The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective

Running title: Andes productivity and carbon cycle

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Summary

- Why do forest productivity and biomass decline with elevation? To address this question, research to date has generally focused on correlative approaches describing changes in growth and biomass against elevation-related variables such as temperature.

- We present a novel, mechanistic approach to this question by quantifying each component of the autotrophic carbon budget in 16 forest plots along a 3300m elevation transect in the Peruvian Andes, where growing season length does not vary with elevation.

- Low growth rates at high elevations appear primarily driven by low gross primary productivity ($GPP$), with little shift in either carbon use efficiency ($CUE$) or allocation of net primary productivity ($NPP$) between wood, fine roots and canopy. Rather than a gradual linear decline in $GPP$ or $NPP$, there is some evidence of a sharp transition between submontane and montane forests. Cloud immersion may be important through either decreased illumination or leaf wetting. Leaf-level photosynthetic parameters do not decline with elevation, implying that neither temperature nor nutrient limitation restrict photosynthesis at high elevations.

- When cloud immersion regimes are accounted for, the lack of relationship between productivity and annual temperature suggest that plant acclimation and community turnover result in little long-term sensitivity of tropical forest productivity to temperature.
Introduction

Wet tropical montane elevation transects can provide valuable insights into the influence of environmental controls, and in particular temperature, on ecosystem productivity and carbon cycling (Malhi et al., 2010). By providing a strong contrast in environmental conditions in a small biogeographical area and a constant twelve-month growing season, they can help us understand the long-term effects of acclimation and community turnover on ecosystem function.

Tropical montane forests have usually been observed to have lower above-ground productivity and biomass than nearby lowland forests (Raich et al., 2006; Spracklen & Righelato, 2014; Girardin et al., 2014a). The question of what drives this low productivity and biomass of tropical montane forests has long intrigued ecologists (Grubb, 1971; 1977; Bruijnzeel & Veneklaas, 1998; Whitmore, 1998). Empirical approaches to address this question have tended to focus on observed correlations between productivity (usually only woody productivity measured via diameter growth rates) or biomass and environmental drivers such as temperature or nutrient availability (e.g. Raich et al., 1997; Wang et al., 2003; Raich et al., 2006; Moser et al., 2011), or nutrient manipulation experiments (Tanner et al., 1998; Homeier et al., 2012; Fisher et al., 2013). Nevertheless, despite research in a number of different tropical montane forest ecosystems, a deeper understanding of the observed changes in productivity and biomass remains lacking.

We present a new dataset and analysis to address this question using a series of measurements of all the major components of the autotrophic carbon budget of forest ecosystems in a number of forest plots along an elevation gradient in Peru. This requires quantification of the major components of gross primary productivity ($GPP$, the total photosynthesis per unit ground area), net primary productivity ($NPP$, the rate of production of new biomass) and autotrophic respiration ($R_a$, the use of photosynthate by the plant’s own metabolism). Such an approach facilitates a quantitative and mechanistic understanding of the relative importance of leaf, whole plant, and stand-level processes in determining the growth rates and biomass of forest ecosystems. The key components are illustrated in Figure 1.
From the perspective of the autotrophic carbon budget, the primary mechanisms that could cause a reduction in growth rates and biomass with increasing elevation are: (1) limitation of rates of photosynthesis and thus declines in GPP; (2) relative increases in autotrophic respiration ($R_a$) and resultant decreases in carbon use efficiency (CUE), which is the ratio NPP/GPP; (3) shifting allocation or storage of NPP away from woody biomass and into canopy or fine roots, or (4) increases in tree mortality rates (decreases in wood residence time) and thus decreases in equilibrium above-ground biomass (Figure 1). We review each of these potential mechanisms in turn.

**Decline in net photosynthesis**

A decline in canopy net photosynthesis could result from either a decline in CO$_2$- and light-saturated leaf photosynthetic capacity, a decline in realized rates of leaf-level photosynthesis below capacity, or through a decline in canopy leaf area. These various declines could occur because of a number of different abiotic drivers, such as decreases in temperature, water status, atmospheric CO$_2$, soil nutrient availability and light. Reductions in temperature could decrease metabolic activity and decrease photosynthetic rates below optimum levels; such temperature dependence is implicit in many ecosystem models. On the other hand, photosynthesis may acclimate to ambient mean temperatures, resulting in little temperature dependence in ecosystem productivity (Lloyd & Farquhar, 2008). The decrease in the partial pressure of CO$_2$ in air that occurs with increasing elevation could decrease photosynthetic rates; however, research to date suggests that this is offset by the increased diffusivity at high elevations and reduced partial pressure of O$_2$, resulting in little net sensitivity of photosynthesis to air pressure (Cordell et al., 1998; 1999). High soil water content and low temperatures with increasing elevation can reduce nitrogen mineralization rates and affect plant available nutrients (Benner et al., 2010), leading to decreases in the supply rate of foliar nitrogen and phosphorus necessary for photosynthesis, although this can be confounded by changes in leaf construction costs and lifetime (Cordell et al., 1998; van de Weg et al., 2009; Wittich et al., 2012). Reduced light availability, occurring as a function of frequent cloud cover, can lead to reductions in realised photosynthetic rates below capacity. There is evidence from montane forests that cloud cover, as well as the accompanying leaf wetting events, can result in reduced photosynthesis rates (Letts et al., 2010; Goldsmith et al., 2013). Finally, declines in GPP can also result from decreases in canopy leaf area, which may be a response to nutrient supply limitation (Weaver & Murphy, 1990; Kitayama & Aiba, 2002; Moser et al., 2007).
Changes in carbon use efficiency

Relative increases in $R_a$ at high elevation, and resultant decreases in $CUE$, may also account for observed decreases in growth and biomass. This could occur if there was increased metabolic investment in processes not directly associated with $NPP$, such as protection against cold, or defence against herbivores or pathogens (though such biotic pressures are expected to decrease with elevation; Metcalfe et al., 2013). While some individual components of respiration have been quantified (e.g. stem respiration; Zach et al., 2009; Robertson et al., 2010), studies of total autotrophic respiration as a function of elevation in tropical forests are exceedingly rare (Leuschner et al., 2013).

