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Simulating forest productivity along a neotropical elevational 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]

INTRODUCTION

Intact tropical forests currently cover 13.9 million km^2 worldwide, or 24% of tropical land area (Pan *et al.* 2011). These forests support the most biodiverse terrestrial ecosystems in existence (Ghazoul & Sheil 2010) and provide a basic livelihood for many millions of people (IPCC 2007), so their importance cannot be overemphasised. Also very significantly, they absorb 1.02 billion tonnes of carbon (Mg C) from the atmosphere every year, approximately 25% of global forest uptake (Malhi 2010; Pan *et al.* 2011), and in so doing they reduce the rate of global warming by 15% (Malhi 2010, 2012), making their conservation a crucial element of current policies concerning climate change (IPCC 2007; Ghazoul & Sheil 2010).

We need a mechanistic understanding of the components of the tropical forest carbon cycle or 'budget' in order to translate carbon balance into future forest cover gains and losses under committed climate change (Malhi *et al.* 1999; IPCC 2007). Quantifying the carbon budget in terms of standard fluxes in (photosynthesis/productivity) and out (respiration) reveals how global atmospheric carbon dioxide (CO_2) levels are affected by forested areas and *vice versa* (Chambers *et al.* 2004; Clark 2004; Malhi *et al.* 2009; Malhi 2010). Additionally, ecosystem health, resilience and productivity are increasingly being measured in terms of carbon budgets and carbon gain (IPCC 2007; Zhang *et al.* 2009). However, until recently field data on forest biomass stocks and changes did not exist from enough tropical areas either to assess carbon budgets or to constrain modelling efforts adequately for a robust estimation (Marthews *et al.* 2012). This has resulted in much debate over whether tropical forests are a net source or sink of carbon (Chambers *et al.* 2001, 2004; Clark 2004; Luyssaert *et al.* 2008; Lewis *et al.* 2009; Houghton *et al.* 2009).

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

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

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

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

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

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

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

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 CO_2 concentration (taken as 285.2 ppmv CO_2 for 1850, IPCC 2007) followed by a *c*. 150 year period of increasing atmospheric CO_2 (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 CO_2 levels from global 'well-mixed' values (Park *et al.* 2007; Pan *et al.* 2011), seasonal cycles in CO_2 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 CO_2/m^{2}s gC/gN for C_3 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/m^2 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/m^2 for trees) (Clark *et al.* 2011).

Therefore, measured values for canopy height and *LAI* were accommodated by specifying appropriate values for the η_{sl} parameter from $\eta_{sl} = \frac{a_{wl} LAI_{eq}^{\frac{2}{3}}}{a_{ws} h_{eq}}$ (Table 1).

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

JULES was run at each study site under several parameter combinations in a full factorial design: (i) with the live stemwood coefficient η_{sl} set at the site-specific value (required to balance known canopy height and *LAI*) and at the default value (Table 1), (ii) with the canopy top-leaf N:C ratio N_{l0} set at the site-specific value and at the value corresponding to the Caxiuanã site (Table 1), (iii) with the proportion of *GPP* 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 explanation of this quantity), (iv) with the Plant Functional Type (PFT) parameters controlling the upper and lower bounds of photosynthesis set to default broadleaf values T_{low}=0°C, T_{upp}=36°C and default needleleaf values T_{low}=-10°C, T_{upp}=26°C (see Clark *et al.* 2011) to test PFT-specific effects (despite the lack of native needleleafs, this tests whether the (broadleaf) cloud forest vegetation behaves as if it has needleleaf temperature tolerances), (v) with the correct meteorological driving data set for the site (as described Appx. I) and with the driving data replaced with the data from Caxiuanã to test meteorology-specific effects. All analyses were done using R version 2.13.1 (R Development Core Team 2011).

RESULTS

With fractional cover held at 100% broadleaf, *JULES* predicted *LAI* to decrease to 0.1 m^2/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 4.5-5.0 m^2/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 Luyssaert *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_{l0} 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 Mg C ha^{-1} 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 Luyssaert *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_{l0} 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 Mg C ha^{-1} 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 Luyssaert *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_{l0} 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 Mg C ha^{-1} yr^{-1} at all sites. Increasing r_g by 0.10 had

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

Net primary productivity (Total *NPP*, the sum of above- and below-ground *NPP*). Apart from San Pedro, Manaus and the measurements of Aragão *et al.* (2009) at Tambopata, in the lower montane and lowland zones *JULES*'s predictions for overall mean *NPP* were higher than both measurements and what the Luyssaert *et al.* (2007) band and Clark *et al.* (2001b) would suggest, although still lower than the assumptions of the precipitation-based *MIAMI* model (Fig. 2d). *JULES* predicted declining *NPP* with decreasing temperature only in the montane zones, but again with too steep a decline in the upper montane zone (Fig. 2d). With Caxiuanã meteorology imposed, *NPP* rose to Caxiuanã levels at all sites confirming that simulated *NPP* is highly sensitive to meteorological conditions in the model. Changing η_{sl} or N_{l0} did not affect *NPP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *NPP* to approximately 10 Mg C ha^{-1} yr^{-1} at all sites. Increasing r_g by 0.10 had the effect of decreasing *NPP* by approximately 13.6% at all sites (and decreasing r_g by 0.10 increased *NPP* by the same amount).

