricatum</i>	- - -	- <1 -	- - -	- - <1	- - -	<1 - -	- - <1 <1	- - <1 -
<i>Myrrhidendron donnellsmithii</i>	- - -	- <1 -	- - -	- - -	- <1 -	- - -	- 1 1 -	1 - - -
<i>Peperomia galioides</i>	- - -	- <1 <1	- - -	- - -	- - -	- - -	<1 - <1	<1 - - -
<i>Ageratina bustamenta</i>	- - -	- - 1	- - -	- - -	- - -	<1 - -	- <1 - -	1 - - -
<i>Cyathea suprastrigosa</i>	- - -	- - -	- 3	- - 1	4 2	- <1 12	- <1 - -	- - 3 4
<i>Grammitis cultrata</i>	- - -	- - -	- <1	- - <1	- <1	- <1 -	- - - -	- - - <1
<i>Ocotea pittieri</i>	- - -	- - -	<1 6	- 5 45	8 12	30 20 -	- 10 1 -	- - - -
<i>Solanum longianicum</i>	- - -	- - -	- <1	<1 <1 <1	- - -	- - -	- <1 <1 <1	- - - -
<i>Peperomia dotana</i>	- - -	- - -	<1 -	- - -	<1 -	- - -	<1 - - -	- - - -
<i>Muehlenbeckia tamnifolia</i>	- - -	- - -	<1 -	- - <1	- - -	- - -	- <1 - -	- - - -
<i>Peperomia hylophila</i>	- - -	- - -	<1 -	<1 - -	- - -	- - -	- - - <1	- - - -
Atlantic Upper Montane Species								
<i>Symbolanthus pulcherrimum</i>	- - -	- - -	- - -	- - -	<1 <1	- - -	- - - -	- - - -
<i>Hedyosmum goudotianum</i>	- - -	- - -	- - -	- - <1	4 6	2 5 3	- - - -	- - - -
<i>Miconia</i> sp. 4 (MK 4996)	- - -	- - -	- - -	- - -	8 5	2 3 -	- - - -	- - - -
<i>Cybianthus pastensis</i>	- - -	- - -	- - -	- - -	<1 <1	- <1 <1	- <1 1 1	1 1 2 3
<i>Dioscorea standleyi</i>	- - -	- - -	- - -	- - -	- <1	<1 <1 <1	- - - -	- - - <1
<i>Celastraceae</i> , sp. 1 (MK 4491)	- - -	- - -	- - -	- - -	<1 -	1 - -	- - - -	- - - -
<i>Gesneriaceae</i> , sp. 1 (MK 5028)	- - -	- - -	- - -	- - -	<1 -	- <1 -	- - - -	- - - -
<i>Podocarpus macrostachyus</i>	- - -	- - -	- - -	- - -	- - -	8 40 6	- - - -	- - - -
<i>Miconia confertiflora</i>	- - -	- - -	- - -	- - -	- - -	10 12 8	- - - -	- - - -
<i>Elaphoglossum alfredii</i>	- - -	- - -	- - -	- - -	- - -	40 <1	- - - -	- - - -
<i>Brunellia costaricensis</i>	- - -	- - -	- - -	- - -	- - -	2 - 5	- - - -	- - - -
<i>Centropogon talamancensis</i>	- - -	- - -	- - -	- - -	- - -	1 2 -	- - - -	- - - -
Pacific - Atlantic Upper Montane Species								
<i>Myrsine coriacea</i>	- - -	- - <1	- - -	- - -	- - -	- 2 <1	3 2 - -	- - - -
<i>Didymaea alsinoides</i>	- - -	- - -	- - -	- - -	- - -	<1 - 2	- <1 - -	- - - -
<i>Pilea pubescens</i>	- - -	- - -	- - -	- - -	- - -	<1 <1	- <1 - -	- - - -
<i>Oxalis spiralis</i> ssp. <i>vulcanicola</i>	- - -	- - -	- - -	- - -	- - -	<1 - <1	- - <1 -	- - - -
<i>Myrsine pellucidopunctata</i>	- - -	- - -	- - -	- - -	- - -	- 1 -	- - 1 -	- - - -
<i>Nertera granadensis</i>	- - -	- - -	- - -	- - -	- - -	<1 - -	<1 - - -	- - - -
<i>Ardisia compressa</i>	- - -	- - -	- - -	- - -	- - -	- - -	5 3 2 1	- - - -
<i>Rhynchospora aristata</i>	- - -	- - -	- - -	- - -	- - -	- - -	- <1 <1 1	- - - -
<i>Alloplectus</i> sp. (MK 3802)	- - -	- - -	- - -	- - -	- - -	- - -	<1 <1 <1	- - - -
<i>Palicourea salicifolia</i>	- - -	- - -	- - -	- - -	- - -	- - -	3 4 - -	- - - -
<i>Cornus disciflora</i>	- - -	- - -	- - -	- - -	- - -	- - -	- - 4 3	- - - -



Table 4 e.

Community	I	I	I	II	II	II	III	III	IV	IV	IV	V	V	VI	VI	VI	VII	VII	VII	VII	VIII	VIII	VIII	VIII
Altitude (x 100 m asl)	20	21	22	23	24	26	20	21	22	23	24	25	26	27	28	29	27	28	29	31	30	32	31	30
Plot Number	52	50	49	48	47	53	82	81	80	79	78	77	76	75	74	73	54	55	56	58	57	60	71	72
Pacific - Atlantic Upper Montane Species (continued)																								
<i>Acaena elongata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	<1	-	-	-	-
<i>Senecio cooperi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	-	-	-	-
<i>Neomirandea araliaefolia</i>	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	<1	<1	-	-	-	-
<i>Senecio costaricensis</i>	-	-	-	-	-	-	-	-	-	-	-	<1	<1	2	<1	<1	-	-	-	-	-	-	<1	<1
<i>Elaphoglossum latifolium</i>	-	-	-	-	-	-	-	-	-	-	-	35	-	7	<1	-	-	-	-	-	-	<1	<1	
<i>Scheffera rodriguesiana</i>	-	-	-	-	-	-	-	-	2	20	5	4	15	1	2	15	8	8	6	5	1	1	1	1
<i>Chusquea talamancensis</i>	-	-	-	-	-	-	-	-	-	25	55	70	90	40	90	20	90	20	20	70	60	20	20	70
<i>Centropogon costaricae</i>	-	-	-	-	-	-	-	-	<1	<1	1	<1	<1	1	<1	<1	<1	<1	<1	<1	1	-	<1	1
<i>Rhamnus oreodendron</i>	-	-	-	1	-	-	-	-	-	4	1	1	-	4	<1	1	2	2	1	-	3	1	-	3
<i>Drymis granadensis</i>	-	-	-	-	-	-	<1	-	-	2	2	3	15	1	-	1	3	-	2	4	2	2	4	2
<i>Blechnum viviparum</i>	-	-	-	-	-	-	<1	-	-	<1	<1	<1	<1	1	-	1	2	1	-	1	-	1	<1	<1
<i>Miconia schnellii</i>	-	-	-	-	-	-	-	-	-	20	-	-	12	<1	-	15	-	7	20	8	-	-	-	-
<i>Peperomia saligna</i>	-	-	-	-	-	-	-	-	-	<1	<1	<1	<1	<1	-	<1	-	<1	-	1	-	1	-	-
<i>Chusquea sp. (MK 4319)</i>	-	-	-	-	-	-	-	1	15	15	40	-	10	-	-	-	-	-	20	35	-	-	-	
<i>Disterigma humboldtii</i>	-	-	-	-	-	-	-	-	<1	-	1	5	1	-	-	-	-	-	-	2	<1	-	-	-
<i>Vriesea williamsii</i>	-	-	-	-	-	-	-	-	<1	-	-	-	-	1	-	-	-	-	1	<1	-	-	-	-
<i>Culcita conifolia</i>	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-
<i>Macleania rupestris</i>	-	-	-	-	-	-	-	-	-	-	-	<1	<1	1	<1	1	3	2	10	2	1	-	-	-
<i>Zanthoxylum scheryi</i>	-	-	-	-	-	-	-	-	-	-	-	-	1	2	4	1	5	25	4	6	-	-	-	-
<i>Maianthemum paniculatum</i>	-	-	-	-	-	-	-	-	-	<1	<1	-	-	1	<1	<1	<1	<1	<1	<1	<1	-	<1	<1
<i>Ilex pallida</i>	-	-	-	-	-	-	-	-	-	5	-	15	-	3	3	-	-	-	-	<1	1	-	-	-
<i>Huperzia pythioides</i>	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	-	-	-	-	-	<1	<1	-	-	-
<i>Grammitis capillaris</i>	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	-	-	-	-	-	<1	-	-	-	-
<i>Quercus costaricensis</i>	-	-	-	-	-	-	-	-	-	-	-	10	60	-	-	-	-	-	40	15	90	80	-	-
<i>Cavendishia bracteata</i>	-	-	-	-	-	-	-	<1	-	-	2	2	<1	-	-	-	-	-	-	1	1	-	-	-
<i>Gaiadendron punctatum</i>	-	-	-	-	-	-	-	-	-	<1	1	-	-	-	-	-	-	-	8	<1	1	-	-	-
<i>Palicourea adusta</i>	-	-	-	-	-	-	-	-	-	<1	<1	2	-	-	-	-	-	-	-	<1	<1	-	-	-
<i>Maxillaria biolleyi</i>	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	20	1	<1	-	-	-
<i>Sphrosperrum cordifolium</i>	-	-	-	-	-	-	-	-	-	<1	1	-	-	-	-	-	-	-	<1	-	2	-	-	-
<i>Dennstaedia cicutaria</i>	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	<1	-	-	-	-
<i>Elaphoglossum fougierianum</i>	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	<1	<1	-	-	-
<i>Grammadenia minor</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	<1	-	-	-	-
<i>Polypodium myriolepis</i>	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	<1	-	-	-	-
<i>Thelypteris gomeziana</i>	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	-	<1	-	-	-	-
<i>Campyloneurum amphostenon</i>	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	<1	-	-	-	-
<i>Peperomia alpina</i>	-	-	-	-	-	-	-	-	-	-	<1	-	-	-	-	-	-	-	-	<1	-	-	-	-
<i>Vaccinium consanguineum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	3	2	2	6	10	-	-
<i>Elaphoglossum furturaceum</i>	-	-	-	<1	-	-	-	-	-	-	-	-	-	<1	2	2	-	<1	1	1	-	-	-	-
<i>Fuchsia microphylla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	<1	<1	<1	<1	<1	<1	-	<1	<1
<i>Ilex discolor var. lamprophylla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	1	2	-	-	4	8	-	-	-	-
<i>Cleyera theaeoides</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	3	2	40	-	3	-	-	-	-	-	-
<i>Persea vesticula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	5	2	5	-	-	-	-	-	-
<i>Hesperomeles heterophylla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	1	1	-	-	-	-	-	-
<i>Eriosorus flexuosus</i>	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	-	-	<1	<1	<1	<1	-	-	-	-
<i>Dendrophthora squamigera</i>	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	-	-	<1	<1	<1	<1	-	-	-	-
<i>Roldana heterogama</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	<1	<1	<1	-	-	-	-
<i>Elaphoglossum squamipes</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	<1	<1	<1	-	-	-
<i>Elaphoglossum mathewsii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	3	-	-	<1	<1	-	-	-
<i>Plagiogyria costaricensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	<1	<1	-	-	-	-
<i>Ageratina subcordata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	1	-	-	-	-	-	-	-
<i>Crossopetalum tonduzii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	<1	<1	<1	-	-	-	-
<i>Grammitis meridensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	-	<1	<1	-	-	-	-
<i>Grammitis moniliformis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	-	<1	<1	<1	-	-	-	-
<i>Comarostaphylis arbutoides</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	60	15	-	-	-
<i>Myrsine pittieri</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	8	5	8	-	-
<i>Weinmannia trianae var. sulcata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	30	50	-	-	-
<i>Clethra gelida</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	<1	-	-	-
<i>Pemettya prostrata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	3	-	-	-	-
<i>Gaultheria erecta</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	2	-	-	-	-
<i>Diplostephium costaricense</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-
<i>Viburnum venustum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	<1	-	-	-	-
<i>Rhynchospora vulcani</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-
<i>Grammitis myriophylla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	<1	<1	-	-	-

