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Tropical montane forests are a larger than expected global carbon store

D. V. Spracklen[1] and R. Righelato[2]

[1]School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK
[2]Environmental Systems Science Centre, University of Reading, Reading, UK

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Correspondence to: D. V. Spracklen (dominick@env.leeds.ac.uk)

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Abstract

Tropical montane forests (TMFs) are recognised for the provision of hydrological services and the protection of biodiversity, but their role in carbon storage is not well understood. We synthesized published observations (n = 89) of above-ground biomass (AGB) from forest inventory plots in TMFs (defined here as forests between 23.5° N and 23.5° S with elevations ≥ 1000 m a.s.l.). We found that mean (median) AGB in TMF is 257 (239) t per hectare of Earth's surface. We demonstrate that AGB declines moderately with both elevation and slope angle but that TMF store substantial amounts of biomass, both at high elevations (up to 3500 m) and on steep slopes (slope angles of up to 40°). We combined remote sensed datasets of forest cover with high resolution data of elevation to show that seventy five percent of the planimetric global area of TMF are on steep slopes (slope angles greater than 27°). We used our remote sensed datasets to demonstrate that this prevalence of steep slopes results in the global land-surface area of TMF (1.22 million km^2) being 40 % greater than the planimetric (horizontal) area that is the usual basis for reporting global land surface areas and remotely sensed data. Our study suggests that TMF are likely to be a greater store of carbon than previously thought, highlighting the need for conservation of remaining montane forests.

1 Introduction

Tropical montane forests (TMFs) are important for the provision of ecosystem services particularly water (Martínez et al., 2009) and biodiversity (Martínez et al., 2009; Gentry, 1992), but their role in global carbon storage is less well known (Bruijnzeel and Veneklaas, 1998). In lowland tropical forests there have been recent advances in our understanding of above-ground biomass (AGB) storage, through synthesis of data from forest inventory plots (Baker et al., 2004; Malhi et al., 2006; Gibbs et al., 2007; Saatchi et al., 2007; Slik et al., 2010; de Castilho et al., 2006; Lewis et al., 2013) and application of remote sensing techniques (Asner et al., 2010; Saatchi et al., 2011; Baccini et al., 2012; Simard et al., 2011). However, knowledge of AGB storage in TMF is still quite poor: persistent cloud cover and steep terrain makes remote sensing difficult (Simard et al., 2011; Castel et al., 2001), there is a paucity of plot-based data which is difficult to acquire on steep slopes (Malhi et al., 2006), and few attempts have been made to synthesise the available observations. Tropical montane forest soils can also contain large amounts of biomass, similar in magnitude to the amount of AGB, though insufficient data are available to include this parameter in our analysis (e.g., Moser et al., 2011; Álvarez-Arteaga et al., 2013; Omoro et al., 2013).

The higher elevations of TMFs result in changes to many important environmental variables including temperature, rainfall, cloud cover, incoming solar radiation, wind speed, nutrient inputs and soil type (Lieberman et al., 1996). The impact of these environmental variables on biomass storage is not well known. TMF are also commonly located on steep slopes, impacting forest structure through altering access to space and light resources (Robert, 2003) and through altering the incidence of landslides (Dislich and Huth, 2012). TMF typically have lower canopy height than lowland forests (Kitayama and Aiba, 2002; Leuschner et al., 2007; Fisher et al., 2013; Girardin et al., 2014a) which may be expected to reduce AGB storage. Studies along elevational transects in the Andes have reported increasing stem density with elevation (Girardin et al., 2014a), but no trends in basal area (Girardin et al., 2014a). Leaf area index appears to either have little trend with elevation (Fischer et al., 2013) or to decline with increasing elevation (Leuschner et al., 2007). Previous studies of AGB along a single elevational transect have found declining (Kitayama and Aiba, 2002; Raich et al., 2006; Girardin et al., 2010, 2014a), increasing (Rai and Proctor, 1986) or no (Culmsee et al., 2010) relationship with elevation. Regional studies suggest that elevation may not be the most important variable in explaining the variability in AGB (Slik et al., 2010; Leuschner et al., 2007), with rainfall and soil characteristics explaining more of the variability in AGB across Borneo compared to elevation. Previous analysis has mainly focused on lowland tropical forests and has correlated AGB with temperature (Raich et al., 2006), rainfall (Malhi et al., 2006; Saatchi et al., 2007; Slik et al., 2010), soils (Malhi et al., 2006; Saatchi et al., 2007; Slik et al., 2010), slope angle (Mascaro et al., 2011) and specifics related to the tree community (Baker et al., 2004). Below ground carbon also varies with elevation, with fine root biomass increasing along elevational transects in the Andes (Kitayama and Aiba, 2002; Leuschner et al., 2007; Moser et al., 2011; Girardin et al., 2013).

To improve our understanding of AGB storage in TMFs we synthesised estimates of live AGB from forest inventory plots that have been reported in the peer reviewed literature. We explored the role of topographical and climatological variables in controlling AGB. We then used satellite remote sensing observations of pan-tropical forest cover and topography to explore the impact of slope angle on AGB storage.

2 Methods

2.1 Forest inventory plots

We synthesised peer reviewed studies of AGB storage in TMFs. We defined TMFs as forests between latitudes of 23.5° N and 23.5° S and at altitudes ≥ 1000 m a.s.l. Where available we also synthesised topographical (elevation and slope angle) and climatological variables (annual mean temperature and annual mean rainfall) from the same plots. AGB was typically reported per unit area of the Earth's surface although some studies reported AGB per unit planimetric area. For the latter, we used information on slope angle to convert AGB to a surface area basis.

We used stepwise multiple linear regression to assess controls on AGB. Regressions of all independent variables (elevation, slope angle, mean annual temperature, mean annual precipitation) were calculated and variables with insignificant correlations ($P > 0.05$, tested using a t test of the correlation coefficient) were discarded. Variables were sorted according to the significance of the correlation coefficient and incorporated into the multiple regression in declining order. This process was repeated until the strength of the correlation did not increase by a preset amount.

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2.2 Remote sensed data

We used remote sensed datasets to analyse the area and topography of TMFs. To analyse the global extent of TMF, we used a remote sensed dataset of humid tropical forest cover at a resolution of 18.5 km for the year 2000 (Hansen et al., 2008). This product uses Landsat 7 ETM+ to calibrate the vegetation continuous field (VCF) product from the MODerate-resolution Imaging Spectroradiometer (MODIS) sensor onboard NASA's Terra satellite (Hansen et al., 2003). The VCF is derived from all 7 bands of the MODIS sensor and contains proportional estimates for vegetation cover (woody vegetation, herbaceous vegetation and bare ground).

To explore the topography of TMF we used the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) 7.5 arc second (~ 250 m horizontal resolution) mean elevation product. GMTED2010 is based on data from 11 different sources with the primary source being the Shuttle Radar Topography Mission. To calculate the elevation of tropical forests we averaged the GMTED data to the same spatial resolution of the forest cover product. We calculated the angle of slope across the tropics at the native resolution of GMTED. Slope was calculated for each pixel of the DEM from the mean height of all the pixel neighbours. Our calculated slope will be a lower limit, primarily due to variability in elevation at spatial resolutions less than 250 m.

3 Results and discussion

We synthesised 89 mean observations of AGB in TMF (Table 1) at locations across the Neotropics (North, Central and South America), Africa and Asia and at elevations up to 3600 m. In our dataset, the AGB in TMF varied from 77 $\mathrm{t\,ha^{-1}}$ to 785 $\mathrm{t\,ha^{-1}}$ of the Earth's surface with mean (median) storage of 257 (239) $\mathrm{t\,ha^{-1}}$. We found that mean AGB in Asian TMF was 257 $\mathrm{t\,ha^{-1}}$ ($n = 31$), greater than the mean AGB in Neotropical TMF which was 219 $\mathrm{t\,ha^{-1}}$ ($n = 51$), although the difference was not significant (Student's t test, $P > 0.1$). Very few data were available for African TMF, where mean AGB was 527 $t\,ha^{-1}$ ($n = 7$). The overall pattern in TMFs matches that observed in lowland forests, where Neotropical forests have significantly less AGB than Asian and African lowland tropical forests (Slik et al., 2010; Paoli et al., 2008), possibly due to the prevalence of large trees in Asian forests (Slik et al., 2013).

