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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 growth and biomass against elevation-related variables such
38 as temperature.

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

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

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

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57 **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.

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

98

99 *Decline in net photosynthesis*

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

124

125 *Changes in carbon use efficiency*

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

134

135 *Shifting allocation of NPP*

136 Although above-ground *NPP* has often been observed to decline with elevation (Marrs *et al.*,
137 1988; Weaver & Murphy, 1990; Girardin *et al.*, 2010; Moser *et al.*, 2011) insights into
138 belowground *NPP*, and thus total *NPP*, remain limited. Many studies have noted an increase
139 in root biomass with increasing elevation (Kitayama & Aiba, 2002; Moser *et al.*, 2008;
140 Girardin *et al.*, 2013), but how this relates to root *NPP* depends on understanding fine root
141 lifetimes. Few studies have quantified root *NPP*; some have observed no strong patterns with
142 elevation (Girardin *et al.*, 2013) while others have observed an increase with elevation
143 (Röderstein *et al.*, 2005; Moser *et al.*, 2011). Nevertheless, it has been hypothesized that
144 declining above-ground *NPP* is compensated for by a concomitant change in belowground
145 *NPP* (Leuschner *et al.*, 2007). The observed increase in fine root production along certain
146 elevation transects and more universal increase for fine root biomass have been proposed as
147 compensation for low nutrient availability.

148

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

154

155 We synthesize 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, which explores the relationships between plant traits
162 and ecosystem function; hence this study presents and explains the benchmark productivity
163 data for various CHAMBASA companion papers (this volume). It also provides a consistent
164 dataset suitable for testing and aiding ecosystem model development. For this specific paper,
165 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 2010)). The cloud climatology of this valley is described by Halladay *et al.* (2012) and the
191 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. Malhi *et al.* (2015) present an analysis of
199 the spatial variability of the carbon cycle in lowland Amazonian forests, including the
200 Allpahuayo and Tambopata sites. Ten of the plots are the focus of the CHAMBASA field
201 programme, a multi-scale project that links field-measured traits to plot-level metrics to
202 airborne remote sensing of this landscape.

203

204 For eight of these plots, all the major components of NPP and R_a were measured, enabling
205 estimation of GPP and CUE ; for the remaining eight only the major components of NPP
206 have thus far been assessed (Table 2). Data collection dates vary between plots, spanning
207 over six years (2007-2012) in four plots (TAM-05, TAM-06, WAY-01, SPD-02), four years
208 (2009-2012) in four plots (SPD-01, ESP-01, ALP-01, ALP-30), three years (2007-2009) in
209 five plots (TON-01, TRU-03, TRU-04, TRU-07, TRU-08) and two years (2013-2015) in
210 three plots (ACJ-01, PAN-02, PAN-03), representing 61 plot-years of intensive monthly data
211 collection efforts in total (Table 1).

212

213 *Field methods*

214

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

222

223 The GEM protocol involves measuring and summing all major components of NPP and
224 autotrophic respiration on monthly or seasonal timescales. For NPP , this includes canopy
225 litterfall ($NPP_{\text{litterfall}}$) at biweekly intervals, estimates of leaf loss to herbivory ($NPP_{\text{herbivory}}$)

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

237

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

245

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

257

$$258 \quad CUE = NPP / GPP = NPP / (NPP + R_a) \quad (1)$$

259

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

269

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

286

287 Many of these measurements have potential systematic uncertainties: we assign sampling or
288 systematic uncertainties to each measurement, and rigorously propagate the uncertainties
289 through our calculations. In particular, it is important to note that our calculation of *NPP* is
290 based on the summation of four independent measurements (litterfall, tree growth, fine root
291 production and branchfall) and our estimate of *GPP* is based on the summation of seven
292 independent measurements (the components of *NPP*, as well as leaf, stem and rhizosphere
293 measurements). While some of these terms can carry substantial measurement and scaling

294 uncertainties, if the uncertainties are independent for each measurement, these uncertainties
295 propagate by quadrature to result in a manageable uncertainty in the final sum *NPP* or *GPP*
296 (Appendix S1). For example, while there may be significant uncertainty in our measurement
297 of root productivity or in our scaling of stem respiration, this does not result in unmanageable
298 uncertainties in our estimates of *GPP*. By contrast, an eddy covariance-based estimate of
299 *GPP* is based on a single type of measurement (of net ecosystem exchange); hence any
300 uncertainties in the method, such as underestimation of night-time respiration in stable
301 atmospheric conditions, can result in an equivalent uncertainty in the final estimate of *GPP*.
302 Hence, a carbon summation measurement comprised of seven independent measurements
303 may potentially be more accurate than an eddy covariance-based estimate comprised of one
304 measurement. Where the two approaches agree, we can have increased confidence that both
305 approaches are capturing the major components of the carbon cycle.

