

10 Structure and Composition of Costa Rican Montane Oak Forests

M. KAPPELLE

10.1 Introduction

Montane forests in the humid tropics differ significantly from tropical lowland forests (Richards 1952; Grubb and Whitmore 1966; Churchill et al. 1995; Hamilton et al. 1995; Kappelle 2004). The diurnal presence of clouds and mist is often the most remarkable characteristic of these forests (Stadtmüller 1987). The specific atmospheric humidity regime and strong diurnal temperature oscillations are probably the main environmental causes generating such a different structure and composition in tropical highland forest systems, compared to tropical lowland rainforests (Bruijnzeel and Veneklaas 1998).

A peculiar forest type frequently found in tropical and subtropical highland regions is the oak/beach-bamboo forest. Mature phases of this forest type generally have a canopy layer dominated by 30- to 50-m-tall fagaceous species, and an understory characterized by 3- to 6-m-tall woody bamboos (Kappelle 1996). Such forests occur in the Americas as well as in Asia. Examples are beach forest (*Fagus*) with *Sasa* bamboo in Japan (Nakashizuka 1988), *Nothofagus* forest with *Chusquea* bamboo in southern South America (Veblen et al. 1981), *Nothofagus* forest with *Nastus* bamboo in Papua New Guinea (van Valkenburg and Ketner 1994), *Castanopsis* forest and *Lithocarpus* forest in Kalimantan and Sumatra (Ohsawa et al. 1985; Kitayama 1992), *Colombobalanus* (formerly known as *Trigonobalanus*) forest in Colombia (van der Hammen and Cleef 1983, Chaps. 1 and 11), and oak forest (*Quercus*) often with *Arundinaria* bamboo in the Himalayas (Saxena and Singh 1982), on Kalimantan and Java (Werner 1986), or with *Chusquea*, *Aulonemia* and *Rhipidocladum* bamboos in tropical Mexico, Central America and Colombia (Lozano and Torres 1974; Soderstrom et al. 1988; Pohl 1991; Widmer 1993; Kappelle 1996; Kappelle and Brown 2001; Chaps. 1, 10 and 11). Figure 10.1 shows the distribution of oak in Costa Rica.

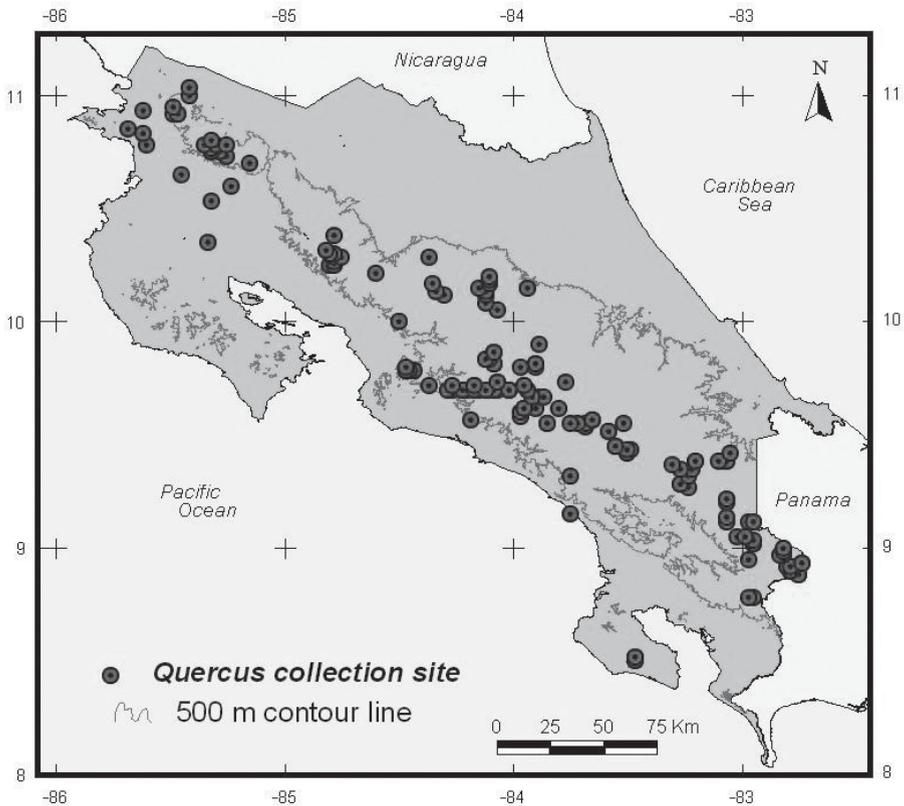


Fig. 10.1. Location of 168 Costa Rican collection sites of *Quercus* specimens stored at INBio's herbarium (INB). The 500-m contour line is drawn to show that most collections are from mid and high elevations. Only *Q. oleoides* has been collected below 500 m elevation, in the drier northern Pacific lowlands of Guanacaste. The collection site on the Osa Peninsula in the southern Pacific region corresponds to a cloud forest at the summit of a >700 m high hill where *Q. rapurahuensis* and *Q. insignis* were found (Kappelle et al. 2003). *Q. costaricensis* and *Q. corrugata* have been included in IUCN's Red List

