

72 Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world

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INTRODUCTION

As indicated in the introductory chapter to this book, knowledge of tropical montane cloud forest (TMCF) occurrence, biodiversity, hydrology, and ecological functioning has increased considerably since the ground-breaking publications of Zadroga (1981), Stadtmüller (1987), and the proceedings of the first international symposium on TMCF held in 1993 in Puerto Rico (Hamilton *et al.*, 1995a). Cloud forests continue to be threatened in several ways, notably by their conversion to pasture and various forms of agriculture, as well as by climatic drying – the numerous hydrological and ecological consequences of which are only poorly understood as yet (Bubb *et al.*, 2004; Mulligan and Burke, 2005a; Pounds *et al.*, 2006; Zotz and Bader, 2009).

The collection of chapters in the present volume further advances our knowledge in the three broad and interrelated areas that were defined in the introduction, viz. (i) cloud forest biogeography and biodiversity, (ii) biophysical and ecological processes, and (iii) management and conservation strategies.

As the recognition of the value of TMCFs as treasure houses of biodiversity and as providers of high-quality water continues to increase, an array of initiatives aimed at their conservation has emerged in recent years, often within a Payment for Ecosystem Services (PES) context (Asquith and Wunder, 2008;

Muñoz-Piña *et al.*, 2008; Porras *et al.*, 2008; Garriguata and Balvanera, 2009; Tognetti *et al.*, this volume). Such PES schemes, but also land and forest managers and policy-makers in general, need to determine (amongst others) which forests under their jurisdiction are the most diverse and valuable biologically, which ones provide the best water supplies, which forests are the most vulnerable to climate change or most threatened by encroachment, and which degraded TMCFs have the best chances for rehabilitation. In short, there is a great need for site-specific information on TMCFs for incorporation into conservation and management plans at various spatial scales.

This final chapter summarizes the current state of knowledge with respect to the three broad categories distinguished above (biodiversity, biophysical functioning, and conservation and management issues including response to a variety of threats). In doing so, a distinction will be made (where possible and necessary) between the different types of cloud forests defined in the introductory chapter (Table 1.1), viz. tall lower montane cloud forest (LMCF), upper montane cloud forest (UMCF) of intermediate stature, and stunted sub-alpine (SACF) and elfin cloud forests (ECF). The rationale for making such a distinction lies in the wetter and cooler conditions that are generally encountered as one moves up from the lower montane to the upper montane and sub-alpine belts, and which are believed to affect the hydrological and ecological

functioning of the respective forest types (Grubb, 1977; Silver *et al.*, 1999; Hafkenscheid, 2000; Bruijnzeel, 2001; Gerold *et al.*, 2008; Roman *et al.*, this volume). The chapter also makes a deliberate attempt at answering the key questions raised in the introductory chapter for each of the above-mentioned broad categories (Scatena *et al.*, this volume) and concludes with a brief discussion of the main global cloud forest conservation initiatives, key remaining information needs, and future research challenges.

CURRENT STATE OF KNOWLEDGE

Global extent, distribution, and climate of tropical montane cloud forests

Key questions regarding the current extent, distribution, and climates of TMCFs include:

- Where do we find cloud forests and under what climatic conditions?
- How much is left of the original forest?

Producing a global map of actual TMCF distribution has proved a daunting task, as described in more detail in the introductory chapter (Scatena *et al.*, this volume). However, knowledge of where TMCFs occur has increased considerably since the 1993 Puerto Rico symposium when the first map was made by having symposium participants place tacks on maps in areas where they were "reasonably confident" that TMCF existed (Hamilton *et al.*, 1995b). In the pioneering analysis of Aldrich *et al.* (1997b) and the second-generation reiteration by Bubb *et al.* (2004), global forest cover assessments were combined with global elevation data and regionally specific altitudinal limits of cloud forests (see Table 1.2 in Scatena *et al.*, this volume) to derive estimates of the potential (i.e. assuming the entire area between the specified altitudinal limits to be forested) and actual areas of TMCF. Using this approach, the *potential* area of TMCF was estimated to be in the order of 380 000 km² (2.5% of the world's tropical forest area), whereas the *actual* area with TMCF (in the year 2000) was estimated at c. 215 000 km² (1.4% of the world's tropical forests; cf. Tables 1.3 and 1.4 in this volume). The area under cloud forest estimated in this way constitutes 6.6% of the area covered by tropical montane forest in the world as defined by Kapos *et al.* (2000). Taking these estimates of actual and potential cloud forest occurrence at face value implies that roughly 56% of the original forest still remains and that c. 165 000 km² of cloud forest have been converted. As to their relative distribution, approximately 43% of all remaining cloud forests can be found in Asia (including northern Australia) and Oceania, 41% in the Americas (including the Hawaiian archipelago) and 16% in Africa (cf. Table 1.3).

No distinction was made by Bubb *et al.* (2004) between different types of cloud forest in terms of forest stature, degree of cloud incidence or rainfall regime (see Table 1.1 and Scatena *et al.* (this volume) for general descriptions). Nevertheless, the more than 560 sites with confirmed cloud forest presence (Aldrich *et al.*, 1997b; Figures 72.1a–c) represent a wide range of climatic conditions (rainfall and temperature, wind) and landscape settings (elevation and exposure, mountain size, distance to sea). Jarvis and Mulligan (this volume) employed spatial data-sets derived from the WorldClim database, to describe the climate at 477 "cloud forest" sites as identified by UNEP-WCMC. Further, comparisons were made between the climate of cloud forest sites and that of randomly generated sites covering forested areas throughout the montane tropics, with the aim of identifying the climatic variables most important in distinguishing TMCF from other tropical forests. TMCFs were found to be wetter (by 184 mm year⁻¹ on average), cooler (by 4.2 °C on average), and less seasonally variable than other montane forests. The most statistically significant differences in climate between TMCFs and other montane forests were: maximum temperature, mean temperature, rainfall, and rainfall seasonality (in order of significance). Cloud forests also tend to be located closer to the coast (particularly in Asia) and at higher altitudes than montane forests not affected by cloud. Furthermore, cloud forests occupy more topographically exposed areas than other montane forests. Interestingly, cloud forest sites in Africa tend to be drier (average annual rainfall less than 1500 mm) and more seasonal than their counterparts in Asia (c. 2150 mm of rain on average), whereas the cloud forests of the Latin American and Caribbean region experience a wide range of rainfall conditions (Jarvis and Mulligan, this volume).

Using a hydro-climatic definition of cloud forest as "forest under frequent and/or persistent exposure to ground-level cloud," Mulligan (this volume) modeled their distribution using new tropics-wide data-sets on satellite-observed cloud frequency, climate and land cover. This approach yielded a much greater global extent of cloud forest cover (2.21 Mkm²) than the previously discussed altitude-based estimates, suggesting that "significantly cloud-affected" forests (CAF) may represent as much as 14.2% of all tropical forests (cf. Table 2.4). The hydro-climatic approach was tested with a high level of success against the more than 560 sites listed by WCMC-UNEP as having confirmed cloud forest presence (Aldrich *et al.*, 1997b), with the best fit between actual and modeled cloud forest presence for sites experiencing ground-level cloud (i.e. fog) conditions for more than 70% of the time (Mulligan, this volume; Figure 72.2). Comparing the potential and actual distributions of CAF obtained in this way suggests that ~45% of the original CAF still remains and that some 2.72 Mkm² of CAF have been lost (Mulligan, this volume).

Differences in results obtained with the two approaches (i.e. elevation- vs. climate-based) are to be expected. The greater

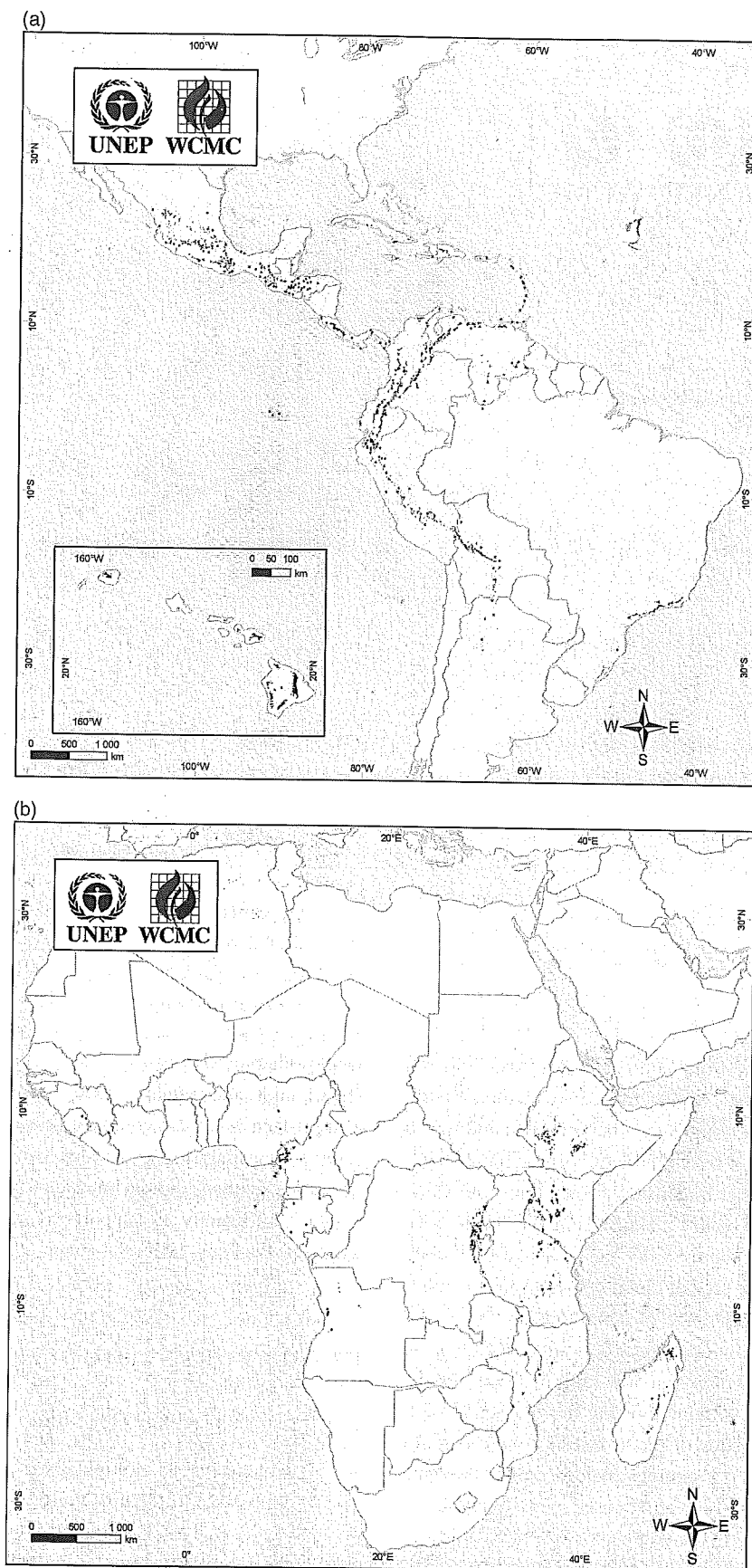


Figure 72.1. Estimated tropical montane cloud forest distribution in (a) the Americas (including the Hawaiian archipelago), (b) Africa and

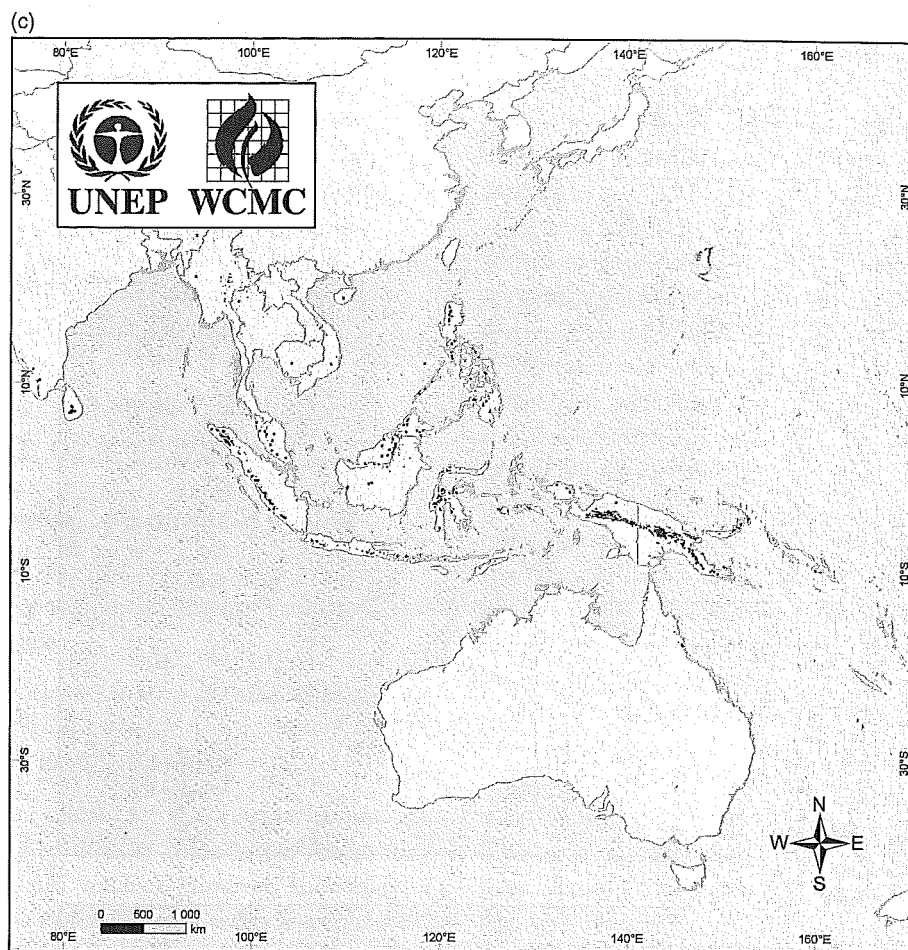


Figure 72.1. (cont.) (c) Asia (including northern Australia and Oceania), based on the altitudinal ranges listed in Table 1.2 (areas indicated by red shading) and known cloud forest site locations according to Aldrich *et al.* (1997b) (green dots). (Reproduced from Figures 1.3, 1.4, and 1.5; See also color plate.)

extent of cloud forest derived from Mulligan's analysis compared to that of Bubb *et al.* (2004) results from two factors; firstly, Mulligan's analysis included fragmented areas of forest and sparse woodland at 500-m resolution through the use of fractional Vegetation Continuous Fields rather than using a fixed threshold value to denote forest cover in a binary classification (cf. Table 2.4). Secondly – and more importantly – by using a hydro-climatic definition of cloud forest, the area of cloud-affected forest is modeled. This may cover a wider range of conditions and structural features than the more narrow ecological definition does (e.g. in terms of mossiness, etc.). Forests in low-rainfall areas can be significantly cloud-affected without showing the full set of traditional ecological characteristics of cloud forests found in high-rainfall areas (cf. Table 1.1). Examples include certain lowland forests (not included in any elevation-based classification; cf. Gradstein *et al.*, this volume) in coastal, peninsular, or island locations where the extra water inputs and reduced evaporation associated with fog occurrence support forest or woodland in areas that

would otherwise be too dry (Aravena *et al.*, 1989; Dawson, 1998; Hildebrandt and Eltahir, 2006; see also García-Santos, 2007; Marzol-Jaén *et al.*, this volume). Less-dense woodland ecosystems such as some of the higher-altitude Miombo woodlands of Tanzania constitute another example in which fog may improve the site water balance sufficiently to support savanna in grassland-dominated areas (cf. Backeus, 1992; Salzmann, 2000).

CLOUD FOREST BIODIVERSITY

Key questions regarding cloud forest biodiversity include:

- Are cloud forests biologically richer than non-cloud forests?
- Is it possible to identify regions and areas with the greatest diversity in TMCF flora and fauna?
- Is there a difference in biological richness between different altitudinal belts on single mountains?

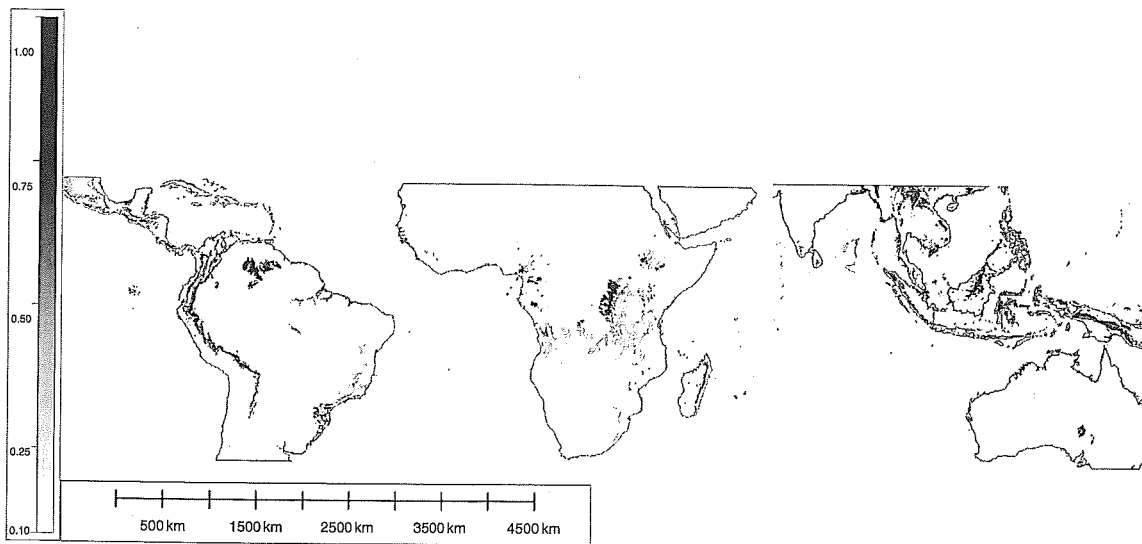


Figure 72.2. Modeled distribution of cloud-affected tropical montane forests (with UNEP–WCMC listed cloud forest sites indicated in red). The darker the shade the greater the fractional cover of forest within the 1-km pixel. (Reproduced from Figure 2.11; See also color plate.)

General considerations

Although the global area of (narrowly defined) TCMF is only about 0.26% of the Earth's land surface (Bubb *et al.*, 2004), it is widely acknowledged that these particular forests are amongst the most species-rich and species-dense ecosystems worldwide, both in terms of flowering plants (Grubb, 1977; Prance, 1982; Stadtmüller, 1987; Groombridge, 1992; Barthlott *et al.*, 1996, 2005; Kappelle, 2004; Mutke and Barthlott, 2005; Richter, 2008; Hemp, this volume #12; Meyer, this volume), mosses (Benzing, 1990; Gradstein *et al.*, 2001), birds (Terborgh, 1977; Long, 1995; Fjeldså and Rahbek, 1997; Watson and Townsend Peterson, 1999), mammals (Leo, 1995; Heaney, 2001; McCain, 2005; cf. Owunji and Plumptre, this volume), amphibians (e.g. frogs, toads, lizards, salamanders; Scott, 1976; Duellman, 1988; Pineda and Halffter, 2004; Cortés *et al.*, 2008), and reptiles (Scott, 1976; Wilson and McCranie, 2004).

TMCFs also appear to be particularly numerous in at least six of the most important biodiversity “hot spots” around the globe, viz. the tropical Andes and Atlantic Forests in South America, the Caribbean Islands, the Eastern Afro-montane peaks scattered along the eastern edge of Africa, the Asian Sundaland which includes the high mountains of Borneo, and Polynesia–Micronesia which includes the islands of Fiji, Hawai'i, and Tahiti (Myers *et al.*, 2000; Figure 72.3).

In addition, TMCFs occur within a significant portion of the 200 biologically most distinct “Ecoregions” of the planet as identified by WWF-US (Olson and Dinerstein, 2002). Ecoregions are defined as large areas of land or water that contain a

geographically distinct assemblage of natural communities that share a large majority of their species and ecological dynamics, share similar environmental conditions, and interact ecologically in ways that are critical for their long-term persistence (Dinerstein *et al.*, 1995; Olson *et al.*, 2001). These “Global 200” Ecoregions were selected on the basis of various features of biodiversity, including species richness, number of endemic species,¹ presence of unusual higher taxa, unusual ecological or evolutionary phenomena, and the global rarity of habitats (Olson and Dinerstein, 2002). The 18 most important “Global 200” Ecoregions (i.e. 9% of the total) that contain tropical cloud forests (and which partly overlap with the above-mentioned six hot spot areas) are, listed per biome: *Afrotropical*: Cameroon Highland forests, Albertine Rift montane forests, Eastern Arc montane forests; *Australasian*: New Guinea montane forests; *Indo-Malayan*: lowland and montane forests in Sumatra and surrounding islands, Peninsular Malaysia, and Borneo, and the montane forests of West Java; *Neotropical*: Greater and Lesser Antillean moist forests, Talamancan–Isthmian Pacific forests, northern Andean montane forests, coastal Venezuelan montane forests, Guayana Highland moist forests, Central Andean Yungas, Brazilian Atlantic forests (*Mata Atlântica*); and *Oceania*: South Pacific Island forests, and Hawaiian moist forests (Olson and Dinerstein, 2002; cf. Figure 72.3).

¹ Endemism refers to the phenomenon that the spatial distribution of a taxon (usually a species) is restricted to a narrowly defined local geographic area. Species that occur only in that specific location and nowhere else in their natural state are called endemics.

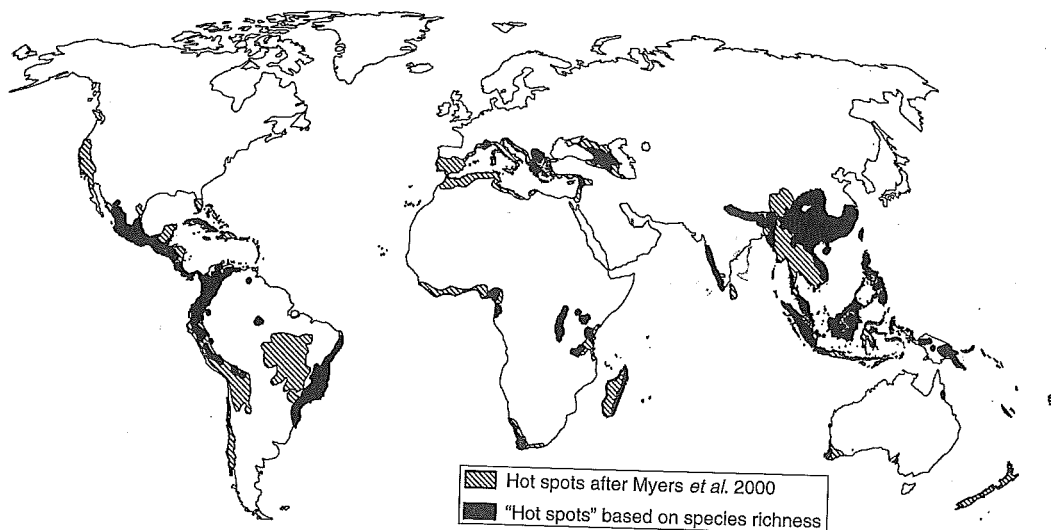


Figure 72.3. Global biodiversity hot spots according to Myers *et al.* (2000) compared with areas with at least 3000 vascular plant species per 10 000 km² (Mutke and Barthlott, 2005).

