The potential negative impacts of global climate change on tropical montane cloud forests

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Abstract

Nearly every aspect of the cloud forest is affected by regular cloud immersion, from the hydrological cycle to the species of plants and animals within the forest. Since the altitude band of cloud formation on tropical mountains is limited, the tropical montane cloud forest occurs in fragmented strips and has been likened to island archipelagoes. This isolation and uniqueness promotes explosive speciation, exceptionally high endemism, and a great sensitivity to climate. Global climate change threatens all ecosystems through temperature and rainfall changes, with a typical estimate for altitude shifts in the climatic optimum for mountain ecotones of hundreds of meters by the time of CO₂ doubling. This alone suggests complete replacement of many of the narrow altitude range cloud forests by lower altitude ecosystems, as well as the expulsion of peak residing cloud forests into extinction. However, the cloud forest will also be affected by other climate changes, in particular changes in cloud formation. A number of global climate models suggest a reduction in low level cloudiness with the coming climate changes, and one site in particular, Monteverde, Costa Rica, appears to already be experiencing a reduction in cloud immersion.

The coming climate changes appear very likely to upset the current dynamic equilibrium of the cloud forest. Results will include biodiversity loss, altitude shifts in species’ ranges and subsequent community reshuffling, and possibly forest death. Difficulties for cloud forest species to survive in climate-induced migrations include no remaining location with a suitable climate, no pristine location to colonize, migration rates or establishment rates that cannot keep up with climate change rates and new species interactions. We review previous cloud forest species redistributions in the paleo-record in light of the coming changes.

The characteristic epiphytes of the cloud forest play an important role in the light, hydrological and nutrient cycles of the cloud forest and are especially sensitive to atmospheric climate change, especially humidity, as the epiphytes can occupy incredibly small eco-niches from the canopy to crooks to trunks. Even slight shifts in climate can cause wilting or death to the epiphyte community. Similarly, recent cloud forest animal redistributions, notably frog and lizard disappearances, may be driven by climate changes. Death of animals or epiphytes may have cascading effects on the cloud forest web of life.

Aside from changes in temperature, precipitation, and cloudiness, other climate changes may include increasing dry seasons, droughts, hurricanes and intense rain storms, all of which might increase damage to the cloud forest. Because cloud forest species occupy such small areas and tight ecological niches, they are not likely to colonize damaged regions. Fire, drought and plant invasions (especially non-native plants) are likely to increase the effects of any climate change damage in...
the cloud forest. As has frequently been suggested in the literature, all of the above factors combine to make the cloud forest a likely site for observing climate change effects in the near future. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: cloud forest; tropical montane cloud forest; climate change impacts; relative humidity; paleovegetation; epiphytes; cloud formation changes

1. Introduction

As one ascends in altitude up a tropical mountain, the trees typically decrease in stature and the leaves become smaller, harder and thicker (Whitmore, 1989). If the mountain intersects the cloud cap, these effects are magnified. Twisted stunted trees are encountered and the leaves become even more akin to desert xeromorphic leaves. The dwarfed trees in the cloud cap are laden with a heavy mass of epiphytes whose roots suspend in air and a new group of animal species distinct from below the cloud cap is encountered. The frequent mists add to the atmosphere and give this special ecosystem its most commonly known name—the cloud forest (Stadtmüller, 1987).

As the global climate changes, the hydrological cycle will undoubtedly change. Increasing sea surface temperatures will increase evaporation from the sea and pump more water into the tropospheric water cycle. At first glance, this may seem to lead to increasing clouds, but detailed studies have indicated a tendency for a decrease in low-level cloudiness that envelopes cloud forests (see Section 3.3). Long-term observations (Pounds et al., 1999) and preliminary modelling (Still et al., 1999; Foster, 2001) at the Monteverde Cloud Forest in Costa Rica suggest that the height of the cloudbank is already rising, resulting in less cloud immersion, and thus driving local extinctions through enhanced dryness.

Exactly how the cloud immersion impacts the forest is unknown, but certain effects are obvious—high relative humidity (RH) and reduced sunshine are two of the most important ones. The enhanced RH contributes to the large epiphyte mass, as the aerial plants capture water directly from the clouds or via enhanced condensation. In addition, a high RH explains the presence of so many kinds of unique amphibian species. However, the explanation of the stunted and twisted nature of the cloud forest trees

<table>
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<tr>
<th>Nomenclature:</th>
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<td><strong>Notation</strong></td>
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remains a puzzle. Many suggestions have been put forth but it remains unclear if any one of them explains all cloud forest attributes (Table 1).

This lack of understanding of the underlying mechanisms of cloud forest morphology make it difficult to predict what the impacts of climate change will be. A further difficulty lies in distinguishing between local climate changes and global ones. Changes in the global climate will cause changes in local circulation patterns. Furthermore, local climate is likely to be affected by local events such as deforestation or dam building. While local changes may be much stronger than global ones at a given site, generalizing about local changes is difficult. In order to mitigate against potentially hazardous changes at a given site, we must understand the different components contributing to the change. This review aims to elucidate the role of global changes on the tropical montane cloud forest.

### Table 1
Listing of some of the principle attributes of the cloud forest

<table>
<thead>
<tr>
<th>Climates Characteristics</th>
<th>Vegetation Characteristics</th>
<th>Slow Nutrient Uptake</th>
<th>Soil and Litter Different</th>
<th>Positive Water Balance</th>
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<tbody>
<tr>
<td>Frequent cloud presence</td>
<td>Abundance of epiphytes</td>
<td>Low transpiration</td>
<td>High organic content in soil</td>
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<tr>
<td>Usually high relative humidity</td>
<td>Stunted trees</td>
<td>Low photosynthesis rates (though capacity not reduced)</td>
<td>High concentration of polyphenols in litter</td>
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<tr>
<td>Low irradiance</td>
<td>Small, thick and hard leaves</td>
<td>Low nutrient uptake</td>
<td>Soils wet</td>
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<tr>
<td>Low Productivity</td>
<td>High endemism</td>
<td>Low sap flow</td>
<td>Additional moisture input from cloud stripping</td>
<td></td>
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<tr>
<td>Low NPP</td>
<td>Low LAI (although locally it can be very high)</td>
<td>Low transpiration</td>
<td>Stream flow/incident rainfall very high</td>
<td></td>
</tr>
<tr>
<td>Low LAI although locally it can be very high</td>
<td>Slow nutrient uptake</td>
<td>Low photosynthesis rates (though capacity not reduced)</td>
<td>Low evapotranspiration and evaporation</td>
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Threats to the cloud forest from global climate change include changes in air quality, hurricane frequency and duration, ultraviolet radiation, rainfall, and temperature (Hamilton et al., 1995b). We will not discuss direct CO2 or air quality impacts in this review (see Korner, 1994), but will address the other effects. This review draws extensively from previous reviews, including: a detailed overview of the cloud forest (Stadtmüller, 1987), the first Tropical Montane Cloud Forest symposium proceedings (Hamilton et al., 1995a, especially its articles on hydrology (Brujinzeel and Proctor, 1995), and plant distributions (Merlin and Juvik, 1995)), the 1998 special issue of Climatic Change (Markham, 1998) on climate change impacts on tropical forests (especially Benzing 1998 on epiphytes and Donnelly and Crump (1998) on amphibians), and an article on atmospheric change impacts on mountain ecosystems (Bensiton et al., 1997).

### 2. The cloud forest

#### 2.1. Characteristics of the cloud forest

##### 2.1.1. Nomenclature

A detailed account of the nomenclature used for cloud forests is given in Stadtmüller (1987), see also Hamilton et al. (1995b). Common names include: dwarf forest, elfin woodlands, mossy forest and montane rainforest or thicket in English; *nuboselva*, *bosque (montano) nubuloso*, and *selva nublada* in Spanish; *forêt néphéliphile* and *forêt de nuage* in French; and *Nebelwald* and *Wolkenwald* in German. For our purposes, the cloud forest will simply refer to forests whose characteristics are tied to the frequent presence of clouds and mist. There are various definitions that distinguish between fog and clouds. One definition defines fog as any cloud which touches the ground and thus one might argue that these forests should be called fog forests. However, other definitions that rely on droplet size or formation mechanisms favor the cloud forest appellation. We will use the common names cloud forest (CF) and tropical montane cloud forest (TMCF).

Several ways to subdivide cloud forests have been presented in the literature. Stadtmüller (1987) stressed the difference between CFs that occur in regions of
abundant rainfall and those that occur on arid mountainsides (Sugden and Robins, 1982a,b, 1983; Cavellier and Goldstein, 1989). The first can be difficult to distinguish from surrounding vegetation, whereas the second can be very distinct from its neighbors. Hamilton et al. (1995b) distinguished band and patch type forests based on their extent and concluded that they typically thrive in continental versus islands climates, respectively. For the purposes of climate change impacts, a classification scheme that includes all isolated cloud forests in one grouping and large band type forests in another will serve to highlight the greater sensitivity of the isolated cloud forests. The isolated CF, regardless of its cause of isolation —such as the Elfin or dwarf cloud forests, will be more sensitive to climate change by virtue of their small fragmented size, which leads to difficulties in relocation and repopulation. Similar to the isolated CF are the Lomas Formations on the western coast of Peru and Chile, where fog water contributions allow the development of ferns, gymnosperms and flowering plants, in an otherwise desert, almost plantless, environment (Follman, 1963; Dillon, 1997). The Lomas may well respond to climatic change in a manner similar to the cloud forests.

2.1.2. Ecotones

On moist tropical mountains, ecosystems grade from lowland rainforest (LRF) to lower montane rainforest (LMRF) to upper montane rainforest (UMRF) (Grubb et al., 1963). These zones are shown in Fig. 1. Grubb and Whitmore (1966) concluded that this zonation results from a gradation in cloud frequency, from negligible (LRF) to frequent (LMRF) to persistent cloudiness (UMRF). Cloud forests occur in LMRF or UMRF locations where cloud immer-

![Fig. 1. Ecotone zonation on tropical mountains. Typical gradation of mountain ecosystem types is shown. From the lowland rainforest (LRF) through the lower montane rainforest (LMRF) up to the upper montane rainforest (UMRF), tree stature decreases. Leaf size also decreases. In the presence of frequent cloudiness, the cloud forest (CF) can occur in either the LMRF or UMRF. Within the cloud forest, tree height and leaf size are even smaller than in standard forests at the same altitude. Accompanying the decrease in size in the CF, trees become twisted and gnarled and leaves become thick and hard. On exposed ridges and peaks these effects can be even more magnified and the crown of trees often assumes an umbrella-like shape. This subclass of cloud forest is sometimes referred to as an elfin forest.](image-url)
sion frequency is enhanced relative to its surroundings.

Following the ground contact of the clouds, the CF typically occurs in narrow altitude belts, and on ridges or mountain peaks, with species distributions that are akin to island archipelagos (Merlin and Juvik, 1995; Vazquez-Garcia, 1995). The altitude of cloud formation, and hence the cloud forest, shows considerable variation as it depends on the moisture content of the air, convective or advective cloud formation processes, the velocity and direction of the wind, the distance to the sea and macro and micro topographical effects. Nonetheless, a typical altitude for cloud forest on large, inland mountains is between 2000 and 3500 m. On coastal and isolated mountains, the cloud forest is found at lower elevations, roughly 1000 m in Hawaii and as low as 500 m in Micronesia and Fiji (Hamilton et al., 1995b). This compression of ecotones, or the Massenerhebung effect, occurs for other montane ecotones as well.