The oak forests of upland Costa Rica are a good example of these tropical montane fagaceous-bamboo forests. They differ in many aspects from oak forests in temperate lowland North America (Hammit and Barnes 1989) and Mediterranean Europe (Romane and Terradas 1992; Roda et al. 1999). This chapter presents a characterization of their distribution, structure, composition and diversity, and serves as an introduction to other chapters in this book on oak forest paleoecology (Chap. 2), non-vascular plants and lichens (Chaps. 6 and 7), population dynamics (Chaps. 15, 18, 23, 24, 25, 26 and 27), ecosystem functioning (Chaps. 21 and 22), and conservation and sustainable use (Chaps. 30, 31, 32 and 33).

10.2 Geographic Forest Distribution

Montane oak forests in Costa Rica are principally found along Pacific slopes at altitudes of 1,500–3,400 m, and along Atlantic slopes at 1,800–3,100 m elevation (see also Chap. 4). Most montane oak forest stands are concentrated in Costa Rica's Talamanca Range, though small, dispersed patches of oak forest stands occur in the volcanic mountain chains to the northwest (Kappelle 1996), including the Monteverde Cloud Forest Preserve (Nadkarni and Wheelwright 2000). Occasionally, highland oak trees may appear in patchy distribu-

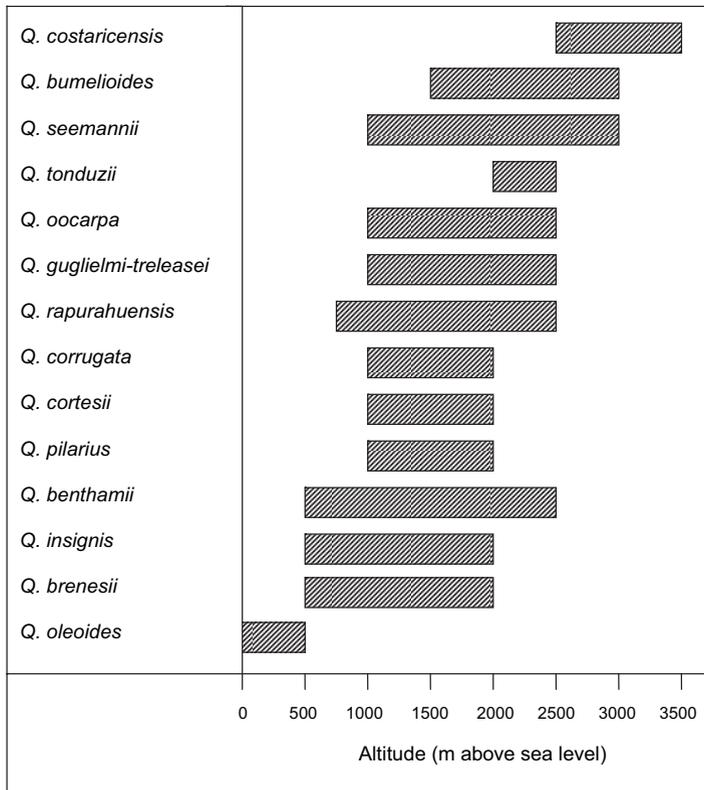


Fig. 10.2. Altitudinal distribution of 14 oak (*Quercus*) species occurring in Costa Rica. Distributions are in accordance with Burger (1977), Kappelle (1987, 1996), and reviews of herbarium specimens at CR and INB. Following Burger (1977), *Q. eugeniaefolia* and *Q. sapotaefolia* have been included in *Q. seemannii*. However, *Q. bumelioides*, which Burger (1977) also classified under *Q. seemannii*, has been treated here as a separate species, as recommended by N. Zamora at INB (personal communication; see www.inbio.ac.cr). *Q. bumelioides* is synonymous with *Q. copeyensis* (K.C. Nixon, personal communication). Previously, *Q. benthamii* and *Q. cortesii* had not been reported for Costa Rica (Burger 1977)

tions at lower elevations. One species of Costa Rican oak, *Quercus oleoides*, is even restricted to dry lowland forests in Costa Rica's northwestern, Pacific Guanacaste region. Only four of 14 *Quercus* species known from Costa Rica reach elevations below 1,000 m a.s.l. (Fig. 10.2).

