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3 **Simulating forest productivity along a neotropical elevational**
4 **transect: temperature variation and carbon use efficiency**
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ABSTRACT

A better understanding of the mechanisms controlling the magnitude and sign of carbon components in tropical forest ecosystems is important for reliable estimation of this important regional component of the global carbon cycle. We used the *JULES* vegetation model to simulate all components of the carbon balance at six sites along an Andes-Amazon transect across Peru and Brazil and compared the results to published field measurements. In the upper montane zone the model predicted a lack of forest vegetation, indicating a need for better parameterisation of the responses of cloud forest vegetation within the model. In the lower montane and lowland zones simulated ecosystem productivity and respiration were predicted with reasonable accuracy, although not always within the error bounds of the observations. Model-predicted carbon use efficiency in this transect surprisingly did not increase with elevation, but remained close to the ‘temperate’ value 0.5. Upper montane forests were predicted to allocate ~50% of carbon fixation to biomass maintenance and growth, despite available measurements showing that they only allocate ~33%. This may be explained by elevational changes in the balance between growth and maintenance respiration within the forest canopy, as controlled by both temperature- and pressure-mediated processes, which is not yet well represented in current vegetation models.

[205 words]

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52 **INTRODUCTION**

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54 Intact tropical forests currently cover 13.9 million km² worldwide, or 24% of tropical land area (Pan *et al.*
55 2011). These forests support the most biodiverse terrestrial ecosystems in existence (Ghazoul & Sheil 2010)
56 and provide a basic livelihood for many millions of people (IPCC 2007), so their importance cannot be
57 overemphasised. Also very significantly, they absorb 1.02 billion tonnes of carbon (Mg C) from the
58 atmosphere every year, approximately 25% of global forest uptake (Malhi 2010; Pan *et al.* 2011), and in so
59 doing they reduce the rate of global warming by 15% (Malhi 2010, 2012), making their conservation a
60 crucial element of current policies concerning climate change (IPCC 2007; Ghazoul & Sheil 2010).

61 We need a mechanistic understanding of the components of the tropical forest carbon cycle or
62 'budget' in order to translate carbon balance into future forest cover gains and losses under committed
63 climate change (Malhi *et al.* 1999; IPCC 2007). Quantifying the carbon budget in terms of standard fluxes in
64 (photosynthesis/productivity) and out (respiration) reveals how global atmospheric carbon dioxide (CO₂)
65 levels are affected by forested areas and *vice versa* (Chambers *et al.* 2004; Clark 2004; Malhi *et al.* 2009;
66 Malhi 2010). Additionally, ecosystem health, resilience and productivity are increasingly being measured in
67 terms of carbon budgets and carbon gain (IPCC 2007; Zhang *et al.* 2009). However, until recently field data
68 on forest biomass stocks and changes did not exist from enough tropical areas either to assess carbon
69 budgets or to constrain modelling efforts adequately for a robust estimation (Marthews *et al.* 2012). This has
70 resulted in much debate over whether tropical forests are a net source or sink of carbon (Chambers *et al.*
71 2001, 2004; Clark 2004; Luysaert *et al.* 2008; Lewis *et al.* 2009; Houghton *et al.* 2009).

72 With the advent of large-scale ecosystem research efforts and regional-scale census networks such as
73 the Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA, Avissar & Nobre 2002;
74 <http://lba.inpa.gov.br/lba/>), the Amazon Forest Inventory Network (*RAINFOR*, Malhi *et al.* 2002; Phillips *et al.*
75 *et al.* 2009; <http://www.geog.leeds.ac.uk/projects/rainfor/>) and the Andes Biodiversity and Ecosystem
76 Research Group (*ABERG*, Malhi *et al.* 2010; <http://darwin.winston.wfu.edu/andes/>), data are increasingly
77 becoming available that allow us to assess carbon budgets component by component (Malhi *et al.* 2009,
78 2011, Mercado *et al.* 2011). Tropical ecosystems vary greatly in their spatial and temporal dynamics
79 (Aragão *et al.* 2009; Zhang *et al.* 2009; Girardin *et al.* 2010; Metcalfe *et al.* 2010; Ghazoul & Sheil 2010)
80 and accurate and precise quantification of tropical carbon cycling is logistically and physically challenging
81 work (Chambers *et al.* 2004; Malhi *et al.* 2009; Metcalfe *et al.* 2009; Girardin *et al.* 2010) so uncertainties in
82 individual fluxes remain high. However, measurement methods are improving and the details of the tropical
83 carbon cycle are finding themselves on an ever-firmer scientific basis.

84 Advances in vegetation models since the mid-1990s, notably the development of Dynamic Global
85 Vegetation Models (DGVMs), have greatly improved the model representation of dynamic canopies and
86 forest biogeochemical cycling (Prentice *et al.* 2007; Landsberg & Sands 2011). DGVMs are sophisticated

87 simulators of vegetation dynamics, making use of process-based algorithms and a wide variety of
88 parameters and forcing variables (e.g. Clark *et al.* 2011; Best *et al.* 2011). However, the current generation
89 of DGVMs remains relatively poorly verified and validated in tropical climates (Alton *et al.* 2007; Prentice
90 *et al.* 2007; Malhi *et al.* 2011, van de Weg *et al.* 2012), despite recent improvements in this direction (e.g.
91 Mercado *et al.* 2007, 2011). Across the Amazon basin and eastern Andes escarpment, for example, there are
92 strong gradients in temperature, precipitation and seasonality (Phillips *et al.* 2009; Malhi *et al.* 2010) and the
93 forests of the region are extremely diverse not only floristically and structurally (Terborgh & Andresen
94 1998; ter Steege *et al.* 2003; Butt *et al.* 2008; van de Weg *et al.* 2009), but also topographically (Grubb &
95 Whitmore 1966; Ashton 2003; Malhi *et al.* 2010), pedologically and hydrologically (Pires & Prance 1985;
96 Bruijnzeel & Proctor 1995) and edaphically (Quesada 2008; Quesada *et al.* 2010). Despite their
97 sophistication, applying DGVMs in a tropical context is necessarily approximate, but nevertheless these
98 kind of model predictions provide the best available benchmark against which to compare field
99 measurements. Such model-data comparisons are a means of identifying not only quantities that need to be
100 measured more accurately but also processes that need to be represented more reliably in models (van de
101 Weg *et al.* 2012).

102 In this study we focus on the standard carbon fluxes describing productivity and respiration (Table
103 2). We have also used Carbon Use Efficiency (*CUE*), defined as the ratio of net carbon gain (Net Primary
104 Productivity, *NPP*) to gross carbon assimilation (Gross Primary Productivity, *GPP*), which is a quantity that
105 has received much recent attention (e.g. Malhi *et al.* 2009). Historically, *CUE* close to 0.50 (i.e.
106 $NPP=GPP/2$) was a common rule-of-thumb in use in temperate forests (Chambers *et al.* 2004), however
107 *CUE* is now assumed to vary generally with disturbance and succession (Mäkelä & Valentine 2001, Yang *et al.*
108 *et al.* 2011; e.g. Landsberg & Sands 2011 suggested that efficiency should decline from $CUE\approx 0.5$ in young
109 forests to $CUE\approx 0.3$ in forests >60 years since disturbance). In the tropics, *CUE* appears to be generally
110 lower than in temperate forests, e.g. Kira (1978) found *CUE* to be 0.35 in Pasoh, Malaysia, Chambers *et al.*
111 (2004) found 0.32 in old-growth Amazon forests and recent work has found a similar value of 0.30-0.40
112 across the Amazon and the Andes (Malhi *et al.* 2009, 2011; Metcalfe *et al.* 2010; Malhi 2012). This
113 temperate-tropical difference is clearly visible in maps of worldwide mean annual *CUE* (e.g. Zhang *et al.*
114 2009), but the mechanisms behind it remain obscure.

115 We applied a global vegetation simulator (the Joint UK Land Environment Simulator DGVM,
116 *JULES*; Best *et al.* 2011; Clark *et al.* 2011) at six tropical forest sites along an Andes-Amazon elevational
117 gradient in South America (Malhi *et al.* 2010). Estimates of annual means of the major carbon fluxes were
118 assembled from current *LBA*, *ABERG* and *RAINFOR* projects and used for model validation (for all field
119 protocols followed, see <http://gem.tropicalforests.ox.ac.uk/>). Finally, feeding back, we carried out additional
120 simulations varying certain model parameters in order to investigate some avenues for the future
121 development of *JULES*.

122 The elevation transect provides a unique opportunity to test the ability of vegetation models to
123 capture the important effects of variation in temperature on ecosystem carbon dynamics (Raich *et al.* 2006).

124 The transect data themselves are the focus of published or parallel papers (Girardin *et al.* 2010; Robertson *et*
125 *al.* 2010; Farfan Amezcuita *et al.* 2012; Huaraca Huasco *et al.* 2012; Silva Espejo *et al.* 2012). In this study
126 we focus on model ability to capture variations in carbon cycling along the transect. We address three
127 research questions: (1) How do simulated forest ecosystem carbon fluxes vary between forests in this
128 Andes-Amazon transect, and how do these fluxes compare with observations? (2) What are the mechanisms
129 in the model that drive variation in carbon flux components across these sites? and (3) Is there a net trend of
130 *CUE* with elevation across these sites? Finally, from a consideration of the factors controlling the
131 magnitudes of these carbon flux components, we suggest modifications to some parameters within the
132 *JULES* model that might improve its performance in future tropical studies and, therefore, in future global
133 simulations of the carbon cycle.

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MATERIALS AND METHODS

We sampled a tropical elevational transect in the South American Andes (Malhi *et al.* 2010), extending out into the lowland Amazon basin, by selecting six sites for model simulation (Fig. 1, Table 1). Meteorological data at all six sites were gap-filled where required to produce model-ready driving data sets (Appx. I). The forest carbon cycle was simulated at all sites using the *JULES* DGVM version 2.2 (released November 2010; Best *et al.* 2011; Clark *et al.* 2011, <http://www.jchmr.org/jules/>) which simulates vegetation productivity from meteorological and forest biometric inputs. For all sites and runs, vegetation cover in *JULES* was fixed at 100% broadleaf with 0% needleleaf (all native tree species in Peru are angiosperms except three uncommon podocarp genera, Pennington *et al.* 2004, and gymnosperms form a similarly negligible component of the Brazilian Amazon forest, <http://floradobrasil.jbrj.gov.br/> so there are no native needleleaf species in any Andes-Amazon biome).

A 650 year spin-up sequence was followed for each simulation, comprising 500 years at pre-industrial levels of atmospheric CO₂ concentration (taken as 285.2 ppmv CO₂ for 1850, IPCC 2007) followed by a *c.* 150 year period of increasing atmospheric CO₂ (slightly longer depending on the starting date of each simulation, see Appx. I) using global historical values (IPCC 2007). Because of a lack of reliable time series data, local deviations of Andes-Amazon atmospheric CO₂ levels from global 'well-mixed' values (Park *et al.* 2007; Pan *et al.* 2011), seasonal cycles in CO₂ concentration (Park *et al.* 2007) and sub-daily cycles (Walsh 1996; Iwata *et al.* 2005) were not simulated. The vegetation dynamics module (TRIFFID) was activated to allow vegetation carbon pools to be updated but not fractional cover.

Default *JULES* photosynthetic parameters (Clark *et al.* 2011) were used for all runs apart from the parameters controlling the nitrogen (N) concentration of top-of-canopy leaves in simulated broadleaf trees (N_{l0}) and photosynthetic capacity (V_{Cmax25}) for which more accurate local values were available (Table 1; note that the constant of proportionality $n_e = V_{Cmax25}/N_{l0}$ was altered from its default value 0.0008 mol CO₂/m²s gC/gN for C₃ vegetation to accommodate this, see Clark *et al.* 2011). Note that, although leaf N concentration was assumed constant down the canopy in previous versions of *JULES* (up to v2.0), the leaf-canopy scale-up option #4 of v2.2 incorporates the work of Mercado *et al.* (2006, 2007) which specifies a leaf N profile exponentially-decreasing from N_{l0} to lower values in the understorey (notably with an exponent different from that describing the decrease in radiation: see Lloyd *et al.* 2010).

