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The Variation of Productivity and Its Allocation Along a Tropical Elevation Gradient: A Whole Carbon Budget Perspective

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33 **Summary**

34

35 • Why do forest productivity and biomass decline with elevation? To address this
36 question, research to date has generally focused on correlative approaches
37 describing changes in woody growth and biomass with elevation.

38 • We present a novel, mechanistic approach to this question by quantifying the
39 autotrophic carbon budget in 16 forest plots along a 3300m elevation transect in
40 Peru,.

41 • Low growth rates at high elevations appear primarily driven by low gross primary
42 productivity (GPP), with little shift in either carbon use efficiency (CUE) or
43 allocation of net primary productivity (NPP) between wood, fine roots and
44 canopy. The lack of trend in CUE implies that the proportion of photosynthate
45 allocated to autotrophic respiration is not sensitive to temperature. Rather than a
46 gradual linear decline in productivity there is some limited but non-conclusive
47 evidence of a sharp transition in NPP between submontane and montane forests,
48 which may be caused by cloud immersion effects within the cloud forest zone.
49 Leaf-level photosynthetic parameters do not decline with elevation, implying that
50 nutrient limitation does not restrict photosynthesis at high elevations.

51 • Our data demonstrate the potential of whole carbon budget perspectives to provide
52 a deeper understanding of controls on ecosystem functioning and carbon cycling.

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55 **Introduction**

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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.

88 From an autotrophic carbon budget perspective, the primary mechanisms that could cause a
89 reduction in growth rates and biomass with increasing elevation are: (1) limitation of rates of
90 photosynthesis and thus declines in GPP; (2) relative increases in autotrophic respiration (R_a)
91 and resultant decreases in carbon use efficiency (CUE), which is the ratio NPP/GPP ; (3)
92 shifting allocation or storage of NPP away from woody biomass and into canopy or fine
93 roots, or (4) increases in tree mortality rates (decreases in wood residence time) and thus
94 decreases in equilibrium above-ground biomass (Figure 1). We review each of these potential
95 mechanisms in turn.

96

97 Decline in net photosynthesis

98 A decline in canopy net photosynthesis could result from either a decline in CO_2 - and light-
99 saturated leaf photosynthetic capacity, a decline in realized rates of leaf-level photosynthesis
100 below capacity, or through a decline in canopy leaf area. These various declines could occur
101 because of a number of different abiotic drivers, such as decreases in temperature, water
102 availability, atmospheric CO_2 , soil nutrient availability and light. Reductions in temperature
103 could decrease metabolic activity and decrease photosynthetic rates below optimum levels;
104 such temperature dependence is implicit in many ecosystem models. On the other hand,
105 photosynthesis may acclimate to ambient mean temperatures, resulting in little temperature
106 dependence in ecosystem productivity (Lloyd & Farquhar, 2008). The decrease in the partial
107 pressure of CO_2 in air that occurs with increasing elevation could decrease photosynthetic
108 rates; however, research to date suggests that this is offset by the increased diffusivity at high
109 elevations and reduced partial pressure of O_2 , resulting in little net sensitivity of
110 photosynthesis to air pressure (Cordell et al., 1998; 1999). High soil water content and low
111 temperatures with increasing elevation can reduce nitrogen mineralization rates and affect
112 plant available nutrients (Benner et al., 2010), leading to decreases in the supply rate of foliar
113 nitrogen and phosphorus necessary for photosynthesis, although this can be confounded by
114 changes in leaf construction costs and lifetime (Cordell et al., 1998; van de Weg et al., 2009;
115 Wittich et al., 2012). Reduced light availability, occurring as a function of frequent cloud
116 cover, can lead to reductions in realised photosynthetic rates below capacity. There is
117 evidence from montane forests that cloud cover, as well as the accompanying leaf wetting
118 events, can result in reduced photosynthesis rates (Letts et al., 2010; Goldsmith et al., 2013).
119 Finally, declines in GPP can also result from decreases in canopy leaf area, which may be a
120 response to nutrient supply limitation (Weaver & Murphy, 1990; Kitayama & Aiba, 2002;
121 Moser et al., 2007).

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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 damage, or defence against herbivores or pathogens (though such biotic pressures are expected to decrease with elevation; Metcalfe et al., 2013), or repair of damaged tissues. 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). A common biosphere model assumption is that autotrophic respiration will increase disproportionately with increasing temperature, leading to a decrease in CUE.

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 the 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.

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

166

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

175

176 **METHODS**

177

178 **Field sites**

179

180 We collected several years (between 2007-2015) of carbon cycling data from 16 one-hectare
181 plots along an elevation gradient in Peru, ranging from the high elevation tree line (~3500 m
182 asl), through the cloud forest-submontane transition (1000-1750 m asl) and into the Amazon
183 lowlands (100-220 m asl). Site descriptions are summarised in Table 1 and provided for some
184 sites in more detail in site-specific papers (del Aguila-Pasquel et al., 2014; Huaraca Huasco
185 et al., 2014; Malhi et al., 2014; Girardin et al., 2014a; 2014b). The montane sites are
186 concentrated in the Kosñipata Valley, and the submontane plots either in the adjacent Tono
187 Valley (TON-01) or in the Pantiacolla front range of the Andes (PAN-02 and PAN-03).
188 These sites have been the subject of on-going, multidisciplinary research by the Andes

189 Biodiversity and Ecosystems Research Group (ABERG: www.andesconservation.org; Malhi
190 et al. 2010)). The cloud climatology of this valley is described by Halladay et al. (2012) and
191 the water budget has been closed by Clark et al. (2014).