Table 5. Stem density and relative abundance of free species (dbh  $\geq$  10 cm) in 0.015 ha subplots at the Chirripó Massif, Costa Rica

Slope	Pac	Pac	Pac	Pac	Pac	Pac	All	All	All	All	All	All	All	All	All	Pac	Pac	Pac	Pac	Pac	Pac	All	All
Community	I	I	I	II	II	II	III	III	IV	IV	IV	V	V	VI	VI	VII	VII	VII	VIII	VIII	VIII	VIII	VIII
Altitude (x 100 m asi)	20	21	22	23	24	26	20	21	22	23	24	25	26	27	28	29	27	28	29	31	30	32	31
Plot number	52	50	49	48	47	53	82	81	80	79	78	77	76	75	74	73	54	55	56	58	57	60	71
Stem density (N / 0.015 ha)	12	17	14	9	9	13	11	12	15	14	16	20	15	16	21	23	11	9	15	23	11	38	10
Relative abundance (%)																							
Lower Montane Species																							
<i>Ocotea leucoxyloides</i>	8.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Inga punctata</i>	8.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ardisia nigropunctata</i>	16.7	17.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guatteria tonduzii</i>	8.3	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rondeletia buddleoides</i>	-	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Croton schiedeanus</i>	-	-	14.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhus striata</i>	-	-	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Verbesina oerstediana</i>	-	-	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ladenbergia brenesii</i>	-	-	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Miconia sp. 5 (MK 3008)</i>	-	-	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyathea caracasana</i>	-	5.9	14.3	-	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eugenia austinsmithii</i>	-	5.9	7.1	-	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bilizia hippocastanum</i>	8.3	-	7.1	-	-	-	-	8.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ardisia costaricensis</i>	-	-	-	22.2	22.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microtropis occidentalis</i>	-	-	-	-	11.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhamnus oreodendron</i>	-	-	-	-	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Alnus acuminata</i>	-	-	-	-	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Magnolia posana</i>	-	-	-	-	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nectandra salicina</i>	16.7	5.9	-	-	-	-	-	-	-	-	6.3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trichilia havanensis</i>	-	5.9	-	-	-	23.1	-	8.3	-	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Alchornea latifolia</i>	-	-	7.1	-	-	-	-	-	13.3	-	6.3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Meliosma glabrata</i>	8.3	-	-	-	-	-	-	-	-	7.1	6.3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ardisia glanduloseomarginata</i>	-	-	-	-	-	-	9.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prunus annularis</i>	-	-	-	-	-	-	9.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Beilucia costaricensis</i>	-	-	-	-	-	-	9.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Miconia platyphylla</i>	-	-	-	-	-	-	9.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tovomitopsis allenii</i>	-	-	-	-	-	-	27.3	8.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mollinedia pinchotiana</i>	-	-	-	-	-	-	-	8.3	6.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guarea tonduzii</i>	-	-	-	-	-	-	-	8.3	20	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ocotea holdridgeliana</i>	-	-	-	-	-	-	-	8.3	6.7	14.3	6.3	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lozania mutisiana</i>	-	-	-	-	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Centronia phlomisoides</i>	-	-	-	-	-	-	-	-	6.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Piper imperiale</i>	-	-	-	-	-	-	-	-	6.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Symplocos austinsmithii</i>	-	-	-	-	-	-	-	-	6.7	-	12.5	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prastoea allenii</i>	-	-	-	-	-	-	-	-	-	14.3	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyathea sp. 1 (MK 5210)</i>	-	-	-	-	-	-	-	-	-	14.3	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Phoebe hammetiana</i>	-	-	-	-	-	-	-	-	-	7.1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nectandra cutodontisii</i>	-	-	-	-	-	-	-	-	-	-	18.8	-	-	-	-	-	-	-	-	-	-	-	-
<i>Miconia cremadena</i>	-	-	-	-	-	-	-	-	-	-	6.3	-	-	-	-	-	-	-	-	-	-	-	-
Lower - Upper Montane Species																							
<i>Magnolia sororum</i>	-	-	7.1	-	-	-	-	8.3	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-
<i>Quercus copeyensis</i>	8.3	-	-	55.6	55.6	23.1	-	8.3	-	-	6.3	30	40	18.8	-	-	-	-	-	-	-	-	-
<i>Hydrangea asterolasia</i>	-	-	-	-	-	-	9.1	-	-	-	-	-	-	-	4.3	-	-	-	-	-	-	-	-
<i>Saurauia veraguasensis</i>	-	11.8	-	-	-	-	-	-	-	-	-	-	-	6.3	4.3	-	-	-	-	-	-	-	-
<i>Styrax argenteus</i>	-	5.9	-	11.1	-	-	-	-	-	-	-	-	6.7	-	-	9.1	-	-	-	-	-	-	-
<i>Quercus saemannii</i>	16.7	17.6	14.3	-	-	-	-	-	-	-	-	-	-	-	-	36.4	33.3	13.3	56.5	-	-	-	-
<i>Cyathea fulva</i>	-	-	-	-	-	-	9.1	8.3	6.7	7.1	-	-	-	6.3	-	-	-	-	-	-	-	-	-
<i>Dicksonia gigantea</i>	-	-	-	-	-	-	9.1	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-
<i>Ocotea austinii</i>	-	-	-	-	-	-	-	-	14.3	6.3	-	-	-	-	-	9.1	11.1	-	-	-	-	-	-
<i>Ardisia palmana</i>	-	-	-	-	-	-	-	-	-	12.5	-	-	-	6.3	-	-	-	-	-	-	-	-	-
<i>Weinmannia pinnata</i>	-	-	-	11.1	-	15.3	9.1	8.3	-	-	5	6.7	12.5	38.1	17.4	18.2	22.2	26.7	-	-	-	-	-
<i>Ocotea pittieri</i>	-	-	-	-	-	-	-	16.7	6.7	7.1	12.5	5	20	37.5	-	-	11.1	-	-	-	-	-	-
<i>Clusia stanophylla</i>	-	11.8	-	-	11.1	-	-	-	-	-	-	-	-	-	9.5	-	18.2	11.1	-	-	9.1	-	5.6

Table 5 Continued.

Slope	Pac	Pac	Pac	Pac	Pac	Pac	Atl	Atl	Atl	Atl	Atl	Atl	Atl	Atl	Atl	Pac	Pac	Pac	Pac	Pac	Pac	Atl	Atl	
Community	I	I	I	II	II	II	III	III	IV	IV	V	V	VI	VI	VI	VII	VII	VII	VII	VIII	VIII	VIII	VIII	
Altitude (x 100 m asl)	20	21	22	23	24	26	20	21	22	23	24	25	26	27	28	29	27	28	29	31	30	32	31	30
Plot number	52	50	49	48	47	53	82	81	80	79	78	77	76	75	74	73	54	55	56	58	57	60	71	72
Stem density (N / 0.015 ha)	12	17	14	9	9	13	11	12	15	14	16	20	15	16	21	23	11	9	15	23	11	38	10	18
Upper Montane Species																								
<i>Miconia</i> sp. 4 (MK 4996)	-	-	-	-	-	-	-	-	-	-	-	15	-	-	-	-	-	-	-	-	-	-	-	-
<i>Symplocos serrulata</i>	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hedyosmum goudotianum</i>	-	-	-	-	-	-	-	-	-	-	-	5	13.3	-	-	-	-	-	-	-	-	-	-	-
<i>Podocarpus macrostachyus</i>	-	-	-	-	-	-	-	-	-	-	-	-	6.3	14.3	4.3	-	-	-	-	-	-	-	-	-
<i>Miconia confertiflora</i>	-	-	-	-	-	-	-	-	-	-	-	-	6.3	14.3	8.7	-	-	-	-	-	-	-	-	-
<i>Cyathea suprastrigosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30.4	-	-	-	-	-	-	-	-	-
<i>Ilex pallida</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.7	-	-	-	-	-	-	-	-	-
<i>Brunellia costaricensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.3	-	-	-	-	-	-	-	-	-
<i>Cleyera theaeoides</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9.1	-	20	-	-	-	-	-	-
<i>Cornus disciflora</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	-	-	-	-	-	-
<i>Schefflera rodrigueziana</i>	-	-	-	-	-	-	-	-	-	-	10	6.7	-	4.8	4.3	-	-	-	4.3	9.1	5.3	10	-	-
<i>Quercus costaricensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	4.8	8.7	-	-	-	63.6	5.3	20	38.9	-	-
<i>Drymis granadensis</i>	-	-	-	-	-	-	-	-	-	-	5	-	-	14.3	4.3	-	-	-	-	-	-	10	5.6	-
<i>Cucurbita conifolia</i>	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	5.6
<i>Vaccinium consanguineum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.1	6.7	-	-	-	-	-	-
<i>Garrya laurifolia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	-	-	-	-	-	-
<i>Viburnum costaricanum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	13	-	-	-	-	-
<i>Zanthoxylum scheryi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13.3	13	-	-	-	5.6
<i>Hesperomeles heterophylla</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.3	-	-	-	-	-	-
<i>Miconia schneelli</i>	-	-	-	-	-	-	-	-	-	-	-	6.7	-	-	-	-	-	8.7	-	-	5.3	20	-	-
<i>Persea vesticula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	18.2	-	-	-	-
<i>Comarostaphylis arbutoides</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	76.3	-	-	-
<i>Viburnum venustum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.6	-	-	-
<i>Escallonia myrtilloides</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.6	-	-	-
<i>Myrsine pittieri</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.6	-	-	11.1
<i>Weinmannia trianae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	30	16.7	-
<i>Ilex discolor</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10	11.1	-

er is better developed in UM oakforest, which is in accordance with trends observed in Andean forests in Colombia (Van Reenen & Gradstein 1984).

