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Tropical Montane Forests

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Introduction

Mid and high-elevation regions near the equator such as are found in the Andes and on Papua New Guinea support tropical montane forests (TMF), which range from relatively dry woodlands to extremely wet forests. TMF forms a major component of several of the world's biodiversity hotspots (e.g., Meso-America and the northern Andes), as it represents an extremely species-rich system, which is highly endangered due to human interference. The most important and diverse of all TMF types is the tropical montane cloud forest (TMCF). This conspicuous ecosystem filters global air masses in such a way that they seize and incorporate water and nutrients from mist and fog into their cycles. It may be even richer than the tropical lowland rainforest (TLRF) when diversity is measured as species density on a per-unit-area basis. TMCF is well known for its important fresh-water resources, which feed the many rivers passing through major mountain cities in the Andes such as Bogotá and Quito, which in turn depend on these resources to supply their human populations with sufficient drinking water. However, today these fragile forests are among the most endangered ecosystems worldwide, due to destructive anthropogenic forces causing forest loss and habitat fragmentation, ultimately leading to species extinction and loss of environmental goods and services which are vital to the regional and local human populations.

The present article presents a brief overview of TMF, emphasizing its most important representative, the TMCF type. A bioclimatic definition is presented and its overall aspects are discussed. Subsequently, its geographic distribution and main determinants are treated. Details on climate, soils, and topography are elaborated. Furthermore, past trends in forest cover are dealt with. This is followed by a detailed discussion of the TMF structure, species composition, dominance, and dynamics as a result of disturbances. Regional subtypes and boundaries with other forest types are listed. Next, the ecological/environmental and sociocultural importance of this specific forest ecosystem is analyzed. Past and current TMF use practices are assessed and some sustainable forest management systems identified. Finally, threats to the survival of species and the integrity of the ecosystem as a whole are evaluated and current and future conservation strategies discussed. Such an analysis ultimately permits the setting of priorities in conservation and sustainable development for the benefit of the peoples living in and depending on TMF systems.

Definition

Forests on Tropical Mountains

TMF is latitudinally restricted to the tropics and may only be found, in its strict sense, at northern and southern latitudes between the tropics of Cancer and Capricorn. In a wider sense, TMF reaches a northern latitude of 23° in Mexico and a southern latitude of 25° in Argentina. Within this latitudinal range, TMF is altitudinally restricted to montane elevations. This is the most difficult part of the elaboration of a concise definition, for scholars have not been able to define the altitudinal limits of the montane belt unanimously. In general, as a rule of thumb, it is assumed that montane forests occur between 500 and 4000 m above sea-level. However, there are places on earth, especially on volcanic islands, where montane forests may occur at 300 m elevation (e.g., in the Caribbean), while there are sites in certain tropical mountain chains such as in the South American Andes where small pockets of montane forests occur in wind-protected valleys at elevations over 4000 m. In the latter case, these montane forests are better known as tropical subalpine forests (TSF) as they often occur just below – or amongst – the treeless, tropical alpine grasslands and shrublands.

