The climate of cloud forests

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Abstract:

This chapter analyzes the climatic conditions prevailing at sites where tropical montane cloud forests have been reported. Spatial data-sets of climate were used to describe the climate at 477 cloud forest sites identified by UNEP-WCMC. Some 85% of the sites are found at altitudes between 400 and 2800 m.a.s.l., with an average altitude of 1700 m. The range of altitudes at which cloud forests are found is extensive (220–5005 m). The climate of cloud forests is highly variable from site to site, with an average rainfall of ~2000 mm yr^{-1} and an average temperature of 17.7 °C. In addition, cloud forests are found in seasonal and aseasonal environments alike, both in terms of rainfall and temperature. There are some clear differences in the climates of cloud forests found in Africa, Latin America and the Caribbean, and those in Asia. Cloud forests are found to be wetter (with incident rainfall being 184 mm yr^{-1} higher on average), cooler (by 4.2 °C on average), and less seasonally variable than other montane forests not affected significantly by fog and low cloud. Cloud forests are also almost completely confined to a zone within 350 km from the nearest coast. Finally, the climatic representativity of 14 intensively studied cloud forest sites (ISS) was analyzed; as a group, the sites provided a fair representation of the climates found in cloud forests, evenly covering the ranges in temperature and rainfall. The majority of cloud forest sites occur in regions with 2000–2600 mm of rainfall and annual mean temperatures of 14–18 ^{o}C. Relatively dry cloud forest sites (< 1000 mm of rain yr^{-1}) are under-represented in the UNEP-WCMC data-base.

Keywords: climatic condition, cloud forest, spatial data-sets, montane forest.

Introduction

Tropical montane cloud forests (TMCF) are defined as tropical forests occurring in areas of frequent or persistent ground-level cloud (Grubb, 1977; Bruijnzeel and Proctor, 1995). They generally occur between 1200 and 2500 m.a.s.l. although they may be found below 500 m and even above 3500 m (La Bastille and Poole, 1978; Stadtmüller, 1987; Hemp, 2010). In this paper these forests are simply referred to as "cloud forests". Strictly speaking, the term montane does not always apply. Whilst the boundary between mountains and hills is usually set at 500 m, not all areas above 500 m elevation are mountains (e.g. some are plateaux), hence mountains proper are defined both by their altitude and by their topographic relief (Meybeck *et al.*, 2001).

This paper examines the variation in climatic conditions of areas in which cloud forests are known to occur. Since climate is likely to be a major control on both the hydrology and ecology of cloud forests, setting the climatic context for cloud forests is fundamental to understanding their structure and functioning, and thus the likely impacts of environmental (notably climatic) change upon them (Foster, 2010). Though the prime interest here is not to predict cloud forest distribution by comparing climatic conditions at known cloud forest sites with those prevailing at sites with other montane forest types (Mulligan, 2010), knowledge of climatic conditions will enable a better understanding of the overall conditions that form and maintain the cloud forest ecosystem. This includes examining the geographical context of sites in terms of such factors as distance to the nearest coast, mountain range size and topographic exposure – which are all known to affect temperature, humidity, rainfall, fog occurrence, wind speeds, etc. For example, TMCFs tend to be found at lower altitudes on small outlying mountains compared with large ones (the "mass-elevation" or "telescoping" effect), and this has been related to the fact that large mountain massifs, by their uptake of solar radiation and its slow release as long-wave radiation, may be better at warming the atmosphere above them than do smaller mountains (Schröter, 1926). It is also likely to be the result of a lowering of the cloud base because of the higher humidity levels prevailing in coastal and island areas (Van Steenis, 1972; Bruijnzeel *et al*., 1993) where outlying small mountains often occur. Whichever is the case at a specific location, climate is likely to play an important role in determining forest type and stature, either directly or indirectly, e.g. through its effect on soil properties (notably degree of water-logging and nitrogen content; (Roman *et al.*, 2010; Benner *et al.*, 2010; Bruijnzeel *et al.*, 2010b).

Part one of this paperr uses climate data from a 1-km gridded climate data-base (WorldClim, available from http://www.worldclim.org; Hijmans *et al.*, 2005) for areas of known cloud forests as represented in the World Conservation Monitoring Centre (WCMC) spatial data-base of protected areas (Aldrich *et al*., 1997; UNEP-WCMC, 2004). The range of climatic and environmental conditions in these cloud forests are examined in a latitudinal and altitudinal context and compared with climates for areas covering the same range of altitudes and which support forest as defined by the 1-km FRA2000 data-set; (FAO, 2005), but which are not TMCF according to the UNEP-WCMC data-base. This is done in order to identify the conditions that characterize TMCF and to understand better the global variation of climatic and topographic contexts within which cloud forests exist.

Part two examines the climatic detail of a number of well-studied TMCF sites in Latin America, Africa and South-east Asia (so-called intensively studied sites, ISS) in order to define the range of temperature and precipitation regimes in which these well-known cloud forests occur. These well-studied cloud forest areas are also placed within the wider climatic context for the known (but not necessarily well-studied) tropical cloud forests of part one. In this way, an indication is obtained of how well existing heavily studied sites represent the range of climatic characteristics in which TMCFs are found. Furthermore, climatic similarities and dissimilarities between well-studied sites are pointed out as a means of understanding differences in the interpretation of their hydrologic and ecological structure and functioning (cf. Bruijnzeel and Proctor, 1995; Bruijnzeel, 2001; Roman *et al.*, 2010; Benner *et al.*, 2010; Bruijnzeel *et al.*, 2010b).

