34 Neotropical Montane Oak Forests: Overview and Outlook

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34.1 Introduction

The preceding chapters of this book discuss scientific research results on natural and managed oak forests growing in the highlands of the American Tropics. Chapter authors highlight evolutionary, ecological and socioeconomic aspects of specific oak forests and identify existing gaps in our understanding. Their work and studies published elsewhere forms the basis for this chapter's overview of the current state of knowledge on ecological patterns and processes which determine the structure and functioning of these magnificent forests. The increasingly important human use and much needed conservation of these biodiverse and threatened habitats are dealt with as well. Cross-cutting trends and issues are discussed and conclusions drawn.

Neotropical montane oak forests are a special type of tropical montane forests (Kappelle 2004), in which tall oak trees (*Quercus*) dominate a 30- to 60-m-high forest canopy, often in pure stands or mixed with pines (*Pinus*) or other predominant trees. Though Neotropical oak forest history, structure, species diversity, species interactions, ecosystem functioning, post-disturbance recovery, and human use may vary considerably over short geographical ranges, regional trends are now becoming evident. Research presented in this book clearly illustrates these large-scale trends. The following sections in this chapter synthesize our knowledge for each of these trends and themes.

34.2 Modern Distribution and Biogeographical History

Highland oak forests in the Tropics of the American continent are latitudinally and longitudinally distributed from central Mexico (i.e. south of the line Mazatlán–Fresnillo–Tampico) through Central America (Guatemala, Belize's Maya Mountains, El Salvador, Honduras, Nicaragua, Costa Rica and Panama) into Andean Colombia (e.g. Antioquia, Boyacá, Cauca, Cundinamarca, Huila and Nariño) just north from Ecuador, where the southernmost native oaks grow at the Pasto Airport in Nariño (Pulido et al. in Chap. 11, Fig. 34.1). Oaks are also found in the insular Caribbean, in the western region of Cuba between Pinar del Río and Matanzas (Nixon in Chap. 1).

   Altitudinally, Neotropical highland oak forests range from 500 m elevation up to 3,300 m in the Colombian Andes (Hooghiemstra in Chap. 2; Chap. 11) and 3,400 m in Costa Rica's Chirripó National Park (Kappelle and Van Uffelen in Chap. 4). *Quercus*, however, is also found at altitudes below 500 m, in lowland forests such as those thriving in Costa Rica's north-western Pacific, dry Guanacaste region (Kappelle in Chap. 10).
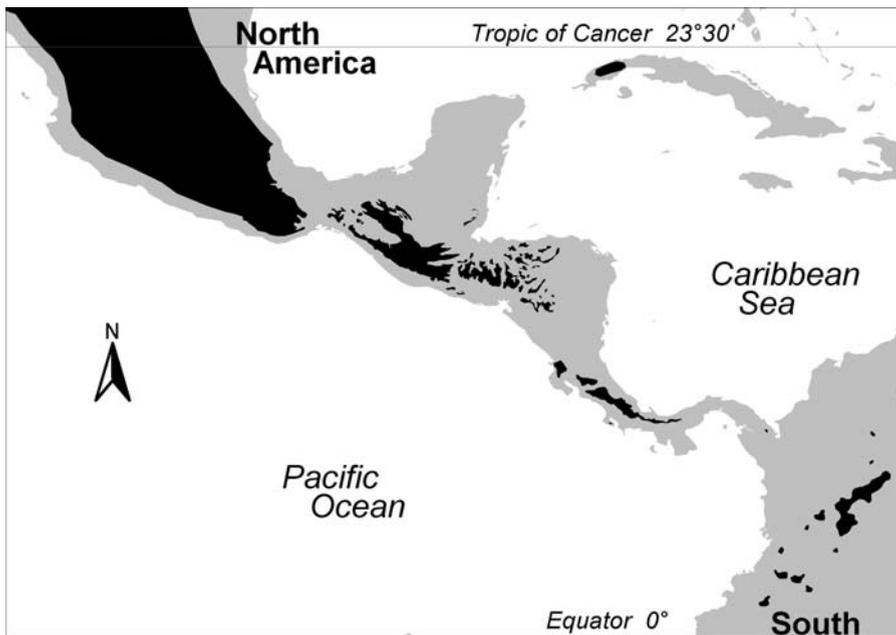

Fig. 34.1. Map showing the distribution of the genus *Quercus* (oak) in the Neotropics. Tropical oak in the Americas is found only in the Northern Hemisphere, at all latitudes between the Tropic of Cancer and the Equator. Most oaks are restricted to elevations over 500 m, such as found in the Mexican and Cuban sierras, the Belizean mountains, the Guatemalan volcanoes, the Honduran and Nicaraguan highlands, the Costa Rican and Panamanian cordilleras, and the Colombian Andes. Map preparation by Marco V. Castro