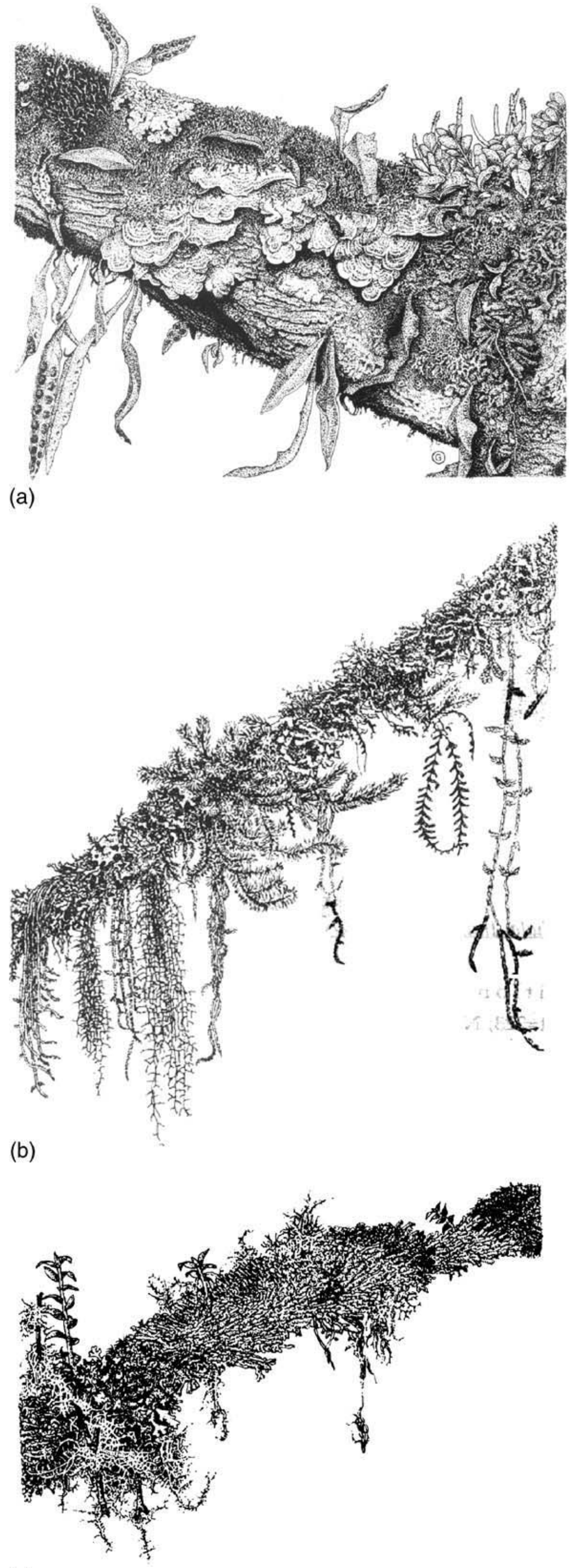
Tropical Montane Cloud Forests

In contrast, TMCF – the cloudy version of TMF – was well defined a decade ago. Specialists now agree that TMCF differs significantly in composition and structure from rainforests in tropical lowlands (TLRF). It typically occurs as a narrow altitudinal belt in tropical highlands where the atmospheric environment is characterized by persistent, frequent, or seasonal cloud cover at vegetation (or ground) level, i.e., the tree crowns are regularly bathed in mist and fog ('canopy wetting'). Although little is known about the hydroecological effect of the mist-forming, enveloping, and wind-driven clouds on the hydrological input in this ecosystem, it has been widely recognized that the frequent cloud and mist presence causes a considerable increase in atmospheric humidity within the forest interior – a phenomenon presently known as 'horizontal precipitation.'

Characterizing Tropical Montane Forests

Limiting climatic factors such as horizontal precipitation (cloud stripping), a reduced photosynthesis due to reduced solar radiation, a periodic water shortage (vapor deficit), strong diurnal temperature oscillations, a general reduction of the evapotranspiration rate, exposure to strong winds, and a limited nutrient uptake, are the most important environmental factors which determine the large array of differences in forest structure and composition when cloudy TMF is compared to TLRF. Some of these striking differences include a particular, often elfin-like physiognomy characterized by a reduced tree stature, an increased tree stem density, frequently gnarled trunks and branches of stunted trees with dense crowns and small-sized, sclerophyllous and coriaceous leaves. At first sight, the branches of trees and shrubs appear typically draped with pendant mosses covered with water droplets and filmy ferns. In fact, a complex mosaic-like assemblage of vascular and nonvascular epiphytes (orchids, bromeliads, ferns, mosses, liverworts, algae, lichens, and fungi) blankets the surface of host trees and shrubs (**Figure 1**).

The epiphytes contribute to an enormous extra above-ground biomass which may retain a significant quantity of additional water from clouds (i.e., the above-mentioned process of cloud stripping). All these diagnostic features, together with the forest's low productivity and low nutrient cycling rates, characterize the general structure and functioning of the TMCF and hence the most typical of all TMF varieties.



(a) (b) (c)

Figure 1 Epiphytic communities of vascular and nonvascular plants on tree branches in Colombian tropical montane forests at elevations of (a) 1980 m, (b) 2550 m, and (c) 3370 m, studied by Jan H.D. Wolf. Courtesy of Gerard Oostermeijer.

Distribution

Geographical Distribution

TMF as well as TMCF occurs between 500 and 4000 m altitude on all three tropical continents (Africa, America, and Asia) and in equatorial

Oceania. The majority of TMF sites are found between 1200 and 2800 m elevation. They are found from central Mexico (Eje Neovolcánico Transversal) south-eastward along the Central American mountain chains (Guatemala, Costa Rica), and further south along the Andes to northern Argentina (Salta-Tucumán). They appear especially well developed in the northern Andes (Venezuela, Colombia, Ecuador, and Peru), on both the eastern and western flanks of their cordilleras. In Central Africa they occur in mountainous countries like Uganda (Bamenda Highlands, Rwenzori Mountains), and in East Africa along the so-called Eastern Arc (e.g., Mount Kilimanjaro, Mount Kenya) and at the drier Ethiopian highland plateaux. Further to the east, they are encountered on the higher parts of Southeast Asia (e.g., Mount Kinabalu in Sabah, East Malaysia; Kalimantan and Irian Jaya in Indonesia; Philippines; Papua New Guinea). They inhabit the mountaintops of many oceanic islands where exceptionally wet, marine, equatorial conditions prevail, as is the case in the Caribbean region (Jamaica, Puerto Rico) and the Pacific Ocean (Fiji, Hawaii; **Figure 2**).

The Massenerhebung Effect

It is well known that TMF formations occur at higher elevations on taller mountains. The upper limit of lowland forest may be brought down to varying degrees below the temperature-determined uppermost limit when the fog characteristic of TMF environment occurs at lower levels. This little understood phenomenon is known as the Massenerhebung or telescope effect, first described for the Alps in Europe. Apparently, the compression and depression of the forest belts on small mountains, such as on tropical islands (e.g., Hawaii) and along coasts, seems mainly associated with a lowering in the level at which cloud habitually forms. More specifically, the altitudinal distribution of TMCF is related to the cloud level itself, which in turn is dependent upon the humidity at the foot of a mountain. The greater the humidity is at the mountain's base, the lower the cloud level occurs (**Figure 3**).

Climate

The average temperature in TMF and cool-humid TMCF depends principally on elevation, as temperature decreases with increasing altitude. Average annual temperatures range from 8°C at 3400 m to 20°C at 1000 m. Average annual rainfall is correlated with slope orientation and fluctuates between 500 and 10 000 mm, although yearly precipitation generally ranges from 1000 to 3000 mm. Ascending air masses bring increased precipitation to mountain slopes (windward slopes; e.g., under the influence of trade winds in the Caribbean) unless they are sheltered from the wind (leeward slopes; rain shadow). As has been said, the net precipitation or throughfall in TMCF is significantly enhanced beyond rainfall contribution through direct canopy interception of cloud water (horizontal precipitation), a process also known as cloud stripping. It is therefore not surprising that TMF is particularly rich in epiphytes, which obtain water directly from the perhumid atmosphere.