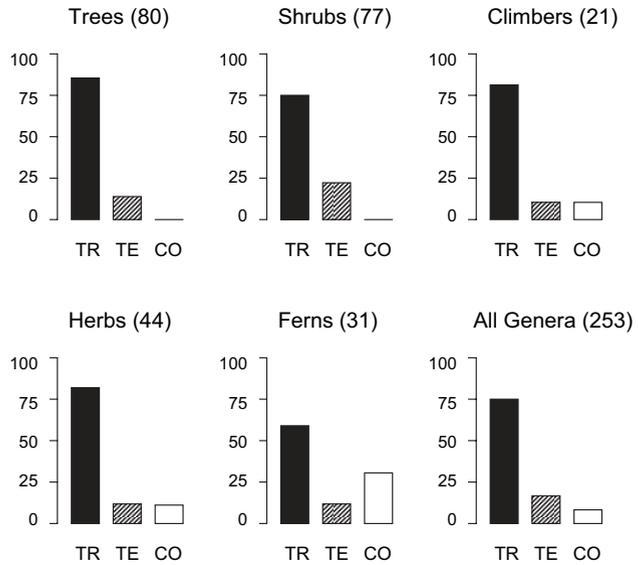
As on many other tropical mountains (e.g., Aiba and Kitayama 1999; Ashton 2003), Talamanca's highland oak forests are zoned in sequential altitudinal belts: the upper montane oak forests (2,200–3,400 m), and the lower montane oak forests (1,500–2,400 m). Upper montane oak forests generally have a higher cloud and mist incidence (persistence) than is the case for lower montane oak forests. In fact, according to Grubb and Stevens (1985), there is a close correlation between the lower–upper montane forest ecotone and the diurnal cloud base. In the tropics, the elevation of the diurnal cloud base is generally set by the relative humidity and rate of cooling of warm lowland air being conducted up slopes as it warms during the morning (Ashton 2003). In Costa Rica, below the lower montane oak forest belt, a premontane belt occurs (Holdridge et al. 1971) – immediately above the lowland rainforest zone – dominated by a mixture of tree species including Lauraceae (Kappelle 2004). At higher elevations, the subalpine (3,100–3,500 m) and alpine (3,300–3,819 m) belts are found. These are generally dominated by cold and humid, low-stature scrub and grasslands known as paramo vegetation (Körner 1999; Kappelle and Horn 2005). Further details on altitudinal gradients and elevational zonation in Costa Rican montane oak forests are given in Chap. 4.

10.3 Plant Geography

In Costa Rica's highlands, differing seasonal patterns of rainfall, superimposed on discontinuous mountain chains, rich mineral volcanic soils, the nearness of large species-rich continental areas, a past history as an archipelago, and the influence of glaciations have all contributed to a dynamic system of high local floristic heterogeneity (Burger 1975, 1980). This is exemplified by the country's Talamancan montane oak forests, in which almost 75 % of 253 censused vascular plant genera (excluding orchids and bromeliads) has a tropical distribution (Kappelle et al. 1992), whereas the remaining 25 % is made up of temperate (17 %) and cosmopolitan (8 %) genera (Fig. 10.3).

Important temperate plant genera include holarctic *Alnus*, *Arenaria*, *Cornus*, *Myrica*, *Quercus*, *Prunus*, *Rhamnus*, *Ribes*, *Rubus*, *Vaccinium* and *Viburnum*, and austral-Antarctic *Acaena*, *Drymis*, *Escallonia*, *Fuchsia*, *Gaiadendron*, *Gaultheria*, *Pernettya*, *Podocarpus* and *Weinmannia*. Within the tropical component, the neotropical element is best represented and contributes to almost half of all recorded genera (46 %). Some characteristic neotropical tree genera are *Billia*, *Brunellia*, *Freziera*, *Guatteria* and *Mollinedia*. The tropical afro-American element is very poorly represented (3 %, *Guarea*, *Lippia*,

Fig. 10.3. Biogeographical distribution of 253 terrestrial vascular plant genera per growth form in upper montane *Quercus* forests in Costa Rica. Closed bars Tropical genera (TR), dashed bars temperate genera (TE), open bars cosmopolitan genera (CO). Y-axis values are percentages of the total number of genera per growth form. Numbers within brackets indicate the number of genera per growth form



Trichilia, *Urera*). Most of the 80 tree genera observed are neotropical, tropical Asian-American or pantropical in distribution. *Clethra*, *Cleyera*, *Hedyosmum*, *Magnolia*, *Meliosma*, *Persea*, *Phoebe*, *Styrax*, *Symplocos* and *Turpinia* are of tropical Asian-American origin. The only cosmopolitan tree genus that has been found is *Ilex*.

Shrubs amount to 77 genera and are principally neotropical (over 60%), pantropical or northern/southern temperate. Neotropical montane shrub genera are mostly Andean-centered, and originated as a result of very active speciation or even explosive evolution as a consequence of tropical Andean orogenesis (Gentry 1982, 1985). Herb genera (44 genera in total) are basically neotropical, pantropical and wide-temperate. Climbers (21) are principally neotropical or pantropical. Ferns (31) show mainly cosmopolitan, pantropical or neotropical distributions. Most cosmopolitan genera are herbs (14%) or ferns (29%).