Figure 2a compares AGB in Asian and Neotropical TMF against that reported in recent syntheses of AGB in lowland forests (Malhi et al., 2006; Slik et al., 2010; de Castilho et al., 2006). We found AGB in TMF to be significantly lower than that in lowland forests both in the Neotropics (Student's t test, $P < 0.01$) and Asia ($P < 0.01$) (Fig. 2a). To explore the relationship between elevation and AGB we combined the montane data synthesised here with lowland data from previous analysis (Malhi et al., 2006; Slik et al., 2010; de Castilho et al., 2006). Across the combined lowland and montane Asian and neotropical data ($n = 309$), elevation has a modest control on AGB ($r^2 = 0.15$) with a reduction of ~ 50 t biomass ha^{-1} for a 1000 m increase in elevation (AGB ($t\,ha^{-1}$) = 362 – 0.057× elevation (m)) (Fig. 2b). Similar relationships were found when the analysis was restricted to the neotropics ($n = 191$) ($r^2 = 0.20$, AGB ($t\,ha^{-1}$) = 303 – 0.038× elevation (m)). This decline in AGB with increasing elevation is consistent with a recent analysis along six Andean elevational transects (Girardin et al., 2014a). We found a weaker relationship between AGB and elevation when we restricted our analysis to TMF ($n = 82, r^2 = 0.001, P > 0.1$). Indeed, within TMF we found no significant difference (Student's t test, $P > 0.1$) between carbon storage in upper-montane (elevation ≥ 2000 m, $n = 32$, mean = 231 $t\,ha^{-1}$) compared to lower-montane (1000 m < elevation < 2000 m, $n = 50$, mean = 235 $t\,ha^{-1}$) forests. So whilst TMF have a lower AGB per unit land surface area compared to lowland forests, montane forests still store substantial amounts of biomass up to elevations of 3500 m.

We also explored the correlation between AGB and climatological and topographical variables. In our combined dataset (TMF and lowland forests where all variables are available, $n = 104$) we find that elevation ($r^2 = 0.15, P < 0.01$), slope angle ($r^2 = 0.14, P < 0.01$, Fig. 2c) and annual mean temperature ($r^2 = 0.16, P < 0.01$) have modest correlations with AGB, whereas there is little correlation with annual mean

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rainfall ($r^2 = 0.01, P > 0.1$) (Table 2 and Fig. 3). We used multiple linear regression to further understand the topographical and meteorological controls on AGB. Our multiple regression model explained 24.3 % of the variance in AGB ($F_{2,104} = 16.2, P < 0.01$) with elevation and slope angle being the two significant variables in the model (AGB, t ha^{-1}) = 349 – 0.032 × elevation (m) – 2.81 × slope angle (°)). Our analysis is restricted to tropical sites, so elevation and temperature and strongly correlated in our dataset ($r^2 = 0.97$). We note that elevation is not a direct controlling factor with many environmental variables varying along elevational gradients (Girardin et al., 2014a). When we restricted our analysis to TMF ($n = 21$, elevations ≥ 1000 m) we found weak correlations with annual mean temperature ($r^2 = 0.05$) and annual mean rainfall ($r^2 = 0.09$) and a modest correlation with slope angle ($r^2 = 0.31$) (Table 2). Lack of strong correlation of AGB with topographic and climatic variables has been previously reported (Slik et al., 2010; Leuschner et al., 2007). Other environmental parameters such as nutrient availability (Fischer et al., 2013), soil properties, ultra-violet light exposure, light exposure, cloud immersion or wind speed may play an important role in AGB storage (Girardin et al., 2014a). Fischer et al. (2013) reported increased nitrogen limitation but decreased phosphorus limitation with increasing elevation. Studies of net primary productivity along elevational transects display abrupt changes at specific elevations that may be associated with factors such as frequency of cloud immersion controlling light and humidity (Girardin et al., 2010, 2014a). Seasonal variability in NPP at two montane forest sites in the Andes is also linked to solar radiation and cloud immersion (Girardin et al., 2014b) potentially implicating these variables as important drivers of AGB storage. Variability in tree species richness, which in the Andes is greatest at mid-elevations (1000–1500 m a.s.l), also has potential implications for carbon storage (Girardin et al., 2014a). Furthermore, it is possible that soil properties which are known to affect AGB in lowland forests (de Castilho et al., 2006; Paoli et al., 2008), may also have a strong affect on AGB in TMF. We were not able to explore the role of such factors because they were not systematically reported in the studies synthesised here. Future

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studies of AGB in TMFs need to observe and report a larger suite of environmental parameters.

Most forest inventory plots are established over a fixed land-surface area (Malhi et al., 2006). For example, the RAINFOR protocol uses land-surface area as the metric for plot establishment (Phillips et al., 2009). AGB from forest plots is typically reported as the biomass stored per unit area of land-surface, whereas remote sensed forest data are reported on a planimetric basis. Alternatively, AGB can be reported as the biomass stored per planimetric (horizontal) area (Mascaro et al., 2011). In regions with gentle slopes there is little difference between land-surface area and planimetric area so the distinction is often assumed to be unimportant. However, on steep slopes the land-surface area can be substantially greater than the planimetric surface area, with the ratio being a factor 1.41 on a 45° slope. This means that biomass storage on a planimetric area basis can be substantially greater than on a land-surface area basis. Across our TMF dataset, at sites where slope angle is reported ($n = 46$), the angle varied from 0° to 40° with a mean slope angle of 18°. This results in AGB storage in our TMF plots being, on average, 7 % greater when calculated per unit of planimetric area compared to when calculated per unit of the Earth's surface (Fig. 2b). On the steepest slopes in our dataset, AGB on a planimetric surface is 31 % greater than that calculated on a land-surface area. In contrast, in the lowland forests plots there is a mean slope of 10° ($n = 86$) resulting in AGB being on average only 3 % greater when calculated per planimetric surface area as compared to land-surface area. The relationship between AGB and elevation in our dataset (TMF and lowland data) is weaker when AGB is calculated on a planimetric surface ($r^2 = 0.07$) compared to when calculated on a surface area basis ($r^2 = 0.14$). Repeating the multi-linear regression analysis using AGB calculated on a planimetric basis reduces the sensitivity of AGB to slope angle by one third compared to the calculation based on surface area ($AGB_{planimetric}$ $(\mathrm{t\,ha^{-1}}) = 347 - 0.032 \times \mathrm{elevation}(m) - 1.82$ slope angle (°), $r^2 = 0.18$, $F_{2,104} = 11.3$). In lowland neotropical forests, previous work has found that slope angle has little (de Castilho et al., 2006) or positive (Mascaro et al., 2011) impact on planimetric AGB. Our

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analysis extends these previous works through including forests plots on slopes with steeper angles and suggests that whilst AGB (planimetric) declines moderately with increasing slope angle, forests on steep slopes (up to angles of 40°) still store substantial amounts of biomass.

The regional and global area of forests is reported as the planimetric surface area and regional biomass stocks are typically calculated by multiplying the biomass storage per unit area by the planimetric area of the forested region (Gibbs et al., 2007; Baccini et al., 2012). If these calculations use biomass storage per unit land surface area, there is the potential to underestimate regional biomass stocks in forests with steep slopes.

To explore whether slope has implications for the regional biomass stocks of TMF we combined a high-resolution (7.5 arc sec; ~ 200 m pixel at the equator) digital elevation model (DEM) with a global dataset of moist tropical forest cover (Hansen et al., 2008). With these datasets, TMF cover 0.88 million km^2 (planimetric area) accounting for 8.3 % of total tropical forest area (Fig. 4a). Figure 1 shows the global distribution of tropical forests as a function of elevation. TMF are distributed across the tropics (47 % in neotropics, 40 % Asia, 13 % Africa) and concentrated in Papua New Guinea, Indonesia, Yunnan Province (China) and throughout the Andes in Central and South America. For each pixel of the DEM we calculated the angle of slope. The frequency of different slope angles is shown in Fig. 4b. In the lowland tropical forests the average slope angle is 11° with 50 % of forests having slope angles of less than 9°. Steeper slopes are more frequent in TMF with the mean slope being 32° and 75 % of forests having slope angles of greater than 27°. We note that the mean slope angle in TMF is greater than that in our forest inventory dataset, confirming biases in the site selection of forest plots to gentle slopes (Malhi et al., 2006).