Soil

TMF soils are quite different from tropical lowland soils. On tropical mountains, the often reddish-brown loamy lowland soils on flat plains become replaced by more yellowish, acid and peaty soil types with organic upper horizons on steep slopes in rugged terrain. TMF soils are frequently water-logged and suffer from podsolization, a soil-forming process, which causes the leaching of nutrients (lixiviation) from upper soil horizons to lower levels. These nutrient-poor, water-saturated soils may experience an anaerobic environment, which in turn originates impeded root respiration, a reduction in below-ground bioactivity, and lower decomposition levels. The final result is the accumulation of humus in the topsoil (histosols) and/or loss of nutrients at top- and mid-soil levels (podsols). However, on a number of mountains (e.g., volcanoes) nutrient-rich soil types may prevail (andosols), as intrusive rocks intermingled with marine sediments become exposed and weathered. Soil characteristics in TMCF appear to correlate strongly with plant community distribution.

Present Forest Cover

Over the last few decades TMF and particularly TMCF has suffered greatly from human interference. Large-scale deforestation for timber, fuelwood, and charcoal production in combination with forest conversion to pastureland has caused uncontrolled habitat fragmentation and severe land degradation. Today, TMF covers an estimated 200 million ha throughout the tropics. This is only 30% of the 700 million ha of the globe's tropical montane landmass. Throughout the 1980s the annual TMF deforestation rate was 2.5 million ha. TMCF makes up less than 1% of the world's closed canopy forests, while in the neotropics it presently covers only 65–75 million ha, about a third to half of which occurs in Colombia. Further research using high-resolution satellite imagery is urgently needed to assess precisely the area currently covered by TMF and TMCF in particular.

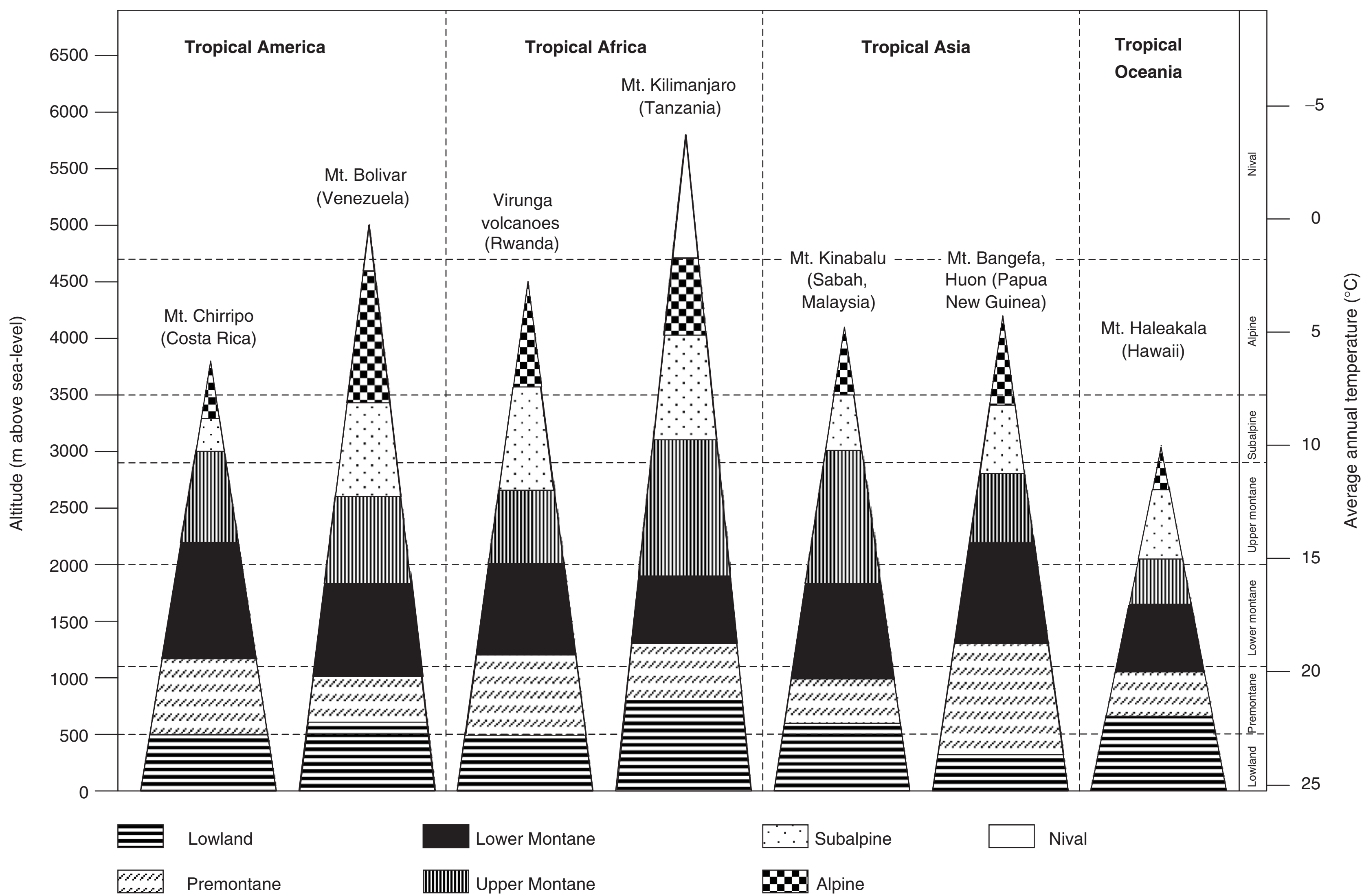


Figure 2 Altitudinal vegetation zonation on selected mountains on all tropical continents. The tropical montane forest (TMF) is strictly found in the lower and upper montane belts, but may occur locally in adjacent zones of the premontane and subalpine belts. The transitional subalpine belt (just below the upper TMF tree line, separating the TMF from alpine scrub) is regionally and locally also known as the ericaceous belt, while the transitional premontane belt (separating the lowland forest from TMF formations) has also been named as the (foot) hill zone or submontane belt.