Stem densities and relative abundances of tree species (dbh  $\geq$  10 cm) for 0.015 ha subplots are given in Table 5. In general stem density between LM and UM forests does not differ clearly. However, a small increase in the average density occurs with increasing altitude (12.9 stems / 0.015 ha in LM vs. 17.7 stems / 0.015 ha in UM forest). Tree density was highest in community VIII (plot 60) at 3200 m asl on the Pacific slope, where *Comarostaphylis arbutoides* Lindl. (rel. abundance: 76.3%) becomes far more abundant than *Quercus costaricensis* Liebm. This forest plot resembles the transition to (non-oak) ericaceous Subalpine Forest just below the upper forest line (Islebe & Kappelle 1994).

Schematic vegetation profile diagrams drawn for transect areas of 5  $\times$  50 m are presented in Figs. 8.a (LM) and 8.b (UM). Canopy and subcanopy trees (dbh  $\geq$  10 cm), as well as major understorey elements are shown. Whereas LM forests display a relatively open and interrupted canopy layer, dominated by emergent oak trees, the UM forests – and especially communities VII and VIII – show a lower and more flattened canopy.

Another conspicuous feature is the abundance of palms such as *Geonoma hoffmanniana* Wendl. ex Spruce and *Prestoea allenii* H. Moore in the understorey of the LM forests vs. the dense clumps of *Chusquea* bamboos in UM forest communities.

#### Classification of montane *Chusquea-Quercus* forest communities

With the help of the TWINSPLAN classification programme eight *Chusquea-Quercus* forest communities were distinguished (Table 4): four LM communities (I, II, III, IV) and four UM communities (V, VI, VII, VIII). Three were only found on the Pacific slope (I, II, VII), four only on the Atlantic slope (III, IV, V, VI), and one (VIII) appeared on both slopes, close to the upper forest line near the continental divide (Fig. 9). Figure 10 illustrates the TWINSPLAN classification through a dendrogram and shows the three-level division into the eight forest communities.

In general, the montane *Chusquea-Quercus* forests on the Chirripó Massif are dominated by *Quercus copeyensis* C. Mueller, *Q. costaricensis* and *Q. seemannii* Liebm. in the canopy layer and *Chusquea* bamboos in the understorey layer. Common tree

species are *Weinmannia pinnata* L. and the hemiepiphytic stilt-rooted *Clusia stenophylla* Standley. Other wide-ranging tree species are *Saurauia veraguasensis* Seemann, *Prunus annularis* Koehne, *Styrax argenteus* Presler, *Viburnum costaricanum* (Oersted) Hemsley, *Ocotea pittieri* (Mez) Van der Werff and the large-leaved *Oreopanax capitatus* (Jacq.) Decne. & Planch. The woody climbers *Hydrangea asterolasia* Diels and *Smilax kunthii* Killip & Morton occur frequently, as does the herbaceous vine *Bomarea acutifolia* (Link & Otto) Herb. Common herbs include *Alloplectus ichtyoderma* Hanst., *Begonia udisilvestris* C. DC. and the aroid *Anthurium concinatum* Schott., which occurs as a terrestrial as well as an epiphytic plant. Abundant ferns are *Asplenium serra* Langsd. & Fisch., *Arachniodes denticulata* (Swartz) Ching, *Elaphoglossum firmum* (Mett.) Urban and *E. eximium* (Mett.) Christ. Various epiphytic species of *Anthurium*, *Elaphoglossum*, *Peperomia* Ruiz & Pavón and *Polypodium* L. inhabit the bases of *Quercus* tree trunks.

#### *Geocological description of lower montane Mollinedia-Quercus forests*

These lauraceous-fagaceous forests occur between about 2000 and 2600 m asl and are characterized by the abundance of understory palms (*Geonoma hoffmanniana*, *Chamaedorea warszewiczii* Wendl. and *Prestoea allenii*), sometimes accompanied by the bamboo *Aulonemia viscosa* (Hitche.) McClure or the cyclanth *Sphaeradenia irazuensis* (Cufod.) Harling. Important tree species are *Quercus copeyensis*, *Mollinedia pinchotiana* Perkins, *Trichilia havanensis* Jacq., *Ardisia glandulosomarginata* Oersted, *Tovomitopsis allenii* Maguirre, *Billia hippocastanum* Peyritsch, *Nectandra salicina* C.K. Allen, *Microtropis occidentalis* Loes., *Guarea tonduzii* C. DC., *Alchornea latifolia* Swartz, *Meliosma glabrata* (Liebmann) Urban, *Miconia platyphylla* (Benth.) L.O. Williams, *Lozania mutisiana* Roemer & Schult., *Ocotea austinii* C.K. Allen and *O. holdridgeana* W. Burger. Important herbaceous taxa (both terrestrial and epiphytic) are *Monstera deliciosa* Liebmann and *Peperomia palmana* C. DC. as well as the ferns *Asplenium harpeodes* Kunze and *Vittaria graminifolia* Kaulf. The climber *Cissus martiniana* Woodson & Seibert is frequently observed.

The LM *Quercus* forests on the Pacific slope are characterized by a unique combination of the tree species *Eugenia austinsmithii* Standley, *Ardisia costaricensis* Lundell, *Oreopanax liebmannii* Marchal, *Gutteria tonduzii* Diels, *Rondeletia buddleioides*

Benth., *Xylosma intermedia* (Seemann) Triana & Planch. and *Dendropanax querceti* J.D. Smith. *Magnolia sororum* Seibert is often a codominant canopy species. Other important elements are the treefern *Cyathea caracasana* var. *maxonii* (Underw. in Maxon) Tryon, the shrubs *Cavendishia talamancensis* Luteyn, *Dicliptera skutchii* Leonard and *Psychotria aubletiana* Steyerem., the bamboo *Chusquea longifolia* Sw. and the climber *Passiflora* L. sp. (MK 3282). The Atlantic LM *Quercus* forests are dominated by the trees *Phoebe hammeliana* W. Burger, *Nectandra cufodontisii* (Schmidt) C.K. Allen and *Miconia cremadena* Gleason, the shrub *Psychotria panamensis* var. *panamensis* Standley and the herbs *Hansteinia ventricosa* and *Anthurium mickelii*. The cyclanth *Asplundia microphylla* (Oersted) Harling occurs in both terrestrial and epiphytic forms.

#### *I. Pacific Ocotea tenera-Quercus seemannii forest community*

This forest community is dominated by 30 to 50 m tall *Quercus seemannii* trees, sometimes accompanied by *Q. copeyensis*. The combination of different bamboos (*Aulonemia viscosa* and *Chusquea longifolia*) and the dwarf palm *Geonoma hoffmanniana* is characteristic of the understory. The forest is made up of the common subcanopy tree species *Eugenia austinsmithii* and the less frequent but exclusive presence of e.g., *Ocotea tenera* Mez & J.D. Smith ex Mez, *O. leucoxyton* (Sw.) Laness. and *Picramnia latifolia* Tulasne. A characteristic shrub is *Palicourea discolor* K. Krause. A diagnostic species in the herbaceous layer is *Tradescantia zanonii* (L.) Sw. Locally, *Magnolia sororum* trees appear with cover values up to 25%. Due to past logging efforts below 2000 m asl at the Pacific slope of the Chirripó Massif, the *Ocotea tenera-Quercus seemannii* forests are restricted to the belt between 2000 and 2250 m asl along this slope. It is expected that this forest community extends down to ca. 1800 m asl in other, less disturbed parts of the Cordillera de Talamanca (see for instance Kappelle *et al.* 1989).

The soil profile in plot 50 (profile VU14) is moderately deep, well-drained, dark-brown, overlaid by a 13 cm thick layer of fibric to sapric organic soil material. Loamy sand overlies a sandy loam containing stones and weathered boulders. Both crumb and subangular blocky structures are observed in the lower part of the soil profile. Mottles are probably a result of very weathered gravel (section of 2 cm), which has lost its original rock structure. Very fine to medium pores are

found. Abundant roots occur in the organic soil material. The soil has been classified as a (Histic) Acric Hapludand (Soil Survey Staff 1975) or a Humi-Haplic Andosol (FAO 1988).

### II. Pacific *Ocotea mollicella-Quercus copeyensis* forest community

Taxa like *Ocotea mollicella* (Blake) Van der Werff and *Chusquea patens* L.G. Clark are diagnostic for this 30 to 40 m tall forest community, although *Quercus copeyensis* and *Clusia stenophylla* are dominant. *Alnus acuminata* Kunth is abundant on steeper sites, probably associated with mass movements. Other important tree species are *Eugenia austinsmithii*, *Microtropis occidentalis*, *Mollinedia pinchotiana* and *Weinmannia pinnata*. The tree fern *Cyathea caracasana* var. *maxonii* is common at open sites with high light intensities. The conspicuous cyclanth *Sphaeradenia irazuensis* shares the understorey with *Geonoma hoffmanniana* and *Chusquea longifolia*. The *Ocotea mollicella-Quercus copeyensis* forests are found between 2250 and 2650 m asl on the Pacific slope.