We used information on slope angle to calculate the ratio of land-surface area to planimetric area across the forested area of the tropics. Figure 5 displays the spatial pattern of this ratio, which reaches a factor 2 across TMF of the Andes, Indonesia and Papua New Guinea. These estimates are likely to be a lower limit due to variability in elevation at scales below the resolution of the DEM. Most lowland tropical forests have ratios less than 1.05 although some lowland forest regions of the Amazon basin (e.g., Guiana Shield) have ratios up to 1.25. Figure 4c compares the global distribution of this ratio in lowland forests and TMF. More than 60 % of lowland forests have a surface area to planimetric area of less than 1.05. In TMF, ratios up to 2 are common with the most frequent ratio being around 1.4. We find the global land-surface area of TMF is 1.22 million km^2, 40 % greater than the planimetric area reported above. The less steep terrain typical of lowland tropical forests results in a 7 % difference between land-surface area (10.4 million km^2) and planimetric area (9.7 million km^2) of these forests.

We have demonstrated that the AGB storage of TMF depends on elevation and slope angle. Forest inventory plots confirm that TMF store considerable biomass both at high elevations (up to 3600 m) and on steep slopes (slope angles up to 40°). On such steep slopes the land-surface area is substantially greater than the planimetric area, meaning that estimation of regional biomass storage in montane forests needs to account for slope.

Here we have restricted our work to analysis of AGB as few comparable data are available for below ground biomass. Previous work has documented the importance of below ground carbon storage within TMF soils (Raich et al., 2006; Leuschner et al., 2007) which in some cases may exceed AGB stores (Frangi and Lugo, 1985) and will further increase the importance of these ecosystems as a global carbon store. Deforestation and degradation of TMFs are ongoing (Armenteras et al., 2003; Cayuela et al., 2006). This, combined with the negative implications of future climate change on ecosystem functioning in TMFs (Foster, 2001), highlights the urgent need for conservation attention. Whilst the majority of focus for the role of carbon finance in forest conservation has been on lowland forests, our analysis highlights the significance of TMF as a global carbon store.

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References

Álvarez-Arteaga, G., García Calderón, N. E., Krasilnikov, P., and García-Oliva, F.: Carbon storage in montane cloud forests in Sierra Norte of Oaxaca, Mexico, Agrociencia, 47, 171–180, 2013.

Alves, L. F., Vieira, S. A., Scaranello, M. A., Camargo, P. B., Santos, F. A. M., Joly, C. A., and Martinelli, L. A.: Forest structure and live above ground biomass variation along an elevational gradient of topical Atlantic moist forest (Brazil), Forest Ecol. Manag., 260, 679–691, 2010.

Armenteras, D., Gast, F., and Villareal, H.: Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia, Biol. Conserv., 113, 245–256, 2003.

Asner, G. P., Powell, G. V. N., Mascaro, J., Knapp, D. E., Clark, J. K., Jacobson, J., Kennedy-Bowdoin, T., Balaji, A., Paez-Acosta, G., Victoria, E., Secada, L., Valqui, M., and Hughes, R. F.: High-resolution forest carbon stocks and emissions in the Amazon, P. Natl. Acad. Sci. USA, 107, 16738–16742, 2010.

Baccini, A., Goetz, S. J., Walker, W. S., Laporte, N. T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P. S. A., Dubayah, R., Friedl, M. A., Samanta, S., and Houghton, R. A.: Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps, Nat. Clim. Change, 2, 182–185, 2012.

Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Lloyd, J., Monteagudo, A., Neill, D. A., Patino, S., Pitman, N. C. A., Silva, J. N. M., and Martinez, R. V.: Variation in wood density determines spatial patterns in Amazonian forest biomes, Glob. Change Biol., 10, 545–562, 2004.

Bruijnzeel, L. A. and Veneklaas, E. J.: Conditions and tropical montane forest productivity: the fog has not lifted yet, Ecology, 79, 3–9, 1998.

Castel, T., Beaudoin, A., Stach, N., Stussi, N., Le Toan, T., and Durand, P.: Sensitivity of space-borne SAR data to forest parameters over sloping terrain, theory and experiment, Int. J. Remote Sens., 22, 2351–2376, 2001.

Cayuela, L., Benayas, J. M. R., and Echeverria, C.: Clearance and fragmentation of tropical montane forests in the Highlands of Chiapas, Mexico (1975–2000), Forest Ecol. Manag., 226, 208–218, 2006.

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Chen, D. X., Li, Y. D., Liu, H. P., Xu, H., Xiao, W. F., Luo, T. S., Zhou, Z., and Lin, M. X.: Biomass and carbon dynamics of a tropical mountain rain forest in China, Sci. China Life Sci., 53, 798–810, 2010.

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., and Holland, E. A.: Net primary production in tropical forests: an evaluation and synthesis of existing field data, Ecol. Appl., 11, 371–384, 2001.

Culmsee, H., Leuschner, C., Moser, G., and Pitopang, R.: Forest aboveground biomass along an elevational transect in Sulawesi, Indonesia, and the role of Fagaceae in tropical montane rain forests, J. Biogeogr., 37, 960–974, 2010.

Cunha, G. D., Gama-Rodrigues, A. C., Gama-Rodrigues, E. F., and Velloso, A. C. X.: Biomass, carbon and nutrient pools in montane Atlantic forests in the North of Rio de Janeiro State, Brazil, Rev. Bras. Cienc. Solo, 33, 1175–1185, 2009.

de Castilho, C. V., Magnusson, W. E., de Araujo, R. N. O., Luizao, R. C. C., Lima, A. P., and Higuchi, N.: Variation in aboveground tree live biomass in a central Amazonian Forest: effects of soil and topography, Forest Ecol. Manag., 234, 85–96, 2006.

Delaney, M., Brown, S., Lugo, A. E., Torres-Lezama, A., and Quintero, N. B.: The distribution of organic carbon in major components of forests located in five life zones of Venezuela, J. Trop. Ecol., 13, 697–708, 1997.

Dislich, C. and Huth, A.: Modelling the impact of shallow landslides on forest structure in tropical montane forests, Ecol. Monitor., 239, 40–53, 2012.

Dossa, G. G. O., Paudel, E., Fujinuma, J., Yu, H., Chutipong, W., Zhang, Y., Paz, S., and Harrison, R. D.: Factors determining forest diversity and biomass on a tropical volcano, Mt. Rinjani, Lombok, Indonesia. PLoS ONE, 8, e67720, doi:10.1371/journal.pone.0067720, 2013.

Edwards, P. J. and Grubb, P. J.: Studies of mineral cycling in a montane rain forest in New Guinea, I. The distribution of organic matter in the vegetation and soil, J. Ecol., 65, 943–969, 1977.

Feshe, J., Hofstede, R., Aguirre, A., Paladines, C., Kooijman, A., and Sevink, J.: High altitude tropical secondary forests: a competitive carbon sink?, Forest Ecol. Manag., 163, 9–25, 2002.

Fisher, J. B., Malhi, Y., Torres, I. C., Metcalfe, D. B., van de Weg, M. J., Meir, P., Silva-Especjo, and Huasco, W. H.: Nutrient limitation in rainforests and cloud forests along a 3000 m elevation gradient in the Peruvian Andes, Oecologia, 172, 889–902, 2013.

BGD
10, 18893–18924, 2013

Foster, P.: The potential negative impacts of global climate change on tropical montane cloud forests, Earth-Sci. Rev., 55, 73–106, 2001.
Frangi, J. L. and Lugo, A. E.: Ecosystem dynamics of a subtropical floodplain forest, Ecol. Monogr., 55, 351–369, 1985.
Gentry, A. H.: Tropical forest biodiversity: distribution patterns and their conservation significance, Oikos, 63, 19–28, 1992.
Gibbon, A., Silman, M. R., Malhi, Y., Fisher, J. B., Meir, P., Zimmermann, M., Dargie, G. C., Farfan, W. R., and Garcia, K. C.: Ecosystem carbon storage across the grassland-forest transition in the high Andes of Manu National Park, Ecosystems, 13, 1097–1111, 2010.
Gibbs, H. K., Brown, S., Niles, J. O., and Foley, J. A.: Monitoring and estimating tropical forest carbon stocks: making REDD a reality, Environ. Res. Lett., 2, 045023, doi:10.1088/1748-9326/2/4/045023, 2007.
Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., Feeleys, K. J., Rapp, J., Silva-Espejo, J. E., Silman, M., Salinas, N., and Whittaker, R. J.: Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes, Glob. Change Biol., 16, 3176–3192, doi:10.1111/j.1365-2486.2010.02235.x, 2010.
Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D., and Silvae, J. E.: Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests, Global Biogeochem. Change, 27, 252–264, 2013.
Girardin, C. A. J., Farfan-Rios, W., Garcia, K., Feeley, K. J., Jørgensen, P. M., Murakami, A. A., Pérez, L. C., Seidel, R., Paniagua, N., Claros, A. F. F., Maldonado, C., Silman, M., Salinas, N., Reynel, C., Neill, D. A., Serrano, M., Caballero, C. J., La Torre-Cuadros, M. D. L. A., Macìa, M. J., Killeen, T. J., and Malhi, Y.: Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects, Plant Ecol. Divers., 1–11, doi:10.1080/17550874.2013.820806, 2014a.
Girardin, C. A. J., Espejob, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca, L., Marthews, T. R., Aragao, L. E. O. C., Farfàn-Rios, W., Garcìa-Cabrera, K., Halladay, K., Fisher, J. B., Galiano-Cabrera, D. F., Huaraca-Quispe, L. P., Alzamora-Taype, I., Eguiluz-Mora, L., Salinas-Revilla, N., Silman, M. R., Meir, P., and Malhi, Y.: Productivity and carbon allocation in a tropical montane cloud forest of the Peruvian Andes, Plant Ecology and Diversity, 7, 107–123, 2014b.