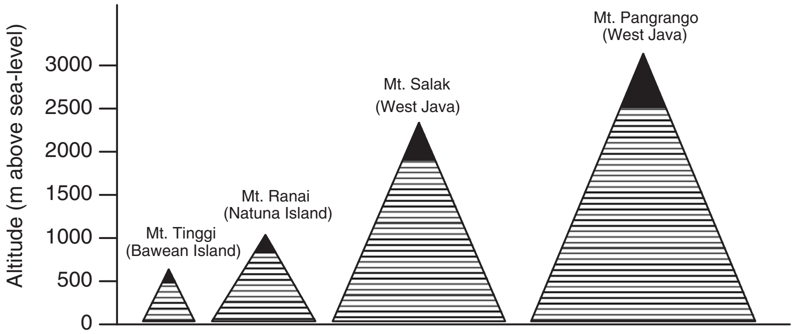


Figure 3 The Massenerhebung or telescope effect of tropical vegetation zonation, exemplified by the occurrence of mossy montane forest at contrasting altitudes on different-sized mountains in South-East Asia. (Adapted with permission from Bruijnzeel LA and Hamilton LS (2000) *Decision Time for Cloud Forests*. Paris: WWF, IUCN, and UNESCO.)

Table 1 Characters of structure and physiognomy used to define the principal tropical lowland and montane rain forest formations

Formation	*TLF (evergreen)*	*TLMF*	*TUMF*
Canopy height	25–45 m	15–33 m	1.5–18 m
Emergent trees	Characteristic, to 60 (80) m tall	Often absent, to 37 m tall	Usually absent, to 26 m tall
Pinnate leaves	Frequent	Rare	Very rare
Principal leaf size class of woody plants[a]	Mesophyllous	Mesophyllous	Microphyllous
Buttresses	Usually frequent, and large	Uncommon, and small	Usually absent
Cauliflory	Frequent	Rare	Absent
Big woody climbers	Abundant	Usually none	None
Bole climbers	Often abundant	Frequent to abundant	Very few
Vascular epiphytes	Frequent	Abundant	Frequent
Nonvascular epiphytes	Occasional	Occasional to abundant	Often abundant

[a] Leaf sizes according to the 1934 Raunkiaer Leaf Sizes Classification System.
TLF, tropical lowland forest; TLMF, tropical lower montane forest; TUMF, tropical upper montane forest.
After Whitmore TC (1984) *Tropical Rain Forests of the Far East*. Oxford, UK: Clarendon, with permission.

Description and Major Features

Forest Formations along an Altitudinal Gradient

When climbing a high tropical mountain, one passes through nearly all climatic and vegetation zones of the world over a relatively short distance. It is therefore no surprise that tropical mountains are extremely rich in species and ecosystems. One may observe a series of forests with different structure, physiognomy, and composition. As the late Tim Whitmore clearly stated, one of the most striking features is the change from mesophyll-dominated forest with an uneven billowing canopy surface to a lower, more even, often pale-colored, microphyll-dominated canopy, of more slender trees, usually with gnarled limbs and very dense subcrowns. At mid-elevation in the northern Andes, the transitional tropical premontane forest (TPMF; 500–1200 m above sea-level) and its adjacent lower montane forest (TLMF; 1200–2400 m) occur with a broad ecotone against the 30–40-m-tall lowland forest formation (TLF; **Table 1**).

At higher elevations, closer to the upper forest line, upper montane forest (TUMF; 2400–3600 m) occurs. The change from frequent cloud cover at vegetation level in TLMF to more persistent cloud cover in TUMF is one of the major factors determining the common boundary between both TMF belts at 2200–2600 m altitude. TUMF is often only 10–25 m tall or less, and its shorter version is sometimes called 'dwarf forest,' 'elfin forest,' 'montane thicket' or – when nonvascular epiphytic plants abound – 'mossy forest.' Its trees may be swathed in bryophytes (mosses, liverworts) and filmy ferns.

On the highest peaks TUMF is replaced by a shorter, much more gnarled formation, stunted by the wind, with even tinier, often xeromorphic leaves (nanophylls). This formation is known as subalpine rainforest (TSF), and has been observed at such geographically disjunctive places as Costa Rica, Ecuador, and New Guinea. The upper tree line (also known as the timber line) on the tallest mountains can be found around 4000 m elevations, although this line is often depressed by human-set fire. Above the tree line occurs a treeless, alpine, cold, wet and misty biome, often dominated by giant stem rosette plants belonging to genera such as *Espeletia*, *Lobelia*, and *Senecio*, shrubs, forbs, bunch grasses, bamboos, sedges, mosses, liverworts, and beard-like lichens. This biome or ecosystem is regionally known as the paramo (Latin America), the afroalpine (Africa), or tropic-alpine (southeast Asia) ecosystem. It is a tundra-like, peaty system extending up to the rocky snowline at about 4500 m elevation, above which the nival belt extends with its mountain glaciers and snowy summits.

Structure and Physiognomy

The structure of the average high-elevation TMF and TMCF has a dwarfish appearance. Small, flattened, sometimes bonsai-like trees display curved trunks due to soil creep on steep slopes. They occur clumped together in an almost impenetrable setting. Twisted branches with thick (pachyphyllous), hard (sclerophyllous), tiny (microphyllous to nanophyllous) leaves, located in thick bunches on dense subcrowns are heavily loaded with woody and herbaceous epiphytes. Without doubt, the abundance of epiphytes causes an enormous increase in aboveground forest biomass and may act as a sponge, retaining water from clouds and fog.