Shifting allocation of $NPP$

Although above-ground $NPP$ has often been observed to decline with elevation (Marrs et al., 1988; Weaver & Murphy, 1990; Girardin et al., 2010; Moser et al., 2011) insights into belowground $NPP$, and thus total $NPP$, remain limited. Many studies have noted an increase in root biomass with increasing elevation (Kitayama & Aiba, 2002; Moser et al., 2008; Girardin et al., 2013), but how this relates to root $NPP$ depends on understanding fine root lifetimes. Few studies have quantified root $NPP$; some have observed no strong patterns with elevation (Girardin et al., 2013) while others have observed an increase with elevation (Röderstein et al., 2005; Moser et al., 2011). Nevertheless, it has been hypothesized that declining above-ground $NPP$ is compensated for by a concomitant change in belowground $NPP$ (Leuschner et al., 2007). The observed increase in fine root production along certain elevation transects and more universal increase for fine root biomass have been proposed as compensation for low nutrient availability.

Hence montane forest growth rates could be suppressed by some combination of reduced photosynthetic capacity, reduced ambient photosynthesis, increasing autotrophic respiratory load or allocation of $NPP$ away from woody biomass production. The systematic evaluation of these alternative mechanisms requires the standardized measurement of all the components of carbon production and allocation across an elevation transect.

We synthesize a unique dataset where we have conducted intensive monitoring of the carbon cycle for multiple years across a series of 16 plots along a 3300 m elevation transect in Peru. This provides an opportunity to understand how the carbon dynamics of tropical forests vary
with elevation, as well as to apply the process-based framework described above to generate
a quantitative comparison of the relative importance of various factors influencing growth
rates and biomass among forests along this elevation transect. These sites are also the
location of the CHAMBASA project, which explores the relationships between plant traits
and ecosystem function; hence this study presents and explains the benchmark productivity
data for various CHAMBASA companion papers (this volume). It also provides a consistent
dataset suitable for testing and aiding ecosystem model development. For this specific paper,
for our study system, we ask the following questions:

1. How do key stand-level aspects of the forest carbon cycle, such as \( GPP \), \( NPP \), \( CUE \),
   and \( NPP \) allocation to canopy, wood and fine roots, vary with elevation?
2. Is the decline in woody growth rates with increasing elevation in this transect
determined by changes in \( GPP \), carbon use efficiency (\( CUE \)), or allocation of \( NPP \)?
3. Are trends with elevation on this transect linear or is there evidence for abrupt
   transitions? If the latter, what factors may be causing such an abrupt transition?
4. Are declines in above-ground biomass with elevation on this transect mainly
determined by changes in growth rates or changes in mortality rates?

METHODS

Field sites

We collected several years (between 2007-2015) of carbon cycling data from 16 one-hectare
plots along an elevation gradient in Peru, ranging from the high elevation tree line (~3500 m
asl), through the cloud forest-submontane transition (1000-1750 m asl) and into the Amazon
lowlands (100-220 m asl). Site descriptions are summarised in Table 1 and provided for some
sites in more detail in site-specific papers (del Aguila-Pasquel et al., 2014; Huaraca Huasco
et al., 2014; Malhi et al., 2014; Girardin et al., 2014a; 2014b). The montane sites are
concentrated in the Kosñipata Valley, and the submontane plots either in the adjacent Tono
Valley (TON-01) or in the Pantiacolla front range of the Andes (PAN-02 and PAN-03).
These sites have been the subject of on-going, multidisciplinary research by the Andes
Biodiversity and Ecosystems Research Group (ABERG: www.andesconservation.org; Malhi,
2010)). The cloud climatology of this valley is described by Halladay et al. (2012) and the
water budget has been closed by Clark et al. (2014).
The lowland Amazonian sites are in two locations: two plots at Tambopata, Madre de Dios, in southeastern Peru (~200 m asl) with a moderate dry season (2-4 month), and another two plots at Allpahuayo, Loreto, in northeastern Peru (~100 m asl) with no dry season. Although Allpahuayo is some distance from the other plots, the availability of similar data allows for better assessment of the site-to-site variability of lowland forests. Neither lowland site has much tree species overlap with the montane sites. Malhi et al. (2015) present an analysis of the spatial variability of the carbon cycle in lowland Amazonian forests, including the Allpahuayo and Tambopata sites. Ten of the plots are the focus of the CHAMBASA field programme, a multi-scale project that links field-measured traits to plot-level metrics to airborne remote sensing of this landscape.

For eight of these plots, all the major components of NPP and $R_a$ were measured, enabling estimation of $GPP$ and $CUE$; for the remaining eight only the major components of $NPP$ have thus far been assessed (Table 2). Data collection dates vary between plots, spanning over six years (2007-2012) in four plots (TAM-05, TAM-06, WAY-01, SPD-02), four years (2009-2012) in four plots (SPD-01, ESP-01, ALP-01, ALP-30), three years (2007-2009) in five plots (TON-01, TRU-03, TRU-04, TRU-07, TRU-08) and two years (2013-2015) in three plots (ACJ-01, PAN-02, PAN-03), representing 61 plot-years of intensive monthly data collection efforts in total (Table 1).

**Field methods**

Our approach is to measure the major components of the autotrophic carbon cycle. Herein, we define “autotrophic” as a focus on the plant processes of photosynthesis, productivity, autotrophic respiration and allocation, rather than heterotrophic processes such as decay and soil organic matter respiration. We employ the field protocol of the Global Ecosystems Monitoring network (GEM: www.gem.tropicalforests.ox.ac.uk). These methods are described in detail in an online manual on the GEM website and in previous individual site papers, and in Appendix S1.

The GEM protocol involves measuring and summing all major components of $NPP$ and autotrophic respiration on monthly or seasonal timescales. For $NPP$, this includes canopy litterfall ($NPP_{litterfall}$) at biweekly intervals, estimates of leaf loss to herbivory ($NPP_{herbivory}$).
from scans of litterfall, above-ground woody productivity of all medium-large (> 10 cm dbh) trees in the plot \(NPP_{\text{ACW} \geq 10 \text{ cm}}\) via three-monthly measurement of dendrometers, as well as a full annual census of all trees, woody productivity of small trees (2-10 cm dbh; \(NPP_{\text{ACW} < 10 \text{ cm}}\)) in annually censused subplots, the turnover of branches on live trees (\(NPP_{\text{branch turnover}}\)) by conducting three-monthly transect censuses of freshly fallen branch material from live trees, fine root productivity (\(NPP_{\text{fine root}}\)) from ingrowth cores installed and harvested every three months, and estimation of course root productivity (\(NPP_{\text{coarse root}}\)) by applying a multiplying factor to above-ground woody productivity. Leaf area index (LAI) is calculated from photographs taken with a digital camera and a hemispherical lens and processed with CAN-EYE software (INRA 2010) in a subset of the plots (TAM-05, TAM-06, ALP-01, ALP-30, SPD-01, SPD-02, ESP-01, WAY-01) every other month.