A common phenomenon observed on Neotropical mountains is the turnover of *Quercus* species along altitudinal gradients (Kappelle and Brown 2001). Oak species appear to be adapted to specific climatic and soil conditions prevailing at determined elevations. In Costa Rica, some 14 *Quercus* species are altitudinally distributed from sea level up to 3,400 m elevation. In this country, highest oak species diversity is found between 1,000 and 2,000 m where some 10–11 species may co-occur (Chap. 10). Similarly, in the small La Chinantla area of Oaxaca, Mexico, at least six species co-occur between 1,000 and 3,000 m elevation (Meave in Chap. 9).

The current latitudinal, longitudinal and altitudinal distribution of the genus *Quercus* and oak forests in the American Tropics is largely defined by the geological and climatic history of the continent, and the evolution of its flora (Kappelle et al. 1992). During the Pleistocene, the distribution of Neotropical montane oak forests was strongly affected by glacial cycles which included recurrent periods of cooling and warming. These climate fluctuations, exemplified by the Younger Dryas cooling event at the Pleistocene–Holocene boundary, made the oak forest altitudinal belt move up and down over considerable elevational distances (Islebe and Hooghiemstra in Chap. 3). As a result of this dynamic geoclimatic history, the modern flora of Neotropical montane oak forests is made up of a blend of tropical (60–75 %), temperate (18–35 %) and cosmopolitan (5–10 %) plant genera (Kappelle et al. 1992). Whereas at higher latitudes northern temperate (Holarctic) genera are more important, closer to the Equator southern temperate (Austral-Antarctic) and Neotropical genera become increasingly abundant (Kappelle in Chap. 10).

Evidence from long marine and terrestrial pollen records show how the distribution of the wind-pollinated Holarctic genus *Quercus* extended southwards from today's North America, through Central America, into northwestern South America (Hooghiemstra in Chap. 2). *Quercus* arrived in western Central Mexico at the start of the late Miocene, about 10 million years ago (Fournier 1982). The closure of the inter-oceanic channel which connected the tropical seas of the modern Atlantic and Pacific Oceans, and the subsequent formation of the Panamanian Isthmus took place some 4–5 million years ago (Keighwin 1982). However, detailed analysis of a long fossil pollen record from Colombia showed that *Quercus* migrated into today's basin of Bogotá not earlier than some 470,000 years before present (Van't Veer and Hooghiemstra 2000). As Hooghiemstra suggests (Chap. 2), the low migration rate of oak from Mexico into Colombia, even after the consolidation of Central America's Isthmus, may be largely due to its dependence on certain animals responsible for the dispersal of the tree's heavy seeds, known as acorns (López Barrera and Manson in Chap. 13, and Van Den Bergh and Kappelle in Chap. 26). Another reason for its slow migration may be the dependence of oak on the presence of specialized fungi with which the tree forms mycorrhizal associations at soil level (Mueller et al. in Chap. 5).

34.3 Forest Structure

Highland oak forests in tropical America vary considerably in structural features. Mature canopy trees may reach heights of 20–30 m in Mexico (Luna et al. in Chap. 8 and Meave et al. in Chap. 9), 35–45 m and occasionally up to 60 m in Costa Rica (Kappelle in Chap. 10), and 40 m in Colombia (Cuatrecasas 1934; Kappelle 1987; Pulido et al. in Chap. 11). In general, tree height decreases with elevation and may be greater on cloudy slopes, compared to drier slopes at the same altitude (Kappelle 1991; Kappelle and Van Uffelen in Chap. 4). Layering of horizontal forest strata is evident in most of these forests, and includes upper and lower canopy tree layers, a shrub layer, and a herb layer.

The upper canopy layer is often dominated by oak (*Quercus*) and pine (*Pinus*) in Mexico and northern Central America (Chaps. 2, 8, 9, 14 and 16). Pine, however, is not native to Costa Rica, Panama and South America (Hooghiemstra in Chap. 2). In the latter countries, highland oak forest tree canopies are dominated by oak and a variety of other tree families such as Araliaceae, Cunoniaceae, Magnoliaceae and Podocarpaceae (Chaps. 10, 17, 18, 21 and 22). As Pulido et al. (Chap. 11) point out, in some rare cases in Colombia oak forests are actually dominated by *Colombobalanus* (syn.: *Trigonobalanus*), a related and physiognomically similar tree, also in the Fagaceae. The lower canopy tree layer includes smaller individuals of tall trees and medium-sized adult trees in a number of families, e.g. Lauraceae, Melastomataceae, Myrsinaceae, Styracaceae and Theaceae (Chaps. 8–11).