JULES assumes that canopy height h (in m) and LAI at equilibrium are allometrically related as

$$LAI_{eq} = \left(\frac{\eta_{sl} a_{ws} h_{eq}}{a_{wl}} \right)^{\frac{3}{2}}$$
 where η_{sl} is a live stemwood coefficient (default value = 0.01 kg C/m² per unit LAI for

broadleaf trees), a_{ws} is the ratio of total to respiring stem carbon (=10 for woody plants) and a_{wl} is an allometric coefficient relating woody biomass to LAI (=0.65 kg C/m² for trees) (Clark *et al.* 2011).

171 Therefore, measured values for canopy height and LAI were accommodated by specifying appropriate values

172 for the η_{sl} parameter from $\eta_{sl} = \frac{a_{wl} LAI_{eq}^{\frac{2}{3}}}{a_{ws} h_{eq}}$ (Table 1).

173 Soil layers 0-10 cm, 10-35 cm, 35-100 cm and 1-4 m were simulated with the van Genuchten soil
174 hydrology option (Hodnett & Tomasella 2002; Marthews *et al.* 2008; Best *et al.* 2011). The standard
175 pedotransfer functions of Cosby *et al.* (1984) were applied to measured soil textures (Table 1) to calculate
176 the parameters of the soil water characteristic, under the assumption that the van Genuchten model
177 parameters may be approximated by Clapp & Hornberger model parameters (see Dharssi *et al.* 2009).

178 *JULES* was run at each study site under several parameter combinations in a full factorial design: (i)
179 with the live stemwood coefficient η_{sl} set at the site-specific value (required to balance known canopy height
180 and LAI) and at the default value (Table 1), (ii) with the canopy top-leaf N:C ratio N_{10} set at the site-specific
181 value and at the value corresponding to the Caxiuanã site (Table 1), (iii) with the proportion of GPP
182 allocated to growth r_g set at $r_g=0.15$, $r_g=0.25$ (default value) and $r_g=0.35$ (see Appx. II for definition and
183 explanation of this quantity), (iv) with the Plant Functional Type (PFT) parameters controlling the upper and
184 lower bounds of photosynthesis set to default broadleaf values $T_{low}=0^\circ\text{C}$, $T_{upp}=36^\circ\text{C}$ and default needleleaf
185 values $T_{low}=-10^\circ\text{C}$, $T_{upp}=26^\circ\text{C}$ (see Clark *et al.* 2011) to test PFT-specific effects (despite the lack of native
186 needleleaves, this tests whether the (broadleaf) cloud forest vegetation behaves as if it has needleleaf
187 temperature tolerances), (v) with the correct meteorological driving data set for the site (as described Appx.
188 I) and with the driving data replaced with the data from Caxiuanã to test meteorology-specific effects. All
189 analyses were done using R version 2.13.1 (R Development Core Team 2011).

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RESULTS

With fractional cover held at 100% broadleaf, *JULES* predicted *LAI* to decrease to $0.1 \text{ m}^2/\text{m}^2$ (i.e. disappearance of almost all vegetation) at Wayqecha, the highest elevation site (3025 m asl), when all other sites supported *LAI* at $4.5\text{-}5.0 \text{ m}^2/\text{m}^2$. This had the effect of reducing all fluxes to minimal (but nonzero) values but *JULES* nevertheless did return a reasonable prediction of *CUE*. This reduction to minimal cover at altitude happened under all parameter combinations (even if the temperature limits for photosynthesis were changed to default needleleaf values) except when the Caxiuanã (lowland) meteorology was used. The minimal vegetation simulated at Wayqecha should be borne in mind when interpreting the following results concerning bulk carbon quantities (see Table 2 for definitions):

Gross primary productivity (GPP). *JULES*'s predictions for overall mean *GPP* were broadly constant with temperature in the lowlands, lying towards the top of the Luysaert *et al.* (2007) band, slightly underestimating *GPP* at Manaus in comparison with measurements (Fig. 2a). *JULES* predicted declining *GPP* with decreasing temperature (i.e. with increasing elevation) in the upper and lower montane zones, but declining faster than measurements would suggest (Fig. 2a). With Caxiuanã (lowland Brazilian Amazon) meteorology imposed, simulated *GPP* rose to Caxiuanã levels at all sites confirming that simulated *GPP* is highly sensitive to meteorological conditions in the model. Changing η_{sl} , N_{10} or r_g did not affect *GPP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *GPP* to approximately $20 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at all sites.

Autotrophic respiration (R_a). *JULES*'s predictions for overall mean R_a were within observation error at Manaus and Caxiuanã, but otherwise lower than both measurements and what the Luysaert *et al.* (2007) band would suggest (Fig. 2b). *JULES* predicted declining R_a with decreasing temperature along the whole transect (Fig. 2b). With Caxiuanã meteorology imposed, R_a rose to Caxiuanã levels at all sites confirming that simulated R_a is highly sensitive to meteorological conditions in the model. Changing η_{sl} or N_{10} did not affect R_a , but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean R_a to approximately $10 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at all sites. Increasing r_g by 0.10 had the effect of increasing R_a by approximately 11.4% at all sites (and decreasing r_g by 0.10 decreased R_a by the same amount).

Heterotrophic respiration (R_h). In most of the lower montane and lowland zones, *JULES*'s predictions for overall mean R_h were higher than both measurements and what the Luysaert *et al.* (2007) band would suggest (Fig. 2c). *JULES* predicted declining R_h with decreasing temperature only in the montane zones, but again with too steep a decline in the upper montane zone (Fig. 2c). With Caxiuanã meteorology imposed, R_h rose to Caxiuanã levels at all sites confirming that simulated R_h is highly sensitive to meteorological conditions in the model. Changing η_{sl} or N_{10} did not affect R_h , but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean R_h to approximately $10 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at all sites. Increasing r_g by 0.10 had

227 the effect of decreasing R_h by approximately 13.6% at all sites (and decreasing r_g by 0.10 increased R_h by
228 the same amount).

229 *Net primary productivity* (Total *NPP*, the sum of above- and below-ground *NPP*). Apart from San Pedro,
230 Manaus and the measurements of Aragão *et al.* (2009) at Tambopata, in the lower montane and lowland
231 zones *JULES*'s predictions for overall mean *NPP* were higher than both measurements and what the
232 Luysaert *et al.* (2007) band and Clark *et al.* (2001b) would suggest, although still lower than the
233 assumptions of the precipitation-based *MIAMI* model (Fig. 2d). *JULES* predicted declining *NPP* with
234 decreasing temperature only in the montane zones, but again with too steep a decline in the upper montane
235 zone (Fig. 2d). With Caxiuanã meteorology imposed, *NPP* rose to Caxiuanã levels at all sites confirming
236 that simulated *NPP* is highly sensitive to meteorological conditions in the model. Changing η_{sl} or N_{10} did not
237 affect *NPP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *NPP* to
238 approximately 10 Mg C ha⁻¹ yr⁻¹ at all sites. Increasing r_g by 0.10 had the effect of decreasing *NPP* by
239 approximately 13.6% at all sites (and decreasing r_g by 0.10 increased *NPP* by the same amount).

240 *Net ecosystem productivity* (*NEP*). In the lower montane and lowland zones *JULES* simulated a small CO₂
241 sink at all sites broadly in line with the Malhi (2010) band, which agreed with measurements at all lowland
242 and lower montane sites, though these sinks were smaller in magnitude than the suggested Luysaert *et al.*
243 (2007) sink (Fig. 2e). *JULES* predicted no consistent trend of *NEP* with elevation or temperature (Fig. 2e).
244 With Caxiuanã meteorology imposed, *NEP* converged to Caxiuanã levels at all sites. Changing η_{sl} or N_{10} did
245 not affect *NEP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *NEP* to
246 approximately 0.6 Mg C ha⁻¹ yr⁻¹ at all sites. Increasing r_g by 0.10 had the effect of decreasing *NEP* by
247 approximately 11.6% at all sites (and decreasing r_g by 0.10 increased *NEP* by the same amount).

248 *Carbon use efficiency* (*CUE*, =*NPP*/*GPP*). Simulated values for overall mean fitted all measurement
249 values except San Pedro fairly well, though with some overestimation (Fig. 2f). *JULES* predicted no
250 consistent trend of *CUE* with elevation or temperature, notably not confirming the consistent increase with
251 elevation expected from the results of Zhang *et al.* (2009) or Piao *et al.* (2010) (Fig.2f). With Caxiuanã
252 meteorology imposed, *CUE* rose to Caxiuanã levels at all sites. Changing η_{sl} or N_{10} did not affect *CUE*, but
253 changing T_{low} and T_{upp} to needleleaf values had the effect of reducing mean *CUE* by approximately 0.04
254 across all sites. Increasing r_g by 0.10 had the effect of decreasing *CUE* by approximately 0.06 at all sites
255 (and decreasing r_g by 0.10 increased *CUE* by the same amount).

256
257 In summary, in the upper montane zone *JULES* predicts a lack of forest vegetation. In the lower montane
258 and lowland zones *JULES* overestimates *NPP* and R_a , underestimates R_h but predicts *GPP*, *NEP* and *CUE*
259 fairly well.

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263 **DISCUSSION**
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265 Forest productivity, respiration and carbon use efficiency are controlled by a variety of factors along our
266 elevational transect, which encompasses several tropical forest biomes and therefore many different species
267 compositions and canopy architectures (see general reviews Friend & Woodward 1990; Malhi & Grace
268 2000; Landsberg & Sands 2011). Although temperature effects are arguably the most important (Friend &
269 Woodward 1990, Raich *et al.* 2006), as Ashton (2003) pointed out, if the boundaries between biomes along
270 elevational gradients were controlled entirely by temperature then the Massenerhebung effect (e.g. Richards
271 *et al.* 1996) would require much greater global variation in lapse rates than is observed in reality (also see
272 Zach *et al.* 2010). We concentrate here on our first two research questions: how do ecosystem carbon
273 budgets vary along our study transect and what are the mechanisms driving this variation?
274

275 *Gross primary productivity (GPP)*
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277 Within the known limits of the vegetation simulator used, our results for simulated *GPP* were in line both
278 with measurements and with the upper half of the range of values suggested by Luysaert *et al.* (2007).
279 Photosynthesis (carbon fixation per unit leaf area) varies with temperature according to the Farquhar - von
280 Caemmerer - Berry model (Cox 2001; Clark *et al.* 2011; Landsberg & Sands 2011) which for these sites,
281 where temperatures are usually below the optimal temperature for photosynthesis (approximately 25°C,
282 Landsberg & Sands 2011), means that *GPP* declines with decreasing temperature (as found by Raich *et al.*
283 2006, also see van de Weg *et al.* 2012). This trend fully supports our *JULES* simulations.

284 *GPP* declines with decreasing radiative input (e.g. Zach *et al.* 2010, van de Weg *et al.* 2012; received
285 SW radiation at Wayqecha was 103 W/m² in annual mean compared to 152 W/m² in the lowland sites) and
286 radiation is one of the drivers of seasonality in at least our upper montane sites (Silva Espejo *et al.* 2012).
287 This trend fully supports our simulations and therefore provides an alternative driver for the decline of *GPP*
288 along our transect. It has also been noted that cloud cover increases the proportion of diffuse radiation and,
289 because diffuse radiation penetrates vegetation canopies more efficiently than direct, this may increase
290 photosynthesis (Graham *et al.* 2003; Mercado *et al.* 2007; Marthews *et al.* 2012), at least in cases where an
291 increase in diffuse radiation is not associated with a decrease in total photosynthetically-active radiation
292 *PAR* (van de Weg *et al.* 2012).

293 Despite their high rainfall and moist climate, tropical forests are well-known to experience
294 significant dry periods (seasonal as well as short spells) (Richards *et al.* 1996; Walsh 1996; Fisher *et al.*
295 2008; Marthews *et al.* 2008; Metcalfe *et al.* 2010) and water limitation can be a control of *GPP* (at sub-
296 annual timescales also called Plant Carbon Expenditure *PCE*, Table 2). Surface soil moisture in the transect
297 is approximately equal in the upper montane and lowland zones, and slightly higher in the lower montane

298 zone because of orographic rainfall at the Andes escarpment (Zimmermann *et al.* 2010), but there are not yet
299 enough data from mid-elevations to show conclusively how much variability in *GPP* is explained by
300 precipitation. Soil texture and nutrients (Pires & Prance 1985; Quesada 2008) are also known to account for
301 some regional variation in carbon fluxes (Friend & Woodward 1990; Chambers *et al.* 2004; Malhi *et al.*
302 2009; Aragão *et al.* 2009), but, as is standard for DGVMs, soil types are only accounted for in the
303 parameterisation of *JULES* in terms of soil hydraulic properties (see Methods). To account for soil moisture
304 stress on photosynthesis, *JULES* uses a multiplicative soil moisture stress factor (β) in its *GPP* calculations
305 (a fraction 0-1 with higher meaning greater soil water availability; Clark *et al.* 2011). The value of β during
306 the simulations was consistently high (mean>0.93 across all simulation time points), indicating almost no
307 water limitation (as found in van de Weg *et al.* 2012), except at Manaus, which experienced several dry
308 periods during its simulation periods (mean=0.53), and possibly Tono (mean=0.81). Surprisingly, according
309 to current data, soil moisture content does not explain the variability in *GPP* along this transect either in
310 simulations or in the field (Zimmermann *et al.* 2010).