For autotrophic respiration, we estimate rhizosphere respiration (\(R_{\text{rhizosphere}}\)) once per month by subtracting the respiration of root-free soil from that of unaltered soil, we estimate above-ground woody respiration (\(R_{\text{stem}}\)) by measuring stem respiration once per month and scaling by a stem surface area allometry, we estimate below-ground course root and bole respiration (\(R_{\text{coarse root}}\)) by applying a multiplier to \(R_{\text{stem}}\), and leaf dark respiration (\(R_{\text{leaf}}\)) by measuring leaf dark respiration rates in two seasons, then scaling by estimates of sun and shade leaf fractions and applying a correction of light inhibition of dark respiration.

The measured components of \(NPP\) and \(R_a\) are then summed to estimate total \(NPP\) and autotrophic respiration \(R_a\) (Appendix S1). In plant-level autotrophic steady state conditions (and on annual timescales or longer where there is little net non-structural carbohydrate storage), gross primary productivity (\(GPP\)), the carbon taken up via photosynthesis, should be approximately equal to plant carbon expenditure (\(PCE\)), the amount of carbon used for \(NPP\) and autotrophic plant respiration (\(R_a\)) if there is no net accumulation of non-structural carbohydrates. Autotrophic steady state condition does not require the total plot carbon cycle to be in equilibrium, the plot can still be gaining or losing biomass or soil carbon stocks, as long as there is no substantial accumulation or loss of non-structural carbohydrates. Hence, we estimated \(GPP\) as the sum of \(NPP\) and \(R_a\). We calculate the carbon use efficiency (\(CUE\)) as the proportion of total \(GPP\) invested in \(NPP\) rather than \(R_a\):

\[
CUE = \frac{NPP}{GPP} = \frac{NPP}{(NPP + R_a)}
\]
Our biometric estimate of GPP is indirect and depends on summing up components of NPP and $R_a$, each with their inherent sampling errors and systematic uncertainties. An alternative approach to estimating GPP (also with inherent errors) is from eddy covariance flux measurements. Reliable eddy covariance measurements would be almost impossible in the complex and steep topography of our montane sites, but comparisons of biometric approaches with flux measurements in 46 forest sites (Campioli et al., unpublished data), including several lowland rainforest sites, demonstrate very good agreement between the two approaches, suggesting that no major terms of the autotrophic carbon budget are being missed.

Somewhat inevitably, any estimate of NPP may be biased towards underestimation because it neglects several small NPP terms, such as NPP lost as volatile organic emissions, non-measured litter trapped in the canopy, or dropped from understory plants below the litter traps. At a site in central Amazonia, volatile emissions were found to be a minor component of the carbon budget (0.13±0.06 Mg C ha$^{-1}$ year$^{-1}$; Malhi et al., 2009). For below-ground NPP, the allocation to root exudates and to mycorrhizae is disregarded. In effect, we treat root exudation and transfer to mycorrhizae as rhizosphere autotrophic respiration rather than as NPP, which could potentially impact our CUE estimates. Recent estimates from a similar network of lowland plots estimate that forests in less fertile sites increased C allocation to the (non-root) rhizosphere by up to ~2.2±1.4 MgC ha$^{-1}$ yr$^{-1}$ compared to fertile sites, an indication that root exudate fluxes are <7% of GPP (Doughty et al., unpublished data). Given that these exudates are labile and rapidly respired by mycorrhizae and soil microfauna in the rhizosphere, this exudate NPP term is very similar to fine root autotrophic respiration in terms of carbon cycling. The fairly close agreement with independent, flux-based estimates of GPP (Campioli et al., unpublished data) suggest that there are no large missing terms or biases at the scale of the whole stand.

Many of these measurements have potential systematic uncertainties: we assign sampling or systematic uncertainties to each measurement, and rigorously propagate the uncertainties through our calculations. In particular, it is important to note that our calculation of NPP is based on the summation of four independent measurements (litterfall, tree growth, fine root production and branchfall) and our estimate of GPP is based on the summation of seven independent measurements (the components of NPP, as well as leaf, stem and rhizosphere measurements). While some of these terms can carry substantial measurement and scaling
uncertainties, if the uncertainties are independent for each measurement, these uncertainties propagate by quadrature to result in a manageable uncertainty in the final sum \(NPP\) or \(GPP\) (Appendix S1). For example, while there may be significant uncertainty in our measurement of root productivity or in our scaling of stem respiration, this does not result in unmanageable uncertainties in our estimates of \(GPP\). By contrast, an eddy covariance-based estimate of \(GPP\) is based on a single type of measurement (of net ecosystem exchange); hence any uncertainties in the method, such as underestimation of night-time respiration in stable atmospheric conditions, can result in an equivalent uncertainty in the final estimate of \(GPP\). Hence, a carbon summation measurement comprised of seven independent measurements may potentially be more accurate than an eddy covariance-based estimate comprised of one measurement. Where the two approaches agree, we can have increased confidence that both approaches are capturing the major components of the carbon cycle.

This ecosystem-level approach was complemented by a leaf-level approach to understanding variation in leaf physiological traits. These leaf gas exchange measurements are reported in detail in Bahar et al (unpublished data) and summarised briefly here. Over the period July-October 2011, measurements were made using a portable photosynthesis system (Licor 6400XT, Li-Cor BioSciences, Lincoln, NE, USA) on 300 canopy trees (~1150 sun-exposed leaves) of about 210 species along the transect. For each tree, branches were collected from the top canopy position, recut under water to ensure xylem water continuity, before starting gas exchange measurements on the most recently fully expanded leaves. \(\text{CO}_2\) response curves of light-saturated photosynthesis (\(A\leftrightarrow C_i\) curves) (with \(\text{PAR} \text{ at } 1800 \mu\text{mol photons m}^{-2} \text{ s}^{-1}\)) were performed within 30–60 minutes of branch detachment, with \(\text{CO}_2\) concentrations inside the 6 cm\(^2\) reference chamber ranging in a stepped sequence from 35 to 2000 \(\mu\text{mol mol}^{-1}\). Block temperatures within the chamber were set to the prevailing day-time air temperature at each site (from 25-28 °C). The resultant \(A\leftrightarrow C_i\) curves were fitted following the model described by Farquhar et al. (1980) in order to calculate \(V_{\text{cmax}}\) and \(J_{\text{max}}\) on a leaf area basis. Rates of \(\text{CO}_2\) exchange were corrected for diffusion through the gasket of the LI-6400 leaf chamber (Bruhn et al., 2002) prior to calculation of \(V_{\text{cmax}}\) and \(J_{\text{max}}\). Fitted parameters were scaled to a reference temperature of 25°C using activation energies of 64.8 and 37.0 kJ mol\(^{-1}\) for \(V_{\text{cmax}}\) and \(J_{\text{max}}\), respectively (Farquhar et al., 1980). The Michaelis constants of Rubisco for \(\text{CO}_2\) (\(K_c\)) and \(\text{O}_2\) (\(K_o\)) at a reference temperature 25°C were assumed to be 404 \(\mu\text{bar}\) and 248 mbar, respectively (von Caemmerer et al., 1994); these values were adjusted to actual leaf temperatures assuming activation energies of 59.4 and 36 kJ mol\(^{-1}\) for \(K_c\) and \(K_o\),
respectively (Farquhar et al., 1980). Finally, rates of $A$ obtained at ambient CO$_2$ concentrations of 400 and 2000 μmol mol$^{-1}$ ($A_{\text{sat}}$ and $A_{\text{max}}$, respectively) were extracted from the $A\leftrightarrow C_i$ curves and reported separately. During measurements, ambient leaf temperature along the transect ranged between 25 and 30°C, while RH varied between 60 and 70%. Leaf samples were then dried and analysed for nitrogen and phosphorus content at the Australian National University, Canberra.