2.1.3. Vegetation characteristics

With increasing altitude, plant species change from lowland species to montane ones. Accompanying the species change, tree stature decreases with increasing altitude. For example, in monsoon Asia, the drop off in tree height can be quite step-like, dropping by a factor of ~ 2 from LRF to LMRF and again from LMRF to UMRF. Leaf sizes also decrease with altitude, ranging from mesophyllous in the LRF, to notophyllous in the LMRF and to microphyllous in UMRF (Ohsawa, 1995b). Epiphyte load tends to increase with altitude. In the cloud forest, these high altitude characteristics are enhanced. Furthermore, cloud forest trees are twisted, gnarled and often assume an umbrella-like crown. Trees are even more stunted on exposed ridges and peaks where many CFs thrive (Werner and Balasubramaniam, 1992; Werner, 1998). Leaves are thicker, harder and smaller than in surrounding vegetation. Epiphyte loads, diversity and endemism explode. Tree species from the Weinmannia family and tree ferns from the Cyatheaceae family (Merlin and Juvik, 1995) are common in the cloud forest worldwide.

2.1.4. Epiphytes

Epiphytes are a defining characteristic of cloud forests, where 1/4 of all plant species may be epiphytes. The following discussion will be most relevant to those CFs which are most abundant in epiphytes, such as the elvin or dwarf CFs. An astonishing percentage of the epiphytes in CFs are often endemic, especially within the isolated CFs (Young and León, 1991; Gentry, 1992; Hietz and Hietz-Seifert, 1995; Benzing, 1998). Thus, it is not surprising that epiphytes can have important roles and even dominate many of the cycles in the cloud forest, including (as summarized by Benzing, 1998) the following points:

(a) The light cycle: the leaf area index (LAI) rarely exceeds 20 in most humid tropical forest but can be as large as 150 on branches densely covered with epiphytes; productivity of epiphytes can exceed other flora.

(b) The water cycle (capture, storage and slow release): water capture by epiphytes via horizontal precipitation, HP or cloud stripping, is typically 5–20% of annual rainfall, although values exceeding 100% have been recorded. Epiphytes also store water (up to 50,000 liters/ha (Sugden, 1981; 3000 liters/ha Richardson et al., 2000) and provide water to canopy animals.

(c) The nutrient cycle (capture, storage and slow release): up to half the total input of NH4+ and NO3− and other important ions and nutrients to the forest can come from water stripped from passing clouds by epiphytes. Up to half the total nutrient pool of the canopy is sometimes found in the epiphytes and their associated humus. Richardson et al. (2000) also noted that of three forests studied, only in the dwarf forest did bromeliads achieve sufficient abundance to become significant in the litter nutrient cycle and to the total net primary productivity.

These factors alone argue for the importance of the health of epiphytes, not only for the life cycle of the canopy, but also in some cases for the ecosystem as a whole. Furthermore, epiphytes provide homes, nesting materials and food for a vast array of animal species, including invertebrates [(which make a considerable contribution to the food chain (Richardson et al., 2000)]], frogs and birds, and even some primates (Benzing, 1998).

Epiphytes can play a critical role in the health of the cloud forest, making their vulnerability to climate change an important issue. Evidence for their sensitive dependence on climate spans many scales. Along
mountain transects, specific epiphyte populations appear and disappear following saturation deficit transects (Benzing, 1998). The distribution of epiphyte families also follows the saturation deficit. The vascular epiphytes, including orchids, ferns and bromeliads, have some capacity to store water, whereas the nonvascular epiphytes do not. The nonvascular epiphytes, including mosses, lichens and liverworts, lack the simple epidermis of their vascular cousins such that they require almost constant high relative humidity. Therefore, their biomass distribution peaks at the altitude of minimum saturation deficit. This altitude is somewhat higher than the peak in vascular epiphytes’ biomass distribution, as higher altitudes have lower temperatures and hence tend to have higher relative humidity (Benzing, 1998).

Aside from altitude zonation, epiphyte species are localized within the cloud forest: some at the edge [cold mesic epiphytes] and some at the center (warmth loving epiphytes (Vazquez-Garcia, 1995)]. Both altitude and intra-forest zonation are found among terrestrial species as well, but the epiphytes show a further recognition of microhabitat distinction: different epiphytes occupy different locations on a tree, from crown, to stem base to knotholes (Hietz and Hietz-Seifert, 1995; Benzing, 1998). Our understanding of the photosynthetic process used by most epiphytes, which appear to be very temperature-sensitive, also supports the observational evidence for climate dependence (Benzing, 1998).

2.1.5. Endemism

The intense microhabitat specialization of epiphytes explains in part their exceptionally high endemism rate in the cloud forest. While tree species diversity generally decreases with altitude, epiphytic biomass increases dramatically within the cloud forest, often accompanied by increases in speciation and extremely high rates of endemism (León and Young, 1996). Indeed, the cloud forests along the base of the Northern Andes and adjacent Central America host the distributional center of epiphytic and herbaceous families, in contrast with the trees’ center which is within Amazonia (Gentry, 1992). The fragmented nature of the CF ecosystem also plays an important role leading to high levels of endemism, with some plants endemic to specific islands or countries or even specific mountain peaks (Raynor, 1995; Merlin and Juvik, 1995). Gentry estimates that endemism can occur in cloud forests as small as 5–10 km² (Gentry, 1986). In South American cloud forests, he estimates local endemism at 10–24%, suggesting that perhaps an entirely different evolutionary mode is operating in these areas (Gentry, 1992). If we are to conserve a broad array of plant species, it seems obvious that the cloud forest is a good place to start. In contrast to most cloud forests, one series of isolated cloud forests, which is surrounded by arid vegetation in South America, shows uncharacteristically low endemism that might suggest a recent origin (Sugden and Robins, 1983).

Animals also show high endemic rates within the cloud forest. Thirty percent of Peru’s endemic birds, mammals and anurans are found primarily in the cloud forest (Leo, 1995). A large-scale, global survey of restricted range birds found that over 20% of restricted range birds use the cloud forest extensively and many of these birds are endangered (see references in Long, 1995).

2.1.6. Soil

Montane slopes host a variety of soil types deriving from the abundance of parent rock types that are highly weathered from frequent rainfall and landslides. Steep slopes and weathering often results in very shallow soils and little horizon development. Furthermore, montane soils often, but not always, have low nitrogen values (Tanner et al., 1990) and low decomposition rates (Hafkenscheid, 2000) and references therein. These factors may lead to the characteristically low primary productivity of montane vegetation (Grubb, 1977), although high aluminum and organic carbon soil contents or low levels of sunlight might also be partly responsible (Grubb, 1977; Kitayama 1995; Bruijnzeel and Veneklaas, 1998; Werner, 1998, Section 2.2). Cloud forest soils are wet and frequently saturated, though rarely waterlogged. Bruijnzeel and Proctor (1995) concluded that of all the observations to date, no cloud forest soil ever showed a water deficit, even during a severe drought. However, at some point the soil water must run out and there has been at least one observation of CF canopy dieback in response to a drought (Werner, 1995).
The capacity of the soil and the epiphytes to absorb and store a great deal of water provides the important services of erosion and flood control as well as dry weather stream flow.

2.1.7. The role of temperature

Current models of ecotone movement rely mainly on average temperature and precipitation (Holdridge, 1947; Prentice et al., 1992; Neilson, 1995). Box’s (1995) model is more complex but still relies on correlations between the prevailing climate and eco-type. Plant responses to climate change may also depend on altered wind regimes, anthropogenic factors or even past forest states (Graumlich, 1994). For these reasons, models of ecotone movement must be based on mechanistic understanding of the climate vegetation relationship rather than correlations. This is particularly obvious when we consider that future climate states may have no analog in the present world.

Nonetheless, observations show that ecotones are strongly correlated with temperature. This is particularly true in eastern Asia, which has abundant rainfall throughout the year and in the absence of man’s influence would be entirely forested (Ohsawa, 1990, 1995a; Fang and Yoda, 1990a,b, 1991). The altitude limit of the forests in humid monsoon Asia appear to correlate quite strongly with a warmth index value of 15°C month (Ohsawa, 1990, 1993; WI = sum of all monthly temperatures exceeding 5°C). This result has been substantiated on the species level by Fang and Yoda (1990a,b), who found that the total averaged value of WI for six forest species at their altitude limit, at 12 different sites, was 15.2°C month (σ = 2.4). Finally, Kitayama (1995) concludes that the upper limit of the cloud forest on Mount Kinabalu in Sabah may be thermally controlled, with a cut-off of WI = 85°C month. In the absence of water stress, there appears to be evidence that forest ecotones are strongly temperature-controlled (Ohsawa, 1995a).

2.1.8. The role of clouds

In humid Southeast Asia, the frequent occurrence of fog has less impact on the vegetation and it can be difficult to pick out the cloud forest from the surrounding vegetation (Ohsawa, 1995b). However, elsewhere the hydrologic impact of frequent cloud cover can be drastic and substantial changes in vegetation occur over a relatively small shift in altitude across the boundary of frequent cloud occurrence (for examples, see Sugden and Robins, 1982a,b; Werner, 1986, 1998; Merlin and Juvik, 1995; Vazquez-Garcia, 1995; Young, 1998). The displacement of standard montane species and/or morphology by CF ones can be quite sharp, suggesting that cloud cover can indeed control floristic assemblages, especially of canopy species (Grubb and Whitmore, 1966; Smith et al., 1995; Kitayama, 1995). Grubb and Whitmore (1966) suggest that the altitude of cloud formation determines the distribution of not only the cloud forest but all tropical montane forests. Whether or not this is true, we know that the characteristic stunting and twisting of trees and small hard leaves of the cloud forest is linked to frequent cloud cover. How the clouds lead to these characteristics is unknown but many suggestions have been put forth, see Section 2.2.

2.1.9. Massenerhebung effect

The Massenerhebung effect is the often noted telescoping, or compression of vegetation zones, on small and coastal islands. It is especially strong for the cloud forest biome, whose lower boundary is typically 1500–2500 m (Stadtmüller, 1987), but drops to as low as 500 m on isolated coastal mountains (Merlin and Juvik, 1995). Lower cloud forest altitudes on island mountains are to be expected, somewhat, as the water vapor content of air at the foot of the island mountain will be higher than that over the large continental mountain range. Wetter air condenses at higher temperatures, and hence lower altitudes, than dry air, given equal lapse rates where $\Gamma = -\frac{dT}{dz}$ is the lapse rate, $T$ the temperature and $z$ the altitude. Further reducing the altitude of cloud formation on small isolated mountains is a steeper lapse rate relative to large mountains. This compresses the temperature profile on small mountains relative to large ones and increases the relative humidity at a given altitude, implying lower cloud formation on the smaller mountain (Hastenrath, 1991). Given steeper lapse rates on shorter mountains, the forest limit/temperature correlations discussed above will produce the telescoping effect. However, there is no evidence that the lapse rates on small mountains are steep enough to reproduce the
500–1000 m altitude differences. Furthermore, the shifting of vegetation zones is not always linear. For instance, in New Guinea, the UMRF appears to have been absent during the late Pleistocene, which would not be expected by a temperature gradient alone (Grubb and Whitmore, 1966, see also Section 7.2).

