

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.

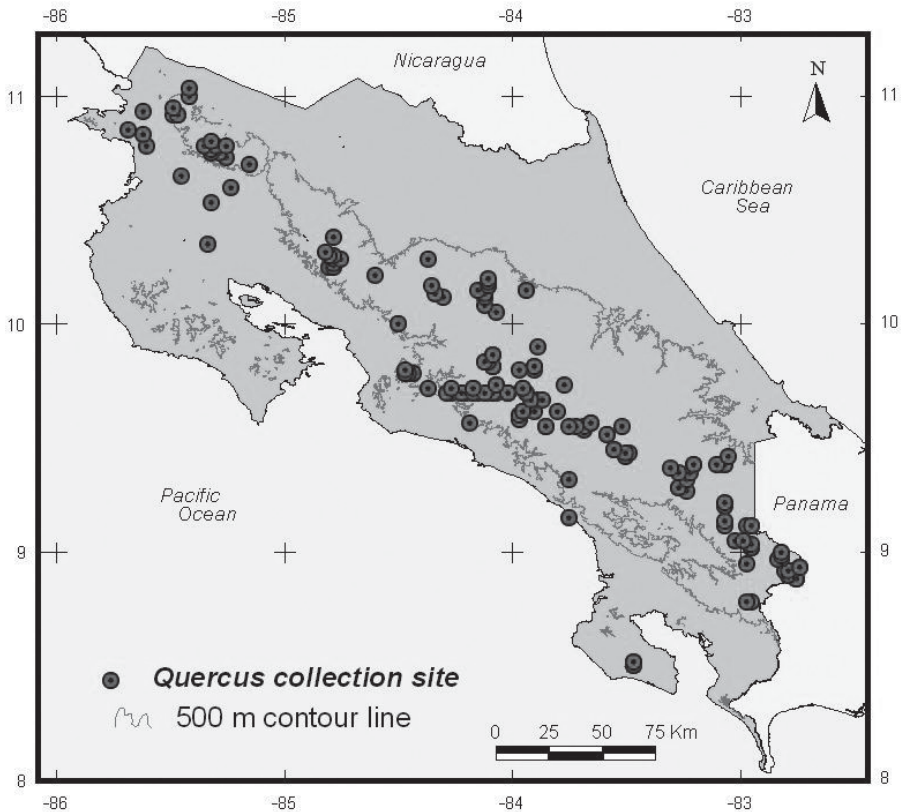


Fig. 10.1. Location of 168 Costa Rican collection sites of *Quercus* specimens stored at INBio's herbarium (INB). The 500-m contour line is drawn to show that most collections are from mid and high elevations. Only *Q. oleoides* has been collected below 500 m elevation, in the drier northern Pacific 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-

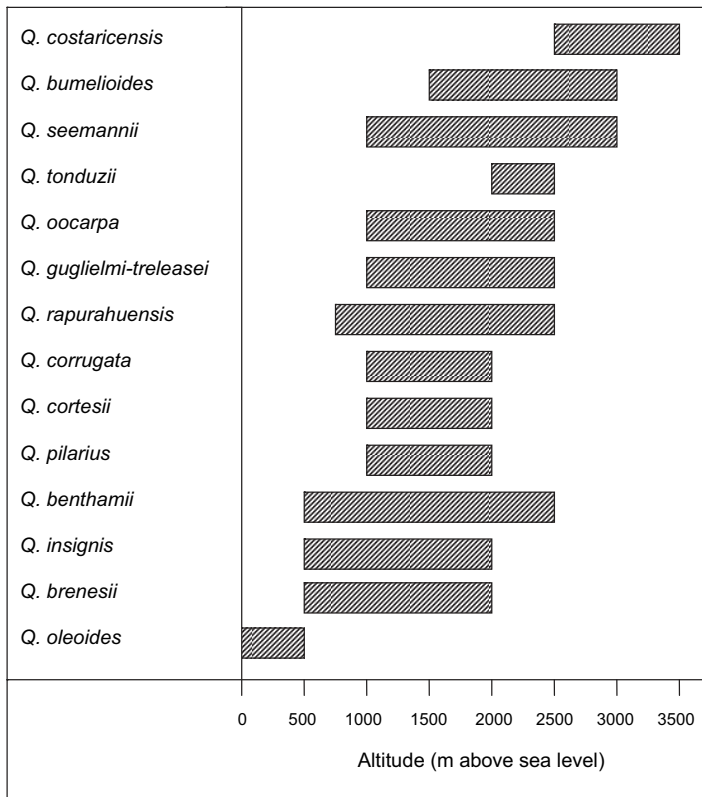


Fig. 10.2. Altitudinal distribution of 14 oak (*Quercus*) species occurring in Costa Rica. Distributions are in accordance with Burger (1977), Kappelle (1987, 1996), and reviews of herbarium specimens at CR and INB. Following Burger (1977), *Q. eugeniaefolia* and *Q. sapotaefolia* have been included 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).

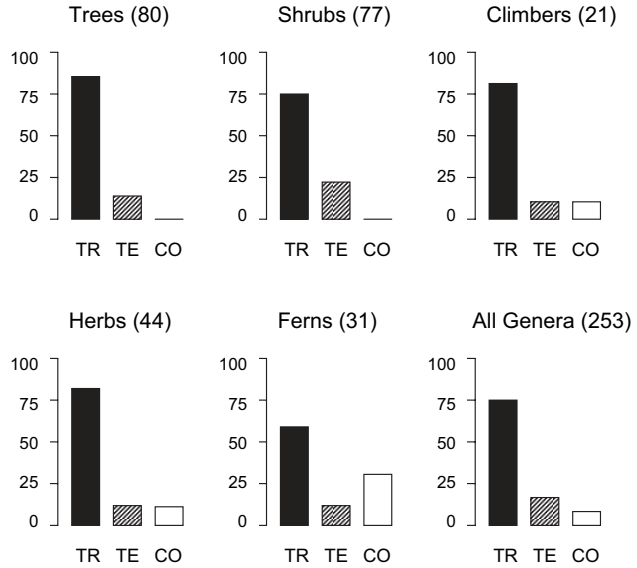
As on many other tropical mountains (e.g., Aiba and Kitayama 1999; Ashton 2003), Talamanca's highland oak forests are zoned in sequential altitudinal belts: the upper montane oak forests (2,200–3,400 m), and the lower montane oak forests (1,500–2,400 m). Upper montane oak forests generally have a higher 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*, *Gutteria* 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.

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