**Analysis framework**

To explore variation in forest carbon production and allocation, we ask: what parameters explain the variation in total NPP, above-ground coarse wood productivity ($\text{NPP}_{\text{acw}}$; hence tree growth rates), and above-ground biomass among sites? To resolve this question, we apply a systematic framework to decompose the relationship between $\text{NPP}_{\text{stem}}$ and GPP into several terms in a productivity-allocation-turnover chain, that we previously introduced to analyse carbon cycling along wet-dry gradients in lowland Amazonia (Malhi et al., 2015) and temporal responses to carbon allocation, seasonality and drought events are explored in (Doughty et al., 2015a; 2015b):

\[ \text{NPP} = \frac{\text{GPP} \times \text{NPP}}{\text{GPP}} \]

(2)

\[ i.e. \ \text{NPP} = \text{GPP} \times \text{CUE} \]

\[ \text{NPP}_{\text{ACW}} = \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_{\text{ACW}}}{\text{NPP}} \]

(3)

\[ i.e. \ \text{NPP}_{\text{ACW}} = \text{NPP} \times \text{woody allocation} \]

For a mature forest, where biomass growth and mortality rates are similar and there is little net change in biomass, the above-ground woody biomass residence time, $\tau_R$, can be estimated as woody biomass divided by woody productivity (Galbraith et al., 2013). Hence biomass can be expressed as:

\[ \text{Biomass}_{\text{ACW}} = \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_{\text{ACW}}}{\text{NPP}} \times \tau_R \]

(4)

**Results**
Climate

Figure 2 shows climatic characteristics as a function of elevation. Temperature demonstrates a steady linear decline with elevation, consistent with an adiabatic lapse rate of -4.4°C km\(^{-1}\) (p < 0.001, \(r^2 = 0.99\); Figure 2a). Total annual precipitation is high along the entire transect (always >1500 mm) and has a strong peak at mid-elevations (1000-2000 m) where night-time cool katabatic winds from the Andean slopes collide with moist Amazonian air to generate a stationary rainfall front (Killeen & Solorzano, 2008) (Figure 2b). Soil moisture shows no trend with elevation (p > 0.05; Figure 2c); it is largely aseasonal along the entire transect, with moderate seasonality only observed in two of the lowland plots (TAM-05 and TAM-06; Malhi et al., 2014) and at the uppermost plots (WAY-01 and ACJ-01; Girardin et al., 2014a). In this generally wet transect, spatial variation in annual mean soil moisture content seems to be determined by soil textural properties rather than by variation in precipitation regimes. Solar radiation declines at mid-elevations, associated with a higher frequency of both cloud occurrence and cloud immersion (Halladay et al., 2012), and then rises again at the uppermost, treeline plot (ACJ-01). Cloud immersion is particularly frequent in June-August, the austral winter, when temperatures are slightly lower and the cloud base is lower (Halladay et al., 2012).

Autotrophic carbon budget

The major components of GPP and NPP for the studied plots are shown in Table 2, with key aspects plotted as a function of elevation in Figure 3. In all cases, we fit either a single linear regression, or a piecewise regression with a break at 1600 m if the latter has a lower Akaike Information Criterion (AIC) score. GPP (from the 8-plot dataset) demonstrates a significant linear decline with elevation (p < 0.02, \(r^2 = 0.62\)), but a notable feature is an apparent transition between 1500 m and 1750 m (Figure 3a). The plot at 1500 m shows values of GPP similar to those of the lowland rainforests, despite being ~6-7°C cooler. The plot at 1750 m shows substantially lower productivity than that at 1500 m, and GPP declines further in the higher elevation plots. Piecewise regression is marginally significant (p = 0.06, \(r^2 = 0.67\)) and demonstrates a similar AIC score (49.0) to that of the simple linear regression (49.5).

NPP (from the full 16-plot dataset) shows a significant decline with elevation (p < 0.001, \(r^2 = 0.61\), and stronger evidence for a transition at 1600 m (Figure 3b). Piecewise regression with a break at 1600 m (p < 0.001, \(r^2 = 0.70\)) has a lower (better) AIC score (67.2) than the simple
linear regression (69.6). Above the 1500-1750 m transition, there is remarkably no overall
trend of NPP with elevation over an elevation range of 1750 m (a change of mean
temperature of 12-13 °C). The same pattern of no trend applies below the 1500 m transition,
though in this case the lack of trend is strongly driven by the high NPP at a single plot, SPD-03.

The carbon use efficiency (CUE), the ratio NPP/GPP, shows no relationship with elevation,
nor do plots at or below 1500 m significantly differ than those above 1500 m (p > 0.1; Figure
3c). Hence, there is no evidence of decreased or increased autotrophic respiratory load at
lower temperatures; CUE does not appear to be a function of temperature. Given the relative
invariance of CUE in our dataset, we apply fixed values of CUE (0.35 ± 0.04 for plots < 1600
m and 0.30 ± 0.05 for plots > 1600 m) to our NPP-only dataset (5 plots) to estimate GPP for
these plots, resulting in an extended dataset of GPP estimates for all 16 plots (Table 2).
However, the derived values of GPP are not plotted in Fig. 3a nor used in the statistical
analysis.