192

193 The lowland Amazonian sites are in two locations: two plots at Tambopata, Madre de Dios,
194 in southeastern Peru (~200 m asl) with a moderate dry season (2-4 month), and another two
195 plots at Allpahuayo, Loreto, in northeastern Peru (~100 m asl) with no dry season. Although
196 Allpahuayo is some distance from the other plots, the availability of similar data allows for
197 better assessment of the site-to-site variability of lowland forests. Neither lowland site has
198 much tree species overlap with the montane sites

199

200 For eight of these plots, all the major components of NPP and R_a were measured, enabling
201 estimation of GPP and CUE; for the remaining eight only the major components of NPP
202 have thus far been assessed (Table 2). Data collection dates vary between plots, spanning
203 over six years (2007-2012) in four plots (TAM-05, TAM-06, WAY-01, SPD-02), four years
204 (2009-2012) in four plots (SPD-01, ESP-01, ALP-01, ALP-30), three years (2007-2009) in
205 five plots (TON-01, TRU-03, TRU-04, TRU-07, TRU-08) and two years (2013-2015) in
206 three plots (ACJ-01, PAN-02, PAN-03), representing 61 plot-years of intensive monthly data
207 collection efforts in total (Table 1).

208

209 Weather data were recorded at a number of automatic weather stations along the transect,
210 including fully automatic stations at or near ACJ-01, WAY-01/ESP-01, SPD-01, TON-01,
211 PAN-02, TAM-05/TAM-06 and ALP-01/03. Other sites had above canopy manual rain
212 gauges, and temperature was estimated from the nearest weather station using the observed
213 temperature lapse rate of $-4.4^\circ\text{C km}^{-1}$. Soil moisture (0-30 cm) was measured every month at
214 every soil respiration measurement point (25 points ha^{-1}).

215

216 Field methods

217

218 Our approach is to measure the major components of the autotrophic carbon cycle. Herein,
219 we define “autotrophic” as a focus on the plant processes of photosynthesis, productivity,
220 autotrophic respiration and allocation, rather than heterotrophic processes such as decay and
221 soil organic matter respiration. We employ the field protocol of the Global Ecosystems
222 Monitoring network (GEM: www.gem.tropicalforests.ox.ac.uk). These methods are described

223 in detail in an online manual on the GEM website and in previous individual site papers, and
224 in Methods S1, Online Supporting Information.

225

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

240

241 For estimation of autotrophic respiration, we estimate (i) rhizosphere respiration ($R_{\text{rhizosphere}}$)
242 once per month by subtracting the respiration of root-free soil from that of unaltered soil; (ii).
243 above-ground woody respiration (R_{stem}) by measuring stem respiration once per month and
244 scaling by a stem surface area allometry; (iii) below-ground course root and bole respiration
245 ($R_{\text{course root}}$) by applying a fixed multiplier to R_{stem} ; and (iv) leaf dark respiration (R_{leaf}) by
246 measuring leaf dark respiration rates of multiple sampled leaves in two seasons, then scaling
247 by estimates of sun and shade leaf fractions and applying a correction of light inhibition of
248 dark respiration.

249

250 The measured components of NPP and R_a are then summed to estimate total NPP and
251 autotrophic respiration R_a (Appendix S1). In plant-level autotrophic steady state conditions
252 (and on annual timescales or longer where there is little net non-structural carbohydrate
253 storage), gross primary productivity (GPP), the carbon taken up via photosynthesis, should
254 be approximately equal to plant carbon expenditure (PCE), the amount of carbon used for
255 NPP and autotrophic plant respiration (R_a) if there is no net accumulation of non-structural
256 carbohydrates. The autotrophic steady state condition does not require the total plot carbon

257 cycle to be in equilibrium; the plot can still be gaining or losing biomass or soil carbon
258 stocks, as long as there is no substantial accumulation or loss of non-structural carbohydrates.
259 Hence, we estimated GPP as the sum of NPP and R_a . We calculate the carbon use efficiency
260 (CUE) as the proportion of total GPP invested in NPP rather than R_a :

261

$$262 \text{ CUE} = \text{NPP} / \text{GPP} = \text{NPP} / (\text{NPP} + R_a) \quad (1)$$

263

264 Our biometric estimate of GPP is indirect and depends on summing up components of NPP
265 and R_a , each with their inherent sampling errors and systematic uncertainties. An alternative
266 approach to estimating GPP (also with inherent errors) is from eddy covariance flux
267 measurements. Reliable eddy covariance measurements would be almost impossible in the
268 complex and steep topography of our montane sites, but comparisons of biometric
269 approaches with flux measurements in 6 sites (Malhi et al., 2015, Fig. S1) and 46 forest sites
270 (M. Campioli et al., unpublished data), including several lowland rainforest sites,
271 demonstrate very good agreement between the two approaches, suggesting that no major
272 terms of the autotrophic carbon budget are being missed.

273

274 Somewhat inevitably, any estimate of NPP may be biased towards underestimation because it
275 neglects several small NPP terms, such as NPP lost as volatile organic emissions, non-
276 measured litter trapped in the canopy, or dropped from understory plants below the litter traps
277 (Clark et al., 2001). At a site in central Amazonia, volatile emissions were found to be a
278 minor component of the carbon budget ($0.13 \pm 0.06 \text{ Mg C ha}^{-1} \text{ year}^{-1}$; Malhi et al., 2009). For
279 below-ground NPP, the allocation to root exudates and to mycorrhizae is disregarded. In
280 effect, we treat root exudation and transfer to mycorrhizae as rhizosphere autotrophic
281 respiration rather than as NPP, which could potentially impact our CUE estimates. Recent
282 estimates from our lowland plots estimate that forests in less fertile sites increased C
283 allocation to the (non-root) rhizosphere by up to $\sim 2.2 \pm 1.4 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ compared to fertile
284 sites, an indication that root exudate fluxes are $< 7\%$ of GPP (C.E. Doughty et al.,
285 unpublished data). Given that these exudates are labile and rapidly respired by mycorrhizae
286 and soil microfauna in the rhizosphere, this exudate NPP term is very similar to fine root
287 autotrophic respiration in terms of carbon cycling.