A comparative, phytogeographical analysis demonstrates a great floristic affinity of Costa Rican montane oak forests with equivalents in the Colombian Andes (Cordillera Oriental, Chap. 11), and lower levels of similarity with Mexican mesophyllous montane oak forests, such as found in the transversal Neovolcanic mountain range and surroundings (Kappelle et al. 1992, Chaps. 8 and 9). The greater affinity with Colombia may be due to climatic similarities between Costa Rica's Talamanca mountains and the Colombian Andes, which both display humid to per-humid conditions. The Mexican Neovolcanic mountain belt is much drier, favoring a set of drought-resistant upland plant genera of northern origin not known in Costa Rica (e.g., *Liquidambar* and

Pinus). Similarly, some moisture-loving plant genera of neotropical or austral-Antarctic origin that are well spread in the Colombian Andes seem to have migrated northward to Costa Rica's Talamanca range, but have not been able to reach the drier Mexican montane oak forests. More in-depth, regional-scale biogeographic studies are needed to help reveal the precise floristic – as well as faunistic, for that matter – affinities and dissimilarities among related biota of neotropical montane oak forests.

10.4 Forest Structure and Physiognomy

Tropical montane oak forests demonstrate a clear vertical structure with a number of horizontal layers, similar to the stratification of temperate oak forests (Kappelle 2004). In mature old-growth stands in Costa Rica, the dominant canopy oaks are normally 25–40 m tall, though some giant, emergent individuals may reach heights of 50–60 m. It has been hypothesized that maximum tree height is principally limited by water transport constraints, leaf water stress, and the resulting reductions in leaf photosynthesis (Koch et al. 2004). Table 10.1 presents some stand structure and diversity data for old-growth oak forest (OGF) at 2,900–3,000 m a.s.l. in Costa Rica.

Immediately below the upper oak forest line at altitudes of 3,000–3,200 m where subalpine forests commence (Islebe and Kappelle 1994), *Q. costaricensis* trees become lower in stature (<25 m) and more stunted (Chap. 4). Here, they may form twisted branches with densely packed, small-sized leaves (Holdridge et al. 1971; Kappelle and Leal 1996). Oak branches and twigs are often thickly covered with epiphytic aroids, bromeliads, ericads, orchids, ferns and parasitic loranth, alternated with pending, atmospheric moisture-capturing mosses, hepatics and lichens (Holdridge et al. 1971; Kappelle et al. 1989; Chaps. 6, 7 and 21). Mature oaks lack real buttresses, but expanded bases do occur on some larger trees (Holdridge et al. 1971).

Stem densities in numbers per ha range from 5,000–8,400 for stems >1 cm DBH (diameter at breast height), to 700–1,000 for stems >5 cm DBH, and 455–510 for stems >10 cm DBH (Blaser 1987; Jiménez et al. 1988). Occasionally, the DBH of giant oaks may reach values over 120 cm. Values of basal area are among the highest found in tropical forests: 50–53 m² per ha for stems >1 cm DBH, 48–51 m² per ha for stems >10 cm DBH, and 32–37 m² per ha for stems >50 cm DBH (Blaser 1987; Jiménez et al. 1988). *Q. costaricensis* and *Q. copeyensis* (now known as *Q. bumelioides*) alone may account for up to 90% of both density and basal area for stems >50 cm DBH, and thousands of juveniles (seedlings, saplings) may fit into a single hectare (Chap. 18).

Family importance values (FIV), which include measures of relative dominance, density and diversity (Mori et al. 1983), were measured for stems >3.0 cm DBH in a 0.1-ha plot of old-growth, mature oak forest. Highest

Table 10.1. Stand structure and diversity data for three 0.1-ha plots in montane old-growth oak forest (OGF) at ~2,950 m a.s.l. in Costa Rica. Values are based on plot data presented in Kappelle et al. (1995a, 1996). Similar data for successional oak forest are presented in Chap. 17

Variable ^a	Plot 1	Plot 2	Plot 3	Mean+1 SE
Canopy height (m)	35	38	35	36.5+2.1
Number of stems ≥ 3 cm DBH per plot	184	197	182	189.5+7.5
Number of stems ≥ 10 cm DBH per plot	69	51	70	60.5+9.5
Number of stems per diameter class				
Stems 3–5 cm DBH per plot	58	81	65	73+8
Stems 5–10 cm DBH per plot	57	65	47	56+9
Stems 10–20 cm DBH per plot	33	27	39	33+6
Stems 20–40 cm DBH per plot	20	13	20	16.5+3.5
Stems 40–80 cm DBH per plot	14	8	8	8+0
Stems ≥ 80 cm DBH per plot	2	3	3	3+0
Stem density (stems ≥ 3 cm DBH per ha)	1,840	1,970	1,820	1,895+75
Basal area for stems ≥ 3 cm DBH ($\text{m}^2 \text{ha}^{-1}$)	64.7	57.5	58.7	58.1+0.6
Species richness per plot (terr. vasc.) ^b	62	79	68	73.5+5.5
Species richness per plot (trees only)	18	21	20	20.5+0.5
Shannon-Wiener's index (terr. vasc.)	3.70	4.45	4.38	4.18+0.24
Shannon-Wiener's index (trees only)	3.27	3.18	3.48	3.33+0.15
Reciprocal Simpson's index (terr. vasc.)	6.30	9.97	11.31	10.64+0.67
Reciprocal Simpson's index (trees only)	6.14	4.87	7.98	6.43+1.56
Species density (terr. vasc.)	20.7	26.3	22.7	24.5+1.8
Evenness or equitability index (terr. vasc.)	0.62	0.71	0.72	0.72+0.01