Maximum canopy tree heights range generally from 7 m at 3400 m elevation (Peru) to 20 m at 1000 m (Monteverde, Costa Rica). Stem densities (diameter at breast height (dbh) > 5 cm) are higher in TMF than at lower elevations in TLF and may fluctuate between 500 stems per hectare at 2700 m elevation in Colombia and Costa Rica and 1000 stems per hectare at 3300 m in Ecuador. If all stems over 2.5 cm dbh are included, a total of 1600 stems per hectare may be recorded (Peru). In the case of 15–35-year-old secondary TMF at 500–3000 m altitude, values of 2500–3500 stems per hectare (dbh > 2.5 cm) seem normal (Costa Rica, Puerto Rico). However, TMF structure data may differ significantly over different slopes (windward versus leeward), along different rainfall gradients, and at different altitudes (temperature variations).

Next to the generally more elfin TMF formations, other TMF types exist in which huge, 35–55-m-tall trees prevail. An example is the tropical montane fagaceous-bamboo forest type found in Central and South America as well as in certain parts of Southeast Asia. In Costa Rica this TMF type is dominated by different species of white and black oak (*Quercus*) in its canopy and *Chusquea* bamboo in its 3–6-m-tall understory. Similar fagaceous-dominated TMF is observed in Andean Colombia where oak trees (*Quercus, Trigonobalanus*) are accompanied by *Chusquea* and *Neurolepis* bamboos, in Indonesia (Sumatra, Kalimantan, Java), where *Castanopsis* and *Lithocarpus* trees form dense stands, as well as on Papua New Guinea, where *Nothofagus* trees spread shade over an understory of climbing *Nastus* bamboos. Other fagaceous–bamboo-dominated montane forests are distributed over more subtropical regions, such as parts of Chile (*Nothofagus* trees with *Chusquea* bamboos), the Himalayas (*Quercus* trees with *Arundinaria* bamboos), and Japan (*Fagus* trees with *Sasa* bamboos).

In Costa Rican TMF at 2500 m elevation (Talamanca mountains), giant oaks (*Quercus*) grow in large quantities and show dbh over 2 m. Below the tall, epiphyte-blanketed oak crowns appears a subcanopy layer with a large number of 10–25-m-tall tree species from both temperate and tropical origin. Temperate plant genera and species begin to appear in TMF at 2000 m elevation. Examples in Costa Rica are alder (*Alnus*), oak (*Quercus*), and willow (*Salix*). Here, values of basal area are among the highest found in tropical forests worldwide: at several places, a basal area value higher than 50 $m^2 ha^{-1}$ was measured. Values of 25 (Ecuador) to 40 (Puerto Rico) $m^2 ha^{-1}$ are more likely for TMF between 1000 and 3000 m above sea-level.

Besides the more common and widespread moist TMF formations (including wet, rain, and cloud forests) discussed so far, there occur in some places seasonally dry tropical montane woody vegetation types (woodlands, bushlands, thickets, shrublands, and other xeromorphic communities). This is especially the case in sections of Africa but also in northern Meso-America (e.g., in Mexico and some parts of Guatemala), where conifers such as the pine tree *Pinus hartwegii* dominate the forest structure and intense droughts and fire appear to be the most frequent disturbance factors.

Biological Diversity and Endemism

TMF species-richness decreases with latitude, with lower per-unit-area values for countries around the tropics of Cancer and Capricorn (e.g., Argentina, Mexico) and highest near the Equator (Costa Rica, Indonesia, Papua New Guinea, Peru). At the same time, TMF species diversity is highest at mid-elevation and decreases towards subalpine elevations (**Figure 4**).

In the neotropics, the northern Andes appear to be a center of speciation, from which originated the radiation of numerous species into the peripheral TMF areas at higher latitudes. Endemism is low at the generic level but high at the species level. Some plant genera such as found in the orchids (e.g., *Epidendrum*) and piperoids (e.g., *Peperomia*) are extraordinarily rich in species. About a decade ago, a new tree family restricted to the neotropical TMF was found

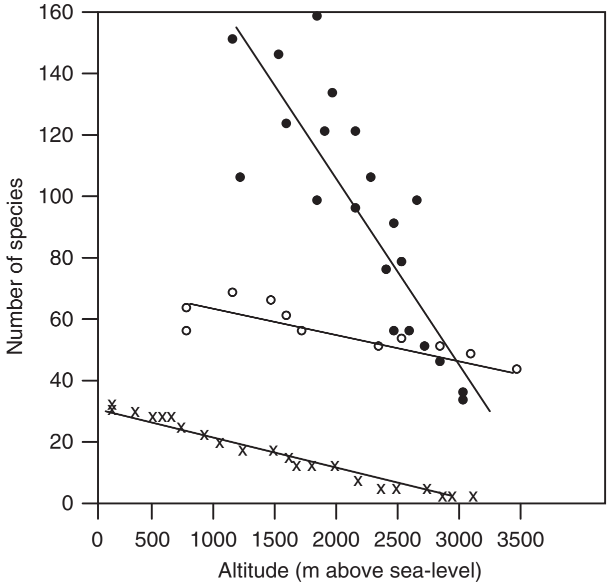


Figure 4 Species-richness in tropical montane forests plotted as a function of altitude, with regression lines. Closed circles represent tree species (diameter at breast height ≥ 2.5 cm) in 0.1 ha plots in Andean forests (data from Gentry AH in Churchill SP, Balslev H, Forero E, and Luteyn JL (eds) (1995) *Biodiversity and Conservation of Neotropical Montane Forests*. New York: New York Botanical Garden); open circles represent numbers of syntopic bird species in Andean Peru, and crosses represent rodents in montane New Guinea (birds and rodents according to Rahbek C in Körner C and Spehn E (eds) (2002) *Mountain Biodiversity: A Global Assessment*. New York: Parthenon).

(Ticodendraceae, Costa Rica). A major reason for these high levels of endemism is the fact that many TMF sites are situated on mountain tops where species populations became isolated from their metapopulations at the end of the ice ages when Pleistocene climatic fluctuations took place. They could therefore evolve into new, locally restricted (endemic) species.