Net ecosystem productivity (*NEP*). In the lower montane and lowland zones *JULES* simulated a small CO_2 sink at all sites broadly in line with the Malhi (2010) band, which agreed with measurements at all lowland and lower montane sites, though these sinks were smaller in magnitude than the suggested Luyssaert *et al.* (2007) sink (Fig. 2e). *JULES* predicted no consistent trend of *NEP* with elevation or temperature (Fig. 2e). With Caxiuanã meteorology imposed, *NEP* converged to Caxiuanã levels at all sites. Changing η_{sl} or N_{l0} did not affect *NEP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *NEP* to 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 approximately 11.6% at all sites (and decreasing r_g by 0.10 increased *NEP* by the same amount).

Carbon use efficiency (*CUE*, *=NPP/GPP*). Simulated values for overall mean fitted all measurement values except San Pedro fairly well, though with some overestimation (Fig. 2f). *JULES* predicted no consistent trend of *CUE* with elevation or temperature, notably not confirming the consistent increase with elevation expected from the results of Zhang *et al.* (2009) or Piao *et al.* (2010) (Fig.2f). With Caxiuanã meteorology imposed, *CUE* rose to Caxiuanã levels at all sites. Changing η_{sl} or N_{l0} did not affect *CUE*, but changing T_{low} and T_{upp} to needleleaf values had the effect of reducing mean *CUE* by approximately 0.04 across all sites. Increasing r_g by 0.10 had the effect of decreasing *CUE* by approximately 0.06 at all sites (and decreasing r_g by 0.10 increased *CUE* by the same amount).

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

DISCUSSION

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

Gross primary productivity (*GPP*)

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

GPP declines with decreasing radiative input (e.g. Zach *et al.* 2010, van de Weg *et al.* 2012; received SW radiation at Wayqecha was 103 W/m^2 in annual mean compared to 152 W/m^2 in the lowland sites) and radiation is one of the drivers of seasonality in at least our upper montane sites (Silva Espejo *et al.* 2012). This trend fully supports our simulations and therefore provides an alternative driver for the decline of *GPP* along our transect. It has also been noted that cloud cover increases the proportion of diffuse radiation and, because diffuse radiation penetrates vegetation canopies more efficiently than direct, this may increase photosynthesis (Graham *et al.* 2003; Mercado *et al.* 2007; Marthews *et al.* 2012), at least in cases where an increase in diffuse radiation is not associated with a decrease in total photosynthetically-active radiation *PAR* (van de Weg *et al.* 2012).

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

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

GPP is known to increase with the leaf N content of canopy leaves (via leaf RuBisCO content and therefore increased photosynthetic capacity V_{Cmax}, see e.g. Mercado *et al.* 2007, 2011; Clark *et al.* 2011 and review in Lloyd *et al.* 2010). A standard theory to explain lower *GPP* at higher elevations is therefore that montane forests are N-limited ecosystems (Bruijnzeel & Proctor 1995; Tanner *et al.* 1998), with reduced *GPP* occurring through direct effects (lower leaf N because of a reduced N mineralisation rate) and also indirect effects (e.g. decreased active *LAI* because of constrained leaf production or an altered vertical profile of leaf density in the canopy) (Moser *et al.* 2011). Leaf measurements however show that only Wayqecha has significantly lower foliar N than lowland values in this transect (Table 1, Salinas *et al.* 2011; Fisher *et al.* 2011; van de Weg *et al.* 2011, 2012) so N limitation can only be significant in our upper montane zone at most (cf. Moser *et al.* 2011 who also found little change in foliar N content with elevation in Ecuador). Although growth often appears to be N-limited (especially on landslide soil, Fetcher *et al.* 1996), it is not clear that montane forests are N limited in general (Bruijnzeel & Proctor 1995; Tanner *et al.* 1998; Benner *et al.* 2010; van de Weg *et al.* 2009, 2011; Lloyd *et al.* 2010). *JULES* does include leaf N effects in its calculations of *GPP* (which assume that V_{Cmax} at 25°C is directly proportional to canopy top-leaf N:C ratio N_{l0}, Table 1), however between-site differences in foliar N are slight in this transect (Table 1) which is why our *JULES* results were insensitive to variation in N_{l0}. From our results, therefore, we cannot conclude that leaf N content and N limitation are important drivers of *GPP* along this transect.