311 *GPP* is known to increase with the leaf N content of canopy leaves (via leaf RuBisCO content and
312 therefore increased photosynthetic capacity V_{Cmax} , see e.g. Mercado *et al.* 2007, 2011; Clark *et al.* 2011 and
313 review in Lloyd *et al.* 2010). A standard theory to explain lower *GPP* at higher elevations is therefore that
314 montane forests are N-limited ecosystems (Bruijnzeel & Proctor 1995; Tanner *et al.* 1998), with reduced
315 *GPP* occurring through direct effects (lower leaf N because of a reduced N mineralisation rate) and also
316 indirect effects (e.g. decreased active *LAI* because of constrained leaf production or an altered vertical
317 profile of leaf density in the canopy) (Moser *et al.* 2011). Leaf measurements however show that only
318 Wayqecha has significantly lower foliar N than lowland values in this transect (Table 1, Salinas *et al.* 2011;
319 Fisher *et al.* 2011; van de Weg *et al.* 2011, 2012) so N limitation can only be significant in our upper
320 montane zone at most (cf. Moser *et al.* 2011 who also found little change in foliar N content with elevation
321 in Ecuador). Although growth often appears to be N-limited (especially on landslide soil, Fetcher *et al.*
322 1996), it is not clear that montane forests are N limited in general (Bruijnzeel & Proctor 1995; Tanner *et al.*
323 1998; Benner *et al.* 2010; van de Weg *et al.* 2009, 2011; Lloyd *et al.* 2010). *JULES* does include leaf N
324 effects in its calculations of *GPP* (which assume that V_{Cmax} at 25°C is directly proportional to canopy top-
325 leaf N:C ratio N_{10} , Table 1), however between-site differences in foliar N are slight in this transect (Table 1)
326 which is why our *JULES* results were insensitive to variation in N_{10} . From our results, therefore, we cannot
327 conclude that leaf N content and N limitation are important drivers of *GPP* along this transect.

328 Finally, it has often been noted that cloud forest leaves exhibit ‘xeromorphic’ features despite the
329 generally wet conditions: leaves are generally smaller (microphylls and notophylls) with a thicker lamina,
330 better-developed palisade tissue and thicker outer epidermal walls and cuticles and more likely to be simple
331 (i.e. not compound) and hypostomatous (Grubb *et al.* 1963; Grubb & Whitmore 1966; Friend & Woodward
332 1990; Bruijnzeel & Proctor 1995; Richards *et al.* 1996; Willmer & Fricker 1996; Waide *et al.* 1998).
333 However, many so-called ‘xeromorphic traits’ appear rather to aid the removal of water from the leaf
334 surface during fog than reduce water loss (Haworth & McElwain 2008). It seems logical to assume that fog

335 and low cloud permeating the canopy depress leaf temperatures, however UV-B radiation is proportionately
336 higher in cloud forests because of differential transmission (Bruijnzeel & Proctor 1995; Foster 2001) and
337 plants in environments with low air temperatures but high radiation loads sometimes also have architectural
338 adaptations that allow tissue temperatures to be higher than air temperatures (see discussions in Friend &
339 Woodward 1990; Haworth & McElwain 2008; Landsberg & Sands 2011). Finally, in cloud forests water
340 films frequently form over leaf surfaces, impeding gas exchange (Richards *et al.* 1996; Dietz *et al.* 2007)
341 and allowing the growth of epiphylls and eukaryotic pathogens which reduce leaf photosynthetic efficiency
342 and shorten leaf longevity (Dietz *et al.* 2007, Salinas *et al.* 2011). These various ‘leaf structural’ effects may
343 have a net positive or a net negative effect on cloud forest *GPP*, but in the absence of better field data we
344 cannot be certain that their net effect is significant in this transect.

345 346 *Autotrophic respiration (R_a)*

347
348 Our values for simulated R_a were underestimates in comparison to both measurements and the range of
349 values suggested by Luysaert *et al.* (2007). Robertson *et al.* (2010) found that stem CO_2 efflux followed a
350 simple exponential trend with decreasing temperature in our transect (with Q_{10} value 1.5), which broadly
351 supports the trend of our *JULES* results, though not their magnitude. Increasing the proportion of *GPP*
352 allocated to growth r_g from its default value (0.25, Appx. II) was the only parameter change of those tested
353 that moved R_a closer to the measurement points, but in the absence of field values for r_g this result must be
354 considered only suggestive (Appx. II).

355 Evidence from Kosñipata suggests that the root component of R_a is fairly independent of temperature
356 (at least, above freezing temperatures), so this temperature dependence is being driven by the aboveground
357 components of R_a (Silva Espejo *et al.* 2012, Huaraca Huasco *et al.* 2012, Farfan Amezcuita *et al.* 2012). In
358 simulating R_a , *JULES* follows a scheme more sophisticated than Q_{10} with R_a following a hump-shaped
359 relationship with temperature based on the carboxylation rate of photosynthesis V_{Cmax} (declining both at low
360 and at high temperatures, Cox 2001, Clark *et al.* 2011 and see discussions in Atkin *et al.* 2005, 2008). Some
361 recent research has additionally included acclimation effects in this scheme (e.g. Atkin *et al.* 2008), but this
362 is not yet in any official release (or in v2.2 of *JULES* used in this study).

363 Apart from a small number of parameters such as *LAI*, canopy height, V_{Cmax} and leaf N
364 concentration, differences between biomes (e.g. differences in the R_a relationship) must be described in
365 *JULES* through introducing new Plant Functional Types (PFTs) (the only default tropical forest vegetation
366 type is “broadleaf tree”). Many groups are working on widening the PFTs available to DGVMs (e.g.
367 Westoby & Wright 2006; Prentice *et al.* 2007; Fisher *et al.* 2010b), which is necessary in the biodiverse
368 tropical zone where a greater proportion of species are specialists (Ghazoul & Sheil 2010). A wider set of
369 PFTs could greatly improve the representation of R_a in this model and in comparison to field data.

370 371 *Heterotrophic respiration (R_h)*

373 Our values for simulated R_h were overestimates in comparison to both measurements and the range of values
374 suggested by Luyssaert *et al.* (2007) below the upper montane zone. Although it is well-accepted that
375 instantaneous within-site variations in R_h follow exponential Q_{10} functions of temperature below oxygen
376 diffusion limitation (Robinson *et al.* 2008), between-site differences do not appear to do so in this transect
377 (Zimmermann *et al.* 2009a, b, 2010). Increasing the proportion of GPP allocated to growth r_g from its
378 default value (0.25, Appx. II) was the only parameter change that moved R_h closer to the measurement
379 points, but in the absence of field values for r_g this result must be considered only suggestive (Appx. II).

380 In general, heterotrophic soil respiration is controlled by substrate supply, microbial biomass and
381 other climate factors such as precipitation in addition to temperature (Zimmermann *et al.* 2010, also see
382 Metcalfe *et al.* 2007, 2011; Cornwell *et al.* 2008; Sayer *et al.* 2011) so these presumably become dominant
383 at larger spatial scales and over longer timescales despite the clear temperature controls on short-term
384 within-site responses, perhaps via plant trait interactions (Cornwell *et al.* 2008). Soil moisture is known to
385 explain much global between-site variation in R_h and soil mineralisation rates (Robinson *et al.* 2008,
386 Ghazoul & Sheil 2010) although in the Kosñipata transect it has proved challenging to distinguish
387 temperature and moisture effects because low temperatures and reduced precipitation occur in the same
388 season, both decreasing respiration rates (Zimmermann *et al.* 2010). Finally, note that Zimmermann *et al.*
389 (2010) found little change in soil respiration with elevation in this transect, so if processes of decomposition
390 and N mineralisation per unit mass decrease in the upper montane zone, as implied by the leaf N values at
391 Wayqecha (see above), then, from the results of a leaf and wood translocation experiment (Salinas *et al.*
392 2011), either the mass of organic material builds up to compensate (to yield a similar flux per unit area) or
393 more complicated effects such as soil priming must be occurring (Sayer *et al.* 2011).

394

395 *Net primary productivity (NPP)*

396

397 Our values for simulated NPP were overestimates in comparison to both measurements and the range of
398 values suggested by Clark *et al.* (2001b) and Luyssaert *et al.* (2007) below the upper montane zone. Because
399 NEP is close to zero for all our sites, long-term mean NPP aligns very closely to R_h as is to be expected
400 under equilibrium conditions. As with GPP , there is much debate over the mechanisms through which NPP
401 varies between biomes (e.g. Malhi *et al.* 2009; Metcalfe *et al.* 2009; Aragão *et al.* 2009; Girardin *et al.* 2010;
402 see also the NPP databases of Scurlock & Olson 2002, Malhi *et al.* 2011). Here, however, because of the
403 mechanistic approach of *JULES* (in common with all DGVMs) GPP and R_a are modelled explicitly and
404 separately and then NPP is calculated as the difference ($GPP - R_a$) (Table 2), so the controlling factors of
405 NPP have already been discussed above as controls either on GPP or on R_a .

406 Increasing the proportion of GPP allocated to growth r_g from its default value (0.25, Appx. II) was
407 the only parameter change that moved NPP closer to the measurement points, but in the absence of field

408 values for r_g this result must be considered only suggestive (Appx. II). However, note that this simple
409 change simultaneously improved the representation of simulated R_a , R_h and NPP in *JULES*.

411 *Net ecosystem productivity (NEP)*

412
413 *JULES* predicts all the study sites to be weak carbon sinks (i.e. carbon is being sequestered in all ecosystems
414 along this transect) and the magnitude of these sinks is only a little below the suggested values of Luysaert
415 *et al.* (2007) and Malhi (2010). Increasing the proportion of *GPP* allocated to growth r_g from its default
416 value (0.25, Appx. II) tended to decrease *NEP* at all sites but not change its sign (as a consequence of
417 increased growth and/or maintenance respiration, see Appx. II). Note that because *JULES* assumes a mass
418 balance under equilibrium conditions: all these nonzero carbon budgets are caused by transient effects (e.g.
419 from successional dynamics, climate variability or the changes in atmospheric CO_2 concentration since c.
420 1850, IPCC 2007).

422 *Carbon use efficiency (CUE)*

423
424 The phrase “carbon use efficiency” is misleading at the ecosystem level and it should not be understood that
425 tropical forests are ‘less efficient’ than their temperate counterparts: overall, they simply appear to allocate
426 proportionately fewer carbon resources to growth (the same argument applies to similar terms such as
427 “biomass production efficiency”, Vicca *et al.* 2012). Low *CUE* may not indicate inefficiency: for example,
428 high respiration may be a necessary consequence of the elevated metabolic rates necessary for
429 photosynthesis in highly-variable light environments (Huaraca Huasco *et al.* 2012 found a depressed value
430 for *CUE* in the transition zone to permanent cloud in our transect, perhaps showing this respiration effect).

431 *JULES* predicts *CUE* values at all sites close to 0.5, clearly higher than measured values (Fig. 2).
432 However, in answer to our third research question, *JULES* does not return the increase of *CUE* with
433 elevation suggested by Zhang *et al.* (2009) and Piao *et al.* (2010). Atkin *et al.* (2005) and Zhang *et al.* (2009)
434 found evidence for temperature-mediated differences in *CUE* and Piao *et al.* (2010) suggested a parabolic
435 relationship between *CUE* and mean annual temperature. Similarly, from a compilation of global trait,
436 biomass and growth data, Enquist *et al.* (2007) found that plant *CUE* increased with elevation from ~0.30 at
437 sea level to >0.60 above 1000 m asl, which implies a direct or indirect correlation with air temperature.
438 However, neither available measurements nor our simulations with *JULES* support this theory in this
439 particular elevational transect.