The soil profile in plot 48 (profile VU13) is moderately deep, well-drained, dark-brown to brownish yellow, with a dark gray eluvial horizon containing some pure quartz grains. Podsolization is taking place. The mineral soil material is overlaid by a 11 cm thick layer of fibric to sapric organic soil material. The structure is weak and subangular blocky. Loamy sand overlies a sandy loam, which contains very weathered gravel resulting in the presence of residual nodules. Micro to very fine pores are common, while few medium pores occur in the lower part. Abundant roots traverse the organic soil material, but are few in the eluvial horizon and the horizon immediately below. The soil has been classified as a (Histic) Alic Hapludand (Soil Survey Staff 1975) or a Humi-Haplic Andosol (FAO 1988).

### III. Atlantic *Persea caerulea-Quercus copeyensis* forest community

This LM forest community is represented by stands of ca. 35 m tall *Quercus copeyensis* with *Mollinedia pinchotiana*, *Phoebe hammeliana*, *Tovomitopsis allenii* and *Weinmannia pinnata* predominant in the sub-canopy layer. Less frequent trees are *Ardisia glandulosomarginata*, *Ocotea pittieri*, *Persea caerulea* (Ruiz & Pavón) Mez. Important shrubs are *Bellucia costaricensis* Cogn., *Besleria formosa*, *Hansteinia ventricosa* and *Psychotria dichroa* (Standley) C.M. Taylor. Oth-

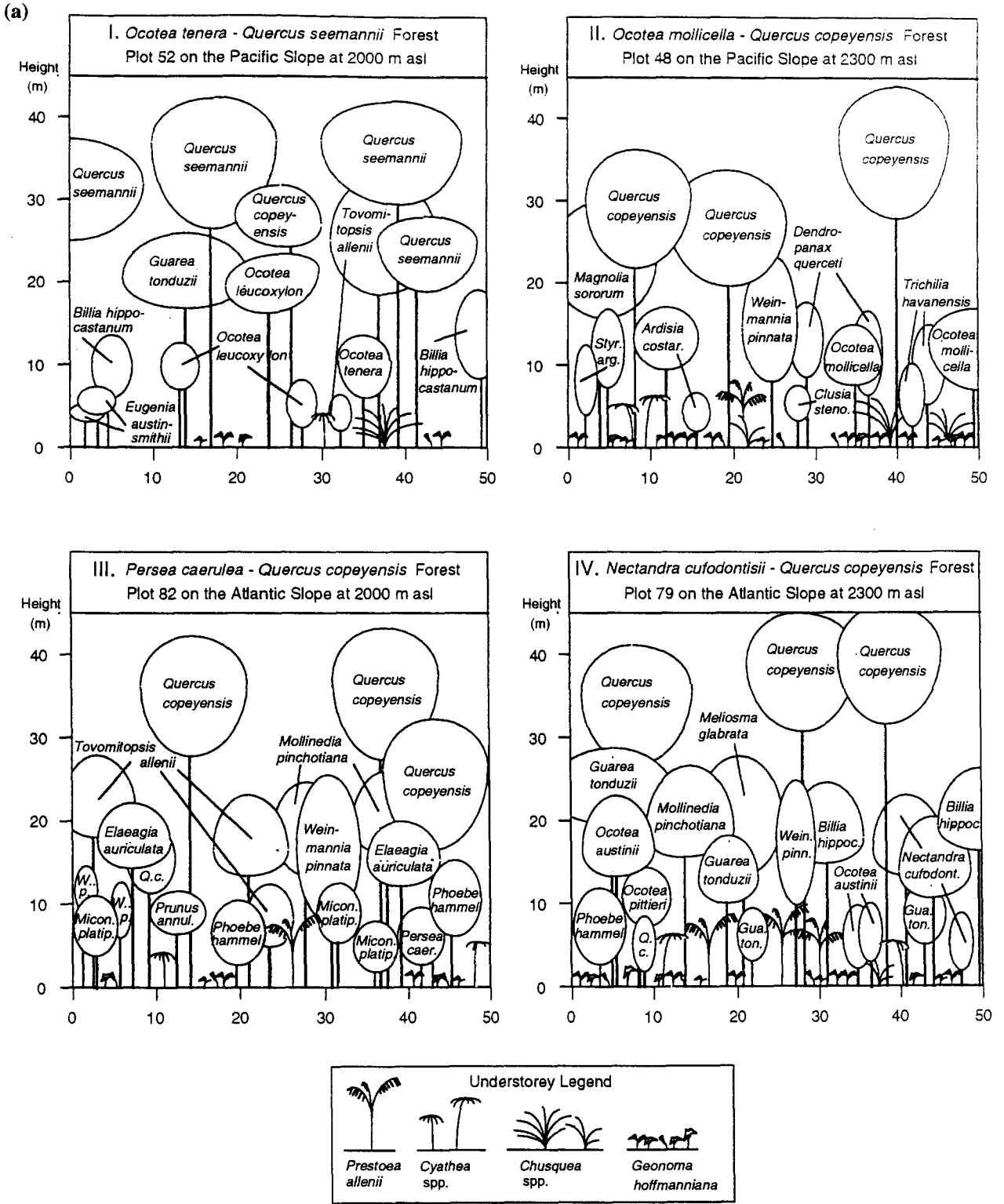
er understorey elements include the tree fern *Cyathea fulva* (Mart. & Gal.) Fée, the palms *Geonoma hoffmanniana* and *Prestoea allenii*, and the epiphytic cyclanth *Asplundia microphylla*. The *Persea caerulea-Quercus copeyensis* forests are found below 2150 m asl on the Atlantic slope and probably extend down to ca. 1800 m asl (M. Kappelle, pers. obs.). However, this is not yet systematically confirmed, as sampling for the present data set took place down to 2000 m asl only.

The soil profile in plot 81 (profile VU32) is moderately deep, moderately well-drained, black to brownish yellow, overlaid by a 20 cm thick layer of fibric to sapric organic soil material. Clayey loam overlies clay containing some very weathered gravel in the lower profile causing mottles. Mottles in the upper profile are a result of accumulated organic matter (filled-up root spaces). Material is slightly sticky and slightly plastic throughout. Structure is moderate to weak subangular blocky. Micro and very fine pores are common. Larger roots abound in the organic soil material and very fine to fine roots common in the first two mineral horizons. The soil has been classified as a (Histic) Typic Hapludand (Soil Survey Staff 1975) or a Humi-Haplic Andosol (FAO 1988).

### IV. Atlantic *Nectandra cufodontisii-Quercus copeyensis* forest community

Diagnostic species for this 30 to 40 m tall forest community are the tree *Nectandra cufodontisii*, the shrub *Besleria barbensis* Hanst. and a cyatheaceous tree fern (MK 5210), as well as the rare *Grammadenia rufa* Lundell and *Solanum incomptum* Bitter. Characteristic species include *Quercus copeyensis*, *Mollinedia pinchotiana* and *Ocotea pittieri*, but also *Alchornea latifolia*, *Ardisia palmana* J.D. Smith, *Billia hippocastanum*, *Guarea tonduzii*, *Symplocos austinsmithii* Standley, *Weinmannia pinnata*. Principal understorey monocots are *Aulonemia viscosa*, *Prestoea allenii*, *Sphaeradenia irazuensis*, and the ubiquitous *Geonoma hoffmanniana*. The rubiaceous *Psychotria panamensis* var. *panamensis* is profuse in the shrub layer. The *Nectandra cufodontisii-Quercus copeyensis* forests are found between 2150 and 2450 m asl on the Atlantic slope.

The soil profile in plot 79 (profile VU31) is moderately deep, moderately well-drained, dark brown to yellowish brown, with a 29 cm thick layer of fibric to sapric organic soil material. Sandy loam overlies loam containing some weathered gravel. Soil material is slightly sticky and slightly plastic throughout, with a moderate subangular blocky structure. Few medium