Methodology

Objectives

Data-sets on cloud forest localities across the globe, gridded climatic data (WorldClim), and elevation data-sets are used in this paper with the following objectives:

- To examine the relationship between the gridded climate data and ground-measured station data for stations within 5 km of UNEP-WCMC cloud forest sites in order to quantify how representative the WorldClim climates are for those measured on the ground, and their utility in the analysis to come.
- To look briefly into the latitudinal and longitudinal distribution of the cloud forest sites.
- To analyze the climate of areas containing known cloud forests and to compare the climate of these sites with all tropical forest sites.
- To compare the geographic setting of UNEP-WCMC cloud forest sites with all tropical montane sites in terms of distance from sea, size of mountain and topographic exposure.
- To examine climatic differences (including cloud cover) with distance from sea, size of mountain and topographic exposure to see to what extent these variables control climate, beyond the control exerted by altitude alone (as inherent in the WorldClim data because of their interpolation). Further, to examine whether the mass-elevation effect is apparent in the cloud forest distributions.
- To examine the distribution of ISS-climates within the context of cloud forest climates as a whole.

Data-sets used

This analysis was carried out using the UNEP-WCMC data-base of global cloud forest point data (UNEP-WCMC, 2004), and global maps of monthly climatic variables from the WorldClim data-base (Hijmans *et al*., 2005). The UNEP-WCMC data-base represents only well-known cloud forests, many of which are protected areas, and thus constitutes only a sample of areas potentially or actually under cloud forest (indeed, only nine of the 14 ISS used in the present analysis occur in the UNEP-WCMC data-base). Furthermore, the data are given as point locations for what may be large sites representing named places. For example, some data points are plotted as a mountain top when in reality the cloud forest is found in a band at lower altitudes on that mountain (P. Bubb, personal communication). A total of 526 cloud forest sites were identified in the UNEP-WCMC data-set at the time of writing of this paper but because some sites occupied the same 1-km grid cell, or had dubious geographic coordinates, only 477 cells were considered to contain cloud forest for certain. Some additional uncertainty is introduced by the fact that not everyone agrees as to what is and what is not cloud forest, and names and definitions are legion (Stadtmüller, 1987; Grubb, 1977; Frahm and Gradstein, 1991; Bruijnzeel and Hamilton, 2000; Hietz, 2010). Indeed, improving the availability and quality of data on cloud forest distribution is a high priority for this and much other related work (Mulligan, 2010; Lawton *et al*., 2010). In this paper, TMCFs were simply taken as to occur in those areas defined as such by the UNEP-WCMC data-base.

In addition, the 1-km resolution gridded Global Forest Resources Assessment (FRA, 2000) of the UN Food and Agricultural Organization (FAO) (USGS, 2000) has been used alongside the STRM (Shuttle Radar Topography Mission) 30-arc-second (1 km) digital elevation model (DEM) (USGS, 2004) to define all montane forests, "montane" being defined as all areas higher than 500 m after (Meybeck *et al*., 2001), thereby incorporating all levels of topographic roughness (both true mountains and plateaux). Mountain range size was also calculated using this same definition. The Digital Chart of the World (DCW) was used to define coasts (including the shores of the Great Lakes of Africa because these are large enough to produce coastal effects on the local climate; cf. Van der Molen *et al.*, 2006), for the calculation of distance from the coast, which was performed using the distance function in Arcview 3.2.

The main climate data-base used here (WorldClim) was developed through the interpolation of data from climate stations covering the entire terrestrial surface, collated from various data sources including international climate data-bases, such as the Global Historical Climatology Network (GHCN), the FAO, the World Meteorological Organization (WMO), the International Centre for Tropical Agriculture (CIAT), R-HYdronet, as well as a number of country-level data-bases (Hijmans *et al.*, 2004). Only stations with more than 10 years of data were used to produce the data-base, with the majority of stations covering the period 1950–1990. This has resulted in some 46,000 stations for rainfall (rf), 26,000 for mean temperature (T_{mean}) and 18,000 for average daily maximum (T_{max}) and minimum (T_{min}) temperatures. Station data were interpolated using thin-plate smoothing splines (Hutchinson, 1995) with elevation (derived from the SRTM 30 arc-sec elevation data-base) as a co-variable. The result is a continuous surface of monthly climate means (rf, T_{mean}, T_{max}, T_{min}) and mean diurnal range in temperature (T_{range}, calculated as the mean of monthly T_{max} - T_{min}), all with a grid resolution of 30 arc-sec (approximately 1 km at the equator). Because the WorldClim data-base does not include data on cloud cover (one of the variables considered to be of considerable importance here; cf. Mulligan, 2010), these data were extracted from the smaller CIAT climate data-base (Jones, 1991) with 2273 stations in 111 countries throughout the world. Although wind-speed data are sometimes available in gridded climate products, wind-direction data for terrestrial areas are not. Thus, it was not possible to accurately characterize wind as a climatic variable in this paper.

The expected error in Worldclim *rf* data is estimated to be < 10 mm mo^{-1} at the majority of places, while temperature errors are estimated at < 0.3 ºC in most areas (Hijmans *et al*., 2005). Nevertheless, the production of the climate surfaces from relatively sparsely distributed station data fails to capture small-scale orographic processes, and so rainfall in some isolated, very wet areas is underestimated, whilst at some dry spots rainfall is overestimated. Given the significant topographic (and thus climatic) variability in cloud forest environments, slight errors in the geographic coordinates of the sites might also cause significant differences between the interpolated climate surface and the climate on the ground. Moreover, local variations in slope- and aspect-related radiation loads, wind funneling (affecting actually received amounts of rain and fog), cloud cover and cloud base height are not incorporated in WorldClim. As such, application to individual areas or sites should be made with caution.

In all cases climatic, forest and topographic data were extracted only for tropical terrestrial areas (taken here as to lie between 23^o N and 28^o S – the latitudinal range of sites in the UNEP-WCMC TMCF data-base). However, the entire data-set for the tropics is very large (> 2.3 million cells) and this creates some significant data-processing limitations. Hence, a randomly distributed sample of 53,519 cells representing montane forest sites (originally 60,000 but reduced somewhat to include only those cells for which data were available for all variables) was extracted for analysis and comparison with the UNEP-WCMC cloud forest data points (477 cells). Data processing was carried out using a combination of ARC/INFO, Arcview 3.2 and PCRASTER GIS systems.