The above-ground coarse woody NPP demonstrates shows substantial site-to-site variation
but a significant linear decline as a function of elevation (p < 0.02, r² = 0.28), with a decrease
of 0.38 Mg C ha⁻¹ yr⁻¹ per 1000 m increase in elevation (Figure 3d). There is no evidence of a
break at 1600 m. Remarkably, fractional allocation of NPP to canopy, wood and roots
demonstrates no significant relationship with elevation and relatively little plot-to-plot
variability, nor do plots below 1600 m significantly differ than those above 1600 m (p > 0.1;
Figures 3d, 3e, 3f). Across the dataset the mean fractional allocations of NPP are 48±5 % to
canopy, 29±4 % to wood and 22±5 % to fine roots. Above-ground live biomass (AGB) shows
large plot-to-plot variation, but also a significant linear decline with elevation (p < 0.03, r² =
0.23; Figure 3g). This is strongly associated with a decline in forest stature, rather than a
decline in basal area. Biomass residence time (τR; calculated as above-ground woody
biomass divided by above-ground woody NPP) shows very large plot-to-plot variation and
little relationship with elevation, nor do plots at or below 1500 m significantly differ than
those above 1500 m (p =0.08; Figure 3h).

Application of analysis framework

We next compare the NPP and respiration components of two upper cloud forest
autotrophic carbon budgets against that of the four lowland plots (Figure 4). The mid-
Elevation plots are here excluded because of their transitional nature. This shows that woody biomass production rates are 50% lower in the upper montane forests than in the lowlands (Figure 4a). This decline can largely be attributed to a 36±7% decline in GPP, together with a moderate (15±10%) decline in carbon use efficiency (although in our broader dataset we see no overall trend in CUE with elevation). There is no significant change in proportional allocation of NPP to woody production, consistent with the larger dataset (Figure 3). As noted above, there is no evidence of an increase in CUE, as might be expected if temperature was a strong positive control on the fraction of photosynthate used in autotrophic respiration.

Our framework shows that the low biomass of the upper montane forests largely reflects these low growth rates (Figure 4b), rather than increases in mortality rates (= decreases in residence time). Biomass is 38±11% lower in the upper montane plots. This largely reflects the fact that woody growth rates are 42±2% lower, slightly offset by residence times being 6±19% longer in this. The wider dataset, however, shows no significant trend of residence time with elevation (Figure 3h).

Hence we can pinpoint a decline in GPP (i.e. total canopy photosynthesis) as the primary cause of the decline in woody growth rates and in forest biomass in upper montane forests, rather than a change NPP allocation or mortality rates. Low CUE may also partially contribute to a decline in woody growth in these particular montane plots, but this decline is not consistent along the whole gradient. We next ask is if this decline in GPP reflects decline in maximum photosynthetic capacity (e.g. limitation by nutrients, low temperatures), or a limitation of realized photosynthetic rates below potential rates (for example, by cloud immersion causing light limitation, and/or causing leaf wetting).

Figure 5 plots key aspects of canopy photosynthetic capacity, including the total leaf area index (LAI), and the maximal area-based rates of CO₂ fixation by Rubisco (Vcmax) and photosynthetic electron transport (Jmax). LAI shows only a modest and largely linear decline with elevation, with no evidence of a sharp transition at mid-elevations (p = 0.03, r² = 0.50; Figure 5a). The LAI is always > 3.5, indicating that canopies are largely closed at all elevations and almost all light is intercepted.

The leaf photosynthetic parameters are shown both at ambient temperatures and using values normalized to a measuring temperature of 25 ºC (i.e. Vcmax,25 and Jmax,25). At ambient
temperatures there was no evidence of a trend of either photosynthetic parameter with elevation (p > 0.1; Figures 5b, 5c). When normalised to 25 °C, site mean values of $V_{cmax,25}$ and $J_{max,25}$ were higher in the uplands (p = 0.052 for $V_{cmax,25}$; p = 0.049 for $J_{max,25}$). On a per-area basis, leaf N shows a slight, but non-significant, increase with elevation (p > 0.1; Figure S1a), and leaf P shows a strong linear increase with elevation (p < 0.001, $r^2 = 0.77$; Figure S2a). Thus, when assessed at a common temperature and when controlling for elevation differences in $C_i$ (by using $V_{cmax}$), photosynthetic N use efficiency was, on average, greater at high elevations. These findings are corroborated by Bahar et al. (unpublished data), who show that upland sites show higher investment of nitrogen in the photosynthetic apparatus, suggesting compensatory acclimation to the lower temperatures.

The magnitudes and trends are broadly consistent with those reported by van de Weg et al. (2009) for this same elevation gradient. This trend is consistent with results from a fertilisation experiment on the transect, which shows that woody growth rates in plots above 1500 m were responsive to N addition (indicating relative limitation of N), and growth rates in plots below 1500 m were responsive to P and N combined, indicating some role for P-limitation (Fisher et al., 2013). Overall, the relative availability of these nutrients appears to have no overall effect on the trend of leaf photosynthetic capacity with elevation.

Discussion

The results present a whole autotrophic carbon budget perspective on the variation of forest growth, productivity and biomass with elevation. This perspective and analytic framework have enabled us to isolate the relative roles and importance of photosynthesis, respiration, allocation and mortality in determining tree growth rates and biomass.

The analysis shows that there is no overall trend in CUE, in NPP allocation, and little overall trend in mortality rate/residence time. This pinpoints changes in gross primary productivity as the primary determinant of general trend for decline in growth and biomass with elevation. In the context of this transect at least, this suggests that many hypotheses related to shifts in allocation (e.g. increased investment in fine roots at high elevations causes a decline in wood production), or to shifts in carbon use efficiency (e.g. there is a greater respiratory load and hence lower CUE at high temperatures) can be rejected when explaining variation with elevation.
The next question is whether the decline in GPP with elevation is related to a decline in canopy photosynthetic capacity or in rates of actual photosynthesis. Canopy photosynthetic capacity is a function of canopy leaf area and leaf-level photosynthetic capacity at ambient temperatures. Strikingly, we do not observe any evidence of a decline in photosynthetic parameters under ambient conditions, and only a modest decline in LAI. This suggests that canopy photosynthetic capacity shows only moderate variation with elevation, and that any declines in capacity are manifest through declines in LAI rather than leaf-level properties.

The lack of any decline in leaf-level photosynthesis is further supported by the lack of change in leaf N per unit area with elevation, and the increase of leaf P per unit area (an observation that was also noted by van de Weg et al., 2009). This suggests that lower temperatures do not lead to less canopy stocks of key nutrients.