The shrub layer is particularly rich in species, especially in Costa Rica and Colombia (Chaps. 10 and 11) where Ericaceae, Piperaceae, Rosaceae, Rubiaceae and Solanaceae predominate. The Mexican pine-oak forests are less rich in shrubs, though Ericaceae and Asteraceae may locally abound (Chaps. 8 and 9). In wetter montane oak forests closer to the Equator, bamboos (principally *Chusquea*) often accompany the bushes of the shrub layer (Widmer 1993, 1998; Chaps. 4, 10, 11, 21 and 22). Understory specialists such as dwarf palms (*Chamaedorea*, *Geonoma*) may locally predominate over bamboos, especially at elevations of 2,000–2,600 m (Groot et al. in Chap. 15). Some understory shrubs may develop very specific plant–pollinator (insect) relations, e.g. with bumblebees which may be vital to successful reproduction (Wesselingh et al. 1999, 2000).

The herb layer is less well developed and may include Acanthaceae, Araceae, Campanulaceae, Gesneriaceae and Scrophulariaceae, among other families (Chaps. 10 and 11). In the Araceae, the genus *Anthurium* – with terrestrial and epiphytic growth forms – may be particularly species rich and well adapted to locally differing light regimes and substrates (Chap. 15).

Mature oak forest densities of stems≥10 cm DBH (diameter at breast height) range from 500–750 individuals per hectare in Costa Rica (Blaser 1987; Jiménez et al. 1988) to 750–1,500 individuals per hectare in Mexico

(Meave et al. in Chap. 9). Occasionally, diameters of giant oaks may reach values over 120 cm (Chap. 10). With a basal area of about 50 m^2 per ha for stems≥10 cm DBH (Blaser 1987; Jiménez et al. 1988), values for mature old-growth montane oak forests in Costa Rica are among the highest found in tropical forests (Chap. 10). In addition, Hertel et al. (Chap. 22) revealed a very large fine root biomass (>1,300 g m^{-2}) for old-growth oak forest in Costa Rica, compared to other mature, humid tropical forests. It should be noted here that vascular epiphytes may also contribute considerably to oak forest biomass, as has been shown by Wolf and Flamenco-S (Chap. 29). These scholars reported a total of about 1,000 kg dry weight of vascular epiphytes per hectare in a little-disturbed old-growth pine-oak forest stand in Chiapas, Mexico.

34.4 Water and Nutrient Fluxes

Montane oak forests in the humid Tropics of the Americas often experience an almost diurnal presence of clouds (Kappelle in Chap. 10). That is why they are frequently called cloud forests (Spanish: *robledales nubosos*, *encinares nublados*), especially in Costa Rica, Panama and Colombia. Although knowledge of the overall effect of clouds through fog or horizontal precipitation on the hydrological input in tropical montane forests is still scanty, it has been widely recognized that, compared to other tropical forests, the specific atmospheric humidity regime of these forests represents one of the main factors causing the large array of differences in forest structure and functioning (Bruijnzeel 2001).

Köhler et al. (Chap. 21) measured incident rainfall (gross precipitation) in Costa Rican montane oak forests, and recorded 2,800–2,900 mm year^{-1}, of which 70–75 % corresponded to throughfall, 2–17 % to stemflow, and 10–25 % to canopy interception – depending on the successional stage of the forest. These authors found that nutrient concentrations in throughfall water exceeded those measured in incident rainfall. In upper canopy trees, they recorded a pH of stemflow water ranging from 4.2 to 5.7, and noted significantly higher nutrient concentrations in stemflow in these trees than in lower canopy trees. Total annual litter production in mature old-growth oak forest was 12,870 kg ha^{-1} year^{-1}. Leaves dominated the litter fraction, which contributed to some 56 % of total litter (Chap. 21).

In Costa Rican mature old-growth oak forests, soils generally have dark-brown humus profiles composed of fine organic material, free of litter fragments, and with only little mineral material. Between 2,000 and 3,000 m elevation, the thickness of soil humus profiles ranges from 10 to 20 cm at the Pacific slope, and up to 40 cm at the Atlantic slope (Kappelle et al. 1995b; Kappelle and Van Uffelen in Chap. 4). In these forests, the soil carbon pool size ranges from about 500 mol m^{-2} in the organic layer to 12.5 mol m^{-2} in the mineral

topsoil, the C/N ratios (molar) in both soil layers fluctuating in the range 25–28. Similarly, N concentrations range from 100 to 150 mol m^{-3}, and P concentrations from 2.5 to 12 mol m^{-3} (Hertel et al. in Chap. 22).