Plant Growth Forms, Species Richness, and Composition

If we take a look at the main plant families and genera making up the average neotropical TMF, we may encounter a large number of broad-leaved canopy trees, subcanopy trees, understory shrubs, a series of ground herbs, some hemiepiphytes, and a few giant native coniferous trees (needle-leaved gymnosperms; **Table 2**).

A very important life form in these forests is the tree fern, which has been considered diagnostic for TMCF. These woody, stemmed, 2–7-m-tall pteridophytes with their enormous leaf rosettes occur in almost all TMCF types around the world. Other conspicuous understory elements include large monocotyledons such as understory bamboos, often-dwarfish palms and colorful heliconias. Bright-green, pteridophytic *Selaginella* species and terrestrial mosses (Polytrichaceae) preferring damp, cool climates may carpet the forest floor. Woody climbers are few, but herbaceous vines may abound.

Vascular epiphytes are extremely diverse and include an almost infinite number of orchids, bromeliads, ferns (including the filmy ferns of the genus *Hymenophyllum*), aroids, ericads, cyclanths, gesneriads, and piperoids. Whereas the number of flowering epiphytes decreases with increasing altitude (lower temperatures), pteridophytic plant groups such as ferns and club mosses (Lycopodiaceae) become more abundant. Epiphytic bryophytes, including mosses (Musci) and liverworts (Hepaticae), are ubiquitous and cover the trunks, branches, and twigs of trees and shrubs. In addition, a diverse set of epiphytic and epilithic yellow, red, brown, green, and white-colored foliose, fruticose, and crustose lichens complete the rich spectrum of TMF life forms.

Animal Diversity

Faunal diversity is also striking. The diversity among birds and amphibians is especially remarkable. Recent research results show that the highest avian biodiversity in South America is found at the transition between Amazon TLF and TMF in the adjacent eastern slopes of the Andes. The Convention on International Trade in Endangered Species (CITES) and The World Conservation Union (IUCN)-listed, endangered spectacled bear (*Tremarctos ornatus*) known from the Andes in South America and the mountain gorilla (*Gorilla gorilla beringei*, with 620 individuals in 2000) inhabiting the Virunga volcanoes on the border of the Democratic Republic of Congo, Uganda, and Rwanda in Africa are probably the best-known 'flagship' mammals still living in TMF, although with populations hunted down, in an ever-decreasing habitat. Other species still to be found in TMF and TMCF include a tapir, large cats (puma, jaguar, ocelot), several deer, marsupials, monkeys, rodents, rabbits, mice, and a fair number of bats, among many others. Studies on TMF arthropods (insects, spiders) have only just begun and species numbers have to be estimated. In most cases, little is known about the distribution, natural history, and population ecology of TMF animal species and further attention from scholars is urgently needed.

Disturbance Regimes

TMF and especially TMCF in the neotropics are often affected by natural disturbance regimes, including factors such as storms and hurricanes. Storm-induced landslides are a common phenomenon on steep slopes in TMF areas and may cause local forest disturbance.

Table 2 Most important vascular plant families and genera observed in neotropical montane forests (data from the author)

Life form	*Family*	*Genus*
Needle-leaved trees	Pinaceae	*Pinus*
	Podocarpaceae	*Podocarpus*, *Prumnopitys*
Broad-leaved trees	Annonaceae	*Guatteria*
	Betulaceae	*Alnus*
	Boraginaceae	*Cordia*
	Brunelliaceae	*Brunellia*
	Caprifoliaceae	*Viburnum*
	Clethraceae	*Clethra*
	Cunoniaceae	*Weinmannia*
	Ericaceae	*Comarostaphylis*, *Vaccinium*
	Escalloniaceae	*Escallonia*
	Euphorbiaceae	*Alchornea*, *Croton*, *Hieronyma*, *Sapium*
	Fabaceae	*Inga*, *Pithecellobium*
	Fagaceae	*Quercus*
	Flacourtiaceae	*Abatia*, *Casearia*, *Xylosma*
	Lauraceae	*Cinnamomum*, *Nectandra*, *Ocotea*, *Persea*
	Loganiaceae	*Buddleia*
	Magnoliaceae	*Magnolia*, *Talauma*
	Meliaceae	*Guarea*, *Trichilia*
	Monimiaceae	*Mollinedia*, *Siparuna*
	Moraceae	*Cecropia*, *Ficus*, *Pourouma*
	Myrtaceae	*Eugenia*, *Myrcia*, *Myrcianthes*
	Sabiaceae	*Meliosma*
	Symplocaceae	*Symplocos*
	Theaceae	*Cleyera*
	Winteraceae	*Drimys*
Trees, shrubs	Actinidiaceae	*Saurauia*
	Aquifoliaceae	*Ilex*
	Celastraceae	*Crossopetalum*, *Maytenus*
	Chloranthaceae	*Hedyosmum*
	Melastomataceae	*Clidemia*, *Miconia*, *Topobea*
	Myrsinaceae	*Ardisia*, *Myrsine*, *Parathesis*
	Rosaceae	*Polylepis*, *Prunus*, *Rubus*
	Rubiaceae	*Elaeagia*, *Faramea*, *Hoffmannia*, *Palicourea, Psychotria*, *Rondeletia*
	Solanaceae	*Acnistus, Cestrum, Solanum*
Trees, hemiepiphytes	Araliaceae	*Dendropanax*, *Oreopanax*, *Schefflera*
	Clusiaceae	*Clusia*, *Tovomita*, *Vismia*
Shrubs, herbs	Asteraceae	*Eupatorium*, *Diplostephium*, *Senecio*
	Hypericaceae	*Hypericum*
	Piperaceae	*Peperomia*, *Piper*
	Urticaceae	*Phenax*, *Pilea*, *Urera*
Herbs	Acanthaceae	*Dicliptera*, *Hansteinia*, *Justicia*
	Campanulaceae	*Burmeistera*, *Centropogon*
	Scrophulariaceae	*Calceolaria*, *Castilleja*, *Hemichaena*
Parasitic shrubs	Loranthaceae s.l.	*Dendrophthora*, *Gaiadendron*, *Phoradendron*, *Struthanthus*
Palms	Arecaceae	*Ceroxylon*, *Chamaedorea*, *Geonoma*
Bamboos	Poaceae	*Aulonemia*, *Chusquea*
Climbers	Asteraceae	*Liabum*, *Mikania*
	Alstroemeriaceae	*Bomarea*
	Dioscoreaceae	*Dioscorea*
	Hydrangeaceae	*Hydrangea*
	Passifloraceae	*Passiflora*
	Vitaceae	*Cissus*