440 Modelled *CUE* follows a daily cycle, increasing as *GPP* declines (and becoming undefined at night),
441 but what about seasonal change? Monteith (1981) assumed minimal change within the growing season (over
442 time periods of at least a few weeks) but *CUE* is also known to depend on successional stage (Mäkelä &
443 Valentine 2001; Malhi *et al.* 2009; Landsberg & Sands 2011) indicating that *CUE* depends not only on
444 growth rates but also on whether high growth is caused by seasonality and mobilisation of stored resources

(change in growth/maintenance allocation, Appx. II) or inherent to a particular plant functional group (e.g. pioneers). Recent evidence suggests that *CUE* does follow an annual cycle at some sites, with storage of carbon during one season as a buffer against another season (Malhi *et al.* 1999; Farfan Amezcuita *et al.* 2012; Huaraca Huasco *et al.* 2012; Silva Espejo *et al.* 2012), however simulations currently do not capture these effects.

Chambers *et al.* (2004) suggested that in nutrient-deficient forests such as central Amazon *terra firme*, more carbon is fixed via photosynthesis than can be utilized by growth and functional respiration, pointing to an edaphic rather than biotic control (e.g. nutrient or moisture limitation) and this perspective is also supported by more recent evidence (Malhi *et al.* 2009; Aragão *et al.* 2009; cf. similar mechanisms reviewed by Lloyd *et al.* 2010, Vicca *et al.* 2012). *CUE* may also be controlled by plant traits (Enquist *et al.* 2007) which may of course themselves be controlled by climate-related and edaphic factors. The model *FUN*, for example, includes a mechanism whereby plants preferentially devote resources (*GPP*) to N acquisition before growth (*NPP*) with the effect that greater N acquisition costs will directly reduce both productivity and *CUE* (Fisher *et al.* 2010a). This mechanism suggests a reduction in *CUE* in N limited ecosystems, e.g. the upper montane zone of this transect. Although our simulations are supported by this trend, this may be coincidental because *JULES* does not include such N allocation routines (Clark *et al.* 2011).

Increasing the proportion of *GPP* allocated to growth r_g from its default value (0.25, Appx. II) simultaneously improved the fit between simulated R_a , R_h and *NPP* and available measurements (see above), and, to a lesser extent, *CUE*. What is the correct value, however? Combining the relationship between r_g (the fraction of carbon allocated to growth), *CUE* and γ (ratio of growth to maintenance respiration) (Appx. II):

$$r_g = \frac{\gamma(1 - CUE)}{\gamma + CUE}$$

with the respiration measurements of Robertson *et al.* (2010) for this transect (Appx. II) suggests that $r_g=0.33$ is a more reasonable value in lowland forest at Caxiuanã (using measured *CUE*=0.33, Table 2, $\gamma=0.32$) and in upper montane forests a lower value for r_g should be appropriate, perhaps as low as 0.05 at Wayqecha (using *CUE*=0.33, Table 2, $\gamma=0.03$).

If *CUE* does not vary greatly with elevation then changes in r_g must be controlled by γ , which is at least partly controlled by pressure (Gale 1972; Friend & Woodward 1990, Raich *et al.* 2006). Moving from Caxiuanã to Wayqecha, mean annual temperature drops from 26.2°C to 12.5°C (Table 2) and total atmospheric pressure from 1023 hPa to 706 hPa (measured annual mean). Therefore the mean equilibrium solubility of oxygen decreases from 8.6 mg O₂/L to 7.7 mg O₂/L (Henry's Law, Appx. III; equivalent to 0.82% v/v O₂ in aqueous solution). Lower dissolved oxygen might impose a constraint on R_a and its components R_g and R_m (e.g. Guo *et al.* 2008), especially in environments where irradiance (and therefore photosynthesis) is intermittent so respiration is more likely to temporarily deplete reserves of O₂ held inside

481 leaf cells (Öpik 1980) and the slow rate of diffusion of O₂ both within cells and across leaf boundary layers
482 will hamper replenishment from the atmosphere and may induce anaerobic respiration (fermentation).
483 Reduced partial pressure of CO₂ can reduce photosynthesis, although this is partially offset by increased
484 diffusivity of CO₂ and reduced photorespiration in C₃ plants (Bowman *et al.* 1999, Raich *et al.* 2006).
485 Metabolically important thresholds for tropical montane vegetation are not well known (Friend &
486 Woodward 1990), but dissolved oxygen concentrations below 4 mg/L are generally accepted to mean “only
487 a few kinds of fish and insects can survive” in rivers in the USA (Behar 1997) and Carrera-Burneo &
488 Gunkel (2003) suggested that 5 mg O₂/L was restrictive to ecosystem function in the Ecuadorean Andes.
489 Equating the health thresholds of water courses to thresholds for cloud forest vegetation is speculative, but it
490 seems reasonable to suggest that low pressure (Gale 1972; Iwabuchi *et al.* 1995; Bowman *et al.* 1999; Guo
491 *et al.* 2008) may be causing some level of stress in cloud forest vegetation in addition to low temperature
492 effects. Reduced diffusive and photosynthetic rates as a consequence of reduced atmospheric partial
493 pressures would have a significant effect on the productivity and carbon balance of tropical montane forests
494 (Friend & Woodward 1990; Körner 1998).

495 In this study we have applied the vegetation model *JULES* at six tropical sites, making use of an
496 elevational transect in the Peruvian Andes (Malhi *et al.* 2010) and data from *RAINFOR* sites across the
497 lowland Amazon basin. Field-based estimation of respiration and productivity in tropical forests is
498 challenging work and very few sites have been intensively monitored with all components of the forest
499 carbon cycle measured *in situ* (Metcalf *et al.* 2009; Malhi *et al.* 2009). The need for good model
500 simulations to fill the gaps between well-studied tropical forests is well-known and we present robust
501 predictions of all ecosystem-level carbon fluxes, forming a uniquely detailed picture of carbon cycling
502 across a wide range of neotropical forests.

503 Simulated forest ecosystem carbon fluxes showed generally close agreement with measurements
504 from lowland and lower montane forests, although not upper montane forests where simulated vegetation
505 died back. From a review of the dominant mechanisms influencing the carbon budget and how its
506 components vary with elevation, temperature and pressure, we conclude that carbon use efficiency in this
507 transect does not increase with elevation as has been found in other studies (Zhang *et al.* 2009, Piao *et al.*
508 2010, but see Zach *et al.* 2010). The carbon efficiency of forests under different temperature regimes has
509 recently received much attention and we develop this viewpoint to suggest that the allocation of carbon to
510 growth and maintenance within the vegetation canopy is also important. Our simulations indicate that better
511 estimates of these parameters will improve the ability of *JULES* to simulate forest carbon cycle components.
512 The variation of all these quantities with elevation has important implications for theories on carbon flows
513 through tropical forests and, therefore, for carbon budget and forest productivity assessment not only in the
514 Andes-Amazon region but across all tropical zones.

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REFERENCES

- Alton P, Mercado L, North P (2007) A sensitivity analysis of the land-surface scheme JULES conducted for three forest biomes: Biophysical parameters, model processes, and meteorological driving data. *Global Biogeochemical Cycles*, **20**, GB1008.
- Amorim Costa J (2005) Análises físicas e fertilidade em solos de terra preta e latossolo amarelo sob florestas na região de Caxiuanã, Pa. *Relatório Final*, Museu Paraense Emílio Goeldi, Brazil.
- Amthor JS (2000) The McCree-de Wit-Penning de Vries-Thornley Respiration Paradigms: 30 Years Later. *Annals of Botany*, **86**, 1-20.
- Anderson LO, Malhi Y, Ladle RJ, *et al.* (2009) Influence of landscape heterogeneity on spatial patterns of wood productivity, wood specific density and above ground biomass in Amazonia. *Biogeosciences Discussions*, **6**, 2039-2083.
- Aragão LEOC, Malhi Y, Metcalfe DB, *et al.* (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences*, **6**, 2759-2778.
- Araújo AC, Nobre AD, Kruijt B, *et al.* (2002) Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: The Manaus LBA site. *Journal of Geophysical Research D*, **107**(D20), 8090(LBA58).
- Ashton PS (2003) Floristic zonation of tree communities on wet tropical mountains revisited. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 87-104.
- Atkin OK, Atkinson LJ, Fisher RA, *et al.* (2008) Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate–vegetation model. *Global Change Biology*, **14**, 2709-2726.
- Atkin OK, Bruhn D, Hurry VW, Tjoelker MG (2005) The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology*, **32**, 87-105.
- Avissar R, Nobre CA (2002) Preface to special issue on the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA). *Journal of Geophysical Research D*, **107**(D20), 8034(LBA1).
- Behar S (1997) Testing the Waters: Chemical & Physical Vital Signs of a River. *Manual*, River Watch Network, Dubuque, Iowa.
- Benner J, Vitousek PM, Ostertag R (2010). Nutrient cycling and nutrient limitation in tropical montane cloud forests. In: *Tropical Montane Cloud Forests* (eds Bruijnzeel LA, Scatena FN, Hamilton LS), pp 90-100. CUP, Cambridge, UK.
- Berberan-Santos MN, Bodunov EN, Pogliani L (1997) On the barometric formula. *American Journal of Physics*, **65**, 404-412.
- Best MJ, Pryor M, Clark DB, *et al.* (2011) The Joint UK Land Environment Simulator (JULES), model description – Part 1: Energy and water fluxes. *Geoscientific Model Development*, **4**, 677-699.

- 572 Bonan G (2008) *Ecological Climatology* (2nd ed.). CUP, Cambridge, UK.
- 573 Bowman WD, Keller A, Nelson M (1999) Altitudinal Variation in Leaf Gas Exchange, Nitrogen and
574 Phosphorus Concentrations, and Leaf Mass per Area in Populations of *Frasera speciosa*. *Arctic,*
575 *Antarctic, and Alpine Research*, **31**, 191-195.
- 576 Bruijnzeel LA, Proctor J (1995). Hydrology and Biogeochemistry of Tropical Montane Cloud Forests: What
577 Do We Really Know? In: *Tropical Montane Cloud Forests* (eds Hamilton LS, Juvik JO, Scatena
578 FN), pp 38-78. Springer-Verlag, New York.
- 579 Butt N, Malhi Y, Phillips O, New M (2008) Floristic and functional affiliations of woody plants with climate
580 in western Amazonia. *Journal of Biogeography*, **35**, 939-950.
- 581 Carrera-Burneo P, Gunkel G (2003) Ecology of a high Andean stream, Rio Itambi, Otavalo, Ecuador.
582 *Limnologica*, **33**, 29-43.
- 583 Chambers JQ, dos Santos J, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-
584 ground net primary production in central Amazon forest. *Forest Ecology and Management*, **152**, 73-
585 84.
- 586 Chambers JQ, Tribuzy ES, Toledo LC, *et al.* (2004) Respiration from a tropical forest ecosystem:
587 partitioning of sources and low carbon use efficiency. *Ecological Applications*, **14**(suppl.), S72-S88.
- 588 Chapin FS, Matson P, Mooney HA (2002) *Principles of Terrestrial Ecosystem Ecology*. Springer, New
589 York.
- 590 Clark DB, Mercado LM, Sitch S, *et al.* (2011) The Joint UK Land Environment Simulator (JULES), model
591 description – Part 2: Carbon fluxes and vegetation dynamics. *Geoscientific Model Development*, **4**,
592 701-722.
- 593 Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and
594 atmospheric composition. *Philosophical Transactions of the Royal Society of London B*, **359**, 477-
595 491.
- 596 Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001a) Measuring net primary
597 production in forests: concepts and field methods. *Ecological Applications*, **11**, 356-370.
- 598 Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA (2001b) Net primary
599 production in tropical forests: an evaluation and synthesis of existing field data. *Ecological*
600 *Applications*, **11**, 371-384.
- 601 Cornwell WK, Cornelissen JHC, Amatangelo K, *et al.* (2008) Plant species traits are the predominant
602 control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065-1071.
- 603 Cosby BJ, Hornberger GM, Clapp RB, Ginn TR (1984) A Statistical Exploration of the Relationships of Soil
604 Moisture Characteristics to the Physical Properties of Soils. *Water Resources Research*, **20**, 682-690.
- 605 Cox PM (2001) Description of the "TRIFFID" Dynamic Global Vegetation Model. *Hadley Centre Technical*
606 *Note*, **24**.
- 607 Dharssi I, Vidale PL, Verhoef A, Macpherson B, Jones C, Best M (2009) New soil physical properties
608 implemented in the Unified Model at PS18. *Met Office Technical Report*, **528**.