34.5 Fungi and Lichens

Fungi are a key component of oak forests worldwide. Neotropical montane oak forests are no exception to that rule. Oaks have evolved often obligatory, highly specialized mutualistic relationships with certain macrofungi, termed ectomycorrhizae, to promote processes such as nutrient cycling, nutrient uptake, and decomposition of organic matter (Mueller and Bills 2004). In Costa Rican highland oak forests, at least 22 woody or tough macrofungi (polypore fungi) have been recorded (Mueller et al. in Chap. 5). According to Mueller et al. (Chap. 5), these species are adapted to significant daily fluctuations in temperature and to high humidity levels throughout the year. To date, an additional 400 species of Agaricales (mushrooms and boletes, in the Basidiomycetes) have been identified from these Costa Rican montane *Quercus*-dominated forests. About half are ectomycorrhizal, the others being putatively saprotrophic (Chap. 5).

Like fungi, lichens form a very important element of Neotropical oak forest biodiversity. Lichen growth in tropical oak forests is often abundant, probably due to the presence of suitable oak substrate and a favourable climate with high precipitation, frequent fog and moderate temperatures (Sipman in Chap. 6). Today, at least 460 lichen species have been recorded by Sipman and colleagues in montane oak forests of Mexico, Guatemala, El Salvador, Costa Rica and Colombia, suggesting that species richness is at least comparable with temperate oak forests, though actual diversity is probably twice as large (Chap. 6).

Epiphytic lichens inhabit a great number of microhabitats on oak trees. Holz (Chap. 7) reported some 60 species of macrolichens dwelling on standing mature oak trees in upper montane Costa Rica. Many demonstrate a specific host preference. Species richness is highly variable, with a mean of 2.7 lichen species per 600 cm^2 of random substrate area. Generally, species richness increases with tree height. Many lichens on the trunks and in the inner canopy tend to grow in pure patches, apparently as a mechanism of adaptation to promote successful interspecific competition for space and light (Chap. 7).

34.6 Plant Species Diversity

Recent work by Nixon (Chap. 1) demonstrates the huge species diversity within the Holarctic genus *Quercus* (oak) in the New World. Probably some 220 species of oak are found on the American continent, distributed from Canada southwards into Colombia. Mexico is the richest country, with some 160–165 species of native *Quercus* (Valencia-A 2004; Valencia-A and Nixon 2004), followed by the USA with 91 recognized species; Cuba and Colombia each harbour only a single native oak species (Nixon 1993 and in Chap. 1). The highlands of central and eastern Mexico have been identified as the major centre of oak species diversity in the Western Hemisphere (Nixon 1993). The best example of Mexico's incredibly large diversity within *Quercus* is found in the state of Oaxaca where some 70 species thrive (48 % of Mexico's total; Valencia-A 2004). This is particularly interesting, considering that only 25 % of this Mexican state is covered by pure oak forests and mixed pine-oak forests (Meave et al. in Chap. 9). In addition, it should be noted that the extra-ordinary diversity in Mexican oaks is also reflected in the enormous richness of non-plant species associated with oak, such as gall-forming insects, particularly gall wasps (Oyama et al. in Chap. 20). Major lineages of gall wasps are thought to have diverged from Mexico and Guatemala (Kinsey 1936), probably as a result of local oak diversity. This co-evolutionary history may be the main reason why morphological variation in galls induced by insects in oak species in Mexico is particularly high (Chap. 20).

Thousands of vascular plant species are believed to inhabit the montane oak forests of the Neotropics. In Costa Rican oak forests, at least 1,300 species have been formally recorded so far (Van Velzen et al. 1993; Kappelle 1996 and in Chap. 10, Kappelle et al. 2000). Over half of these are dicot species. Almost 500 terrestrial woody plants and some 130 pteridophytes have been documented along a single montane oak forest transect in Costa Rica's Chirripó National Park (Kappelle and Gómez 1992; Kappelle et al. 1995b; Kappelle and Van Uffelen in Chap. 4). Further to the northwest, Wolf and Flamenco-S (Chap. 29) confirm the presence of at least 720 species of vascular epiphytes in the highland pine-oak forests of Chiapas. Apparently, the vascular epiphyte diversity of these Mexican oak forests is strongly dependent on past levels of anthropogenic disturbance (Wolf 2005, and Chap. 29).

Plant diversity in other parts of the oak-inhabited Neotropical highlands may be as great or even greater. However, Pulido et al. (Chap. 11) are convinced that plant species richness of modern Colombian oak forest (577 recorded vascular plant species) is smaller than for similar forest in Costa Rica (Kappelle et al. 1996). This pattern may well be due to the long-lasting human activities which have strongly impacted the oak forests of the Northern Andes, for centuries, if not millennia (Van der Hammen and Gonzalez 1963; Herrera et al. 1989; Hooghiemstra in Chap. 2). Further analysis of large

floristic databases, such as currently assembled for the highlands of Chiapas, may reveal specific and detailed patterns in, for example, montane oak forest tree species diversity (González-Espinosa et al. 2004 and in Chap. 16) and vascular epiphyte species richness (Wolf and Flamenco-S 2003 and in Chap. 19).