288

289 Many of these measurements have potential systematic uncertainties: we assign sampling or
290 systematic uncertainties to each measurement, and rigorously propagate the uncertainties

291 through our calculations. In particular, it is important to note that our calculation of NPP is
292 based on the summation of four independent measurements (litterfall, tree growth, fine root
293 production and branchfall) and our estimate of GPP is based on the summation of seven
294 independent measurements (the components of NPP, as well as leaf, stem and rhizosphere
295 measurements). While some of these terms can carry substantial measurement and scaling
296 uncertainties, if the uncertainties are independent for each measurement, these uncertainties
297 propagate by quadrature to result in a manageable uncertainty in the final sum NPP or GPP
298 (Appendix S1). For example, while there may be significant uncertainty in our measurement
299 of root productivity or in our scaling of stem respiration, this does not result in unmanageable
300 uncertainties in our estimates of GPP. Hence, a carbon summation measurement comprised
301 of seven independent measurements may potentially be more accurate than an eddy
302 covariance-based estimate comprised of one measurement.

303

304 This ecosystem-level approach was complemented by a leaf-level approach to understanding
305 variation in leaf physiological traits. These leaf gas exchange measurements are reported in
306 detail in Bahar et al. (in press, this volume) and summarised briefly here. Over the period
307 July-October 2011, measurements were made using a portable photosynthesis system (Licor
308 6400XT, Li-Cor BioSciences, Lincoln, NE, USA) on 300 canopy trees (~1150 sun-exposed
309 leaves) of about 193 species along the transect, along 12 plots along the full elevation
310 gradient (typically 10-14 species per plot). For each tree, branches were collected from the
311 top canopy position, recut under water to ensure xylem water continuity, before starting gas
312 exchange measurements on the most recently fully expanded leaves. CO₂ response curves of
313 light-saturated photosynthesis ($A \leftrightarrow C_i$ curves) (with PAR at 1800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) were
314 performed within 30–60 minutes of branch detachment, with CO₂ concentrations inside the 6
315 cm² reference chamber ranging in a stepped sequence from 35 to 2000 $\mu\text{mol mol}^{-1}$. Block
316 temperatures within the chamber were set to 28 °C in the lowlands and 25 °C in the highlands
317 (ambient mean leaf temperatures at time of measurement ranged between typically 30 °C in
318 the lowlands and 23 °C in the highest plots). The resultant $A \leftrightarrow C_i$ curves were fitted following
319 the model described by Farquhar et al. (1980) in order to calculate V_{cmax} and J_{max} on a leaf
320 area basis. Rates of CO₂ exchange were corrected for diffusion through the gasket of the LI-
321 6400 leaf chamber (Bruhn et al., 2002) prior to calculation of V_{cmax} and J_{max} . Any variation in
322 mesophyll conductance is not accounted for in these estimates. Fitted parameters were scaled
323 to a reference temperature of 25°C using activation energies of 64.8 and 37.0 kJ mol⁻¹ for
324 V_{cmax} and J_{max} , respectively (Farquhar et al., 1980). The Michaelis constants of Rubisco for

325 CO₂ (K_c) and O₂ (K_o) at a reference temperature 25°C were assumed to be 404 μbar and 248
 326 mbar, respectively (von Caemmerer et al., 1994); these values were adjusted to actual leaf
 327 temperatures assuming activation energies of 59.4 and 36 kJ mol⁻¹ for K_c and K_o, respectively
 328 (Farquhar et al., 1980. During measurements, RH varied between 60 and 70%. Leaf samples
 329 were then dried and analysed for nitrogen and phosphorus content at the Australian National
 330 University, Canberra.

331

332 Analysis framework

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

341

$$342 \quad NPP = GPP \times \frac{NPP}{GPP}$$

343

(2)

344 i.e. $NPP = GPP \times CUE$

$$345 \quad NPP_{ACW} = GPP \times \frac{NPP}{GPP} \times \frac{NPP_{ACW}}{NPP} \quad (3)$$

346 i.e. $NPP_{ACW} = NPP \times \text{woody allocation}$

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

$$351 \quad Biomass_{ACW} = GPP \times \frac{NPP}{GPP} \times \frac{NPP_{ACW}}{NPP} \times \tau_R \quad (4)$$

352

353 **Results**

354 Climate

355 Figure 2 shows climatic characteristics as a function of elevation. Temperature
356 demonstrates a steady linear decline with elevation, consistent with an adiabatic lapse rate of
357 $-4.4^{\circ}\text{C km}^{-1}$ ($p < 0.001$, $r^2 = 0.99$; Figure 2a). Total annual precipitation is high along the
358 entire transect (always >1500 mm) and has a strong peak at mid-elevations (1000-2000 m)
359 where night-time cool katabatic winds from the Andean slopes collide with moist Amazonian
360 air to generate a stationary rainfall front (Killeen & Solorzano, 2008) (Figure 2b). Soil
361 moisture shows no trend with elevation ($p > 0.05$; Figure 2c); it is largely aseasonal along the
362 entire transect, with moderate seasonality only observed in two of the lowland plots (TAM-
363 05 and TAM-06; Malhi et al., 2014) and at the uppermost plots (WAY-01 and ACJ-01;
364 Girardin et al., 2014a). In this generally wet transect, spatial variation in annual mean soil
365 moisture content seems to be determined by soil textural properties rather than by variation in
366 precipitation regimes. Solar radiation declines at mid-elevations, associated with a higher
367 frequency of both cloud occurrence and cloud immersion (Halladay et al., 2012), and then
368 rises again at the uppermost, treeline plot (ACJ-01). Cloud immersion is particularly frequent
369 in June-August, the austral winter, when temperatures are slightly lower and the cloud base is
370 lower (Halladay et al., 2012).

371

372 Autotrophic carbon budget

373 The major components of GPP and NPP for the studied plots are shown in Table 2, with key
374 aspects plotted as a function of elevation in Figure 3. In all cases, we applied an ANCOVA
375 (response~elevation*location), where location is a categorical variable indicating “above” or
376 “below” the zone of transition from submontane to cloud forest at 1600 m). We then applied
377 stepwise model reduction and provide the best fit lines for each panel. Thus, the outcomes
378 include lines with different slopes (i.e. interaction), a single line with a slope (i.e. no
379 interaction), or horizontal line(s) at different or the same intercept (i.e. no slope). This
380 approach enabled us to evaluate evidence for a sharp transition at cloud base. We plot all data
381 against elevation as a purely geographical variable free of a priori assumptions; in Fig. S2, we
382 plot against temperature as a potential response variable; the resulting significance statistics
383 are almost identical.