continued

Table 2 Continued

Life form	*Family*	*Genus*
Tree ferns	Cyatheaceae	*Alsophila*, *Cyathea*, *Lophosoria*
	Dicksoniaceae	*Culcita*, *Dicksonia*
Ferns	Adiantaceae	*Adiantum*, *Cheilanthes*, *Eriosorus*
	Aspleniaceae	*Asplenium*
	Blechnaceae	*Blechnum*
	Dryopteridaceae	*Dryopteris*, *Polystichum*
	Elaphoglossaceae	*Elaphoglossum*
	Grammitidaceae	*Ceradenia*, *Grammitis* s.l.
	Hymenophyllaceae	*Hymenophyllum*, *Trichomanes*
	Polypodiaceae	*Campyloneurum*, *Polypodium*
	Pteridaceae	*Pteris*
	Thelypteridaceae	*Thelypteris*
	Vittariaceae	*Vittaria*
Fern-allies	Lycopodiaceae	*Huperzia*, *Lycopodium*
	Selaginellaceae	*Selaginella*
Vascular epiphytes	Araceae	*Anthurium*, *Monstera*, *Philodendron*
	Ericaceae	*Cavendishia*, *Macleania*, *Psammisia*, *Satyria*
	Bromeliaceae	*Pitcairnea*, *Puya*, *Tillandsia*, *Vriesea*
	Cyclanthaceae	*Asplundia*, *Sphaeradenia*
	Gesneriaceae	*Alloplectus*, *Solenophora*
	Orchidaceae	*Cattleya*, *Epidendrum*, *Malaxis*, *Maxillaria*, *Stelis*, *Telipogon*

Studies conducted in the TMF of the Luquillo mountains in Puerto Rico demonstrate the importance of disturbance, both natural and anthropogenic, in controlling both the structure and functioning of these forests. On a smaller scale, the same is true for tree fall gaps caused by the natural death of senescent TMF trees. However, many successional plant species, pioneers as well as late-secondary elements, appear to be well adapted to the sudden occurrence of natural gaps, which they may colonize within a short period of time. A whole gamut of fast-growing pioneer herbs and soft-wooded shrubs may fill a gap within a few weeks or months, particularly in the wet season, although full recovery following a large-scale disturbance may take decades or up to a century or more. A study of TMF recovery taking place after a period of clearing, burning, and years of grazing in Costa Rica resulted in a conservative estimate of 65–85 years as the theoretically minimum time needed for recovery of the terrestrial structure and floristic composition of the forest. An additional 50 years may be necessary for a natural recovery of the full epiphytic biomass and flora present before the disturbance took place (**Figure 5**).

Conservation and Utilization

Forest Conversion and Habitat Loss

TMF has suffered a long history of transformation by human beings. Particularly in the Andes, TMF conversion took place long before the arrival of the Hispanic culture some 500 years ago. Near Bogotá, Colombia, large groups of gatherers and hunters lived in the TMF altitudinal belt some 12 500 years before the present time, while indigenous artifacts in the TMF zone at the flanks of the Llalo volcano in Ecuador date from some 14 000 years before now. Intensive maize agriculture started in the Colombian Andes some 2500–3000 years ago.

The current situation of TMF is alarming, as it has become one of the most threatened tropical ecosystems worldwide. Over the centuries, as mountain roads were constructed, TMF has been cleared to harvest timber, fuelwood, and charcoal, and cut and burned for crop and grazing land. The loss of about half of the Mexican TMF, and especially its mesophyllous TMF, is just one of many striking examples. In Colombia, only 10–20% of the original TMF cover (i.e., as present in pre-Columbian times) remains today. Due to habitat fragmentation, endemic bird and frog species concentrated in TMF may become threatened with extinction. In Central American TMF the dwindling resplendent quetzal (*Pharomachrus mocinno*) has become the flagship bird species in conserving remnant TMF fragments. The golden toad (*Bufo periglenes*) – now believed to be extinct due to climate change (e.g., loss of cloud cover) and habitat loss – has become the symbol of the destructive human impact on TMCF worldwide. Moreover, invasive alien species have become an