Not only vascular plant diversity is high in Neotropical montane oak forests; non-vascular plant species richness – especially that of bryophytes – is also extraordinarily large (Holz in Chap. 7). In a recent inventory conducted in Costa Rican highland oak forests, 251 bryophyte species (128 hepatics, one hornwort, and 122 mosses) were recorded (Holz et al. 2002; Holz and Gradstein 2005). The same study revealed the occurrence of 108 epiphytic bryophytes (67 hepatics and 41 mosses) dwelling on stems and branches of a total of 15 oak trees (Chap. 7). Many of these species are considered ecological indicator species which can be used to measure and monitor changes in microclimatic and substrate conditions of disturbed and recovering oak forest (Chaps. 7 and 29).

34.7 Animal Habitat Preferences and Diets

The largest mammal inhabiting the montane oak forests of Mesoamerica is the endangered Baird's tapir, *Tapirus bairdii* (Naranjo and Vaughan 2000). This herbivore mammal has an important impact on the structure and plant diversity of its habitat, as it disperses seeds which are ingested wholly and dropped intact (Tobler 2002; Tobler et al. in Chap. 27). Other large mammals observed in montane oak forest include feline carnivores such as the jaguar, *Panthera onca*, and the puma, *Puma concolor* (Aranda and Sánchez-Cordero 1996), still little studied in the Neotropical highlands (Almeida 2000).

Baird's tapir seems to prefer undisturbed oak forests, tending to avoid patches impacted by human activity. In Mexico and Costa Rica, relative tapir abundance in undisturbed areas is more than twice as high as that in disturbed zones (Chap. 27). Agricultural areas are considered important barriers to tapir movement, and may result in significant fragmentation of tapir populations. Following habitat loss, hunting is the second most important threat to tapir populations. Analysis of tapir faeces demonstrated the importance of leaves and stems as key components of this herbivore's diet, whereas fruits contribute to less than 10 % of its food. In Costa Rica, remains of *Quercus costaricensis* were frequently encountered in tapir faecal samples (Chap. 27).

Rats and mice (Muridae and Heteromyidae) may abound in tropical montane oak forests – especially in years following mast seeding (López-Barrera Manson in Chap. 13; Van den Bergh and Kappelle in Chap. 26). Species of some myomorph genera prefer closed, mature oak forest (e.g. *Heteromys* and *Oryzomys*) whereas others are more numerous in open, shrubby or grassy

habitats such as abandoned pastures (*Reithrodontomys*; Chap. 26). They are among the principal consumers and dispersers of acorns and other seeds (Chap. 13).

During a short field study in Costa Rican montane oak forests, some 20 birds have been observed foraging on over 20 different tree and shrub fruits, resulting in a total of 68 bird–plant frugivorous interactions (Wilms and Kappelle in Chap. 24). Lauraceous tree species within the genera *Ocotea* and *Nectandra* were most frequently fed upon. Small to medium-sized birds foraged mainly on fruits of fast-growing, light-dependent trees, whereas medium to large-sized birds preferred the fruits and seeds of slow-growing, mature forest tree species. Most of the birds observed displayed a preference for intact oak forest over open, disturbed habitats. Resplendent Quetzals, for instance, were much more abundant in mature old-growth forest than in pastures (Chap. 24). These birds prefer higher-elevation forests as their principal habitat, though they are known to altitudinally migrate as seasonal fruit availability changes (Wheelwright 1983). In Costa Rica, higher relative abundance of quetzals was found between February and June, coinciding with the breeding season (García-Rojas in Chap. 25).

34.8 Seed Predation and Dispersal

Many forest vertebrates depend on the availability of fruits and seeds which serve as main sources of food. Similarly, numerous plants depend on the presence and abundance of fruit- and seed-consuming vertebrates responsible for the dispersal of their seeds. It has been widely recognized that frugivorous and granivorous birds and mammals play a key role in the dispersal of seeds of trees, shrubs, herbs and climbers in tropical forests (e.g. Guevara et al. 1986; Adler 1995; Ceballos 1995; Janzen and Forget 2001; Levey et al. 2005; Wilms and Kappelle in Chap. 24; García-Rojas in Chap. 25).