384

385 We only collected data on autotrophic respiration (and thereby derived GPP) for eight plots.
386 GPP (from the 8-plot dataset) demonstrates a significant linear decline with elevation ($p <$
387 0.01 , $r^2 = 0.62$ (Fig.3a). The plot at 1500 m shows values of GPP similar to those of the

388 lowland rainforests, despite being $\sim 6\text{-}7^\circ\text{C}$ cooler, but overall there is no strong statistical
389 support for a break at cloud base. If the overall trend is interpreted as a temperature response
390 alone, the resulting sensitivity of GPP to temperature would be estimated as $-1.02 \text{ Mg C } ^\circ\text{C}^{-1}$.
391

392 NPP (from the full 16-plot dataset) shows a significant decline with elevation ($p < 0.001$, $r^2 =$
393 0.61), and stronger evidence for a transition at 1600 m (Fig. 3b). Regression with a break at
394 1600 m ($p < 0.001$, $r^2 = 0.68$) has a lower (better) AIC score (66.3) than the simple linear
395 regression (69.6). Above the 1500-1750 m transition, there is remarkably no overall trend of
396 NPP with elevation over an elevation range of 1750 m (a change of mean temperature of 12-
397 13°C). The same pattern of no trend applies below the 1500 m transition, though in this case
398 the lack of trend is strongly driven by the high NPP at a single plot, SPD-02. If this
399 influential plot is removed, there is a significant decline of NPP with elevation in the
400 lowland/submontane plots ($p < 0.001$, $r^2 = 0.79$ for full ANCOVA, Fig. S3).

401
402 The carbon use efficiency (CUE), the ratio NPP/GPP, shows no relationship with elevation,
403 nor do plots at or below 1500 m significantly differ than those above 1500 m ($p > 0.1$; Fig.
404 3c). Hence, there is no evidence of decreased or increased autotrophic respiratory load at
405 lower temperatures; CUE does not appear to be a function of temperature. Given the relative
406 invariance of CUE in our dataset, we apply fixed values of CUE (0.35 ± 0.04 for plots < 1600
407 m and 0.30 ± 0.05 for plots > 1600 m) to our NPP-only dataset (8 plots) to estimate GPP for
408 these plots, resulting in an extended dataset of GPP estimates for all 16 plots (Table 2).
409 However, the derived values of GPP are not plotted in Fig. 3a nor used in the statistical
410 analysis of CUE and GPP trends.

411
412 The above-ground coarse woody NPP demonstrates shows substantial site-to-site variation,
413 but a significant linear decline as a function of elevation ($p < 0.02$, $r^2 = 0.28$), with an
414 estimated mean decrease of $0.38 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ per 1000 m increase in elevation (Fig. 3d).
415 However, the best fit model is in two different constant values of NPP_{acw} above and below
416 1600m (AIC score of 30.1 vs. 35.8). This holds true even when the influential plot SPD-02 is
417 removed (Fig. S3). Remarkably, fractional allocation of NPP to canopy, wood and roots
418 demonstrates no significant relationship with elevation and relatively little plot-to-plot
419 variability, nor do plots below 1600 m significantly differ than those above 1600 m ($p > 0.1$;
420 Figs. 3d, 3e, 3f). Across the dataset the mean fractional allocations of NPP are $48 \pm 5\%$ to

421 canopy, 29 ± 4 % to wood and 22 ± 5 % to fine roots. Above-ground live biomass (AGB) shows
422 large plot-to-plot variation, but also a significant linear decline with elevation ($p < 0.03$, $r^2 =$
423 0.23 ; Fig. 3g). This is strongly associated with a decline in forest stature, rather than a decline
424 in basal area. Biomass residence time (τ_R ; calculated as above-ground woody biomass
425 divided by above-ground woody NPP) shows very large plot-to-plot variation and little
426 relationship with elevation, nor do plots at or below 1500 m significantly differ than those
427 above 1500 m ($p = 0.3$; Figure 3h).

428

429 Application of analysis framework

430 We next compare the NPP and respiration components of two upper cloud forest
431 autotrophic carbon budgets against that of the four lowland plots (Figure 4). The mid-
432 elevation plots are here excluded because of their transitional nature. Woody biomass
433 production rates are 50% lower in the upper montane forests than in the lowlands (Figure 4a).
434 This decline can largely be attributed to a 36 ± 7 % decline in GPP, together with a moderate
435 ($15\pm 10\%$) decline in carbon use efficiency (although in our broader dataset we see no overall
436 trend in CUE with elevation). There is no significant change in proportional allocation of
437 NPP to woody production, consistent with the larger dataset (Figure 3). As noted above, there
438 is no evidence of an increase in CUE, as might be expected if temperature was a strong
439 positive control on on autotrophic respiration.

440

441 The low biomass of the upper montane forests largely reflects these low growth rates
442 (Figure 4b), rather than increases in mortality rates (= decreases in residence time). Biomass
443 is $38\pm 11\%$ lower in the upper montane plots. This largely reflects the fact that woody growth
444 rates are $42\pm 2\%$ lower, slightly offset by residence times being $6\pm 19\%$ longer in this. The
445 wider dataset, however, shows no significant trend of residence time with elevation (Figure
446 3h).

447

448 Hence we can clearly pinpoint a decline in GPP (i.e. total canopy photosynthesis) as the
449 primary cause of the decline in woody growth rates and in forest biomass in the upper
450 montane forest plots, rather than a change NPP allocation or mortality rates. Low CUE may
451 also partially contribute to a decline in woody growth in these particular montane plots, but
452 this decline is not consistent along the whole gradient. We next ask is if this decline in GPP
453 may reflect decline in maximum photosynthetic capacity (e.g. limitation by nutrients, low

454 temperatures), or a reduction in realized photosynthetic rates below potential rates (for
455 example, by cloud immersion causing light limitation, and/or causing leaf wetting).