Analyzing cloud forest climates

Representativity of the WorldClim data-set - WorldClim station data are interpolated in a manner which does not retain values for the individual stations that form the basis of the interpolation (in order to produce smoothed rather than locally pitted and peaked surfaces). Before using this data-base one needs to ascertain how well the interpolated surfaces represent station data near cloud forest sites. Therefore, as a first step, a basic analysis was made to examine the proximity of cloud forest sites to the nearest climate station(s), and the representativity of the positions of the climate stations in the landscape in terms of topographic exposure. Next, to quantify the correlation between interpolated climatic and observed records, WorldClim climatic data for the 1-km cell above each ground station were compared with all available station data within a 5-km radius of the UNEP-WCMC cloud forest sites (150 stations for rainfall and 107 for temperature). Whilst it would have been better to compare WorldClim climates derived for UNEP-WCMC cloud forest points with independent station data, a literature review produced less than ten comparable and long-term climate time-series. In addition, even where such data did exist, they were invariably measured at altitudes different to the average grid-cell altitude in the WorldClim data-base, and usually more indicative of micro-scale climates rather than the more macro-scale climates examined here. Thus, the current test is not an independent test of the quality of the WorldClim data-set (since the very station data that produced the surfaces were used), but rather a test of the extent to which the smoothed data-set still represents on-the-ground climate conditions near observed cloud forest sites.

Geographic distribution of UNEP-WCMC cloud forest sites - the latitudinal and longitudinal distributions of the 477 cloud forest sites in the UNEP-WCMC data-base were examined by producing frequency distributions of cloud forest occurrence in 1-degree classes of latitude and longitude. To avoid location bias introduced by the global distribution of land, the cloud forest site frequencies (grouped into 10-degree classes of longitude and 5-degree classes of latitude) were divided by the area of land within the tropics within each respective band of latitude and of longitude. Land area was calculated from the DCW combined with grids of the latitude and longitude classes. Further, to take account of any bias due to the latitudinal and longitudinal distribution of mountains (altitudes > 500 m), the SRTM 30 arc-sec elevation data-base was used to calculate mountain areas and these were aggregated into the same latitudinal and longitudinal classes as the cloud forest frequencies. The frequencies were then converted to sites per unit mountain area.

Climates of UNEP-WCMC cloud forest sites - for each identified cloud forest site the monthly climate data were extracted from the WorldClim climate surface, and general patterns in temperature and rainfall examined. A rainfall seasonality index was also calculated using a method developed by Markham (1970). The index ranges from 0 to 1, with 0 representing climates with no intra-annual variation, and 1 representing climates with all rain falling in one single month. For the analysis of cloud cover, the CIAT climate data-base was used (consisting of data from 2272 meteorological stations across the globe) and a simple analysis was made of average annual fractional cloud cover as a function of altitude, distance to the nearest coast, and mountain range size to see whether the often cited “mass-elevation” effect was apparent in the data. To better understand the relationship between climate variables and distance from coast, the climate data were extracted for three natural break classes of mountain range size (small: 72,000 km^2 on average, medium: 6.8 million km^2 on average, and large: 14 million km^2 on average) for comparison. Since initial analysis gave reason to suspect that the three mountain range size classes corresponded to the three continents, the analysis was repeated for Latin America and the Caribbean only, so as to confirm whether any climate differences between mountain range size classes were due to mountain range size rather than the geographic configuration of each continent.

Comparison of cloud forest climates with climates of other tropical forests - climate data were extracted for the 477 raster cells with confirmed presence of cloud forest and compared with those extracted for all tropical forests (a random sample of 53,519 forested raster cells) and then for only tropical *montane* forests (also 53,519 forested raster cells found in areas >500m). In each case, the data were examined for each variable by means of frequency distributions and tables. To assess the statistical significance of differences between distributions, a two-sample Kolmogorov-Smirnov (K-S) test was carried out on the distributions in S-Plus 2000 using a 95% confidence level for two independent samples. For a single sample of data, the K-S test was used to test whether or not the sample was consistent with a specified distribution function. For two samples of data, it was used to test whether or not these two samples might reasonably be assumed to come from the same distribution (note that the K-S test does not assume that the data population are normally distributed).

Topographic and geographic setting of cloud forests - a number of climatically-related topographic attributes were calculated using the SRTM 30 arc-sec elevation data-base. Distance from the nearest coast was calculated using DCW data. Mountain range size was approximated by calculating the area that falls inside the 500 m contour (in km^2). This gave large values for parts of large mountain chains and plateaux (primarily the Andes and the African highlands), and smaller values for isolated peaks.

Topographic exposure was calculated using the so-called toposcale procedure of Zimmermann (2004). Toposcale is an ARC-AML algorithm for multi-scale topographic exposure analysis. It applies circular moving-windows with increasing radii to a DEM, and calculates the difference between the average elevation of the window and the elevation of the central cell of the window. The topographic exposure can be interpreted as a ridge or peak if the central cell in the moving window has a higher elevation than the average elevation of the cells in the surrounding window. Integration into a single multi-scale measure is achieved by starting with the standardized exposure values of the largest window, then adding standardized values from smaller windows where they exceed the values of the larger-scale map. In this analysis search radii of 3–15 cells were used (i.e. a maximum search radius of approximately 15 km). Although other techniques for the calculation of directional exposure are available (e.g TOPEX; Ruel *et al.*, 2002), these require wind-direction data which are generally not available at the global scale. Moreover, toposcale has practical advantages over such large grids because of its operation in ARC-INFO and its computational ease compared with TOPEX. The multi-scale approach of toposcale is also preferable in this case where the scale at which exposure is important is unknown. Next, the resulting distance to coast, mountain range size and topographic exposure data were extracted and compared for all tropical mountains and cloud forest sites. Data examination and testing for statistical significance of differences between the two distributions were carried out as described in the previous paragraph. Key climatic variables were examined as a function of topographic exposure. In each case a random sample of 53,519 cells in the montane tropics was extracted for analysis.