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Grimm, U. and Fassbender, H. W.: Ciclos bioquímicos en un ecosistema forestal de los Andes Occidentales de Venezuela, I. Inventario de las reservas organicas y minerales (N, P, K, Ca, Mg, Mn, Fe, Al, Na), Turrialba, 31, 27–37, 1981.

Hansen, M., DeFries, R. S., Townshend, J. R. G., Carroll, M., Dimiceli, C., and Sohlberg, R. A.: Global percent tree cover at a spatial resolution of 500 meters: first results of the MODIS Vegetation Continuous Fields Algorithm, Earth Interact., 7, 1–15, 2003.

Hansen, M. C., Stehman, S. V., Potapov, P. V., Loveland, T. R., Townshend, J. R. G., DeFries, R. S., Pittman, K. W., Arunarwati, B., Stolle, F., Steininger, M. K., Carroll, M., and DiMiceli, C.: Humid tropical forest clearing from 2000 to 2005 quantified using multi-temporal and multi-resolution remotely sensed data, P. Natl. Acad. Sci. USA, 105, 9439–9444, 2008.

Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., and Leuschner, Ch.: Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests, Forest Ecol. Manag., 258, 1904–1912, 2009.

Hofstede, R. and Aguirre, N.: Biomasa y dinámica del carbono en relación con las actividades forestales en la Sierra del Ecuador, in: El Páramo Como Espacio de Mitigación de Carbono Atmosferico, Serie Páramo 1, edited by: Medina, G. and Mena, P., Ediciones Abya Yala, Quito, 29–51, 1999.

Kitayama, K. and Aiba, S. I.: Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo, J. Ecol., 90, 37–51, 2002.

Leuschner, C., Moser, G., Bertsch, C., Roderstein, M., and Hertel, D.: Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador, Basic Appl. Ecol., 8, 219–230, 2007.

Lewis, S. L., Sonke, B., Sunderland, T., Begne, S. K., Lopez-Gonzalez, G., van der Heijden, G. M. F., Phillips, O. L., Affum-Baffoe, K., Baker, T. R., Banin, L., Bastin, J.-F., Beeckman, H., Boeckx, P., Bogaert, J., De Canniere, C., Chezeaux, E., Clark, C. J., Collins, M., Djagbletey, G., Djuikouo, M. N. K., Droissart, V., Doucet, J.-L., Ewango, C. E. N., Fauset, S., Feldpausch, T. R., Foli, E. G., Gillet, J.-F., Hamilton, A. C., Harris, D. J., Hart, T. B., de Haulleville, T., Hladik, A., Hufkens, K., Huygens, D., Jeanmart, P., Jeffery, K. J., Kearsley, E., Leal, M. E., Lloyd, J., Lovett, J. C., Makana, J.-R., Malhi, Y., Marshall, A. R., Ojo, L., Peh, K. S.-H., Pickavance, G., Poulsen, J. R., Reitsma, J. M., Sheil, D., Simo, M., Steppe, K., Taedoumg, H. E., Talbot, J., Taplin, J. R. D., Taylor, D., Thomas, S. C., Toirambe, B., Verbeeck, H., Vlem-

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inckx, J., White, L. J. T., Willcock, S., Woell, H., and Zemagho, L.: Above-ground biomass and structure of 260 African tropical forests, Phil. Trans. R. Soc. B, 368, 1625, 20120295, doi:10.1098/rstb.2012.0295, 2013.

Lieberman, D., Lieberman, M., Peralta, R., and Hartshorn, G. S.: Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica, J. Ecol., 84, 137–152, 1996.

Malhi, Y., Wood, D., Baker, T. R., Wright, J., Phillips, O. L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T. J., Laurance, S., G., Laurance, W. F., Lewis, S. L., Monteagudo, A., Neill, D. A., Vargas, P. N., Pitman, N. C. A., Quesada, C. A., Salomão, R., Silva, J. N. M., Lezama, A. T., Terborgh, J., Martínez, R. V., and Vinceti, B.: The regional variation of aboveground live biomass in old-growth Amazonian forests, Glob. Change Biol., 12, 1107–1138, 2006.

Martínez, M. L., Pérez-Maqueo, O., Vázquez, G., Castillo-Campos, G., García-Franco, J., Mehltreter, K., Equihua, M., and Landgrave, R.: Effects of land use change on biodiversity and ecosystem services in tropical montane cloud forests of Mexico, Forest Ecol. Manag., 258, 1856–1863, 2009.

Mascaro, J., Asner, G. P., Muller-Landau, H. C., van Breugel, M., Hall, J., and Dahlin, K.: Controls over aboveground forest carbon density on Barro Colorado Island, Panama, Biogeosciences, 8, 1615–1629, doi:10.5194/bg-8-1615-2011, 2011.

Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N., and Iost, S.: Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment, Glob. Change Biol., 17, 2211–2226, 2011.

Nadkarni, N. M., Schaefer, D., Matelson, T. J., and Solano, R.: Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica, Forest Ecol. Manag., 198, 223–236, 2004.

Omoro, L. M. A., Starr, M., and Pellikka, P. K. E.: Tree biomass and soil carbon stocks in indigenous forests in comparison to plantations of exotic species in the Taita Hills of Kenya, Silva Fenn., 47, 935, 2013.

Paoli, G. D., Curran, L. M., and Slik, J. W. F.: Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo, Oecologia, 155, 287–299, 2008.

Phillips, O., Baker, T., Feldpausch, T., and Brienen, R.: RAINFOR field manual for plot establishment and remeasurement, available at: http://www.rainfor.org/upload/ManualsEnglish/

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RAINFOR_field_manual_version_June_2009_ENG.pdf (last access: 15 November 2013), 2009.
Proctor, J., Anderson, J. M., Chai, P., and Vallack, H. W.: Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak: I. forest environment, structure and floristics, J. Ecol., 71, 237–260, 1983.
Rai, S. N. and Proctor, J.: Ecological studies on four rainforests in Karnataka, India, J. Ecol., 74, 439–454, 1986.
Raich, J. M., Russell, A. E., and Vitousek, P. M.: Primary productivity and ecosystem development along an elevational gradient on Manua Loa, Hawaii, Ecology, 78, 707–721, 1997.
Raich, J. W., Russell, A. E., Kitayama, K., Parton, W. J., and Vitousek, P. M.: Temperature influences carbon accumulation in moist tropical forests, Ecology, 87, 76–87, 2006.
Robert, A.: Simulation of the effect of topography and tree falls on stand dynamics and stand structure of tropical forests, Ecol. Monitor., 167, 287–303, 2003.
Román-Cuesta, R. M., Salinas, N., Asbjornsen, H., Oliveras, I., Huaman, V.Gutiérrez, Y., Puelles, L., Kala, J., Yabar, D., Rojas, M., Astete, R., Jordán, D. Y., Silman, M., Mosandl, R., Weber, M., Stimm, B., Günter, S., Knoke, T., and Malhi, Y.: Implications of fires on carbon budgets in Andean cloud montane forest: the importance of peat soils and tree resprouting, Forest Ecol. Manag., 261, 1987–1997, 2011.
Saatchi, S. S., Houghton, R. A., dos Santos Alvalá, R. C., Soares, J. V., and Yu, Y.: Distribution of aboveground live biomass in the Amazon basin, Glob. Change Biol., 13, 816–837, 2007.
Saatchi, S. S., Harris, N. L., Brown„ S., Lefsky, M., Mitchard, E. T. A., Salas, W., Zutta, B. R., Buermann, W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M., and Morel, A.: Benchmark map of forest carbon stocks in tropical regions across three continents, P. Natl. Acad. Sci. USA, 108, 9899–9904, doi:10.1073/pnas.1019576108, 2011.
Saner, P., Loh, Y. Y., Ong, R. C., and Hector, A.: Carbon stocks and fluxes in tropical lowland Dipterocarp rainforests in Sabah, Borneo, PLoS one, 7, e29642, doi:10.1371/journal.pone.0029642, 2012.
Scatena, F. N., Silver, W., Siccama, T., Johnson, A., and Sanchez, M. J.: Biomass and nutrient control of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989, Biotropica, 25, 15–27, 1993.
Sierra, C. A., del Valle, J. I., Orrego, S. A., Moreno, F. H., Harmon, M. E., Zapata, M., Colorado, G. J., Herrera, M. A., Lara, W., Restrepo, D. E., Berrouet, L. M., Loaiza, L. M., and