Overall diversity tends to decline away from the equator and – at least for vascular plants – has been explained in terms of temperature, moisture availability, and topographic heterogeneity, with the latter becoming particularly important in humid montane areas (Kreft and Jetz, 2007). The extraordinary diversity of such taxonomic groups as bryophytes, vascular plants, birds, and amphibians in cloud forests is often the result of past explosive evolutionary radiation (e.g. Gentry, 1982, 1988, 1992; Duellman, 1988; Benzing, 1990; Long, 1995; Gradstein *et al.*, 2001). The tropical Andes, for example, appears to have served as an important center of speciation for a variety of taxa including mosses and liverworts (Benzing, 1990; Wolf, 1993, 1995; Nadkarni *et al.*, 1995), orchids and bromeliads (Sugden and Robins, 1979; Wolf, 1994), ericaceous herbs and shrubs (Luteyn, 1989), bamboos (Clark, 1995), ferns (Kessler, 2002; Kessler and Lehnert, 2009), frogs and salamanders (Duellman, 1988), hummingbirds (Bleiweiss, 1998), and other avian groups (Fjeldså and Rahbek, 1997), as well as geometrid moths (Brehm *et al.*, 2007, 2008). Because of the high levels of endemism in TMCs, new species are still regularly discovered. For example, only two decades ago a whole new tree family (Ticodendraceae, restricted to Neotropical TMCs) was discovered in Costa Rica (Gómez-Laurito and Gómez, 1991), a country where the study of TMCs may be considered as being amongst the most advanced in the tropical world. Similarly, even in well-known groups such as birds, several new narrowly endemic species were discovered in the Ecuadorian, Peruvian, and Colombian Andes in the 1990s (Krabbe *et al.*, 1999; O'Neill *et al.*, 2000; Cuervo *et al.*, 2001; Salaman *et al.*, 2003), while Brehm *et al.* (2008) expect to find at least 200 additional species of geometrid moths along an elevational transect (1040–2670 m.a.s.l.) in the montane forests of southern

Ecuador, despite previous intensive sampling over 4 years during which some 1223 species of geometrid moths had been identified already. Such extraordinary richness in species and endemics is thought to reflect the interaction of isolation and the creation of numerous new habitat niches during the uplift of the Andes (Gentry, 1982, 1988). Also, past climatic fluctuations (including glacial cycles) caused the montane forest altitudinal belts in Central and South America to move up and down over considerable elevational distances (Van der Hammen, 1974; Van der Hammen and Hooghiemstra, 2001; Islebe and Hooghiemstra, 2006). As a result of this dynamic geoclimatic history, the modern-day flora of Neotropical montane cloud forests is made up of a blend of pan-tropical, Neotropical, Andean-endemic, northern temperate (Holarctic), southern temperate (Austral-Antarctic), and cosmopolitan plant genera (e.g. Kappelle *et al.*, 1992; Van der Hammen and Hooghiemstra, 2001; Holz and Gradstein, 2005a), thereby adding to their overall diversity (cf. Kreft and Jetz, 2007). Other examples of high diversity are given in the subsequent section on regional patterns of species and endemism richness.

Are cloud forests biologically richer than non-cloud forests?

There are as yet no pan-tropical analyses that explicitly indicate the most important cloud forests with respect to overall floristic or faunal biodiversity. However, the hot spots of vascular plants identified by Mutke and Barthlott (2005) and the overall biodiversity hot spots identified by Myers *et al.* (2000) shown in Figure 72.3 exhibit a striking overlap with the distribution of cloud-affected forests derived by Mulligan (this volume) in Figure 72.2.

There are several approaches through which one can go beyond the individual plot- or transect-scale study of species occurrence or richness in particular taxonomic groups in cloud forests so as to obtain a pan-tropical overview. Quantification of the total biodiversity at many TMCF sites is a near-impossibility (Brehm *et al.*, 2008), let alone for all cloud forests worldwide. However, by concentrating on some of the better-known groups (such as flowering plants, mammals, amphibians, and birds) one can make use of the best available data on their known ranges to obtain an indication of biogeographic patterns of richness and endemism. Pan-tropical to global studies of this nature exist for vascular plants (Mutke and Barthlott, 2005; Kreft and Jetz, 2007), and plant diversity in general (Kier *et al.*, 2005), for threatened vertebrates (Grenyer *et al.*, 2006), as well as for various environmental proxies for biodiversity (e.g. Kleidon and Mooney, 2008). Range data are available for threatened amphibians (IUCN *et al.*, 2008a) and mammals (IUCN *et al.*, 2008b), as well as for birds of the western hemisphere (Ridgely *et al.*, 2007) and these were used as a means of understanding the relative biological importance of cloud forests and the potential geographic variation in biological importance across the known cloud forests. The range maps included each of the 6260 species of amphibians known to science (as of the end of 2007), 5488 species (including *Homo sapiens*), 412 sub-species, and 21 sub-populations of mammals, and 4273 species of birds. This information was developed through an extensive process of scientific contribution and review coordinated by the World Conservation Union (IUCN), Conservation International (CI), The Nature Conservancy (TNC), and various universities (see Appendix 72.1 for details). Despite their various limitations (described in Appendix 72.1) and despite the fact that the bird data pertain to the western hemisphere only, these are some of the best available data for a pan-tropical assessment of cloud forest faunal biodiversity. There are no similar data for vascular plants in the public domain though previous analyses confirm the broad patterns of diversity observed for the groups analyzed here (cf. Kier *et al.*, 2005; Mutke and Barthlott, 2005).

Kier and Barthlott (2001) defined endemism richness as the “specific contribution of an area to global biodiversity” and regarded this as a better measure of conservation value than species richness per se as endemism richness accounts for range-size rarity. The contribution of a specific area to the global species inventory is known as its *C*-value. For the 10 × 10 km raster grids used here the *C*-value of a pixel for a given species was calculated as $1/G$, where *G* is the global range size (i.e. the number of pixels in which the species occurs). Where species have a large range, the *C*-value is low, and where their range is restricted, the *C*-value is high. Endemism richness of a site is then the sum of *C*-values for all the species for which range data are available. Species richness and endemism richness were calculated for each group and then averaged within areas defined

Table 72.1 *Measures of species richness and endemism richness inside and outside of cloud forests*

Group	Mean species richness		Mean endemism richness	
	Cloud forest	Non-cloud forest	Cloud forest	Non-cloud forest
Amphibians	24.69	23.50	0.027	0.0034
Mammals	107.75	74.65	0.014	0.0037

as cloud-affected forest (according to the hydro-climatic definition of Mulligan, this volume) and also for areas outside of these CAFs.

Table 72.1 compares mean species- and endemism-richness values inside and outside of cloud-affected forests (i.e. comparing cloud forests as an ecosystem against all other terrestrial ecosystems) for mammals and amphibians across the tropics and for birds within the Neotropics. For amphibians, CAFs do not appear to be more species-rich on average than the (much more extensive) non-cloud forest ecosystems, but they are an order of magnitude richer in endemics. *Thus, for amphibians, CAFs contribute an order of magnitude more to global biodiversity than do non-cloud forest areas.* As for mammals, species richness in CAF is distinctly higher than outside of cloud forests (by more than 40%), whereas *endemism richness for mammals in CAFs is almost four times higher than in non-cloud-affected forests* (Table 72.1). Although the mean bird species richness in tropical Latin American cloud forests is similar to that outside of cloud forests, CAFs cover only 4.73% of the land surface of tropical Latin America and thus support many more bird species per unit area. Also, endemism richness for birds is 3.4 times higher within cloud-affected forests (Table 72.1).

Can regions and areas with the greatest diversity in TMCF flora and fauna be identified?

FLORA

As indicated earlier, there are no global surveys of plant diversity focusing explicitly on TMCF. However, the general patterns of species richness of vascular plants shown in Figure 72.4 gives some indication and confirms the importance of the various biodiversity hot spots containing areas with cloud forest as identified earlier in Figure 72.3. The following paragraphs briefly discuss the floristic richness of several of these areas in the respective regions.

Costa Rican TMCF is estimated to hold up to at least 5000 vascular plant species (Kappelle, 2001, 2006), while similar forests in Asia (e.g. in Peninsular Malaysia and Borneo) may harbor up to 4000 species (Kumaran *et al.*, this volume). In the Costa Rican cloud forest area of Monteverde alone

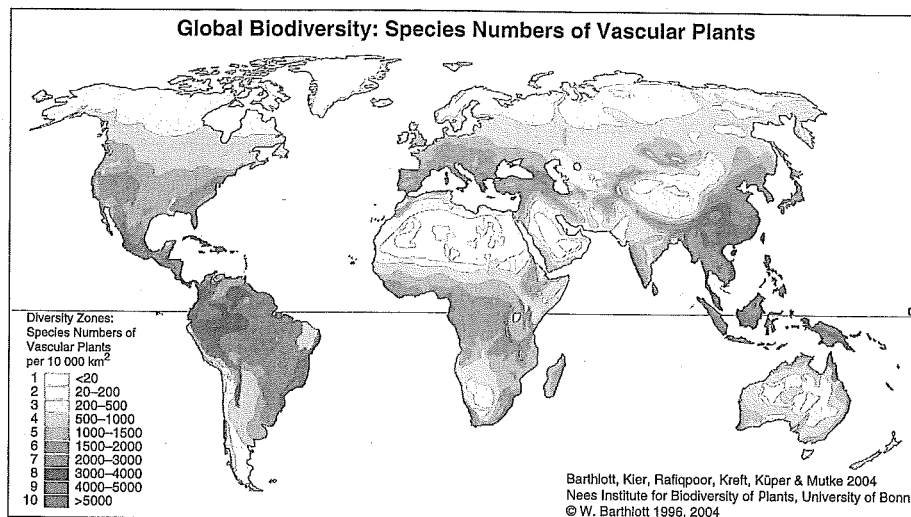


Figure 72.4. World map of species richness of vascular plants (Mutke and Barthlott, 2005). (See also color plate.)

(700–1840 m.a.s.l.) a total of 3020 different plant species have been collected – roughly corresponding with 25–30% of all Costa Rica's plant species – including at least 755 species of tree and 350 fern species (Haber, 1991, 2000; Nadkarni *et al.*, 1995; Bigelow and Kukle, 2000). Further south in Costa Rica, along the Pacific and Atlantic slopes of Mt. Chirripó (3819 m.a.s.l.), almost a hundred fern species, several gymnosperms (Podocarpaceae), nearly 300 terrestrial dicots (trees, shrubs, herbs, lianas, etc.), as well as some 50 monocots (bamboos, palms, cyclanths, orchids, bromeliads, aroids, etc.) were collected from oak-dominated cloud forest stands between 2000 and 3200 m.a.s.l. (Kappelle *et al.*, 1995b; Kappelle and Van Uffelen, 2006).

In Mexico, cloud forests cover less than 1% of the country's territory but they contain about 12% of its 3000 plant species (Rzedowski, 1996). Up to 30% of these are endemic to the country. All in all, about half of the 90 000 known higher plant species in the Neotropics – the world's richest flora – are found in the montane zone (Churchill *et al.*, 1996).

African tropical high mountains (Mt. Kilimanjaro, Mt. Elgon, Mt. Kenya, Mt. Meru, and the Ruwenzori Mountains) and their cloud forests are also characterized by a high biodiversity and a high degree of plant endemism (Hemp, this volume #12). The Eastern Arc Mountains in Tanzania are considered true "hot spots" of biodiversity and endemism due to (more or less) constantly favorable climatic conditions and the presence of a permanent forest cover over very long periods of time (Rodgers and Homewood, 1982; Newmark and Senzota, 2003; C. Hemp, this volume). Over 1200 plant species have been reported for the TMCs on the slopes of Mt. Kilimanjaro (5895 m.a.s.l.), representing about half of the vascular flora on this mountain (Hemp, this volume #12). On Mt. Kinabalu (4101 m.a.s.l.) – the highest mountain in Asia between the Himalayas and the snow-capped peaks of New Guinea – plant diversity is equally

remarkable. Together with a portion of adjacent sub-montane forest, the 745 km² Kinabalu Park contains representatives from more than half the families of all flowering plants. The mountain boasts 1000 or more species of orchids. This represents about half the number of orchid species found on the entire island of Borneo, which itself counts about one-tenth of the world total. In addition, over 600 species of fern are found on Mt. Kinabalu, representing one-fifth of the world's pteridophytes. The particular biological richness found on the mountain – despite its comparatively young age (c. 1 million years) – is believed to reflect the fact that Mt. Kinabalu acted as a refuge for montane plants from other high-elevation parts of Borneo that were eroded away at a time when Mt. Kinabalu was thrust up (Luping *et al.*, 1978; McKinnon *et al.*, 1996; cf. Kumaran *et al.*, this volume).

In the Pacific Ocean, many Polynesian island groups (e.g. Samoa, Tahiti in the Society Islands, and the Cook, Hawaiian, Austral, and Marquesas Islands) share a common set of flowering plants (Meyer, this volume). Furthermore, TMCs in French Polynesia (e.g. Tahiti) contain the floristically most diverse of all plant communities, with the highest rate of endemism and the highest number of biological types (Meyer, this volume).

FAUNA

The distribution of species richness and endemism richness (or at least current knowledge of these) within cloud-affected forests for amphibians and mammals is shown in Figures 72.5 and 72.6, respectively. With respect to *amphibians*, the importance of the Atlantic cloud forests of Brazil, the eastern slopes of the Andes, the Guyana shield, eastern Madagascar, the Guinean cloud forests of West Africa, and the cloud forests of northern Borneo is confirmed, both in terms of species richness and endemism richness. Locally, endemism richness for amphibians is high in

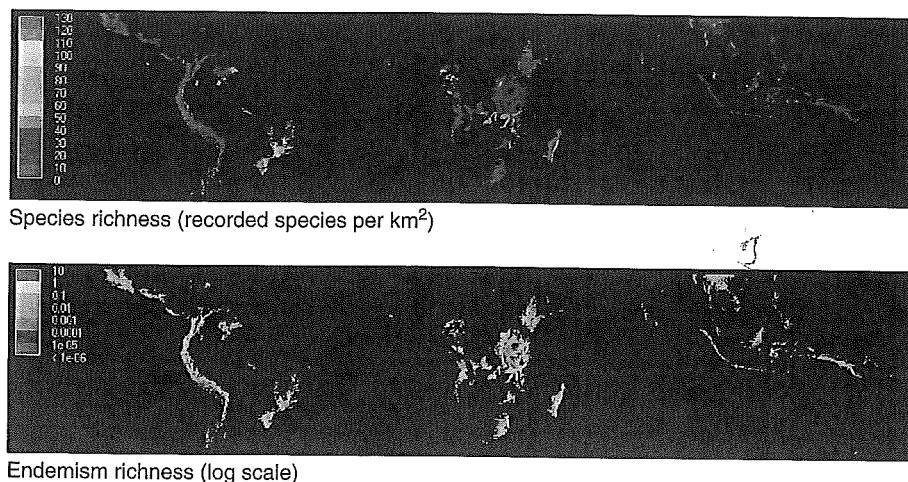


Figure 72.5. The distribution of species richness and endemism richness for amphibians in areas with cloud-affected forest. See text for explanation. (See also color plate.)

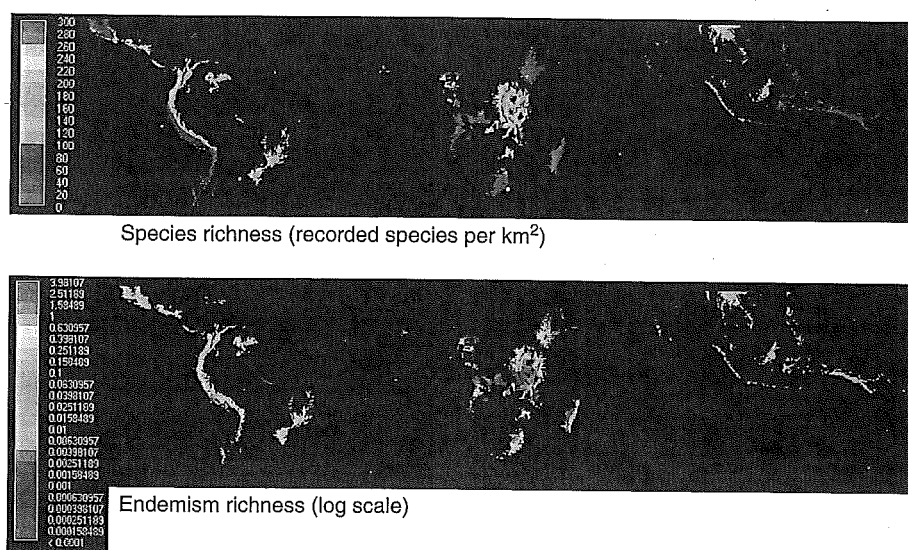


Figure 72.6. The distribution of species richness and endemism richness for mammals in areas with cloud-affected forest. See text for explanation. (See also color plate.)

parts of Costa Rica, the Andean peaks of Colombia, Ecuador, and northern Perú, in the eastern Atlantic forests of Brazil, the Eastern Arc Mountains of Tanzania and Kenya, and in isolated areas in northern Borneo, Papua New Guinea, the Philippines, Malaysia, and Indonesia (Figure 72.5).

The overall patterns derived for *mammals* are broadly similar to those for *amphibians*, with some notable differences in South-East Asia and Madagascar. Mammal species richness (or at least current knowledge of it) appears to be greatest in South-East Asia and in the north-eastern Andean cloud forests. Endemism richness for mammals is highest in parts of the Andes, in various East African cloud forests (see also Owunji and Plumptre, this volume), and in parts of Indonesia (Figure 72.6).

The spatial distribution of species richness for *birds* in the Neotropics is greatest in the cloud-affected forests of the Atlantic Coast of Brazil, the Guyana shield, and the eastern Andes. Endemism richness is greatest in the CAFs of Costa Rica, the Sierra Nevada de Santa Marta (Colombia), and the Andean mountains of Venezuela, Colombia, Ecuador, and Perú (Figure 72.7).

The present analysis by and large confirms the results of an early pan-tropical survey of avifaunal diversity of TMCF by Long (1995) who reported over 2500 species of birds confined to TMCF, of which nearly 1000 species occurred in the Neotropics (675 in South America, 180 in Central America, and 140 in the Caribbean). Outside the Neotropics, more than

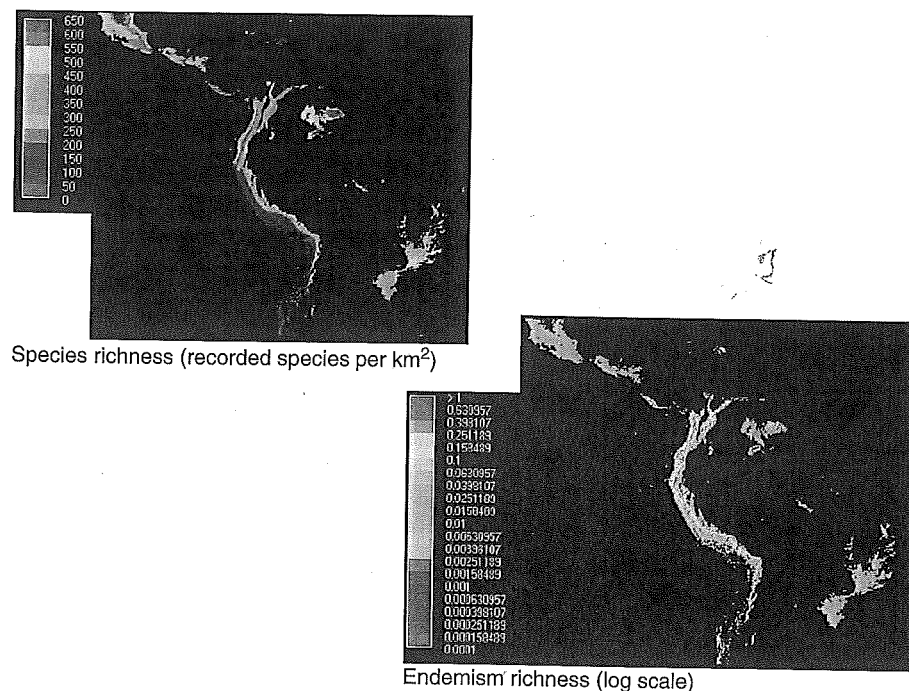


Figure 72.7. The distribution of species richness and endemism richness for birds in Latin American cloud-affected forests. See text for explanation. (See also color plate.)

600 species have been recorded in South-East Asia and New Guinea, and some 185 in the rest of Asia. Corresponding numbers for Africa and the Pacific are 390 in the Pacific, and over 320 in Africa. Areas of primary importance in terms of bird diversity and endemism (known as Endemic Bird Areas, EBAs) are found in the TCMF regions of Africa (e.g. Albertine Rift area, Eastern Arc Mountains, Kenyan Mountains, Cameroon Mountains, Canary Islands), northern/central Asia (Eastern Himalayas, Western Ghats, Sri Lanka), South-East Asia (Peninsular Malaysia, the Indonesian islands, Papua New Guinea, and the Philippines), the Pacific (Micronesian islands, Fiji, Samoa, Solomon, Hawaiian, and Cook Islands, New Caledonia), Latin America (southern Mexico, Central American highlands, northern tropical Andes, southern Brazilian coastal cloud forests), and the insular Caribbean, e.g. Hispaniola (Long, 1995).

Superimposed upon these large-scale diversity patterns are local-scale variations incurred by topography and micro-climatic conditions (e.g. exposure to strong winds). Studies carried out at Monteverde, Costa Rica, have demonstrated differences in bird diversity between windward and leeward slopes. Here, avifaunal richness ranged from 165 species in drier pre-montane forest on the leeward Pacific slope to 315 species in wetter pre-montane forest on the windward Caribbean slope, with 121–187 species occurring in various forest formations at the very wet and windy Continental Divide (1600–1800 m.a.s.l.) (Young and McDonald, 2000; see also Häger and Dohrenbusch, this volume).

Summarizing, the best data available to date for biodiversity confirm the importance of cloud-affected forests (CAF) in terms of species richness per unit area and, particularly, in terms of endemism richness, thereby confirming the very high conservation value of CAFs. In addition, whilst there is considerable geographic variation in species and endemism richness values, a number of well-defined hot spots of diversity can be identified (Figures 72.3–72.7). Further work is needed on mapping plant diversity and endemism in specific tropical cloud forest areas and between cloud forest types within specific areas.

Does biological richness differ between different altitudinal belts on single mountains?

PLANTS

Within individual mountain systems the general trend observed in most TCMFs is a decrease in overall woody plant species diversity and forest stature with increasing elevation (e.g. Grubb, 1977; Gentry, 1988, 1995; Proctor *et al.*, 1988; Kappelle *et al.*, 1995b; Cavellier, 1996; Lieberman *et al.*, 1996; Aiba and Kitayama, 1999; Hemp, 2002, 2005a; Homeier *et al.*, 2008; Paulsch *et al.*, 2008). Gradient analysis has further shown that cloud forest plant species diversity is typically highest at mid-elevations (500–2000 m.a.s.l.) and decreases toward higher, sub-alpine altitudes (Gentry, 1988; Kitayama, 1995; Kappelle *et al.*, 1996; Lieberman *et al.*, 1996; Hemp, this volume #12). Average

altitudinal range widths of individual plant species have been reported as being close to 500 m in Bolivian TMCF (Bach *et al.*, 2007) vs. 200–800 m on Mt. Kinabalu, Borneo (Kitayama, 1995) and Mt. Chirripó in Costa Rica (Kappelle *et al.*, 1995b). The causes determining species turnover patterns with elevation are still poorly understood but most probably involve climatic variables such as temperature and humidity, rainfall excess (and therefore soil water status; Kitayama, 1995; Schawe *et al.*, this volume), light and nutrient availability and therefore ecosystem productivity (cf. Grubb, 1977; Raich *et al.*, 1997; Schuur and Matson, 2001; Letts *et al.*, this volume; Benner *et al.*, this volume), as well as historical and evolutionary processes, and dispersal limitations (Kessler and Kluge, 2008). According to Kessler and Kluge (2008), the distribution patterns of endemic species along tropical elevation gradients differ from those of species richness in that richness generally decreases with altitude whilst the number of endemics tends to increase with elevation. In addition, on large mountains endemism tends to peak above 2000 m.a.s.l. This is probably due to a combination of the small size of the area available for speciation (in turn determined by topography and erosion and landslide hazards), long-term climatic stability, and taxon-specific traits like host specificity among epiphytes and very specific, co-evolved plant–pollinator relations in the case of orchids (see also Brehm *et al.*, 2008).

Whilst the number of flowering epiphytes decreases with altitude (lower temperatures), pteridophytic plant groups such as ferns and club mosses (Lycopodiaceae) become more abundant at higher elevations. Non-vascular epiphytes such as bryophytes – which include mosses (Musci) and liverworts (Hepaticae) – become highly diverse, abundant, and dominant in upper montane cloud forests, and cover the trunks, branches, and twigs of numerous trees and shrubs (e.g. Frahm and Gradstein, 1991; Zotz, 1999; Richardson *et al.*, 2000; Gradstein *et al.*, 2001; Nieder *et al.*, 2001; Holz *et al.*, 2002). Epiphylls – bryophytic epiphytes and lichens that grow on the surface of the leaves of vascular plants – may abound in perhumid parts of the forest understory at mid-elevation, e.g. close to shaded rocky outcrops near rivulets and cascades. Of an estimated 4000 species (2700 mosses, 1300 liverworts) occurring in tropical America, about 80% of the liverworts and 50% of the mosses are confined to montane cloud forests (Gradstein and Pócs, 1989).