Seedling emergence from soil seed bank material collected in Costa Rican montane oak forests and pastures demonstrated that at least one third of all plant species which emerged under greenhouse conditions had been dispersed zoochorously (Ten Hoopen and Kappelle in Chap. 23). Under natural conditions, emergence may be affected by litter (López-Barrera and González Espinoza 2000). In the particular case of oak (e.g. *Quercus rugosa*), animal-dispersed seeds (acorns) are likely to germinate soon after they are shed (Guariguata and Sáenz 2002; Bonfil in Chap. 12). Acorns cannot retain their viability long enough to survive until the next rainy season while forming part of the soil seed bank. The combination of these characteristics may be the main reason why acorns were not present in the collected soil seed bank material used during the seedling emergence observation study (Chap. 23).

Important fruit and seed predating and dispersing mammals at tropical latitudes include tapirs, monkeys, peccaries, bats, squirrels, rats and mice (Barnett 1977; Janzen 1983; Price and Jenkins 1986; Van den Bergh and Kappelle 1998 and in Chap.26; Demattia et al. 2002; López-Barrera and Manson in Chap. 13; García-Rojas in Chap. 25; Tobler et al. in Chap. 27).

Tropical montane oak seeds (acorns) are predated upon and/or dispersed by small mammals, particularly rodents (e.g. *Peromyscus* spp. and *Sciurus granatensis*; Chaps. 13 and 26). The huge amounts of tropical acorns available during mast seeding years may considerably affect local rodent populations, as has been demonstrated by a study on *Quercus laurina*, *Q. crassifolia* and *Q. rugosa* in the Chiapas highlands of Mexico (Chap. 13). It is well known that acorns are dispersed by jays in temperate oak forests. Jays seem to form a symbiotic relation with oaks. The same may apply for Neotropical montane oak forests which are inhabited by, e.g. the Silvery-Throated Jay (*Cyanolyca argentigula*, Chap. 24).

Certainly, a large percentage of tropical forest bird species strongly depend on fruits for their diet (Stiles 1985). Probably, frugivorous birds form the most important group of seed dispersers in the high-elevation oak forests of the tropical Americas, particularly in view of the low abundance of monkeys and bats in this cool 'temperate' highland ecosystem (Kappelle 1996). About half (34) of all bird species recorded in a Costa Rican montane oak forest showed frugivorous behaviour (Chap. 24). During a short survey, these avian dispersers were observed to forage on at least 22 fruit-bearing, endozoochorous tree species.

Many of these birds are considered key restoration agents, as they transport ornithochorous tree seeds from mature closed forest into neighbouring non-forested secondary growth and pastures on cleared forest lands (Chap. 24). In pastures, birds often drop seeds around isolated remnant forest trees, which offer them shelter on their way to distant forest fragments. Such scattered trees may act as seed traps and trigger forest succession at cleared sites (Guevara and Laborde 1993, and Chap. 24). A good example of a tropical oak forest bird accelerating forest recovery is that of the Resplendent Quetzal (*Pharomachrus mocinno*). This spectacular bird is recognized for its key ecological function in maintaining montane forest dynamics (Guindon 1997). Its behaviour increases the probabilities of seed survival and allows for light gap colonization, enrichment of isolated forest patches, and maintenance of tree species populations with limited distribution ranges (Chap. 25).

34.9 Responses to Disturbance

During the last 50 years, the clearing of large tracts of Neotropical montane forests, including oak forests, has led to severe land degradation in general,

and to biodiversity depletion in particular (e.g. Rzedowski 1981; Budowski 1982; Monasterio et al. 1987; Bonfil 1991; González-Espinosa et al. 1995; Kappelle 1996). Since the early 1980s, vegetation and species response to tropical montane forest disturbance has received increased attention from scientists (Ewel 1980; Sugden et al. 1985; Brown and Lugo 1990; González-Espinosa et al. 1991; Walker et al. 1991; Kappelle 1993). A major conclusion of these studies concerns the decrease of the recovery rate with increasing elevation (e.g. Ewel 1980; Kappelle et al. 1995a, 1996). Regrowth following disturbance of tropical oak forests, for instance, appears to be extremely slow in the upper montane forest belt (2,400–3,200 m elevation), compared to faster recovery rates occurring at mid-elevation (1,500–2,400 m; Ewel 1980; Kappelle et al. 1994).

Recovery of oak species following disturbance may strongly depend on the availability of acorns and the activity of seed-dispersing animals (Chaps. 12 and 13). A study addressing seedling and population dynamics of *Quercus rugosa* on the slopes of the Ajusco Volcano, south of Mexico City, demonstrated that oak seedlings, once they emerged from dispersed acorns, were very fragile and had to survive a dry period of variable length in order to become vigorous saplings (Bonfil in Chap. 12). Therefore, only in years with higher than average winter rains (i.e. a reduced dry season) were conditions met for abundant seedling establishment. In average years, newly germinated seedlings died during their first dry season (Chap. 12).