The WI-forest limit argument might possibly avoid these failings as it is computed with a non-linear sum of temperatures exceeding a certain limit, but it also fails to explain the distribution of all forest species in the moist forests of China (Fang and Yoda, 1990a,b). Flenley also argues that the lapse rate change–Massenerhebung effect connection is not satisfactory, as it does not explain the CF tree stunting. As discussed below, Flenley ties the stunting of cloud forest trees to excessive UV-B radiation. UV-B intensity increases with altitude and may be enhanced by reflection off cloud surfaces. He argues that it is possible that on island mountains, UV-B radiation is further enhanced by reflection off the sea surface, thus moving the CF location down slope (Flenley, 1995). For the cloud forest at any rate, the Massenerhebung effect is certainly tied to lower altitude cloud formation on shorter mountains.

2.2. The cause of CF morphology

Whatever the cause of stunting, one thing is clear: cloud forests are enveloped in clouds. Grubb and Whitmore’s (1966) suggestion that the frequency of cloud contact is the most important factor in limiting the stature of montane forest is continually reinforced by descriptive reports (Bruijnzeel and Veneklaas, 1998). Somehow, the frequent cloud cover is closely linked to the occurrence of short and twisted trees and xeromorphic leaves. Since wind commonly accompanies cloudiness, it might be responsible for some of the odd morphology (Merlin and Juvik, 1995; Werner, 1995). Other factors that accompany frequent cloud contact are: an extra hydrological input, a distinct chemical input, reductions in irradiance of 10–50% and persistent leaf wetness leading to a reduction of photosynthesis (Bruijnzeel and Veneklaas, 1998). Perhaps one of these effects leads to the odd morphology.

2.2.1. Polyphenols and UV-B radiation

In control experiments, plants that underwent enhanced UV-B radiation showed CF-like stunted growth and small thick leaves (see references in Flenley, 1992c). Under exposure to high UV-B, plants protect themselves by producing phenolic compounds, flavonoid and alkaloids, that absorb UV-B radiation. Fresh leaf litter on the floor of cloud forests shows high concentrations of polyphenols (Bruijnzeel and Proctor, 1995; Hafkenscheid, 2000). In turn, polyphenols may interfere with photosynthesis, cell division in fine roots, transpiration and ion uptake. While the photosynthetic capacity of the CF does not appear to be systematically lower than other forests, the net productivity of the CF is reduced. Two measures of productivity, above ground NPP (net primary productivity) and LAI (leaf area index), are markedly lower in the CF relative to other forests at comparable altitudes (Bruijnzeel and Veneklaas, 1998), although locally the LAI can be quite high (Benzing, 1998). Transpiration rates also appear to be reduced relative to lowland forests and nutrient uptake rates also operate at below their maximum capacity (Bruijnzeel and Proctor, 1995; Hafkenscheid, 2000). Other impacts of high polyphenol concentrations in the soil are slow decomposition (Kuiters, 1990) and the reduction of the impact of both aluminum toxicity (Hue et al., 1986) and low nitrogen concentrations (Northup et al., 1995) in the soil, all of which have been reported for a number of cloud forest soils (Hafkenscheid, 2000). The correlation of the presence of polyphenols, low productivity and uptake and stunted growth does suggest that polyphenols, perhaps driven by UV-B radiation, may play a significant role in stunting. But why the correlation with cloudiness? Furthermore, UV-B radiation only becomes sufficiently strong above 2500–3000 m to cause harm (Caldwell et al., 1980), well above the altitude of many cloud forests.

Several environmental characteristics of cloudy days may explain the enhancement of the UV-B effect in cloud forests. Low levels of visible light and abundant water tend to make plants more sensitive to enhanced UV-B radiation (Ziska et al., 1992). In addition, the common daily regime of cloud formation below the altitude of the cloud forest in the morning and enveloping clouds in the afternoon may increase the insolation of UV-B radiation in the morning through reflection and prevent visible light driven repairs in the afternoon, making the CF habitat particularly unacceptable to non-adapted plants.
(Flenley, 1992c). Thus, the UV-B hypothesis is consistent with the Massenerhebung effect and can also neatly explain the disappearance of the CF at some sites during the last glacial maximum (see Section 7.2). These, in combination with the explanation of CF tree stunting and the high concentration of pheno- lyps in the leaf litter, make the UV-B theory well worth further research.

2.2.2. Other stunting hypotheses

With high humidity and low insolation of the cloud forest, one expects to find moisture-loving leaves rather than leaves that resemble drought-re- sistant ones (Flenley, 1995). This oddity led to the suggestion that periodic water shortages caused the xeromorphic characteristics and stunted tree growth, but soil water shortages have never been observed in a cloud forest (Bruijnzeel and Proctor, 1995). On the other hand, CF soils are usually wet and this may lead to the observed low transpiration of plants by imped-ing root respiration, which in turn might cause the unusual morphologies to arise. Reduced nutrient uptake is generally seen in mountain sites (Körner, 1994) and is further reduced within the cloud forest, which correlates well with the general trend for stunting on mountains and its exaggerated mani- festation in cloud forests (Hafkenscheid, 2000). Bruijnzeel (1995) concludes that the answer lies somewhere within the soil and is perhaps linked to exposure to harmful UV-B radiation as discussed above.

Above the soil, another explanation for the twist- ing and stunting of trees is wind, which might ex- plain the exaggerated stunting found on exposed ridges and peaks (Merlin and Juvik, 1995; Werner, 1995). Another hypothesis is that low leaf tempera- tures may cause stunting since temperature decreases with increasing altitude and is further reduced under cloud cover. However, Bruijnzeel et al. (1993) showed that temperature depression was not the cause of stunting on Gunung Silam. Neither temperature depression nor wind obviously explain the disappearance of the CF in New Guinea during the Late Pleistocene (Flenley, 1992b, Section 7.2), although a separate cause or a complex chain of effects might be responsible for this effect. Given the many characteristics of the cloud forest, different factors may be responsible for different aspects and manifesta-

3. Possible climate changes with relevance to the cloud forest

3.1. High altitude sites

Projecting climate change on tropical mountain sites is fraught with difficulties. Current global climate models, GCMs, do not model current day mountain climates well because they do not resolve the topography, which is particularly important for capturing precipitation and cloudiness. Further, not enough detail is known about mountain climates to adequately test current mountain climate simulations. This lack of basic understanding stems from a paucity of climate data, little theoretical attention to mountain climatology and the complexity of mountain weather (Barry, 1994). This ignorance is particularly dangerous in light of the fact that higher altitude sites may be affected by climate change even more strongly than lowland sites. This arises because as the climate warms, more water will be pumped into the atmosphere and the lapse rate is expected to decrease—approaching the saturated lapse rate. If this occurs, high altitude sites will be less cold relative to the surface ($T = -dT/dz$ is decreasing) than they were in the cooler climate, i.e. high altitude sites will warm more than lower altitude sites. Tropical montane temperature records (Bensiton et al., 1997), the retreat of tropical glaciers (Schubert, 1992; Hastenrath and Kruss, 1992), ice core temperature records (Thompson et al., 1993), and freezing heights (Bensiton et al., 1997) strongly suggest that tropical high elevation sites may already be showing this enhanced warming (Bensiton et al., 1997). However, recent results show that although the tropical lapse rate decreased prior to 1979, since then it has shown a slight increase. Furthermore, while glaciers continue to retreat, tropical freezing levels have lowered in the 1980s and 1990s (Gaffen et al., 2000). Many of these changes appear to be linked to sea surface temperature changes, although the recent in-
crease in lapse rates does not appear to be (see Section 3.3).

3.2. Increases in water stress and intense events

The moisture available to an ecosystem affects both the kind and the amount of the vegetation that will grow (Woodward, 1987). The soil serves as an important water reservoir for terrestrial plants for non-rainy days, dry seasons and droughts. Climate change will likely change the balance of current water tables by increasing loss through evaporation, via higher temperatures, and by changing rainfall inputs. Few studies have focused on climate change impacts on the hydrological cycle in the tropics; but one study, the Hulme and Viner analysis of the UK Met Office’s GCM, shows increasing water stress in many tropical regions. They find decreasing soil moisture throughout the tropics (although they caution that this result is crude). Furthermore, with the exception of east and northeast Africa through the Middle East and into monsoon India, the length of the dry season in the tropics increased. The same regions also showed a decrease in the relative humidity field when averaged over four other GCMs (see Section 3.3). These predictions suggest increasing water stress, which if it occurs will cause damage to trees and epiphytes, implying more fire and drought. Fire and drought tend to degrade tropical forests to grasses, bushes and fire-tolerant trees, such as Pinus (Goldammer and Price, 1998).

Hulme and Viner’s analysis also points to more intense rainfall events, as seen in other GCMs as well (Fowler and Hennessey, 1995, although Bensiton et al., 1996 concludes that it is still uncertain whether extreme events will increase). Typhoons and hurricanes may also increase in frequency although results for this are even more uncertain. If extreme events do increase in intensity, wind damage to trees and soil erosion will increase (Emanuel, 1987; Hulme and Viner, 1998). Soil erosion leads to a multiple of woes—including drought, nutrient leaching and complete slope failure, all of which can effectively reduce available soil moisture with devastating consequences for mountain forests. El Niño events may increase in frequency (Timmermann et al., 1999) and many authors have linked drought at particular sites to El Niño conditions (Sri Lanka—Werner, 1998, Sabah—Kitayama, 1995, Hawaii—Chu, 1989). Just how much drought, low soil moisture and increased water demands from increasing temperatures a forest can withstand is very site-dependent, but certainly some cloud forests will not be able to survive the coming climate change. Decreases in cloud immersion, discussed below, will also lead to increased stress through decreases in water input and increases in water loss.

3.3. Changes in cloudiness

3.3.1. Cloud formation and rainfall

Clouds form when water vapor condenses to form liquid water droplets. Theoretically, this can occur via chance collisions, but this requires highly supersaturated air (of the order 300–400%) that rarely occurs in nature. Instead, clouds usually form via the collection of water droplets onto a foreign substance, or an aerosol particle. For a given particle size, condensation then occurs when the RH exceeds a much lower critical value. Typically, this occurs when air rises and cools adiabatically, thus lowering its saturation vapor pressure and increasing its RH. For instance, over the warm tropical oceans, convection acts to draw air upwards and thereby forms cumulus clouds. These types of clouds often provide a lot of the annual rainfall in cloud forests, but another type of cloud, orographic clouds, often provides the daily regime of cloud immersion.

Orographic clouds are formed when wind is forced upward by topographic relief, and in the case of the tropical montane cloud forests, it is often the trade winds running into a mountain. The bottom of the clouds typically forms at the level of the lifting condensation level. The top of the cloud is often limited by the trade wind inversion, which causes an increase in temperature with altitude. If this occurs, the thickness of the cloud, and hence the size of rain droplets that can form, are limited. If the droplets are prevented from becoming large enough to overcome the frictional resistance of air, no rain will fall. (Hastenrath, 1991; Houze, 1993). This is essentially the case for some cloud forests along the Caribbean coast of South America, where annual rainfall is very low and lowland vegetation is of the arid type. Yet, cloud forests thrive above about 800 m. Every day, high altitude small clouds form above the mountain
peaks and in late afternoon, when temperatures cool, the cloud base descends, covering the forest mainly at night. In cooler higher sites, clouds cover the forests mainly in the afternoon (Cavelier and Goldstein, 1989).