If canopy photosynthetic capacity plays only a small part in explaining the decline of GPP, this suggests that trends in ambient or actual photosynthesis may be more important in explaining the trend, and that actual photosynthesis does not track potential photosynthesis. One possible factor explaining the suppression of ambient photosynthesis below maximum levels is the observed decline in solar radiation (Figure 2), which is almost entirely explained by cloud occurrence and also occasional cloud immersion. Cloud immersion tends to reduce total solar radiation, although the effect of reduction in total solar radiation may be partially offset by the greatly increased diffuse fraction and less vertical stratification of available light. The canopy in the montane forest may have the ability for high levels of photosynthesis under sunny conditions, but immersion during cloud events reduce actual photosynthesis rates. However, the uppermost plot, Acjanaco, which sits in sunnier conditions at the treeline, does not record an increase in GPP. In the cloud forest zone (above ~1500-1750 m), an additional suppressing factor may be leaf wetting as a result of cloud immersion, which can reduce transpiration (Goldsmith et al., 2013; Gotsch et al., 2014).

A key point to consider is whether the trends in forest properties with elevation are broadly linear, or whether there is an abrupt transition in the region 1500-1750 m. Figure 3a and 3b are suggestive of an abrupt decline in GPP and NPP around this zone, which coincides with the appearance of many typical cloud forest features such as abundant epiphytic bryophytes (Horwath, 2012), tree ferns and other characteristic cloud forest features and species (W. Farfan Rios, unpublished data), increased leaf waxiness (S. Feakins, unpublished data),
shortened canopy stature (Asner et al., 2014) and a changed tree architecture from straight boles (competing for stratified light) to gnarled and twisted boles. This abrupt transition to a cloud forest type suggests that increase in cloud frequency and particularly cloud immersion drives the decline in GPP, and hence the decline in NPP and woody growth.

A remarkable feature is that the 1500 m plot exhibits GPP and NPP as high as that in the Amazon lowlands, despite being 6-7 °C cooler. In contrast, the 1750 m has values more characteristic of the higher cloud forest, but very high biomass. Focussing on the larger NPP dataset rather than the smaller GPP one, NPP shows no significant trend with elevation in the range 100-1500 m, and no significant trend with elevation in the range 1750-3537 m. The overall decline of NPP with elevation is driven by the submontane - cloud forest transition. Our analysis demonstrates how cloud immersion rather than temperature may drive the productivity and biomass of tropical montane forest ecosystems.

In conclusion, we have demonstrated the value of a whole carbon-budget perspective to provide insight into how and why growth and biomass tend to decline with elevation along a tropical elevation gradient. For this transect, we show that a decline in GPP with elevation is the main determinant of declining growth and biomass, with little trend in CUE, allocation of NPP, or biomass residence times. The results could have been very different. For example, for wet-dry gradients in lowland Amazonia, Malhi et al. (2015) demonstrated that the observed decline in GPP going from wet to dry forests was offset by increases CUE and increased allocation to woody growth, leading to little trend in woody growth rates with rainfall. The low biomass of dry forests was instead driven by low woody biomass residence times. The other striking result here is the lack of variation in leaf photosynthetic capacity with elevation, with the overall decline of GPP and NPP driven by a transition near cloud base. This suggests that temperature has little direct influence on productivity, with ecosystems acclimating their ecophysiology or shifting in composition to optimise productivity for their particular climate regime. For example, in colder forests, lower rates of nutrient mineralisation and uptake are compensated for longer leaf lifetimes and nutrient retention periods, and peak photosynthetic rates are likely optimised to lower temperatures.

There is large turnover of tree species between plots; individual species may be constrained by temperature, but the constant changes in species portfolio result in a relatively invariant potential GPP. Such results are consistent with a recent global analysis that suggests NPP is largely determined by stand age and biomass, and not by climate (Michaletz et al., 2014, but
note the critique by Chu et al. (2015). Such insights have yet to be incorporated into global vegetation models (Matthews et al., 2012), which tend to predict a high sensitivity of tropical GPP to temperature (Galbraith et al., 2010).

The sensitivity of biomes, and in particular tropical biomes, to warming temperatures is one of the key questions in global change ecosystems research. While this tropical elevation transect by its nature does not extend to the warmer lowland temperatures of a future warmer world, it does highlight the important processes of acclimation and community turnover that can result in relatively low long-term sensitivity of primary productivity to temperature. Tropical elevation transects are particular powerful tools for examining temperature relationships, as they do not have the confounding influence of varying length of a dormant winter season (Malhi et al., 2010). However, cloud immersion may confound attempts to use long elevation gradients as proxies for temperature changes alone. In a warming world, tropical cloud base is like to be rising (Still et al., 1999), and some of the most dramatic responses in carbon cycling and species composition may occur at this cloud immersion ecotone.

Finally, we acknowledge that the results reported here come from only one gradient study. Tropical montane regions are highly variable, and other transects may show different results emerging from a different permutation of ecology, cloud climatology, soils, topography and biogeographical context. For example, in the only other direct assessment of GPP and NPP in a tropical elevation gradient, for three plots spanning 1000-3000 m in Ecuador, Leuschner et al. (2013) did note a decline in GPP (from ~21 Mg C ha\(^{-1}\) yr\(^{-1}\) at 1000 m to ~9 Mg C ha\(^{-1}\) yr\(^{-1}\) at 3000 m) associated with a strong decline in LAI (from 5-6 at 1000 m to 2-3 at 3000 m), and an increased allocation of NPP towards roots at high elevations. We encourage the development of similar studies in other tropical elevation gradients and attempts at synthesis of insights across such studies. Our study shows how a whole autotrophic carbon budget perspective can yield new insights into these longstanding ecological questions, and also rephrase the types of questions that we ask.

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Author Contributions
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Röderstein M, Hertel D, Leuschner C. 2005. Above- and below-ground litter production in

**Spracklen DV, Righelato R. 2014.** Tropical montane forests are a larger than expected global carbon store. *Biogeosciences* **11**: 2741–2754.

**Still CJ, Foster PN, Schneider, SH. 1999.** Simulating the effects of climate change on tropical montane cloud forests. *Nature* **398**: 608-610.


**Weaver PL, Murphy PG. 1990.** Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* **22**: 69–82.


### Table 1. Environmental characteristics of 1 ha study sites occurring along a 2800 m tropical montane elevation transect.