FAUNA

A recent global analysis of elevational diversity trends for non-volant small mammals revealed a clear pattern of mid-elevational peaks in species richness, while diversity peaked at higher elevations on taller mountains (McCain, 2005). Shukor (2001) assessed diversity patterns of small mammals along an elevational transect on Mt. Kinabalu in Malaysia, utilizing data from previously existing sources and a new field study. Species richness of small mammals (e.g. shrews, squirrels, murid

rodents) showed a mid-elevation bulge at about 1200–1400 m.a.s.l. (i.e. below the cloud forest belt that starts at about 1800–2000 m.a.s.l. on Mt. Kinabalu; Kitayama, 1995), with numbers declining rapidly upon entering the wet upper montane cloud forest. Generally speaking, the number of animal species (e.g. amphibians, birds, butterflies – but not moths) on Mt. Kinabalu exhibits a downward trend with increasing elevation; cf. McKinnon *et al.*, 1996; Kumaran *et al.*, this volume). Likewise, on Mt. Mulu (2371 m.a.s.l.) in Sarawak, there is a progressive decline in the number of bird species with increasing altitude, ranging from 171 species in the lowland rain forest to only 12 species at the lower boundary of the UMCF at 1300 m.a.s.l., where a different avifauna takes over. Most species dropped out above 900 m.a.s.l. (McKinnon *et al.*, 1996). A similar discontinuity in bird species found in New Guinean LMRF and UMCF has been reported by Kikkawa and Williams (1971) who also noted that the niches occupied by forest birds changed with elevation. With increasing altitude the proportion of tree-nesting insectivorous species increased, whereas tree-nesting frugivores decreased and omnivores stayed about the same. In addition, the proportion of predatory birds decreased, while the proportion of ground-living birds increased with elevation. These changes were explained in terms of decreasing food resources, especially of fruit and small vertebrates, with increasing altitude (Kikkawa and Williams, 1971).

At mid-elevations in Latin American TMCF at least ten orders of mammals – volant and non-volant – have been recorded, with some 121 species in 25 families found in Costa Rican highland cloud forest (Monteverde): Marsupialia (opossums), Insectivora (shrews), Chiroptera (bats), Primates (monkeys), Xenarthra (sloths, armadillos, anteaters), Lagomorpha (rabbits), Rodentia (porcupines, squirrels, rats, mice, pacas, agoutis), Carnivora (large cats, coyote, gray fox, skunks, raccoons), Perissodactyla (tapir), and Artiodactyla (peccaries, deer) (Timm and LaVal, 2000). Over 40% of the Monteverde cloud forest mammals are bats. Preliminary observations suggest a decline in vertebrate diversity with increasing altitude in Costa Rica (M. Kappelle, personal observations) but more work is needed on the abundance, zonation, and biogeography of most tropical highland mammals (Timm and LaVal, 2000; cf. Williams *et al.*, 2003). Also at Monteverde, some 161 species of reptiles and amphibians are known, with a total of 79 species thriving in the higher and wetter TMCF zones (Pounds, 2000). On Mt. Kinabalu, 40 species of amphibians have been found above 1000 m.a.s.l., as were 27 species of lizards and 36 species of snakes, but no reptiles have been recorded above 2400 m.a.s.l. (i.e. in the UMCF belt). Similar observations were made on Mt. Kerinci (3805 m.a.s.l., Sumatra; McKinnon *et al.*, 1996). Faunal biodiversity associated with tank bromeliads was studied along an elevational gradient in the Luquillo Mountains of Puerto Rico (Richardson *et al.*, 2000). Animal species richness within the bromeliads showed a

mid-elevation peak while animal abundance declined with elevation.

Finally, the altitudinal distribution of the main groups of soil macrofauna (ants, termites, etc.) has been studied on a few locations only, e.g. on Mt. Mulu (Sarawak, East Malaysia, 2371 m.a.s.l.; Collins *et al.*, 1984) and Mt. Silam (889 m.a.s.l., Sabah, East Malaysia; Leahey and Proctor, 1987). On Mt. Mulu, strong decreases were observed in total numbers of soil invertebrates with elevation, with earthworms and some beetles replacing termites as the chief detritivores in lower montane forest just below the main cloud condensation level. In the peaty soils of the upper montane forest, beetles became dominant in association with earthworms, fly larvae, and cockroaches. In the most exposed, stunted vegetation zones near the summit, several groups fell away entirely (Collins *et al.*, 1984). On Mt. Silam – a small ultrabasic coastal mountain where a daily cloud cap develops around 700 m.a.s.l. (Bruijnzeel *et al.*, 1993) – no clear trends emerged for individual soil faunal groups with elevation except for a strong decline in the number and biomass of earthworms above the altitude at which the dipterocarps disappeared (610 m.a.s.l.; Leahey and Proctor, 1987). However, no such decline was observed on Mt. Mulu where the disappearance of the dipterocarps between 800 and 1130 m.a.s.l. was not accompanied by a reduction in earthworm densities and biomass (Collins, 1980). Likewise, both earthworm biomass and species richness increased with elevation from LMRF to elfin forest in the Luquillo Mountains of Puerto Rico and was highest in the ECF (Gonzalez *et al.*, 2007).

Summarizing, with the exception of ferns and non-vascular epiphytes (mosses and liverworts), species richness and abundance (numbers of individuals) of both plants and animals (including birds) tend to decline with increasing elevation. A mid-elevation maximum (located within or beneath the cloud belt) tends to be observed for plant, bird, and mammal diversity.

CLOUD FOREST HYDROMETEOROLOGY AND HYDROLOGY

With respect to the hydrological functioning of TMCF, the following questions assume key importance:

- Do lower montane, upper montane, and sub-alpine/elfin cloud forests differ in terms of their rainfall and cloud water inputs, net precipitation, and general hydrometeorology?
- Are there regional contrasts in water inputs via cloud water interception and wind-driven rain (e.g. “maritime” vs. “continental” situations)?

- Does water use (evapotranspiration) differ between different types of TMCF?
- How are annual and seasonal water yields affected by converting different types of TMCF to pasture, annual crops, or coffee plantations?

Hydrometeorology of different types of TMCF

WATER INPUTS AND NET PRECIPITATION

The proper quantification of the total amounts of water inputs received by TMCF and the relative contributions by precipitation, cloud water interception (CWI), and horizontal (wind-driven) rain is fundamental to assessing the hydrological importance of intact and converted cloud forest areas. This is illustrated by the results obtained by several early studies from Central America that arguably have contributed to the reputation of TMCFs as suppliers of high amounts of streamflow throughout the year. Zadroga (1981) compared the rainfall and streamflow regimes for two groups of watersheds in northern Costa Rica, one located on the windward Atlantic side of the Continental Divide and the other on the leeward Pacific side. Annual streamflow from the Pacific watersheds amounted to 34% of the rainfall and showed a clear seasonal flow pattern that followed that for precipitation, while annual streamflow from the Atlantic watersheds roughly equaled precipitation (102%) and even exceeded rainfall inputs for seven out of 12 months (Figure 72.8). Whilst acknowledging that the high runoff coefficient derived for the Atlantic watersheds was partly due to underestimation of rainfall inputs in the higher, rainier parts of the watersheds that lacked measurement stations, Zadroga (1981) attributed the very high streamflows primarily to unmeasured inputs of cloud water, emphasizing the fact that months with excess streamflow over precipitation coincided with the dominant occurrence of moisture-laden clouds that were brought in from the

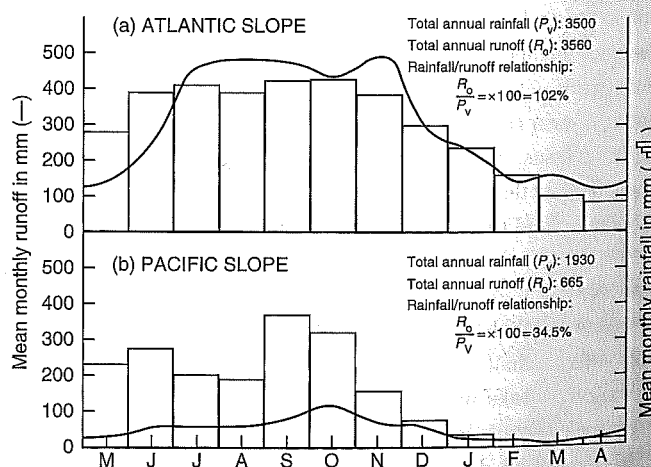


Figure 72.8. Contrasting rainfall and streamflow regimes for watersheds on the Atlantic and Pacific slopes of northern Costa Rica (after Zadroga, 1981).

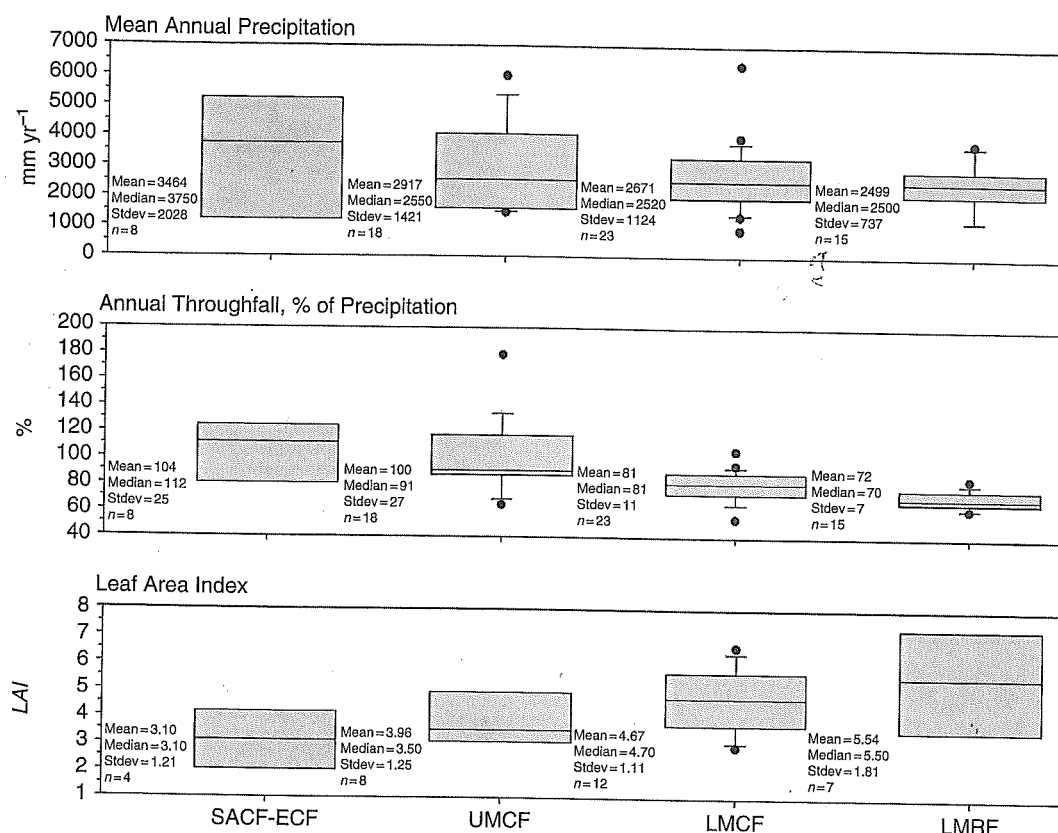


Figure 72.9. Mean and median annual rainfall, relative amounts of throughfall (% of rainfall), and leaf area index (*LAI*) for lower montane rain forest (LMRF), lower montane cloud forest (LMCF), upper montane cloud forest (UMCF), and sub-alpine/elfin cloud forest (SACF-ECF). Error bars denote 1 standard deviation from the mean. Data listed in Appendix 72.2.

Caribbean by the trade winds. In addition, he recognized that evaporative losses from these cloud-ridden slopes would be low.

Zadroga's contentions were confirmed by measurements of rainfall, streamflow, and climatically based estimates of evapotranspiration for another Atlantic watershed located further south in Costa Rica (Calvo, 1986). Whilst both of these early investigations must be considered "black box" studies that did not quantify the underlying hydrological processes, further support came from comparative observations of rainfall and throughfall (*TF*, also called crown drip) in Atlantic cloud forests in Costa Rica (Caceres, 1981) and Honduras (Stadtmüller and Agudelo, 1990). These studies showed that annual *TF* at cloud-exposed locations could attain values of as much as 110–180% of measured rainfall.

To what extent are these observations exemplary for the hydrological behavior of TMCFs in general, and how reliable are such direct comparisons of rainfall and *TF* in view of such potentially disturbing factors as wind losses around the rain gage and ungaged contributions of inclined rainfall (as opposed to horizontally moving clouds or rain)? Earlier reviews of the hydrometeorological literature on TMCF (Bruijnzeel and Proctor, 1995; Bruijnzeel, 2001, 2005) lacked sufficient data for a meta-analysis but the proliferation of local studies of net precipitation (i.e.

amounts of water arriving at the forest floor as *TF* plus stemflow, *SF*) – and to a lesser extent forest water use – during the last 5–10 years (many of which are reported upon in this volume) allows an analysis of some of these questions and whether different types of TMCF do exhibit different net precipitation fractions or water use.

Appendix 72.2 lists net precipitation data for lower montane rain forests little or not affected by fog and low cloud (LMRF, $n = 15$), tall lower montane cloud forest subject to moderate cloud incidence (LMCF, $n = 23$), upper montane cloud forest of intermediate stature and subject to frequent cloud incidence (UMCF, $n = 18$), and stunted sub-alpine and elfin cloud forests (SACF-ECF, $n = 8$)². Figure 72.9 shows the average amounts of rainfall, the fraction of rainfall becoming *TF*, and the leaf area index (*LAI*) for the respective forest types, while Figure 72.10 shows scatter-plots of annual *TF* vs. rainfall amounts at individual study sites grouped per forest type.

² Note that elfin cloud forest (ECF) represents a small-statured forest irrespective of elevation. As such, ECF is azonal and may refer to the most stunted facies of forest near the timber-line at high elevations, or to stunted wind-exposed forest on ridges and summits. The latter may occur at high or low elevation, with the lowermost occurrences reported at 300–500 m.a.s.l. (cf. Scatena *et al.*, this volume).

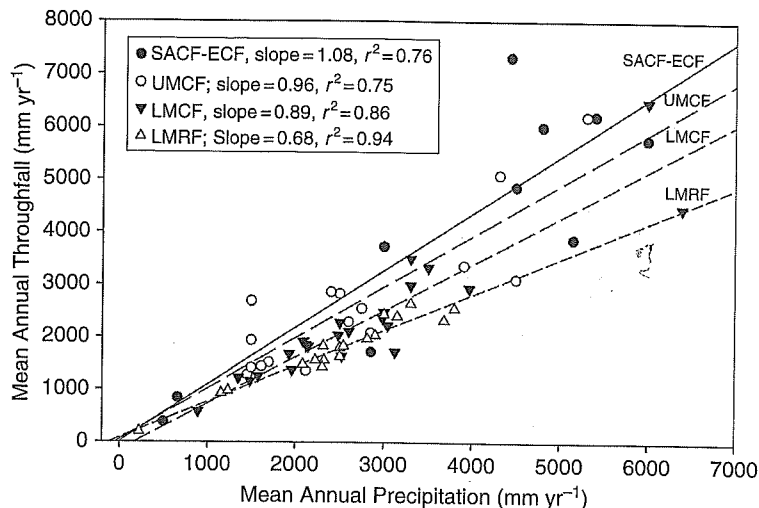


Figure 72.10. Linear regression relationships linking amounts of throughfall (TF) and rainfall (P) in lower montane rain forest (LMRF), lower montane cloud forest (LMCF), upper montane cloud forest (UMCF), and sub-alpine/elfin cloud forest (SACF-ECF). Data listed in Appendix 72.2.

Based on more than 60 local studies, the following patterns emerge: (i) average LAI values per forest type decrease from LMRF through LMCF and UMCf to SACF-ECF; (ii) rainfall at SACF-ECF sites tends to be higher than that at sites representing the other three forest categories which do not exhibit much difference between one another; and (iii) the TF fraction of rainfall (P) increases steadily from LMRF to SACF, viz. from $72 \pm 7\%$ (SD) in LMRF, to $81 \pm 11\%$ in LMCF, $100 \pm 27\%$ in UMCf, and $104 \pm 25\%$ in SACF-ECF (Figure 72.9).

Rigorous comparisons of the statistical differences in TF/P between the different forest types is limited by the small and uneven sample sizes and differences in sampling methodologies of the various studies. Nevertheless, comparisons of means and medians using t -tests, Mann-Whitney rank sum tests, and analysis of variance (ANOVA) where appropriate support the patterns observed in Figure 72.9. Moreover, there are significant differences (at $p = 0.05$) between the means or medians of TF/P for UMCf and both LMCF and LMRF (but not SACF-ECF). The median TF/P value for LMCF is also significantly higher than the median value for LMRF.

Comparison of the slopes of rainfall vs. TF graphs per forest type also indicates that TF exceeds rainfall as measured in the open at SACF-ECF sites, whereas the two are similar at UMCf sites (Figure 72.10). To obtain the total amount of precipitation reaching the forest floor (i.e. net precipitation), the fraction of the rainfall arriving as stemflow (SF) should be added to the amount of TF . Not all studies of net precipitation measured SF but values observed in LMRF and LMCF are typically very low (<1 – 2% of incident rainfall), although occasionally higher values have been reported (see Appendix 72.2 for details). SF fractions obtained for UMCf vary widely (0.1 – 30.5%) with an overall average approaching 10% of rainfall and a median of 3% ; the

Thus, whilst overall amounts of net precipitation (i.e. throughfall + stemflow) reaching the forest floor in LMRF and LMCF are only slightly higher (73% and 83% , respectively) on average than the more widely measured amounts of throughfall alone, net precipitation in UMCf and SACF-ECF may well exceed throughfall by 5 – 10% on average and by more than 10% in specific cases.

corresponding range and average for SACF-ECF read 3 – 18% and 6.7% , respectively (Appendix 72.2).

The rather low TF fraction observed for most LMRF (Figure 72.9) is often attributed to the high epiphyte loads of these forests (e.g. Cavelier *et al.*, 1997; Ataroff, 1998; cf. Fleischbein *et al.*, this volume). Interestingly, although both LMCF and UMCf typically have a much higher epiphytic biomass than LMRF (Frahm and Gradstein, 1991; Wolf, 1993; Köhler *et al.*, 2007), this does not seem to have a reducing effect on the magnitude of the TF fraction in the various types of cloud forests (Figure 72.9 and Appendix 72.2). Based on measurement and modeling of the water dynamics of epiphytes and bryophytes in a montane forest in Costa Rica, Hölscher *et al.* (2004) concluded that – whilst the *potential* water storage capacity of the epiphytes is very high – their *actual* (effective) capacity to absorb additional moisture is modest at best because the epiphytes are usually kept wet by the frequent rain and fog occurring in these forests (cf. Köhler *et al.*, this volume; Tobón *et al.*, this volume #26; Oesker *et al.*, this volume).

Although the high TF fractions obtained for UMCf and SACF-ECF must partly reflect “occult” contributions by CWI and wind-driven rain captured by the canopy but missed by a standard-type rain gage (cf. Zadroga, 1981), it should be noted

that wind speeds at exposed UMCF and SACF-ECF sites tend to be (much) higher than those experienced lower down on the slopes by the more sheltered LMCF and LMRF (Holwerda, 2005; Motzer, 2005; Bendix *et al.*, 2008). Therefore, rainfall amounts measured at exposed, windy sites are in danger of being (grossly) underestimated and need to be corrected for wind losses around the gage (Førland *et al.*, 1996; Yang *et al.*, 1998; Nešpor and Sevruk, 1999) and for the interactive effects of inclined rainfall falling onto steeply sloping terrain (Sharon, 1980; Herwitz and Slye, 1992). To date, only a few studies in TMCF have applied such corrections (Holwerda *et al.*, 2006; McJannet *et al.*, 2007a,b; cf. García-Santos, 2007; Giambelluca *et al.*, this volume). The magnitude of such corrections may be substantial, depending on the local situation. As such, the higher *TF* fractions derived for UMCF and SACF-ECF are almost certainly influenced by an underestimation of incident rainfall by many studies (see e.g. Prada *et al.*, 2009 for a recent example), although the data do not permit a quantification of the effect for different sites.

Local topography and slope aspect also exert a major influence on atmospheric inputs, as demonstrated by the high small-scale variability in relative and absolute amounts of *TF* vis-à-vis topographic position reported by Weaver (1972) for cloud forests in Puerto Rico (cf. Holwerda *et al.*, this volume #29), by Juvik and Ekern (1978) in Hawai'i (cf. DeLay and Giambelluca, this volume; Giambelluca *et al.*, this volume), by Stadtmüller and Agudelo (1990) in Honduras (cf. Häger and Dohrenbusch, this volume) and by García-Santos (2007) in La Gomera (Canary Islands; cf. Marzol-Jaén *et al.*, this volume). Future work will need to explicitly quantify inputs of wind-driven rain and fog in a spatially distributed manner. Although several powerful modeling approaches of various degrees of complexity are available (e.g. Yin and Arp, 1994; Walmsley *et al.*, 1996, 1999; Blocken *et al.*, 2005, 2006; Mulligan and Burke, 2005b), validation of model predictions through field measurements remains a challenge, largely because of the difficulties of adequately measuring rainfall inputs under windy conditions in complex terrain (Blocken *et al.*, 2006). Arguably, the recently developed spherical rain gage of Chang and Flannery (2001) and the "potential rain gage" of Frumau *et al.* (2006a) – which allows quantification of the angle of incidence of the rain – may prove useful in this regard. In addition, use can be made of conventional fog gages for comparative site characterization (cf. Juvik and Nullet, 1995a; Rollenbeck *et al.*, 2007; Frumau *et al.*, this volume; Marzol-Jaén *et al.*, this volume), rainfall radar systems for the quantification of the spatial extent of rain fields (Mulligan, 2006a; Rollenbeck *et al.*, 2007; Rollenbeck *et al.*, this volume), and remotely sensed cloud extent and characteristics (Mulligan, 2006b; Nair *et al.*, 2008; Welch *et al.*, 2008; Lawton *et al.*, this volume).

The estimation of amounts of *CWI* by a forest canopy has evolved considerably in recent years, from a simplistic equating

of the catch by some type of fog gage to that by a live canopy (e.g. Ataroff, 1998), or simply assigning all excess *TF* over rainfall to *CWI* (e.g. Holder, 2003), via comparisons of *TF* vs. rainfall relationships for times with and without fog (e.g. Harr, 1982; Hafkenscheid *et al.*, 2002) or times with and without strong winds (Tanaka *et al.*, this volume), to the more recently developed process-based wet-canopy water-budget method (Holwerda *et al.*, 2006; McJannet *et al.*, 2007b,d; Holwerda *et al.*, this volume #29; Giambelluca *et al.*, this volume; Schmid *et al.*, this volume), and direct measurement using sophisticated eddy covariance and spectrometer equipment (Eugster *et al.*, 2006; Holwerda *et al.*, 2006; Beiderwieden *et al.*, 2008; Schmid *et al.*, this volume). Arguably, results obtained with the wet-canopy water budget method may be considered the most realistic but the confidence limits of the estimates are wide due to the accumulation of error associated with the measurement of the respective components (see discussion in Holwerda *et al.*, 2006; McJannet *et al.*, 2007b).

Whilst the currently available measurements of (absolute) amounts of *CWI* do not permit the identification of regional patterns other than higher values being associated with windier and wetter places (Bruijnzeel and Proctor, 1995; Bruijnzeel, 2005; DeLay and Giambelluca, this volume; Häger and Dohrenbusch, this volume), these can be modeled using some of the approaches referred to in the previous paragraphs. An example is given in Figure 72.11 for the whole of Costa Rica, showing the clear influence of topographic exposure and elevation (Mulligan and Burke, 2005b; cf. Bendix *et al.*, 2008; Lawton *et al.*, this volume). At the same time, there remains a clear need to validate such model predictions using field measurements of *CWI* and wind-driven rain. Arguably, this could be done most profitably in data-rich areas such as (amongst others) Puerto Rico, northern Costa Rica, southern Ecuador, several of the Canary Islands, and Hawai'i. Furthermore, when trying to unravel the relative importance of inputs via cloud water capture and wind-driven rain under different climatic and topographic circumstances, use can be made of the contrast in stable isotope signatures of fog and wind-driven rain observed at several (but not all) locations (Scholl *et al.*, this volume; cf. Rhodes *et al.*, 2006; Guswa *et al.*, 2007).