306

307 This ecosystem-level approach was complemented by a leaf-level approach to understanding
308 variation in leaf physiological traits. These leaf gas exchange measurements are reported in
309 detail in Bahar et al (unpublished data) and summarised briefly here. Over the period July-
310 October 2011, measurements were made using a portable photosynthesis system (Licor
311 6400XT, Li-Cor BioSciences, Lincoln, NE, USA) on 300 canopy trees (~1150 sun-exposed
312 leaves) of about 210 species along the transect. For each tree, branches were collected from
313 the top canopy position, recut under water to ensure xylem water continuity, before starting
314 gas exchange measurements on the most recently fully expanded leaves. CO₂ response curves
315 of light-saturated photosynthesis ($A \leftrightarrow C_i$ curves) (with PAR at 1800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$)
316 were performed within 30–60 minutes of branch detachment, with CO₂ concentrations inside
317 the 6 cm² reference chamber ranging in a stepped sequence from 35 to 2000 $\mu\text{mol mol}^{-1}$.
318 Block temperatures within the chamber were set to the prevailing day-time air temperature at
319 each site (from 25-28 °C). The resultant $A \leftrightarrow C_i$ curves were fitted following the model
320 described by Farquhar *et al.* (1980) in order to calculate V_{cmax} and J_{max} on a leaf area basis.
321 Rates of CO₂ exchange were corrected for diffusion through the gasket of the LI-6400 leaf
322 chamber (Bruhn *et al.*, 2002) prior to calculation of V_{cmax} and J_{max} . Fitted parameters were
323 scaled to a reference temperature of 25°C using activation energies of 64.8 and 37.0 kJ mol⁻¹
324 for V_{cmax} and J_{max} , respectively (Farquhar *et al.*, 1980). The Michaelis constants of Rubisco
325 for CO₂ (K_c) and O₂ (K_o) at a reference temperature 25°C were assumed to be 404 μbar and
326 248 mbar, respectively (von Caemmerer *et al.*, 1994); these values were adjusted to actual
327 leaf temperatures assuming activation energies of 59.4 and 36 kJ mol⁻¹ for K_c and K_o ,

328 respectively (Farquhar et al., 1980). Finally, rates of A obtained at ambient CO₂
 329 concentrations of 400 and 2000 μmol mol⁻¹ (A_{sat} and A_{max} , respectively) were extracted from
 330 the $A \leftrightarrow C_i$ curves and reported separately. During measurements, ambient leaf temperature
 331 along the transect ranged between 25 and 30°C, while RH varied between 60 and 70%. Leaf
 332 samples were then dried and analysed for nitrogen and phosphorus content at the Australian
 333 National University, Canberra.

334

335 *Analysis framework*

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

344

$$345 \quad NPP = GPP \times \frac{NPP}{GPP}$$

$$346 \quad (2)$$

$$347 \quad i.e. \quad NPP = GPP \times CUE$$

$$348 \quad NPP_{ACW} = GPP \times \frac{NPP}{GPP} \times \frac{NPP_{ACW}}{NPP} \quad (3)$$

$$349 \quad i.e. \quad NPP_{ACW} = NPP \times \text{woody allocation}$$

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

$$354 \quad Biomass_{ACW} = GPP \times \frac{NPP}{GPP} \times \frac{NPP_{ACW}}{NPP} \times \tau_R \quad (4)$$

355

356 **Results**

357 *Climate*

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

374

375 *Autotrophic carbon budget*

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

386

387 *NPP* (from the full 16-plot dataset) shows a significant decline with elevation ($p < 0.001$, $r^2 =$
388 0.61), and stronger evidence for a transition at 1600 m (Figure 3b). Piecewise regression with
389 a break at 1600 m ($p < 0.001$, $r^2 = 0.70$) has a lower (better) AIC score (67.2) than the simple

390 linear regression (69.6). Above the 1500-1750 m transition, there is remarkably no overall
391 trend of *NPP* with elevation over an elevation range of 1750 m (a change of mean
392 temperature of 12-13 °C). The same pattern of no trend applies below the 1500 m transition,
393 though in this case the lack of trend is strongly driven by the high *NPP* at a single plot, SPD-
394 03.

395

396 The carbon use efficiency (*CUE*), the ratio *NPP/GPP*, shows no relationship with elevation,
397 nor do plots at or below 1500 m significantly differ than those above 1500 m ($p > 0.1$; Figure
398 3c). Hence, there is no evidence of decreased or increased autotrophic respiratory load at
399 lower temperatures; *CUE* does not appear to be a function of temperature. Given the relative
400 invariance of *CUE* in our dataset, we apply fixed values of *CUE* (0.35 ± 0.04 for plots < 1600
401 m and 0.30 ± 0.05 for plots > 1600 m) to our *NPP*-only dataset (5 plots) to estimate *GPP* for
402 these plots, resulting in an extended dataset of *GPP* estimates for all 16 plots (Table 2).
403 However, the derived values of *GPP* are not plotted in Fig. 3a nor used in the statistical
404 analysis.