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Benjumea, J. F.: Total carbon stocks in a tropical forest landscape of the Porce region, Colombia, Forest Ecol. Manag., 243, 299–309, 2007.
Simard, M., Pinto, N., Fisher, J. B., and Baccini, A.: Mapping forest canopy height globally with spaceborne lidar, J. Geophys. Res., 116, G04021, doi:10.1029/2011JG001708, 2011.
Slik, J. W. F., Aiba, S. I., Brearley, F. Q., Cannon, C. H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A. D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E., and van Valkenburg, J. L. C. H.: Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests, Global Ecol. Biogeogr., 19, 50–60, 2010.
Slik, J. W.F., Paoli, G., McGuire, K., Amara, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.-L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.-F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Nagamasu, A. A.-M., H., Nilus, R., Nurtjahya, E., Oliveira, A., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-Aguilar, G. E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.-G., and Zweifel, N.: Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics, Global Ecol. Biogeogr., 22, 1261–1271, doi:10.1111/geb.12092, 2013.
Spracklen, D. V. and Righelato, R.: Carbon storage and sequestration in tropical montane forests of southern Ecuador, World Land Trust, Halesworth, Suffolk, UK, 2005.
Tanner, E. V. J.: Studies on the biomass and productivity in a series of montane rain forests in Jamaica, J. Ecol., 68, 573–588, 1980.
Weaver, P. L. and Murphy, P. G.: Forest structure and productivity in Puerto Rico's Luquillo Mountains, Biotropica, 22, 69–82, 1990.

Table 1. Synthesis from the literature of above-ground biomass (AGB) measurements in tropical montane forests (elevation ≥ 1000 m a.s.l.). AGB values marked with * are reported on a planimetric basis. All other values reported on a land-surface basis. We also synthesis literature values from the pre-montane zone (defined here as elevations between 300 m and 1000 m a.s.l.).

Location	Lat., Lon.	Elevation (m)	AGB ($t\,ha^{-1}$)	MAT (°C)	Rainfall ($mm\,yr^{-1}$)	Slope (°)	Reference
Lowland forest, Puerto Rico	~ 18.4° N, ~ 66.1° W	320	226				Scatena et al. (1993)
Montane moist forests, Andes, Venezuela	8.62° N, 71.35° W	2250	409	13.5	1500		Grimm and Fassbender (1981)
Lowland moist forest, Caimital, Venezuela	9.5° N, 70° W	150	308	26	1500		Delaney et al. (1997)
Lowland moist forest, Ticoporo, Venezuela	9° N, 64° W	240	396	25.5	2850		Delaney et al. (1997)
Montane moist forest, Rio Grande, Venezuela	9.5° N, 71° W	2400	395	15	2433		Delaney et al. (1997)
Upper montane wet forest, Mucuy, Venezuela	10.5° N, 71° W	2820	354	10.5	1968		Delaney et al. (1997)
Montane wet forest, Bismarck Range, Papua New Guinea	6.0° S, 145.18° E	2500	310	13	3980		Edwards and Grubb (1977)
Upper montane wet forest, South-Ecuador	~ 4° S, ~ 79° W	2800	149				Hofstede and Aguiree (1999)
Montane wet forest, Pacific Slope, Ecuador	~ 3° S, ~ 80° W	2300	255				Hofstede and Aguiree (1999)
Oyacachi Alnus forest, Cayambe-Coca Ecological Reserve, Napo Province Ecuador	0.22° S, 78.05° W	3200	241	10.5	2250		Feshe et al. (2002)

Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t\,ha^{-1}$)	MAT (°C)	Rainfall ($mm\,yr^{-1}$)	Slope (°)	Reference
Pifo Polyepis forest, Pichincha province, Ecuador	0.23° S, 78.25° W	3600	366	8	1500		Feshe et al. (2002)
Metrosideros stands, Hawaii	19.75° N, 155.25° W	700	123	19.5	6000		Raich et al. (1997)
		1660	81	13.0	2600		
Montane tropical forest, Lore Lindu National Park, Sulawesi, Indonesia	1.44° S, 120.18° E	1050	308.7	21.3	1894	5	Culmsee et al. (2010)
		1400	304.6	19.5	1975	5	
		1800	301.4	17.3	1891	5	
		2400	322.6	14.1	2131	5	
Tropical forest, SE Peru	12.83° N, 69.27° W	194	330	26.4	2730		Girardin et al. (2010)
	12.84° N, 69.28° W	210	300	26.4	2730		
Montane tropical forest, SE Peru	12.95° N, 71.57° W	1000	159	20.7	3087		Girardin et al. (2010)
	13.05° N, 71.53° W	1500	205.6	18.8	2631		
	13.07° N, 71.55° W	1855	111.2	18	2472		
	13.07° N, 71.55° W	2020	77.2	17.4	1827		
	13.11° N, 71.58° W	2720	131.8	13.5	2318		
	13.11° N, 71.6° W	3020	94	11.8	1776		
	13.18° N, 71.58° E	3025	129.8	12.5	1706		
Montane cloud forest, Monteverdre, Puntarenas Province, Costa Rica	10.3° N, 84.8° W	1480	245.1				Nadkarni et al. (2004)[a]
Montane cloud forest, CordilleriaCentral, Costa Rica	10.4° N, 84.0° W	100	278	24	4000	0	Lieberman et al. (1996)[a, b]
		300	325	23	6000	0	
		500	261	22	7000	0	
		750	346	20.5	8000	0	
		1000	261	19	7000	0	
		1250	145	17.5	6000	0	
		1500	215	16	5000	0	
		1750	268	14.5	4000	0	
		2000	271	13	3500	0	
		2300	349	11	3500	0	
		2600	362	10.5	3300	0	

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Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t\,ha^{-1}$)	MAT (°C)	Rainfall ($mm\,yr^{-1}$)	Slope (°)	Reference
Porce region, Columbia	6.75° N, 75.1° W	1200	247.8	21.5			Sierra et al. (2007)
Lore Lindu National Park, Sulawesi, Indonesia	1.5° S, 120.05° E	1050	286			0	Hertel et al. (2009)
Serra do Mar Mountains, São Paulo State, Brazil	23.43° S, 45.12° W	400 400 1000	208.9* 253.8* 283.2*			20 40 40	Alves et al. (2010)
Puu Kolekole, Hawaii, USA	21.15° N, 156.8° W	1210	137	16	2500		Clark et al. (2001)
Laupahoehoe, Hawaii, USA	19.95° N, 155.3° W	1170	266	16	2500		Clark et al. (2001)
Kokee, Hawaii, USA	22.05° N, 159.5° W	1134	206	16	2500		Clark et al. (2001)
Kohala, Hawaii, USA	20.05° N, 155.9° W	1122	145	16	2500		Clark et al. (2001)
Puerto Rico, USA	18.42° N, 66° W	750	229	19.7	3725	10	Frangi and Lugo (1985)
Luquillo Mountains, Puerto Rico	~ 18.3° N, ~ 65.8° W	725 450 1000	138.5 197.9 82.9	20 21 19	3725 3000 4300		Weaver and Murphy (1990)
Blue Mountains, Jamaica	18° N, 77° W	1615 1600 1590 1570	229 312 239 230	15.8 15.5 15.5 15.3	2230 2230 2230 2230		Tanner (1980)
Manu National Park, Peru	12.35° S, 71.52° W	3345	126.8	11	2200		Gibbon et al. (2010)
Montane Atlantic forests, Rio de Janeiro State, Brazil	21.62° S, 42.08° W	900 600	148.4 167.9		1440 1440		Cunha et al. (2009)
Podocarpus National Park, Ecuador	4.1° S, 78.96° W 4.1° S, 78.96° W 4.0° S, 79.0° W 4.0° S, 79.0° W 4.1° S, 79.2° W	1050 1540 1890 2380 3060	285.1* 167.5* 173* 99.8* 112.2*	18.9 16.7 14.9 12.3 8.6	2230 2300 1950 5000 4500	26 10 31 28 27	Moser et al. (2011); Leuschner et al. (2007)