456

457 Figure 5 plots key aspects of canopy photosynthetic capacity, including the total leaf area
458 index (LAI), and the maximal area-based rates of CO₂ fixation by Rubisco (V_{cmax}) and
459 photosynthetic electron transport (J_{max}). LAI shows only a modest and largely linear decline
460 with elevation, with no evidence of a sharp transition at mid-elevations ($p = 0.03$, $r^2 = 0.50$;
461 Figure 5a). The LAI is always > 3.5 , indicating that canopies are largely closed at all
462 elevations and almost all light is intercepted.

463

464 The leaf photosynthetic parameters are shown both at ambient temperatures and using
465 values normalized to a measuring temperature of 25 °C (i.e. $V_{\text{cmax},25}$ and $J_{\text{max},25}$). At ambient
466 temperatures there was no evidence of a trend of either photosynthetic parameter with
467 elevation ($p > 0.1$; Figures 5b, 5c). When normalised to 25 °C, site mean values of $V_{\text{cmax},25}$
468 and $J_{\text{max},25}$ were higher in the uplands ($p = 0.05$). On a per-area basis, leaf N shows a slight,
469 but non-significant, increase with elevation ($p > 0.1$; Figure S1a), and leaf P shows a strong
470 linear increase with elevation ($p < 0.001$, $r^2 = 0.77$; Figure S2a). Thus, when assessed at a
471 common temperature and when controlling for elevation differences in C_i (by using V_{cmax}),
472 photosynthetic N use efficiency was, on average, greater at high elevations. These findings
473 are corroborated by Bahar et al. (2016, this volume), who show that upland sites show higher
474 investment of nitrogen in the photosynthetic apparatus, suggesting compensatory acclimation
475 to the lower temperatures.

476

477 The magnitudes and trends are broadly consistent with those reported by van de Weg et
478 al. (2009) for this same elevation gradient. This trend is consistent with results from a
479 fertilisation experiment on the transect, which shows that woody growth rates in plots above
480 1500 m were responsive to N addition (indicating relative limitation of N), and growth rates
481 in plots below 1500 m were responsive to P and N combined, indicating some role for P-
482 limitation (Fisher et al., 2013). Overall, the relative availability of these nutrients appears to
483 have no overall effect on the trend of leaf photosynthetic capacity with elevation.

484

485 **Discussion**

486

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

491

492 The analysis shows that there is no overall trend with elevation/temperature in CUE, in
493 NPP allocation, or mortality rate/residence time. This pinpoints changes in gross primary
494 productivity as the primary determinant of general trend for decline in growth and biomass
495 with elevation. This suggests that many hypotheses related to shifts in allocation (e.g.
496 increased investment in fine roots at high elevations causes a decline in wood production), or
497 to shifts in carbon use efficiency (e.g. there is a greater respiratory load and hence lower CUE
498 at high temperatures) can be rejected when explaining variation with elevation in this
499 transect. The lack of trend in CUE with temperature is remarkable, and consistent with some
500 prior studies in tropical and temperate regions (Ryan et al., 1997; Litton et al., 2007), and
501 provides a key result against which vegetation model representation of autotrophic respiration
502 can be tested.

503

504 The next question is whether the decline in GPP with elevation is related to a decline in
505 canopy photosynthetic capacity or in rates of actual photosynthesis. Canopy photosynthetic
506 capacity is a function of canopy leaf area and leaf-level photosynthetic capacity at ambient
507 temperatures. Strikingly, we do not observe any evidence of a decline in photosynthetic
508 parameters under ambient conditions, and only a modest decline in LAI. This suggests that
509 canopy photosynthetic capacity shows only moderate variation with elevation, and that any
510 declines in capacity are manifest through declines in LAI rather than leaf-level properties.
511 The lack of any decline in leaf-level photosynthesis is further supported by the lack of change
512 in leaf N per unit area with elevation, and the increase of leaf P per unit area. This suggests
513 that lower temperatures do not lead to less canopy stocks of key nutrients.

514

515 If canopy photosynthetic capacity plays only a small part in explaining the decline of
516 GPP, this suggests that trends in ambient or actual photosynthesis may be more important in
517 explaining the trend, and that actual photosynthesis does not track potential photosynthesis.
518 One possible factor explaining the suppression of ambient photosynthesis below maximum
519 levels is cloud immersion. Cloud immersion tends to reduce total solar radiation, although the
520 effect of reduction in total solar radiation may be partially offset by the greatly increased

521 diffuse fraction and less vertical stratification of available light. The canopy in the montane
522 forest may have the ability for high levels of photosynthesis under sunny conditions, but
523 cloudiness reduces actual photosynthesis rates. An additional suppressing factor may be leaf
524 wetting as a result of cloud immersion, which can reduce transpiration (Goldsmith et al.,
525 2013; Gotsch et al., 2014), and increase pathogen loads. However, the uppermost plot,
526 Acjanaco, which sits in sunnier (but still frequently cloud-immersed) conditions at the
527 treeline, does not record an increase in GPP.

528

529 A key point to consider is whether the trends in forest properties with elevation are broadly
530 linear, or whether there is an abrupt transition in the region 1500-1750 m. Figure 3b is
531 suggestive of an abrupt decline in NPP around this zone. NPP shows no significant trend
532 with elevation in the range 100-1500 m (unless we discount the SPD-02 plot), and no
533 significant trend with elevation in the range 1750-3537 m. The transition zone for NPP (1500
534 m – 1700 m) coincides with the appearance of many typical cloud forest features such as
535 abundant epiphytic bryophytes (Horwath, 2012), tree ferns and other characteristic cloud
536 forest features and species (W. Farfan Rios, unpublished data), increased leaf waxiness (S.
537 Feakins, unpublished data), shortened canopy stature (Asner et al., 2014) and a changed tree
538 architecture from straight boles (competing for stratified light) to gnarled and twisted boles.
539 This abrupt transition suggests that increase in cloud frequency and particularly cloud
540 immersion drives the decline in GPP, and hence the decline in NPP and woody growth.
541 However, the evidence from the smaller GPP dataset equally supports a simple linear fit as
542 opposed to a step-decline at 1600 m, so the support for cloud immersion as a key driver is not
543 conclusive.