<table>
<thead>
<tr>
<th></th>
<th>Allpahuayo A</th>
<th>Allpahuayo C</th>
<th>Tambopata V</th>
<th>Tambopata VI</th>
<th>Pantiacolla 2</th>
<th>Pantiacolla 3</th>
<th>Tono</th>
<th>San Pedro 1500 m</th>
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<td>ALP30</td>
<td>TAM05</td>
<td>TAM06</td>
<td>PAN02</td>
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<td>n/a</td>
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<td>(P_{\text{total}}) (mg kg(^{-1}))</td>
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<th>Esperanza</th>
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<td><strong>Solar radiation (GJ m⁻² yr⁻¹)</strong></td>
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<td>n/a</td>
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<td>2472</td>
<td>1827</td>
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<td>Umbrisol</td>
<td>Umbrisol</td>
<td>Umbrisol</td>
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<td><strong>P total (mg kg⁻¹)</strong></td>
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<tr>
<td><strong>Total C (%)</strong></td>
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<td><strong>Soil C stock (Mg C ha⁻¹ from 0-30 cm)</strong></td>
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<td>97.1</td>
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<td>231.6</td>
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<td>36</td>
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Table 2. Components of the carbon cycle as measured in 1 ha study sites occurring along a 2800 m tropical montane elevation transect. Where appropriate, values are means ± 1 SE. NPP$_{\text{Herbivory}}$, NPP$_{\text{ACW}}$, and NPP$_{\text{Branch Turnover}}$ are estimated. All NPP and respiration component measurements are in Mg C ha$^{-1}$ yr$^{-1}$, NPP allocation fractions are unitless, above-ground biomass values are in Mg C ha$^{-1}$, and residence time is in years.

<table>
<thead>
<tr>
<th></th>
<th>Allpahuayo A</th>
<th>Allpahuayo C</th>
<th>Tambopata V</th>
<th>Tambopata VI</th>
<th>Pantiacolla 2</th>
<th>Pantiacolla 3</th>
<th>Tono</th>
<th>San Pedro 1500 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>GPP</td>
<td>39.05 ± 4.59</td>
<td>41.88 ± 4.60</td>
<td>35.47 ± 3.55</td>
<td>34.47 ± 3.53</td>
<td>32.41 ± 4.16</td>
<td>26.90 ± 3.57</td>
<td>28.27 ± 2.58</td>
<td>38.57 ± 4.13</td>
</tr>
<tr>
<td>NPP</td>
<td>12.21 ± 0.96</td>
<td>14.27 ± 0.95</td>
<td>14.28 ± 0.83</td>
<td>11.60 ± 0.59</td>
<td>11.34 ± 0.66</td>
<td>9.42 ± 0.64</td>
<td>9.90 ± 0.90</td>
<td>12.08 ± 0.49</td>
</tr>
<tr>
<td>CUE</td>
<td>0.31 ± 0.04</td>
<td>0.34 ± 0.04</td>
<td>0.4 ± 0.05</td>
<td>0.34 ± 0.04</td>
<td>0.35 ± 0.05</td>
<td>0.31 ± 0.04</td>
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<tr>
<td>NPP$_{\text{Canopy Allocation}}$</td>
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<td>0.45 ± 0.07</td>
<td>0.43 ± 0.04</td>
<td>0.49 ± 0.06</td>
<td>0.48 ± 0.04</td>
<td>0.48 ± 0.05</td>
<td>0.55 ± 0.06</td>
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<td>NPP$_{\text{Wood Allocation}}$</td>
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<td>0.33 ± 0.03</td>
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<td>0.26 ± 0.03</td>
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<tr>
<td>NPP$_{\text{Root Allocation}}$</td>
<td>0.25 ± 0.03</td>
<td>0.25 ± 0.03</td>
<td>0.32 ± 0.05</td>
<td>0.18 ± 0.02</td>
<td>0.16 ± 0.03</td>
<td>0.14 ± 0.05</td>
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<tr>
<td>NPP$_{\text{Canopy}}$</td>
<td>4.70 ± 0.86</td>
<td>6.42 ± 0.81</td>
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<td>5.64 ± 0.41</td>
<td>4.78 ± 0.46</td>
<td>3.97 ± 0.33</td>
<td>5.41 ± 0.36</td>
<td>5.99 ± 0.22</td>
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<td>NPP$_{\text{Leaf}}$</td>
<td>2.68 ± 0.66</td>
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<td>3.71 ± 0.39</td>
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<td>NPP$_{\text{Coarse root}}$</td>
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<td>0.72 ± 0.04</td>
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<td>0.29 ± 0.04</td>
<td>0.64 ± 0.09</td>
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<tr>
<td>NPP$_{\text{Fine root}}$</td>
<td>3.02 ± 0.29</td>
<td>3.50 ± 0.38</td>
<td>4.54 ± 0.71</td>
<td>2.11 ± 0.31</td>
<td>1.80 ± 0.37</td>
<td>1.29 ± 0.48</td>
<td>2.42 ± 0.81</td>
<td>1.89 ± 0.30</td>
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<td>$R_a$</td>
<td>24.92 ± 4.48</td>
<td>27.46 ± 4.51</td>
<td>20.5 ± 3.45</td>
<td>20.27 ± 3.38</td>
<td>26.63 ± 4.11</td>
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<tr>
<td>$R_{\text{Leaf}}$</td>
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<td>11.35 ± 3.50</td>
<td>8.86 ± 2.84</td>
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<td>7.06 ± 2.48</td>
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<td>8.11 ± 2.55</td>
<td>5.43 ± 1.77</td>
<td>7.62 ± 2.48</td>
<td>8.91 ± 2.82</td>
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<td>4.44 ± 0.92</td>
<td>6.38 ± 0.93</td>
<td>5.07 ± 0.61</td>
<td>4.62 ± 0.57</td>
<td>8.79 ± 1.36</td>
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<tr>
<td>$R_{\text{Coarse root}}$</td>
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<td>1.62 ± 0.83</td>
<td>1.14 ± 0.59</td>
<td>1.60 ± 0.82</td>
<td>1.87 ± 0.95</td>
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<td>65.23</td>
<td>40.47</td>
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<td>27.5</td>
<td>66.29</td>
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<td>Trocha Union VII</td>
<td>Trocha Union IV</td>
<td>Esperanza</td>
<td>Wayqecha</td>
<td>Trocha Union III</td>
<td>Acjanaco</td>
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<td>GPP</td>
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<td>24.19 ± 4.55</td>
<td>13.97 ± 2.66</td>
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<td>21.76 ± 2.57</td>
<td>25.93 ± 3.10</td>
<td>17.23 ± 3.30</td>
<td>26.31 ± 4.64</td>
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<td>NPP</td>
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<td>7.77 ± 0.37</td>
<td>7.73 ± 0.42</td>
<td>7.86 ± 0.47</td>
<td>5.61 ± 0.26</td>
<td>7.89 ± 0.45</td>
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<td>NPP_Canopy Allocation</td>
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<td>0.47 ± 0.02</td>
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<td>0.45 ± 0.04</td>
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<td>0.18 ± 0.03</td>
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<td>0.14 ± 0.03</td>
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<td>1.51 ± 0.29</td>
<td>4.14 ± 0.02</td>
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<td>2.91 ± 0.33</td>
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<td>NPP_Leaf</td>
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<td>NPP_Herbivory</td>
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<td>0.35 ± 0.01</td>
<td>0.25 ± 0.04</td>
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<td>NPP_ACW</td>
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<td>0.77 ± 0.08</td>
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<td>2.17 ± 0.22</td>
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<td>NPP_Coarse root</td>
<td>0.43 ± 0.06</td>
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<td>0.16 ± 0.02</td>
<td>0.25 ± 0.04</td>
<td>0.46 ± 0.07</td>
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<td>0.21 ± 0.03</td>
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<tr>
<td>NPP_Fine root</td>
<td>1.22 ± 0.23</td>
<td>3.26 ± 0.73</td>
<td>1.80 ± 0.18</td>
<td>1.63 ± 0.34</td>
<td>1.41 ± 0.21</td>
<td>1.90 ± 0.35</td>
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<td>1.13 ± 0.21</td>
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<tr>
<td>R_a</td>
<td>24.4 ± 4.01</td>
<td>14.70 ± 2.54</td>
<td>17.90 ± 3.07</td>
<td>24.04 ± 1.02</td>
<td>6.10 ± 1.92</td>
<td>5.18 ± 1.63</td>
<td>4.87 ± 1.54</td>
<td>7.69 ± 2.42</td>
</tr>
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<td>R_leaf</td>
<td>6.55 ± 2.17</td>
<td>6.10 ± 1.92</td>
<td>5.18 ± 1.63</td>
<td>4.87 ± 1.54</td>
<td>6.10 ± 1.92</td>
<td>5.18 ± 1.63</td>
<td>4.87 ± 1.54</td>
<td>7.69 ± 2.42</td>
</tr>
<tr>
<td>R_stem</td>
<td>9.70 ± 3.07</td>
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<td>7.69 ± 2.42</td>
<td>2.71 ± 0.36</td>
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<tr>
<td>R_Rhizosphere</td>
<td>6.11 ± 0.96</td>
<td>2.71 ± 0.36</td>
<td>3.42 ± 0.50</td>
<td>2.71 ± 0.36</td>
<td>2.71 ± 0.36</td>
<td>3.42 ± 0.50</td>
<td>2.71 ± 0.36</td>
<td>3.42 ± 0.50</td>
</tr>
<tr>
<td>R_Coarse root</td>
<td>2.04 ± 1.02</td>
<td>1.02 ± 0.52</td>
<td>1.61 ± 0.81</td>
<td>1.02 ± 0.52</td>
<td>1.02 ± 0.52</td>
<td>1.61 ± 0.81</td>
<td>1.02 ± 0.52</td>
<td>1.61 ± 0.81</td>
</tr>
<tr>
<td>Aboveground biomass</td>
<td>144.37</td>
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<tr>
<td>Residence time</td>
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<td>68.92</td>
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</table>
Figure Legends