Representativity of intensively studied cloud forest sites - the climates extracted for the 14 ISS were compared with the data for the 477 UNEP-WCMC cloud forest sites. To understand the interaction between climatic factors and to place the ISS within the wider context of all identified cloud forest sites, a summary table of ISS climates was produced, as well as a simple scatter-plot of T_{mean} versus rainfall, presenting the position of the ISS within the total range of TMCF sites. Although this probably captured the most important climatic factors, multivariate statistics were then applied so as to capture the variability across the remaining climatic factors. Principal components analysis (PCA) was applied to annual means of T_{mean}, T_{max}, T_{min} and T_{range}, as well as to annual rainfall, and monthly seasonality of rainfall. The first two principal components were then plotted, again with the ISS highlighted amongst all UNEP-WCMC cloud forest sites. Finally, in order to assess the degree of climatic similarity between the 14 ISS, a cluster analysis was performed using Ward's method (Ward, 1963) and the variables cited above.

Results

Testing the interpolation of the WorldClim data-set

It is encouraging to note that the average distance between cloud forest sites and the nearest climate station in the WorldClim data-base proved relatively small: on average 21 km for rainfall, vs. 38 km for T_{mean} and 53 km for T_{max} and T_{min}. The minimum distance was zero km while maximum distances were as high as 122 km for rainfall and 342 km for T_{mean} (367 km for T_{min} and T_{max}). Nevertheless, in a montane setting a station some 21 km from its nearest cloud forest can have a very different altitude, aspect and exposure, and thus a very different climate. The climate stations were found across a range of topographic exposures, with 56% of the stations having neutral levels of topographic exposure, while 25% were located at topographically exposed sites and 19% at unexposed sites.

The comparison of gridded WorldClim data (WC) and station data (ST) for cells close to cloud forests showed good qualitative correspondence for the 130 stations with a rainfall of less than 3000 mm yr^{-1} ($Rain_{WC} = 0.85Rain_{ST} + 230$, $r^2 = 0.75$), but for stations with more than 3000 mm of rain ($n = 18$) the relationship broke down ($Rain_{WC} = 0.22Rain_{ST} + 2430$, $r^2 = 0.26$). For all rainfall values the best relationship proved to be logarithmic ($Rain_{WC} = 1373.1\mathrm{Ln}(Rain_{ST}) - 8370$, $r^2 = 0.81$) indicating that locally high rainfalls are reduced in the interpolated data. For all 130 stations with annual rainfall below 3000 mm, the average residual indicated a remarkable conformity, with the gridded rainfall being only 10.5 mm less than the corresponding station rainfall as positive and negative residuals cancelled each other out. However, individual stations did show large residuals, with the average absolute residual being 83.7 mm yr^{-1}. For the 18 stations with rainfall in excess of 3000 mm the average residual indicated that the gridded data were about 1204 mm yr^{-1} lower than the equivalent station data. These 18 stations are distributed across altitudes ranging from 500 m to 2900 m, with 69% of the stations being located at topographically exposed sites. Clearly, rainfall data are only sufficiently reliable for the present analysis in the case of stations receiving less than 3000 mm annually.

WorldClim annual mean temperatures also showed good qualitative correspondence with ground data (T_{WC} = 0.9971*T_{ST}, r^2 = 0.87; n = 103) and the average residual indicated T_{WC} to be only 0.05°C higher than T_{ST}. The absolute residual showed individual grid cells to differ on average by around 0.05°C compared with the stations underneath them, implying an interpolation error inferior to the expected measurement error of the temperature sensors themselves. As such, for temperature (which is a much simpler function of altitude than rainfall), the errors are low, both overall and at-a-station, thereby increasing confidence in interpolations for individual cloud forest sites. By and large, the WorldClim data constitute a good representation of the station data from which they were produced, and where stations are within close proximity to cloud forests the WorldClim data will represent those forest climates well. However, where stations are further away or climatic gradients steep, the WorldClim data will be less representative.

Geographic distribution of UNEP-WCMC cloud forest sites

The 477 cloud forest sites of the UNEP-WCMC data-base are spread across 62 countries. Countries with more than ten confirmed sites include: Indonesia, Mexico, Malaysia, Venezuela, Ecuador, Philippines, Papua New Guinea, Colombia, Honduras, Perú, Kenya, Sri Lanka, Costa Rica and Panamá. The latitudinal distribution of the cloud forests shows a significant clustering close to the equator, with the majority of sites (83%) found in the northern hemisphere tropics. Arguably, this is to be expected because 60% of the tropical terrestrial surface and nearly 83% of tropical mountains (land above 500 m) lie north of the equator. However, even when expressed per unit mountain area there are still proportionally more confirmed cloud forests north of the equator (by a factor of four). The longitudinal distribution of cloud forests is also highly unequal.Even when taking into account the land mass at each longitude, some longitudes have ten times the number of cloud forests sites as others, also after expressing the number of sites per unit area of mountains at each longitude. This inequality in latitudinal and longitudinal distributions may reflect disparities in sampling effort but is also likely to reflect climatic or topographic differences.

Climates of UNEP-WCMC cloud forest sites

Because of the high spatial variability in the climate of tropical mountain ranges, along with the smoothing induced by the climatic interpolation and inaccuracies in cloud forest classification and geographic position, there will be random errors in the distribution of climates across the UNEP-WCMC sites with confirmed cloud forest presence. Such errors are expected to be most pronounced at climatic extremes and for small sites located along steep topographic and climatic gradients. Nevertheless, one would expect the general patterns to be representative.