Moisture, nutrient availability and light regime are among the most important factors affecting successful establishment of oak seedlings (Quintana-Ascencio et al. 1992). Most Neotropical oaks may be considered early successional species, as they require relatively large forest gaps or clearings for recruitment (Quintana-Ascencio et al. 2004; González-Espinosa et al. in Chap. 16). Some oaks may also regenerate along oak forest edges (Oosterhoorn and Kappelle 2000; López-Barrera et al. 2005, and Chaps. 13 and 16). Along such edges, microclimatic differences expressed in locally dry environments may affect oak seedling growth and physiological response, depending on the requirements of the species concerned (López-Barrera 2003, and Chap. 13; Asbjornsen et al. in Chap. 19). Mortality of oak seedlings (*Quercus acutifolia* and *Q. castanea*) in the Mixteca Alta region of Oaxaca, Mexico, is indeed significantly greater at open microsites – where moisture stress is higher – than at understory microsites (Asbjornsen et al. 2004, and Chap. 19). Compared to other broad-leaved trees and conifers in Chiapas, Mexico, seedling survival under field conditions (successional habitats) was highest for oaks (Ramírez-Marcial et al. 2005 and in Chap. 14). Survival rates of oak seedlings under greenhouse conditions, however, do not differ much from rates established for conifers (Chap. 14).

A recent analysis of the effects of reduced impact logging on oak forest regeneration in Costa Rica demonstrates that, at low harvesting intensities, the annual mortality rate for seedlings exceeds that recorded at moderate harvesting intensity (Sáenz and Guariguata 2001). This difference is probably

related to variations in post-logging overhead light conditions. Comparing individual species, results for *Quercus costaricensis* and *Q. bumelioides* showed the largest, statistically significant differences in diameter growth rates among logging treatments, demonstrated by Guariguata et al. (Chap. 18). Guariguata's results revealed that, at the applied harvesting intensities, juveniles of *Quercus* (particularly *Q. costaricensis*) performed better in terms of radial growth than the other, non-oak study species.

During the last 15 years, community-level recovery of Neotropical montane oak forest has received increased attention as well (e.g. González-Espinosa et al. 1991; Kappelle et al. 1995a, 1996). The available studies on oak forest succession have mainly used chronosequences, particularly after agricultural field (e.g. *milpa*) and pasture abandonment. Research conducted in Chiapas, Mexico, and in the high Talamancas, Costa Rica, has revealed a series of successional pathways and sequential plant associations which occur after abandonment of old fields and pastures (Kappelle et al. 1994; González-Espinosa et al. in Chap. 16; Kappelle in Chap. 17). As expected, species diversity, structural complexity, stand height, basal area and accumulated litter increased with time (Chaps. 16, 17 and 22). Hertel et al. (Chap. 22), for instance, detected a significant linear increase in fine root mass with increasing age of secondary oak forests in highland Costa Rica.

However, recovery may take place at differing rates as a result of specific local stand or patch conditions. To gain a better insight into recovery rates, Kappelle et al. (1995a, 1996) estimated the theoretically minimum time required for abandoned montane pastures to return – via a successful natural recovery pathway – to a state in which their stand structure and floristic richness were within the ranges known for undisturbed mature oak forest. Analysis of beta diversity of terrestrial vascular plants led to an estimation of a minimum floristic recovery time of approximately 65 years. Similarly, a recovery period of 80–90 years was calculated for an abandoned pasture to become structurally similar, in terms of canopy height and basal area, to intact old-growth forest (Chap. 17).

To conclude, as González-Espinosa and colleagues correctly pointed out, floristic replacement probably delineates the major successional trends towards closely related sets of Neotropical old-growth oak forest types within certain ranges of altitudinal, climatic and edaphic conditions (Chaps. 16 and 17). The specific pathways followed by successional processes taking place on abandoned lands, and their characteristic levels of floristic and structural recovery will without doubt depend on the types and intensities of previous land use practices applied to Neotropical highland sites (González-Espinosa et al. 1991; Kappelle and Juárez 1995; Chaps. 16, 17, 18, 19, 21, 22 and 30).

34.10 Conservation and Sustainable Use

In the American Tropics, mountain oak forests have been used by people for centuries, if not millennia (Kappelle and Brown 2001). Probably, the indigenous peoples of the Mexican sierras, Guatemalan and Costa Rican highlands, and Colombian Andes were the first to use and manage Neotropical oak forests (e.g. Ramírez-Marcial et al. 2001; González-Espinosa et al. in Chap. 16). In pre-Columbian times, it is likely that these ethnic peoples relied heavily upon highland oak forests for obtaining food, fodder, fibre, fuel, medicines, dyes, gums, oils, antioxidants, spices, poisons, ornamental plants and pets (e.g. Kappelle et al. 2000). However, it is only recently that the Mesoamerican and Colombian montane oak forests have been significantly fragmented and degraded, as commercial logging and large-scale forest conversion for agricultural land and pastures became common practice (e.g. González-Espinosa et al. 1995; Kappelle 1996; Van Omme et al. 1997; Etter and Van Wijngaarden 2000; Helmer 2000).