For the sake of the following sections, note that climate models are incapable of resolving the cloud microphysics discussed above. Instead, cloud formation has to be parameterized. In a study correlating microphysics discussed above, Slingo (1987) found that an RH > 80% and an updraft correlated well with cloud occurrence. Grubb and Whitmore (1966) found that 80% was a useful cutoff as well because the RH climbed to 80% when rain or cloudiness interrupted clear spells in an LMRF in Ecuador. Many GCMs use schemes related to these observations, adding conditions that are more detailed but essentially relying on the relative humidity in a grid box to determine if a cloud is present. The modeling of cloud formation and rainfall remains one of the essential tasks of the climate community.

3.3.2. Sea surface temperatures and cloudiness

In the late 1970s, tropical sea surface temperatures (SSTs) underwent a step-like increase of several tenths of a degree (Guilderson and Schrag, 1998). This shift has been linked to a number of recent changes in the hydrological cycle of the tropics including increased El Niño frequency and intensity (Guilderson and Schrag, 1998), as well as the 100-m upwards shift of tropical glaciers and freezing heights (Diaz and Graham, 1996). This SST shift also correlates with changes in the trends of tropical lapse rates, which decreased from 1960–1979 and increased from 1979–1997. The decrease has been reproduced in an ensemble of simulations with a GCM forced with observed SST values. However, results of the second period, from 1979–1997, also predict a lapse rate decrease rather than the observed increase (Gaffen, 2000), suggesting that SSTs are not the only factor in driving the value of the tropical lapse rate. Indeed, Santer et al. (2000) concluded that anthropogenic and volcanic effects may be partially responsible for the lapse rate shift. The lapse rate observations suggest less cloudiness before 1979, and more after 1979, as the greater lapse rate in the latter period implies greater convective instability and hence more cloudiness. However, lapse rates are only an indication of potential cloudiness—sufficient vertical velocity is also needed to initiate convection. A better indicator of cloudiness is humidity, as discussed previously.

Graham (1995) was able to reproduce observed trends in specific humidity using a GCM driven with SST changes alone. The specific humidity profile has changed in the following way: over the Western Pacific, at and above 1000 mb, the specific humidity increased from the early 1970s through the 1980s (Flohn and Kapala, 1989; Gaffen et al., 1991; Gutzler, 1992). The largest increase was observed at the 1000 mb layer with smaller increases both upwards to the 700 and 300 mb layers and downwards to the surface. In terms of relative humidity, the observed surface RH actually decreased slightly at all four stations used in Gutzler’s (1992) study. This hints at decreased surface cloud formation as cloud formation correlates with RH (Wallace and Hobbs, 1977; Houze, 1993), especially low-level clouds (Slingo, 1987). Observations of CFs on tropical Pacific Islands might provide a link to these changes in the hydrological cycle and thus provide an early warning system of climate changes over the ocean.

Results of GCMs driven by SST increases also suggest decreased low-level cloudiness upon SST warning. For example, a GCM driven with a uniform SST increase showed a decrease in the globally averaged low-level cloudiness (Schneider et al., 1978). Other simulations that looked at cloudiness in climates warmer than today also found decreases in low-level cloudiness (Rind, 1986; Mitchell and Ingram, 1992). Surface observations (Pounds et al., 1999) and modeling efforts (Still et al., 1999; Foster, 2001) at the Montevearde Cloud Forest (see the next section) also suggest decreasing low level cloudiness at that site. In summary, GCM results suggest that an increase in SST may result in decreased low-level cloudiness, at least in certain locations, and concurrent observations of increased SSTs but decreased RH at the surface in the western Pacific and cloudiness at Montevearde support the causal link.

3.3.3. Cloudiness at the Montevearde Cloud Forest

Pounds et al. (1997, 1999) have linked changes in climate, cloud formation and animal abundance pat-
terns at the Monteverde Cloud Forest in Costa Rica. Bird, lizard and anuran species abundances all correlate with the number of dry days in the dry season, which is linked to cloud immersion frequency. Included in the changes are bird species now colonizing the cloud forest, which were previously restricted to lower altitudes, highland endemic lizard declines and disappearances, and in 1987 an exceptionally large disappearance of 25 of 50 frog and toad species. Given the increase in the number of dry days, and a decrease in the diurnal temperature range (DTR), Pounds et al. suggested that the cloudbank at Monteverde has been rising. The subsequent decrease in cloud immersion would increase the number of dry days but not decrease the overhead cloud cover, which would cause the DTR to increase rather than decrease as observed. Still et al. (1999) found consistently similar results in a study of expected shifts of ecotones for four cloud forest sites, one of which was Monteverde (see Section 4.2). Incidentally, the increase in dry days is consistent with the upward shift of ecotones discussed above, if the number of dry days decreases with altitude. Since rainfall typically increases with altitude, just such a negative

![Fig. 2.](image)

Fig. 2. (a) Changes in the surface relative humidity field from 1960–1990 to 2060–2090 as modeled in four GCMs. The results of four GCM simulations for today and 2 × CO₂ concentrations are compared and shown for the four seasons. The relative humidity change is given as a fraction from 0.20 to −0.20 (or 20% to −20%). Most of the tropical land area shows a decrease in RH of 5–10%. This could imply decreases in low-level cloudiness and consequent damage to the cloud forest. See the text for details of the models and implications. (b) The standard deviation of the relative humidity averages shown in panel a. The value of the standard deviation of the relative humidity averages often is as large as the average itself, suggesting the average results are not entirely robust. However, a large portion of the deviation comes from one GCM and it does appear that there is a trend towards lower RH over tropical land areas. See the text for details.
correlation between dry days and altitude is expected and, indeed, has been observed at the Luquillo Experimental Forest in Puerto Rico, which harbors a cloud forest at its peak (Garcia-Martino et al., 1996).

Foster (2001) has used the regional area model RAMS to test the hypothesis of a rising cloud bank at Monteverde in more detail. Modeling 2 years that bracketed the anuran species crash, 1979 and 1987, she was able to reproduce the increase in dry days and indeed found it was due to a rise in the cloud bank. The driving force for modeling the decrease in moisture was the large-scale ECMWF (European Centre for Medium-Range Weather Forecasts) RH field, which among other atmospheric variables, was used as a boundary condition to drive the limited area simulation. This large-scale RH field showed a very slight increase over the Pacific from 1979 to 1987. Meanwhile, the Monteverde RH decreased, both in the ECMWF data and in the simulation. This suggests that if the tropical tropospheric hydrological cycle continues to increase, there may be further decreases in low-level cloudiness and consequently more damage to the cloud forest (see previous section). Since the enhancements in the tropical tropospheric hydrological cycle may be driven by anthropogenic effects (Graham, 1995), the drying at Monteverde may also be driven by human-induced climate change rather than natural fluctuations.

3.3.4. The relative humidity changes of four GCMs in a $2 \times CO_2$ world

I looked at the expected response to climate change of the relative humidity field, as a proxy for cloudiness, in four different global climate models.
While these models are relatively coarse in resolution and do not show altitudinal zonation or mountain climates, I expect local cloudiness responses to follow the value of the large-scale relative humidity field.

I compared the evolution of the RH field at the surface in the following four GCMs during the course of $2 \times CO_2$ transient IS92 simulations: Echam3/LSG-DKGG, CCSR/NIES CGCM-NIGG, HADCM3-HC3GG and CCCma's CGCM-CCGG models, available online from the IPCC at http://ipcc-ddc.cru.uea.ac.uk/ipcc_ddc. First, I calculated the seasonally averaged RH field for each of the four models: December–February (DJF), March–May (MAM), June–August (JJA) and September–November (SON). Then, I averaged the seasonal averages into period averages from 1960–1990 and from 2060–2090, except for the Echam3 model which was only averaged from 2060–2085 because subsequent years were not available. Next, I differenced the period averages to find predicted changes in the RH field from today to a $2 \times CO_2$ world. Using a nearest neighbor assignment, I interpolated each field onto a $128 \times 64$ grid so that I could average all four models and present the results in Fig. 2a. To assess the robustness of these results, I present the standard deviation of the averages of the four models in Fig. 2b. The pattern of the standard deviation roughly follows the peaks in the difference plot.

In Fig. 2a, the light blue–green color represents little to no change in RH and this covers most of the ocean surfaces. Blue to dark blue represents a decrease in surface RH and appears over most land surfaces with an average value of about $-5\%$, though some decreases are as large as $20\%$. Yellow ($+5\%$) and red areas ($+15\%$) are relatively rare appearing over central Africa and the Middle East in the tropical regions. This is dominated by the CCSR/NIES model, which has the largest RH increase of all four models, with increases in Central Africa, the Middle East and northern South America. Since both the CCC and HADCM3 models show decreases in RH over the entire globe, the areas of increase in the CCSR/NIES model appear as regions of high standard deviation in Fig. 2b. The largest increase in the averaged RH field appears over the Middle East, where the Echam3 model adds to the CCSR/NIES' RH increase. Except for the regions noted, the remainder of the cells over land tropics in all four models primarily shows decreases in RH. These results highlight the fact that the RH response to global warming is complex and even given similar assumptions, different predictions are possible. However, there appears to be a trend towards decreasing RH in these models over most tropical land surfaces. Since surface RH is likely to be correlated to low level cloudiness, this may indicate a trend towards less ground touching clouds and hence may indicate a severe threat to cloud forest species.

4. Climatically suitable zone

4.1. Introduction

In what follows, we will discuss the shifting of climatically suitable regions, so-called ecotones. Typically ecotones are defined by temperature and precipitation regimes and do not consider cloud immersion that is so essential to the cloud forest. Nevertheless, the general results of biogeography models provide some insight into expected changes on tropical mountains. Ecosystems as a whole will not shift to new locations under different climates, because ecosystems are composed of many species, which will each respond to climate change in its own way. This is exemplified in the fossil record, which contains past climate states and vegetation distributions, which have no analog in today's world. This may also be the case for future changes (Graumlich, 1994). Biogeography models attempt to overcome this limitation by grouping plants by functional type and linking these groups to prevailing climate conditions. However, these models are still fundamentally co-relational rather than process-based and may not be appropriate for climate change scenarios. We also do not know if plants can migrate rapidly enough to keep up with the changes in climate that may occur. Other barriers for successful migration are natural and man-made obstacles, such as rivers, valleys, cities, roads and farms in the migration path. These obstacles can both block movement and occupy land of a potential new colony. This is especially true of mountain habitats that are naturally fragmented and small. However, there is some evidence that at least
some cloud forest species have successfully leapt from mountain peak to mountain peak (Werner and Balasubramaniam, 1992; Werner, 1998). In the following section, we discuss where an ecosystem might possibly thrive under the possible climate changes.

4.2. Biogeography models

Biogeography models, such as BIOME (Prentice et al., 1992), MAPSS (Neilson, 1995), Box’s (1995) model and Holdridge’s (1947) life zones do a decent job of predicting the location of current day ecosystems based on temperature and rainfall profiles, as well as sunshine and soil characteristics. Assuming that the correlation relationships between the climatic variables and the dominant ecosystems hold, the models can be used to make predictions about the change in location of ecosystems under changing climates. For a uniform temperature rise, the prime viable location for ecosystems on mountains shifts upward to maintain the same temperature regime. This has been summarized as Hopkins bioclimatic law, which states that for a 3°C increase, species ranges will shift upward 500 m (Peters and Darling, 1985). However, temperatures are not expected to rise uniformly, either horizontally or vertically (see Section 3.3), and other climate changes and vegetation responses complicate the expected outcome.