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Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t ha^{-1}$)	MAT (°C)	Rainfall ($mm yr^{-1}$)	Slope (°)	Reference
Buenaventura Reserve, Ecuador	∼ 4° S, ∼ 79° W	1000	183				Spracklen et al. (2005)
Tapichalaca Reserve, Ecuador	∼ 4.28° S, ∼ 79° W	2250	195				Spracklen et al. (2005)
Bannadpare, South India	12.08° N, 75.7° E	200	227	27	5310		Rai and Proctor (1986)
Agumbe, Karnataka, southern India	13.52° N, 75.1° E	575	420	22.2	7670		Rai and Proctor (1986)
Kagneri, Karnataka, southern India	12.82° N, 75.6° E	500	460	28.6	6100		Rai and Proctor (1986)
South Bhadra, Karnataka, southern India	13.25° N, 75.25° E	800	649	21	6520		Rai and Proctor (1986)
Uganda BUD-17	1.72° N, 31.5° E	1062	603.9	23.1	1326		Lewis et al. (2013)
Cameroon TNP-08	6.31° N, 9.37° E	1217	249.2	21.3	2145		Lewis et al. (2013)
Taita Hills, Kenya	3.37° S, 38.34° E	1826	607			14	Omoro et al. (2013)
Taita Hills, Kenya	3.47° S, 38.34° E	1535	785			14	Omoro et al. (2013)
Taita Hills, Kenya	3.3° S, 38.5° E	1390	767			14	Omoro et al. (2013)
Mt. Rinjani, Lombok	8.4° S, 116.4° E	1000	110			22	Dossa et al. (2013)
		1000	160			22	
		1000	230			22	
		1200	210			22	
		1200	240			22	
		1200	270			22	
		1400	205			22	
		1400	245			22	
		1400	255			22	
		1600	215			22	
		1600	140			22	
		1600	110			22	
		1800	280			22	
		1800	210			22	
		1800	205			22	
		2000	205			22	
		2000	130			22	
Tanzania VTA-30	6° S, 37.72° E	1012	283.5	20.9	1108		Lewis et al. (2013)

Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t ha^{-1}$)	MAT (°C)	Rainfall ($mm yr^{-1}$)	Slope (°)	Reference
Uganda MPG01	0.21° N, 32.29° E	1219	396.2	21.3	1286		Lewis et al. (2013)
Sierra Norte Oaxaca, Mexico	17.83° N, 96.17° W	1500 1950 2050 2400 2500	377 271 263 254 444	16.5	5800		Álvarez-Alteaga et al. (2013)
Jianfengling National Natural Reserve, Hainan, China	18.72° N, 108.88° E	893 867	422.2 479.7	19.8 19.8	2449 2449		Chen et al. (2010)
Mount Kinabalu, Sabah, Malaysia	6.08° N, 116.55° E	650 700 1560 1860 2590 2700 3080	437 548 294 238 308 122 215	24.5 24 18.5 17 12.5 12 10	2300 2300 2300 2300 2300 2300 2300	19 11 17 24 20 22 27	Kitayama and Aiba (2002)
Belalong, Brunei	4.54° N, 115.21° E	332	543.8				Slik et al. (2010)
Carapa Pila, Sarawak	2.71° N, 113.87° E	338	604.3				Slik et al. (2010)
Danum Valley, Sabah	4.96° S, 117.79° E	300	315.5				Slik et al. (2010)
Enggeng, East Kalimantan	3.21° N, 115.79° E	819	577.9				Slik et al. (2010)
Gunung Kinabalu, Sabah	6.04° N, 116.71° E 6.04° N, 116.54° E	774 1958	513.9 405.0				Slik et al. (2010)
Gunung Lumut, East Kalimantan	1.46° S, 115.96° E 1.46° S, 115.96° E	413 466	254.3 356.4				Slik et al. (2010)
Gunung Mulu, Sarawak	4.15° N, 114.88° E 4.14° N, 114.88° E 4.04° N, 114.86° E 4.02° N, 114.82° E	170 300 225 50	470* 380* 650* 250*	24 23.5 24 25	5700 5700 5110 5090	2 27 17 0	Proctor et al. (1983)
Gunung Rara, Sabah	4.54° N, 117.04° E	614	492.4				Slik et al. (2010)
ITCI concession, East Kalimantan	0.96° S, 116.54° E	322	312.7				Slik et al. (2010)
Long Barang, East Kalimantan	1.87° N, 115.12° E	1026	359.1				Slik et al. (2010)
Long Jalan, East Kalimantan	2.87° N, 116.12° E	581	500.8				Slik et al. (2010)
Luran, East Kalimantan	2.87° N, 115.46° E	991	340.8				Slik et al. (2010)

Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t\,ha^{-1}$)	MAT (°C)	Rainfall ($mm\,yr^{-1}$)	Slope (°)	Reference
Malinau, East Kalmintan	2.82° N, 116.14° E	547	443.5				Slik et al. (2010)
Malinau, East Kalmintan	3.12° N, 115.54° E	378	596.2				Slik et al. (2010)
Puak Highlands, East Kalmintan	2.87° N, 115.70° E	1349	765.5				Slik et al. (2010)
Rantau Layung, East Kalimantan	1.54° S, 115.96° E	416	443.5				Slik et al. (2010)
Saan, East Kalimantan	2.46° N, 115.46° E	855	271.0				Slik et al. (2010)
Sempatung, West Kalimantan	1.04° N, 110.04° E	501	469.0				Slik et al. (2010)
Semule, East Kalimantan	2.29° N, 115.29° E	929	412.8				Slik et al. (2010)
Sungai Wain, East Kalimantan	1.12° N, 116.79° E	737	508.1				Slik et al. (2010)
Tubu, East Kalimantan	3.46° N, 116.21° E	490	421.1				Slik et al. (2010)
Ulu Temai, Sarawak	2.21° N, 113.62° E	442	585.4				Slik et al. (2010)
Challabamba, Manu National Park, Peru	13° N, 71.6° W	3100	198 (197)			33	Román-Cuesta et al. (2011)[c]
Laguna-Acjanaco Manu National Park, Peru	13° N, 71.6° W	3400	169 (171)			24	Román-Cuesta et al. (2011)[c]
Pahititi Manu National Park	13° N, 71.6° W	2920	120 (125)			37	Román-Cuesta et al. (2011)[c]
Sondor National Park	13° N, 71.6° W	2850	241 (236)			17	Román-Cuesta et al. (2011)[c]
Malinau, East Kalimantan	3.2604° N, 116.542° E	110	679.2				Slik et al. (2010)
Gong Solok, East Kalimantan	3.3741° N, 116.541° E	66	436.5				Slik et al. (2010)
Kalsel, South Kalimantan	3.709° S, 115.207° E	51	432				Slik et al. (2010)
Malinau, East Kalimantan	3.0407° N, 116.541° E	257	515.7				Slik et al. (2010); Slik et al. (2010)
Kalsel, South Kalimantan	3.5423° S, 115.207° E	249	321				Slik et al. (2010)
East Kalimantan, Berau	1.9575° S, 117.291° E	74	375.3				Slik et al. (2010)
Kalsel, South Kalimantan	3.459° S, 115.124° E	114	271.8				Slik et al. (2010)