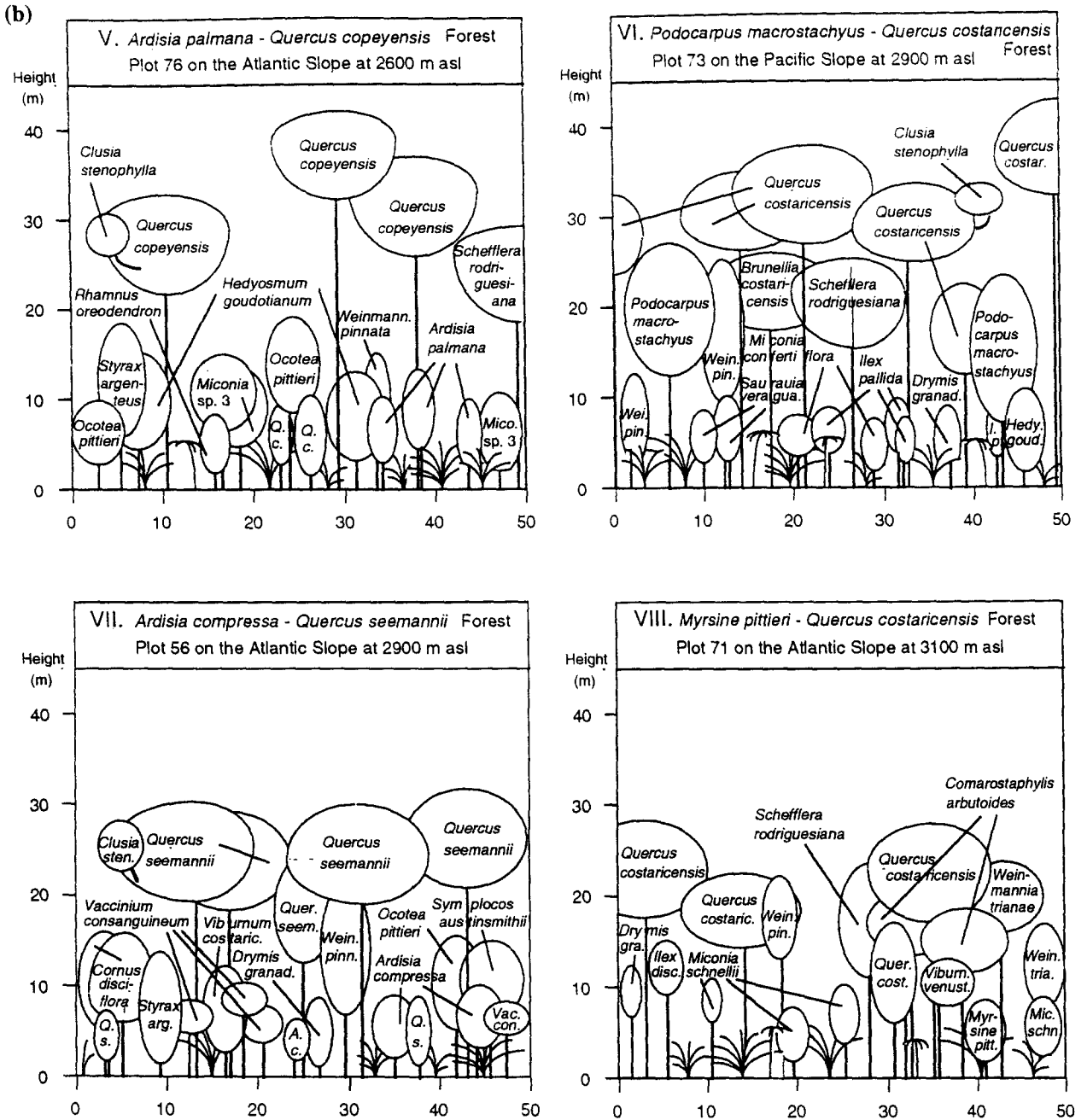


Fig. 8. (a) Schematic vegetation profile diagrams (50 × 5 m) of Lower Montane *Quercus* forest communities (I–IV) in Chirripó National Park, Costa Rica. (b) Schematic vegetation profile diagrams (50 × 5 m) of Upper Montane *Quercus* forest communities (V–VIII) in Chirripó National Park, Costa Rica. Legend as in (a).

pores occur in the upper profile. Roots are abundant in the organic soil material. The soil has been classified as a (Histic) Andic Humitropept (Soil Survey Staff 1975) or a Humi-Andic Dystric Regosol (FAO 1988).

*Geocological description of upper montane Schefflera-Quercus forests*

The myrsinaceous-fagaceous UM *Schefflera-Quercus* Forests (2600–3200 m asl) are characterized by an understorey completely dominated by the bam-

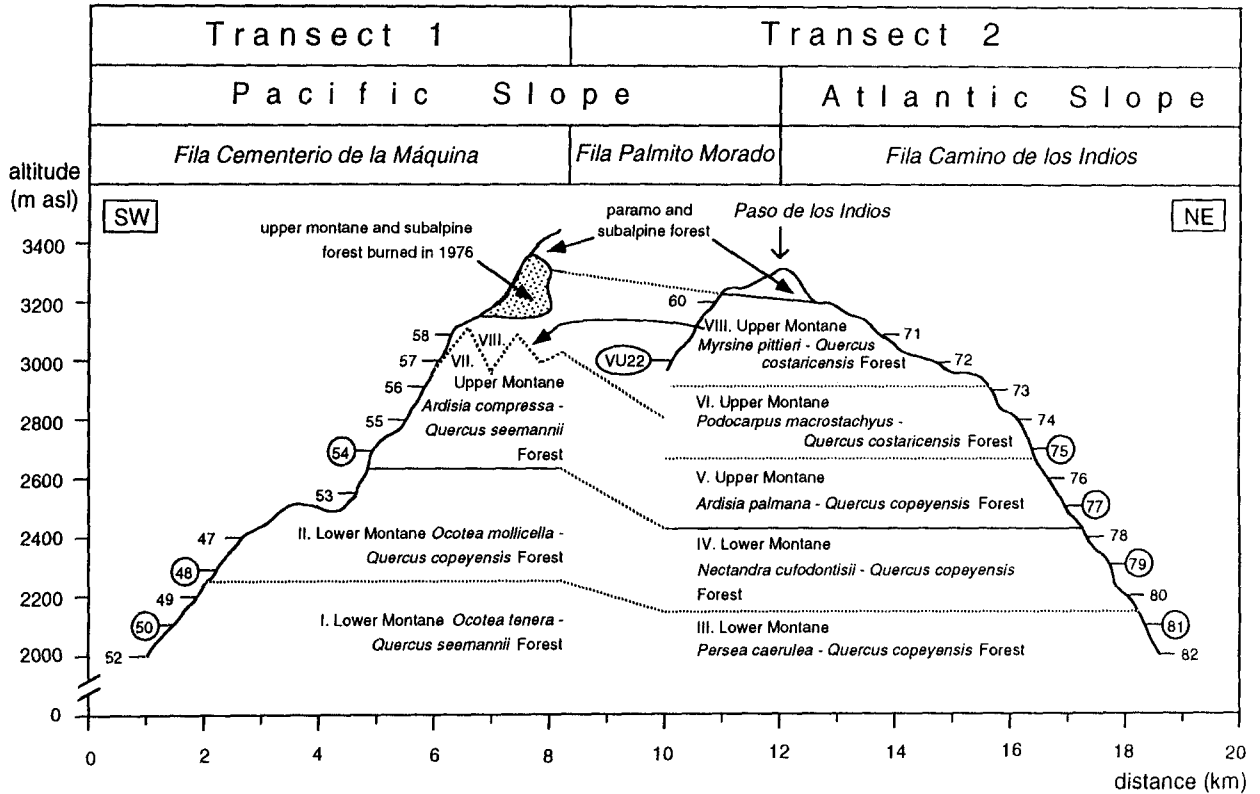


Fig. 9. Schematic mountain profile showing the altitudinal zonation of montane *Quercus* forest communities along two transects through Chirripó National Park, Costa Rica. Plot numbers are indicated along the transects. Numbers in circles refer to plots in which soil profiles were studied. The location of the transects is shown in Fig. 1.

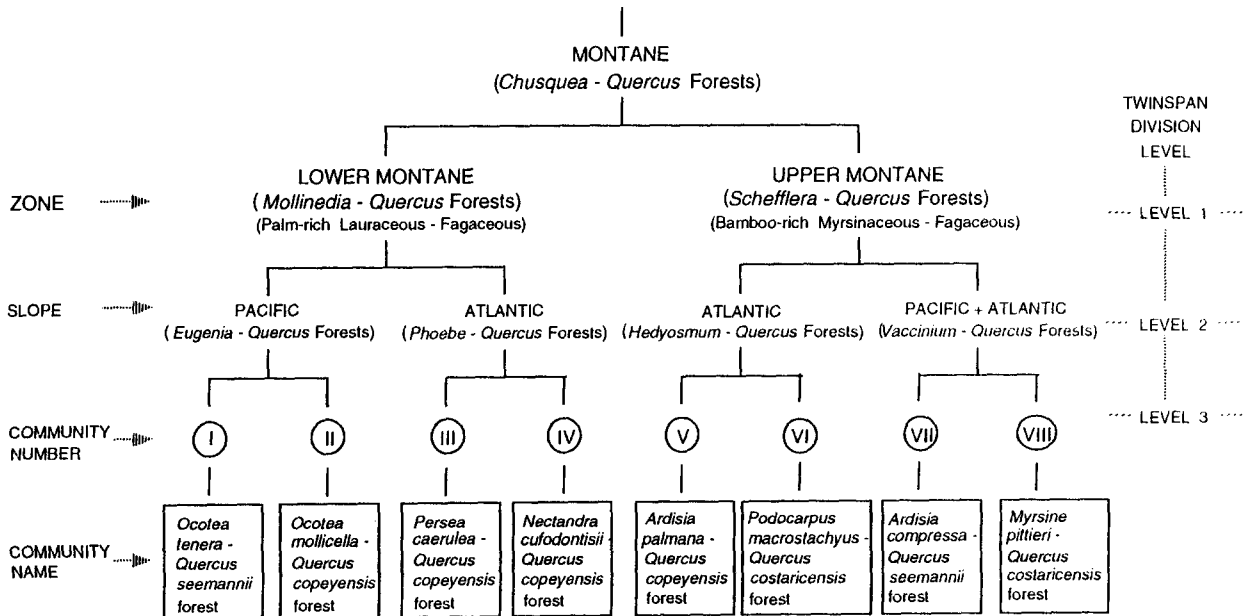


Fig. 10. Dendrogram of the TWINSPLAN vegetation classification of the montane *Quercus* forest communities in Chirripó National Park, Costa Rica.



boo genus *Chusquea*. In the canopy layer *Quercus* (mainly *Q. costaricensis*) is accompanied by *Schefflera rodriguesiana* Frodin. Subcanopy trees often include *Rhamnus oreodendron* L.O. Williams, *Drimys granadensis* L.f., *Miconia schnellii* Wurdack, *Zanthoxylum scheryi* Lundell and *Ilex pallida* Standley. *Chusquea talamancensis* Y. Widmer & L.G. Clark and *C. sp.* (MK 4319) characterize the understorey. They are often accompanied by terrestrial and epiphytic ericaceous shrubs such as *Disterigma humboldtii* (Klotzsch) Niedenzu, *Cavendishia bracteata* (Ruiz & Pavón ex J. St. Hil.) Hoer., *Macleania rupestris* (Kunth) A.C. Smith and *Sphyrospermum cordifolium* Benth. The ground cover is made up of the herbs *Maianthemum paniculatum* (Mart. & Gal.) La Frankie, *Centropogon costaricae* (Vatke) McVaugh and *Peperomia saligna* Kunth, the ferns *Blechnum viviparum* (Broadh.) C. Chr. and *Elaphoglossum latifolium* (Swartz) J. Smith, and the terrestrial bromeliad *Vriesea williamsii* L.B. Smith.

The UM *Quercus* forests on the Pacific slope are characterized by the diagnostic *Cleyera theaeoides* (Swartz) Choisy, *Hesperomeles heterophylla* (Ruiz & Pavón) Hook. and *Persea vesticula* Standley & Steyerl. The small-leaved *Vaccinium consanguineum* Klotzsch and *Fuchsia microphylla* Kunth, the coriaceous *Ilex discolor* var. *lamprophylla* (Standley) Edwin as well as the ferns *Elaphoglossum furfuraceum* (Mett.) Christ and *Eriosorus flexuosus* (Kunth) Copel. occur frequently. The Atlantic UM *Quercus* forests are recognized by the presence of the widely-distributed understorey trees *Hedyosmum goudotianum* Solms-Laubach and *Miconia* Ruiz & Pavón sp. 4 (MK 4996), and the less frequent shrub *Cybianthus pastensis* (Mez) Agostini and the climber *Dioscorea standleyi* C. Morton. The trees *Ocotea pittieri* and *Weinmannia pinnata* are often observed. High cover values of the terrestrial fern *Elaphoglossum firmum* (Mett.) Urban are common.