For instance, rainfall patterns are sure to change. One approach to modeling the effect of changing rainfall and temperature on ecosystems distributions is to impose a uniform temperature rise and a uniform percentage change in rainfall to the current climate, and then apply biogeography models to the shifted climate. A transect study of the La Amistad Biosphere Reserve, Costa Rica, found that for a 3.6°C temperature increase and a 10% precipitation increase (as found in two GCM simulations for the Costa Rica area (Smith et al., 1995)), there was a non-uniform reorganization of the current ecotones, with a general trend upslope (Halpin, 1994). Three of the ecotones along the transect were entirely lost, including the climate associated with the dwarf cloud forest, currently on the peak in this region (Smith et al., 1995; in agreement with Still et al.’s (1999) conclusions). The lower elevation ecotones expanded and moved upslope in the model with the alternate climate. Lending confidence to the trend for wider (and therefore fewer) ecotones in a warmer world are paleo-reconstructions of vegetation distributions during colder eras that show narrower ecotone bands (Halpin, 1994, adapted from Flenley, 1979), although Colinvaux et al.’s (1997) pollen fossil study suggests that Andean vegetation zones were not compressed during the last glacial period. In a study similar to Halpin’s Costa Rican transect study, Scatena (1998) used temperature and rainfall profiles on the Luquillo mountains of Puerto Rico to estimate that either a 2.5°C temperature rise or a 11% reduction in rainfall would be sufficient for the Tabonuco forest to replace the next highest forest type, the Colorado forest. Either of the increases, which are well within the boundaries expected for a 2 × CO₂ scenario, would result in no part of the mountain having the climate conditions that the peak residing dwarf cloud forest currently experiences. This cloud forest, too, may be pushed out of existence. In any event, as the ecotone of the cloud forest moves upward, its viable land area will decrease as there is less land at higher altitudes on any given mountain. Aside from issues of migration, competition and secondary growth, cloud forest diversity is expected to decrease simply because biodiversity scales with area (see Fig. 4a).

Instead of assuming simplistic uniform increases of temperature and precipitation, GCMs can be used to predict the climatic changes. Still et al. (1999) looked at several atmospheric variables thought to correlate with cloud forest location in three GCM simulations of the GENESIS model (Thompson and Pollard, 1997), corresponding to the present, the last glacial maximum and a 2 × CO₂ atmosphere. They found that the warmth index (see Section 2.1) and the absolute humidity surfaces both move upslope by 200–300 m at four cloud forest locations in a 2 × CO₂ world. The similar altitude shifts of the AH and WI surfaces, representing water and temperature regimes, suggest that the water balance of the CF may well be reproduced at this shifted altitude. This argument is strengthened by the 200–300 m down slope shift of the WI and AH surfaces in the LGM simulation, which is consistent with pollen records of cloud forest species during the LGM (see Section 7.1).

This predicted CF altitude shift of 200–300 m in a 2 × CO₂ world is somewhat smaller than other
estimates, probably because it is based on a very coarse GCM, which does not resolve the topography well. Other estimates for the shifting of tropical montane ecotones are: Costa Rica—500 m (Halpin, 1994), Puerto Rico—400 m (Scatena, 1998), mountains everywhere—500 m for a 3°C rise (Hopkin’s bioclimatic law, Peters and Darling, 1985). These shifts are very significant relative to the current altitude range of cloud forest species. Tropical ecotones typically have very narrow elevation ranges because there are strong climate gradients along tropical mountains, due to a lack of seasonal blurring of temperature averages. Halpin (1994) surmises that the trees in Costa Rica live in altitude ranges of about 500 m. Estimates of cloud forest vertical extent are often around 500 m as well (for example: Thailand, Werner and Santisuk, 1993; the Upper Guayllabamba River Basin, Ecuador, Sarmiento, 1995; El Rey National Park, Argentina, Brown, 1995, Serranıa de Mauira, Colombia, Sugden and Robins, 1982a,b), although larger ranges do exist. A 500-m shift in the viable climate range of an ecotone, which spans 500 m, suggests complete replacement of the current range. Even smaller upward shifts of 200–300 m may well push peak residing cloud forests out of existence, with perhaps even less needed to push many Central American cloud forests out of existence.

4.3. Latitudinal changes

Latitudinally, there may be less change in cloud forest distributions. The high latitude limit of tree type seems strongly tied to minimum annual temperatures whereas the equator-ward limit is apparently determined by competition, with no apparent high temperature limit. So the tropical evergreen broadleaf tree, which is the most competitive physiology given ample moisture and temperature, is expected to expand its limits somewhat pole-ward. If the tropical cloud forest does expand pole ward, it may displace the Cryptomerica-dominated temperate cloud forest (Ohsawa, 1995b). The hypothesis that tropical ecotones will expand into current temperature ranges is based mainly on temperature changes, not cloudiness changes that are of paramount importance to the CF. Speculating about latitudinal changes in the cloudiness regime is risky, we note only that an enhancement of rainfall may reduce the CF distribution by reducing the relative importance of horizontal precipitation (Juvik and Nullet, 1995). It is likely that the impact of large-scale changes in the hydrological cycle will be very site-dependent.

5. Implications of climate change for the cloud forest

Exactly how direct contact with clouds changes the cloud forest ecosystem is unknown. What we do know is that the postulate of Grubb and Whitmore (1966), that long persistent cloudiness is the primary factor determining the stature of cloud forests, is borne out by many descriptive studies. Since we do not know the underlying relationships, it is difficult to predict what a change in cloudiness will mean for the cloud forest. However, in the following we make some educated guesses.

5.1. Deforestation, flooding and dry weather flow

Conservationists have argued that the cloud forest plays an important role in reducing flooding and providing water during dry seasons for the forest itself as well as for downhill ecosystems and cities. Cloud forest deforestation, via chainsaws, fire or climate change, may therefore result in increased flooding and reduced stream flow in dry weather (Zadroga, 1981; Stadtmüller, 1987; Werner, 1998; Becker, 1999). Since these consequences are so grave, we will now discuss the possible impact of deforestation on the water budget in detail.

5.1.1. The cloud forest’s water budget

Hydrologically, the frequent contact of clouds on the vegetation has multiple implications. The vegetation gains an additional source of water by stripping water out of the passing clouds, either through direct contact or through condensation, in a process known as horizontal precipitation (hereafter HP, sometimes referred to as cloud stripping). Bruinjizeel and Proctor (1995) reviewed the hydrological cycle of cloud forests and found that HP inputs varied from 70-mm/year (in Venezuela) up to over 1160 mm/year in Honduras, but that typical values were around 5–20% of rainfall. This can be especially significant
during the dry season and droughts, or in cloud forests located in the rain shadow of mountains (Juvik, 1995) or in arid regions (Sugden and Robins, 1983). Subsequent estimates of HP have confirmed this range (Schellekens et al., 1998; Hafkenscheid et al., 1998; Holder, 1998), with an exceptionally high value of HP (1365 mm of HP in a 100-day period, 406% of the rainfall) measured at Alakahi, Hawaii (Juvik and Nullet, 1995).

In addition to increasing the water input, the frequent presence of clouds reduces evapotranspiration (ET), further reducing potential water stress. Bruijnzeel (1999) gives ranges of ET for various montane forests from (a) 275, (b) 500–700, (c) 830–980 to (d) 1155–1380 mm/year for (a) dwarf cloud forests, (b) TMCF in UMRF with several hours of clouds per day, (c) TMCF in LMRF that only get modest amounts of cloud water, and finally (d) cloud-free LMRF at similar or higher elevations. Bruijnzeel cautions against using these estimates blindly, as they are based on indirect evidence. Furthermore, a recent detailed measurement of ET in a lowland tropical rain forest below 600 m gave values of ET in excess of 2000 mm/year (Schellekens et al., 2000)—exceeding all of the rates given by Bruijnzeel (1999). Nevertheless, the strength of the decreasing trend of evaporation with increasing cloudiness, as well as theoretical considerations, strongly suggests that evaporation is indeed reduced in the cloud forest.

5.1.2. Bucket model

The impact of deforestation on the water balance is very complicated, but in essence, it depends on the water holding capacity of the system. Water is primarily held in the soil, so although the canopy can also store a lot of water in the CF, we will ignore it for the time being. If the soil is considered as an open bucket with infinite depth, it can absorb any amount of rainfall, preventing flooding and slowly releasing the stored water, providing dry weather flow to systems down slope. Various factors complicate this simple model. First, the amount of water reaching ground level, the top surface of our bucket, is different under the montane rain forests, pasture land and cloud forests. The canopy of montane and cloud forests intercepts and subsequently evaporates rainfall, so that less water reaches the soil than at pasture sites for equal incident rainfall amounts. On the other hand, the through fall of water in the cloud forest is enhanced relative to the standard montane forest (Bruijnzeel, 1999), apparently through the additional input of horizontal precipitation and the reduced evaporative demands. So given equal amounts of incident rainfall, the bucket is perhaps filled up most in the cloud forest, followed by pasture land and perhaps least in the standard forest. This relation is strengthened by the rate at which the bucket is emptied. Evapotranspiration of the standard forest is greater than that of the CF. These conjectural relationships between the water fluxes are shown graphically in Fig. 3.

This model concurs with observations that stream flow increased following deforestation of some ‘standard’ tropical forests in controlled experiments, dominated mainly by an increase in dry weather flow (the pasture’s bucket is fuller than the standard forest’s and thus provides more dry weather flow). The CF’s full bucket implies the largest dry weather flow, which is corroborated by observations that the stream flow to incident rainfall ratio of the CF is among the highest of all tropical forests (Bruijnzeel, 1990). Further arguments that CFs are a good source of dry weather flow and flood prevention, are the fact that CF soils are nearly always saturated (Bruijnzeel and Proctor, 1995), the huge water storage capacity of the canopy (Sugden, 1981), and mounting observational evidence that cloud forest destruction leads to reduced dry weather flow (Bruijnzeel, 1999; Becker, 1999). The bucket model is overly simplistic, of course. The consequences of forest loss will really depend on the relative amounts of water table input and output, as well as the soil and canopy characteristics of each forest.

5.1.3. Soil compaction

In the event of a complete loss of forest, a further complication may be soil compaction: either via trucks, cattle or incident raindrops. In essence, the top of the bucket will be at least partly closed. In this case, flooding may be more common and more intense. If flooding does occur, it will lead to further soil erosion and more flooding. A much-reduced dry weather flow is expected in the event of soil compaction, as much less water will penetrate the soil to fill up the bucket. Since some form of soil degrada-
Fig. 3. The speculative relative water budgets of the cloud forest, montane forest and grassland. In this figure, three ecosystems are represented: the cloud forest, the montane forest and grasslands. The size of the arrows for a given water flux is an estimate of the size of the flux relative to the other ecosystems. For example, throughfall and dry weather flow are greatest in the cloud forest and least in the montane forest. Similarly, the amount of soil moisture is represented by the shaded area under the surface and again it is greatest under the cloud forest and least under the montane forest. Relative values are speculative, but based on the current best estimates. This figure demonstrates the water services that the cloud forest probably provides: increased dry weather flow and flood prevention.
tion is likely to accompany any form of deforestation, this outcome may be the most likely. Control experiments that showed enhanced dry weather flow following tropical rainforest deforestation may have been unrealistically gentle on the soil (Bonnell, 1998).