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Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t ha^{-1}$)	MAT (°C)	Rainfall ($mm yr^{-1}$)	Slope (°)	Reference
East Kalimantan, Berau	1.8741° N, 117.207° E	105	386.3				Slik et al. (2010)
East Kalimantan, Lempake	0.4591° S, 117.124° E	29	448.7				Slik et al. (2010)
ITCI concession, East Kalimantan	0.9591° S, 116.624° E	141	537.8				Slik et al. (2010)
East Kalimantan, Berau	2.0408° S, 117.124° E	59	510.2				Slik et al. (2010)
Sarawak, Gunung Mulu	4.0407° N, 114.791° E	70	312.7				Proctor et al. (1983); Slik et al. (2010)
Ladan, Brunei	4.624° N, 114.707° E	28	546.9				Slik et al. (2010)
Sawat, Brunei	4.5407° N, 114.541° E	27	374.2				Slik et al. (2010)
Andalau, Brunei	4.624° N, 114.541° E	61	437.3				Slik et al. (2010)
East Kalimantan, Samboja	0.9591° S, 116.957° E	62	340.9				Slik et al. (2010)
Ulu Dapoi, Sarawak	3.1241° N, 114.457° E	213	450.3				Slik et al. (2010)
East Kalimantan, Bukit Bangkirai	1.03° S, 116.868° E	72	297.2				Slik et al. (2010)
Langap, East Kalimantan	3.1241° N, 116.457° E	118	504.7				Slik et al. (2010)
Badas, Brunei	4.5407° N, 114.374° E	38	405.9				Slik et al. (2010)
East Kalimantan, Sungai Wain	1.1258° E 116.791° E	35	407				Slik et al. (2010)
Malinau, East Kalimantan	3.0407° N, 116.457° E	138	456.4				Slik et al. (2010)
Lahei, Central Kalimantan	1.8757° S, 114.207° E	39	247.1				Slik et al. (2010)
ITCI concession, East Kalimantan	0.7924° S, 116.374° E	109	353.2				Slik et al. (2010)
Bok Tisam, Sarawak	3.6241° N, 114.124° E	77	618.3				Slik et al. (2010)
Malinau, East Kalimantan	3.0407° N, 116.374° E	207	598.4				Slik et al. (2010)
Lambir, Sarawak	4.124° N, 114.041° E	23	436.6				Slik et al. (2010)
Lio Mutai, East Kalimantan	2.9574° N, 116.374° E	234	383.2				Slik et al. (2010)
Ulu Bakong, Sarawak	4.2907° N, 114.041° E	41	584				Slik at el. (2010)
Gunung Meratus, East Kalimantan	0.8758° S, 116.291° E	103	550.1				Slik et al. (2010)
Lambir, Sarawak	4.2074° N, 114.041° E	111	731				Slik et al. (2010)
Kalsel, South Kalimantan	3.709° S, 115.541° E	14	369.9				Slik et al. (2010)

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Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t ha^{-1}$)	MAT (°C)	Rainfall ($mm yr^{-1}$)	Slope (°)	Reference
Barito Ulu, Central Kalimantan	0.1258° S, 114.041° E	287	328.2				Slik et al. (2010)
Kalsel, South Kalimantan	3.3757° S, 115.541° E	252	608				Slik et al. (2010)
Kalsel, South Kalimantan	3.6257° S, 115.374° E	45	395.3				Slik et al. (2010)
Kalsel, South Kalimantan	3.2923° S, 115.374° E	268	580.8				Slik et al. (2010)
Gunung Niut, West Kalimantan	0.7075° N, 109.874° E	118	489.5				Slik et al. (2010)
Kalsel, South Kalimantan	3.2923° S, 115.24° E	55	413.8				Slik et al. (2010)
Sunujuh, West Kalimantan	1.4575° N, 109.458° E	27	461.2				Slik et al. (2010)
Nyabau, Sarawak	3.2074° N, 113.124° E	44	778.5				Slik et al. (2010)
Gunung Mersing, Sarawak	2.5408° N, 113.124° E	231	541.1				Slik et al. (2010)
Bukit Raya, Sarawak	1.9575° N, 112.957° E	141	584.7				Slik et al. (2010)
Segan, Sarawak	2.9574° N, 112.957° E	160	556.7				Slik et al. (2010)
Bukit Iju, Sarawak	2.7074° N, 112.707° E	111	554.2				Slik et al. (2010)
Sangai, Central Kalimantan	1.4591° S, 112.541° E	97	386.2				Slik et al. (2010)
Sangai, Central Kalimantan	1.294° S, 112.374° E	248	495.4				Slik et al. (2010)
Bako, Sarawak	1.7075° N, 110.458° E	58	352.3				Slik et al. (2010)
Gunung Santubong, Sarawak	1.6241° N, 110.374° E	9	389.4				Slik et al. (2010)
Gunung Palung, West Kalimantan	1.2924° S, 110.208° E	280	563.9				Slik et al. (2010)
Serimbu, West Kalimantan	0.7075° N, 110.124° E	129	526				Slik et al. (2010)
Kembera, West Kalimantan	0.0425° S, 110.041° E	29	438.1				Slik et al. (2010)
Sabah, Gunung Silam	4.9573° S, 118.124° E	245	232.5				Slik et al. (2010)
Sabah, Sepilok	5.874° S, 118.041° E	17	475.6				Slik et al. (2010)

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Table 1. Continued.

Location	Lat., Lon.	Elevation (m)	AGB ($t\,ha^{-1}$)	MAT (°C)	Rainfall ($mm\,yr^{-1}$)	Slope (°)	Reference
Sabah, Sepilok	5.874° S, 117.957° E	32	335.1				Slik et al. (2010)
Danum Valley, East Sabah, Malaysia	5.31° N, 117.45° E	250	266.7			20	Saner et al. (2012)

[a] Biomass converted to carbon using a conversion factor of 0.5.
[b] Stand volume converted to biomass assuming a wood specific density of 0.56 $g\,cm^{-3}$ which is the mean reported by Culmsee et al. (2010).
[c] Individual site values are not reported. We calculate AGB values for each site through weighting the average value for all sites with basal area × height for each site. Weighting using the natural logarithm of (basal area × height) changes the AGB values only slightly (reported in parentheses).

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Table 2. Correlation (R^2) of above ground biomass (AGB) with topographical and meteorological variables. Correlations are shown separately for all sites (bold), neotropics (italics) and Asia (normal text) for the subset of sites where data on elevation, slope, temperature and rainfall are all available. Asterisks indicate significant ($P < 0.01$) correlations.

	AGB TMF[a]	AGB TMF + lowland[b]	E	S	T	R
AGB	1	1	–	–	–	–
Elevation (E)	**0.03**	**0.15***	1	–	–	–
	–	0.23*				
		0.42*				
Slope (S)	**0.31**	**0.14***	0.03	1	–	–
	–	0.27*				
		0.04				
Annual mean temperature (T)	**0.05**	**0.16***	0.97	0.02	1	–
	–	0.23*				
		0.44				
Annual mean rainfall (R)	**0.09**	**0.01**	0.05	0.04	0.11	1
		0.08				
		0.15				

[a] TMF only. All sites: $n = 21$.
[b] TMF + lowland. All sites: $n = 104$, Neotropics: $n = 89$; Asia: $n = 15$.

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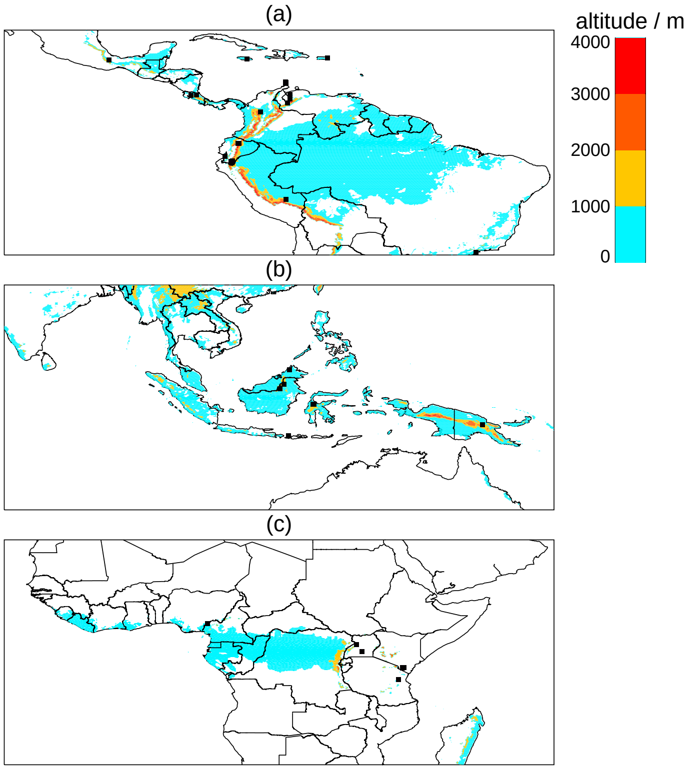

Fig. 1. Location of tropical montane forest inventory plots (solid squares) where data of above ground biomass has been synthesised for this analysis. Background colour shows elevation of tropical forests (coloured where vegetation continuous field from MODIS is > 25 %).