405

406 The above-ground coarse woody *NPP* demonstrates shows substantial site-to-site variation
407 but a significant linear decline as a function of elevation ($p < 0.02$, $r^2 = 0.28$), with a decrease
408 of $0.38 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ per 1000 m increase in elevation (Figure 3d). There is no evidence of a
409 break at 1600 m. Remarkably, fractional allocation of *NPP* to canopy, wood and roots
410 demonstrates no significant relationship with elevation and relatively little plot-to-plot
411 variability, nor do plots below 1600 m significantly differ than those above 1600 m ($p > 0.1$;
412 Figures 3d, 3e, 3f). Across the dataset the mean fractional allocations of *NPP* are 48 ± 5 % to
413 canopy, 29 ± 4 % to wood and 22 ± 5 % to fine roots. Above-ground live biomass (*AGB*) shows
414 large plot-to-plot variation, but also a significant linear decline with elevation ($p < 0.03$, $r^2 =$
415 0.23 ; Figure 3g). This is strongly associated with a decline in forest stature, rather than a
416 decline in basal area. Biomass residence time (τ_R ; calculated as above-ground woody
417 biomass divided by above-ground woody *NPP*) shows very large plot-to-plot variation and
418 little relationship with elevation, nor do plots at or below 1500 m significantly differ than
419 those above 1500 m ($p = 0.08$; Figure 3h).

420

421 *Application of analysis framework*

422 We next compare the *NPP* and respiration components of two upper cloud forest
423 autotrophic carbon budgets against that of the four lowland plots (Figure 4). The mid-

424 elevation plots are here excluded because of their transitional nature. This shows that woody
425 biomass production rates are 50% lower in the upper montane forests than in the lowlands
426 (Figure 4a). This decline can largely be attributed to a $36\pm 7\%$ decline in *GPP*, together with
427 a moderate ($15\pm 10\%$) decline in carbon use efficiency (although in our broader dataset we
428 see no overall trend in *CUE* with elevation). There is no significant change in proportional
429 allocation of *NPP* to woody production, consistent with the larger dataset (Figure 3). As
430 noted above, there is no evidence of an increase in *CUE*, as might be expected if temperature
431 was a strong positive control on the fraction of photosynthate used in autotrophic respiration.

432

433 Our framework shows that the low biomass of the upper montane forests largely reflects
434 these low growth rates (Figure 4b), rather than increases in mortality rates (= decreases in
435 residence time). Biomass is $38\pm 11\%$ lower in the upper montane plots. This largely reflects
436 the fact that woody growth rates are $42\pm 2\%$ lower, slightly offset by residence times being
437 $6\pm 19\%$ longer in this. The wider dataset, however, shows no significant trend of residence
438 time with elevation (Figure 3h).

439

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

448

449 Figure 5 plots key aspects of canopy photosynthetic capacity, including the total leaf area
450 index (LAI), and the maximal area-based rates of CO_2 fixation by Rubisco (V_{cmax}) and
451 photosynthetic electron transport (J_{max}). LAI shows only a modest and largely linear decline
452 with elevation, with no evidence of a sharp transition at mid-elevations ($p = 0.03$, $r^2 = 0.50$;
453 Figure 5a). The LAI is always > 3.5 , indicating that canopies are largely closed at all
454 elevations and almost all light is intercepted.

455

456 The leaf photosynthetic parameters are shown both at ambient temperatures and using
457 values normalized to a measuring temperature of $25\text{ }^\circ\text{C}$ (i.e. $V_{\text{cmax},25}$ and $J_{\text{max},25}$). At ambient

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

468

469 The magnitudes and trends are broadly consistent with those reported by van de Weg *et al.*
470 *al.* (2009) for this same elevation gradient. This trend is consistent with results from a
471 fertilisation experiment on the transect, which shows that woody growth rates in plots above
472 1500 m were responsive to N addition (indicating relative limitation of N), and growth rates
473 in plots below 1500 m were responsive to P and N combined, indicating some role for P-
474 limitation (Fisher *et al.*, 2013). Overall, the relative availability of these nutrients appears to
475 have no overall effect on the trend of leaf photosynthetic capacity with elevation.

476

477 **Discussion**

478

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

483

484 The analysis shows that there is no overall trend in *CUE*, in *NPP* allocation, and little
485 overall trend in mortality rate/residence time. This pinpoints changes in gross primary
486 productivity as the primary determinant of general trend for decline in growth and biomass
487 with elevation. In the context of this transect at least, this suggests that many hypotheses
488 related to shifts in allocation (e.g. increased investment in fine roots at high elevations causes
489 a decline in wood production), or to shifts in carbon use efficiency (e.g. there is a greater
490 respiratory load and hence lower *CUE* at high temperatures) can be rejected when explaining
491 variation with elevation.