FOREST WATER USE

Comprising only 15 studies in total, the current data-set on cloud forest water use (both for transpiration E_t and total evapotranspiration ET , i.e. including wet-canopy evaporation E_i) is much smaller than that for throughfall and stemflow. Nevertheless, considerable progress has been made in the last 5 years with the quantification of E_t and ET in montane tropical forests. Whilst Bruijnzeel and Proctor (1995) were unable to report any annual totals for E_t other than indirect (and therefore highly approximate) estimates derived with the water budget method

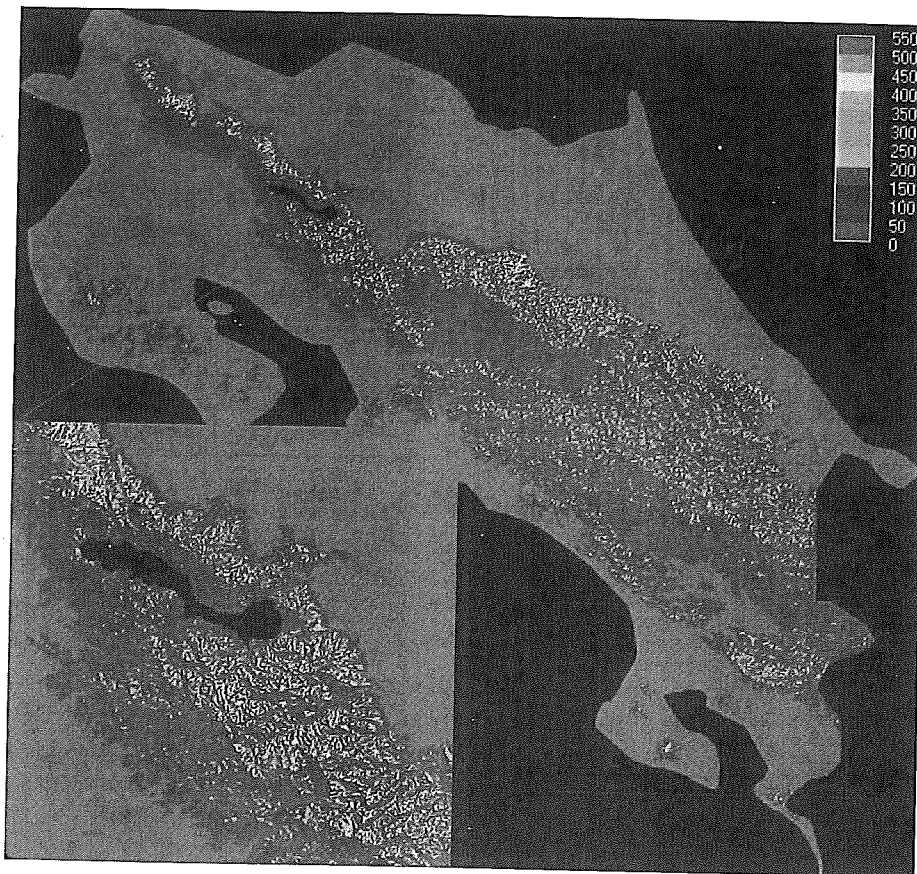


Figure 72.11. Modeled annual fog interception input (mm) at 90-m resolution across Costa Rica (after Mulligan and Burke, 2005b; reproduced with permission). (See also color plate.)

at the watershed scale, the number of studies using sapflow equipment – and to a lesser extent micrometeorological methods – has been increasing steadily in recent years (Appendix 72.3). A preliminary analysis of the available data is offered below, although the conclusions need to be viewed with caution given the small number of replications for UMCf and SACf–ECf in particular.

Figure 72.12 summarizes the average annual totals of ET and its two main components (transpiration E_t and wet-canopy evaporation E_i) for the three types of cloud forests distinguished. No comparative data on transpiration for LMRF are available (cf. Bruijnzeel and Proctor, 1995) but average total ET for these forests is $1280 \pm 72 \text{ mm year}^{-1}$ ($n = 7$). At $1188 \pm 239 \text{ mm year}^{-1}$ ($n = 9$) the average value for LMCF is not significantly different from that for LMRF, but ET totals for UMCf ($783 \pm 112 \text{ mm year}^{-1}$, $n = 3$) and ECf ($547 \pm 25 \text{ mm year}^{-1}$, $n = 2$) are distinctly lower. And although the small number of observations for the latter forest types precludes statistical testing, the data do confirm the need to distinguish between lower montane (cloud) forests on the one hand, and upper montane (and elfin) forests on the other (cf. Appendix 72.3). Combining averaged data on precipitation inputs (Figure 72.9) with averaged ET

values per cloud forest type (Figure 72.12) gives some indication of the corresponding precipitation-excess values – and therefore the probability of waterlogged conditions. Although such estimates are obviously approximate, the derived average precipitation-excess values show a clear increase from $\sim 1200 \text{ mm}$ and $\sim 1500 \text{ mm year}^{-1}$ in LMRF and LMCF, respectively, to $\sim 2100 \text{ mm year}^{-1}$ in UMCf and $\sim 2900 \text{ mm year}^{-1}$ in ECf (cf. Kitayama, 1995; Schawe *et al.*, this volume). The potential consequences of this increasing wetness with elevation for forest productivity and nutrient availability will be discussed in the corresponding section below.

As was found earlier for ET , average annual amounts of transpiration (E_t) also decrease gradually with elevation from $\sim 645 \text{ mm}$ in LMCF to $\sim 385 \text{ mm}$ in UMCf and $\sim 355 \text{ mm}$ in ECf (Figure 72.12). Interestingly, both E_t and ET (not shown) are significantly related to forest LAI, especially after normalization for net radiation input (cf. Figure 72.13 below). In addition, the fraction of available energy used by the respective forest types for transpiration (E_t/R_n) shows a marked reduction from 0.61 ± 0.08 in lowland evergreen rain forest (LERF), to 0.48 ± 0.14 in LMCF, 0.37 ± 0.06 in UMCf, and 0.26 ± 0.01 in ECf. These important findings will be revisited in the section on forest

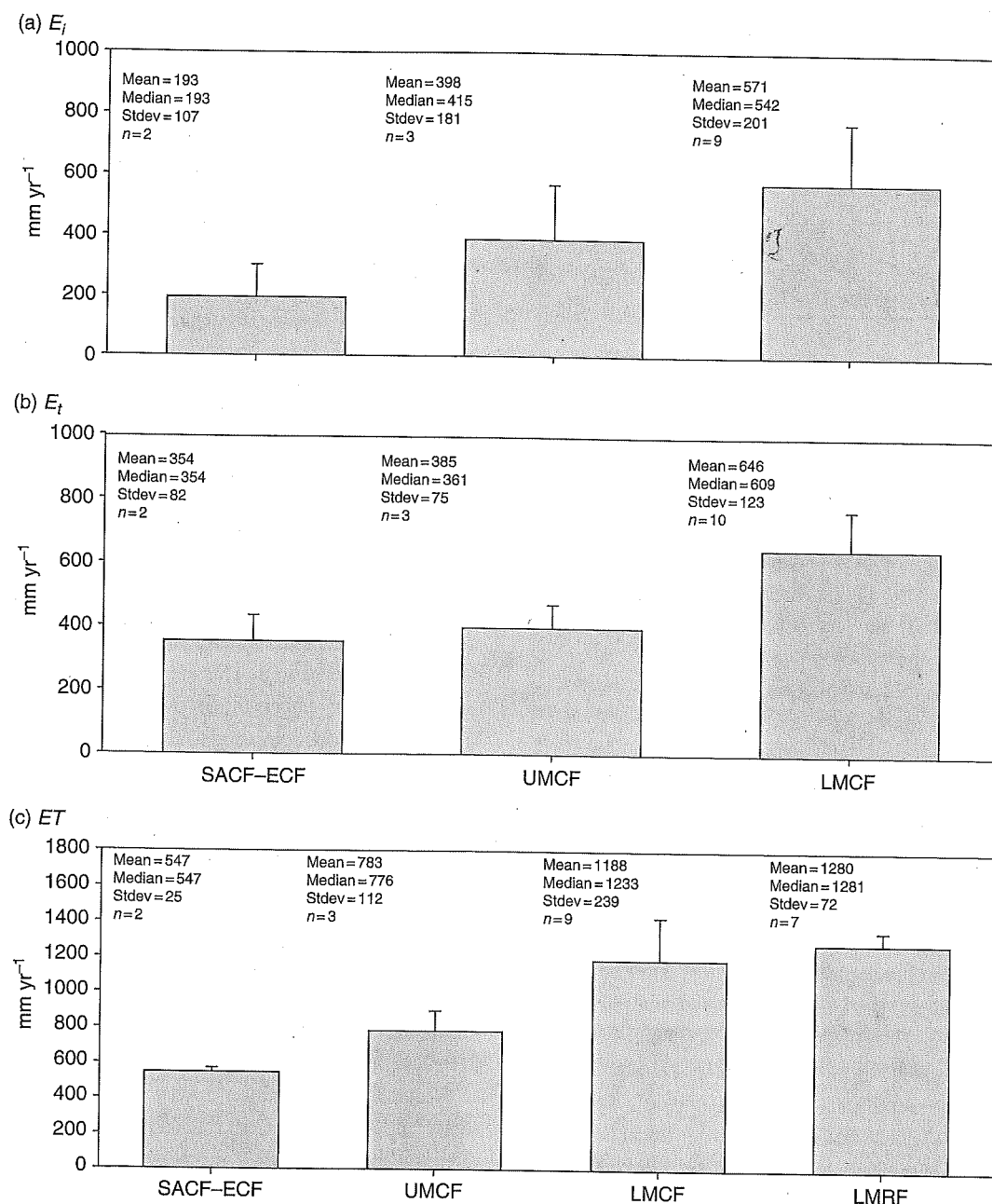


Figure 72.12. Mean and median annual (a) rainfall interception, (b) transpiration, and (c) total evapotranspiration for lower montane rain forest (LMRF, ET only), lower montane cloud forest (LMCF), upper montane cloud forest (UMCF), and sub-alpine/elfin cloud forest (SACF-ECF). Error bars denote 1 standard deviation from the mean. Data listed in Appendix 72.3.

productivity below. Across all sites listed in Appendix 72.3, mean annual precipitation (MAP) is negatively correlated with net radiant inputs, forest water use (E_t), and LAI . Overall, up to 42% of the variance in E_t between sites can be explained by the combination of MAP , mean air temperature, and net radiation (which is controlled in turn by the frequency and degree of cloud cover). In addition, the relationship between E_t and LAI is particularly strong, also after normalizing E_t for the evaporation equivalent of available net radiant energy (Figure 72.13).

Overall, the available information indicates that relative contributions by transpiration E_t to total evaporative water loss ET are roughly as important as those by wet-canopy evaporation E_i (c. 50% each) in both LMCF and UMCF. However, there are insufficient data for meaningful statements in this regard for SACF-ECF (see Appendix 72.3 for details). Occasionally, however, very high values have been derived for E_i (e.g. for several near-coastal forests in northern Queensland; McJannet *et al.*, 2007d). It is not clear to what extent this finding reflects

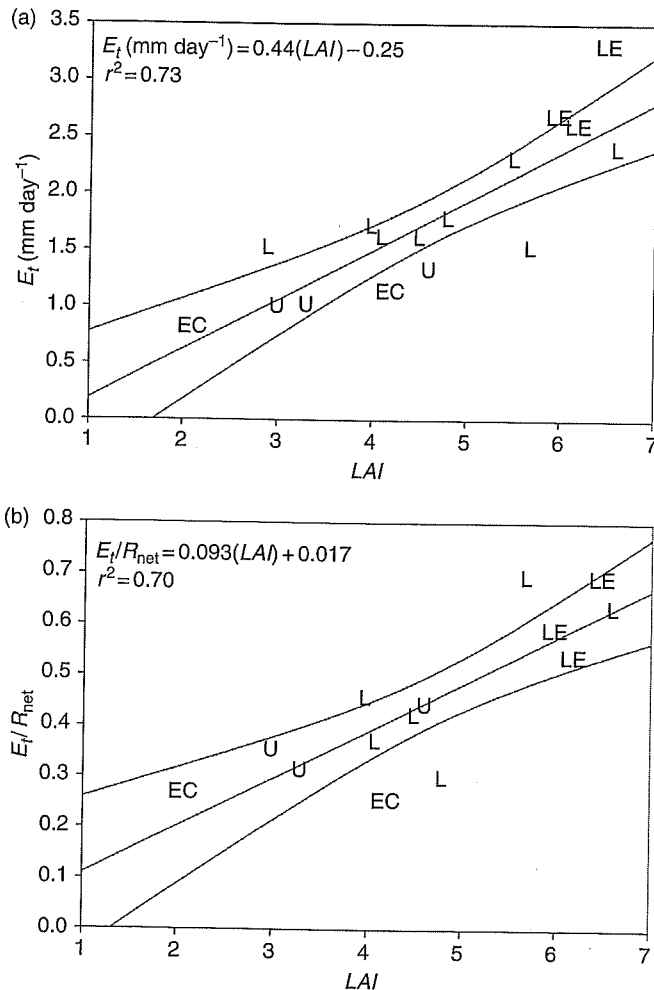


Figure 72.13. Cloud forest transpiration (E_t) vs. leaf area index (LAI): (a) daily E_t values, (b) normalized for the evaporative equivalent of net radiant energy (R_{net}). LE, lowland evergreen rain forest; L, lower montane cloud forest; U, upper montane cloud forest; EC, elfin cloud forest.

differences in methodology or a physical reality (e.g. advected energy from the ocean or deforested lowlands sustaining high evaporation rates during rainfall) given that various other “maritime” sites (Puerto Rico, Hawai’i, Costa Rica) do not exhibit similarly high values (Appendices 72.2 and 72.3). There is a need for additional observations of evaporation in UMcF and SACF–ECF in particular.

Cloud forest conversion and water yield

Based on the very large contrast in streamflow produced by windward and leeward forests in northern Costa Rica (Figure 72.8), Zadroga (1981) postulated that conversion of Atlantic cloud forest might well result in significantly reduced streamflows. However, the recent results of detailed hydrological field and modeling studies in cloud forest and pasture

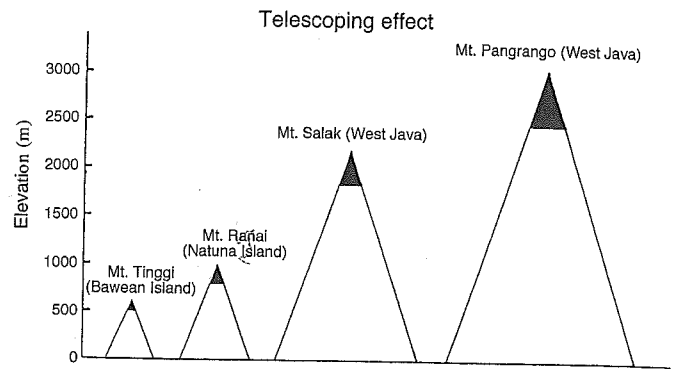


Figure 72.14. The “telescoping effect” of vegetation zonation on differently sized mountains (after Van Steenis, 1972).

in the same area raise questions about the validity of some of the standard assumptions as to why cloud forests produce such high amounts of streamflow. Conversion of cloud forest to pasture in northern Costa Rica did *not* lead to the expected decreases in annual or even seasonal water yield; rather the effect on streamflow was more or less neutral. This surprising finding was attributed to the compensatory effects of: (i) low additional inputs by CWI under forested conditions compared to rough pasture, under conditions of very high rainfall (including wind-driven rain), and (ii) the lower water use of pasture compared to cloud forest (Bruijnzeel, 2006; Schellekens, 2006). Whilst runoff response to rainfall (“quick-flows”) at the small watershed scale (<10 ha) were roughly doubled after conversion to grazed pasture – presumably due to diminished infiltration opportunity and increased overland flow on compacted cow trails (Tobón *et al.*, this volume #54; cf. Zimmermann and Elsenbeer, 2008) – the effect was not detectable at the operational watershed scale (100 km²; Bruijnzeel, 2006; Schellekens, 2006).

Whilst CWI constituted only a small contribution to overall water inputs in the Costa Rican case, the situation may be different in areas with a more seasonal rainfall regime where CWI may become important during the dry season – as for instance in parts of Pacific Central America (Holder, 2003; Mulligan and Burke, 2005b; cf. Figure 72.11). Recent work on CWI and forest and pasture water use in central Veracruz, eastern Mexico – an area with strongly seasonal rainfall and reportedly receiving substantial amounts of occult precipitation (Vogelmann, 1973) – demonstrated that cloud forest conversion would lead to a major local *increase* in flows (Muñoz-Villers, 2008; Gomez-Cárdenas, 2009), amongst other reasons because of low CWI by the local cloud forest (Holwerda *et al.*, 2010; cf. Ponette-González *et al.*, 2009) and a much higher water consumption by the cloud forest than by pasture (Holwerda *et al.*, 2007; Gomez-Cárdenas, 2009). Finally, partial clearing of Douglas fir forest in the Pacific Northwest of the USA – an area subject to heavy fog incidence (Harr, 1982) – caused a

temporary decrease in baseflows during the dry summer months. Interestingly, the effect gradually disappeared after 5–6 years, as the regenerating trees were apparently effective at capturing sufficient amounts of cloud water again (Ingwersen, 1985).

Reliable information on the effect of cloud forest conversion to agricultural cropping (with or without associated soil degradation and ensuing negative effects on dry-season flows; cf. Bruijnzeel, 2004, 2005) or conversion to shade-coffee plantations is not available, although the effect on water yield could be modeled from information on plantation water use (Holwerda *et al.*, 2007) and rainfall and cloud water interception (Ponette-González *et al.*, 2009).

Summarizing, the direction and magnitude of changes in water yield (if any) after TMCF conversion depend on the outcome of multiple interactions, and are therefore highly contextual and site-specific. Where cloud water interception is low and forest water use comparatively high, water yields are likely to increase upon cloud forest conversion, and vice versa.

CLOUD FOREST PRODUCTIVITY: SOIL VS. CLIMATIC EFFECTS

The changes in forest structure and physiognomy observed as one ascends wet tropical mountains have, in the words of Whitmore (1989) “puzzled and irritated” scientists for a long time. Of these changes the most notable are a decrease in forest stature and leaf size from tall lower montane forest to increasingly stunted upper montane and sub-alpine cloud forests with increasing altitude (Grubb, 1977; Moser *et al.*, 2007). A related phenomenon is the occurrence of (often stunted) mossy forest at lower altitudes on small outlying mountains (often on islands or in coastal areas) compared to larger mountains away from the coast (Van Steenis, 1972; Richards, 1996; Figure 72.14). This is generally thought to reflect a combination of the higher atmospheric moisture contents prevailing under “maritime” conditions (cf. Foster, this volume; Jarvis and Mulligan, this volume) and the smaller heat-storing capacity of smaller mountains compared to larger ones.

Regardless of the elevation at which these mossy forests occur, the common denominator appears to be the high frequency of fog (cf. Mulligan, this volume; Jarvis and Mulligan, this volume), which is thought to influence an array of ecological processes controlling forest stature (Grubb, 1977; Bruijnzeel *et al.*, 1993; Cavelier, 1996; Silver *et al.*, 1999; Benner *et al.*, this volume). This leads to the following key questions:

- What causes the lower stature of certain types of cloud forests compared to forest not affected appreciably by frequent fog? Are the dominant controls primarily soil- or climate-related or both?

- Do soils under lower and upper montane cloud forests differ and if so, in what respect and what are the consequences for nutrient availability and forest productivity?

Possible reasons that have been advanced to explain the stunting of UMCF and SACF–ECF on wet tropical mountains (summarized and discussed by Grubb, 1977; Flenley, 1995; Cavelier, 1996; Bruijnzeel and Veneklaas, 1998; Tanner *et al.*, 1998; see also Benner *et al.*, this volume; Roman *et al.*, this volume) are manifold and include:

- Periodic water shortage, especially in the case of shallow and stony soils;
- Chronic soil saturation and impeded root respiration due to oxygen deficiency;
- Reduced leaf temperatures and reduced photosynthetic capacity associated with low radiation inputs;
- Limited nutrient uptake due to (i) climatically controlled reduction in soil water uptake rates (transpiration, E_t), (ii) extreme soil acidity or low fertility or both, often coupled with (iii) reduced decomposition and mineralization of leaf litter, and (iv) elevated levels of toxic substances in the soil water, notably “free” aluminum and polyphenols;
- Exposure to strong winds, notably in the trade-wind belt and at exposed upper slopes and summit locations; and
- Exposure to high intensities of UV-B radiation.

Waide *et al.* (1998) drew attention to the fact that several of these factors are known to co-vary and thus may act in a synergistic manner such that it is difficult to unravel the relative importance of individual factors. However, in the last decade a number of important studies have been made of the changes in forest structural characteristics, and of the corresponding changes in climate, soils, eco-physiology, and nutrient dynamics along elevational or soil fertility gradients. Much of this work has been concentrated at a relatively small number of intensively studied sites, both in the maritime tropics (notably Hawai’i, Jamaica, Sabah (East Malaysia), and Puerto Rico; see Benner *et al.*, this volume for a fuller discussion) and under more continental conditions, e.g. the Yungas of Bolivia (Schawe *et al.*, 2007; Gerold *et al.*, 2008; Schawe *et al.*, this volume), the eastern Andes of southern Ecuador (Beck *et al.*, 2008a; cf. Wilcke *et al.*, this volume), and to a lesser extent the Cauca region of south-western Colombia (Letts *et al.*, this volume), northern Thailand (Tanaka *et al.*, 2003; Tanaka *et al.*, this volume), and Mt. Kilimanjaro, Tanzania (Schrumpp, 2004).

Whilst it remains difficult to identify the relative importance of several co-varying factors (e.g. radiation, temperature, rainfall, humidity vs. elevation), this new work does allow the formulation of a hypothesis that goes a long way toward explaining cloud forest stunting, both at higher elevations on large

mountain massifs (UMCF and SACF-ECF) and at much lower elevations on small outlying mountains (ECF) across the humid tropics. First, however, the various hypotheses listed above are discussed briefly in the light of the new evidence.

DROUGHT VS. WATERLOGGING

Both early (as reviewed by Cavelier, 1990, 1996; Bruijnzeel and Proctor, 1995; Bruijnzeel and Veneklaas, 1998) and more recent data on soil water dynamics in different cloud forest types (Silver *et al.*, 1999; Cavelier *et al.*, 2000; Hafkenscheid, 2000; Santiago *et al.*, 2000; García-Santos, 2007; Moser *et al.*, 2008; Schawe *et al.*, this volume) confirm that drought is not an important determinant of tropical montane forest stature, even under conditions of low rainfall, as long as fog inputs are consistent (Cavelier *et al.*, 2000; García-Santos, 2007). Productivity (e.g. trunk increment) has been shown to be reduced during (and after) major drought years (Aiba *et al.*, this volume) but observations of leaf litter standing crop after a severe drought did not suggest major water stress in cloud-affected forest, in contrast to forests below the cloud belt which showed strong increases in leaf litterfall after a drought (Bruijnzeel *et al.*, 1993). Also, whilst many cloud forests have xeromorphic-looking leaves ("sclerophylls"), these leaves are not particularly drought-tolerant (reviewed by Turner, 1994). Reports of severe water stress in cloud-affected forest (as discussed in Bruijnzeel and Proctor, 1995) appear to pertain exclusively to forests located on very shallow soils.