The results discussed in this section on the water budget are based primarily on intentional deforestation rather than forest loss due to climate change. Therefore, caution must be exercised in extending these conclusions to the future. For instance, if climate change does cause deforestation, it may not necessarily be harmful to the soil. While there is a chance that newly exposed soil will be compacted by incident raindrops, and hence effectively cut off from infiltration, it is more likely that grasses will grow and provide the soil with some protection, as occurred in the Andean paramo (Sarmiento, 1997a,b).

5.2. Epiphytes and climate change

The biomass of a forest, or individual plant for that matter, is strongly influenced by water availability—no water, no plants (Woodward, 1987). Trees can survive dry seasons and droughts by accessing underground water supplies that build up over the course of previous wet periods. However, in the event of a major climate change, with permanently increased dry seasons, this water source may eventually be used up and some forests will probably die, to be replaced by more drought-resistant ecosystems. Epiphytes, however, respond much sooner to changes in the moisture cycle as they do not have access to ground water and rely entirely on atmospheric moisture. Furthermore, their extreme microhabitat colonization (see Section 2.1) argues for sensitivity to even small changes in moisture availability. Because epiphytes occupy so many microhabitats in a given canopy, there may be some ability for them to reorganize within the canopy to take advantage of shifted climate regimes. This may be limited, however, because epiphytes are sensitive not only to climate, but also to other factors in their microenvironment such as the light regime, substrate depth and so forth. Observations of epiphyte reactions to longer than usual dry spells include the expected wilting of epiphytes (Grubb and Whitmore, 1966; Lowry et al., 1973) as well as whole scale canopy die back in the event of severe drought (Werner and Balasubramaniam, 1992). If the drying trends outlined above are truly underway (Section 3.3), the effects may first be seen in the epiphyte communities of cloud forests. Benzing (1998) stresses that epiphytes are important components of several cycles within the CF. In some instances, therefore, death of the epiphytes may directly harm the underlying vegetation and alter resource allocation. However, there have been cases where hurricanes have destroyed the epiphyte community and the tree community continued to thrive (Scatena, personal communication).

5.3. Impacts on animals

Animals will be affected both directly and indirectly by climate change. For example, consider the impact of the loss of epiphytes due to climate change. Almost all CF terrestrial invertebrate taxa and many lower vertebrates use the moisture or nutrients that epiphytes store and produce, including seeds, fruit, nectar and pollen (Benzing, 1998). Epiphytes also provide nesting materials and water services to canopy animals. Some animals, especially birds and insects, have co-evolved symbiotic relationships with one specific plant species. Epiphyte reduction and disappearance may lead to the death of many animals and probably to some extinctions. Like the epiphytes, animals also play a key role in forest dynamics. For instance, many birds and mammals distribute seeds, which highlights the complex web of interactions of life within a forest—death of one component can have far-reaching consequences. Two high profile cloud forest mammals are the mountain gorilla of Virunga of which less than 500 survive in the wild and the spectacled bear of South America. While they are not likely to be directly affected by climate change, the collapse of their forest could certainly cause their disappearance.

One group of cloud forest animals that may be directly affected by climate change is the class Amphibia, including frogs, toads, salamanders and caecilians. Amphibian skins and eggs are permeable, making them sensitive to changes in temperature and moisture as well as pollutants. Worldwide, amphibian populations have been declining and while some decline is expected, rates of decline are greater than population model predictions. Many of these de-
clines are linked to habitat destruction, but some have occurred in seemingly undisturbed places. There are many postulates as to why these declines are occurring (Alford and Richards, 1999). These include the direct effect of desiccation on the moisture-sensitive animals, and the indirect effects of less energy for reproductive activities, suppression of the immune system, parasite growth and the loss of food source, i.e. insects, which in turn are climate-sensitive. The possible reduction of water input to the CF (Section 3.2) may cause CF amphibians the following problems: difficulty in finding suitable egg-laying spots, crowding at ponds that do form, the drying up of ponds before pond-frog tadpoles hatch, the drying up of eggs of leaf-laying frog eggs, and so forth and so on (Donnelly and Crump, 1998).

At this point one can only conclude that specialist species, be they dietary or habitat specialists, are likely to be more affected, just as we concluded for the microhabitat colonization of epiphytes. And, since so many amphibian specialist species are found within the cloud forest, once again, the cloud forest inhabitants face a heightened risk. Local extinctions will have impacts on the food chain, both up and down, as well as impacts on competitive balances with other species.

Cloud forest frogs have not escaped the worldwide decline in frog abundances. We discussed a striking case earlier (Section 3.3) in which 25 of 50 species of frogs and toads disappeared in 1987 from the Monteverde Cloud Forest. Some scientists claim that this is normal population dynamics, but it seems unlikely given the failure of 20 of those 25 lost species to reappear in the intervening time (Pounds et al., 1999). Furthermore, anuran and other vertebrate species abundances within the Monteverde cloud forest are correlated to the number of dry days. Bird species that were previously confined to altitudes below the CF are now regularly breeding in what was strictly CF habitat. Two highland endemic lizard species have disappeared from the CF recently, while one drier climate adapted lizard has shown no distributional changes. The changes in all three classes, birds, lizards and anurans, are significantly correlated with the number of dry days in the dry season. Pounds et al. (1999) and Foster (2001) argued that a complete chain of reasoning connects anthropogenic climate change to the increase in dry days at Monteverde and hence to the Monteverde extinctions. Long-term animal and climate studies at other sites may soon reveal similar patterns.

6. Recovery from disturbances in cloud forests

6.1. Canopy openings and invasions

CF plants at the edge of the CF in Sri Lanka appear to be relatively frost-tolerant while those at the center are not well adapted to frost (Werner and Balasubramaniam, 1992). Similarly, CF plant species appear to be intolerant of fire. So whenever there is a canopy opening, and frost or fire is a threat, CF species along the new opening are likely to die, which can result in a spread of the opening (Werner, 1995, 1998). This arises partly because cloud forest trees are relatively slow growing and thus will not compete well with fast growing pioneer species in the openings. Non-native pioneer species can be especially threatening as the resident cloud forest species will not have evolved any defenses against them.

Canopy openings can arise from a number of events—hurricanes, typhoons, logging and even drought. While there is evidence that CF trees can withstand some amount of drought (Bruijnzeel and Proctor, 1995), drought-induced canopy die-backs have been observed in the Sri Lankan CF. Subsequently, fire and frost, which were previously suppressed in the CF interior, prevented tree growth in the newly opened canopy and promoted the expansion of grass areas. Now, Rhododendron arboreum is the only tree species found above 1500 m in the grasslands that replaced the CF of Sri Lanka (Werner, 1995). Similarly, in Tahiti, the montane forest has been invaded by the fast growing South American melastome tree following two destructive hurricanes (Merlin and Juvik, 1995). In a short-term (3 year) but detailed study of Andean mountain forest succession in pastures, Sarmiento (1997a,b) showed that introduced non-native grasses limited the dispersal success of montane tree species into the pasture, via seedling competition. In the past, anthropogenic burning led to the spread of Andean grasslands, paramo, but with native species with which the local shrubs and trees evolved and can eventually success-
fully compete. Sarmiento concludes that these non-native tussocks must be removed before the natural progression from grassland to shrubs to forest can occur, otherwise the succession may follow the path of forest to pasture. In Hawaii, feral pigs damage the CF vegetation and non-native species are invading (Medeiros et al., 1995). Olander et al. (1998) found that non-endemic species found at disturbed sites did not spread far into the undisturbed cloud forest at the Luquillo Experimental Forest. This suggests that the CF may have some resiliency against invasions if it remains undisturbed, but in areas with disturbed soil, it loses the competitive battle against non-native invaders. This seems reasonable in light of the slow growth rate of CF species (see the following section) and the lack of co-evolution which would prevent the development of defense mechanisms against non-native species.

6.2. Recovery rates

Byer and Weaver (1977) concluded that the TMCF has the slowest recovery rate of all tropical forests. Olander et al. (1998) quantified recovery rates in the cloud forest of the Luquillo Experimental Forest, Puerto Rico. They found that cloud forest recovery in areas where the root mat was removed is much slower than in other forest types at Luquillo and extrapolated their observations to estimate a 200- to 300-year recovery time. In cases where the soil was not so disturbed, recovery rates were much faster. (Weaver, 1990; Olander et al., 1998). Compacted soil can also lead to cascading damage via enhanced flooding and more soil erosion. Scatena (1995) points out that simple foot trails in Luquillo that have been nearly abandoned for 25 years were still recognizable. Except for the possible increase of more high intensity rainfall events, climate change may not have such drastic consequences for the soil. Consequently, under the pressure of changing climate the CF may be able to reestablish themselves faster than the 200–300-year recovery rate estimated for the Luquillo Forest. However, it seems plausible that other stresses may arise, which in conjunction with climate change will counterbalance this shorter recovery rate.

Another important factor in the recovery and reloca
tion of CF species is competition with nonnative species that can halt regeneration altogether (Myers, 1991; Werner, 1995; Merlin and Juvik, 1995; Sarmiento, 1997b). In one CF in Hawaii, the removal of feral pigs has resulted in an unusually rapid recovery. This has probably arisen because other common threats, especially fire, are lacking and that most of the alien plants there are disturbance specialists. In this case, once the disturbance was removed, the native CFs were able to recover. In the event of climate change-induced openings, recovery will probably depend on the presence of further disturbances including fire, frost, invaders and soil health.

6.3. Secondary forest—poor in biodiversity?

In cases where the cloud forest has recently recovered from destructive events, both the biodiversity and the biomass tend to be very low. For instance in the Solomon Islands, which frequently experiences typhoons and is also under pressure from an increasing human population, most of the cloud forest is in some stage of regeneration. The flora on this island is markedly poor relative to other tropical Pacific islands, with numerous species poorly represented or completely absent (Merlin and Juvik, 1995). On the other hand, tree species richness might be expected to recover relatively rapidly with respect to other tropical forests. This is because there is less tree diversity and hence fewer successional stages within the CF. The case for the epiphytes also has competing effects. Epiphytes are characteristically quick and successful colonizers and hence might be expected to recover rapidly. However, it seems that they will be limited in the secondary forest, which lacks the old trees that harbor many microclimates and carry the bulk of epiphytic mass in old growth cloud forests (Hietz and Hietz-Seifert, 1995).

In summary, the combination of increased water stress and increased strong wind events is likely to result in more frequent CF canopy die backs. Subsequently, nonnative grass invasions, fire, frost, animal grazing and so forth may slow or prevent cloud forest recovery and may even spread the canopy gaps. In the event of recovery, it may take centuries to rebuild the biomass of the trees and hence the richness of the epiphyte community to the level of the old growth forests. But clearly, cloud forests have survived typhoons and extreme events in the
past. Perhaps the cloud forest can recover on timescales longer than we have presently observed, maybe with input from nearby non-damaged cloud forests. It is currently unclear if cloud forests can survive the combined stresses of increasing isolation and fragmentation, increased temperatures, drought, rainfall and wind, as well as direct anthropogenic pressures, not to mention the catastrophic consequences of the loss of cloud contact with forest conjectured in Section 3 above! It is difficult to know if the above cases of slow recovery or failure to recover are our first glimpses of the large-scale breakdown of CFs or the result of peculiar combinations of stresses.