#### V. Atlantic *Ardisia palmana-Quercus copeyensis* forest community

This forest is the only UM community dominated by 30 to 35 (45) m tall *Quercus copeyensis* trees. The presence of several *Geonoma hoffmanniana* individuals – a typical LM understorey species – at 2500 m asl suggests an almost transitional stand just above the limit with LM forests. *Symbolanthus pulcherrimum* Gilg. is the single diagnostic species found. Prominent trees include *Ardisia palmana*, *Miconia schnellii*, *Ocotea pittieri*, *Prunus annularis*, *Rhamnus oreodendron*,

*Schefflera rodriguesiana*, *Styrax argenteus* and *Weinmannia pinnata*. Predominating taxa in the understorey are *Chusquea talamancensis* and *C. sp.* (MK 4319). Locally, *Sphaeradenia irazuensis* becomes important. The fern *Elaphoglossum latifolium*, *E. firmum* and *E. erinaceum* (Fée) T. Moore may cover together over half of the ground surface. The *Ardisia palmana-Quercus copeyensis* forests are found between 2450 and 2650 m asl on the Atlantic slope.

The soil profile in plot 77 (profile VU30) is shallow, imperfectly drained, black to yellowish brown, with a very weak developed iron pan. A layer of 25 cm fibric to sapric organic soil material overlies the eluvial horizon, while podsolization is taking place. Sandy clayey loam and loam overlie a sandy loam, all containing weathered to very weathered gravel and stones causing mottles. Micro and very fine pores are common. Large roots are abundant in sapric organic matter, but very fine to fine roots are few and prevail in the eluvial horizon. The soil has been classified as a (Histic) Placic Humitropept (Soil Survey Staff 1975) or a Humi-Dystric Regosol (FAO 1988).

#### VI. Atlantic *Podocarpus macrostachyus-Quercus costaricensis* forest community

This community is easily recognized by the occurrence of *Podocarpus macrostachyus* Parl., the only gymnosperm tree species found along the montane Chirripó transects. Other diagnostic species are the broad-leaved trees *Brunellia costaricensis* Standley and *Miconia confertiflora* Almeda, the herb *Centropogon talamancensis* Wilbur and the ground-dwelling fern *Elaphoglossum alfredii* Rosenst. *Quercus costaricensis* with individuals over 35 m tall is the dominant canopy species. *Quercus seemannii* is occasionally observed. Abundant woody taxa are *Drimys granadensis*, *Ilex pallida*, *Ocotea pittieri*, *Saurauia veraguasensis*, *Schefflera rodriguesiana* and *Weinmannia pinnata*. Dense clumps of *Chusquea talamancensis* and *Chusquea sp.* (MK 4319) are frequent in the understorey. The epiphytic ericad *Cavendishia bracteata* and the climbing *Hydrangea asterolasia* occur frequently. The *Podocarpus macrostachyus-Quercus costaricensis* forests are found between 2650 and 2950 m asl on the Atlantic slope.

The soil profile in plot 75 (profile VU29) is shallow, imperfectly drained, very dark grayish brown to yellowish brown, with a dark gray, weakly developed, eluvial horizon, overlaid by a 30 cm thick layer of fibric to sapric soil material. Podsolization is taking place.

Soil texture ranges from sandy loam with a little gravel to loam frequently containing gravel. Some gravel is very weathered causing mottling. Soil consistence is slightly plastic and sticky. Micro to fine pores occur in all horizons. Roots are abundant in the organic soil material. The soil has been classified as a (Histic) Typic Placudand (Soil Survey Staff 1975) or a Humi-Mollic Andosol (FAO 1988).

#### VII. Pacific *Ardisia compressa-Quercus seemannii* forest community

*Ardisia compressa* Kunth, *Cleyera theaeoides*, *Persea vesticula* and *Vaccinium consanguineum* are characteristic tree species in this ca. 30 m high forest community. The canopy layer is almost exclusively made up of *Quercus seemannii* individuals. The hemiepiphytic species *Clusia stenophylla* is abundant. Other prominent trees include *Ilex pallida*, *Rhamnus oreodendron*, *Schefflera rodriguesiana*, *Styrax argenteus*, *Viburnum costaricanum* and *Zanthoxylum scheryi*. The understory is occupied by the dominant bamboo *Chusquea talamancensis*. The epiphytic ericad *Macleania rupestris* is commonly found on *Quercus* trunks. The ground cover is made up of *Anthurium concinatum* and ferns such as *Elaphoglossum furfuraceum*. The pioneering *Senecio megaphyllus* Greenman thrives in open areas, such as tree fall gaps. The *Ardisia compressa-Quercus seemannii* forests are found between 2650 and 3150 m asl on the Pacific slope.

The soil profile in plot 54 (profile VU11) is moderately deep, well-drained, black to olive yellow, with a very dark grayish brown eluvial horizon overlaid by a 13 cm thick layer of fibric to sapric organic soil material. Podsolization is taking place. Soil texture is loamy sand with an increase of gravel and stones to the lower part of the profile, being weathered or very weathered. Structural development is weak. Material is sticky and plastic in the horizon underlying the eluvial horizon. Very fine and fine pores, as well as abundant roots occur in the organic soil material. The soil has been classified as a (Histic) Typic Hapludand (Soil Survey Staff 1975) or a Humi-Umbric Andosol (FAO 1988).

#### VIII. Pacific-Atlantic *Myrsine pittieri-Quercus costaricensis* forest community

This 20 to 25 (30) m tall community was previously recognized and described by Kappelle *et al.* (1989), who later divided it into two subcommunities: a moist Pacific *Comarostaphylis arbutoides-Quercus costari-*

*ensis* forest and a wet Atlantic *Ilex discolor-Quercus costaricensis* forest (Kappelle 1992). The forest plots included in the present study fit within these earlier descriptions.

The *Myrsine pittieri-Quercus costaricensis* forests are the uppermost montane forests present in Costa Rica and are dominated by *Quercus costaricensis* in the ca. 20–25 m high canopy layer, and *Chusquea talamancensis* up to 6 m tall in the understory. *Comarostaphylis arbutoides*, *Myrsine pittieri* (Mez) Lundell and *Weinmannia trianae* Wedd. var. *sulcata* (Engl.) Cuatrecasas are the more important diagnostic tree species, with *C. arbutoides* prevailing on the Pacific slope and *W. trianae* on the Atlantic slope. Abundant woody species include *Clusia stenophylla*, *Drimys granadensis*, *Miconia schnellii*, *Oreopanax capitatus*, *Schefflera rodriguesiana*, *Vaccinium consanguineum* and *Zanthoxylum scheryi*. *Macleania rupestris* is a common epiphyte, while its congener *M. talamancensis* Wilbur & Luteyn is only rarely observed. The large orchid *Maxillaria biolleyi* (Schltr.) L.O. Williams appears as a terrestrial element. Near the border with the gnarled Subalpine Dwarf Forest, woody taxa like *Clethra gelida* Standley, *Gaiadendron punctatum* (Ruiz & Pavón) Don and *Viburnum venustum* C. Morton prevail. Species preferring the upper portion of the Pacific slope are *Diplostephium costaricense* Blake, *Gaultheria erecta* Vent., *Pernettya prostrata* (Cav.) DC. and to a lesser extent *Persea vesticula* and *Weinmannia pinnata*. Some taxa thriving better on the Atlantic slope are *Grammitis myriophylla* (Mett. ex Baker) Morton and *Rhynchospora vulcani* Boeckeler, but also *Cavendishia bracteata*, *Elaphoglossum latifolium*, *Palicourea adusta* Standley and *Senecio costaricensis* R.M. King. The *Myrsine pittieri-Quercus costaricensis* forests are found between 2950 and 3250 m asl on the Pacific slope (*Comarostaphylis arbutoides-Quercus costaricensis* forest *sensu* Kappelle 1992)), and between 2950 and 3150 m asl on the Atlantic slope (*Ilex discolor-Quercus costaricensis* forest *sensu* Kappelle (1992)).

Soil profile VU22 near plot 60 is moderately deep, well-drained, dark-brown to dark yellowish brown, with a 10 cm thick layer of sapric organic soil material. Loamy sand overlies a sandy loam containing very frequently fresh gravel and stones. The structure is medium granular and subangular blocky, but material becomes structureless in parts of the B-horizon. Soil consistence is slightly sticky to sticky, and slightly plastic to plastic. Micro (vesicular) pores are more or less common. Roots are abundant in the organic soil

material. The soil has been classified as a (Histic) Typic Hapludand (Soil Survey Staff 1975) or a Humi-Haplic Andosol (FAO 1988).

## Discussion

### *Changes along Chirripó's altitudinal gradient*

In montane oakforests on the slopes of Cerro Chirripó, a series of climatic, geologic, geomorphologic, edaphic and vegetation changes occur with increasing elevation. The most important environmental factor correlated with the distribution of oak forest communities is the average air temperature, which drops from c. 17.6 °C at 2000 m asl (LM forest) to 13.6 °C at 2700 m asl (UM forest). Soil temperatures measured at 30 cm soil depth decrease significantly as altitude increases. According to Lauer (1981), soil temperatures below ca. 8–10 °C critically reduce the water absorption capacity of roots. Figure 6 shows that all soil temperatures measured range above 8 °C and, therefore, do not necessarily restrict tree growth. If the regression lines are extrapolated below 8 °C, one will arrive at altitudes of c. 3150–3350 m asl, which coincide with the change to the treeless páramo zone, just above the upper forest line. Thus, the temperature data recorded on Cerro Chirripó support Lauer's suggestion. In this context, Chirripó's LM and UM oakforests easily fit within Central America's 'Tierra Fría' belt (1800–3200 m asl), where the average annual temperature ranges from c. 10 to 17 °C (Troll 1959, 1968; Lauer 1968, 1976).

The thickness of the humus profile on Chirripó's montane slopes (2000–3200 m asl) is highest between 2300 and 2700 m asl, probably as a consequence of low temperatures and high precipitation (soil saturation), which account for a low degree of soil bioactivity and subsequently slow decomposition process (cf. Odum 1970). The size of the humus layer is probably also due to high levels of soil acidity. In general, accumulation of organic material appears to be higher at places where soil moisture contents are higher (high precipitation levels).