492

493 The next question is whether the decline in *GPP* with elevation is related to a decline in
494 canopy photosynthetic capacity or in rates of actual photosynthesis. Canopy photosynthetic
495 capacity is a function of canopy leaf area and leaf-level photosynthetic capacity at ambient
496 temperatures. Strikingly, we do not observe any evidence of a decline in photosynthetic
497 parameters under ambient conditions, and only a modest decline in LAI. This suggests that
498 canopy photosynthetic capacity shows only moderate variation with elevation, and that any
499 declines in capacity are manifest through declines in LAI rather than leaf-level properties.
500 The lack of any decline in leaf-level photosynthesis is further supported by the lack of change
501 in leaf N per unit area with elevation, and the increase of leaf P per unit area (an observation
502 that was also noted by van de Weg *et al.*, 2009). This suggests that lower temperatures do not
503 lead to less canopy stocks of key nutrients.

504

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

519

520 A key point to consider is whether the trends in forest properties with elevation are broadly
521 linear, or whether there is an abrupt transition in the region 1500-1750 m. Figure 3a and 3b
522 are suggestive of an abrupt decline in *GPP* and *NPP* around this zone, which coincides with
523 the appearance of many typical cloud forest features such as abundant epiphytic bryophytes
524 (Horwath, 2012), tree ferns and other characteristic cloud forest features and species (W.
525 Farfan Rios, unpublished data), increased leaf waxiness (S. Feakins, unpublished data),

526 shortened canopy stature (Asner *et al.*, 2014) and a changed tree architecture from straight
527 boles (competing for stratified light) to gnarled and twisted boles. This abrupt transition to a
528 cloud forest type suggests that increase in cloud frequency and particularly cloud immersion
529 drives the decline in *GPP*, and hence the decline in *NPP* and woody growth.

530

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

539

540 In conclusion, we have demonstrated the value of a whole carbon-budget perspective to
541 provide insight into how and why growth and biomass tend to decline with elevation along a
542 tropical elevation gradient. For this transect, we show that a decline in *GPP* with elevation is
543 the main determinant of declining growth and biomass, with little trend in *CUE*, allocation of
544 *NPP*, or biomass residence times. The results could have been very different. For example,
545 for wet-dry gradients in lowland Amazonia, Malhi *et al.* (2015) demonstrated that the
546 observed decline in *GPP* going from wet to dry forests was offset by increases *CUE* and
547 increased allocation to woody growth, leading to little trend in woody growth rates with
548 rainfall, The low biomass of dry forests was instead driven by low woody biomass residence
549 times. The other striking result here is the lack of variation in leaf photosynthetic capacity
550 with elevation, with the overall decline of *GPP* and *NPP* driven by a transition near cloud
551 base. This suggests that temperature has little direct influence on productivity, with
552 ecosystems acclimating their ecophysiology or shifting in composition to optimise
553 productivity for their particular climate regime. For example, in colder forests, lower rates of
554 nutrient mineralisation and uptake are compensated for longer leaf lifetimes and nutrient
555 retention periods, and peak photosynthetic rates are likely optimised to lower temperatures.
556 There is large turnover of tree species between plots; individual species may be constrained
557 by temperature, but the constant changes in species portfolio result in a relatively invariant
558 potential *GPP*. Such results are consistent with a recent global analysis that suggests *NPP* is
559 largely determined by stand age and biomass, and not by climate (Michaletz *et al.*, 2014, but

560 note the critique by Chu *et al.* (2015). Such insights have yet to be incorporated into global
561 vegetation models (Marthews *et al.*, 2012), which tend to predict a high sensitivity of tropical
562 GPP to temperature (Galbraith *et al.*, 2010).

563

564 The sensitivity of biomes, and in particular tropical biomes, to warming temperatures is
565 one of the key questions in global change ecosystems research. While this tropical elevation
566 transect by its nature does not extend to the warmer lowland temperatures of a future warmer
567 world, it does highlight the important processes of acclimation and community turnover that
568 can result in relatively low long-term sensitivity of primary productivity to temperature.

569 Tropical elevation transects are particular powerful tools for examining temperature
570 relationships, as they do not have the confounding influence of varying length of a dormant
571 winter season (Malhi *et al.*, 2010). However, cloud immersion may confound attempts to use
572 long elevation gradients as proxies for temperature changes alone. In a warming world,
573 tropical cloud base is like to be rising (Still *et al.*, 1999), and some of the most dramatic
574 responses in carbon cycling and species composition may occur at this cloud immersion
575 ecotone.