7. Past climate change impacts on the cloud forest

7.1. Forest retreat and expansion

In the past, tropical forest have expanded and retreated in response to climate changes. The pollen fossil record of the tropics for the last 18,000 years was concisely summarized by Flenley (1998) and shows forest advances and retreats as well as altitude shifts in forest boundaries. By comparing records from sites at various altitudes, Flenley estimated that the forest limit in the tropical regions of Latin America, Southeast Asia, the west Pacific and in Africa descended approximately 1000 m during the Last Glacial Maximum (LGM). Similarly, all three regions show evidence for montane species (including cloud forest ones) descending to lowland sites during the LGM (descents of 1000 m and more are documented in Latin America, Colinvaux et al., 1996a,b; 1200 m in Indonesia, Van der Kaars and Dam, 1997; 600 m in Africa, Maley, 1991).

7.2. Disappearance of CF species in the pollen fossil record

The altitude shifts for the lower and upper limit of a given ecosystem are not expected to be the same, meaning ecotone altitude ranges will change (see Section 4.2). In the Late Pleistocene, species of the mossy forest of New Guinea almost completely disappeared from the pollen fossil record (Walker and Flenley, 1979). According to Flenley (1997), similar phenomena have been reported for the sub-alpine shrubbery in the Colombian Andes (an ecosystem similar to the CF with stunted growth and small thick leaves) and for the UMRF at Pedro Palo. Alpine grasslands appear to have expanded to fill the gap. Temperature decreases acting alone would shift the vegetation zonation downwards, but would not pinch out a given ecotone. An alternative explanation is the UV-B theory and it is discussed below.

The New Guinea cloud forests currently range from about 2800 to 3700 m (Flenley, 1992a). Above the tree line, a small scrub zone sometimes exists for roughly 200 m in altitude, eventually grading into alpine grassland. Flenley argues that the upper limit of this mossy forest is apparently determined by low temperatures; low temperatures kill woody plant types including CF trees. Below the lower limit of the cloud forest, at about 2800 m, LMRF plants thrive. Flenley argues that within the cloud forest, above 2800 m, UV-B radiation is so high that unless plants have some protective mechanism they cannot survive. One such protective measure is the production of flavinoids in the leaves, which absorb harmful UV-B radiation, and in turn lead to stunting (see Section 2.2). LMRF plants cannot survive in the high UV-B radiation at high altitudes, and the twisted stunted CF plants are at a competitive disadvantage at lower altitudes, thus a UV-B cutoff marks the LMRF/CF boundary at 2800 m. Flenley (1992b,c) conjectures that under climate change, this altitude would probably not change much as it is dependent on the intensity of UV-B radiation, although cloudiness may act to magnify this effect and could thus play a role in adjusting the altitude of this boundary. During the late Pleistocene, when temperatures dropped, the forest limit dropped to about 2000 m, below the UV-B cutoff. The zone where the special UV-B protecting characteristics of stunted vegetation have a competitive advantage, above 2800 m, was then above the forest limit, and the CF species disappear. If this is indeed the main mechanism driving CF morphology and its lower limit, then future climate change may drive a potentially large expansion of CF areas as the lower UV-B limit is expected to remain at the same altitude, but the tree line will probably rise. However, we must remember that the UV-B mechanism is probably a secondary
consideration to CF altitude distribution; cloud cover apparently dominates CF distributions. However, the UV-B mechanism could well limit CF distribution and explains many aspects of the CF, whereas other mechanisms seem to explain only one.

An alternative explanation for the loss of stunted vegetation zones during the LGM is the low CO$_2$ concentration documented for this era (Street-Perrott, 1994). Low CO$_2$ levels are known to favor grasses (C4 plants) over trees (C3), perhaps explaining the expansion of the grasslands. This CO$_2$ theory does not explain the Massenerhebung effect or stunting, but it is not necessarily the same mechanism that causes stunting and controls the forest boundary. The CO$_2$ or UV-B theory can also help explain apparent temperature depression discrepancies during the LGM. Pollen records from tropical mountains record a vegetation descent, which, if based solely on temperature, imply a decrease of some 6–10$^\circ$C during the LGM. This is larger than estimates of SST cooling rates, even the larger rates found for corals of 5$^\circ$C (Guilderson and Schrag, 1994). Flenley (1997) suggests that either the UV-B theory or the CO$_2$ theory could have been responsible for part of the observed descent rather than solely temperature responses.

7.3. Tropical Africa, cloud types and Podocarpus

7.3.1. The pollen record

Maley et al. have studied changes in forest distributions in tropical west Africa and found evidence of changes in the distribution of species found only in the cloud forest today, *Olea capensis* and *Podocarpus latifolius* (Maley and Brenac, 1998). These two montane taxa sometimes show different reactions to a given change in climate. *O. capensis* favors slightly drier climates than *P. latifolius* (Maley and Brenac, 1998). This cautions us to be very careful in making statements about the retreat or advance of entire biomes based on just one species. The pollen fossil record of Lake Barombi Mbo shows a maximum in *Podocarpus* 3800–3400 years ago, when *O. capensis* abundance is quite low. The shores of Barombi Mbo itself may not have hosted the *Podocarpus*, because *Podocarpus* pollen is able to move over long distances, so the pollen may have floated in from nearby Mount Kupe. However, the fossil abundance maximum in this cloud forest species, and a concurrent widespread synchronous increase of *Podocarpus* at several other mountains in equatorial Africa, suggest an increase in wet cloud forest habitat. Seemingly in contradiction is the Lake Bosumtwi core in western Africa. It shows a dramatic lake level drop of about 130 m at the start of the *Podocarpus* maximum, 3700/3800 years ago. Furthermore, there is evidence that a nearby forest retreated a few hundred years later, from 3000–2000 years BP, although there are indications that the forest retreat may have started earlier (Maley, 1991). Apparently some cloud forest species’ ranges are expanding during a time when at least one lake level dropped and other forests may have been shrinking. This picture is consistent with a decrease in overall rainfall, but enhanced cloudiness at mountain sites where cloud forests reside. This suggests an increase in stratiform clouds, which do not necessarily rain (see Section 3.3) but still provide the cloud forest characteristics of enhanced horizontal precipitation and reduced evaporation (Maley, 1997; Maley and Brenac, 1998).

7.3.2. Cloudiness changes and SSTs

Maley (1997) points out that the increased stratiform cloud formation from 3700/3800 to about 3000 years ago is also consistent with SST depressions in the Gulf of Guinea (Morley and Dworetzky, 1993). As SSTs drop, uplift is replaced by subsidence and stratiform clouds replace cumulous clouds. (see Zheng et al., 1999 for a recent study of correlations between tropical Atlantic SSTs and west African rainfall). The cold SSTs are related to an enhanced upwelling in the ocean driven by high trade wind stress, which in turn are linked to anti-cyclonic activity. This is a close analogy to the Pacific’s El Niño phenomenon. In fact, the dry stratiform phase in western Africa appears to be in phase with wet conditions in South America and a wet Sahara—characteristics of current El Niño modes. The period before 3700/3800 years ago has opposite moisture trends and corresponds to a La Niña-like phase.

Perhaps the most striking lesson to be learned from Maley’s work in the context of this review is that climate change dramatically alters cloud forest species extents. Maley also notes that the 3700/3800 years ago climate shift coincides with the end of the

Tenerean Neolithic (Roset, 1987) civilization in the Sahara and the Harapan–Indus civilization in India (Bryson and Swain, 1981), which is another sobering lesson about the potential impacts of climate change.

Further back in time, the Lake Bosumtwi pollen core shows the characteristic montane taxa descent during the LGM. From around 28,000 to 9000 years BP, montane species dominated the core and lowland rain forest species practically disappear. One of the typical montane elements found in the core for the LGM period, *Olea hochstetteri*, today resides on mountains 700 km away from the lake at an altitude of about 1200 m asl. The lake is only at 100 m asl but nearby hills, with altitudes of 400–550 m asl, may have hosted *O. hochstetteri* during the LGM, implying a minimum descent of 600 m (Maley, 1991).

### 7.4. Plant migrations

Whether or not plants will be able to survive future shifts in their climatically optimal range is a complicated question. Barriers to successful recolonization include:

1. the existence of a suitable site, both (a) climatically, and (b) undisturbed by mankind;
2. physical barriers such as rivers, mountains, oceans, roads, and cities in the migration path;
3. migration rates versus climate change rates;
4. competition at the new site with perhaps previously unencountered species;
5. the slow maturation rate of the CF.

#### 7.4.1. Methods of migration

We know that forest species have successfully shifted their latitudinal and altitudinal ranges in the past. We also know that even in the event of nearly complete disappearance of species in the pollen record at a given site, the species can reestablish itself, as happened with cloud forest species in New Guinea during the LGM (see above). Evidence for long distance distribution of montane taxa comes from similar montane taxa inhabiting widespread African forests. This has led some authors to conclude that montane taxa and animals descended to the plains during the last LGM and migrated to different mountains (Maley and Elenga, 1993; Maley, 1996). This plane flooding seems reasonable in light of the documented descents of montane species and forest extensions throughout the tropics during the LGM and evidence of apparently relic montane patches at low altitudes where there is persistent cloudiness and fog (Maley and Brenac, 1998).

On the other hand, some authors interpret the presence of the same species residing on different mountains as evidence that the seeds somehow jump from site to site (Vazquez-Garcia, 1995; Werner, 1998). Common island species must have evolved in this manner, so this theory is sometimes referred to as the archipelago theory of speciation. Sugden and Robins (1982a,b, 1983) favor such an interpretation for the isolated Serranía de Macuira cloud forest whose non-endemic, widespread, early successional species suggest recent favorable cloudiness changes and the aerial arrival of CF seeds. Merlin and Juvik (1995) provide a useful survey of species at isolated island cloud forests in the Pacific and conclude that the widespread occurrence of Weinmannia and the tree fern *Cyathea*, common if not dominant CF species at these sites, suggests that they are dispersed by wind. Paleo-records of woody species in Europe and North America during the Holocene show rapid horizontal dispersal rates, 50–2000 m/year. This suggests that there was either long distance seed dispersal, or that there may have been pre-existing ‘infection sites’ that spread under climate change (Melillo et al., 1996). In summary, whatever the mechanism of montane plant migrations—flooding of the plains during cold spells, mountain hopping or advance infection sites—there is abundant evidence that plants have migrated across long distances and sometimes quite rapidly.

#### 7.4.2. Migration rates

However, future climate changes are expected to require migration rates 10 times faster than that which is typically observed in the pollen fossil record (Melillo et al., 1996). Estimates for the migration rates of montane species are much slower than those of lowland species. For example, the expansion growth rate of one dominant alpine species (*Carex curvula*) has been estimated at 0.5 mm/year (Grabherr et al., 1978)—far too slow to track even the lower estimate of climate change shift rates of 2 m/year (see the following paragraph).
Apart from arriving at a new site, species must complete their life cycle before the climate envelope has moved on. Estimates for the establishment of new montane forest indicate it is a slow process. Körner (1994) concludes that paleo-ecological evidence for montane tree line migration indicates that new mature montane tree lines take at least 200 years to establish. Walker and Chen (1987) found that doubling times for the areal expansion of various rainforest tax in the early Holocene, a time whose warming is thought to be similar to predicted changes in the next 100 years, were on order of 100 years for many species. Podocarpus, a characteristic CF species, was found to have a doubling time of 200–400 years. This timescale is similar to Körner’s 200-year estimate for montane tree line establishment and Olander et al.’s (1998) estimate for recovery of the cloud forest. So let us assume it will take at least 200 years for the cloud forest to move—anywhere. Given current cloud forest altitude bands of about 500 m, and an altitude shift rate of 200 m/100 years, a lower limit (see Section 4.2), we estimate that in 200 years the entire climate optimum belt of cloud forest will be relocated. This is roughly the same as the speculative relocation timescale discussed above. Perhaps cloud forest species will be able to spread just fast enough to keep up with climate change.