Forest stature becomes more compressed at higher elevations. While average canopy tree height declines, the shrub, herb and bryophyte layers retain their stature rather well. On the other hand, with increasing elevation a small increase in stem density and a decrease in average stem diameter are observed. The upper UM forest canopy is more flattened and less interrupted

than in stands at lower altitudes. The strong wind prevailing near the higher crests, especially on the Atlantic slope, is the main factor responsible for the shaping and smoothening of the canopy surface. Furthermore, the considerable effect that hurricanes have on the shape of tree canopies in the Caribbean region – to which Talamanca's Atlantic slope climatically belongs – has been recognized in the past (cf. Odum & Pigeon 1970; Brokaw & Walker 1991).

Floristic changes along the altitudinal gradient are best expressed in the significant drop in species richness with increasing elevation (Fig. 7). First, the TWINSPLAN classification immediately separates species-rich LM forests from less diverse UM forests, and secondly distinguishes between Pacific and Atlantic forests (Fig. 10). Next, the shift from dwarf palms in the understorey at lower altitudes to bamboos at higher elevations is evident. In the subcanopy layer, the large number of Lauraceae found in LM forests are replaced by Myrsinaceae in UM forests. At the same time, one notes the substitution of terrestrial shrubs belonging to the Rubiaceae and Gesneriaceae by members of the Ericaceae and Asteraceae.

### *Comparison with other studies on Talamanca montane Quercus forests*

The present study represents one of the first detailed studies on the changes in the ecology of Costa Rica's montane *Quercus* forests as found along an altitudinal gradient. However, several previous studies on the botany of Talamanca's montane oakforests have laid the basis for this research (e.g., Weber 1958; Holdrige *et al.* 1971; Blaser 1987; Jiménez *et al.* 1988; Kappelle *et al.* 1989; Orozco 1991). Weber (1958) was the first to note clear changes in Chirripó's floristic composition with increasing altitude. Between 1900 and 2100 m asl he observed epiphyte-rich cloud forest dominated by *Quercus* and accompanied by stilt-rooted *Clusia* species, *Weinmannia pinnata*, orchids, *Elaphoglossum*, Hymenophyllaceae, the epiphytic ericad *Satyria*, and the understorey cyclanth *Sphaeradenia*. At ca. 2450 m asl he observed a compositional change, coinciding with the transition from LM to UM oakforest, and then came upon the sudden appearance of numerous *Myrsine* treelets. This immediate change justifies the use of the term 'myrsinaceous' as an adjective to characterize UM oakforest. In this forest stand Weber (1958) came across clumps of *Chusquea* bamboos, a dominant *Elaphoglossum* cover on the forest floor, and scattered *Prestoea* palm trees. At 2850 m asl he found

a patch of burned oakforest with pioneering *Bocconia*, *Gnaphalium*, *Phytolacca*, *Pteridium*, and *Senecio* as well as some undisturbed fragments with epiphytic *Anthurium*, *Peperomia*, bromeliads and bryophytes. We observed a similar shrubby postfire vegetation near 3100 m asl along Transect 1 (Fig. 9). On the transition from UM forest to the páramo Weber (1958) accounted for a number of woody species of *Buddleja*, *Drimys*, *Gaultheria*, *Myrrhidendron* and *Vaccinium*, all characteristic for the Subalpine (Dwarf) Forest (Islebe & Kappelle 1994). A decade later Holdridge *et al.* (1971) presented an in-depth survey of forest environments occurring from sea level to Talamanca's summits. The oak forests they studied at El Empalme (LM, 2350 m asl), La Chonta (LM, 2400 m asl) and Villa Mills (UM, 3080 m asl) – sites that were revisited by Kappelle *et al.* (1989) – much resemble those observed at Cerro Chirripó. Oak forests at the La Chonta site are very similar to the here-described *Ocotea tenera-Quercus seemannii* community (no. I), while the Villa Mills forest stand is comparable to the common *Myrsine pittieri-Quercus costaricensis* community (no. VIII), known from different localities in the western Cordillera de Talamanca (Kappelle *et al.* 1989; Kappelle 1992; this study). The El Empalme oak forest corresponds to Kappelle *et al.*'s (1989) *Quercus seemannii-Q. copeyensis* community, a forest type not explicitly observed along the transects on Cerro Urán and Cerro Chirripó. More recently, Blaser (1987) gave descriptions of an Atlantic *Quercus copeyensis*-dominated 'White Oak Forest' (Villa Mills, 2650–2700 m asl), which represents a stand belonging to our UM *Ardisia palmana-Quercus copeyensis* community (no. V; cf. plot 76 at 2600 m, presented in Fig. 8b). His 'Black Oak Forest' with almost equal quantities of *Quercus copeyensis* and *Q. costaricensis* corresponds to a transition from Chirripó's *Ardisia palmana-Quercus copeyensis* community to the *Podocarpus macrostachyus-Quercus costaricensis* community. Kappelle *et al.* (1989) previously recognized this transition in the western Talamanca's as a wide-spread *Quercus copeyensis-Q. costaricensis* community. Blaser (1987), Kappelle *et al.* (1989), but also Orozco (1991) found this transitional association to occur at lower elevations than one was to be expected at Cerro Chirripó. This is probably explained by the 'Massenerhebung' Effect *sensu* Grubb (1971; see also Schröter's (1926) first account on this phenomenon in the Alps), which states that vegetation belts in the Tropics are pressed down on smaller mountains, such as near Villa Mills at Cerro de La Muerte

(Buenavista Massif), which is c. 300 m less high than Cerro Chirripó. However, the exact phytosociological position of this mixed, transitional oak forest type is still not fully understood, as it has not been recorded in the transects along the slopes of Cerro Chirripó. Orozco (1991) following Blaser (1987) gave descriptions of six oak forest stands (stems  $\geq 10$  cm dbh) between 2000 and 2850 m asl in the area between El Empalme and Villa Mills, at a distance of ca. 30 to 60 km W of Cerro Chirripó. One of her Villa Mills sites at 2700 m asl (the same location as Blaser's (1987) 'White Oak Forest' plot) as well as a stand at Macho Gaff (2600 m asl) correspond to Chirripó's UM *Ardisia palmana-Quercus copeyensis* community. Another Villa Mills site (the same location as Blaser's (1987) 'Black Oak Forest' plot) and the forest Orozco (1991) studied at 2850 m asl on the slopes of Cerro Asunción, again represent the transitional *Quercus copeyensis-Q. costaricensis* community described by Kappelle *et al.* (1989). Orozco's (1991) two other study sites at (Pacific) División (2050 m asl) and (Atlantic) Macho Mora (2550 m asl), respectively, are characterized by LM mixed oakforest belonging to Kappelle *et al.*'s (1989) *Quercus seemannii-Q. copeyensis* community, which – like the other mixed oakforest type – is not known from the Chirripó National Park. Furthermore, Kappelle *et al.* (1989) discussed two other montane oakforest types: (i) the *Myrsine pittieri-Quercus costaricensis* forest community (2900–3100 m) near the Cerros Las Vueltas, De la Muerte and Urán (Kappelle 1992; This study); and (ii) the *Geonoma hoffmaniana-Quercus copeyensis* community (2400–2800 m asl) on the Pacific slope near La Esperanza del Guarco, Providencia and Trinidad de Dota. More detailed studies on this forest type in the Western Talamancas are needed in order to find out which of Chirripó's *Geonoma*-rich *Quercus copeyensis* forest communities can be regarded as its equal or closest relative.

#### *Comparison with extra-Talamancan montane Quercus forests in Costa Rica*

Along the (Atlantic) La Selva-Volcán Barva altitudinal transect in the Costa Rican Cordillera Volcánica Central, Hartshorn & Peralta (1988) found 'lower montane' (LM) forest between 1450 and 2500 m asl, and 'montane' (UM) forest between 2500 and the volcano's summit at 2906 m asl ('names' *sensu* Holdridge 1969). Canopy heights in LM and UM forest on Volcán Barva's slopes were considerably lower (c. 15–25 m) than

in the Chirripó Park, a difference probably explained by the low number of (large) oaks at Barva's mid-elevations and the possibly stronger influence of the Caribbean Trade Winds, which cause a flattening of the canopy surface. Barva's LM forests were dominated by genera such as *Billia*, *Guatteria*, *Hieronyma* and *Turpinia*, and the oak species *Quercus tonduzii*. The main understorey element was *Geonoma hoffmanniana* – just as in LM forest on Cerro Chirripó – in association with *Chusquea pohlii*. UM forest at Barva included taxa well-known from the Talamanca's: *Brunellia costaricensis*, *Drimys granadensis*, *Ilex vulcanicola*, *Weinmannia pinnata* and *Didymopanax pittieri* (= *Schefflera rodiguesiana*). Heaney & Proctor (1990) present additional information on 1.0 ha forest plots along the same transect and mention for a 20–25 m tall LM forest at 2000 m asl the presence of *Ardisia*, *Miconia*, *Viburnum*, Hamamelidaceae and treeferns, whereas *Clethra* was found in a 20–23 m tall UM forest at 2600 m asl. Along the La Selva – Volcán Barva transect tree species richness (stems  $\geq 10$  cm dbh) decreased from 69 at 2000 m asl to 35 at 2600 m asl, thus in a similar way as in Chirripó's oak forests (Fig. 7). Although Marss *et al.* (1988) provided information on soil changes along the same transect and discovered a rise in organic carbon and exchangeable elements with increasing elevation, no such significant increases were recorded for Chirripó's montane oakforests. Soil acidity levels registered along the slopes of Volcán Barva (Marss *et al.* 1988) are very close to those found at Chirripó. Other, very similar forests occur on the slopes of the nearby Volcán Poás, Cordillera Volcánica Central (Macey 1975). Here, at ca. 2450–2550 m asl a 20–22 m tall *Quercus-Podocarpus-Schefflera* forest predominates, which is most similar to Chirripó's *Podocarpus macrostachyus-Quercus costaricensis* community (no. VIII). Further north, in the Monteverde Cloud Forest Reserve (Cordillera de Tilarán) Lawton & Dryer (1980) distinguished at 1800–1850 m asl a 18–25 m tall LM 'Oak Ridge Forest' dominated by *Quercus corrugata* and *Q. seemannii*, resembling much Chirripó's *Ocotea tenera-Quercus seemannii* community (no. I). The higher altitudinal position of the latter as compared to Monteverde's 'Oak Ridge Forest' can be related to the 'Massenerhebung' Effect *sensu* Grubb (1971; Brujinzeel *et al.* 1993).