Conversely, the averaged precipitation-excess values cited in the previous section for the respective cloud forest types suggest the soils of UMCF experience roughly twice the amount of water percolating through soils under LMRF. The corresponding volume for SACF-ECF is nearly three times that in LMRF. As such, soils of UMCF tend to be wet to saturated for most of the time and those of SACF and ECF in high-rainfall areas tend to be frequently, if not persistently, saturated (see examples in Bruijnzeel and Proctor, 1995; cf. Silver *et al.*, 1999; Hafkenscheid, 2000; Santiago *et al.*, 2000; Moser *et al.*, 2008; Schawe *et al.*, this volume). This contention is confirmed by numerous soil profile descriptions made along elevational transects in South-East Asia (e.g. Tie *et al.*, 1979; Van Reuler, 1987; Bruijnzeel *et al.*, 1993; Mangen, 1993), East Africa (e.g. Schrumph, 2004), the Caribbean (e.g. Wadsworth and Bonnet, 1951; Lyford, 1969), Hawai'i (Kitayama and Müller-Dombois, 1994), and South America (e.g. Hetsch and Hoheisel, 1976; Schrumph *et al.*, 2001; Schawe *et al.*, 2007) which all report increased occurrence of hydromorphic characteristics beneath the more stunted forest types. In addition, at a given elevation (and therefore climatic conditions), forest stature is often reported to decline with increasing soil wetness (typically in association with a reduction in slope steepness; e.g. Hetsch and Hoheisel, 1976; Lawton and Dryer, 1980; Mangen, 1993; Silver *et al.*, 1999; Santiago *et al.*,

2000; Vernimmen *et al.*, 2007; cf. Häger and Dohrenbusch, this volume; Roman *et al.*, this volume). However, on young soils derived from volcanic ash – which typically have very high porosity and permeability values and which tend to be very well-drained (cf. Tobón *et al.*, this volume #52) – waterlogging (and associated forest stunting) is observed only under conditions of extreme rainfall (>5000 mm year⁻¹) and low topographic gradients (cf. Häger and Dohrenbusch, this volume). Also, where SACF occurs above the level of most frequent cloud occurrence and maximum rainfall – such as in the Hawaiian archipelago above the trade-wind inversion (cf. Kitayama and Müller-Dombois, 1994; Juvik and Nullet, 1995b) and on Mt. Kilimanjaro above 2800 m.a.s.l. in the *Erica* forest belt (Hemp, this volume #12) – rainfall-excess values will be much smaller due to a combination of comparatively high evaporation and reduced rainfall (Giambelluca and Nullet, 1992; Kitayama and Müller-Dombois, 1994; cf. Røhr, 2003). Nevertheless, even in the sub-humid higher parts of Mt. Kilimanjaro, Schrumph (2004) observed waterlogged and poorly drained soils in the SACF zone due to the presence of bedrock at shallow depths. Similarly, soil moisture levels in low-elevation ECF have been reported to remain very high (although not reaching full saturation) due to regular nocturnal cloud immersion even under conditions of low rainfall (Cavelier *et al.*, 2000).

Summarizing, high and often excessive soil moisture levels are present in most UMCF and, especially, SACF and ECF settings below the trade-wind inversion. Also, forest stature and leaf area at a given elevation tend to be inversely related to the degree of soil waterlogging.

TEMPERATURE, RADIATION LEVELS, AND PLANT PHOTOSYNTHETIC CAPACITY

The observation that very similar-looking waterlogged ECF can develop at vastly different elevations – and therefore experience highly different temperature and radiation regimes (including UV-B radiation) – already suggests that precipitation excess (read: soil water status) overrides any temperature or radiation effects (Cavelier *et al.*, 2000; Gerold *et al.*, 2008; cf. Schawe *et al.*, this volume). Further support for this contention comes from observations of very tall (30–50 m) montane forests at 2200–3000 m.a.s.l. on well-drained volcanic soils in Papua New Guinea despite reportedly frequent fog (Hyndman and Menzies, 1990; Mangen, 1993). Indeed, although radiation inputs and photosynthetic photon flux densities (*PPFD*) at sites with UMCF or SACF-ECF are typically reduced compared to sites with LMCF (by 30–40%) or compared to lowland forest (by $>50\%$) (Cavelier and Mejia, 1990; Hafkenscheid, 2000; Holwerda, 2005; Gerold *et al.*, 2008), it is pertinent to note that *PPFD* values in low-statured SACF-ECF have been

reported to be very similar to those measured in taller UMCF lower down on the same mountain (Schawe *et al.*, this volume). More importantly, at 650–800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, average PPFD values observed at a number of UMCF sites are well above the light-saturation level of most plants ($\sim 400\text{--}500 \mu\text{mol m}^{-2} \text{s}^{-1}$; Aylett, 1985; Cordell *et al.*, 1998; Hafkenschied, 2000) and should therefore not be limiting photosynthesis and growth in these places (e.g. Turton, 1990; Hafkenschied, 2000; cf. Cordell *et al.*, 1998; Schuur and Matson, 2001; Leuschner *et al.*, 2007). In addition, in areas where average values of PPFD on cloudy days are around the light-saturation level, maximum values still occur for 3–4 hours day⁻¹ in UMCF and SACF-ECF vs. $\sim$ up to 4–5 hours day⁻¹ in LMRF (Cavelier and Mejia, 1990; Gerold *et al.*, 2008; Giambelluca *et al.*, 2009; Schawe *et al.*, this volume) although Letts *et al.* (this volume) report very low PPFD values for an LMCF in Colombia during the wet season.

Further support for the contention that light is not limiting intrinsic plant productive capacity in LMCF, UMCF, or ECF comes from the observation that maximum stomatal conductances in various types of TMCF (Aylett, 1985; Cavelier, 1990; Bruijnzeel and Veneklaas, 1998; Cordell *et al.*, 1998; Santiago *et al.*, 2000; Tanaka *et al.*, 2003; Küppers *et al.*, 2008; Letts *et al.*, this volume) are not lower than those found in tall evergreen lowland rain forest (Roberts *et al.*, 2005). Also, values of net photosynthetic capacity *per unit leaf surface area* (A_{max}) of LMCF and of several UMCF do not exhibit any significant trends with elevation or forest stature (Cordell *et al.*, 1998; Hafkenschied, 2000; cf. Bruijnzeel and Veneklaas, 1998; Letts *et al.*, this volume). However, because forest LAI decreases markedly with increasing elevation – and therefore from LMRF to LMCF, UMCF, and SACF-ECF (Moser *et al.*, 2007; Figure 72.9) – rates of photosynthesis (A) and water uptake (Et) at the stand scale also decline with elevation (cf. Figure 72.12). In addition, it is pertinent to note that although Et is strongly related to LAI (Figure 72.13a), the fraction of available radiation used by the respective forest types for transpiration (Et/R_{net}) shows a gradual reduction with elevation (see previous section on hydrometeorology). In other words, factors other than radiation and (by implication) temperature, must be responsible for the observed decrease in Et with altitude. Further support for this contention comes from the observation that forest LAI (and therefore Et and A) at a given elevation (and therefore experiencing similar climatic conditions) decreases sharply as the degree of persistent soil wetness increases (Santiago *et al.*, 2000; Vernimmen *et al.*, 2007).

NUTRIENT AVAILABILITY

Foliar nutrient analyses in the more stunted cloud forest types (UMCF, SACF-ECF) and various fertilization experiments

Summarizing, light levels do not appear to be limiting plant productive capacity in UMCF or SACF-ECF but the declining leaf area with increasing elevation leads to lowered rates of photosynthesis and soil water uptake at the stand level. Also, soil water uptake decreases more rapidly with increasing elevation than do levels of available net radiant energy. Similar trends in leaf area and soil water uptake are found along gradients of soil wetness, with the smallest values being observed under the wettest conditions.

involving comparatively high doses (compared to atmospheric inputs) of nutrient additions in various combinations have indicated various nutrient deficiencies (notably of nitrogen; Hafkenschied, 2000; Soethe *et al.*, 2008a,b; Benner *et al.*, this volume). However, unlike foliar nutrient concentrations, amounts of plant-available nutrients in mineral soil horizons do not necessarily decrease with increasing elevation and have sometimes even been reported to increase with altitude (e.g. Soethe *et al.*, 2008b; cf. Roman *et al.*, this volume). Conversely, C:N ratios and C:P ratios in the organic layer generally increase with elevation, suggesting mineralization of plant litter to be slowed down, thereby reducing the availability of nitrogen and phosphorus to plant roots (e.g. Soethe *et al.*, 2008b; cf. Benner *et al.*, this volume). Also, the foliar N:P ratios found at different elevations suggest nitrogen supply becomes more critical than phosphorus supply at higher elevations (Soethe *et al.*, 2008a,b; Benner *et al.*, this volume). Whilst such reduced rates of litter decomposition have often been attributed to the lower temperatures prevailing at higher elevations, there is increasing evidence that moisture levels override any temperature effects (Schuur, 2001; cf. Silver *et al.*, this volume). This would explain the slow decomposition rates that have been observed in stunted ECFs on permanently wet soils at low elevations despite favorable ambient temperatures (Cavelier *et al.*, 2000; Benner *et al.*, this volume; Silver *et al.*, this volume). As indicated earlier, excessive soil moisture levels tend to limit soil oxygen availability (Silver *et al.*, 1999; Santiago *et al.*, 2000), which, in turn, may affect the activity of various decomposer communities, particularly fungi (Schuur, 2001). In addition, leaves from wetter sites have higher lignin concentrations (possibly in response to lowered nitrogen availability) rendering them even less amenable to decomposition (Schuur, 2001; Benner *et al.*, this volume). Pertinently, experimental aeration has been shown to greatly increase rates of nitrogen mineralization (Cavelier *et al.*, 2000; cf. Marrs *et al.*, 1988; Schuur and Matson, 2001). Cavelier *et al.* (2000) pointed out that for low mineralization rates to occur, the soil does not necessarily have to be saturated all the time – consistently high moisture levels will produce the same effect.

On the other hand, the few available studies of cloud forest soil nutrient budgets indicate that the trees take up only a mere

fraction of the amounts of readily available nutrients in net precipitation arriving at the forest floor or contained in leaf litter leachate (Bruijnzeel *et al.*, 1993; Hafkenscheid, 2000). This suggests that the roots have difficulty in making full use of what nutrients are available. Although the precise mechanism is still being debated (Benner *et al.*, this volume; see also below) and although the cited estimates of nutrient uptake concerned the production of above-ground biomass only, *it is clear that the persistently wet to saturated conditions prevailing in UMCF and SACF–ECF soils severely limit opportunities for exploitation of mineral soil horizons by the roots* (Silver *et al.*, 1999; Santiago *et al.*, 2000; Soethe *et al.*, 2006). The occurrence of adventitious roots (i.e. above the soil surface) capturing nutrient-rich stemflow before it reaches the soil – as reported for some excessively wet forests – may be interpreted along similar lines (Herwitz, 1991). Various other adaptations in root architecture are required to improve tree anchorage on such shallow and saturated slopes, particularly under conditions of high wind (Soethe *et al.*, 2006, 2007; see also below).

Alternatively, toxic concentrations of “free” aluminum or hydrogen ions in the soil solution have also been invoked to explain reduced nutrient uptake (Hafkenscheid, 2000). Aluminum concentrations have been reported to increase with site wetness (Schoor and Matson, 2001) and reduced site fertility (Hafkenscheid, 2000; cf. Schumpf *et al.*, 2001; Schawe *et al.*, 2007). To neutralize potentially toxic levels of aluminum (or hydrogen), the roots are considered to produce phenolic compounds that, in addition, immobilize nitrogen by organic complexation, thereby preventing leaching of precious nitrogen in dissolved form (Northup *et al.*, 1995, 1998; Hafkenscheid, 2000). Interestingly, although concentrations of aluminum in the soil solution in a series of montane forests in Hawai’i increased with site wetness, foliar concentrations of aluminum decreased along the gradient, suggesting the roots were effectively excluding aluminum uptake (Schoor and Matson, 2001). In addition, lignin concentrations in leaf litter at these sites were higher – and nitrogen concentrations lower – as the soils became wetter (Schoor, 2001). Although no measurements were made of phenolic concentrations, these are known to be related positively to lignin concentrations and inversely to nitrogen concentrations (Bruijnzeel *et al.*, 1993; Hafkenscheid, 2000). The mechanisms linking plant phenol production in montane tropical forests – both in leaves and roots – with soil biological and chemical processes, site fertility, and forest productivity require more work before generalizations can be made (Northup *et al.*, 1995, 1998; Hafkenscheid, 2000; Hättenschwiler *et al.*, 2003).

The trees of the more stunted tropical montane forest types appear to respond to these adverse soil conditions in several ways: increased leaf scleromorphism (Turner, 1994), increased leaf longevity (Moser *et al.*, 2007), and increased investment of carbon in below-ground biomass and productivity (Leuschner *et al.*, 2007).

Although the leaves of many of the more stunted types of cloud forest look distinctly xeromorphic, there is ample evidence

(reviewed by Turner, 1994) that this is not an adaptation to better withstand drought conditions but rather a response to reduced nutrient availability. Scleromorphic features appear to be closely associated with long-lived leaves (Turner, 1994). Whilst information on leaf lifespan in tropical montane forests is comparatively rare, recent data from an elevational transect in Ecuador suggest that leaves remain significantly longer on the trees in cloud-affected forests than below the cloud belt, although no differences were observed between different types of cloud forest (Moser *et al.*, 2007). However, a meta-analysis of fine-root production data from more than 80 tropical moist forest stands from the lowlands and the montane belt indicates that upper montane forests in the Neotropics have significantly higher average fine-root production ($1721 \text{ g m}^{-2} \text{ year}^{-1}$) than do either lowland forests ($405 \text{ g m}^{-2} \text{ year}^{-1}$) or lower montane forests not affected by significant cloud ($540 \text{ g m}^{-2} \text{ year}^{-1}$; Hertel and Leuschner, this volume). This increased investment of carbon in below-ground biomass under the more adverse (acid, wet, poor in nitrogen) soil conditions prevailing in UMCF and ECF (Roman *et al.*, this volume) is apparently realized at the expense of above-ground productivity and biomass, and represents a marked shift in carbon allocation from shoot to root with increasing elevation or degree of soil wetness (Leuschner *et al.*, 2007; Moser *et al.*, 2007; Hertel and Leuschner, this volume).

WIND

Although wind is rarely a definitive factor determining montane forest stature, the occurrence of persistently high winds on wet, exposed upper slopes and summit locations acts as an added stress factor (Lawton, 1982; Cordero, 1999; cf. Fetcher *et al.*, 2000). The combination of high wind loading and the shallow rooting patterns caused by shallow soil depths or prolonged saturated conditions described above produces various architectural adaptations, including greater occurrence of stilt and aerial roots, a greater proportion of coarse roots, asymmetrical extensions of the soil root plate, and increased sprouting from fallen logs (Gill, 1969; Soethe *et al.*, 2006, 2007). On the other hand, it may well be disadvantageous for trees to be tall and highly productive in such wet and windy environments. Increased height and canopy growth will result in increased wind stress and in enhanced capture of cloud water and wind-driven rain (and thus wetter soils?), which might ultimately be counter-productive. Future research on the causes of cloud forest stunting should also take into account the ecological costs of forest productivity.

CLOUD FORESTS AND CLIMATE CHANGE

During the “anthropocene” (Crutzen and Stoermer, 2000) most of Earth’s ecosystems – cloud forests included – have become subject to sustained human impact. This raises a number of

In summary, regardless of elevation, reduced forest stature on wet tropical mountains is typically associated with persistently wet and shallow soils, reduced rooting depth, reduced nitrogen availability, and possibly enhanced soil toxicity. Wind and steep topography constitute additional stress factors at exposed locations. The forests respond to these adverse soil conditions by investing much more carbon in below-ground biomass (i.e. the root system) at the expense of above-ground biomass, and to a lesser extent in the production of harder, thicker, and longer-lasting leaves.

important questions with regard to the impacts of climate change on cloud forest biodiversity and the ecosystem services that these forests provide. These questions include:

- Where and how are different types of TMCF expected to be affected by climatic drying (reduction in precipitation or cloud frequency)?
- What ecosystem component or functions are most affected by climatic change?

Observed and projected climate change for cloud forests

Before the above questions can be answered it is helpful first to look at climate change scenarios for cloud forests. Based on preliminary modeling for selected cloud forest sites, Still *et al.* (1999) and Foster (2001) concluded that climate change resulting from anthropogenic greenhouse gas emissions will significantly affect the temperature and humidity of cloud forest environments worldwide. Similarly, both observational (e.g. Pounds *et al.*, 1999; Barradas *et al.*, this volume) and experimental evidence is on the increase that montane areas carrying cloud forest may warm up locally as a result of deforestation in adjacent lowlands (Lawton *et al.*, 2001; Van der Molen, 2002; Ray *et al.*, 2006; Nair *et al.*, this volume). Scatena (1998) interpreted the presence of isolated stands of large and very old (>600 years) Colorado trees (*Cyrilla racemiflora*) in the Luquillo Mountains of eastern Puerto Rico at elevations well below the current cloud base that experience comparatively lower rainfall (<3000 mm year⁻¹) as evidence of a gradual upward shift in vegetation zonation over the past several centuries. *Cyrilla* is currently a dominant tree in areas above the cloud base (>600 m.a.s.l.) and is most common where mean annual rainfall exceeds 4000 mm. Similarly, Brown *et al.* (1996) reported the occurrence of pockets of mossy cloud forest below the current average cloud base in Honduras. According to the temperature lapse rates prevailing on most tropical mountains (0.5–0.65 °C per 100 m rise in elevation), a projected rise in temperature of 3 °C would imply a rise in cloud-base level of 450–600 m (Foster, 2001).

Since cloud forest environments are defined by the presence of ground-level cloud (i.e. fog), the rises in cloud-base levels implied by global or regional warming (Foster, 2001; Foster, this volume) can be expected to have profound impacts upon many aspects of the cloud forest ecosystem, ranging from changes in biological diversity (Pounds *et al.*, 1999; Nadkarni and Solano, 2002; Williams *et al.*, 2003; Colwell *et al.*, 2008) to changes in ecological (Raich *et al.*, 1997; Aiba *et al.*, this volume) and, possibly, hydrological functioning (Hemp, 2005b; Ponette *et al.*, 2009; Hemp, this volume #58;). Generally speaking, because of the fragmented nature of TMCF distributions and their occurrence along narrow elevational bands in heterogeneous mountain landscapes (Vázquez-García, 1995; Scatena *et al.*, this volume), cloud forests must be considered highly vulnerable to both local and regional climate change (Mulligan, this volume; Nair *et al.*, this volume). This is true both in terms of the very real possibility of “mountain-top extinctions” (where summit ecotones are driven out of existence upon lifting of the cloud base), and in terms of spatial discontinuities between current and projected elevational ranges for groups of species (Williams *et al.*, 2003; Colwell *et al.*, 2008). In addition, due to their often exposed locations (Jarvis and Mulligan, this volume), cloud forests in areas affected by hurricane passage (notably the Caribbean, Central America, East Asia, North Queensland, and the southwestern Pacific; cf. Scatena *et al.*, 2005) may become subjected to increasingly frequent or intense disturbance by tropical cyclones due to the global warming of the oceans, although the topic is still a matter of much debate (e.g. Emanuel, 2005; Webster *et al.*, 2005; McBride *et al.*, 2006; cf. Mann *et al.*, 2007).

Because of the lack of precise information on the location of (different types of) cloud forests, there has been little research to date looking at the potential impacts of climate change on cloud forests as a whole and which areas are more likely to be impacted than others (cf. Still *et al.*, 1999; Foster, 2001; Williams *et al.*, 2007). Mulligan and Burke (2005a) used the modeled distributions of cloud-affected forest (CAF) discussed in Chapter 2 to analyze both historically observed and future projected climate change in areas with CAF (cf. Mulligan, this volume) and their hydrological impacts. Mulligan and Burke first used the climatic data-set of New *et al.* (2000) to examine whether a change was detectable between the mean temperatures in areas with CAF for the periods 1901–1946 and 1947–1993. The observed change was a cooling of around 1 °C over all CAF except those in the southern Andes, in contrast to the warming observed for tropical lowlands over the same period. This cooling may be insignificant or could be the result of reduced nocturnal cloud cover leading to lower night-time temperatures. The pattern for historic rainfall change in areas with CAF as derived by Mulligan and Burke (2005a) was less clear, with some areas indicating stationarity, others drying and yet others wetting. In almost all cases the observed changes were modest and within 20% of the 1901–1993 mean rainfall.

Cloud frequency is perhaps the most significant climate variable for cloud-affected forest. To assess changes in cloud cover, Mulligan and Burke (2005a) used the HIRS cloud climatology data-set of the University of Wisconsin (cf. Jin *et al.*, 1996) – which at that time spanned a period of 22 years (1979–2001). They extracted annual cloud frequency data for all areas with known cloud forest according to the UNEP–WCMC database (Aldrich *et al.*, 1997b) and calculated the change in the frequency of clear-sky (i.e. no cloud) observations between the periods 1979–1990 and 1991–2001. The results indicated a decrease in the number of clear days (i.e. an increase in cloudiness) for cloud forests near the equator, and the reverse (decreased cloudiness) for the 10–20° latitudinal belts to the north and south. Observed cloud frequency declined particularly over cloud forest areas in South-East Asia whereas in Latin America there was a decline in Mexico, Central America, and northern Colombia, and an increase in cloud frequency in Perú and Bolivia. The maximum observed changes in cloud-free days were around 4% per decade.

Having found mixed signals of climate change in the limited historic data (a modest temperature decline, small-scale positive or negative changes in rainfall, and small-scale positive or negative changes in cloud frequency), Mulligan and Burke (2005a) examined the results of two different general circulation models (GCMs) – ECHAM5 and HADCM3 – using the SRES A2 CO₂ scenarios prepared for the Intergovernmental Panel on Climate Change Third Assessment Report published in 2001. The monthly gridded GCM data were split into two periods, 1950–2000 and 2000–2050, and mean values for temperature and rainfall were calculated for the two periods and then compared (see also Mulligan, this volume). HADCM3 predicted a mean global temperature increase of 3.3 °C between the two periods, with CAF seeing changes between +2 and +5 °C. The greatest temperature changes were derived for the most continental cloud forests (in the African interior), and the smallest for cloud forests on small islands (cf. Figure 2.14). A similar spatial pattern was predicted by ECHAM5 although the magnitude of the changes was somewhat less than those obtained with HADCM3 (cf. Figure 2.15). Given the typical elevational range of ~500 m observed for many tree species (Kappelle *et al.*, 1995b; Kitayama, 1995; Bach, 2004) and the often narrower ranges for a host of animals (cf. Williams *et al.*, 2003; Colwell *et al.*, 2008; Rovito *et al.*, 2009), such changes in temperature are bound to have major ecological consequences (see corresponding section below).

The GCM results for changes in rainfall were both more extreme and more uncertain than those for temperature, especially at the regional and sub-regional scale. Predicted changes in rainfall over cloud forest areas between 1950–2000 and 2000–2050 indicate a potential loss in rainfall (of 100 to 1000 mm year⁻¹ over the period) for some areas (e.g. Colombia, Mexico, Central Africa) and a potential gain in others (e.g. Perú, Madagascar, and the South-East Asian islands (+100 to

+1000 mm year⁻¹ over the period) according to HADCM3 (cf. Figure 2.16). Conversely, according to ECHAM5 almost all cloud forest areas will experience an increase in rainfall of a few hundred mm year⁻¹, with the exception of Madagascar, West Africa, and a few of the South-East Asian islands (cf. Figure 2.17). Thus, differences in predicted changes in rainfall between different GCMs are large but so are the expected magnitudes of change in relation to current mean rainfall (Mulligan and Burke, 2005a; cf. Mulligan, this volume).

IMPACTS OF CLIMATE CHANGE ON TMCF WATER BALANCE

Mulligan and Burke (2005a) developed a simple model to illustrate spatial and temporal patterns in water balance across the tropics (23.5° N – 35° S). The model has a spatial resolution of 1 km and operates at a monthly time-step. Grid-cell water balance is calculated as precipitation (including modeled contributions by wind-driven rain but not cloud water) minus potential evapotranspiration (*PET*). Using grids of current climate data, baseline conditions were simulated (see map in Mulligan and Burke, 2005a, p. 59) to allow preliminary evaluation of the spatial changes in monthly water budget as predicted by the model after applying the changes in temperature, solar radiation and rainfall projected by the ECHAM5 GCM for the period 2000–2050 (Figure 72.15).

The predicted impact of projected climate change on the water balance of cloud-affected forests is variable, with some areas having projected increased precipitation surplus (e.g. the Andes and Central Africa) whilst others show a significant drying (West Africa, Madagascar, South-East Asia, the Brazilian Atlantic cloud forests, and the CAFs of the Guyana shield; Figure 72.15). These results should be viewed as highly preliminary. First of all, because rainfall dominates the water balance signal, the simulated impacts are highly dependent on the rainfall projections of the GCM used. As shown in the previous section, these tend to differ between GCMs, both in terms of direction and magnitude. Moreover, the present simulations do not take into account the effect of seasonal changes in rates of glacial melting at higher elevations (cf. Kaser *et al.*, 2005; Juen *et al.*, 2007), nor the complex relationships between changes in lowland energy budget and upland cloud-base height (cf. Ray *et al.*, 2006; Van der Molen *et al.*, 2006; Nair *et al.*, this volume; Van der Molen *et al.*, this volume). However, Mulligan and Burke (2005a) considered the hydrological impacts of the applied rainfall change scenario to be more important than those simulated using a scenario for all observed forest conversion until 2001.