544

545 In conclusion, we have demonstrated the value of a whole carbon-budget perspective to
546 provide insight into how and why growth and biomass tend to decline with elevation along a
547 tropical elevation gradient. For this transect, we show that a decline in GPP with elevation is
548 the main determinant of declining growth and biomass, with little trend in CUE, allocation of
549 NPP, or biomass residence times. The results could have been very different. For example,
550 for wet-dry gradients in lowland Amazonia, Malhi et al. (2015) demonstrated that the
551 observed decline in GPP going from wet to dry forests was offset by increases CUE and
552 increased allocation to woody growth, leading to little trend in woody growth rates with
553 rainfall. The low biomass of dry forests was instead driven by low woody biomass residence
554 times. The other striking result here is the lack of variation in leaf photosynthetic capacity

555 with elevation, with the overall decline of GPP and NPP driven by a transition near cloud
556 base. This suggests that temperature has little direct influence on productivity, with
557 ecosystems acclimating their ecophysiology or shifting in composition to optimise
558 productivity for their particular climate regime. For example, in colder forests, lower rates of
559 nutrient mineralisation and uptake are compensated for longer leaf lifetimes and nutrient
560 retention periods, and peak photosynthetic rates are likely optimised to lower temperatures.
561 There is large turnover of tree species between plots; individual species may be constrained
562 by temperature, but the constant changes in species portfolio result in a relatively invariant
563 potential GPP. Such results are consistent with a recent global analysis that suggests NPP is
564 largely determined by stand age and biomass, and not by climate (Michaletz et al., 2014, but
565 note the critique by Chu et al. (2015)). Such insights have yet to be incorporated into global
566 vegetation models (Marthews et al., 2012), which tend to predict a high sensitivity of tropical
567 GPP to temperature (Galbraith et al., 2010).

568

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

581

582 Finally, we acknowledge that the results reported here come from only one gradient
583 study. Tropical montane regions are highly variable, and other transects may show different
584 results emerging from a different permutation of ecology, cloud climatology, soils,
585 topography and biogeographical context. For example, in the only other direct assessment of
586 GPP and NPP in a tropical elevation gradient, for three plots spanning 1000-3000 m in
587 Ecuador, Leuschner et al. (2013) did note a decline in GPP (from $\sim 21 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at 1000
588 m to $\sim 9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at 3000 m) associated with a strong decline in LAI (from 5-6 at 1000

589 m to 2-3 at 3000 m), and an increased allocation of NPP towards roots at high elevations. We
590 encourage the development of similar studies in other tropical elevation gradients and
591 attempts at synthesis of insights across such studies. Our study shows how a whole
592 autotrophic carbon budget perspective can yield new insights into these longstanding
593 ecological questions, and also rephrase the types of questions that we ask.

594

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596

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608

609 **Author Contributions**

610 YM, CAJG, DBM, LEOCA, NS planned and designed the research. YM, CAJG, DBM,
611 LEOCA, CED, WHH, JES-E, JAP, FFA, RG, FYI, WF-R conducted fieldwork, OLP and MS
612 contributed plot data, NB and GRG contributed to data analysis, YM and GRG wrote the
613 manuscript, with contributions from CAJG, LEOCA, CED, OLP, WF-R and PM.

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Tables

Table 1. Environmental characteristics of 1 ha study sites occurring along a 2800 m tropical montane elevation transect. n/a indicates data are not available.

	Allpahuayo A	Allpahuayo C	Tambopata V	Tambopata VI	Pantiacolla 2	Pantiacolla 3	Tono	San Pedro 1500 m
RAINFOR site code	ALP11/ALP12	ALP30	TAM05	TAM06	PAN02	PAN03	TON01	SPD02
Latitude	-3.95	-3.9543	-12.8309	-12.8385	-12.64957	-12.6383	-12.9592	-13.0491
Longitude	-73.4333	-73.4267	-69.2705	-69.296	-71.26267	-71.2745	-71.5658	-71.5365
Elevation (m)	120	150	223	215	595	848	1000	1527
Slope (deg)	1.4	1.5	4.5	2.2	n/a	n/a	8	27.1
Aspect (deg)	n/a	196	186	169	n/a	n/a	n/a	125
Solar radiation (GJ m ⁻² yr ⁻¹)	n/a	5.22	n/a	4.8	3.82	n/a	n/a	4.08
Mean annual air temperature (°C)	25.2	25.2	24.4	24.4	23.5	21.9	20.7	18.8
Precipitation (mm yr ⁻¹)	2689	2689	1900	1900	2366	2835	3087	5302
Soil moisture (%)	26.8	10.8	21.8	35.5	n/a	n/a	39.8	37.3
Soil type	Alisol/Gleysol	Arenosol	Cambisol	Alisol	Plinthosol	Alisol	Cambisol	Cambisol
P _{total} (mg kg ⁻¹)	125.6	37.6	256.3	528.8	n/a	n/a	751	1630.7
Total N (%)	0.1	0.08	0.16	0.17	n/a	n/a	0.42	0.9
Total C (%)	1.19	1.13	1.51	1.2	n/a	n/a	5.01	13.6
Soil C stock (Mg C ha ⁻¹ from 0-30 cm)	92.95	16.4	43.7	37.4	n/a	n/a	78.6	93.5
Soil organic layer depth (cm)	12	10	13	37	n/a	n/a	35	30

Table 1 Continued.