576

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

589

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591

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603

604 **Author Contributions**

605 Y.M., C.G, D.M., L.A., N.S. planned and designed the research. Y.M., C.G, D.M., L.A.,
606 W.H.H., J.E.S., J.A.P., F.F.A., R.G., F.Y.I., W.F.R. conducted fieldwork, O.P and M.S.
607 contributed plot data, N.B. and G.G. contributed to data analysis, Y.M. and G.G. wrote the
608 manuscript, with contributions from C.G., L.A., C.D., L.A., O.P. W.F.R. and P.M.

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Tables

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

	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

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

1

2 **Figure Legends**

3

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

8

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

12

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

19

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

23

24 Figure 5. Variation in key canopy attributes influencing canopy photosynthetic capacity along
25 the 2800 m tropical montane elevation transect, including (a) Leaf Area Index (LAI); (b)
26 maximal area-based rates of CO₂ fixation by Rubisco at ambient temperatures (V_{cmax}) and
27 normalised to 25°C ($V_{cmax,25}$); (c) photosynthetic electron transport at ambient temperatures
28 (J_{max}) and normalised to 25°C ($J_{max,25}$).

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30

31 **Supporting Information**

32

33 **Figure S1.** Relationship between foliar nutrients and elevation.

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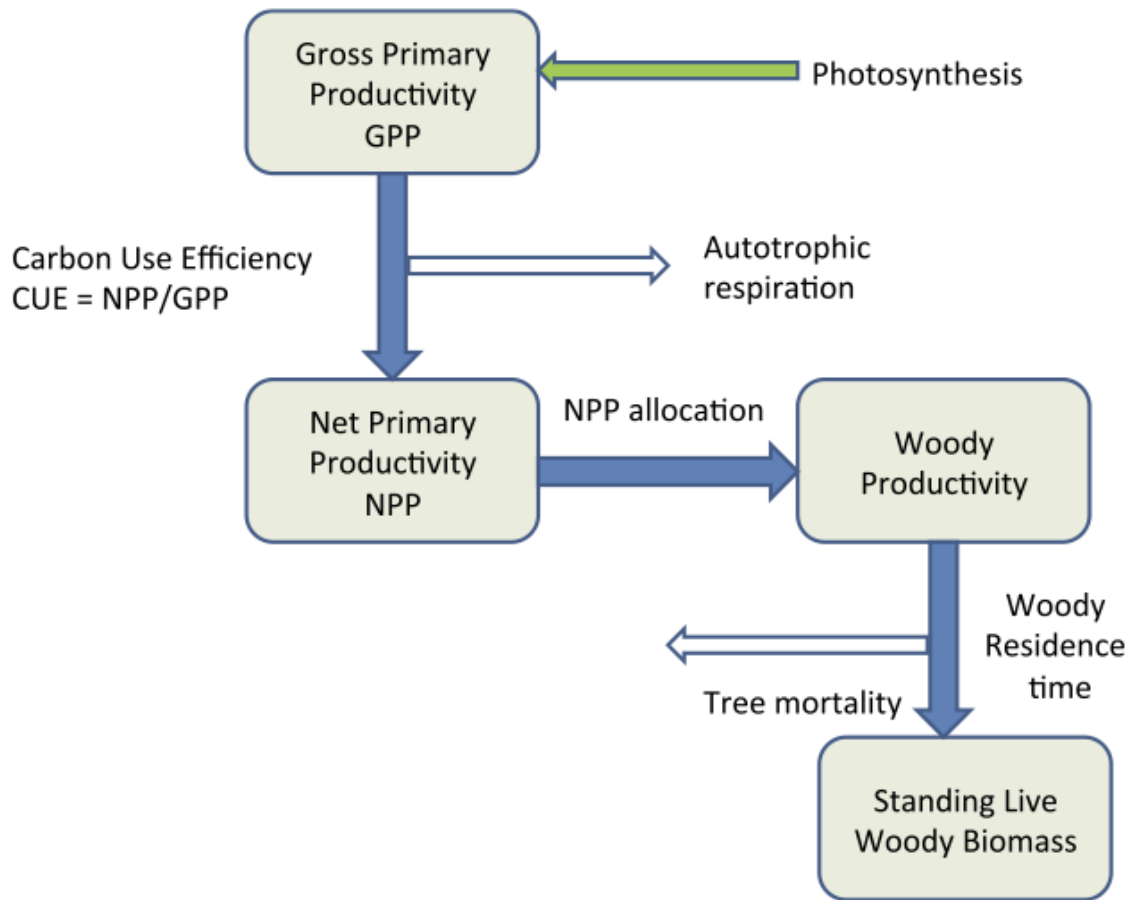
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38 Fig 1.