<Figure 1>

Figure 1 presents frequency histograms of altitude, annual rainfall and rainfall seasonality, as well as of T_{mean}, T_{max}, and T_{min} at the 477 UNEP-WCMC cloud forest sites. Table I lists averages and maximum and minimum values of these variables for all the sites, whereas Table II gives the average climatic parameters separated by continent. In general, the histograms cover a wide range of climatic conditions. The average altitude of the cloud forest sites is slightly less than 1700 m, with 77% of all sites lying between 500 m and 2800 m. One site is registered as low as 22 m, but this is most likely an artifact of a small error in the geographic coordinates over steep terrain. As many as 48 UNEP-WCMC cloud forest sites (10%) are registered below the 500 m altitude threshold used here to define montane forest. Some of these may, again, be due to erroneous coordinates, or represent island sites where cloud forests have been documented to occur at lower than usual altitudes (Stadtmüller, 1987). This may also occur due to considerable altitudinal variation within a 1-km grid cell. Within-cell altitudinal variation reached as much as 5517m in the Himalayas, and had a global upper quartile range of 550 m (Hijmans *et al*., 2005), indicating that the cloud forest site might be in a higher elevation sector of the grid cell.

<Table I>

The average annual rainfall for all sites is ~2000 mm (Table I), with 94% of sites having between 800 mm and 3400 mm. The wettest site is located at Bukit Batu Bora in Malaysia, receiving 4500 mm annually, although high rainfall sites are likely to be significantly underestimated in this analysis. T_{mean} for all sites is 17.7^{o}C, spanning a large range. The lowest value (allegedly ~1 ^{o}C) concerns Puncak Jaya/Mount Carstensz in Irian Jaya (Indonesia) at 3800 m but this is very likely an example of location error in the cloud forest points data-set. The maximum value is 27.3 ^{o}C, at Mount Halcon ("22 m") in the Philippines. Levels of rainfall seasonality also vary a great deal between sites, with the index showing a negative skew and ranging from just 0.01 (practically homogenous rainfall distribution as found in Santa Cruz, Ecuador) to 0.76 (highly seasonal, with a long pronounced dry season, in the Simen Mountains in Ethiopia). The high coefficients of variation calculated for each climatic variable indicate the high degree of variability in climates between cloud forests sites.

<Table II>

<Figure 2>

Examining the climatic conditions for each continent (Table II and Figure 2), some clear differences become apparent. Cloud forest sites in Africa tend to be drier (average rainfall less than 1500 mm yr^{-1}), with Asia tending to have significantly wetter cloud forests (~ 2150 mm of rain on average) and the Latin American and Caribbean (LAC) region experiencing a wide range of rainfall conditions (Figure 2). African cloud forests also have the highest rainfall seasonality and LAC ones the lowest. Average temperatures are fairly similar for each continent, but Asian cloud forests tend to have a lower diurnal temperature range (9.3 ^{o}C compared with 10.3 ^{o}C and 10.4 ^{o}C for Latin America and Africa, respectively) whereas African cloud forests also tend to be warmer. However, such differences are likely to be as much a function of differences in overall climate between the regions as differences in the climates favoured by cloud forests, since the distribution of cloud forests is also limited by other, non-climatic factors.

Comparison of cloud forest climates with climates of other tropical montane forests

Comparing cloud forest climates with those for all tropical montane forests gives a clearer distinction of the specific climatic characteristics of cloud forests compared with their nearest neighbours. The differences are presented as tabulated averages (Table III), and the frequency distributions for cloud forests alongside those for tropical montane forests in general are shown in Figure 3. Annual rainfall for cloud forests is on average 184 mm higher than for other tropical montane forests (2027 mm vs. 1842 mm), with the minimum cloud forest rainfall being ~320 mm higher than for other montane forests. Variations between sites are similar (CVs of ~41% in both cases). Mean temperature is some 4.2 °C lower for cloud forests than for other montane forests. Site-to-site variability in all temperature variables is higher for cloud forests but rainfall seasonality is lower for cloud forests as is T_{range} (although it is more variable between sites).

Cloud forests are negatively skewed towards higher rainfall regimes (even though these are probably underestimated) compared with tropical montane forests in general. The rainfall seasonality index for cloud forests is positively skewed (i.e. they are generally less seasonal) compared with tropical montane forests. T_{mean} is significantly negatively skewed for cloud forests compared with tropical montane forests in general (i.e. cloud forests occur in cooler environments) whereas the same patterns exist for T_{max} and T_{min}. Finally, T_{range} is positively skewed for cloud forests compared with all tropical montane forests (i.e. they occur in diurnally less variable environments).

<Table III>

<Figure 3>

The results of the Kolmogorov-Smirnov (KS) tests (Table IV) indicate that the distributions for cloud forest and all tropical montane forests are all statistically dissimilar (p-values < 0.05 in all cases), although some distributions are more different than others. The greatest differences occur in T_{max} (*KS*-value 0.49), and T_{mean} (0.47) whereas the distributions are most similar for rainfall seasonality (0.19) and rainfall (0.25).

<Table IV >

Topographical and geographical settings of cloud forests

Describing and comparing the topographical and geographical settings of cloud forests may help to explain the climatic patterns observed, but also point to other potentially important factors that interact with these climatic factors to determine the distribution of cloud forests, such as distance to coast, or mountain range size and site exposure. A correlation analysis between altitude, mountain range size, topographical exposure and distance to coast showed low correlations between the variables, the highest correlation coefficient being 0.27 for altitude vs. exposure. The respective variables are therefore sufficiently independent and the climatic effects assigned to each variable in the following analyses are thus the result of that variable and not due to co-linearity with other variables.

Altitude - the identified cloud forest sites had an average altitude of 1687 m (Table I) compared with 993 m for other montane tropical forests. The altitude of the cloud forests was highly variable between sites (CV = 56%) and they occurred over a much wider range of altitudes compared with all tropical montane forests (Figure 4a). The K-S results for this variable indicated a significant difference between the two distributions (*KS* = 0.43; Table IV).

<Figure 4>

Distance to coast - the distance from the nearest coast at which known cloud forests are found was also highly variable (Figure 4b), averaging 103 km but ranging from just 50 m (for some island cloud forests) to nearly 950 km for Pico de Neblina in Brazil (Table I). Asian sites are much closer to the coast (on average 57 km), with Latin American and African sites on average being situated over twice that distance from the coast (Table II). This is likely to reflect the characteristics of available land in these regions as much as the tolerances of the cloud forest communities themselves. Cloud forests tend to be much closer to coasts than other tropical montane forests (Figure 4b, with average distances of 103 km and 445 km, respectively). Indeed, known cloud forests are almost completely confined to within 350 km from the nearest coast (Figure 4b) and occur relatively rarely in continental interiors (< 5 % of sites). The K-S analysis also shows a very significant difference between the cloud forest and general montane forest distributions (*KS* = 0.48; Table IV).