Figure 1. The pathway leading from the conversion of photosynthate to standing live woody biomass provides a framework for understanding the processes which can ultimately lead to reduced growth and standing biomass in tropical montane forests as compared to tropical lowland forests. Adapted from (Malhi, 2012).

Figure 2. Variation in climate along the 2800 m tropical montane elevation transect, including (a) mean annual air temperature, (b) direct precipitation, (c) soil moisture and (d) solar radiation.

Figure 3. Variation in carbon cycle characteristics along the 2800 m tropical montane elevation transect, including (a) gross primary productivity (GPP), (b) net primary productivity (NPP), (c) carbon use efficiency, the fraction $NPP/GPP$, (d) aboveground course woody NPP ($NPP_{acw}$), (e) fractional NPP allocation to canopy components, (f) fractional NPP allocation to woody components, (g) fractional NPP allocation to roots, (h) above-ground live biomass (AGB) and (i) woody residence time.

Figure 4. The ratio of key carbon cycle attributes of the two upper montane cloud forest plots (Wayqecha and Esperanza) relative to the four lowland forest plots (Tambopata and Allpahuayo).

Figure 5. Variation in key canopy attributes influencing canopy photosynthetic capacity along the 2800 m tropical montane elevation transect, including (a) Leaf Area Index (LAI); (b) maximal area-based rates of CO$_2$ fixation by Rubisco at ambient temperatures ($V_{cmax}$) and normalised to 25ºC ($V_{cmax,25}$); (c) photosynthetic electron transport at ambient temperatures ($J_{max}$) and normalised to 25ºC ($J_{max,25}$).
Supporting Information

Figure S1. Relationship between foliar nutrients and elevation.
Fig 1.

Gross Primary Productivity (GPP) → Photosynthesis

Carbon Use Efficiency (CUE) = NPP/GPP

Net Primary Productivity (NPP) → Autotrophic respiration

NPP allocation

Woody Productivity

Woody Residence time

Tree mortality

Standing Live Woody Biomass
Fig 3.

(a) GPP (Mg C ha⁻¹ yr⁻¹)
(b) NPP (Mg C ha⁻¹ yr⁻¹)
(c) Carbon use efficiency
(d) NPP mean (Mg C ha⁻¹ yr⁻¹)
(e) Fractional NPP allocation to canopy
(f) Fractional NPP allocation to wood
(g) Fractional NPP allocation to roots
(h) AGB (Mg C ha⁻¹)
(i) Residence time (yrs)
Fig. 4

EQ(4) \[ \text{AGB}_\text{acw} = \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_\text{acw}}{\text{NPP}} \times \tau_W \]

EQ(3) \[ \text{NPP}_\text{acw} = \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_\text{acw}}{\text{NPP}} \]

Difference in process component (\%)
-60
-40
-20
0
20
40

Allocation

EQ(4) \[ \text{AGB}_\text{acw} = \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_\text{acw}}{\text{NPP}} \times \tau_W \]

EQ(3) \[ \text{NPP}_\text{acw} = \text{GPP} \times \frac{\text{NPP}}{\text{GPP}} \times \frac{\text{NPP}_\text{acw}}{\text{NPP}} \]
Fig. 5

(a) LAI vs. Elevation (m)

(b) $V_{c\text{max}}$ vs. Elevation (m)

(c) $J_{\text{max}}$ vs. Elevation (m)