ECOLOGICAL IMPACTS OF CLIMATE CHANGE

Apart from any changes in water budget, climate change is also likely to affect cloud forest biodiversity (both in terms of abundance and elevational zonation), and ecological functioning.

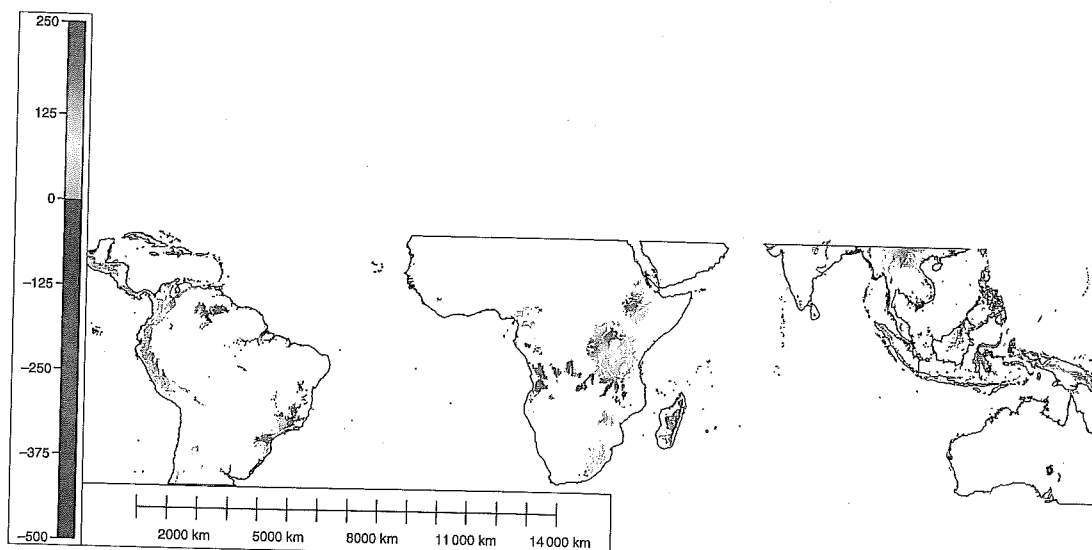


Figure 72.15. Impact of projected climate change (2000–2050) on the water balance (in mm year^{-1}) of cloud-affected forest areas across the tropics. (See also color plate.)

Whilst comparatively little is known as yet of such ecological effects, there are various signs on the wall that do not bode well. Nadkarni and Solano (2002) and Nadkarni (this volume) have documented the major changes in epiphyte and bryophyte diversity that may occur upon climatic drying or opening up of cloud forest canopies. Indeed, given their exposed position and dependence on rainfall and fog inputs and the nutrients contained therein (Hietz, this volume; cf. Chang *et al.*, this volume; Liu *et al.*, this volume), epiphytes and bryophytes in the upper parts of the canopy must be regarded particularly vulnerable to climatic drying (Zotz and Bader, 2009; cf. Lugo and Scatena, 1992; Colwell *et al.*, 2008; Köhler *et al.*, this volume) and their demise or disappearance is likely to change the canopy's cloud-water intercepting capacity in ways that are as yet not fully understood (cf. Chang *et al.*, this volume; Mulligan *et al.*, this volume #25; Tobón *et al.*, this volume #26).

Also, amphibian declines and extinctions have become a common feature in many habitats around the world, including protected TMCF reserves, suggesting that the phenomenon cannot be explained solely by localized habitat destruction (Stuart *et al.*, 2004; Rovito *et al.*, 2009; cf. Pineda and Halfpeter, 2004). At Monteverde (Costa Rica), for instance, a species of harlequin frog (*Atelopus* sp.) and the famous golden toad (*Bufo perigrinus*) have vanished due to pathogen outbreaks that have been linked to global warming (Pounds *et al.*, 2006). The agent is a pathogenic chytrid fungus which causes a skin disease amongst the frogs and toads, ultimately leading to mass extinctions (Pounds and Crump, 1994; Pounds *et al.*, 1999, 2006; Lips *et al.*, 2003). Similarly, Rovito *et al.* (2009) recently reported dramatic declines in salamander populations in UMCF in Mexico and Guatemala. The species in decline comprise several major evolutionary lineages of tropical salamanders, underscoring the

fact that significant portions of the phylogenetic diversity of Neotropical salamanders are at risk (Rovito *et al.*, 2009). Cloud forest frogs on other continents are also significantly threatened. For instance, the frog *Philautus poppiae*, a native of Sri Lankan closed canopy cloud forest, has been classified as Endangered on the IUCN *Red List of Threatened Species* due to the continued decline in the quality and extent of its habitat. As many as 19 Sri Lankan frog species have gone extinct so far. Apart from habitat loss caused by subsistence farming activities and logging, climatic drying and the use of agrochemicals in cardamom cultivation are considered additional causes. Apparently, no other country in the world has more documented amphibian extinctions, including a number of cloud forest frog species (IUCN, 2009). In short, given their often narrow elevational range of occurrence, cloud forest amphibians must be considered particularly sensitive to climate change (Williams *et al.*, 2003; Rovito *et al.*, 2009).

As for vertebrates, Williams *et al.* (2003) developed bioclimatic models of the current spatial distribution of regionally endemic vertebrates in the rain forests of northern Australia – a World Heritage Site and therefore well protected – to aid in the prediction of distributional changes after various degrees of climatic warming (examined range: 1–7 °C). Even after a 1-°C rise in temperature – a change that is considered inevitable in the next few decades – 63 out of the 65 considered species were predicted to experience significant changes in their distribution already, whereas species losses increased rapidly beyond a temperature increase of 2 °C due to the loss of “core environments.” It is pertinent to note that these distribution models only considered the effects of increasing temperature. Apart from the expected deleterious effects of a raised cloud base on amphibians as documented earlier for Monteverde (Pounds *et al.*, 1999, 2006),

Williams *et al.* (2003) also emphasized the increase in habitat fragmentation that tends to accompany a rise in cloud condensation levels in complex mountainous topography (and leading to separation of populations on different peaks). Last but not least, they identified a number of additional adverse effects on vertebrate diversity and distribution, including raised CO₂ levels rendering canopy tree leaves tougher to eat and less nutritional, thereby affecting endemic ringtail possums, tree kangaroos, and many insects; increasingly unpredictable rainfall affecting insectivorous and frugivorous bird populations, as well as changes in litter decomposition and mineralization rates affecting soil fauna and microbial activity and, ultimately, forest nutrient supply (cf. Benner *et al.*, this volume). On a related note, Boy *et al.* (2008) demonstrated increased nutrient loading of montane tropical forests due to biomass burning in (sometimes far away) lowlands (cf. Rollenbeck *et al.*, this volume).

Summarizing, whilst the extent of, and impacts on, cloud forest biodiversity, hydrology, and ecology of impending climate change are only poorly documented as yet, they are likely to be highly significant.

CLOUD FOREST CONSERVATION, MANAGEMENT, AND RESTORATION

Cloud forests face many threats, including exploitation for timber and other forest products, fragmentation, and conversion to other forms of land use – notably cattle ranching, cultivation of temperate vegetables, and coffee plantations (Amelung and Diehl, 1992; Etter and Van Wijngaarden, 2000; Brown and Kappelle, 2001; Cayuela *et al.*, 2006; Beck *et al.*, 2008a; Ponette-González *et al.*, 2009). In addition, there are the more subtle ecological changes associated with regional and global climate change (Scatena, 1998; Pounds *et al.*, 1999; Foster, 2001; Nadkarni and Solano, 2002; Williams *et al.*, 2003; Rovito *et al.*, 2009) and the increased risk of fire due to climatic drying (Asbjornsen and Garnica-Sánchez, this volume). Apart from direct clearing, several studies have shown that the construction of roads and power lines (Olander *et al.*, 1998; Beck *et al.*, 2008c) and the continued harvesting of fuelwood (Rüger *et al.*, 2008), as well as recreational visits (Honey, 2008) can all have long-term impacts on TMCF. In some areas, old-growth forest continues to be cleared to make way for pastures that replace other pastures suffering from decreasing productivity or invasion by bracken (Paulsch *et al.*, 2001; Hartig and Beck, 2003). In other areas, abandonment follows outmigration from rural areas to urban centers as a result of changes in economic conditions, thereby potentially favoring ecosystem recovery (Kappelle *et al.*, 1995a, 1996; Aide and Grau, 2004) and offering opportunities

for forest restoration (Holl and Kappelle, 1999; Grau *et al.*, 2003, 2008; Grau *et al.*, this volume).

The majority of the remaining TMCFs are only fragments of their original extent (Bubb *et al.*, 2004; Mulligan, this volume) whereas many of those that still exist continue to be exposed to the various threats listed above. It is widely recognized that, to be successful, any effort to conserve, manage, or restore TMCF needs to be both science-based and community-based (Hamilton *et al.*, 1995a; Aldrich *et al.*, 2000; Kappelle and Brown, 2001; Báez *et al.*, this volume; Hofstede *et al.*, this volume). Thus, science should guide conservation strategies and tactics to achieve sustainable cloud forest use, and scientists should inform land managers and the general public about such diverse themes as the impacts of regional and global climate change on cloud forests, how the environmental services provided by cloud forests can be valued, and how integrated planning of protected forest areas and surrounding land is to be organized most effectively.

This section discusses various key elements of cloud forest conservation and management for which research has produced relevant scientific knowledge in the past few decades.

Sustainable use and management of cloud forests

For centuries trees in the taller types of TMCF have been felled to be used in local construction, whereas fuelwood has been harvested both for subsistence and for commercial purposes (Kappelle and Brown, 2001). However, over the past few decades the concept of forest management has broadened significantly, evolving from the traditional focus on timber harvesting toward more sustainable practices reflecting changes in the societal perception of nature (Sheil and Lawrence, 2004; Wolf, 2005; Herrera and Chaverri, 2006). Indeed, modern society has come to recognize that tropical highland forests are not just a source of timber, but are also important, multifunctional ecosystems offering an array of non-timber forest products (NTFPs; Kappelle *et al.*, 2000; Wolf, 2005) as well as a variety of ecosystem services including high-quality water, carbon sequestration, biodiversity, and scenic beauty (Scatena, 1995; Calvo, 2000; Pagiola, 2002; Aylward, 2005; Barrantes Moreno, 2006). This new perception is reflected in current definitions of sustainable forest management (Herrera and Chaverri, 2006), which highlight the importance of managing permanent forest land without undue reduction of its inherent values and future productivity, and without undue undesirable effects on the biophysical and social environment (ITTO, 1992). Given the very slow growth rates of most upper montane and elfin cloud forests (Weaver and Murphy, 1990; Kappelle *et al.*, 1996; Raich *et al.*, 1997; Aiba *et al.*, 2005; Aiba *et al.*, this volume) and the generally excessively wet soil conditions prevailing in these forests (Bruijnzeel and Veneklaas, 1998; Roman *et al.*, this volume; Schawe *et al.*, this

volume), logging and timber extraction is not an option for this type of cloud forest (Scatena, 1995; Hamilton, 2005).

Reduced-impact logging (RIL) can help enhance juvenile recruitment and growth of economically important tree species in the more productive types of cloud forest and therefore should be considered when developing more sustainable silvicultural systems for TMCFs (Guariguata *et al.*, 2006; Günter *et al.*, 2008). Likewise, measures like RIL, the adoption of longer cutting cycles, and increasing the traditional minimum felling diameter generally leads to higher timber yields, reduced damage to the soil and the remaining stand, and improved conservation of biodiversity compared to standard logging techniques (Brünig, 1996; Cassells and Bruijnzeel, 2005; Günter *et al.*, 2008). However, although various silvicultural principles and approaches (e.g. improvement felling) are universally applicable, the sustainable management of highly diverse tropical montane forest ecosystems requires case-specific silvicultural approaches meeting local socio-economic, biophysical, and ecological conditions. In contrast to the situation for lowland evergreen rain forests rich in high-value timber species (such as the dipterocarp forests of South-East Asia), for which various nominally sustainable timber harvesting schemes have been developed (Brünig, 1996; Thang and Chappell, 2005) there is almost no knowledge on the ecological and economic viability of silvicultural systems in montane cloud forests which tend to have low numbers of large, harvestable trees (cf. Guariguata *et al.*, 2006; Günter *et al.*, 2008). The first results obtained during a recently initiated comprehensive study of the silvicultural and ecological consequences of light selective logging in an Ecuadorian LMCF suggested no significant changes in the overall diversity of various animal groups, although changes were observed at the level of population structure and species composition (Günter *et al.*, 2008). Günter *et al.* (2008) concluded that ecologically sustainable management of Neotropical montane forest is possible as long as the disturbance intensity is kept low (i.e. few gaps of modest size) and provided the disturbed areas are embedded within a matrix of undisturbed forest to allow recruitment and recovery of the affected taxa. Epiphytes on trees located in the vicinity of newly created gaps showed a reduction in the number and size of new leaves during the first year after the disturbance, suggesting a response to gap creation. However, variability within disturbed and non-disturbed experimental groups was very high and results sometimes differed in direction as well (Günter *et al.*, 2008). In view of the slow growth rates of many epiphytes, much longer observation periods are required to demonstrate the eventual effects of selected logging on epiphyte assemblages (Barthlott *et al.*, 2001; cf. Gradstein, 2008).

In a related context, Wolf and colleagues assessed the possibility of harvesting ornamental epiphytes (bromeliads) in the Highlands of Chiapas, Mexico, in an ecologically sustainable manner as an alternative to traditional, destructive wood

extraction (Wolf and Konings, 2001; Wolf and Flamenco-Sandoval, 2006; Wolf, this volume). Field observations demonstrated that *Tillandsia vicentina* plants need c. 5 years to develop from seed to a commercially viable size of 20 cm, allowing for a 4-year rotational harvesting scheme with an annual harvest from the lower forest stratum of c. 700 epiphytic rosettes (Wolf, this volume). These results have since been used to help define criteria for sustainable bromeliad harvesting in the cloud forests of Chiapas, thereby improving overall forest management by indigenous communities in the area.

Sustainable forest management must take into consideration the main threats affecting the forest's viability. Amongst these, fire is typically not perceived as a key threat to TMCFs since these forests' regular immersion in cloud would theoretically render them fire-resistant, although charcoal fragments found in various cloud forest soils indicate that fire may have occurred in the past during times of exceptional drought (Wård *et al.*, this volume). However, recent widespread fires in south-eastern Mexico have shown that the ecological integrity of modern-day TMCF in seasonal climates may very well be at risk as wildfires may become more frequent and severe due to climatic drying (Asbjornsen and Garnica-Sánchez, this volume; cf. Mulligan, this volume). The chapter by Asbjornsen and Garnica-Sánchez assesses the technical and organizational aspects involved in suppressing the severe wildfires that occurred in Mexican cloud forests during the 1998 El Niño Southern Oscillation (ENSO). In doing so, they highlight some valuable lessons learned about fire-suppression techniques during extreme fire behavior (including persistent below-ground fires) and suggest that the integration of local community-based and external government-based fire management approaches is critical to achieve effective forest protection and fire suppression (Asbjornsen and Garnica-Sánchez, this volume).

Where and what are the priorities for cloud forest conservation?

As indicated previously in the section on biodiversity, many cloud forest sites occur in six of the most important biodiversity hot spots around the globe (Myers *et al.*, 2000) – viz. the Tropical Andes and Atlantic Forests in South America, the Caribbean Islands, the Eastern Afro-montane peaks, the Asian Sundaland (including the mountains of Borneo), and the Polynesia–Micronesia hot spot that includes the islands of Fiji, Hawai'i, and Tahiti. Cloud forests are also found in 18 of the 200 biologically most distinct "Ecoregions" of the planet (Olson and Dinerstein, 2002) which partly overlap with, and complement these six hot spot areas. Listed per biome, these include the following (cf. Figure 72.3):

- *Afrotropical*: Cameroon Highland forests, Albertine Rift montane forests, Eastern Arc montane forests;
- *Australasian*: New Guinea montane forests;

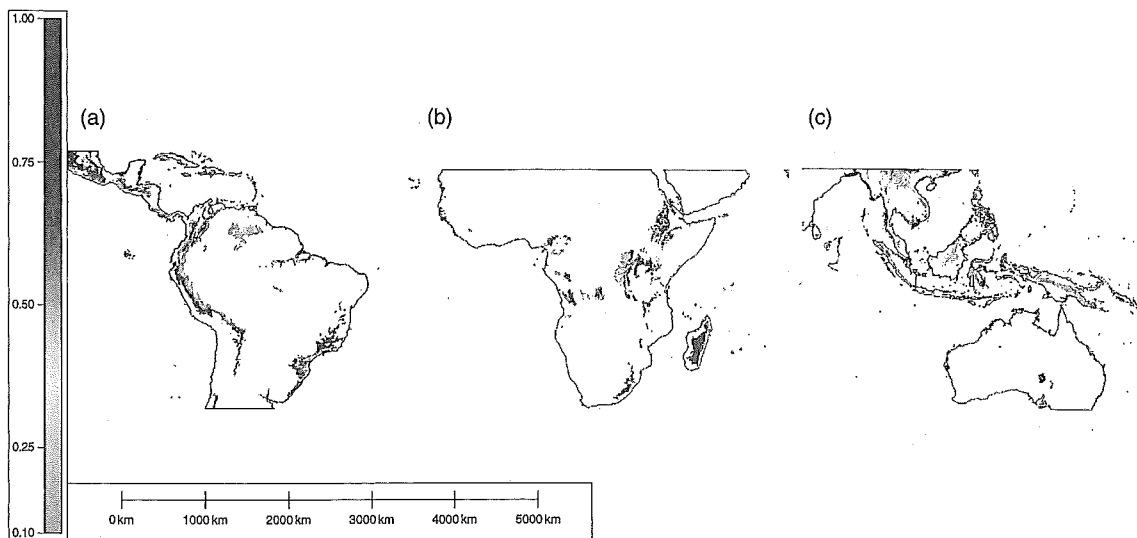


Figure 72.16. Fractional cloud-forest loss according to MODIS_VCF satellite product for (a) Latin America, (b) Africa, and (c) South-East Asia. The darker the shade of red, the greater the forest loss. Red: > 60% forest loss, green < 25% forest loss. (Reproduced from Figure 2.13; See also color plate.)

- *Indo-Malayan*: montane forests in Sumatra and surrounding islands, Peninsular Malaysia, and Borneo, and the montane forests of West Java;
- *Neotropical*: Greater and Lesser Antillean moist forests, Talamancan–Isthmian Pacific forests, northern Andean montane forests, coastal Venezuelan montane forests, Guayana Highland moist forests, Central Andean Yungas, Brazilian Atlantic forests (*Mata Atlantica*); and
- *Oceania*: South Pacific Island forests, and Hawaiian moist forests.

The hydro-climatically based distribution of cloud-affected forest (CAF) derived by Mulligan (this volume) may be combined with the *World Database on Protected Areas* (WDPA Consortium, 2004) to examine the conservation status and priorities of CAF in more spatial detail than is possible on the basis of the general hot spot areas cited above. Similarly, by comparing hydro-climatically based potential and current distributions of CAF, estimates and spatial patterns of cloud forest loss may be obtained (see Mulligan and Burke (2005a) and Mulligan (this volume) for details).

Mulligan's assessment suggests a total cloud forest loss to date of 2.72 Mkm² (or 55% of the originally estimated cover of 4.93 Mkm²). By comparison, application of the same methodology indicates that 47% of all tropical forests have been lost (Mulligan and Burke, 2005b). Extensive loss is inferred to have occurred throughout Latin America, with intensive losses in much of Mexico, the Colombian western and central Cordilleras, western Ecuador, Perú and Bolivia, and the Brazilian Atlantic forests. The most intact remaining Latin American CAFs are found on the eastern flanks of the Andes and in southern Venezuela (Figures 72.2 and 72.16). Significant inferred losses in Africa

Summarizing, more than half of the original cover of CAF has been converted to other land uses and some countries have very little of their original cloud forest remaining. The largest and most intact areas of CAF are found in southern Venezuela, eastern Democratic Republic of Congo, and maritime South-East Asia (Borneo, Celebes, Irian Jaya, and Papua New Guinea). Losses can be expected to continue in all areas with CAF but particularly in those that have shown rapid loss to date.

are concentrated in Madagascar, Ethiopia and Eritrea, South Africa, Uganda, Kenya and Tanzania. In South-East Asia, the most extensive losses are inferred for Indonesia, southern China, Laos and Vietnam (cf. Table 2.7 and Figure 72.16).

Comparing the current extent and distribution of cloud-affected and non-cloud-affected forests with those of Protected Areas (WDPA Consortium, 2004) suggests that 10% (or 1.57 Mkm²) of the tropical *tree-covered* area (15.64 Mkm²) is at least nominally protected, compared with 14.7% (0.38 Mkm²) of the forest area classified as CAF (2.21 Mkm²). Thus, protected CAF makes up ~9% of the total tropical tree-covered area and almost one-fourth (24%) of the total protected tropical tree-covered area (Mulligan, this volume).

A number of Protected Areas contain mostly cloud forest, particularly in Venezuela, Costa Rica, the Philippines, Madagascar, Vietnam, Laos, Cameroon, and Indonesia. The largest individual protected cloud forests are found in Venezuela, Indonesia, and Colombia (see Mulligan and Burke, 2005b for details). To indicate which Protected Areas with CAF are particularly threatened, a ranking was made of the absolute and relative losses of CAF.

Protected Areas with the greatest *proportion* of deforested land formerly under CAF occur throughout Central America and the Caribbean, as well as in Thailand and Indonesia. Protected Areas that have lost the greatest *absolute* areas of CAF are largely located in more continental settings, where one also finds some of the largest Protected Areas and the largest areas CAF (cf. Table 2.8; see Mulligan (this volume) for a discussion of the limitations of the analysis with respect to results obtained for individual sites).

Finally, by examining on a national basis, countries that have significant areas of CAF outside of Protected Areas (as listed in WPDA Consortium, 2004) it is possible to identify areas with further potential for (and likely need of) cloud forest protection. Countries with the largest absolute areas of unprotected CAF include the Democratic Republic of Congo, Brazil, Indonesia, Perú, and Colombia. Similarly, those with the greatest proportion of their CAF unprotected include Laos, Burundi, Papua New Guinea, Taiwan, Honduras, and Ecuador (see Table 2.9 in Mulligan (this volume) for details). In these countries, conservation of CAF assumes particular importance. The same holds for countries where very small areas of remaining and unprotected CAF represent the sole refuge for threatened endemic species. Examples include the Comoros, Eritrea, and Cambodia.

Last, but certainly not least, the host of wild varieties of agricultural crop species found in CAF are of particular interest to society and their source areas require adequate protection to ensure the preservation of gene pools needed for continued improvement of agricultural crops (Debouck and Libreros Ferla, 1995; McNeely and Scherr, 2003; Bubb *et al.*, 2004). Examples from Latin American CAFs include avocado, bean, blackberry, papaya, passion fruit, pepper, potato, sweet cucumber, tomato, and tree tomato (Brown and Kappelle, 2001).

Regeneration and restoration of cloud forests

With the exception of some early work on cloud forest regeneration after disturbance by hurricanes (Weaver, 1986, 1999; cf. Bellingham, 1991) or roadside clearing (Ewel, 1980), most research on the regeneration and restoration of TMCFs is comparatively recent and limited to only a few locations (e.g. Cavelier, 1995; Kappelle *et al.*, 1995a, 1996; Olander *et al.*, 1998; González-Espinosa *et al.*, 2008; Günter *et al.*, 2008, 2009; Martínez *et al.*, 2008; Aide *et al.*, this volume). Whilst the leaf area of regenerating cloud forest stands tends to approach values observed for old-growth forests after 10–15 years (Gomez-Cárdenas, 2009; Hölscher *et al.*, this volume), full recovery in terms of forest structure and terrestrial flora may take up to a century for UMCF at altitudes of 2500 m.a.s.l. and higher, even if seed sources are near (Kappelle *et al.*, 1995a, 1996). Recovery of epiphyte biomass and diversity may well

take much longer, although data on which to base such estimates are few (Van Dunné and Kappelle, 1998; Dunn, 2000; Holz and Gradstein, 2005b; Gradstein, 2008; Hölscher *et al.*, this volume; Köhler *et al.*, this volume; Krömer and Gradstein, this volume). Similarly, under the adverse climatic and soil conditions prevailing in most upper montane, elfin, and sub-alpine cloud forests, growth – and therefore regeneration – is inherently slow (Weaver and Murphy, 1990; Ráich *et al.*, 1997; Aiba *et al.*, 2005). Based on 18 years of observations of forest succession after an airplane crashed into low-elevation ECF in Puerto Rico, Weaver (1990) estimated that full recovery of the original biomass might take at least 200 years. Olander *et al.* (1998) considered a period of 200–300 years to be necessary for disturbed roadsides within the same forest type to return to near-original conditions. Again, the more stunted and wetter types of cloud forest should thus be treaded upon as lightly as possible (cf. Scatena, 1995; Hamilton, 2005).