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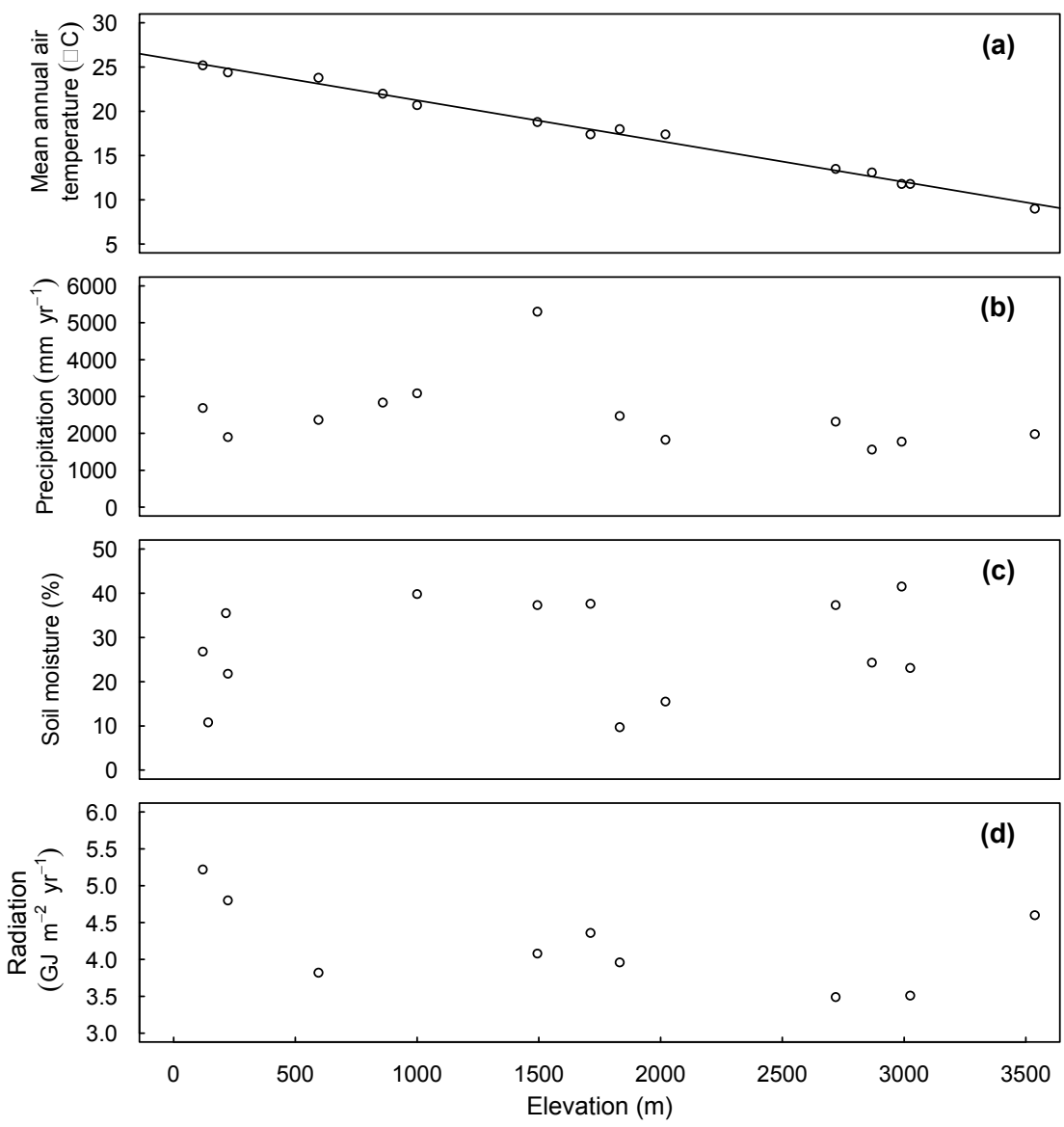
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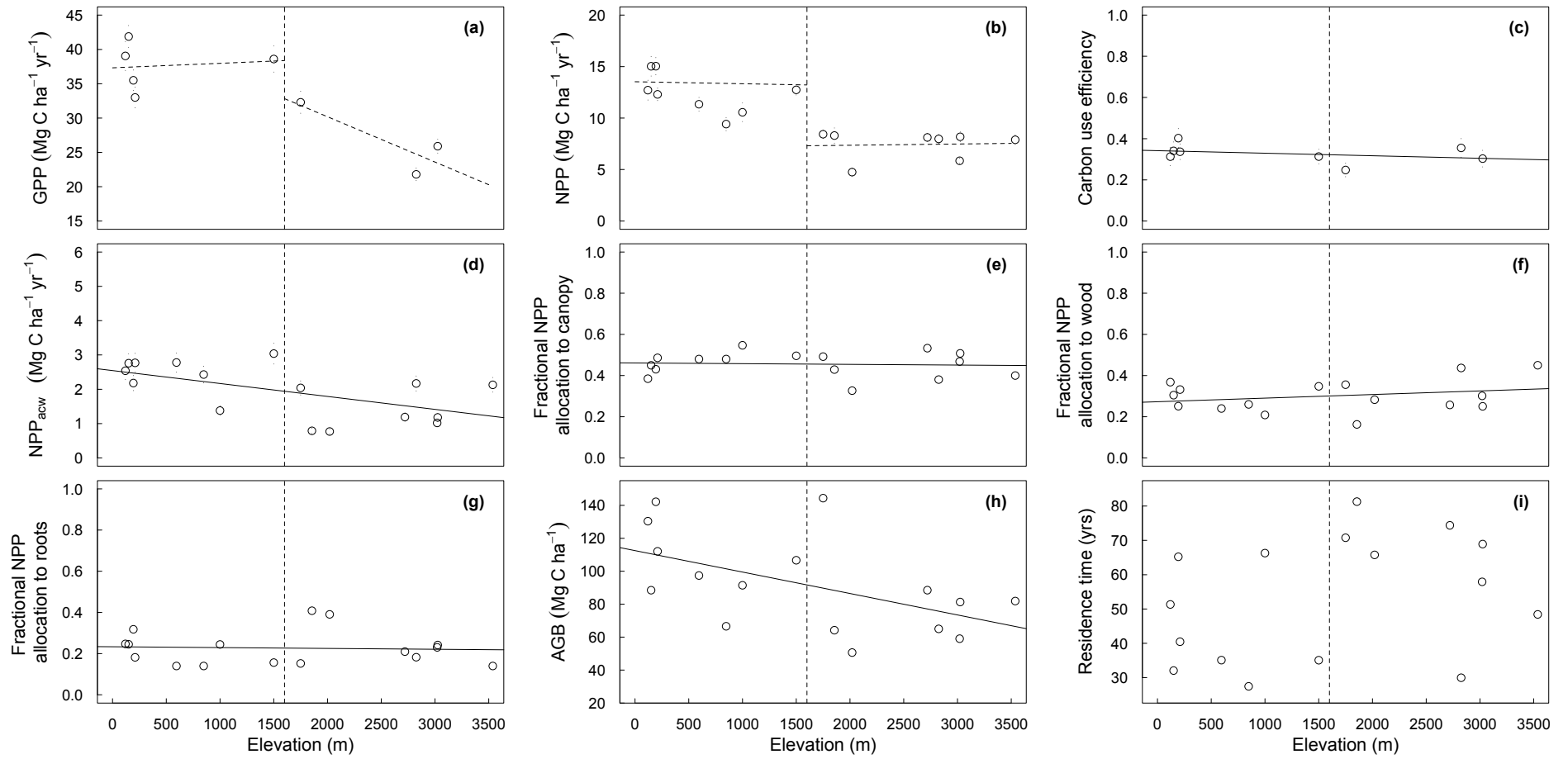