	San Pedro 1750 m	Trocha Union VIII	Trocha Union VII	Trocha Union IV	Esperanza	Wayqecha	Trocha Union III	Acjanaco
RAINFOR site code	SPD01	TRU08	TRU07	TRU04	ESP01	WAY01	TRU03	ACJ01
Latitude	-13.0475	-13.0702	-13.0733	-13.1055	-13.1751	-13.1908	-13.1097	-13.1469
Longitude	-71.5423	-71.5559	-71.5588	-71.5893	-71.5948	-71.5874	-71.5995	-71.6323
Elevation (m)	1776	1885	2020	2758	2863	3045	3044	3537
Slope (deg)	30.5	38.8	18	21.2	27.3	30	22.4	36.3
Aspect (deg)	117	158	n/a	118	302	112	114	104
Solar radiation (GJ m ⁻² yr ⁻¹)	4.36	3.96	n/a	3.49	n/a	3.51	n/a	4.6
Mean annual air temperature (°C)	17.4	18	17.4	13.5	13.1	11.8	11.8	9
Precipitation (mm yr ⁻¹)	5302	2472	1827	2318	1560	1560	1776	1980
Soil moisture (%)	37.6	9.7	15.5	37.3	24.3	23.1	41.5	n/a
Soil type	Cambisol	Cambisol	Cambisol	Umbrisol	Umbrisol	Umbrisol	Umbrisol	Cambisol
P _{total} (mg kg ⁻¹)	1071.1	496	562.8	746.8	980.8	1413.6	787.3	n/a
Total N (%)	1.2	0.81	1.23	1.99	1.48	0.88	1.55	n/a
Total C (%)	22.7	14.25	28.66	28.33	28.59	19.33	27.22	n/a
Soil C stock (Mg C ha ⁻¹ from 0-30 cm)	75.6	97.1	83.7	289	133.9	231.6	82.4	n/a
Soil organic layer depth (cm)	32	30	80	20	50	36	36	n/a

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 \pm 1 SE. $NPP_{\text{Herbivory}}$, NPP_{ACW} , and $NPP_{\text{BranchTurnover}}$ are estimated. All NPP and respiration component measurements are in $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, NPP allocation fractions are unitless, above-ground biomass values are in Mg C ha^{-1} , and residence time is in years.

	Allpahuayo A	Allpahuayo C	Tambopata V	Tambopata VI	Pantiacolla 2	Pantiacolla 3	Tono	San Pedro 1500 m
GPP*	39.05 \pm 4.59	41.88 \pm 4.60	35.47 \pm 3.55	34.47 \pm 3.53	32.41 \pm 4.16	26.90 \pm 3.57	28.27 \pm 2.58	38.57 \pm 4.13
NPP	12.21 \pm 0.96	14.27 \pm 0.95	14.28 \pm 0.83	11.60 \pm 0.59	11.34 \pm 0.66	9.42 \pm 0.64	9.90 \pm 0.90	12.08 \pm 0.49
CUE	0.31 \pm 0.04	0.34 \pm 0.04	0.4 \pm 0.05	0.34 \pm 0.04			0.35 \pm 0.05	0.31 \pm 0.04
$NPP_{\text{Canopy Allocation}}$	0.38 \pm 0.10	0.45 \pm 0.07	0.43 \pm 0.04	0.49 \pm 0.06	0.48 \pm 0.04	0.48 \pm 0.05	0.55 \pm 0.06	0.50 \pm 0.03
$NPP_{\text{Wood Allocation}}$	0.37 \pm 0.04	0.30 \pm 0.03	0.24 \pm 0.02	0.33 \pm 0.03	0.24 \pm 0.02	0.26 \pm 0.03	0.21 \pm 0.02	0.35 \pm 0.03
$NPP_{\text{Root Allocation}}$	0.25 \pm 0.03	0.25 \pm 0.03	0.32 \pm 0.05	0.18 \pm 0.02	0.16 \pm 0.03	0.14 \pm 0.05	0.24 \pm 0.08	0.16 \pm 0.03
NPP_{Canopy}	4.70 \pm 0.86	6.42 \pm 0.81	6.15 \pm 0.35	5.64 \pm 0.41	4.78 \pm 0.46	3.97 \pm 0.33	5.41 \pm 0.36	5.99 \pm 0.22
NPP_{Leaf}	2.68 \pm 0.66	4.05 \pm 0.56	4.03 \pm 0.27	3.71 \pm 0.39	3.53 \pm 0.29	3.04 \pm 0.29	3.48 \pm 0.21	4.12 \pm 0.18
$NPP_{\text{Herbivory}}$	0.50 \pm 0.12	0.76 \pm 0.11	0.76 \pm 0.05	0.70 \pm 0.07	0.62 \pm 0.05	0.53 \pm 0.05	0.66 \pm 0.04	0.66 \pm 0.03
NPP_{ACW}	2.54 \pm 0.25	2.76 \pm 0.28	2.18 \pm 0.22	2.77 \pm 0.28	2.78 \pm 0.28	2.43 \pm 0.24	1.38 \pm 0.14	3.04 \pm 0.30
$NPP_{\text{Branch turnover}}$	1.42 \pm 0.14	1.01 \pm 0.10	0.95 \pm 0.10	0.50 \pm 0.05	0.65 \pm 0.07	0.57 \pm 0.06	0.40 \pm 0.06	0.52 \pm 0.07
$NPP_{\text{Coarse root}}$	0.53 \pm 0.08	0.58 \pm 0.08	0.46 \pm 0.07	0.58 \pm 0.08	0.72 \pm 0.04	0.63 \pm 0.03	0.29 \pm 0.04	0.64 \pm 0.09
$NPP_{\text{Fine root}}$	3.02 \pm 0.29	3.50 \pm 0.38	4.54 \pm 0.71	2.11 \pm 0.31	1.80 \pm 0.37	1.29 \pm 0.48	2.42 \pm 0.81	1.89 \pm 0.30
R_a	24.92 \pm 4.48	27.46 \pm 4.51	20.5 \pm 3.45	20.27 \pm 3.38				26.63 \pm 4.11
R_{Leaf}	8.92 \pm 3.00	11.35 \pm 3.50	8.86 \pm 2.84	6.43 \pm 2.07				7.06 \pm 2.48
R_{Stem}	9.63 \pm 3.05	8.11 \pm 2.55	5.43 \pm 1.77	7.62 \pm 2.48				8.91 \pm 2.82
$R_{\text{Rhizosphere}}$	4.44 \pm 0.92	6.38 \pm 0.93	5.07 \pm 0.61	4.62 \pm 0.57				8.79 \pm 1.36
$R_{\text{Coarse root}}$	1.93 \pm 0.98	1.62 \pm 0.83	1.14 \pm 0.59	1.60 \pm 0.82				1.87 \pm 0.95
Aboveground biomass	130.4	88.5	142.2	112.1	97.4	66.6	91.48	106.67
Residence time	51.34	32.07	65.23	40.47	35.1	27.5	66.29	35.09