Forest recovery on some abandoned crop fields and pastures – particularly after repeated use of fire during the period of agricultural usage – may be hampered severely by bracken fern or similarly fire-resistant grasses, particularly on slopes of low gradients where the bracken fern tends to shade out other species. The effect is less pronounced on steep, exposed slopes where wind-dispersed shrub species manage to germinate underneath the ferns, creating a successional mosaic of dense patches of bracken interspersed with low bush (Kappelle *et al.*, 1994; Hartig and Beck, 2003; Beck *et al.*, 2008c). Invasion by such fire-resistant species creates a so-called “resilient degraded system” in which forest recovery is essentially inhibited by positive feedbacks maintaining the degraded state (Hobbs and Norton, 1996; Suding *et al.*, 2004; Aide *et al.*, this volume). For example, the grass *Melinis minutiflora* invades recently burnt land and its resinous and highly flammable leaves tend to promote additional fires, thereby effectively inhibiting forest regeneration (D’Antonio and Vitousek, 1992; cf. Sarmiento, 1997; Cavelier *et al.*, 1998). Grau *et al.* (this volume) suggest similar feedbacks to be important in north-western Argentina where resilient degraded grasslands are not invaded by cloud forest species even after land-use intensity decreases and rainfall conditions become favorable for tree establishment. In addition, seeds and fruits of many cloud forest tree species are predominantly dispersed by birds and bats which tend to avoid such extended tree-less landscapes (Wilms and Kappelle, 2006; Gomes *et al.*, 2008). Finally, as distance to any remnant patches of old-growth forest increases, chances of seed inputs are diminished accordingly (Cubifia and Aide, 2001; Günter *et al.*, 2006; Ten Hoopen and Kappelle, 2006; Weber *et al.*, 2008).

As for cloud forest *restoration*, few restoration projects have been conducted in TMCF as such, and conclusions have to be based primarily on studies conducted in tropical montane forests less affected by fog (Aide *et al.*, this volume). As stated above, competition with invasive grasses and ferns plus poor seed

dispersal appear to be the most important factors limiting natural cloud forest regeneration. To overcome these barriers, one of the most cost-effective ways to accelerate vegetation recovery is to promote the establishment of shrubs, which help to shade out invasive grasses and ferns and create more appropriate conditions for seedling growth. Although this strategy can reduce competition, additional tree planting will generally be required to recover a species composition similar to that of intact forest, because most forest species are rarely dispersed far from forest stands (Holl *et al.*, 2000; Günter *et al.*, 2006; Aide *et al.*, this volume). As such, tree planting – including enrichment planting – is generally regarded as the main restoration tool to catalyze native forest regeneration on degraded tropical lands (Parrotta *et al.*, 1997; Zimmerman *et al.*, 2000), including montane cloud forest settings (Holl *et al.*, 2000; Mosandl and Günter, 2008; Stimm *et al.*, 2008; Günter *et al.*, 2009; Williams-Linera *et al.*, this volume). However, current efforts are often based on mono-specific tree plantings and frequently involve fast-growing exotic species (notably pines and eucalypts) that may have various adverse environmental impacts (González-Espinosa *et al.*, 2008; see also discussion in Günter *et al.*, 2009).

Forest restoration studies in the cloud forest belt that have employed native tree species are comparatively rare, mostly because the ecological requirements of such species are still poorly known. However the use of indigenous tree species in restoration efforts is on the increase, because they are not only potentially better adapted to local site conditions but also better at fulfilling the needs of the local people (e.g. Wilms and Kappelle, 2006; González-Espinosa *et al.*, 2008; Stimm *et al.*, 2008; Weber *et al.*, 2008; Günter *et al.*, 2009; Williams-Linera *et al.*, this volume). Clearly, restoration efforts targeting degraded, human-dominated cloud forest landscapes are likely to be more successful if biophysical, ecological, and social criteria are combined with local ethno-biological knowledge and integrated in the project design (cf. Pohle, 2008; Günter *et al.*, 2009; Báez *et al.*, this volume).

In Mexico and elsewhere, a major challenge to cloud forest restoration efforts is the large spatial diversity in micro-environmental conditions, species composition, and structure (Williams-Linera, 2002; Williams-Linera *et al.*, 2005; González-Espinosa *et al.*, 2008; cf. Günter *et al.*, 2009). Tree seedling planting experiments in Mexican cloud-affected forest interiors, adjacent agricultural fields, and old-fields indicated that the performance of different tree species depends on site disturbance level. Some species appear to have the potential to be used effectively in restoration of disturbed areas and others in plantation enrichment efforts; another sub-set of species may be used to expand the cloud forest area, and yet others can survive and grow in forests other than those in which they are naturally present (Williams-Linera *et al.*, this volume). These findings strengthen the point made by Holl *et al.* (2003) that the great site-to-site variability in tropical

Summarizing, it is clear that compared with many other ecosystems, cloud forests take much longer to recover and are much more costly to restore. As such, cloud forests (particularly the more stunted and wetter variants) should be treaded upon as lightly as possible.

montane cloud forests may also be viewed as an asset rather than merely as a constraint to ecological restoration at the landscape level. Different tree species respond differently to different site characteristics, thereby enhancing floristic heterogeneity.

Maintaining the ecosystem services provided by cloud forests

Arguably, among the many demonstrated “ecosystem services” that cloud forested headwaters provide to humans, the most important in economic terms are a stable supply of high-quality water that may be used for downstream irrigation, drinking water, industry, or hydropower generation (Scatena, 1995; Aylward, 2005; Barrantes Moreno, 2006; cf. Rhodes *et al.*, this volume #45) – and their unique biodiversity with its considerable ecological (e.g. regional crop pollination; Ricketts *et al.*, 2004), pharmaceutical (e.g. Kappelle *et al.*, 2000; Setzer *et al.*, 2003), and ecotourism potential (Honey, 2008). The taller and more productive types of cloud-affected forest (mostly LMCF) also provide timber (Guariguata *et al.*, 2006; Herrera and Chaverri, 2006; Günter *et al.*, 2008), fuelwood (e.g. Rüger *et al.*, 2008), and various non-timber forest products, such as honey, ornamental plants, game, etc. (Doumenge *et al.*, 1995; Kappelle *et al.*, 2000; Bubb *et al.*, 2004; Shiel and Lawrence, 2004; Wolf, 2005; Báez *et al.*, this volume; Wolf, this volume).

The presence of cloud forest is widely assumed to increase streamflow volumes because of the extra amounts of water captured from passing clouds, beyond that provided by regular precipitation (cf. Zadroga, 1981; Calvo, 1986; Bubb *et al.*, 2004). In addition, the forest helps to reduce the number of shallow landslides and prevents surface erosion, thereby maintaining better water quality (Sidle *et al.*, 2006; cf. Bruijnzeel, 2004). Such considerations lie at the heart of many Payment for Ecosystem Services (PES) schemes in which downstream users pay a certain fee for (mostly hydrological) services rendered by montane cloud forests as compensation to upstream forest owners for conserving their forests instead of converting them to economically more profitable land uses (Pagiola, 2002; Rodrigues-Zuñiga, 2003). Numerous PES schemes have been initiated in recent years in upland settings containing cloud forest, mostly in Central and South America (reviewed by Porras *et al.*, 2008; cf. Tognetti *et al.*, this volume).

Whilst potentially a powerful tool to help conserve threatened upland forests, current PES schemes tend to be based on

generalized beliefs with respect to the hydrological role of forests in general, and of cloud forests in particular. In addition, monitoring activities are often confined to changes in land use only, whereas hydrological monitoring efforts (if any) are rarely of sufficient rigor and duration to allow solid conclusions to be drawn with respect to the hydrologic effectiveness of the scheme (Porrás *et al.*, 2008; Le Tellier *et al.*, 2009). As discussed earlier in this chapter, the few available site-specific studies of the hydrological impacts of cloud forest conversion to pasture have yielded contradictory results. Flows increased in one case (eastern Mexico) but decreased in another (Pacific Northwest of USA), whereas no change was observed under particularly wet conditions (Costa Rica). Given the difficulties associated with predicting the impact of cloud forest conversion on watershed hydrological behavior it will not come as a great surprise to learn that few, if any, PES initiatives have actually been able to demonstrate a measurable hydrological effect of their activities (Rojas and Aylward, 2003; Porrás *et al.*, 2008; Le Tellier *et al.*, 2009). This may well have consequences for buyers and influence their continued willingness to pay (Aylward, 2005; Muñoz-Piña *et al.*, 2008; Porrás *et al.*, 2008; Tognetti *et al.*, this volume).

A related problem concerns the difficulty of adequately quantifying – in economic and social terms – the various environmental services provided by cloud forests (Scatena, 1995; Aylward, 2005; Barrantes Moreno, 2006; Porrás, 2008); additional challenges relate to the long time periods needed to build sufficient trust between service buyers and providers (Asquith *et al.*, 2008), securing equitable access to (and avoiding conflict about) ecosystem services amongst different groups of stakeholders, and establishing the proper institutional arrangements for the payments (see Tognetti *et al.*, this volume for a fuller discussion). Arguably, each situation is more or less unique and requires tailor-made arrangements (cf. Asquith and Wunder, 2008).

Nevertheless, Calvo-Alvarado *et al.* (this volume) describe the creation of the institutional, legal, and operational capacities that were required for the successful development and implementation of the nationwide PES scheme in Costa Rica, along with the development of a domestic water market benefiting many farmers with small- and medium-sized holdings who are willing to conserve the forest on their land (see also Pagiola, 2008; Porrás, 2008). Calvo-Alvarado *et al.* are convinced that the Costa Rican accomplishments can be repeated in other Meso-American countries, with appropriate adjustments to fit other ecological, social, and political situations. However, because the economic value of hydrological ecosystem benefits alone are unlikely to cover all conservation needs, a truly integrated multiple-services approach is needed (Tognetti *et al.*, this volume).

In this regard, ecotourism appears to be a particularly promising additional “service” that cloud forests may offer to local populations (Kappelle and Brown, 2001), as long as the limited

carrying capacity of these often fragile sites is taken duly into account (Honey, 2008; cf. Scatena, 1995). The famous Monteverde Cloud Forest Preserve in northern Costa Rica (10 500 ha), for example, received around 3100 ecotourists annually in the early 1980s, a number that increased to ~50 000 in the early 1990s, and exceeded 200 000 by 2005 (Honey, 2008). Whilst such numbers are indeed excessive and not representative of the situation encountered at the majority of cloud forest sites, they do illustrate the need to limit the influx of visitors and the excessive use of local resources. Only in this way will it be possible to achieve a form of sustainable ecotourism that contemplates socially equitable and ecologically sustainable economic development (Lindbergh and Hawkins, 1993; Honey, 2008). It goes without saying that local communities should be involved at all stages of planning and implementing cloud forest ecotourism and conservation efforts (Lindbergh and Hawkins, 1993; Bubb *et al.*, 2004; Shiel and Lawrence, 2004; cf. Báez *et al.*, this volume; Hofstede *et al.*, this volume).

Summarizing, whilst Payment for Ecosystem Services (PES) schemes – in which such key services as a stable freshwater supply from montane cloud forests are valued in monetary terms – constitute a potentially powerful tool to help conserve these forests, demonstrating the hydrological effectiveness and economic sustainability of PES schemes remains a major challenge. The most suitable arrangements are likely to vary from place to place in response to the local biophysical, social, and economic situation.

OUTLOOK

Global cloud forest conservation efforts

Although the hydrological and biological importance of cloud forests – as well as the recognition that these unique forests are seriously at risk of disappearing altogether – has been realized for decades (e.g. Daugherty, 1973; LaBastille and Pool, 1978), global efforts to promote the conservation and sustainable use of montane cloud forests were initiated comparatively recently only (Hamilton, 1995; Aldrich *et al.*, 1997a,b). The Mountain Cloud Forest Initiative was established in 1999 as a collaborative effort by the UNEP–World Conservation Monitoring Centre (WCMC), the World-Wide Fund for Nature (WWF International), the World Conservation Union (IUCN), and UNESCO’s International Hydrological Programme (IHP) (Aldrich *et al.*, 2000), extending and consolidating IUCN’s earlier *Campaign for Cloud Forests* (Hamilton, 1995). The Initiative envisioned a world in which mountain communities and downstream users value and protect cloud forests for their unique plant and animal species, and for their role in supplying clean water; and in which the

global community recognizes the value of cloud forests as sensitive indicators of global climate change (Aldrich *et al.*, 2000). As a first step toward this long-term goal the Initiative paid particular attention to raising awareness about the existence and uniqueness of cloud forests, the important services they provide to humanity, and the various threats that imperil their continued existence in various parts of the world (Aldrich *et al.*, 1997a, 2000; Bruijnzeel and Hamilton, 2000). In doing so, the Initiative directed its efforts primarily to organizations active in tropical forest conservation, management, and research, to policy- and decision-makers in countries with cloud forests, and to the international environment and development community, urging for immediate action. In 2004, the Initiative produced a *Cloud Forest Agenda* which focused on the integration of cloud forest conservation and sustainable livelihoods for the populations living in and around cloud forests (Bubb *et al.*, 2004). Whilst currently no longer active, it is probably fair to say that the Initiative has played a significant role in raising global awareness of the importance of, and threats faced by TMCFs, as manifested by their inclusion in various recent UN Conventions on Biological Diversity (e.g. SCBD, 2003a,b,c, 2004). In addition, the publication of several alarming findings in high-impact scientific journals in recent years was followed by much publicity and debate, adding further general awareness of the threats faced by cloud forests. Examples include the massive decline in numbers of many species of amphibians, and of the extinction of several others (Pounds *et al.*, 1999, 2006), and the fact that lowland deforestation may well impact cloud formation in adjacent uplands carrying cloud forests (Lawton *et al.*, 2001).

On a related note, following the proclamation of the International Year of the Mountains in 2002, a series of actions to promote sustainable mountain development were undertaken by the UN Convention on Biological Diversity (CBD), including the adoption of a Programme of Work on Mountain Biological Diversity (PoW-MBD) and the recommendation to include a host of other international agreements and bodies, institutions, and program initiatives in the PoW-MBD (SCBD, 2004). The latter include (amongst others): the Ramsar Convention on Wetlands of International Importance, the UN Framework Convention on Climate Change (UNFCCC), the UN Food and Agriculture Organization (FAO), UNESCO, the International Centre for Integrated Mountain Development (ICIMOD), the International Partnership for Sustainable Development in Mountain Regions, the International Human Dimensions Programme on Global Environmental Change (IHDP), the Centre for Mountain Studies, the *Consortio para el Desarrollo de la Ecoregion Andina* (CONDESAN), the Mountain Research Initiative (MRI), the Global Mountain Biodiversity Assessment (GMBA), the International Union of Forest Research Organizations (IUFRO), the Alpine Convention, and UNEP's World Conservation Monitoring Centre (UNEP-WCMC) (SCBD, 2004). To this long list can be added the UN

Intergovernmental Forum on Forests (IFF), which stated recently that "*mountain cloud forests are of particular concern*" with respect to soil and watershed protection and the conservation of biological diversity in environmentally critical areas.

Furthermore, within the context of cloud forest research and conservation, the GMBA under the auspices of DIVERSITAS is of particular interest (Körner and Spehn, 2002; Spehn *et al.*, 2006). The GMBA serves as a cross-cutting network that actively seeks to explore and explain the great biological richness of the mountains of the world –with an emphasis on cloud forests, amongst others in the Andes and the south-eastern Himalayas (cf. Wangda and Ohsawa, this volume). It also provides scientific inputs to policy-makers and various stakeholder groups involved in the conservation and sustainable use of biodiversity in mountain regions. Synthesizing often hidden and fragmented results of research on mountain biodiversity is one of the initiative's key activities (Spehn *et al.*, 2006). A similar global initiative to stimulate and link cloud forest hydrological research is lacking.

Research for the advancement of cloud forest conservation and sustainable use

The information contained in the many chapters of this book is clear evidence that knowledge of cloud forest environments, biodiversity, soils, productivity, and hydrological functioning has greatly increased since the 1993 Puerto Rico cloud forest symposium. We not only have a much better idea now of where cloud-affected forests (CAFs) may be found (based on an analysis of satellite imagery of cloud frequency across the tropics; Figure 72.2) but also where the largest contingent areas of CAF still exist, what the proportional losses are in different regions (Figure 72.16), and where significant areas of CAF are not included as yet in any protected area system (Mulligan, this volume). In addition, global analyses of vascular plant diversity (Figure 72.4), and pan-tropical comparisons of species richness and level of endemism in CAF for amphibians, mammals, and (Neotropical) birds (Figures 72.5–72.7) all point to the existence of a number of well-defined biodiversity hot spots that include significant amounts of CAF (Figure 72.3).

Knowledge of the hydro-meteorology of different types of cloud forest has equally increased in recent years. Whilst total evaporative losses (*ET*) from tall lower montane cloud forest (LMCF) do not appear to be significantly lower than those from lower montane rain forest (LMRF) not affected by fog and low cloud, *ET* from upper montane cloud forest (UMCF) of intermediate stature, and from stunted elfin cloud forest (ECF) in particular is significantly reduced (Figure 72.12). This, together with the higher rainfall observed at many ECF locations, produces significantly greater precipitation excess values – and therefore greater degree of soil wetness and streamflow volumes – in areas with UMCF and ECF compared with LMRF and, to a lesser extent

LMCF. Average estimated increases in total annual water production (i.e. including possible underground flows not detected by stream gaging stations) for different types of cloud forest compared to LMRF range from ~300 mm in the case of LMCF, to ~900 mm for UMCF, and as much as ~2900 mm for ECF (cf. Appendix 72.3). Furthermore, amounts of net precipitation arriving at the forest floor (i.e. throughfall plus stemflow) increase steadily from LMRF to LMCF, UMCF, and ECF, with values for the latter two categories equaling or exceeding conventionally measured rainfall amounts (Figure 72.9 and Appendix 72.2) whereas soil water uptake (transpiration, E_t) decreases steadily for the respective forest types (Figure 72.12 and Appendix 72.3).

Our capacity to measure on-site fog deposition, interception of wind-driven fog and rain by the vegetation, and evaporative losses from cloud forests has improved enormously in recent years (see chapters in Parts III–V in this book; cf. Bruijnzeel, 2005; Holwerda, 2005; Frumau *et al.*, 2006a; McJanet *et al.*, 2007a,c; Beiderwieden *et al.*, 2008). In addition, the increased availability of remotely sensed information on topography, vegetation type, and surface characteristics (including reflection coefficient, leaf area index, surface temperature, etc.), as well as rainfall and cloud characteristics has greatly expanded the possibilities for modeling the spatial and temporal variations in hydrological processes (e.g. Walmsley *et al.*, 1996, 1999; Mulligan and Burke, 2005a,b; Mulligan, 2006a,b; Wu *et al.*, 2006; Welch *et al.*, 2008; Ray *et al.*, 2009; Lawton *et al.*, this volume). Arguably, what is needed now is the integration of on-site measurements of climate, hydrological processes, and streamflow volumes emanating from cloud forest headwater areas, with observations made by national networks in countries with cloud forest (e.g. García-García and Zarraluqui, 2008) and with spatially explicit model predictions (cf. Mulligan and Burke, 2005b; Bruijnzeel, 2006; Wu *et al.*, 2006).

The reduced stature and productivity of certain types of cloud forest – as well as their occurrence at lower elevations on small, isolated mountains compared to larger mountain chains (Figure 72.14) – has puzzled scientists for decades and numerous theories have been advanced over the years to explain the phenomenon. However, much has been learned in this regard too in recent years. Amongst others, there is a major shift in carbon allocation by the plants from above-ground biomass to below-ground biomass (i.e. roots) with elevation, i.e. going from LMRF to UMCF and ECF (Hertel and Leuschner, this volume). This implies, amongst others, that overall ecosystem productivity decreases much less with elevation than previously thought. Whilst foliar nutrient analysis in the more stunted cloud forest types and various fertilization experiments suggest certain nutrient deficiencies (notably for nitrogen; Benner *et al.*, this volume), the few available studies of cloud forest nutrient budgets all show that the trees take up only a mere fraction of the amounts of nutrients dissolved (and therefore readily

available) in net precipitation and leaf litter leachate (Bruijnzeel *et al.*, 1993; Hafkenscheid, 2000). This suggests that the roots have difficulty to make full use of available nutrients. Although the precise mechanism is still being debated (Benner *et al.*, this volume), it is clear that the persistently wet to saturated conditions prevailing in most if not all UMCF and ECF, cause strong reductions in soil aeration levels (Silver *et al.*, 1999) – which in turn have various ecophysiological consequences (Santiago *et al.*, 2000; Santiago *et al.*, this volume) and affect rates of decomposition (Schoor, 2001). In addition, opportunities for exploitation of mineral soil horizons by the roots are strongly reduced in waterlogged soils (Soethe *et al.*, 2006). Finally, nitrogen availability has been shown to be much improved upon aeration (Cavelier *et al.*, 2000; cf. Marrs *et al.*, 1988; Schoor and Matson, 2001). An added stressor at many exposed ridge-top and summit locations is the persistence of high winds (Lawton, 1982).

On the downside, there is still considerable uncertainty about the hydrological consequences of converting (different types of) cloud forest to pasture or vegetable cropping. In some cases an increase in flows has been inferred, in others a decrease, and in yet another case no change was found. There are no rules of thumb in this regard, although the greatest effect would be expected where inputs from wind-driven fog and rain during the dry season are highest and where contrasts in evaporative losses from forest and pasture are largest. More site-specific work is needed. Likewise, there is great uncertainty about the magnitude and even the direction of changes in rainfall associated with climatic warming (Mulligan, this volume), and therefore about the potential hydrological (cf. Figure 72.15) and ecological consequences. Finally, although information on the carbon dynamics and productivity of various types of cloud forest is on the increase (Weaver and Murphy, 1990; Raich, 1998; Röderstein *et al.*, 2005; Moser *et al.*, 2007; Hertel and Leuschner, this volume), overall carbon budgets in different types of cloud forests have not been quantified as yet (cf. Schoor *et al.*, 2001).

Sutherland *et al.* (2009) presented a list of 100 questions of importance to the conservation of global biological diversity, following a strict protocol involving over 750 individuals that generated almost 2300 questions which were shortlisted and refined by workshop participants representing 24 international organizations. On the basis of Sutherland *et al.*'s global list a sub-set of practical research questions was prepared,³ that, if answered, may be considered to contribute the most toward conserving and sustainably using the biological diversity of cloud forests in practice. These core questions relate to the following strategic themes: ecosystem function and services

³ Questions prepared by M. Kappelle.

(6 questions), climate change (9), protected areas (4), ecosystem management and restoration (6), and species management (6).

Ecosystem function and services

(1) Do critical thresholds exist at which the loss of cloud forest species diversity, or the loss of particular species, disrupts ecosystem functions and services, and how can these thresholds be predicted? (2) How can cloud forest biodiversity considerations be integrated into economic policies to reflect the monetary and non-monetary value of cloud forest biodiversity, ecosystem processes, goods, and services? (3) To what extent can (and need) cloud forest ecosystems be managed to increase protection of humans and biodiversity from extreme events (e.g. floods and droughts, hurricanes)? (4) How, where, and when has cloud forest biodiversity loss affected human welfare? (5) What strategies for distributing the material benefits derived from cloud forests most effectively foster environmental stewardship and the conservation of biological and hydrological values? (6) How can cloud forest protected area networks be designed so as to increase carbon storage benefits and help to mitigate climate impacts, with these benefits acting as possible incentives to further support conservation actions?