- 609 Dietz J, Leuschner C, Höscher D, Kreilein H (2007) Vertical patterns and duration of surface wetness in an
610 old-growth tropical montane forest, Indonesia. *Flora*, **202**, 111-117.
- 611 Enquist BJ, Kerkhoff AJ, Stark SC, Swenson NG, McCarthy MC, Price CA (2007) A general integrative
612 model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*, **449**, 218-222.
- 613 Eva HD, Huber O, Achard F, *et al.* (2005) A proposal for defining the geographical boundaries of
614 Amazonia. *Report*, European Communities, Luxembourg.
- 615 Farfan Amezcuita F, Doughty CE, Silva Espejo JE, *et al.* (submitted 2012) The productivity, metabolism
616 and carbon cycle of two lowland tropical forest plots in SW Amazonia, Peru.
- 617 Fetcher N, Haines BL, Cordero RA, Lodge DJ, Walker LR, Fernández DS, Lawrence WT (1996) Responses
618 of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology*, **84**, 331-
619 341.
- 620 Fisher JB, Malhi Y, Torres IC, *et al.* (in review 2011) Nutrient limitation in rainforests and cloud forests
621 along a 3000 m elevation gradient in the Peruvian Andes. *Oecologia*.
- 622 Fisher JB, Sitch S, Malhi Y, Fisher RA, Huntingford C, Tan SY (2010a) Carbon cost of plant nitrogen
623 acquisition: A mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and
624 fixation. *Global Biogeochemical Cycles*, **24**, GB1014.
- 625 Fisher R, McDowell N, Purves D, *et al.* (2010b) Assessing uncertainties in a second-generation dynamic
626 vegetation model caused by ecological scale limitations. *New Phytologist*, **187**, 666-681.
- 627 Fisher RA, Williams M, Ruivo MdL, de Costa AL, Meir P (2008) Evaluating climatic and soil water
628 controls on evapotranspiration at two Amazonian rainforest sites. *Agricultural and Forest
629 Meteorology*, **148**, 850-861.
- 630 Fogg PGT, Sangster JM (2003) *Chemicals in the Atmosphere - Solubility, Sources and Reactivity*. Wiley,
631 Chichester, UK.
- 632 Foster P (2001) The potential negative impacts of global climate change on tropical montane cloud forests.
633 *Earth-Science Reviews*, **55**, 73-106.
- 634 Friend AD, Woodward FI (1990) Evolutionary and Ecophysiological Responses of Mountain Plants to the
635 Growing Season Environment. *Advances in Ecological Research*, **20**, 59-124.
- 636 Fyllas NM, Patiño S, Baker TR, *et al.* (2009) Basin-wide variations in foliar properties of Amazonian forest:
637 phylogeny, soils and climate. *Biogeosciences*, **6**, 2677-2708.
- 638 Gale J (1972) Availability of carbon dioxide for photosynthesis at high altitudes: theoretical considerations.
639 *Ecology*, **53**, 494-497.
- 640 Ghazoul J, Sheil D (2010) *Tropical Rain Forest Ecology, Diversity, and Conservation*. OUP, Oxford, UK.
- 641 Girardin CAJ, Malhi Y, Aragão LEOC, *et al.* (2010) Net primary productivity allocation and cycling of
642 carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, **16**,
643 3176-3192.
- 644 Gohil HL, Correll MJ, Sinclair T (2011) Predicting the effects of gas diffusivity on photosynthesis and
645 transpiration of plants grown under hypobaria. *Advances in Space Research*, **47**, 49-54.

- 646 Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2003) Cloud cover limits net CO₂ uptake and
647 growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of*
648 *Sciences USA*, **100**, 572-576.
- 649 Grubb PJ, Lloyd JR, Pennington TD, Whitmore TC (1963) A comparison of montane and lowland rain
650 forest in Ecuador I. The forest structure, physiognomy, and floristics. *Journal of Ecology*, **51**, 567-
651 601.
- 652 Grubb PJ, Whitmore TC (1966) A comparison of montane and lowland rain forest in Ecuador II. The
653 climate and its effects on the distribution and physiognomy of the forests. *Journal of Ecology*, **54**,
654 303-333.
- 655 Guo S, Tang Y, Gao F, Ai W, Qin L (2008) Effects of low pressure and hypoxia on growth and development
656 of wheat. *Acta Astronautica*, **63**, 1081-1085.
- 657 Hodnett MG, Tomasella J (2002) Marked differences between van Genuchten soil water-retention
658 parameters for temperate and tropical soils: a new water-retention pedo-transfer functions developed
659 for tropical soils. *Geoderma*, **108**, 155-180.
- 660 Houghton RA, Gloor M, Lloyd J, Potter C (2009). The Regional Carbon Budget. In: *Amazonia and Global*
661 *Change* (eds Keller M, Bustamante M, Gash J, Silva Dias P), pp 409-428. American Geophysical
662 Union, Washington, DC.
- 663 Huaraca Huasco W, Girardin CAJ, Doughty CE, *et al.* (submitted 2012) Seasonal production, allocation and
664 cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant*
665 *Ecology & Diversity*.
- 666 Intergovernmental Panel on Climate Change (2007) Climate Change 2007: the Fourth IPCC Assessment
667 Report. CUP, Cambridge, UK.
- 668 Iwabuchi K, Goto E, Takakura T (1995) Effect of O₂ pressure under low air pressure on net photosynthetic
669 rate of spinach. *Acta Horticulturae*, **399**, 101-106.
- 670 Iwata H, Malhi Y, von Randow C (2005) Gap-filling measurements of carbon dioxide storage in tropical
671 rainforest canopy airspace. *Agricultural and Forest Meteorology*, **132**, 305-314.
- 672 Jarvis PG, Leverenz JW (1983). Productivity of Temperate, Deciduous and Evergreen Forests. In:
673 *Physiological Plant Ecology IV* (eds Lange OL, Nobel PS, Osmond CB, Ziegler H), pp 233-280.
674 Springer-Verlag, Berlin, Germany.
- 675 Kira T (1978). Community architecture and organic matter dynamics in tropical lowland rain forests of
676 Southeast Asia with special reference to Pasoh Forest, West Malaysia. In: *Tropical trees as living*
677 *systems* (eds Tomlinson PB, Zimmerman MH), pp 561-590. CUP, Cambridge, UK.
- 678 Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, **115**,
679 445-459.
- 680 Landsberg J, Waring RH (2004). Top-down Models and Flux Measurements are Complementary Methods
681 of Estimating Carbon Sequestration by Forests: Illustrations using the 3-PG Model. In: *Forests at the*

682 *Land-Atmosphere Interface* (eds Mencuccini M, Grace J, Moncrieff J, McNaughton KG), pp 37-50.
683 CABI Publishing, Wallingford, UK.

684 Landsberg J, Sands P (2011) *Physiological Ecology of Forest Production*. Academic Press, Amsterdam,
685 Netherlands.

686 Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF (2009) Changing Ecology of Tropical Forests:
687 Evidence and Drivers. *Annual Review of Ecology, Evolution and Systematics*, **40**, 529-549.

688 Lisboa PLB (1997). A Estação Científica Ferreira Penna/ECFPn. In: *Caxiuanã* (ed Lisboa PLB), pp 20-49.
689 Museu Paraense Emílio Goeldi, Belém, Brazil.

690 Lloyd J, Patiño S, Paiva RQ, Nardoto GB, Quesada CA, Santos AJB, Baker TR, Brand WA, Hilke I,
691 Gielmann H, Raessler M, Luizão FJ, Martinelli LA, Mercado LM (2010) Optimisation of
692 photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest
693 trees. *Biogeosciences*, **7**, 1833-1859.

694 Lovett GM, Cole JJ, Pace ML (2006) Is Net Ecosystem Production Equal to Ecosystem Carbon
695 Accumulation? *Ecosystems*, **9**, 1-4.

696 Luysaert S, Inglima I, Jung M, *et al.* (2007) CO₂ balance of boreal, temperate, and tropical forests derived
697 from a global database. *Global Change Biology*, **13**, 2509-2537.

698 Luysaert S, Schulze E, Börner A, *et al.* (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213-
699 215.

700 Mäkelä A, Valentine HT (2001) The ratio of NPP to GPP: evidence of change over the course of stand
701 development. *Tree Physiology*, **21**, 1015-1030.

702 Malhi Y (2010) The carbon balance of tropical forest regions, 1990-2005. *Current Opinion in*
703 *Environmental Sustainability*, **2**, 237-244.

704 Malhi Y (2012) The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of*
705 *Ecology*, **100**, 65-75.

706 Malhi Y, Aragão LEOC, Metcalfe DB, *et al.* (2009) Comprehensive assessment of carbon productivity,
707 allocation and storage in three Amazonian forests. *Global Change Biology*, **15**, 1255-1274.

708 Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests.
709 *Plant, Cell and Environment*, **22**, 715-740.

710 Malhi Y, Doughty C, Galbraith D (2011) The allocation of ecosystem net primary productivity in tropical
711 forests. *Philosophical Transactions of the Royal Society B*, **366**, 3225-3245.

712 Malhi Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. *Tree*, **15**, 332-337.

713 Malhi Y, Pegoraro E, Nobre AD, Pereira MGP, Grace J, Culf AD, Clement R (2002) Energy and water
714 dynamics of a central Amazonian rain forest. *Journal of Geophysical Research*, **107**(D20), LBA45.

715 Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA (2008) Climate Change, Deforestation, and the
716 Fate of the Amazon. *Science*, **319**, 169-172.

- 717 Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S (2010) Introduction: Elevation gradients in the
718 tropics: laboratories for ecosystem ecology and global change research. *Global Change Biology*, **16**,
719 3171-3175.
- 720 Marthews TR, Burslem DFRP, Paton SR, Yangüez F, Mullins CE (2008) Soil drying in a tropical forest:
721 Three distinct environments controlled by gap size. *Ecological Modelling*, **216**, 369-384.
- 722 Marthews TR, Malhi Y, Iwata H (2012) Calculating downward longwave radiation under clear and cloudy
723 conditions over a tropical lowland forest site: an evaluation of model schemes for hourly data.
724 *Theoretical and Applied Climatology* **107**, 461-477.
- 725 Mercado LM, Huntingford C, Gash JHC, Cox PM, Jogireddy V (2007) Improving the representation of
726 radiation interception and photosynthesis for climate model applications. *Tellus B*, **59**, 553-565.
- 727 Mercado L, Lloyd J, Carswell F, Malhi Y, Meir P, Nobre AD (2006) Modelling Amazonian forest eddy
728 covariance data: a comparison of big leaf versus sun/shade models for the C-14 tower at Manaus I.
729 Canopy photosynthesis. *Acta Amazonica*, **36**, 69-82.
- 730 Mercado L, Lloyd J, Dolman AJ, Sitch S, Patiño S (2009) Modelling basin-wide variations in Amazon forest
731 productivity – Part 1: Model calibration, evaluation and upscaling functions for canopy
732 photosynthesis. *Biogeosciences*, **6**, 1247-1272.
- 733 Mercado LM, Patiño S, Domingues TF, *et al.* (2011). Variations in Amazon forest productivity correlated
734 with foliar nutrients and modelled rates of photosynthetic carbon supply. *Philosophical Transactions*
735 *of the Royal Society B*, **366**, 3316-3329.
- 736 Metcalfe DB, Fisher RA, Wardle DA (2011) Plant communities as drivers of soil respiration: pathways,
737 mechanisms, and significance for global change. *Biogeosciences*, **8**, 2047-2061.
- 738 Metcalfe DB, Meir P, Aragão LEOC, *et al.* (2007) Factors controlling spatio-temporal variation in carbon
739 dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern
740 Amazon. *Journal of Geophysical Research G*, **112**, G04001.
- 741 Metcalfe DB, Meir P, Aragão LEOC, *et al.* (2010) Shifts in plant respiration and carbon use efficiency at a
742 large-scale drought experiment in the eastern Amazon. *New Phytologist*, **187**, 608-621.
- 743 Metcalfe D, Phillips O, Baker T, *et al.* (2009) Measuring Tropical Forest Carbon Allocation And Cycling.
744 *RAINFOR* Field Manual. URL http://www.geog.leeds.ac.uk/projects/rainfor/pages/manuals_eng.html
- 745 Monteith JL (1981) Climatic variation and the growth of crops. *Quarterly Journal of the Royal*
746 *Meteorological Society*, **107**, 749-774.
- 747 Moser G, Leuschner C, Hertel D, Graefe S, Iost S (2011) Elevation effects on the carbon budget of tropical
748 mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology*,
749 **17**, 2211-2226.
- 750 Niinemets Ü, Anten NPR (2009). Packing the Photosynthetic Machinery: From Leaf to Canopy. In:
751 *Photosynthesis in silico: Understanding Complexity from Molecules to Ecosystems* (eds Laisk A,
752 Nedbal L, Govindjee), pp 363-399. Springer, Dordrecht, Netherlands.
- 753 Öpik H (1980) *The Respiration of Higher Plants*. Edward Arnold, London, UK.