^a Shannon-Wiener's index, reciprocal Simpson's index, species density, and evenness index were measured following procedures presented in Magurran (1988)

^b Terr. vasc., all terrestrial vascular plant species

FIV values were recorded in Fagaceae (122), followed by Myrsinaceae (30), Cunoniaceae (22), Styracaceae (18), Araliaceae (16), Lauraceae (15), and Theaceae (11) (Kappelle et al. 1996).

10.5 Plant Diversity

Costa Rican montane oak forests are extraordinarily rich in vascular plant species. For information on the diversity of non-vascular plant species, fungi and lichens, I refer to Chaps. 5, 6, 7 and 21. Epiphytic vascular species are particularly abundant, with at least 100 orchid and 25 bromeliad species (Kappelle 1996). As some 1,000 native orchid species are known to reside in Costa Rica (N. Zamora, personal communication), we may assume that – given the size of the country and the extent of intact montane oak forest – many more

orchid species than the 100 recorded grow in the high canopies of these oak forests.

To date, a total of 1,300 vascular plant species has been recorded for old-growth and recovering Talamancan montane oak forest (2,000–3,400 m elevation; Atlantic and Pacific slopes). For species lists, the reader is referred to Kappelle et al. (1991, 2000), Kappelle and Gómez (1992), van Velzen et al. (1993), Kappelle (1996), Kappelle and van Omme (1997), and MNCR (2001). Almost 500 of these species are woody, and include hundreds of trees and shrubs as well as a few woody climbers such as *Hydrangea* and hemi-epiphytes such as *Clusia* (Kappelle and Zamora 1995). Angiosperms account for some 1,000 species, and are distributed between 750 species of dicots (Magnoliopsida) and 250 species of monocots (Liliopsida). Only three species are native gymnosperms (conifers), belonging to Podocarpaceae. Over 300 species are pteridophytes, including at least 250 ferns, 35 clubmosses (Lycopodiaceae, Selaginellaceae), one quillwort (*Isoetes*), and one horsetail (*Equisetum*).

Most speciose angiosperm plant families are Asteraceae (>60 species), Ericaceae (>30), Lauraceae (>35), Melastomataceae (>35), Myrsinaceae (>20), Piperaceae (>40), Poaceae (>20), Rosaceae (>20), Rubiaceae (>50), and Solanaceae (>30). The most diverse fern families are Adiantaceae (>20), Grammitidaceae (>40), Hymenophyllaceae (>25), Lomariopsidaceae (>35), and Polypodiaceae (>35). Tree ferns account for at least 14 species, spread over Cyatheaceae (11), Dicksoniaceae (3), and Lophosoriaceae (1). Extremely rich epiphytic vascular genera include the tongue fern *Elaphoglossum* (>30 species), the small, sclerophyllous dicot herb *Peperomia* (>25), and the orchid *Maxillaria* (>20). The most speciose terrestrial vascular plant genus is the shrub *Miconia* (>20 species). Diverse vascular genera with at least 15 species are the epiphytes *Anthurium* (see also Chap. 15), *Asplenium*, *Begonia*, *Epidendrum* and *Huperzia*, the bamboo *Chusquea*, the shrubs *Piper*, *Psychotria* (including *Cephaelis*) and *Solanum*, the climber *Passiflora*, and the lauraceous tree *Ocotea*, an important fruit tree for the Resplendant Quetzal (Chap. 25). Other, less diverse but still rich genera with over ten species include the ground-rooted tree *Ficus*, the hemi-epiphytic tree *Oreopanax*, the dwarf palm *Chamaedorea*, and the shrubs *Palicourea* and *Rubus* (Kappelle and Zamora 1995; Kappelle 1996; MNCR 2001).

Alpha diversity was measured for terrestrial vascular plants in three separate 0.1-ha mature old-growth oak forest plots, using different diversity indices (Magurran 1988; Table 10.1). Species richness varied in the range 62–79 species per plot, species density was 20.7–26.3, Shannon-Wiener's index 3.70–4.45, Simpson's reciprocal index 6.30–11.31, and the equitability index – a measure of evenness – showed rounded values of 0.62–0.72 (Kappelle et al. 1995a; Table 10.1).