Topographical exposure - a topographical exposure analysis indicated that the average exposure for all montane sites was –0.81 (slightly sheltered) vs. 96.3 (exposed) for cloud forest sites. The distributions are clearly different (Figure 4c) and a Kolmogrov-Smirnov test indicated that the difference between the two distributions is the most significant of all climate and topographic variables analyzed (*KS* = 0.51, Table IV). Since exposure is directionally dependent it would be useful to repeat the analysis for exposure relative to the (idealized) locally dominant wind directions throughout the tropics.

Mountain range size and the "mass-elevation" effect - average mountain range size for the tropical montane forest group was determined at 8.24 million km^2, compared with 3.26 million km^2 for cloud forests. The associated frequency distributions (Figure 4d) are dominated by the broken distribution of mountain range sizes which correspond to the Andes (the smallest cluster), the African Highlands and the Himalayas. The K-S test indicated that size of mountain area is also a significant variable in distinguishing cloud forests sties from tropical montane forest sites (*KS* = 0.44, Table IV).

An analysis of the relationship between altitude and mountain range size, and altitude and distance from coast yielded no significant correlation when all cloud forests sites were used, nor when the analysis was restricted to LAC-cloud forest sites ($r^2 < 0.1$ in all cases). However, an analysis of the relationship between altitude and the climate variables for stations separated into classes of mountain range size showed that the climate vs. altitude relationships differed for the three classes of mountain range size distinguished here. Because the analysis might be confounded by the fact that the mountain range size classes occupy different continents (which may have different altitude–climate relationships for other reasons than the mountain range sizes themselves) the analysis was repeated just for the LAC-region (n = 30,300). Mountain range size data for the latter conveniently separated into two equal-sized groups: (i) Andean (part of the large mountain region that covers the entire Andes, average mountain area 14.6 million km^2) and (ii) non-Andean (smaller, isolated mountain ranges, islands etc., mean mountain area 1.72 million km^2). Altitude was, on average, lower for mountains in the "large" mountain category (899 m compared with 1081 m) and thus T_{mean} was also higher for this group (22.6 °C vs. 21.3 °C), although annual rainfall was lower (1517 mm for the large mountains and 2200 mm for the smaller mountains).

The altitude–climate relationships show some important differences between the two classes of mountain (Figures 5 and 6). The adiabatic lapse rate for T_{mean} is slightly less (but not statistically significant) for large mountains (0.51 °C 100 m^{-1}) compared with small mountains (0.53 °C 100 m^{-1}), although average T_{mean} at sea-level is some 0.5°C higher in the vicinity of large mountains. At a given altitude, temperature is generally higher for larger mountains and, especially, the difference in maximum or minimum temperature with mountain range size increase with altitude (Figure 5). As a result, T_{range} also increases much more with altitude for larger mountains than for smaller ones. This conforms with the idea that small mountains have a steeper adiabatic lapse rate due to the “mass-elevation” effect, although the differences are small. Theoretically, this effect might be confounded if smaller mountains tend to occur nearer to coasts where climates tend to be more humid and cloud condensation (and thus cloud forest occurrence) tends to happen at lower elevations than further inland. However, a correlation analysis showed no significant correlation between mountain range size and distance to coast for the global tropical montane data-set (n = 53,519, r^2 = 0.19) so this is unlikely. The difference in average lapse rates between large and small mountains suggests that clouds would form some 43 m lower on small mountains than on large mountains (assuming the same base temperature). The average difference of 0.5 ^{o}C in base temperatures between small and large mountains has more than double this effect, with clouds forming ~100 m lower over small mountains. Together, the two effects cause cloud formation on average to be about 143 m lower over small mountains compared with larger mountains.

<Figure 5 >

Variations in rainfall with altitude in the LAC-cloud forest data were much more diverse than for temperatures (Figure 6) and no clear patterns emerged. Large mountains show a decrease in rainfall with altitude, particularly above 1500 m. Small mountain ranges, on the other hand, sometimes show no major change in rainfall with altitude and sometimes increased rainfall since at these smaller scales precipitable water is less likely to be limiting and orographic effects will dominate. Thus, the diversity of patterns reflects the diversity in orographical and meso-climatic settings found in mountainous Latin America and the Caribbean.

<Figure 6 >

Cloud cover

Although annual average cloud cover fraction is highly variable at any given altitude (Figure 7a), the minimum observed cloud cover increases with altitude so that one can find sites with low cloud cover at low altitudes, but much less so at high altitudes. Areas of high and low cloud cover are found at low altitudes but above 2000 m elevation the majority of sites have annual average cloud cover fractions greater than 0.5. There is also a general (but weak) decrease in average cloud cover with increasing distance from the coast. The minimum observed annual average cloud cover increases with distance from coast but the maximum decreases at the same time (Figure 7b).

<Figure 7>

Looking into the cloud-cover data on a frequency basis adds some clarity to these patterns. By aggregating altitude, distance to sea, and mountain range size into classes and then calculating the frequency of sites with annual average cloud cover greater than 50% (0.5 fraction) in each of these classes (Figure 8), it becomes clear that from 0–2000 m altitude the percentage of sites with cloud cover >50% decreases from 60% to around 40% but then increases dramatically to close to 100% from 2000 m to over 3000 m before falling off again (Figure 8a). In terms of distance to coast, 60% of the sites have >50% cloud cover at the coast, increasing to 80% at ~100 km inland and then falling off to 30% at ~500 km inland (Figure 8b). Sample sizes beyond 500 km inland were too small for any robust analysis.