- 754 Pan Y, Birdsey RA, Fang J, *et al.* (2011) A Large and Persistent Carbon Sink in the World's Forests.
755 *Science*, **333**, 988-993.
- 756 Park S, Jiménez R, Daube BC, *et al.* (2007) The CO₂ tracer clock for the Tropical Tropopause Layer.
757 *Atmospheric Chemistry and Physics*, **7**, 3989-4000.
- 758 Patiño S, Lloyd J, Paiva R, *et al.* (2009) Branch xylem density variations across the Amazon Basin.
759 *Biogeosciences*, **6**, 545-568.
- 760 Pennington TD, Reynel C, Daza A (2004) Illustrated guide to the Trees of Peru. David Hunt, Sherborne,
761 UK.
- 762 Phillips OL, Aragão LEOC, Lewis SL, *et al.* (2009) Drought Sensitivity of the Amazon Rainforest. *Science*,
763 **323**, 1344-1347.
- 764 Piao S, Luysaert S, Ciais P, *et al.* (2010) Forest annual carbon cost: a global-scale analysis of autotrophic
765 respiration. *Ecology*, **91**, 652-661.
- 766 Pires JM, Prance GT (1985) The Vegetation Types of the Brazilian Amazon. In: *Amazonia* (eds Prance GT,
767 Lovejoy TE), pp 109-145. Pergamon Press, Oxford, UK.
- 768 Prentice IC, Bondeau A, Cramer W, *et al.* (2007). Dynamic Global Vegetation Modeling: Quantifying
769 Terrestrial Ecosystem Responses to Large-Scale Environmental Change. In: *Terrestrial Ecosystems*
770 *in a Changing World* (eds Canadell JG, Pataki DE, Pitelka LF), pp 175-192. Springer, Berlin,
771 Germany.
- 772 Quesada CA (2008) Soil vegetation interactions across Amazonia. *PhD thesis*, University of Leeds, UK.
- 773 Quesada CA, Lloyd J, Schwarz M, *et al.* (2010) Variations in chemical and physical properties of Amazon
774 forest soils in relation to their genesis. *Biogeosciences*, **7**, 1515-1541.
- 775 R Development Core Team (2011) R: A language and environment for statistical computing, version 2.13.1.
776 R Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org>
- 777 Raich JW, Russell AE, Kitayama K, Parton WJ, Vitousek PM (2006) Temperature influences carbon
778 accumulation in moist tropical forests. *Ecology*, **87**, 76-87.
- 779 Richards PW, Walsh RPD, Baillie IC, Greig-Smith P (1996) The tropical rain forest (2nd ed.). CUP,
780 Cambridge, UK.
- 781 Robertson AL, Malhi Y, Farfan-Amezquita F, Aragão LEOC, Silva Espejo JE, Robertson MA (2010) Stem
782 respiration in tropical forests along an elevation gradient in the Amazon and Andes. *Global Change*
783 *Biology*, **16**, 3193-3204.
- 784 Robinson DA, Campbell CS, Hopmans JW, *et al.* (2008) Soil Moisture Measurement for Ecological and
785 Hydrological Watershed-Scale Observatories: A Review. *Vadose Zone Journal*, **7**, 358-389.
- 786 Ryan MG (1991) Effects of climate change on plant respiration. *Ecological Applications*, **1**, 157-167.
- 787 Rymes M (1998) The SolPos algorithm. National Renewable Energy Laboratory, Golden, Colorado. URL
788 <http://rredc.nrel.gov/solar/codesandalgorithms/solpos>

- 789 Salinas N, Malhi Y, Meir P, *et al.* (2011) The sensitivity of tropical leaf litter decomposition to temperature:
790 results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian
791 forests. *New Phytologist*, **189**, 967-977.
- 792 Sayer EJ, Heard MS, Grant HK, Marthews TR, Tanner EVJ (2011) Soil carbon release enhanced by
793 increased tropical forest litterfall. *Nature Climate Change*, **1**, 304-307.
- 794 Scurlock JMO, Olson RJ (2002) Terrestrial net primary productivity — A brief history and a new worldwide
795 database. *Environmental Reviews*, **10**, 91-109.
- 796 Seinfeld JH, Pandis SN (2006) Atmospheric chemistry and physics (2nd ed.). Wiley, Hoboken, New Jersey.
- 797 Silva Espejo JE, Girardin CAJ, Doughty C, *et al.* (submitted 2012) Productivity and Carbon Allocation in a
798 High Elevation Tropical Mountain Cloud Forest of the Peruvian Andes. *Plant Ecology & Diversity*.
- 799 Tanner EVJ, Vitousek PM, Cuevas E (1998) Experimental investigation of nutrient limitation of forest
800 growth on wet tropical mountains. *Ecology*, **79**, 10-22.
- 801 ter Steege H, Pitman N, Sabatier D, *et al.* (2003) A spatial model of tree α -diversity and tree density for the
802 Amazon. *Biodiversity and Conservation*, **12**, 2255-2277.
- 803 Terborgh J, Andresen E (1998) The composition of Amazonian forests: patterns at local and regional scales.
804 *Journal of Tropical Ecology*, **14**, 645-664.
- 805 van de Weg MJ, Meir P, Grace J, Atkin OK (2009) Altitudinal variation in leaf mass per unit area, leaf
806 tissue density and foliar nitrogen and phosphorus content along an Amazon-Andes gradient in Peru.
807 *Plant Ecology and Diversity*, **2**, 243-254.
- 808 van de Weg MJ, Meir P, Grace J, Ramos GD (2011) Photosynthetic parameters, dark respiration and leaf
809 traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia*, DOI: 10.1007/s00442-
810 011-2068-z.
- 811 van de Weg MJ, Meir P, Williams M, Malhi Y, Silva-Espejo J, Grace J (in review 2012) Modelling the
812 Gross Primary Productivity of a high elevation tropical montane cloud forest. *Ecology*.
- 813 van Oijen M, Schapendonk A, Höglind M (2010) On the relative magnitudes of photosynthesis, respiration,
814 growth and carbon storage in vegetation. *Annals of Botany*, **105**, 793-797.
- 815 Vicca S, Luysaert S, Peñuelas J, Campioli M, Chapin FS, Ciais P, Heinemeyer A, Höglberg P, Kutsch WL,
816 Law BE, Malhi Y, Papale D, Piao SL, Reichstein M, Schulze ED, Janssens IA (2012) Fertile forests
817 produce biomass more efficiently. *Ecology Letters* doi: 10.1111/j.1461-0248.2012.01775.x.
- 818 Waide RB, Zimmerman JK, Scatena FN (1998) Controls of primary productivity: lessons from the Luquillo
819 Mountains in Puerto Rico. *Ecology*, **79**, 31-37.
- 820 Walsh RPD (1996). Microclimate and hydrology. In: *The tropical rain forest* (2nd ed.) (eds Richards PW,
821 Walsh RPD, Baillie IC, Greig-Smith P), pp 206-236,503-540. CUP, Cambridge, UK.
- 822 Wang Q, Kakubari Y, Kubota M, Tenhunen J (2007) Variation on PAR to global solar radiation ratio along
823 altitude gradient in Naeba Mountain. *Theoretical and Applied Climatology*, **87**, 239-253.
- 824 Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Tree*, **21**, 261-268.
- 825 Willmer C, Fricker M (1996) Stomata (2nd ed.). Chapman, Hall, London, UK.

- 826 Yang Y, Luo Y, Finzi AC (2011) Carbon and nitrogen dynamics during forest stand development: a global
827 synthesis. *New Phytologist*, **190**, 977-989.
- 828 Zach A, Horna V, Leuschner C, Zimmermann R (2010) Patterns of wood carbon dioxide efflux across a
829 2,000-m elevation transect in an Andean moist forest. *Oecologia*, **162**, 127-137.
- 830 Zhang Y, Xu M, Chen H, Adams J (2009) Global pattern of NPP to GPP ratio derived from MODIS data:
831 effects of ecosystem type, geographical location and climate. *Global Ecology and Biogeography*, **18**,
832 280-290.
- 833 Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2009a) Climate dependence of heterotrophic
834 soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal
835 gradient. *European Journal of Soil Science*, **60**, 895-906.
- 836 Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2009b) Litter contribution to diurnal and
837 annual soil respiration in a tropical montane cloud forest. *Soil Biology and Biochemistry*, **41**, 1338-
838 1340.
- 839 Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2010) Temporal variation and climate
840 dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient.
841 *Global Biogeochemical Cycles*, **24**, GB4012.
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845 **FIGURE LEGENDS**

846

847 **Fig. 1:** The six study sites and a vertical profile of the Andes-Amazon transition in relation to Amazonia as
 848 defined in Eva *et al.* (2005). On the map, the broken black outline shows *Amazonia sensu stricto* (the
 849 Amazon basin below 700 m asl, Eva *et al.* 2005). On the graph, shading represents Puna grassland above the
 850 treeline at approximately 3400 m asl (Girardin *et al.* 2010), upper montane forest above the consistent cloud
 851 base at approximately 1500 m asl (Ashton 2003), lower montane forest and the lowlands in Amazonia *sensu*
 852 *stricto*. All sites are part of the *RAINFOR* network (Malhi *et al.* 2002) and the nearby flux towers at Manaus
 853 and Caxiuanã are part of the LBA experiment (Avisar & Nobre 2002). Base map used with permission
 854 from the Joint Research Centre, Institute for Environment and Sustainability, © European Communities,
 855 2005.