10.6 Floristic Composition

The 20- to 40-m-tall canopy layer of old-growth stands of Talamanca's montane oak forests is almost exclusively dominated by the genus *Quercus*. At elevations over 2,000 m, endemic *Q. copeyensis*, endemic *Q. costaricensis* and wide-ranging *Q. seemannii* dominate, each within its specific altitudinal range (Burger 1977; Kappelle et al. 1989, 1991). *Q. oocarpa* and *Q. rapurahuenensis* are also frequently observed, albeit in lower numbers, mainly at mid elevation (2,000–2,400 m) along less wet Pacific slopes. Other important canopy tree genera are *Magnolia*, *Podocarpus*, *Prumnopitys*, *Schefflera* and *Weinmannia* (Kappelle et al. 1995b; MNCR 2001). *Clusia* may occasionally occur as an (hemi)epiphytic tree on canopy branches of oak. Parasitic Loranthaceae, including Viscaceae, such as *Dendrophthora*, *Phoradendron* and *Struthantus*, share oak – and other species' – branches and twigs with epiphytic non-parasitic vascular genera in the Araceae, Begoniaceae, Bromeliaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Orchidaceae, Piperaceae and ferns.

The 5- to 20-m-tall subcanopy layer of mature oak forest is composed of a complex mixture of tree species. They include genera such as *Abatia*, *Aiouea*, *Alchornea*, *Alfaroa*, *Alnus*, *Ardisia*, *Billia*, *Brunellia*, *Buddleja*, *Cinnamomum* (including *Phoebe*), *Clethra*, *Cleyera*, *Clusia*, *Comarostaphylis*, *Cornus*, *Croton*, *Dendropanax*, *Drimys*, *Escallonia*, *Eugenia*, *Freziera*, *Guatteria*, *Guarea*, *Hedyosmum*, *Ilex*, *Inga*, *Ladenbergia*, *Lippia*, *Lozania*, *Meliosma*, *Monnina*, *Myrcianthes*, *Myrsine*, *Nectandra*, *Ocotea*, *Oreopanax*, *Panopsis*, *Parathesis*, *Persea*, *Picramnia*, *Prunus*, *Quetzalia* (synonymous with *Microtropis*), *Rhamnus*, *Rondeletia*, *Roupala*, *Salix*, *Sapium*, *Saurauia*, *Styrax*, *Symplocos*, *Ticodendron*, *Trichilia*, *Turpinia*, *Ulmus*, *Vaccinium*, *Viburnum* and *Zanthoxylum*. Often, these species are accompanied by young trees of *Magnolia*, *Quercus*, *Podocarpus*, *Schefflera* and *Weinmannia*, waiting for a tree fall to continue their journey to the higher canopy (Kappelle et al. 1989, 1991, 1995a).

The 1- to 5-m-high understorey layer is dominated largely by bamboo species of the genus *Chusquea* and, to a lesser extent, *Aulonemia*. Most common are *Chusquea longifolia*, *C. talamancensis* and *C. tomentosa*. Bamboos are often associated with dwarf palms (*Chamaedorea*, *Geonoma*), cyclanths (*Asplundia*, *Sphaeradenia*) and treeferns (*Alsophila*, *Cnemidaria*, *Culcita*, *Cyathea*, *Dicksonia*, *Lophosoria* and *Sphaeropteris*); see also Kappelle et al. (1989, 1995b). In this layer, shrubs in the Ericaceae, Melastomataceae, Rubiaceae and Solanaceae are also common. Climbers include *Bomarea*, *Cissus*, *Cyclanthera*, *Cynanchum*, *Dioscorea*, *Iresine*, *Hydrangea*, *Passiflora*, *Sechium*, *Smilax* and *Tropaeolum* (Kappelle 1996).

Ground-dwelling vascular plant species shorter than 1 m, and often recorded in forest tree fall gaps and at forest edges, include a number of herbs in the Acanthaceae, Apiaceae, Asteraceae, Brassicaceae, Campanulaceae, Caryophyllaceae, Commelinaceae, Convallariaceae, Cyperaceae, Gen-

tianaceae, Geraniaceae, Gesneriaceae, Gunneraceae, Heliconiaceae, Iridaceae, Juncaceae, Lamiaceae, Malvaceae, Onagraceae, Oxalidaceae, Phytolaccaceae, Piperaceae, Plantaginaceae, Rosaceae, Scrophulariaceae, Urticaceae, Valerianaceae and Violaceae (Kappelle 1996).

10.7 Conclusions

The current chapter provides some insight into the structure, composition and diversity of Costa Rica's montane oak forest. It is meant to set the stage on this particularly rich and voluminous forest, in order to better understand its spatial and temporal patterns and processes, and above all, its functioning as an ecosystem. In subsequent chapters (Chaps. 15, 17, 23, 24, 26 and 30), these themes will be dealt with by the author, co-authors and colleagues who have studied the magnificent Talamanca montane oak forest environment over the last two decades.

Acknowledgements I am very grateful to friends, colleagues and students who supported my research in Costa Rica's montane oak forest over the last 20 years. I especially want to thank Antoine M. Cleef at the University of Amsterdam (UvA), and Luis Poveda, Nelson Zamora, and the late Adelaida Chaverri (1947–2003) at Costa Rica's National University (UNA) and National Biodiversity Institute (INBio). Marco Castro prepared Fig. 10.1. Major funding was provided by UvA, UNA, INBio and NWO-WOTRO. Research permission was granted by MINAE.