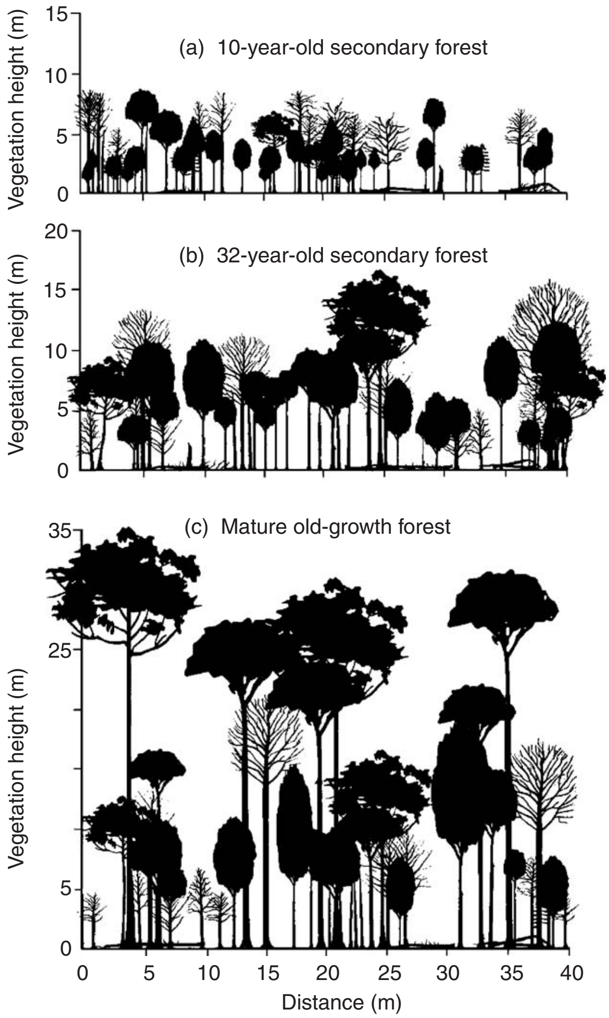


Figure 5 Schematic lateral profiles of three successional stages of tropical montane oak-bamboo forest at 2700–2900 m elevation in Costa Rica (Talamanca mountains). (a) 10-year-old secondary forest (following clearing, grazing, and abandonment); (b) 32-year-old secondary forest (following clearing, grazing, and abandonment); (c) over-250-year-old mature forest (data from the author).

increasing threat to native and often endemic plant and animal species (e.g., the African kikuyu grass which was introduced in tropical montane America).

Sustainable Forest Management

It appears to be extremely difficult to manage TMF in a sustainable way, due to the unfavorable conditions in climate (high rainfall), topography (steep slopes in rugged, highly dissected terrain) and soils (fragile, susceptible to erosion). Moreover, TMF has an important hydrological function, especially in the upper watersheds where water resources are accumulated which serve as drinking and irrigation water for human communities and as generators of hydroelectricity for households. Once mountain roads are constructed and the TMF has been removed, these hydrological services vital to people living down-slope are almost irrevocably lost. Soil erosion and landslides take place and may lead to the ultimate rise of badlands, which cannot be used by humans. Down-slope, runoff of sediment-loaded water (e.g., mud flows) may cause uncontrolled flooding, affecting mid-elevation and lowland villages. Many slopes in areas formerly covered by TMF have been converted into badlands and are now one of the best examples worldwide of how we have mismanaged nature and its natural resources.

Therefore, it is of utmost importance to develop sustainable ways of TMF use. Currently, numerous projects directed at sustainable forest management are underway worldwide. A successful example in TMF areas is the growth and use of secondary forests on previously grazed but now abandoned pasturelands where once old-growth, mature TMF grew. These naturally regenerated, restored forests are subsequently used in a selective way by coppicing and controlled fuelwood extraction, as elements of agroforestry systems or as bird-watching sites to be visited by ecotourists.

Valuation of Traditional and Potential Uses of Biodiversity

On all tropical continents (America, Africa, Asia, and Oceania), TMF products and services have extensively been used for many centuries and probably millenniums, to maintain local human populations. Traditionally, but also in modern times, rural communities have gathered numerous timber and nontimber forest products from TMF, including food, fodder, fiber, fuel, medicine, dyes, gums, oils, antioxidants, spices, poisons, ornamental plants and pets. Examples are found among populations in Central America, the Andes, the African Eastern Arc, the Himalayas, Western Ghats, Indonesia and Papua New Guinea.

An ethnobotanical survey of traditional knowledge in a Costa Rican TMF revealed the use of almost 25% of all 590 species of plants by a local farming community for medicinal, food, ornamental, and construction purposes or as sources of combustibles, dye, fodder, gum, oil, and poison. Indeed, among the planet's TMF species are many wild relatives of some of the world's major food plants (e.g., wild potato and tomato plants in the Andes, avocado trees in Central America, and coffee shrubs in Africa). The preservation of their genetic resources in protected areas is essential to society.

TMF harbors species of plants, animals, and microorganisms, many of which are endemic and/or threatened, and many of which are not yet known to science. They may have a potential in future medicine and may only be revealed after being discovered and screened by biodiversity prospecting and biochemical analysis. These species only flourish if they can maintain minimum viable populations in minimum-sized habitats where ecological integrity is guaranteed. Therefore, it is of utmost importance to conserve and, where necessary, restore their habitat in today's fragmented TMF landscape mosaic.

Conservation and Sustainable Development

At present, only about one-third (23 million ha) of the neotropical TMCF area has some kind of protected status. If we are to preserve a large part of TMF's 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. This is particularly vital as a prerequisite for long-term conservation and sustainable use, for it is the recognition of the overall set of environmental goods and services offered by TMF to the local and regional peoples – and thus strategies including compensation payments to forest-owners for these goods and services – which will make its conservation economically necessary, sociopolitically feasible, and ecologically successful.

See also: **Biodiversity**: Biodiversity in Forests. **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Harvesting**: Forest Operations under Mountainous Conditions. **Health and Protection**: Diagnosis, Monitoring and Evaluation. **Hydrology**: Hydrological Cycle; Impacts of Forest Management on Water Quality; Soil Erosion Control. **Landscape and Planning**: Landscape Ecology, the Concepts. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Resource Assessment**: Forest Change. **Silviculture**: Natural Regeneration of Tropical Rain Forests; Treatments in Tropical Silviculture. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation; Overview. **Tree Physiology**: Forests, Tree Physiology and Climate. **Tropical Forests**: Tropical Moist Forests.

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