856

857 **Fig. 2:** Simulated carbon fluxes for all sites plotted against mean annual temperature and compared to field
 858 measurements: (a) Gross Primary Productivity (*GPP*), (b) Autotrophic respiration (R_a), (c) Heterotrophic
 859 soil respiration (R_h), (d) Total Net Primary Productivity (*NPP*), (e) Net Ecosystem Productivity (*NEP*) with
 860 an inset expanding the values close to $NEP=0$ and (f) Carbon Use Efficiency ($CUE=NPP/GPP$) as defined
 861 in Table 2. Units in plots (a-e) are $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (left vertical axis) or equivalent mean annual flux in Mg
 862 $\text{C ha}^{-1} \text{ yr}^{-1}$ (right axis; n.b. 1 $\text{Mg C/ha per year} = 100 \text{ g C/m}^2 \text{ per year} = 0.264 \mu\text{mol C/m}^2 \text{ per second}$).
 863 *JULES* results are shown as lines: overall means (solid), daylight means (broken) and nighttime means
 864 (dotted, undefined in f) to show daily variation at each site. Measurement points are from Farfan Amezquita
 865 *et al.* (2012), Huaraca Huasco *et al.* (2012), Silva Espejo *et al.* (2012) (all three follow the same methods; all
 866 shown as \blacktriangle , $\pm 1\text{SE}$), Aragão *et al.* (2009, \bullet , $\pm 1\text{SE}$), Malhi *et al.* (2009, Δ , $\pm 1\text{SE}$) and Girardin *et al.* (2010,
 867 \circ , $\pm 1\text{SE}$; n.b. respiration from coarse woody debris was not included in their measurements so they may
 868 have underestimated R_h by possibly as much as 50%) (q.v. Table 2). Site names (e.g. WAY=Wayqecha) are
 869 displayed above/below their corresponding points (sites between Wayqecha and San Pedro (q.v. Table 2) are
 870 shown for reference only and were not used in any analysis). Grey bands on (a-d) show the range of values
 871 found by Luysaert *et al.* (2007) for tropical humid evergreen forests, and also for reference we show: on (d)
 872 the average of the ‘low’ an ‘high’ *NPP* regressions against temperature found by Clark *et al.* (2001b) in old
 873 growth tropical forest sites up to 2500 m asl (lower grey curve) and the global *NPP* regression against
 874 precipitation used in the *MIAMI* model widely used in the 1970s (Scurlock & Olson 2002) (upper grey
 875 curve); on (e) the pantropical (forest) synthesis of Malhi (2010) (lower grey curve) and the range of values
 876 found by Luysaert *et al.* (2007) for tropical humid evergreen forests (upper grey curve); on (f) the *CUE*
 877 regression against temperature found by Piao *et al.* (2010) from a global database of eddy covariance and
 878 direct field measurements from 60 sites including 4 tropical forests (lower grey curve) and the global *CUE*
 879 relationship against altitude proposed by Zhang *et al.* (2009) (upper grey curve). Also for reference, a $y=0$

880 line is shown on all plots except (f) where a $CUE=0.5$ line is shown, and vertical dashed lines show the
881 transition zone at 1500-1800 m asl above which cloud cover is consistent (upper montane forest, Ashton
882 2003) and the boundary at 700 m asl below which is lowland forest (Eva *et al.* 2005). Finally, note that
883 during the night $GPP=0$ so CUE should be undefined, but nevertheless the plotted daylight mean does not
884 coincide with the overall mean line. This is because at timesteps shortly after dusk on many simulated days
885 *JULES* predicts slightly negative NPP (caused by nonzero R_a , perhaps indicating investment in new
886 structures such as buds or leaves or general remobilisation of stored carbon, van Oijen *et al.* 2010) and small
887 but nonzero GPP as GPP tends to zero (due to lag effects), giving a negative nighttime mean for CUE .

888
889 **Fig. A1:** The theoretical variation of r_g with CUE and for example values of Y_g and α (see text for
890 definitions). Uncertainty in the value of Y_g does affect r_g (lines show values at $Y_g=0.75$ and grey bands show
891 values for the range $0.7 < Y_g < 0.8$), with higher values of Y_g giving lower values of r_g . The arrow shows the
892 theoretical direction of forest succession (Landsberg & Sands 2011 suggested that CUE decreases from ≈ 0.5
893 in young to ≈ 0.3 in mature forests, and this may be combined with an increase in carbon storage from $\alpha \approx 0$ in
894 early successional stages to $\alpha \approx CUE$ in mature patches to give r_g decreasing from 0.25 to 0). The $r_g=0.25$
895 estimate of *JULES* (Cox 2001, Clark *et al.* 2011) may be understood as a maximal value for vegetation with
896 negligible storage (high growth), $CUE < 0.6$ and $Y_g = 0.75$.

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TABLE CAPTIONS

Table 1: Characteristics of the six study sites. Values for $V_{C_{max25}}$, the photosynthetic capacity (maximum rate of RuBisCO carboxylation) at 25°C, were taken from van de Weg *et al.* (2011), applying their lowland (Manaus) value to all sites up to San Pedro because of their broadly similar values for N_{10} . For reference, the *JULES* default values for broadleaf vegetation are $N_{10}=0.046$ g N/g C and $V_{C_{max25}}=36.8$ $\mu\text{mol CO}_2/\text{m}^2\text{s}$, so the constant of proportionality $n_e = V_{C_{max25}}/N_{10} = 0.0008$ mol $\text{CO}_2/\text{m}^2\text{s} \cdot \text{g C/g N}$ (a measure of photosynthetic nitrogen use efficiency, Cox 2001; Clark *et al.* 2011).

Table 2: Measured forest carbon fluxes (definitions follow IPCC 2007, e.g. http://www.ipcc.ch/publications_and_data/publications_and_data_glossary.shtml). Sites used for *JULES* simulation runs in this study in bold (Table 1) and some nearby sites where data are available are included for reference. Note that the ‘plant respiration’ *respP* and ‘soil respiration’ *respS* in outputs from *JULES* correspond to R_a (= whole plant respiration including root respiration) and R_h (= soil respiration minus root respiration) as defined here (Clark *et al.* 2011). All confidence intervals are mean \pm 1SE except for those from Metcalfe *et al.* (2010) which are mean \pm 95% CI. Note: in this text we calculate Carbon Use Efficiency (*CUE*) at subdaily timesteps, despite this being arguably difficult to interpret because forests are known to store photosynthates for later use over daily periods. A carbon flux of 1 Mg C ha⁻¹ yr⁻¹ = 100 g C/m² per year and, when considered over sub-daily time periods, = 0.264 $\mu\text{mol C}/\text{m}^2\text{s}$ = 0.264 $\mu\text{mol CO}_2/\text{m}^2\text{s}$ (and when converted to biomass units - i.e. g dry matter rather than g C - these productivities may be thought of as growth rates).

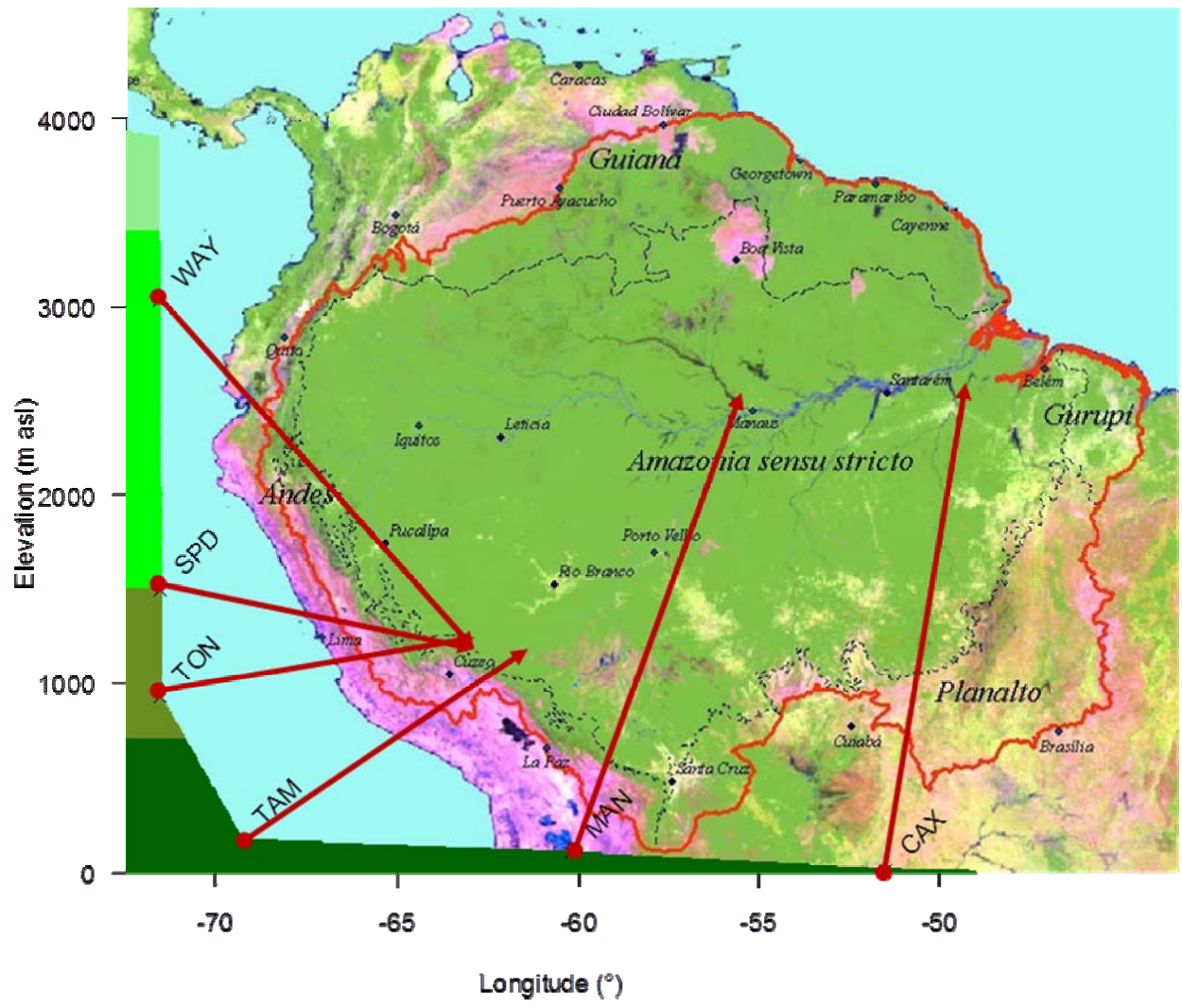


Fig. 1:

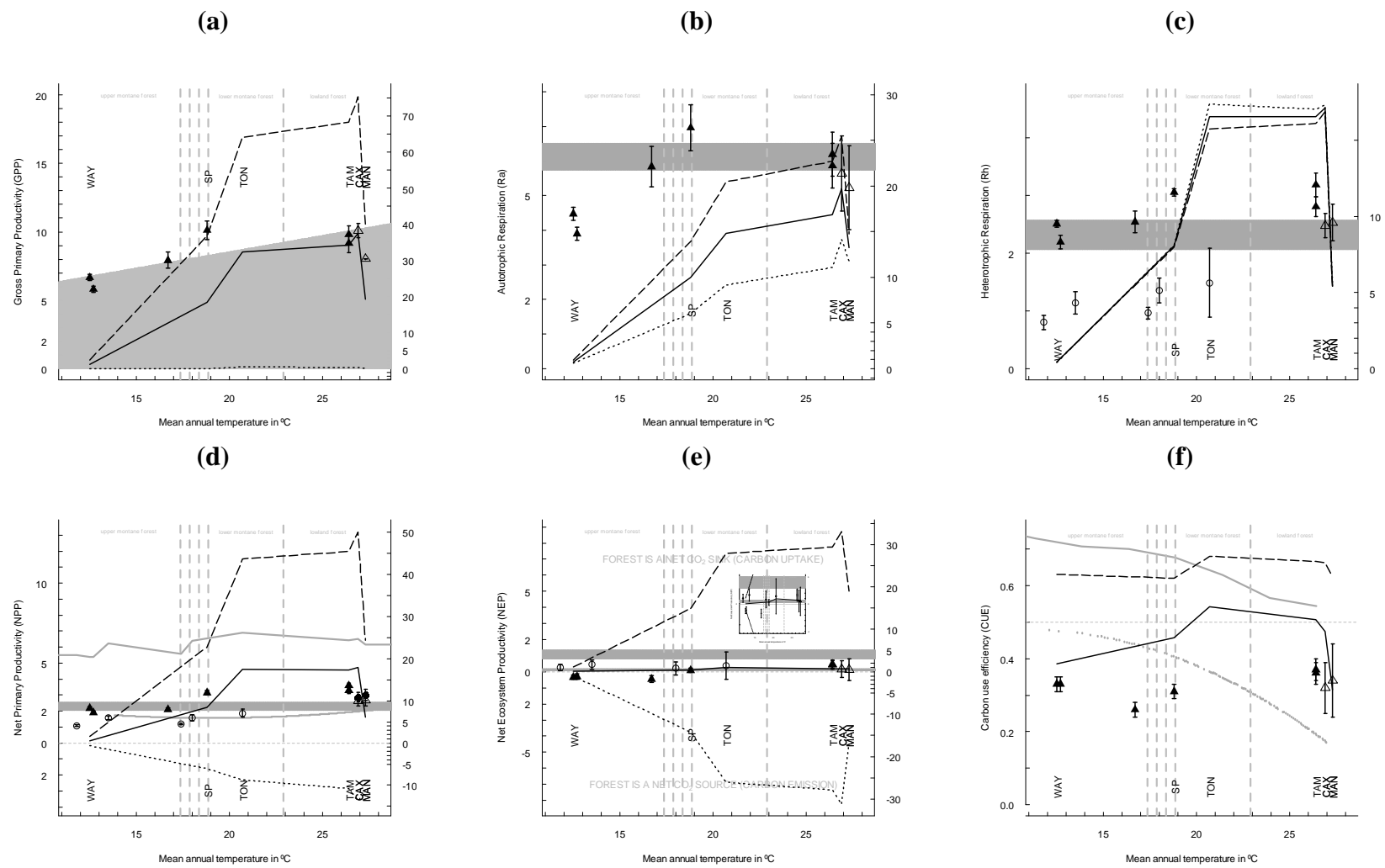


Fig. 2:

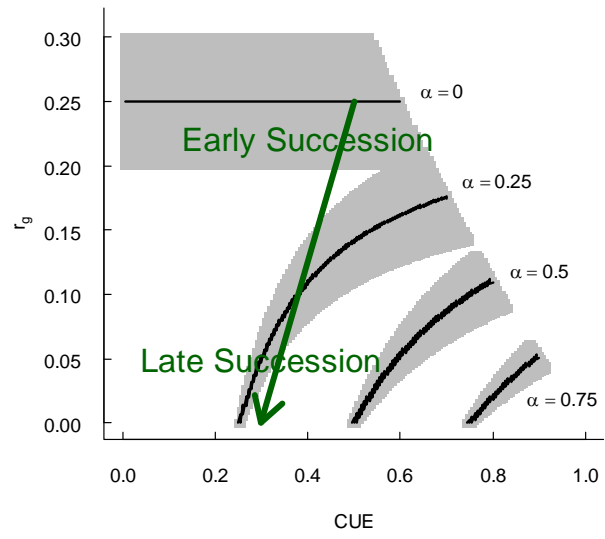


Fig. A1:


Table 1:

Plot	Location	Biome	Elevation above sea level (m)	Mean annual temperature (°C)	Annual precipitation (mm)	Canopy height (<i>h</i> , m)	Leaf Area Index (<i>LAI</i> , m ² /m ²)	Live stemwood coefficient η_{sl} (kg C/m ² per unit <i>LAI</i>)	Soil texture (% clay, % sand)	Canopy top-leaf N:C ratio N_{10} (g N/g C)	Maximum rate of carboxylation of RuBisCO at 25°C V_{Cmax25} ($\mu\text{mol CO}_2/\text{m}^2\text{s}$)	$n_e = V_{Cmax25}/N_{10}$ (mol CO ₂ /m ² s · g C/g N)
Wayqecha n,p,r,t,u	Intensive census plot WAY-01 (WA_3000) at the Estación Biológica Wayqecha	Cusco, Peru	3025 ^v	12.5 ^r	1706 ^r	14 ^{t,w}	4 ^y	0.012	16%, 12% ^p	0.024 ^{z,bb}	55.6 ^{aa}	0.00232
San Pedro plot 2 n,p,r,t,u	Census plot SPD-02 (SP_1500) in the Kosñipata transect	Cusco, Peru	1500 ^v	18.8 ^r	2631 ^r	18.5 ^{t,w}	5 ^y	0.010	16%, 13% ^p	0.054 ^{z,cc}	42.8 ^{aa}	0.00079
Tono plot 1 n,p,r,t,u	Census plot TON-01 (TO_1000) in the Kosñipata transect	Cusco, Peru	925 ^v	20.7 ^r	3087 ^r	29 ^{t,w}	5 ^y	0.007	5%, 64% ^p	0.050 ^{z,dd}	42.8 ^{aa}	0.00086
Tambopata plot 4 i,j,n,p,r,t,u	Intensive census plot TAM-06 (Tambopata plot 4) at the Centro de Investigaciones Tambopata	Madre de Dios, Peru	200 ^f	26.4 ^r	2730 ^r	30 ^j	5 ^s	0.006	7%, 66% ^p	0.051 (=24.80/485) g	42.8 ^{aa}	0.00084

Plot	Location	Biome	Elevation above sea level (m)	Mean annual temperature (°C)	Annual precipitation (mm)	Canopy height (h, m)	Leaf Area Index (LAI , m^2/m^2)	Live stemwood coefficient η_{sl} (kg C/m ² per unit LAI)	Soil texture (% clay, % sand)	Canopy top-leaf N:C ratio N_{10} (g N/g C)	Maximum rate of carboxylation of RuBisCO at 25°C V_{Cmax25} ($\mu mol CO_2/m^2s$)	$n_e = V_{Cmax25}/N_{10}$ (mol CO ₂ /m ² s · g C/g N)
Manaus, K34 Tower b,i,j,k	A mean of census plots MAN-01 and MAN-02 close to the LBA K34 eddy covariance flux tower	Amazonas, Brazil	104 ^q	27.3 ^h	2250 ^f	30 ^m	5.58 ^x	0.007	68%, 20% ^f	0.045 (=22.33/491 from the nearby Jacaranda site) ^g	42.8 ^{aa}	0.00095
Caxiuana Tower plot a,i,j,k,s	Intensive census plot CAX-06 at the Estação Científica Ferreira Penna	Pará, Brazil	12 ⁱ	26.9 ^j	2314 ^j	35 ^{dj}	5.25 ^x	0.006	44%, 38% ^c	0.042 (=19.80/468) _g	42.8 ^{aa}	0.00102

^a Lisboa (1997), ^b Araújo *et al.* (2002), ^c Amorim Costa (2005), ^d Iwata *et al.* (2005), ^e Quesada (2008), ^f Fyllas *et al.* (2009), ^g Patiño *et al.* (2009), ^h Shuttle Radar Topography Mission (SRTM) elevations from Anderson *et al.* (2009) with canopy height subtracted, ⁱ Aragão *et al.* (2009), ^k Malhi *et al.* (2009), ^m Mercado *et al.* (2009), ⁿ van de Weg *et al.* (2009), ^p Zimmermann *et al.* (2009a,b, 2010), ^q A. C. Araújo pers. comm. to N. Restrepo-Coupe July 2009, ^r Girardin *et al.* (2010), ^s Metcalfe *et al.* (2010), ^t Robertson *et al.* (2010), ^u Salinas *et al.* (2011), ^v Global Positioning System (GPS) reading taken by J. Rapp, ^w Maximum measured tree height, J. Fisher and I. Torres (unpubl. data), ^x Patiño *et al.* (unpubl. data), ^y Estimated for this study (Wayqecha value is close to the 4.17 m²/m² in van de Weg *et al.* 2012), ^z N. Salinas (unpubl. data), ^{aa} van de Weg *et al.* (2011), ^{bb} Mean of sun leaves sampled from *Clusia cretosa*, *Hesperomeles ferruginea* and *Weinmannia crassifolia* trees, the commonest species in this plot, ^{cc} Mean of sun leaves sampled from *Vismia* sp., *Alchornea latifolia* and *Tachigali* sp. trees, the commonest species in this plot, ^{dd} Mean of sun leaves sampled from *Symphonia globulifera*, *Perebea guianensis* and *Virola elongata* trees, the commonest species in this plot.

Table 2:

 Plot (code)	Forest bulk carbon fluxes outside large disturbance events ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$, where “bulk” means summed over all plants and soil to make a canopy-averaged, per ha figure)					Carbon Use Efficiency (ratio of net carbon gain to gross carbon assimilation; the fraction of carbon fixed that is allocated to growth; $CUE = NPP/GPP = 1 - (R_a/GPP)$)
	Gross Primary Productivity (gross carbon fixation/assimilation; gross photosynthesis less photorespiration) <i>GPP</i>	Autotrophic (plant-derived) Respiration R_a	Heterotrophic (not derived from plants) Respiration $R_h (=R_{eco} - R_a$ where R_{eco} is ecosystem respiration)	Net Primary Productivity (the carbon equivalent of above- and below-ground biomass production; short-term net carbon uptake) $NPP (=GPP - R_a)$	Net Ecosystem Productivity (medium-term net carbon uptake) $NEP_{a,b}$ ($=NPP - R_h = GPP - R_{eco}$)	
Wayqecha (WAY-01)	25.23±0.83 ^c	16.97±0.72 ^c	9.52±0.23 ^c	8.26±0.41 ^c	-1.26±0.47 ^{c,d}	0.33±0.02 ^c
Wayqecha	21.97±0.83 ^c	14.78±0.73 ^c	8.32±0.45 ^c	7.20±0.39 ^c	-1.12±0.60 ^{c,d}	0.33±0.02 ^c
Esperanza plot			3.05±0.47 ^c	4.11±0.26 ^c	1.06±0.73 ^{c,d}	
Trocha Union plot 3 (TRU-03)			4.31±0.74 ^c	5.98±0.39 ^c	1.67±1.13 ^{c,d}	
Trocha Union plot 4 (TRU-04)			3.66±0.38 ^c	4.50±0.20 ^c	0.84±0.58 ^{c,d}	
Trocha Union plot 7 (TRU-07)			5.14±0.80 ^c	5.97±0.73 ^c	0.83±1.53 ^{c,d}	
Trocha Union plot 8 (TRU-08)						
San Pedro plot 1 (SPD-01)	30.03±2.25 ^f	22.11±2.21 ^f	9.64±0.71 ^f	7.92±0.39 ^f	-1.72±0.81 ^{f,d}	0.26±0.02 ^f
San Pedro plot 2 (SPD-02)	38.31±2.54 ^f	26.39±2.50 ^f	11.59±0.25 ^f	11.92±0.46 ^f	0.33±0.52 ^{f,d}	0.31±0.02 ^f
Tono plot 1 (TON-01)			5.64±2.25 ^e	7.07±0.98 ^e	1.43±3.23 ^{e,d}	
Tambopata plot 3 (TAM-05)	37.11±2.50 ^g	23.48±2.42 ^g	12.07±0.78 ^g	13.63±0.65 ^g	1.56±1.02 ^{g,d}	0.37±0.03 ^g
Tambopata plot 4 (TAM-06)	34.69±2.53 ^g	22.24±2.43 ^g	10.64±0.66 ^g	12.45±0.71 ^g	1.81±0.97 ^{g,d}	0.36±0.03 ^g
Manaus, K34 Tower	30.4 ^{h,i}	19.8±4.6 ⁱ	9.6±1.2 ⁱ	10.1±1.4 ⁱ , 11.40±1.29 ^j	0.5±2.6 ^{i,d}	0.34±0.10 ⁱ
Caxiuanã Tower plot (CAX-06)	38.2±2.0 ⁱ , 33.0±2.9 ^k , 32.0±4.1 ^l	21.4±4.1 ⁱ , 22.4±2.8 ^k , 24.4±4.1 ^l	9.4±0.8 ⁱ , 10.2±1.0 ^k , 9.9±0.8 ^l	10.0±1.2 ⁱ , 10.90±1.11 ^j , 10.6±0.9 ^k , 10.6±0.7 ^l	0.6±2.0 ⁱ , 0.4±1.9 ^k , 0.7±1.5 ^l	0.32±0.07 ⁱ , 0.32±0.04 ^k , 0.33±0.05 ^l

^a Positive *NEP* means that the carbon pool of the ecosystem is usually expanding, i.e. it is a net carbon sink outside large disturbance events. We avoid the term Net Ecosystem Exchange (*NEE*) because this is sometimes defined as the net CO_2 flux to the atmosphere (outside large disturbances), which equals $-NEP$ (e.g. Clark *et al.* 2001a, Malhi *et al.* 2009, Houghton *et al.* 2009) and sometimes defined to equal *NEP* (e.g. Chapin *et al.* 2002, Landsberg & Waring 2004, Luyssaert *et al.* 2007, Bonan 2008), ^b There is often confusion between *NEP* and the related concept of Net Biome Productivity (*NBP*, which is long-term net carbon uptake ($'NEP$ minus disturbance') i.e. net ecosystem productivity averaged over both normal productivity and large disturbance events, IPCC 2007): see Malhi *et al.* (1999) and Lovett *et al.* (2006) for discussions, ^c Silva Espejo *et al.* (2012), ^d Calculated here from $NPP - R_h$, ^e Girardin *et al.* (2010; *n.b.* respiration from coarse woody debris was not included in their measurements so they may have underestimated R_h by possibly as much as 50%), ^f Huaraca Huasco *et al.* (2012), ^g Farfan Amezcuita *et al.* (2012), ^h Malhi & Grace (2000), ⁱ Malhi *et al.* (2009), ^j Aragão *et al.* (2009), ^k Metcalfe *et al.* (2010; taking *GPP* = plant carbon expenditure *PCE* which is legitimate for annual fluxes: because of seasonal storage terms, *PCE* may differ from *GPP* at sub-annual timescales), ^l Malhi *et al.* (2011)