For instance, since the early 1800s large oak forest areas in Mexican, Central American and northern Andean mountains have made way for coffee plantations and pastures for cattle ranching (Kappelle and Juárez 1995; Etter and Van Wijngaarden 2000). Due to increased population density, the last remaining tracts are now significantly threatened, since they are still being indiscriminately cut for timber, fuelwood and charcoal (Aus der Beek et al. in Chap. 31) throughout large parts of the region. This is especially alarming because these mountainous oak forests provide a large proportion of the drinking water and hydro-energy needed in large urban centres such as Guatemala City, San José and suburbs in Costa Rica, and Bogotá, Colombia.

Fortunately, over the last decades, society has come to value and recognize that tropical montane oak forests are not only sources of timber, but also critical ecosystems for water production (Barrantes Moreno in Chap. 33), sources of medicines (Kappelle and Juárez in Chap. 30), carbon sinks and reservoirs (Helmer and Brown 2000), areas for recreation (Chap. 30), and landscapes of great scenic beauty (see also Daily 1997, and Dawkins and Philip 1998). The now recognized multi-functionality of forests is reflected by current definitions of sustainable forest management which attempt to balance forest use and conservation (Castañeda 2000). In this context, Herrera and Chaverri (Chap. 32) stress the need for a clear definition of principles, criteria and indicators (C&I) necessary to assess and monitor sustainable forest management in highland oak forests. Such an approach, in combination with a sound understanding of natural oak forest dynamics (e.g. regeneration), is vital for the successful management of both silvicultural forest systems and protected forest areas (Olvera-Vargas et al. in Chap. 28). Only when C&I-based management guidelines for preservation and silvicultural purposes are in place will a sustainable balance between use and conservation be possible (Chaps. 28 and

32). The proposed framework for sustainable harvesting of bromeliads in the oak forests of Chiapas, Mexico, may serve as a good example of how a sound management plan may considerably enhance overall oak forest conservation while sustainably providing profit to local people (Wolf and Konings 2001; Wolf and Flamenco-S in Chap. 29).

If we are to preserve a large part of the remaining Neotropical montane oak forest and its variety of life as expressed in its genes, species and ecosystem types in the long term, we will need to elaborate a conservation strategy in which not only networks of protected core areas, buffer zones, and corridors form a fundamental component, but also participatory planning strategies in which different local and regional stakeholder groups and decision-makers are involved, in order to establish a broad-based, consensus-oriented conservation framework (Calderón et al. 2004; Kappelle 2004).

This new approach is well illustrated by the creation of the 'Alliance for the Conservation of the Pine-Oak Forest Ecoregion and its Birds in Meso-America' in 2003 (E. Secaira, The Nature Conservancy (TNC) and S. Pérez, Defensores de la Naturaleza, personal communications). The aim of this broad-based conservation partnership is to develop a regional conservation plan to save the montane oak forests of the highlands of southern Mexico (Chiapas), Guatemala, El Salvador, Honduras and Nicaragua, and in this way ensure the preservation of the winter habitat of Neotropical migratory birds threatened with extinction. Special focus is on an umbrella species known as the Golden Cheeked Warbler (*Dendroica chrysoparia*; Spanish: chipe mejilla dorada), which migrates during the boreal fall from the USA to its winter habitat, the montane pine-oak forests of southern Mexico and north-western Central America (Kroll 1980; King and Rappole 2000; Rappole et al. 2000).

The alliance is formed by a number of country-based non-governmental organizations (NGOs) including Pronatura-Chiapas, Instituto Montebello and Instituto de Historia Natural y Ecología (INHE) in Mexico, Fundación Defensores de la Naturaleza and Asociación de Reservas Naturales Privadas (Proyecto Cuchumatanes) in Guatemala, Salvanatura in El Salvador, Fundación EDUCA in Honduras, and the Alianza para las Áreas Silvestres (ALAS) in Nicaragua, as well as several international conservation organizations including TNC, the Texas Park and Wildlife Department (TPWD), and the Zoo Conservation Outreach Group.

It is hoped that such multi-country, multi-scale, multi-stakeholder initiatives will generate the ecosystem-based tools and knowledge urgently needed to help decision-makers find a way to sustainably manage and restore (Holl and Kappelle 1999) the threatened, species-rich highland oak forest ecoregions of the New World, for human well-being.

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