<Figure 8 >

Representativity of intensively studied cloud forest sites

Intensively studied sites (ISS) with an established body of research were selected based on a review of cloud forest research, principally the studies listed in Hamilton *et al.* (1995), and the key research sites selected by Bruijnzeel (2001). In all, 14 sites were selected (see Figure 9 for locations), covering Maui in the Hawaiian archipelago (one site), Latin America and the Caribbean (eight sites), Africa (two sites), and Asia (three sites). This list is not exhaustive, but does attempt to be representative of the many sites across the globe where intensive studies have been conducted. ISS are found at altitudes ranging from 350 m (Luquillo Mountains, Puerto

Rico) to 2700 m (Rwenzori Mountains, Uganda), averaging 1400 m. Relative to other cloud forest sites they are closer to coasts (average distance 41 km), with the Estacion San Francisco in southern Ecuador being the most distant ISS from the coast (141 km).

The climates of the ISSs (Table V and Figures 10–14) tend to cover a broad range of conditions. Monteverde (Costa Rica) and Krakatau (Indonesia) are the wettest sites (with 3105 mm and 3180 mm of rain yr^{-1}, respectively), but they differ in terms of T_{mean}, Monteverde being significantly cooler (20.9 ^{o}C) than Krakatau (24.8 ^{o}C). The Rwenzori Mountains (Uganda), Gunung Silam (East Malaysia), and Luquillo (Puerto Rico) have the least seasonality in rainfall, whilst El Rincon (Mexico), Serrania de Macuira (Colombia), and Sierra de las Minas (Guatemala) have the highest levels of seasonality.

Figure 10 shows the mean temperatures and annual rainfall totals for all UNEP-WCMC cloud forest sites as well as for the ISS. On the whole, the intensively studied sites provide a fair representation of the climates found in cloud forests, evenly covering the ranges in temperature and rainfall (with the proviso that WorldClim rainfall estimates for some of the ISS may be underestimates). The majority of cloud forest sites occur in regions with 2000–2600 mm of rainfall and annual mean temperatures of 14–18 ^{o}C, with five ISS clustering in this range (Mount Cameroon, Blue Mountains, San Francisco, Sierra de las Minas, and East Maui). However, relatively dry cloud forest sites (< 1000 mm of rain yr^{-1}) are under-represented, and low-temperature sites (mean temperatures 10–13 ^{o}C) are also lacking.

<Figure 10 >

Examining only rainfall and temperatures fails to account for many other important climatic factors which strongly affect the biology and hydrology of cloud forests. The multivariate principal components analysis performed on the seven variables described earlier provided two components which accounted for 72.5% of the total variance. Figure 11 presents a plot of these two variables, which provides greater detail in examining the representativity and similarity of ISS in the wider cloud forest context. The first principal component contains high positive loadings for T_{mean}, T_{max} and T_{min}, whilst the second component has a high positive loading for mean annual rainfall, and a high negative loading for rainfall seasonality. The ISS are well distributed throughout the multivariate space, once again confirming that they are representative of the range of climates found in cloud forests.

<Figure 11 >

Figure 12 provides a further analysis of the similarity between sites using cluster analysis. Broadly speaking, these two figures highlight three main clusters within the ISS. The first cluster containing El Rincon and Serrania de Macuira, represents relatively hot and dry, and highly seasonal conditions. The second cluster (Krakatau, Gunun Silam, Monteverde, East Maui, Luquillo, San Francisco, and Rwenzori) have average to high rainfall, relatively warm climates and very low seasonality. The third and final cluster (Yuangyang Lake, Tambito, Blue Mountains, Sierra de las Minas and Mount Cameroon) are characterized by lower temperatures, intermediate levels of seasonality, relatively high rainfall, and low diurnal ranges in temperature. The Hawaiian site in East Maui is perhaps the most atypical cloud forest site (at least in terms of the variables examined here) whereas the Serrania de Macuira stands out as an extreme site with very low rainfall (600 mm) and high mean temperature (24.0 ^{o}C).

<Figure 12 >

Discussion and conclusions

Cloud forests in the UNEP-WCMC data-base show a preferential distribution towards northern hemisphere latitudes close to the equator and they also cluster longitudinally. Both clusterings occur irrespective of any bias that might be introduced due to the uneven distribution of tropical mountains. The climatic conditions leading to the generation and maintenance of cloud forests must be prevalent in these areas.

It has been shown here through coupling of a series of global data-sets that 85% of the 526 known cloud forest sites are found at altitudes between 400 and 2800 m, with an average altitude of slightly less than 1700 m. The range of altitudes at which cloud forests are found is impressive (220–5005 m). The climate of cloud forests is highly variable from forest to forest, with an average rainfall of about 2000 mm yr^{-1} and an average temperature of 17.7 °C. In addition, cloud forests are found in seasonal and in aseasonal environments alike, both in terms of rainfall and temperature. There are some clear differences in the climates of cloud forests found in Africa, Latin America and the Caribbean, and Asia.

Compared with other tropical montane forests, cloud forests are wetter (by 184 mm yr^{-1} on average) and cooler (by 4.2 °C on average) whereas individual cloud forests are also more climatically varied than tropical montane forests in general. At the same time, cloud forests are less seasonally variable in terms of rainfall than other montane forests. The most statistically significant climatic differences between cloud forests and other montane forests in order of significance are: maximum temperature > mean temperature > rainfall > rainfall seasonality.

Cloud forests are almost completely confined to within 350 km from the nearest coast, and are located closer to coasts than montane forests in general. Cloud forests also occupy more topographically exposed areas and differently sized mountains than montane forests in general. The order of significance for geographic differences between cloud forests and montane forests in general is: topographic exposure > distance to coast > mountain range size > altitude, and these variables show little to no co-linearity. Overall, the order of statistical difference in geographical and climatic variables for cloud forests compared with montane forests in general as expressed by the Kolmogorov-Smirnov test is: topographic exposure (0.51) > distance to coast (0.49) ≈ maximum temperature (0.49) > mean annual temperature (0.47) > mountain range size (0.44) > altitude (0.43) >> rainfall (0.25) > rainfall seasonality (0.19).