These relocation and reestablishment timescales should not be confused with the timescales for other possible climate changes. For instance, the impact of increasing CO$_2$ on patterns in the global temperature field may already be being detected (Santer et al., 2000). Other predictions of the impact of the increase of CO$_2$ on particular aspects of the climate, such as the predictions for the relative humidity field in Fig. 2, are typically given for the time when the CO$_2$ content of the atmosphere has doubled relative to pre-industrialized levels. This is expected to occur sometime in the following century.

Aside from the migration race against climate change, another barrier to migration will exist in the future, which did not hamper past migrations. Fewer and fewer natural areas are now available to colonize as humans continue to transform wild lands into farms, roads and towns. It is often speculated that such human structures may cause a physical barrier to orderly migration routes, but given the island-like nature of cloud forests, CF may have already overcome this kind of barrier through long distance seed dispersal. However, the loss of areas to colonize represents a serious threat to the cloud forest, which may just be able to move upslope in time. For the many cloud forests that reside on mountain peaks, these details are irrelevant—these cloud forests are likely to be pushed out of existence.

8. Summary

Mountains host an incredible array of climatic variability, soil types and site exposure, resulting in small isolated eco-niches. This is even more pronounced in the cloud forest, which, of course, relies on regular immersion in low-lying clouds. Within the cloud forest itself are also microhabitat zonations, which the epiphytes and fauna have evolved to exploit (Benzing, 1998). The fragmentary nature of the cloud forest, and especially of its epiphyte and anuran communities, promotes both explosive speciation and exceptionally high rates of endemism (Gentry, 1992; León and Young, 1996), making cloud forests valuable as biological hotspots, but also highly susceptible to climate change (not to mention direct anthropogenic disturbances—Young, 1994). In a summary statement of the 1993 TMCF conference, Markham (1998) concluded that of all tropical forests, the TMCF may be especially vulnerable to climate change and we can only concur. One hopeful aspect of this highly differentiated climate is that the fragmentation itself might provide an excellent opportunity for nearby relocations of climate sensitive species in the event of climate change (Young, 1992; Peters and Darling, 1985). However, many other problems in relocation are expected to arise, which may be especially difficult for the slow growing cloud forest to overcome.

In response to climate changes, the cloud forest is not expected to shift en masse to a new location (Colinvaux et al., 1997, 2000). Plants have a vast array of behaviors, from low temperature limits, to reproduction based on day length, and consequently individual species will respond differently to climate change. Some plants will move to new locations, some will stay where they are and some will die (see
Fig. 4. (a) Possible altitude changes in the suitable climatic region. The current location of the ecotone boundaries is represented by solid lines and a projected ecotone shifting of about 500 m is represent by dashed lines. This amount of altitude shift is arrived at in several ways, but relies mostly on temperature increases. Lower altitude ecotones may expand more than upper ones (see Section 4.2), and pinch out some ecotones. This effect is represented in the figure as in increase in the LRF and UMRF's altitude range. The current cloud forest location is represented by the dark clouds. If the UV-B hypothesis explains the lower limit of the cloud forest, rather than temperature constraints, it is possible that the extent of possible cloud forest habitat may expand in the future. Such a case is represented as the dashed semi-circle, but it seems most likely that the cloud forest will relocate where cloud contact is most frequent (see Section 7.2) as represented by the light grey clouds in the figure. Cloud forests residing at the top of mountains may be pushed into extinction. (b) Relocation of cloud forest species. Speculative impacts on different species within the cloud forest are shown. Three different futures are represented: relocation to a new site (→), staying in the current location (○) and death (×). Of the species that move, some may move upslope, some to other mountain sites and some off the tops of mountains into extinction. Higher altitude species within the cloud forest are more likely to still experience frequent cloud cover (if cloud bases move up in altitude). Therefore, the figure shows a tendency for lower altitude species dying and higher ones surviving. However, all high altitude species may not survive as along with the reshuffling of species mixes, new competitive struggles will be encountered. Furthermore, although new climatically suitable regions may exist, there may be other problems involved in relocation, including migration barriers and rates and no undisturbed location to colonize.
A period when there was no suitable region for CF species appears to have occurred during the LGM in New Guinea when cloud forest species disappeared from the pollen record (Walker and Flenley, 1979) and such a state with no analog climate for CF species may occur again in the future. In the case of epiphytes, not only must the microclimate be reproduced but also the substrate, nutrient input and anchoring conditions. In the case of cloud forests currently residing on peaks and ridges, it seems very plausible that they will be pushed into oblivion.

If an analog climate does exist somewhere in an undisturbed site on the mountain side, cloud forest species’ seeds appear to be capable of traversing long distances to reach a given site. There is evidence for long distance dispersal of cloud forest seeds in both paleo-recorded shifts of distributions and the archipelago-like family grouping of cloud forests (Merlin and Juvik, 1995; Vazquez-Garcia, 1995). But even if the seeds get this far, the battle is still not over. It may take the mature cloud forest 200–300 years to become established, longer than other tropical forests. It is unclear if the suitable climate envelope will have moved on by this time (see Section 7.4). Part of the establishment of a mature forest is a competitive battle with other plants. If non-native species are present, the battle can be much harder to win, as the cloud forest species will not have evolved defenses against these intruders. This appears to have occurred in the tropical montane forests of the Andes where non-native tussocks of grass appear to be arresting the regeneration the cloud forest (Sarniento, 1997a) and similarly in Sri Lankan cloud forests (Werner, 1998).

Aside from the shifting of the climatically suitable region, other climate change threats may increase. For instance, there may be more typhoons, more intense rainstorms and enhanced wind damage in the future. This is particularly devastating for the cloud forest as openings in the canopy of the cloud forest appear to be very slow to regenerate, and in a few cases did not recover at all. Fire, frost and soil damage all act to spread the gap, and prevent regeneration. And once again, the invasion of non-endemic grass species even seems to arrest regeneration (Section 6). Other climate threats include changes in seasonal timing to which plants are very sensitive (Bazzaz, 1998). And of course, there are characteristics of the cloud forest which are little understood, such as the tie between the stunting of trees, the xeromorphic leaves and the frequent cloud cover (Section 3.3). Until this riddle is solved, it is difficult to predict the implications that climate change will have on the cloud forest.

In the case of wholesale loss of old growth forest, much will be lost. Loss or reduction of the cloud forest habitat will mean a loss of endemic species and loss of genetic diversity, with consequent losses to crop cross breeding, local people’s livelihoods, potential medicines and much more. As plants die, the animals that rely on them will also die. Some animals will themselves be directly impacted by climate changes (see Section 5.3). Even if secondary forest can establish itself, it is markedly poorer in biomass and biodiversity (Section 6.3). For instance, old growth trees harbor many more microclimates for epiphytes, which in turn provide food, water and homes for animals. The CF epiphyte community is very dependent on the high humidity of the CF and thus is likely to be adversely affected by increases in water stress from increasing temperatures, decreasing cloudiness and other climate changes (see Fig. 5). Benzing (1998) argues that epiphytes play a large role in the light, water and nutrient cycles of the forest. This suggests that their death may have cascading effects on the CF. Aside from biological loss, destruction of the cloud forest may increase flooding and decrease dry weather flow to downstream ecosystems and human settlements that rely on the cloud forest to provide these water services (Section 5.1). This is particularly alarming as high intensity rainfall events and droughts may both increase under global warming (Section 3.2). Many of these impacts are presented in the flowchart of Fig. 5.

It is often stated in the literature that the intense sensitivity of the cloud forest to climate can be used as an early warning system. In addition to the tight coupling of the life in the cloud forest to climate, the changes in climate at cloud forest locations may change faster than in other regions. As the globe warms, we expect more moisture to be pumped into the atmosphere. This is likely to have two effects that will directly affect the cloud forest. First, the increased atmospheric moisture may shift the value of lapse rate, the change in temperature with altitude,
Fig. 5 Flow chart of potential impacts of climate change. At the top of the figure, potential climate changes are printed in five different colors. A (+) indicates if the effect is expected to increase, and a (−) if a decrease is expected. Potential results of a given climate change are listed below the climate change and are connected by solid lines of the same color as the source climate change. Similarly, subsequent results of impacts that could be the result of all five climate changes, such as water stress or loss of the cloud forest, are connected by dashed lines of the same color as the source climate change. Events that may cause impacts printed above them in the chart are connected by dashed lines with arrows. This chart is not comprehensive but it does list some of the likely outcomes from climate change on the bottom line. The lines leading off of the figure at the top left and right represent common outcomes of increasing dry seasons and extreme events: both will lead to increased soil erosion and wind damage. See the text for discussion.
towards the saturated lapse rate such that high altitude sites experience a greater amount of warming than nearby lowland sites (see Section 3.1). Second, the cloudiness regime will certainly change. Several GCMs suggest that relative humidity in the tropics is likely to decrease by several percent by the time that the CO$_2$ content of the atmosphere has doubled. Other GCMs concur and predict that low-level cloudiness will decrease with warming. A series of studies at the Monteverde Cloud Forest concludes that a recent changes in frog, bird and lizard abundances are linked to a rising cloud base (Section 3.3). Perhaps the warning bell is already ringing.

While climate change is certainly a big threat to the cloud forest, no discussion of the cloud forest would be complete without mentioning the current high-pitched frenzy of rainforest cutting. It has been estimated that TMCFs comprise roughly 1/4 of all tropical montane forests (Persson, 1974) with an annual deforestation rate for tropical hills and mountains of 1.1% (Doumenge et al., 1995). This deforestation rate exceeds that of other tropical forests (0.8%) primarily because montane forests have been left relatively untouched until recently. The TMCFs high altitude and twisted trees, often accompanied by steep slopes, make logging and agriculture difficult. For this reason, they often remain quite pristine and provide a habitat not only for their many endemic species, but serve as a refuge for other montane species whose habitats have been destroyed. This makes the 1.1%/year deforestation rate even more disturbing.

Deforestation pressures on the cloud forest are similar to those on other tropical forests, including logging, mining, road building and clearance for farming and grazing. Furthermore, all forests are threatened by climate change, but the TMCFs appear to be exceptionally vulnerable to climate change. To most effectively save these biologically rich regions will require understanding the roles of human-induced local and global climate change in order to best establish mitigation measures. Yet, we already know enough to state that to save TMCFs requires establishing them as protected forests, as soon as possible, with ample buffer zones around their boundaries to allow for potential altitudinal and latitudinal migration of TMCF species. These protected areas should include mountain ranges and lowland areas that physically connect distinct TMCFs to allow for migration and repopulation.

The UNEP World Conservation Monitoring Centre (http://www.unepwcmc.org/forest/cloudforest/english/homepage.htm) is coordinating a much-needed conservation effort for the TMCF. The mutual support of their program and local people will be essential in the program’s success, see the fascinating case study of the protection of a cloud forest in Ecuador (Becker, 1999). Education will be required to teach conservation measures—both how and why, including how to sustainably farm or harvest the forest. The excellent color brochure by Bruijnzeel and Hamilton (2000) outlining the importance of, and threats to, the cloud forest will certainly be a useful educational tool. Those of us who live in developed countries must do our part to ensure that our personal and government’s money support sustainable forestry. More involvement from scientists in battles to help indigenous people save their sustainable ways of life and protect the world’s forests is desperately needed.

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