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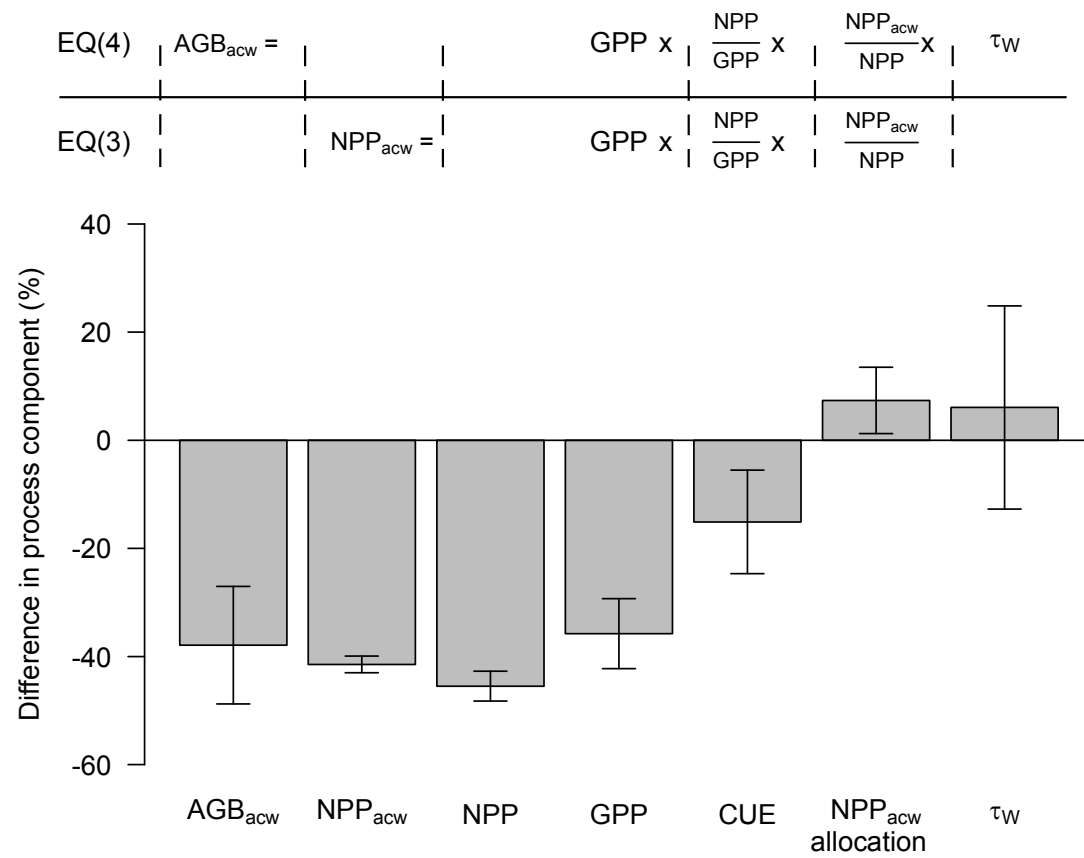
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51 Fig. 4