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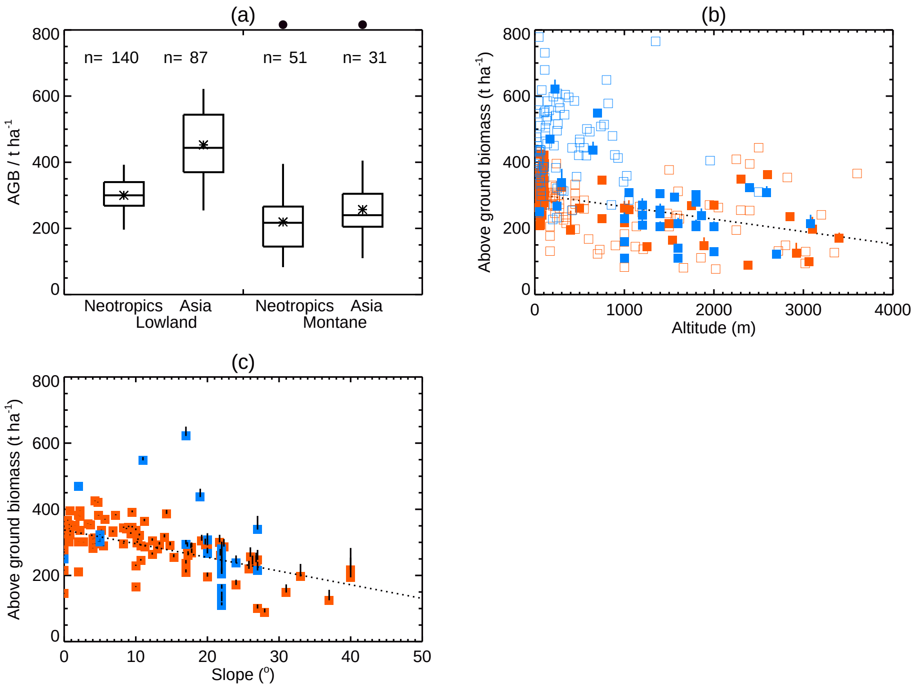

Fig. 2. Above ground biomass (AGB) storage observed in forest inventory plots. **(a)** Comparison of AGB (on a land-surface area basis) in tropical montane forests (elevation ≥ 1000 m) with that in lowland tropical forests. Significant differences between lowland and montane (Student's *t* test, $P < 0.01$) indicated by a solid circle above panel. **(b)** Relationship between AGB and elevation (neotropics: red, Asia: blue). Open symbols show sites where no information on slope is available. **(c)** Relationship between angle of slope and AGB. In **(b)** and **(c)**, symbols show AGB per land-surface area (linear relationship for the neotropics is shown with a dotted line), top of bars show AGB per planimetric area.

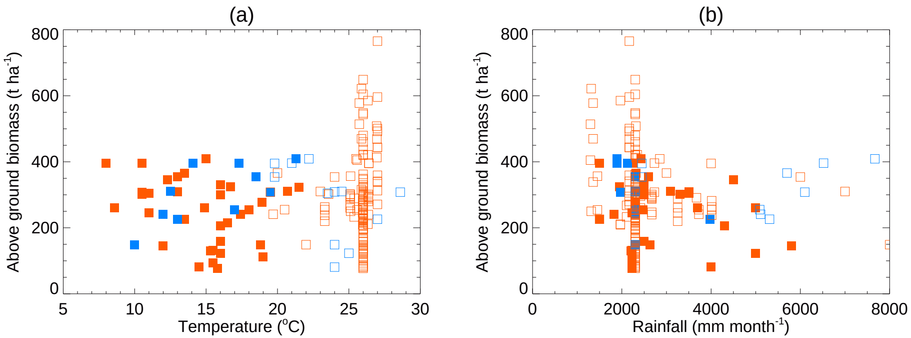

Fig. 3. Relationship between AGB and annual mean **(a)** temperature, **(b)** rainfall (neotropics: red, Asia: blue). Solid points are for TMF (elevation ≥ 1000 m), open points are for lowland forests.

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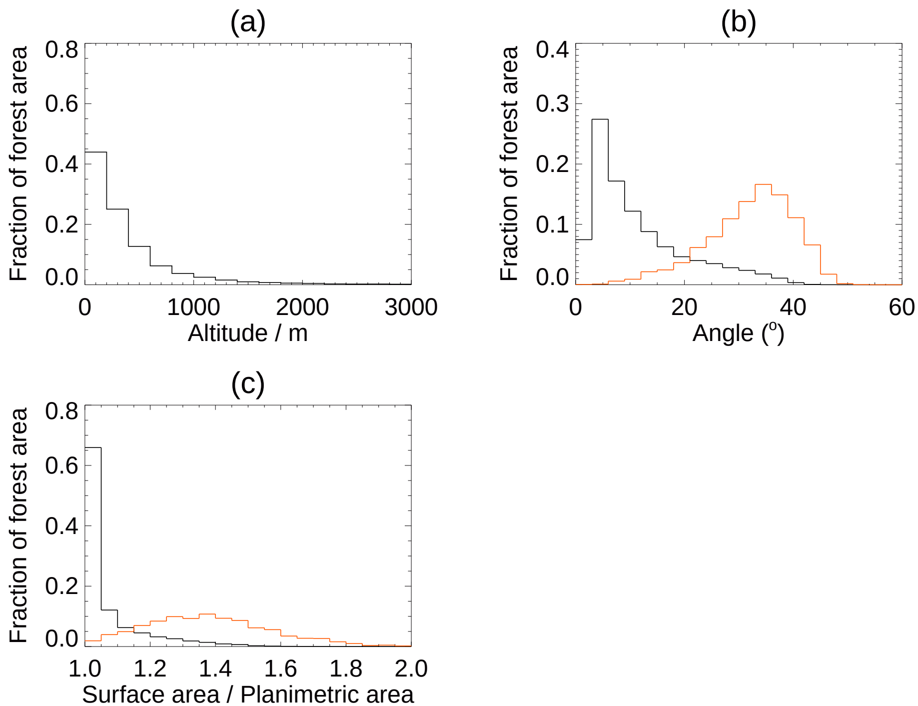

Fig. 4. Distribution of global tropical forests as a function of **(a)** elevation, **(b)** slope angle. **(c)** Ratio of surface area to planimetric area (lowland (elevation < 1000 m) tropical forest: black, tropical montane forest (elevation ≥ 1000 m): red).

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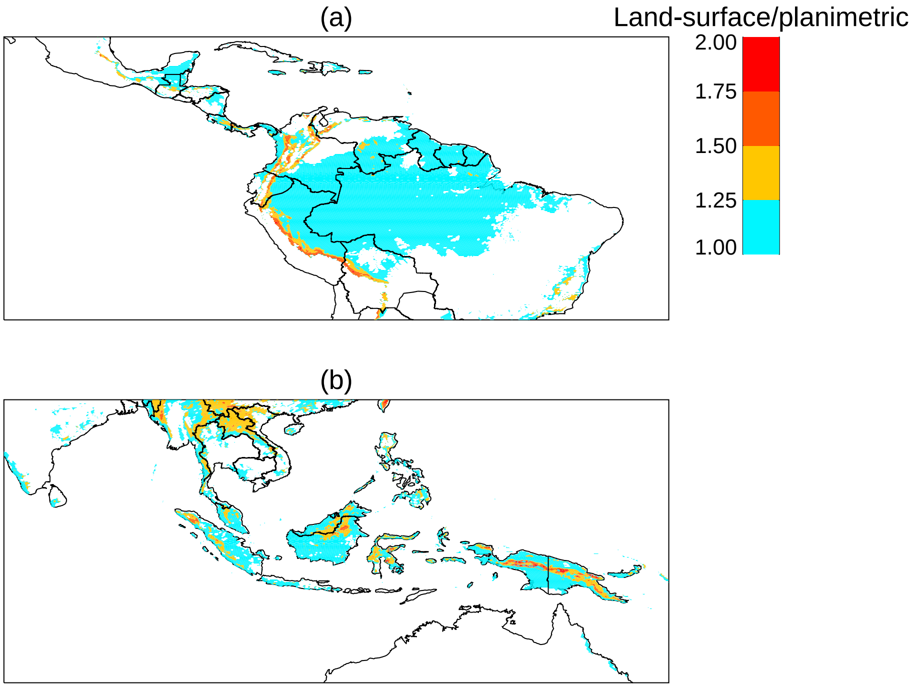

Fig. 5. Impact of slope on the area of tropical forests. Colour shows the ratio of land-surface area to planimetric area in **(a)** neotropics, **(b)** Asia.

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