References

- Aiba S, Kitayama K (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecol* 140:139–157
- Ashton P (2003) Floristic zonation of tree communities on wet tropical mountains revisited. *Perspect Plant Ecol Evol Syst* 6(1/2):87–104
- Blaser J (1987) Standortliche und waldkundliche Analyse eines Eichen-Wolkenwaldes (*Quercus* spp.) der Montanstufe in Costa Rica. PhD Thesis, Georg-August Universität, Göttingen
- Brujinzeel LA, Veneklaas EJ (1998) Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Ecology* 79(1):3–9
- Burger WC (1975) The species concept in *Quercus*. *Taxon* 24:45–50
- Burger WC (1977) Fagaceae. In: Burger WC (ed) *Flora costaricensis*. *Field Bot Ser* 40:59–80
- Burger WC (1980) Why are there so many kinds of flowering plants in Costa Rica? *Brenesia* 17:371–388

- Churchill SP, Balslev H, Forero E, Luteyn JL (eds) (1995) Biodiversity and conservation of Neotropical montane forests. New York Botanical Garden Press, Bronx, NY
- Gentry AH (1982) Neotropical floristic diversity: phytogeographical connections between Central and South America: Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann Missouri Bot Gard* 69:557–593
- Gentry AH (1985) Contrasting phytogeographic patterns of upland and lowland Panamanian plants. In: D'Arcy WG, Correa MD (eds) *The botany and natural history of Panama*. Missouri Bot Gard Press, St Louis, MO
- Grubb PJ, Stevens PF (1985) The forests of the Fatima Basin and Mount Kerigomna, Papua New Guinea. Research School of Pacific Studies, Australian National University, Canberra
- Grubb PJ, Whitmore TC (1966) A comparison of montane and lowland rain forest in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forests. *J Ecol* 54:303–333
- Hamilton LS, Juvik JO, Scatena FN (eds) (1995) *Tropical montane cloud forests*. Springer, Berlin Heidelberg New York, Ecological Studies, vol 110
- Hammit WE, Barnes BV (1989) Composition and structure of an old-growth oak-hickory forest in southern Michigan over 20 years. In: Rink G, Budelsky CA (eds) *Proc 7th USDA Forest Service Central Hardwood Conf*, St Paul, MN. Gen Tech Rep NC-132, pp 247–253
- Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi JA Jr (1971) *Forest environments in tropical life zones: a pilot study*. Pergamon Press, Oxford, UK
- Islebe GA, Kappelle M (1994) A phytogeographical comparison between subalpine forests of Guatemala and Costa Rica. *Feddes Rep* 105:73–87
- Jiménez W, Chaverri A, Miranda R, Rojas I (1988) Aproximaciones silviculturales al manejo de un roble (*Quercus* spp.) en San Gerardo de Dota, Costa Rica. *Turrialba* 38(3):208–214
- Kappelle M (1987) A phytosociological analysis of oak forests in the western Talamanca Range, Costa Rica. MSc Thesis, University of Amsterdam, Amsterdam, The Netherlands
- Kappelle M (1996) Los bosques de roble (*Quercus*) de la Cordillera de Talamanca, Costa Rica: biodiversidad, ecología, conservación y desarrollo. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica
- Kappelle M (2004) Tropical montane forests. In: Burley J, Evans J, Youngquist JA (eds) *Encyclopedia of Forest Sciences*, vol 4. Elsevier, Oxford, UK, pp 1782–1793
- Kappelle M, Brown AD (eds) (2001) *Bosques nublados del Neotrópico*. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica
- Kappelle M, Gómez LD (1992) Distribution and diversity of montane pteridophytes of the Chirripó National Park, Costa Rica. *Brenesia* 37:67–77
- Kappelle M, Horn SP (eds) (2005) *Páramos de Costa Rica*. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica
- Kappelle M, Leal ME (1996) Changes in leaf morphology and foliar nutrient status along a successional gradient in a Costa Rican upper montane *Quercus* forest. *Biotropica* 28(2):331–344
- Kappelle M, van Omme E (1997) Lista de las plantas de los bosques nubosos subalpinos de la Cordillera de Talamanca en Costa Rica. *Brenesia* 47/48:55–71
- Kappelle M, Zamora N (1995) Changes in woody species richness along an altitudinal gradient in Talamancan montane *Quercus* forests, Costa Rica. In: Churchill SP, Balslev H, Forero E, Luteyn JL (eds) *Biodiversity and conservation of Neotropical montane forests*. New York Botanical Garden Press, Bronx, NY, pp 135–148
- Kappelle M, Cleef AM, Chaverri A (1989) Phytosociology of montane *Chusquea-Quercus* forests, Cordillera de Talamanca, Costa Rica. *Brenesia* 32:73–105