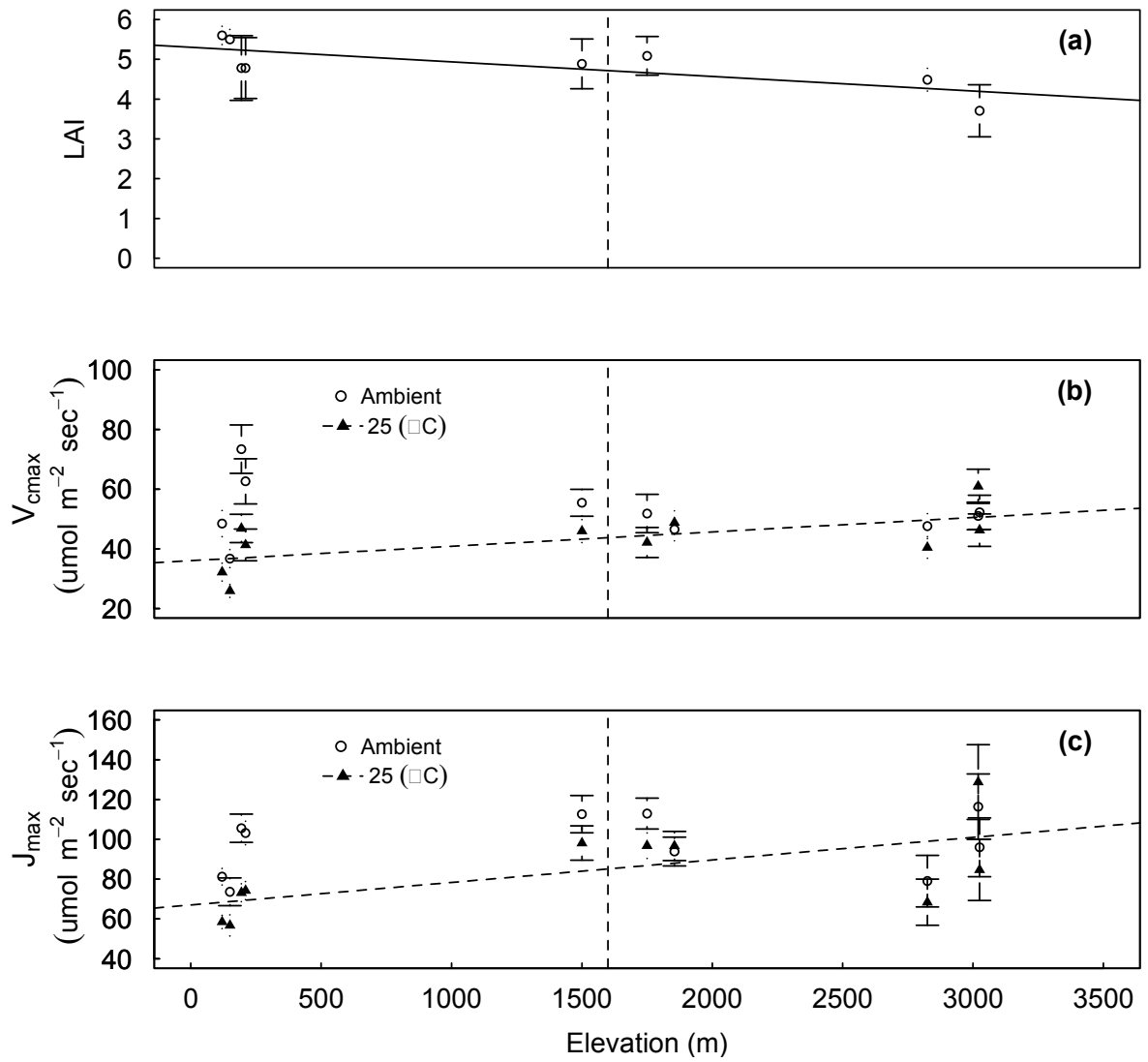
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54 Fig. 5

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