Climate change

(1) Which elements of cloud forest biodiversity, and in which locations, are most vulnerable to climate change, including extreme events (hurricanes, droughts, massive rainfall, and landsliding)? (2) How is the resilience of cloud forest ecosystems to climate change affected by local and regional human activities and interventions? (3) How will climate change, together with other environmental stressors, alter the distribution and prevalence of diseases of wild species (e.g. as in the case of the pathogenic chytrid fungus that affects frogs' health and survival)? (4) How will climate change affect the hydrological behavior of different types of cloud forest? (5) How might cloud forest biodiversity policies and management practices be modified and implemented to accommodate climate change? (6) How might emerging carbon markets affect cloud forest conservation through their impacts on the protection, management, and creation of cloud forest habitats? (7) What are the potential effects of feedbacks between climate change and cloud forest ecosystem dynamics (e.g., drought, forest dieback) on the effectiveness of policy measures to sequester carbon and protect biodiversity? (8) How much carbon is sequestered by cloud forest ecosystems, including their soils, and how can these lands be managed – and if necessary restored – to contribute most effectively to the mitigation of climate change? (9) How will climate change affect the distribution and impacts of climate-dependent disturbance regimes in cloud forests, such as forest fires and hurricanes?

Protected areas

(1) How effective are different types of protected areas (e.g. strict nature reserves, hunting reserves, and national parks) at conserving cloud forest biodiversity and providing ecosystem services? (2) What are the costs per hectare of cloud forest required to manage cloud forests effectively, and how do these vary with management category, geography, and levels of threats? (3) What are the costs and benefits of cloud forest protected areas in terms of human well-being, how are these distributed geographically, and how do they vary with governance, resource tenure arrangements, and site characteristics? (4) How does the management of cloud forest protected areas affect conservation beyond the boundaries of the protected area, such as through the displacement of human populations, hunting, etc.?

Ecosystem management and restoration

(1) What are the trade-offs for cloud forest biodiversity, stream-flow regime and water quality under different forest management systems, such as timber harvesting from natural forest or plantation forests? (2) What was the condition of cloud forest ecosystems before significant human disruption in different geographic areas, and how can this knowledge be used to improve current and future management? (3) What, and where, are the most significant opportunities for large-scale cloud forest ecosystem restoration that benefits both biodiversity and human well-being (including improved hydrological functioning)? (4) How can cloud forest ecosystem management systems be designed to better emulate natural processes, notably natural disturbance regimes (including fire), and to what extent does this improve cloud forest conservation effectiveness? (5) What is the contribution of cloud forest areas that are intensively managed for production of commodities (such as food, timber, etc.) to conservation of cloud forest biodiversity at the landscape scale? (6) Under what circumstances can afforestation, reforestation, and reduced emissions from deforestation and degradation (REDD) benefit cloud forest biodiversity conservation, reduce emissions, and help to achieve more sustainable livelihoods?

Species management

(1) Under what conditions is trade in captive or wild-harvested cloud forest species beneficial for wild populations of the traded species? (2) What is the relative effectiveness of different methods for facilitating movement of a cloud forest species between disjunct patches of its habitat? (3) What is the cost-effectiveness of different contributions to cloud forest species conservation programs such as education, captive breeding, and habitat management? (4) What are the ecosystem benefits of efforts to conserve charismatic, flagship, or umbrella cloud forest

species? (5) What are the likely risks, costs, and benefits of reintroducing or translocating cloud forest species as a response to climate change? (6) What are the most effective approaches for reversing range and population collapse in top predators (e.g. large cats), large herbivores (e.g. tapirs), and other species that exert disproportionate effects on cloud forest ecosystem structure and function?

CONCLUDING REMARKS

With populations and pressure on the land on the increase in many tropical montane areas, the wet, windy, and steep environments characterizing mossy forests often no longer provide the *de facto* protection they did historically (Mosandl *et al.*, 2008). Climate change aside, cloud forests continue to be seriously at risk and may even disappear completely during this century if no major conservation action is taken in the coming decades (Bubb *et al.*, 2004; Mulligan, this volume). The many underlying issues such as poverty, insecurity of land ownership, failed forest policies, and the lack of effective law enforcement continue to challenge our globalized society. As a result, montane forest clearing, accelerated soil erosion and landslips, as well as disruptions of the hydrological regime, and, ultimately, species extinction will continue to take place.

Fortunately, awareness of the importance and value of cloud forests has increased considerably in recent decades, both amongst people living in and near cloud forests and at national and global levels. There is now a better understanding of the importance of cloud forests in terms of the various environmental goods and services they provide, such as biodiversity, recreation and tourism, protection against soil erosion, and perhaps most importantly, the stable hydrological flow regimes that are indispensable for agricultural crop irrigation, hydro-electric power generation, and drinking water for downstream populations.

In addition, during the last 50 years an increasing number of tropical montane cloud forest sites have received some kind of protected area status, ranging from multiple-use protected landscapes and forest reserves, to restricted-use national parks and absolute reserves. However, if one is to preserve a large part of cloud forest variety of life in the long term, a conservation strategy will be needed that not only goes beyond the current networks of protected core areas, buffer zones, and corridors, but also considers the implications of climate change for the future elevational range of cloud forest occurrence. This will require a concerted, global effort with focused local action, in which government agencies, local authorities, scientists, NGOs, private enterprises, and civil society all work together, to develop and implement strategies that halt the threats of invasive species,

deforestation, and fragmentation, and so ensure that cloud forests can continue to serve both nature and humankind in the long run. An essential element of such an effort is the institutionalized participation of all relevant stakeholder groups in the decision-making process at all levels of scale and, where necessary, across borders, so as to establish a broad-based, consensus-oriented conservation framework. Such consensus is a prerequisite for long-term conservation and sustainable forest use, for it is the recognition and valuation of the overall set of environmental goods and services offered by cloud forests to local, regional, and even global communities which will make their preservation and wise management an economic necessity, socio-politically feasible, culturally rewarding, and ecologically balanced. It is hoped that the contents of this book will inspire readers to contribute to this goal.

APPENDIX 72.1 BIOGEOGRAPHIC PATTERNS OF BIODIVERSITY IN CLOUD-AFFECTED FORESTS: BACKGROUND INFORMATION

Range data available for threatened amphibians (IUCN *et al.*, 2008a), birds of the western hemisphere (Ridgely *et al.*, 2007) and mammals (IUCN *et al.*, 2008b) were used as a means of understanding the relative biological importance of cloud forests for biological conservation and the potential geographic variation in biological importance across the known cloud forests. The data-sets were developed through an extensive process of scientific contribution and review coordinated by the World Conservation Union (IUCN), Conservation International, and NatureServe (for amphibians); by IUCN, Conservation International, Arizona State University, Texas A&M University, University of Rome, University of Virginia, and the Zoological Society London (for mammals); and by NatureServe in collaboration with Robert Ridgely, James Zook, The Nature Conservancy's Migratory Bird Program, Conservation International-CABS, World Wildlife Fund-US, and Environment Canada (for birds).

Ranges were determined by interpolation of occurrence between known locations if the ecological conditions seemed appropriate, but not allowing extrapolation beyond known locations. Some species may therefore occur more widely than has been mapped so that some regions are recorded as having lower diversity (and higher endemism) than may actually be the case. Also, for parts of the world that remain poorly known the current data-sets miss any species that are as yet undiscovered. Nevertheless, these are some of the best available data for pan-tropical assessment of cloud forest biodiversity.

Appendix 72.2 Throughfall (*TF*), stemflow (*SF*) and *apparent* rainfall interception (*E_i*) fractions as measured in different types of tropical montane rain forest.

Location and forest type	Elevation (m.a.s.l.)	Mean annual precipitation (mm)	LAI/H –/(m)	Epiphyte biomass (t ha ⁻¹)	<i>TF</i>	<i>SF</i> (% of <i>P</i>)	<i>E_i</i>	Remarks
<i>Montane rain forests little affected by fog</i>								
Bolivia, Yungas ¹	1850	2310	–/20	–	79	–	<21	10 roving gages, 3 mo, weekly
Colombia, Cordillera Central ²	1700	3150	–/35	–	76	–	<24	6 roving gages, 15 mo, weekly
	1950	2200	–/35	–	85	–	<15	Idem
Ecuador ³	1950	2320	7.3/25	–	67	1.1	32	Transect 2 only; 15–36 fixed gages, 36 mo, weekly
Idem ⁴	1960	2080	–/27	13.4	71	–	<29	31 fixed gages, 12 mo, weekly
Costa Rica, Monteverde ⁵	1200	2500	3.5/29	26.0	72	–	<28	5 fixed gages, 12 mo, biweekly
Costa Rica, Talamanca ⁶	2900	2810	7.7/35	2.96	70	2.0	28	UMRF, 30 fixed gages, 46 weeks, weekly
Guatemala ⁷	2100	2500	–	–	65	–	<35	36 fixed gages, 44 weeks, weekly; <i>P</i> likely overestimated since measured at 2550 m; forest grading into LMCF
Indonesia (Sulawesi) ⁸	1042	2900	6.4/23	–	70	0.3	30	Site NF4, 30 fixed gages, 15–17 events
Malaysia, Peninsular ⁹	1600	2300	–/14	–	62	2.2	36	20 roving gages, 68 weeks, 2–3 days
Panama ¹⁰	1200	3680	–/30	–	63	0.4	37	50 troughs (0.05 m ²), 12 mo, daily
Papua New Guinea ¹¹	2500	3800	5.5/30	2.0	67	<1	32	32 fixed gages, 8 mo, bi-weekly
Perú, Central Cordillera ¹²	2470	2220	2.9/20	–	70	0.1	30	20 troughs (0.1 m ²), 54 weeks, weekly
Tanzania, Usambara Mts. ¹³	1500	1230	–/35	2.1 ¹⁴	79	1	20	8 fixed gages, 30 mo, daily
<i>Lower montane cloud forests</i>								
Australia, SE Queensland ¹⁵	1000	1350	5.0/35	–	90	2	8	25 troughs, 31 mo, 2–3 weekly
Australia, N Qld, UB site ^{16,17}	1050	2985	4.1/25	–	79	8.8	12	4–6 troughs (2.4–3.6 m ²), 25 mo, continuous recording
Idem, Mt. Lewis site ^{16,17}	1100	3040	4.5/32	–	73	3	24	Idem, 23 mo
Bolivia, Yungas ¹	2600	3970	–/18	–	74	–	<26	10 roving gages, 3 mo, weekly, forest grading into UMCF
China, Yunnan, Ailao Mt. ¹⁸	2500	1930	5.8/25	1.4	87	2	11	12 fixed gages, 24 mo, 1–3×/day
Idem, Xishuang banna ¹⁹	750	1485	5.0/36	–	78	4.8	17	6 fixed collectors (0.6 m ²), 36 mo, event-based
Colombia, Central Cordillera ^{20,21}	2550	2115	–/23	–	87.5	–	12.5	20 fixed gages, 12 mo, weekly

Appendix 72.2 (cont.)

Location and forest type	Elevation (m.a.s.l.)	Mean annual precipitation (mm)	LAI/H —/(m)	Epiphyte biomass (t ha ⁻¹)	TF	SF (% of P)	E _i	Remarks
Costa Rica, Monteverde								
Windward forest ⁵	1200	6390	3.4/28	—	70	—	<30	5 fixed gages, 12 mo, biweekly
Leeward forest ^{22,5}	1500	2520	3.6/25	33	65	—	<35	20 fixed gages, 12 mo, 1–3 days
Costa Rica, Monte de los Olivos ²³								
Windward forest	1500	3300	—40	—	90.5	—	<9.5	20 troughs (0.1 m ²), 12 mo, daily
Idem	1500	3300	—/25	—	106	—	—7	Idem
Ecuador ⁴	2030	2140	5.7/20	5.3	85	1	14	31 fixed gages, 12 mo, weekly
Idem ⁴	2175	2500	4.9/15	11.6	91	1	8	Idem
Guatemala ²⁴	2200	2600	—/—	—	81	<1	18	3–6 fixed collectors (0.22 m ²), 12 mo, 2×/week
(windward)								
Hawaii, Maui (leeward) ²⁵	1220	890	—/2.5	—	65	—	<35	4 fixed collectors (0.24 m ²), 6 mo, continuous recording
Honduras ²⁴	900–1400	>3500	—/—	—	95	—	<5	3–6 fixed collectors (0.22 m ²), 12 mo, 2×/week?
Indonesia (W Java) ²⁶	1750	3300	—/—	—	80	—	<20	4 collectors of 1 m ² , 12 mo, weekly
Mexico, Veracruz ²⁷	2100	3000	6.6/27	—	82.5	—	17	4 roving collectors (1.2 m ² each), 12 mo, continuous recording
Tanzania, Mt. Kilimanjaro ²⁸	2250	2480	—/40	—	82	<1	17	10 fixed gages, 12 mo, weekly
Idem, dry year		1960	—/40	—	70	<1	29	Idem
Thailand, Kog Ma ²⁹	1265	2085	4.0/25	—	89	1.5	9.5	30 fixed gages, 48 mo, daily
Venezuela, San Eusebio ³⁰	2300	1575	—/27	2.9	79.5	1	19.5	30 fixed gages, 12 mo, 1–2×/week
Venezuela, La Mucuy ³¹	2350	3125	2.9/25	—	54	0.2	46	6 fixed collectors (0.6 m ²), 12 mo, weekly
Upper montane cloud forests								
Australia, Queensland, BK ^{16,17}	1560	5300	3.3/8	—	117	14	—31	4–6 troughs (totaling 2.4–3.6 m ²), 21 mo, continuous recording
Colombia, Central Cordillera ³	3000	1700	—/—	—	89	—	<11	6 roving gages, 15 mo, weekly
Idem, Central Cordillera ^{20,21}	3370	1455	—/22	12.0	87.5	0.1	12.5	20 fixed gages, 12 mo, weekly
Idem, Zipaquirá ³²	3250	1615	3.6/15	—	89	2	9	20 roving gages, 24 mo, weekly
Costa Rica, Monteverde ^{5,33}	1500	4310	3.4/10	4.7	118	—	—18	5 fixed gages, 12 mo, biweekly
Idem ³⁴	1450	6000	3.0/22	16.2 ³⁵	108	1	—9	30 roving gages, 12 mo, daily ^a

Appendix 72.2 (*cont.*)

Location and forest type	Elevation (m.a.s.l.)	Mean annual precipitation (mm)	LAI/H —/(m)	Epiphyte biomass (t ha ⁻¹)	TF	SF (% of P)	E _i	Remarks
Guatemala ²⁴ (windward)	2400	2500	—/—	—	113	1	—14	3–6 fixed collectors (0.22 m ²), 12 mo, 2×/week
Guatemala ⁷ (windward)	2550	2600	—/—	—	88	1	11	36 fixed gages, 44 weeks, weekly
Hawaii ²⁵ (windward)	1950	2400	—/6	—	119	—	—19	4 fixed collectors (0.24 m ²), 9 mo, continuous recording
Honduras ³⁶	1795	1500	—/—	—				4 fixed collectors (0.25 m ²), 12 mo, daily
Concave slope					94	—	6	
Convex slope					129	—	—29	
Ridge top					179	—	—79	
Jamaica, PMull forest ³⁷	1810	2850	5.0/12	—	73	12	14	12 roving gages, 12 mo, 3–4 days; + 1 recording trough
Malaysia, Peninsular ⁹	2030	2115	—/7.5	—	64	30.5	5.5	20 roving gages, 68 weeks, weekly
Perú, Central Cordillera ¹²	2815	2750	2.5/14	—	92.5	<0.1	7.5	20 fixed collectors (0.115 m ²), 12 mo, weekly
Philippines, Luzon ³⁸	2200	3910	—/9	—	86	12	2	16 fixed collectors (0.041 m ²), 60 mo, daily
Puerto Rico Palm forest ³⁹	900	4500	4.6/11	—	69	26	5	20 roving collectors (0.0254 m ²), 6 months, daily
<i>Elfin and sub-alpine cloud forests</i>								
Bolivia, Yungas ¹	3050	5150	—/10	—	75	—	<25	10 roving gages, 3 mo, weekly
Hawaii ⁴⁰	2600	500	—/8	—	75	—	<25	2 fixed collectors (0.125 m ²), 12 mo, continuous recording
Jamaica, MMor Forest ^{37, 41}	1825	2855	4.1/8	2.8	60 ^b	18	22	12 roving gages, 12 mo, 3–4 days; + 1 recording trough
Puerto Rico, East Peak Elfin, windward ^{42,43}	1000	5400	2.0/ 2.5	7.4	115	5	—20	60 fixed collectors, 8 mo, daily
Idem, ridge	1015	4800	—/—	4.4	125	9.5	—35	Idem
Idem, leeward	930	6000	—/—	4.8	96	3	1	Idem
Idem, sheltered ⁴⁴	970	4500	2.1/3	(4.4)	108	(5)	—13	45 roving and 22 fixed gages, 97 d, twice/week; + 3 troughs (1.0 m ²)
Réunion, France ⁴⁵	2150	3000	—/3	—	124	—	—24	8 fixed gages, 8 mo, continuous
Spain, La Gomera ⁴⁶	1290	660	4.2/9	—	126	2.8	—29	2 fixed collectors (0.20 m ²), 19 mo, continuous

¹ Gerold *et al.* (2008).² Vis (1986).³ Fleischbein *et al.* (2006).⁴ Oesker *et al.* (this volume).⁵ Haeger and Dohrenbusch (this volume).

Appendix 72.2 (*cont.*)

- ⁶ Hoelscher *et al.* (2004).
- ⁷ Holder (2004).
- ⁸ Dietz *et al.* (2006).
- ⁹ Kumaran (2008).
- ¹⁰ Cavelier *et al.* (1997).
- ¹¹ Edwards (1982).
- ¹² Gomez-Peralta *et al.* (2008).
- ¹³ Lundgren and Lundgren (1979).
- ¹⁴ Pócs (1980).
- ¹⁵ Hutley *et al.* (1997).
- ¹⁶ McJannet *et al.* (2007a).
- ¹⁷ McJannet *et al.* (2007b).
- ¹⁸ Liu *et al.* (2002).
- ¹⁹ Liu *et al.* (2007).
- ²⁰ Veneklaas and van Ek (1990).
- ²¹ Veneklaas *et al.* (1990).
- ²² Clark *et al.* (1998).
- ²³ Fallas (2002).
- ²⁴ Brown *et al.* (1996).
- ²⁵ Giambelluca *et al.* (this volume).
- ²⁶ Gonggrijp (1941).
- ²⁷ Holwerda *et al.* (2009).
- ²⁸ Schrumpf *et al.* (this volume).
- ²⁹ Tanaka *et al.* (2005).
- ³⁰ Steinhardt (1979).
- ³¹ Ataroff and Rada (2000).
- ³² Tobón (2009).
- ³³ Nadkarni (1984).
- ³⁴ K. F. A. Frumau (personal communication).
- ³⁵ Köhler *et al.* (2007).
- ³⁶ Stadtmueller and Agudelo (1990).
- ³⁷ Hafkenscheid *et al.* (2002).
- ³⁸ Mamanteo and Veracion (1985).
- ³⁹ Holwerda (2005).
- ⁴⁰ Juvik and Nullet (1995b).
- ⁴¹ Tanner (1980).
- ⁴² Weaver (1972).
- ⁴³ Weaver *et al.* (1986).
- ⁴⁴ Holwerda *et al.* (this volume #29).
- ⁴⁵ Gabriel and Jauze (2008).
- ⁴⁶ García-Santos (2007).

^aAlthough classified as LMCF on the basis of forest stature alone, this forest is considered to behave as an UMCF due to very wet and windy conditions; relatively tall stature may be explained by well-drained volcanic soils despite excessive rainfall.

^bProbably underestimated.

Appendix 72.3 Transpiration (E_t), wet canopy (interception) evaporation (E_i), and total evapotranspiration (ET) as measured in different types of tropical rain forest

Location and forest type	Elevation (m.a.s.l.)	Mean annual precipitation (mm)	LAI ($m^2 m^{-2}$)	E_t (mm year $^{-1}$)	E_i (mm year $^{-1}$) ^a	ET (mm year $^{-1}$)	E_i/E_t (%)	E_i/R_n (—)	Setting/method for E_t or ET
<i>Lowland evergreen rain forest</i>									
Central Amazonia, Ducke ¹	80	2500	6.0	980	330	1310	25	0.59	Continental (C), micrometeo
Pasoh, Peninsular Malaysia ²	100	1800	6.5	1206	242	1448	17	0.69	Maritime (M), micrometeo
Lambir Hills, Sarawak ³	50	2740	6.2	946	357	1303	27	0.54	M, micrometeo
<i>Lower montane rain forest little affected by fog</i>									
Madagascar, Périnet ⁴	1010	2080			1295				M, watershed budget for ET
Colombia, Sierra Nevada ⁵	1150	1985			1265				Idem
Ecuador ⁶	1950	2050	7.3	626	655	1281			C, watershed budget for ET and E_t
Kenya, Kericho ⁷	2200	2130			1337				C, watershed budget for ET
Idem, sub-basin ⁷	2350	2015			1240				Idem
Kenya, Kimakia ⁸	2440	2305			1156				Idem
Tanzania, Mbeya ⁹	2500	1925			1381				Idem
<i>Lower montane cloud forest</i>									
Queensland, Gambubal ¹⁰	1000	1350	5.5	845	414	1259	33	—	C/M, sapflow, soil water budget
Idem, Upper Barron ¹¹	1050	2985	4.1	591	854	1445	59	0.37	M, sapflow
Idem, Mt. Lewis ¹¹	1100	3040	4.5	579	880	1459	60	0.42	M, sapflow
Hawai'i, Volcano NP ¹²	1219	2500	4.8	645	588 ¹³	1233	48	0.30	M, micrometeo
Indonesia, Java ¹⁴	1750	3300	—	510	660	1170	56	—	M, watershed budget for ET and E_t
Ecuador ^{15,16}	2030	2140	5.7	555	364	919	40	0.69	C, sapflow
Mexico, Veracruz ^{17,18}	2100	3100	6.6	876	542	1418	38	0.63	C/M, sapflow
Thailand, Kog-Ma ^{19,20}	1268	1768	4.0	626	530	812	46	0.46	C, sapflow and micrometeo
Venezuela, San Eusebio ²¹	2300	1465	—	675	305	980	31	0.44	C/M, energy and water budgets
Venezuela, La Mucuy ²²	2350	3125	2.9	558					C, porometry for E_t
<i>Upper montane cloud forest</i>									
Costa Rica, Monteverde ^{23,24}	1450	6000	3.0	361	415 ^b	776	53	0.36	M, micrometeo
Queensland, Bellenden Ker ¹¹	1560	7470	3.3	349	549	898	61	0.31	M, sapflow

Appendix 72.3 (cont.)

Location and forest type	Elevation (m.a.s.l.)	Mean annual precipitation (mm)	LAI (m ² m ⁻²)	E _t (mm year ⁻¹)	E _i (mm year ⁻¹) ^a	ET(mm year ⁻¹)	E _i /E _t (%)	E _i /R _n (-)	Setting/method for E _t or ET
Puerto Rico, Luquillo Mts. ²⁵	900	4450	4.6	484	190	674	28	0.44	M, micrometeo
<i>Elfin cloud forest</i>									
Puerto Rico, Luquillo Mts. ²⁵	1010	4500	2.1	296	268 ^b	564	47	0.27	M, micrometeo
La Gomera, Canary Islands ²⁶	1270	900	4.2	412	117	529	22	0.26	M, sapflow

¹ Shuttleworth (1988).² Tani *et al.* (2003).³ Kumagai *et al.* (2005).⁴ Bailly *et al.* (1974).⁵ Hermann (1971).⁶ Fleischbein *et al.* (2006).⁷ Blackie (1979a).⁸ Blackie (1979b).⁹ Edwards (1979).¹⁰ Hutley *et al.* (1997).¹¹ McJannet *et al.* (2007d).¹² Giambelluca *et al.* (2009).¹³ T. W. Giambelluca (personal communication).¹⁴ Gonggrijp (1941).¹⁵ Motzer *et al.* (this volume).¹⁶ Oesker *et al.* (this volume).¹⁷ Gomez-Cardenas (2009).¹⁸ Holwerda *et al.* (2009).¹⁹ Tanaka *et al.* (2003).²⁰ Tanaka *et al.* (this volume).²¹ Steinhardt (1979).²² Ataroff and Rada (2000).²³ Bruijnzeel (2006).²⁴ K.F.A. Frumau (personal communication).²⁵ Holwerda (2005).²⁶ García-Santos (2007).^a Based on wet-canopy water budget method.^b Wet variant of Penman-Monteith equation.

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