#### *Comparison with other tropical montane forest zones*

In general, climatic changes as observed in the Chirripó Park do not differ much from those found along altitudinal transects in the Colombian Andes (Van der Hammen 1984; Witte, in press). On both the Sierra Nevada de Santa Marta and the Nevado del Ruíz the diurnal climate is much more pronounced than the yearly cycle – an aspect typical for tropical mountains (Troll 1955; Ohsawa *et al.* 1985). Temperatures are stable over the year, but oscillate largely during the course of a specific day – regardless of the season. A similar trend is found in the relative air humidity regime, although the dry season is, indeed, much drier and characterized by a strong humidity dip at noon. In this way, the course of Chirripó's diurnal climate follows those of Andean Peru (Ellenberg 1975, 1979) and Colombia (Wolf 1993b). Annual rainfall distributions are bimodal in both regions – as well as in montane Ecuador (Grubb & Whitmore 1966) – with highest precipitation during May and September-October. At Chirripó a temperature drop of  $0.58\text{ }^{\circ}\text{C} \cdot 100\text{ m}^{-1}$  increase in altitude was recorded. This value coincided with the one estimated for an Andean forest in Venezuela (Walter 1985) and is very near to the value of  $0.60\text{ }^{\circ}\text{C} \cdot 100\text{ m}^{-1}$  as measured at the slopes of the Colombian Nevado del Ruíz Massif (Witte, in press) and in the Eastern Himalayas (Ohsawa *et al.* 1985) as well as to Kitayama's (1992) value of mean air temperature decline ( $0.55\text{ }^{\circ}\text{C} \cdot 100\text{ m}^{-1}$ ) measured at Mt. Kinabalu on Borneo. The soil temperature on Cerro Chirripó changes in a similar way – reflecting annual air temperatures – and is also comparable to results from the Colombian Andes (Thouret 1983a; Van der Hammen 1984). The great similarity in climate for the Costa Rican, Colombian and Venezuelan montane sites are very likely to be caused by the regional influence of the Inter Tropical Convergence Zone (ITCZ), the strong Trade Winds originating in the Caribbean region, and the formation of condensation belts at mid-elevations.

Changes in soil characteristics on Cerro Chirripó are less marked along the altitudinal gradient, than between Pacific and Atlantic slopes. A similar trend is seen along E and W slopes in Andean forests of Colombia (Thouret 1989). Like on other tropical mountains (Kitayama 1992), edaphic factors at Chirripó play a less important role than climatic aspects in controlling the altitudinal distribution of plant species and forest communities. With respect to organic carbon

levels, soils on Cerro Chirripó are very similar to those in New Guinea and Jamaica (Edwards & Grubb 1977, 1982; Tanner 1977). Regarding exchangeable elements (bases), soils at Chirripó are somewhat poorer than their equivalents in Jamaica or Borneo (Tanner 1977; Kitayama 1992), but close to values measured along the La Selva-Volcán Barva altitudinal transect in the Costa Rican Cordillera Volcánica Central (Marss *et al.* 1988). However, contents of Ca and extractable P resemble those recorded for Mt. Kinabalu (Kitayama 1992). Soil pH does not change along the Chirripó transects, just as on Borneo, and levels of acidity fit within the range established for a Puerto Rican montane tabonuco forest (Johnston 1992) and SE Asian montane forests (Kitayama 1992). Furthermore, Chirripó's soils are very well-drained, a feature also observed at Mt. Kinabalu above ca. 1900 m asl (Kitayama & Mueller-Dombois 1993a, 1993b).

Soil types at Cerro Chirripó are most comparable to those found in the northern Andes. Just as in high altitude Costa Rica, Andosols (Andepts) dominate in Colombia, especially along the transects through montane forest (2300–3800 m asl) on El Nevado del Ruíz (Thouret 1983b, 1989). A number of edaphic features are shared by both neotropical mountains: (i) recent soil development in volcanic ashes (tephra), (ii) thick (dark) humiferous organic layers, (iii) podsolization – although Thouret (1983b, 1989) rather refers to 'crypto-podsolization' (spodic horizons), (iv) presence of a large amount of weatherable parent material, (v) high levels of acidity, and (vi) high soil moisture content. With regard to (ii) and (vi), Thouret (1989) pointed out that the more humus-rich soils are to be found on the wetter slope of tropical mountains, such as the W slope of El Nevado del Ruíz. Our results from Cerro Chirripó, such as thick (often histic) organic layers on the wetter Atlantic slope, confirm this hypothesis.

According to our data and results presented by Sevink (1984) and Thouret (1989), only brown Humitropepts seem to be shared between the montane forest belts of Cerro Chirripó and the Colombian Andes (Sierra Nevada de Santa Marta and El Nevado del Ruíz). However, several other Inceptisols (USDA nomenclature of the Soil Survey Staff 1975) are known from this girdle in both the Colombian Cordillera Central (Thouret 1989) and the Costa Rican Cordillera de Talamanca (CATIE 1983; Blaser 1987; Otárola & Alvarado 1976). These soils mainly fall into two suborders: (a) Andepts with Dystrandeps, Hydrandeps, and Placandeps; (b) Tropepts with Dystropepts. In Costa Rica they occur between ca. 1500–3000 m asl, and

in Colombia between ca. 2300–3800 m asl, but with Tropepts (Dystropepts, and especially Humitropepts) frequently extending down to c. 1200 m asl. Sevink (1984), on the other hand, found Aquepts (Tropepts) to be more important between 2500 and 3300 m asl in the Buritaca transect along the Sierra Nevada de Santa Marta than, for instance, Andepts. This is probably explained by the hydromorphic character of Santa Marta's soils: leaching in rather acid soils is excessive between 1800 and 2800 m asl (Sevink 1984). Above these montane (Andean) edaphic zones, páramo vegetation is found in Costa Rica on mainly zonal Histosols (Tropofolists; Tropofibrists) in the Cordillera de Talamanca (Blaser 1987; Van Uffelen 1991) and in Colombia on either Inceptisols such as Plaquepts and Cryaquepts at the Santa Marta Massif (Sevink 1984) or Cryandeps and Vitrandeps at the Nevado del Ruíz (Thouret 1989). However, their characteristics and interrelationships are beyond the scope of the present paper.

With regard to its altitudinal vegetation sequence, Cerro Chirripó is not particularly different from other tropical mountains, such as the Sierra Nevada de Santa Marta in Colombia (Cleef *et al.* 1984), Mt. Elgon in Kenya (Hamilton & Perrott 1981) or the SE Asian Mts. Kerinci Sumatra, Kinabalu Borneo) and Kerigomna Papua New Guinea), (Edwards & Grubb 1977; Ohsawa *et al.* 1985; Kitayama 1992). As is to be expected, phytogeographic similarities on the generic level are greatest with Andean forests (Kappelle *et al.* 1992) and, to a lesser extent, with forested mountain ranges N of Costa Rica, like the Guatemalan Sierra de los Cuchumatanes (Islebe & Kappelle 1994). Tropical montane fagaceous forests are certainly not restricted to Central America. On the contrary, they are known to occur in a number of other equatorial countries. *Quercus*, for instance, also forms extensive forests in the northern Andes (Cuatrecasas 1934; Vega 1964; Lozano & Torres 1974), (sub)tropical Himalayas (Saxena & Singh 1982) and on Java and Borneo (Werner 1986; Kitayama *et al.* 1993), but is absent in Sri Lankan montane forests (Werner 1986). *Nothofagus* dominates large forest areas in Chile (Veblen *et al.* 1981) and in Papua New Guinea (Read *et al.* 1990), while *Castanopsis* and *Lithocarpus* are major constituents in (upper) montane rainforest on Borneo and Sumatra, respectively (Ohsawa *et al.* 1985; Bratawinata 1986, Kitayama *et al.* 1993). Furthermore, *Trigonobalanus*, a Tertiary relict, is locally important in Colombia (Lozano *et al.* 1979, 1980; Van der Hammen & Cleef 1983). The other major element of Chirripó's cloud forests, the bamboos, predominate

in many other tropical montane forests too. *Chusquea* is found in the Neotropics from Mexico through Central America, along the Andes to Chile and Argentina, and in eastern Brazil (Clark 1989). An example are the Chilean *Nothofagus* forests, in which different species of *Chusquea* characterize the understorey (Veblen *et al.* 1981). In Africa on the wetter slopes of Mt. Elgon and Mt. Kenya between ca. 2400 and 3000 m asl, a separate Bamboo Forest Zone is distinguished, characterized by *Arundinaria* and probably of natural origin (Hamilton & Perrott 1981). According to these authors this bamboo zone is part of what Hedberg (1951) earlier described as the (Afro) Montane Forest Belt (see also White 1978, and Lovett 1993).

Comparing Chirripó's montane forests to those along transects through the Colombian Andes (e.g., Cleef *et al.* 1984), the main similarity observed between both neotropical cloud forest regions concerns the altitudinal position of the limit between the LM (or Subandean) and the UM (or Andean) forest zones. In Costa Rica and Colombia this major boundary is found at c. 2400–2600 m asl, depending on the maximum elevation at each particular massif. In this way, the LM-UM limit occurs at a slightly more elevated position along the slopes on the northern Andes, e.g., at the higher Santa Marta Massif (Cleef *et al.* 1984). Another important feature shared between Costa Rican and Colombian montane forests has already been mentioned above: a great floristic similarity at the generic level. Over 70% of the terrestrial vascular genera occurring in the montane belt of the Cordilleras in central Colombia are shared with the Cordillera de Talamanca (Kappelle *et al.* 1992). However, Chirripó's vascular flora on the species level is largely endemic to the (Costa Rican-Panamanian) Cordillera de Talamanca: about 30 to 40% of the ca. 10,000 species of woody and herbaceous plants in the 612,570 ha Amistad Biosphere Reserve are believed to be endemic (Gómez 1989).

For this and other reasons, the biological wealth of this threatened World Heritage Site – with the Chirripó National Park in its heart – has to be safeguarded for coming generations. To reach such a goal a better understanding of the ecology and distribution of Talamanca's montane oakforests is indispensable. A more complete panorama of these threatened forests is urgently needed. Therefore, the full integration of all previous research on western Talamancan montane oakforest communities is recommended as a basis for Amistad's long-term biodiversity conservation.

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