Thus, cloud forests tend to occur in fairly coastal climates and environments with lower maximum and mean temperatures and higher altitudes compared with other montane forests. Where this is not the case, cloud forests occur in areas with higher rainfall coupled with lower rainfall seasonality than other montane forests. This is no paradigm shift compared to earlier qualitative descriptions (Stadtmüller, 1987; Hamilton *et al.*, 1995; Bruijnzeel and Veneklaas, 1998), but it is important that these trends are observed in the global data-sets used in the present analysis. The fact that topographical exposure is an important characteristic defining cloud forests is indicative that other climatic variables may be important (particularly wind speed), and further macro-scale analyses of cloud forest climates are required to better understand these relationships.

Analysis of the WorldClim data has shown that temperature at a given altitude is higher for larger mountains, which is in agreement with the “mass-elevation” effect, with smaller mountains having a steeper adiabatic lapse rate and thus a potentially lower cloud condensation level, leading in turn to a lowered occurrence of cloud forest (cf. Foster, 2010). The presently used method of calculation of mountain range size excluded mountains less than 500 m high (by definition) and this may have had implications for the observed lack of relationship between mountain range size and distance to coast, as well as the frequency distribution of mountain range sizes for tropical montane (cloud) forests. Large mountains also have a much greater diurnal range in temperature (i.e. lower minimum and higher maximum temperatures) at a given altitude, which probably results from the climatic effects of the mountain on local air masses. The effect is not small: the altitude at which a maximum temperature of 20 °C is reached is some 800 m lower for the smaller mountains in the LAC region than for the larger ones (cf. Figure 5).

High cloud cover (> 60%) is frequent near sea-level and above 2000 m and within 100 km from the coast and this is likely to be one of the most significant climatic variables for cloud forests and the reason why altitude, temperature and distance to coast are important to cloud forest distribution (cf. Van Steenis, 1972). Furthermore, the fact that cloud forests are shown here to occur preferentially at topographically exposed sites indicates that exposure to the climate is critical. Exposed sites where ground-level cloud is frequent, are likely to receive additional water inputs from this source while evaporative losses are reduced (Bruijnzeel and Proctor, 1995, Bruijnzeel, 2001).

Whilst the data used here have been useful in demonstrating broad patterns, some important improvements are necessary to allow more regional analyses to be made and enhanced robustness of some of the results presented here, especially at the extremes of the climatic distributions. First and foremost, a data-base of cloud forest sites is needed that incorporates more of the actual cloud forests and includes more precise information on their extent as well as location and type (cf. Mulligan, 2010; Bruijnzeel et al., 2010a). This could be achieved by coupling satellite-derived cloud-base altitudes with remotely sensed data on forest cover (cf. Nair *et al.*, 2008; Lawton *et al.*, 2010). Moreover, improvements in the incorporation of small-scale rainfall variability in the WorldClim data-base would be of use, as would be the availability of further climate parameters that may be of importance for cloud forest climates (notably wind speed and direction, fog inputs, wind-driven rain, and solar radiation). At the national to regional scale, incorporation of these variables has proved useful in identifying water budget “hot spots” in montane tropical areas, and in identifying priority areas for conservation (Mulligan and Burke, 2005).

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	Annual Precipitation (mm)	Annual Mean Temperature (^{o}C)	Maximum Temperature (^{o}C)	Minimum Temperature (^{o}C)	Range in Temperature (^{o}C)	Seasonality Index	Altitude (m)	Distance to Coast (km)
Average	2027	17.70	22.41	12.95	9.47	0.32	1687	102.71
Max	4541	27.29	34.03	23.64	16.78	0.76	5005	946.71
Min	405	0.93	3.99	-2.07	1.80	0.01	22	0.05
Stand. Coeff. Var. (%)	41.0	28.6	23.2	40.3	26.4	57.2	56.1	120.7

Table I. Summary of annual climatic variables for all WCMC sites, using the WorldClim climate data-base.

Continent	Annual Precipitation (mm)	Annual Mean Temperature (^{o}C)	Maximum Temperature (^{o}C)	Minimum Temperature (^{o}C)	Range in Temperature (^{o}C)	Seasonality Index	Altitude (m)	Distance From Coast (km)
Latin America + Hawaii	1779	17.48	22.60	12.31	10.29	0.35	1747	121.57
Africa	1489	18.36	23.53	13.13	10.40	0.39	1619	135.22
Asia	2150	17.63	22.23	12.98	9.26	0.30	1687	56.90

Table II. Summary of climatic conditions for all WCMC sites separated by continent.

Cloud forest minus all tropical forest	T_{mean}	T_{max}	T_{min}	T_{range}	Annual Rainfall	Rainfall Seasonality Index
Average	-7.0	-7.4	-6.5	-0.9	-63	-0.03
Max	-1.8	-2.3	-1.3	-2.4	-3497	-0.11
Min	-3.3	-5.1	-1.1	-2.1	320	0.01
Coeff. Var	18.4	15.0	25.1	6.6	6.17	3.47

Table III. Climate data on aggregate for cloud forest sites compared with all other tropical forests. Negative values indicates variable value is less for cloud forest compared with tropical forest in general and positive values indicate the variable value is greater for cloud forest than tropical forest in general.

Cloud forest minus all tropical *montane* **forest**	T_{mean}	T_{max}	T_{min}	T_{range}	**Annual Rainfall**	**Rainfall Seasonality Index**
Average	-4.2	-5.0	-3.4	-1.6	185	-0.06
Max	-0.7	-1.4	0.9	-2.4	-2316	-0.09
Min	2.6	1.0	4.2	-1.9	320	0.01
Coeff. Var	15.0	11.6	20.4	4.6	-0.16	-0.58

Table IV. Climate data on aggregate for cloud forest sites compared with all other tropical *montane* forests. Negative values indicates variable value is less for cloud forest compared with tropical montane forest in general and positive values indicate the variable value is greater for cloud forest than tropical montane forest in general.