*GPP is Gross Primary Productivity, NPP is Net Primary Productivity, CUE is Carbon Use Efficiency, the three allocation variables indicate the fraction of NPP allocated to canopy, wood and fine roots. The various subscripts of NPP indicate the amount of NPP allocated to total canopy, to leaves, lost to leaf herbivory, allocated to ACW (above-ground coarse wood production), to branch turnover, to coarse root production and to fine root production. The various subscripts of R indicates the total autotrophic respiration R_a , and the amounts of this respiration in leaves, the woody stem, rhizosphere and coarse roots.

Table 2 Continued.

	San Pedro 1750 m	Trocha Union VIII	Trocha Union VII	Trocha Union IV	Esperanza	Wayqecha	Trocha Union III	Acjanaco
GPP	32.33 ± 4.03	24.19 ± 4.55	13.97 ± 2.66	23.54 ± 4.55	21.76 ± 2.57	25.93 ± 3.10	17.23 ± 3.30	26.31 ± 4.64
NPP	8.01 ± 0.40	7.98 ± 0.74	4.61 ± 0.36	7.77 ± 0.37	7.73 ± 0.42	7.86 ± 0.47	5.61 ± 0.26	7.89 ± 0.45
CUE	0.25 ± 0.03	0.33 ± 0.07	0.33 ± 0.07	0.33 ± 0.07	0.36 ± 0.05	0.30 ± 0.04	0.33 ± 0.07	
NPP _{Canopy} Allocation	0.49 ± 0.04	0.43 ± 0.04	0.33 ± 0.07	0.53 ± 0.03	0.39 ± 0.05	0.51 ± 0.05	0.47 ± 0.02	0.40 ± 0.04
NPP _{Wood} Allocation	0.36 ± 0.03	0.16 ± 0.02	0.28 ± 0.03	0.26 ± 0.02	0.44 ± 0.04	0.25 ± 0.05	0.29 ± 0.03	0.45 ± 0.04
NPP _{Root} Allocation	0.15 ± 0.03	0.41 ± 0.10	0.39 ± 0.05	0.21 ± 0.04	0.18 ± 0.03	0.24 ± 0.05	0.23 ± 0.04	0.14 ± 0.03
NPP _{Canopy}	3.94 ± 0.24	3.42 ± 0.02	1.51 ± 0.29	4.14 ± 0.02	2.94 ± 0.28	3.99 ± 0.28	2.66 ± 0.01	2.91 ± 0.33
NPP _{Leaf}	2.63 ± 0.17	2.42 ± 0.02	1.12 ± 0.21	2.69 ± 0.01	1.96 ± 0.23	2.52 ± 0.18	1.78 ± 0.01	2.20 ± 0.20
NPP _{Herbivory}	0.42 ± 0.03	0.31 ± 0.01	0.15 ± 0.03	0.35 ± 0.01	0.25 ± 0.04	0.32 ± 0.02	0.23 ± 0.01	0.28 ± 0.03
NPP _{ACW}	2.04 ± 0.20	0.79 ± 0.08	0.77 ± 0.08	1.19 ± 0.12	2.17 ± 0.22	1.18 ± 0.12	1.02 ± 0.10	2.13 ± 0.21
NPP _{Branch turnover}	0.38 ± 0.04	0.34 ± 0.05	0.37 ± 0.06	0.56 ± 0.08	0.75 ± 0.07	0.54 ± 0.05	0.41 ± 0.06	0.82 ± 0.08
NPP _{Coarse root}	0.43 ± 0.06	0.17 ± 0.02	0.16 ± 0.02	0.25 ± 0.04	0.46 ± 0.07	0.25 ± 0.04	0.21 ± 0.03	0.62 ± 0.03
NPP _{Fine root}	1.22 ± 0.23	3.26 ± 0.73	1.80 ± 0.18	1.63 ± 0.34	1.41 ± 0.21	1.90 ± 0.35	1.31 ± 0.23	1.13 ± 0.21
R _a	24.4 ± 4.01				14.70 ± 2.54	17.90 ± 3.07		
R _{Leaf}	6.55 ± 2.17				6.10 ± 1.92	5.18 ± 1.63		
R _{Stem}	9.70 ± 3.07				4.87 ± 1.54	7.69 ± 2.42		
R _{Rhizosphere}	6.11 ± 0.96				2.71 ± 0.36	3.42 ± 0.50		
R _{Coarse root}	2.04 ± 1.02				1.02 ± 0.52	1.61 ± 0.81		
Aboveground biomass	144.37	64.22	50.65	88.52	65.03	81.32	59.08	81.9
Residence time	70.77	81.29	65.78	74.39	29.97	68.92	57.92	38.4

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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 3300 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 3300 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 coarse 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. The best model fit (according to AIC) is shown when significant, either a single horizontal line or slope, or two lines split at 1600 m (cloud base).

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). Error bars indicate standard errors.

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 25°C ($V_{cmax,25}$); (c) photosynthetic electron transport at ambient temperatures (J_{max}) and normalised to 25°C ($J_{max,25}$). Error bars indicate standard errors.

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33 **Supporting Information**

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35 **Figure S1.** Relationship between foliar nutrients (nitrogen and phosphorus) and elevation.

36 **Figure. S2** Relationship between primary productivity and temperature.

37 **Figure. S3** Relationship between primary productivity and elevation when the sometimes_

38 influential plot SPD-02 is excluded.