- Kappelle M, Zamora N, Flores T (1991) Flora leñosa de la zona alta (2000-3819 m) de la Cordillera de Talamanca, Costa Rica. *Brenesia* 34:121-144
- Kappelle M, Cleef AM, Chaverri A (1992) Phytogeography of Talamanca montane *Quercus* forests, Costa Rica. *J Biogeogr* 19(3):299-315
- Kappelle M, Kennis PAF, de Vries RAJ (1995a) Changes in diversity along a successional gradient in a Costa Rican upper montane *Quercus* forest. *Biodiv Conserv* 4:10-34
- Kappelle M, van Uffelen JG, Cleef AM (1995b) Altitudinal zonation of montane *Quercus* forests along two transects in the Chirripó National Park, Costa Rica. *Vegetatio* 119:119-153
- Kappelle M, Geuze T, Leal ME, Cleef AM (1996) Successional age and forest structure in a Costa Rican upper montane *Quercus* forest. *J Trop Ecol* 12:681-698
- Kappelle M, van Omme E, Juárez ME (2000) Lista de la flora vascular terrestre de la cuenca superior del Río Savegre, San Gerardo de Dota, Costa Rica. *Acta Bot Mex* 51:1-38
- Kappelle M, Castro M, Acevedo H, González L, Monge H (2003) Ecosystems of the Osa Conservation Area (ACOSA), Costa Rica. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica
- Kitayama K (1992) An altitudinal transect study of the vegetation of Mount Kinabalu, Borneo. *Vegetatio* 102:149-171
- Koch GW, Sillet SC, Jennings GM, Davis SD (2004) The limits to tree height. *Nature* 428:851-854
- Körner C (1999) *Alpine plant life*. Springer, Berlin Heidelberg New York
- Lozano G, Torres JH (1974) Aspectos generales sobre la distribución, sistemática fitosociológica y clasificación ecológica de los bosques de robles (*Quercus*) en Colombia. *Ecol Trop* 1(2):45-79
- Magurran AE (1988) *Ecological diversity and its measurement*. Croom Helm, London
- MNCR (2001) Caracterización de la vegetación de la cuenca del Río Savegre. Proyecto Araucaria, Museo Nacional de Costa Rica (MNCR) and Instituto Nacional de Biodiversidad (INBio), San José, Costa Rica
- Mori SA, Boom BM, de Carvalho AM, dos Santos TS (1983) Southern Bahian moist forest. *Bot Rev* 49:155-232
- Nadkarni N, Wheelwright N (eds) (2000) *Monteverde: ecology and conservation of a tropical cloud forest*. Oxford Univ Press, Oxford
- Nakashizuka T (1988) Regeneration of beech (*Fagus crenata*) after simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecol Res* 3:21-35
- Ohsawa M, Nainggolan PHJ, Tanaka N, Anwar C (1985) Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of east Asia. *J Trop Ecol* 1:193-216
- Pohl RW (1991) Blooming history of the Costa Rican bamboos. *Rev Biol Trop* 39(1):111-124
- Richards PW (1952) *The tropical rain forest*. Cambridge Univ Press, Cambridge, UK
- Roda F, Retana J, Gracia CA, Bellot J (eds) (1999) *Ecology of Mediterranean evergreen oak forests*. Springer, Berlin Heidelberg New York, *Ecological Studies*, vol 137
- Romane F, Terradas J (eds) (1992) *Quercus ilex ecosystems: function, dynamics and management*. Springer, Berlin Heidelberg New York, *Advances in Vegetation Science*, vol 13
- Saxena AK, Singh JS (1982) A phytosociological analysis of woody species in forest communities of a part of Kumaun Himalaya. *Vegetatio* 50:3-22
- Soderstrom TR, Judziewicz EJ, Clark LG (1988) Distribution patterns of neotropical bamboos. In: Heyer WR, Vanzolini PE (eds) *Proc Worksh Neotropical Distribution Patterns*, Academia Brasileira de Ciências, Rio de Janeiro, pp 121-157

- Stadtmüller T (1987) Cloud forests in the humid tropics: a bibliographic review. United Nations University (UNU), Tokyo, Japan
- Van der Hammen T, Cleef AM (1983) *Trigonobalanus* and the tropical amphi-pacific element in the North Andean forest. *J Biogeogr* 10:437–440
- Van Valkenburg JLCH, Ketner P (1994) Vegetation changes following human disturbance of mid-montane forest in the Wau area, Papua New Guinea. *J Trop Ecol* 10:41–54
- Van Velzen, HP, Wijtzes WH, Kappelle M (1993) Lista de especies de la vegetación secundaria del piso montano pacífico, Cordillera de Talamanca, Costa Rica. *Brenesia* 39/40:147–161
- Veblen TT, Donoso C, Schlegel FM, Escobar B (1981) Forest dynamics in south-central Chile. *J Biogeogr* 8:211–247
- Werner WL (1986) A comparison between two tropical montane ecosystems in Asia: Pidurutalagala (Ceylon/Sri Lanka) and Pangrango-Gede (Java). *Mount Res Dev* 6:335–344
- Widmer Y (1993) Bamboo and gaps in the oak forests of the Cordillera de Talamanca, Costa Rica. *Verh Gesell Ökol* 22:329–332