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

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

Autotrophic respiration (R_a)

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

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

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

Heterotrophic respiration (R_h)

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

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

Net primary productivity (*NPP*)

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

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

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

Net ecosystem productivity (*NEP*)

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

Carbon use efficiency (*CUE*)

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

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

Modelled *CUE* follows a daily cycle, increasing as *GPP* declines (and becoming undefined at night), but what about seasonal change? Monteith (1981) assumed minimal change within the growing season (over time periods of at least a few weeks) but *CUE* is also known to depend on successional stage (Mäkelä & Valentine 2001; Malhi *et al.* 2009; Landsberg & Sands 2011) indicating that *CUE* depends not only on 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 Amezquita *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, γ=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, γ=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 O_2/L to 7.7 mg O_2/L (Henry's Law, Appx. III; equivalent to 0.82% v/v O_2 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 O_2 held inside

leaf cells (Öpik 1980) and the slow rate of diffusion of O_2 both within cells and across leaf boundary layers will hamper replenishment from the atmosphere and may induce anaerobic respiration (fermentation). Reduced partial pressure of CO_2 can reduce photosynthesis, although this is partially offset by increased diffusivity of CO_2 and reduced photorespiration in C_3 plants (Bowman *et al.* 1999, Raich *et al.* 2006). Metabolically important thresholds for tropical montane vegetation are not well known (Friend & Woodward 1990), but dissolved oxygen concentrations below 4 mg/L are generally accepted to mean "only a few kinds of fish and insects can survive" in rivers in the USA (Behar 1997) and Carrera-Burneo & Gunkel (2003) suggested that 5 mg O_2/L was restrictive to ecosystem function in the Ecuadorean Andes. Equating the health thresholds of water courses to thresholds for cloud forest vegetation is speculative, but it seems reasonable to suggest that low pressure (Gale 1972; Iwabuchi *et al.* 1995; Bowman *et al.* 1999; Guo *et al.* 2008) may be causing some level of stress in cloud forest vegetation in addition to low temperature effects. Reduced diffusive and photosynthetic rates as a consequence of reduced atmospheric partial pressures would have a significant effect on the productivity and carbon balance of tropical montane forests (Friend & Woodward 1990; Körner 1998).

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

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

[6701 words excl. Abstract, Figures, Table & Appendices]

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843
844
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 (Avissar & 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 μmol CO_2 m^{-2} s^{-1} (left vertical axis) or equivalent mean annual flux in Mg
862 C ha^{-1} yr^{-1} (right axis; n.b. 1 Mg C/ha per year = 100 g C/m^2 per year = 0.264 μmol C/m^2 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 ▲, ±1SE), Aragão *et al.* (2009, ●, ±1SE), Malhi *et al.* (2009, Δ, ±1SE) and Girardin *et al.* (2010,
867 ○, ±1SE; *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 Luyssaert *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 Luyssaert *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

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

Fig. A1: The theoretical variation of r_g with *CUE* and for example values of Y_g and α (see text for definitions). Uncertainty in the value of Y_g does affect r_g (lines show values at Y_g=0.75 and grey bands show 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 theoretical direction of forest succession (Landsberg & Sands 2011 suggested that *CUE* decreases from ≈0.5 in young to ≈0.3 in mature forests, and this may be combined with an increase in carbon storage from $\alpha\approx0$ in 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 estmate of *JULES* (Cox 2001, Clark *et al.* 2011) may be understood as a maximal value for vegetation with negligible storage (high growth), $CUE<0.6$ and Y_g=0.75.

TABLE CAPTIONS

Table 1: Characteristics of the six study sites. Values for V_{Cmax25}, 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_{l0}. For reference, the *JULES* default values for broadleaf vegetation are N_{l0}=0.046 g N/g C and V_{Cmax25}=36.8 µmol CO_2/m^2s, so the constant of proportionality $n_e = V_{Cmax25}/N_{l0}$ = 0.0008 mol CO_2/m^2s · 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±1SE except for those from Metcalfe *et al.* (2010) which are mean±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/m^2 per year and, when considered over sub-daily time periods, = 0.264 µmol C/m^2s = 0.264 µmol CO_2/m^2s (and when converted to biomass units - i.e. g dry matter rather than g C - these productivities may be thought of as growth rates).

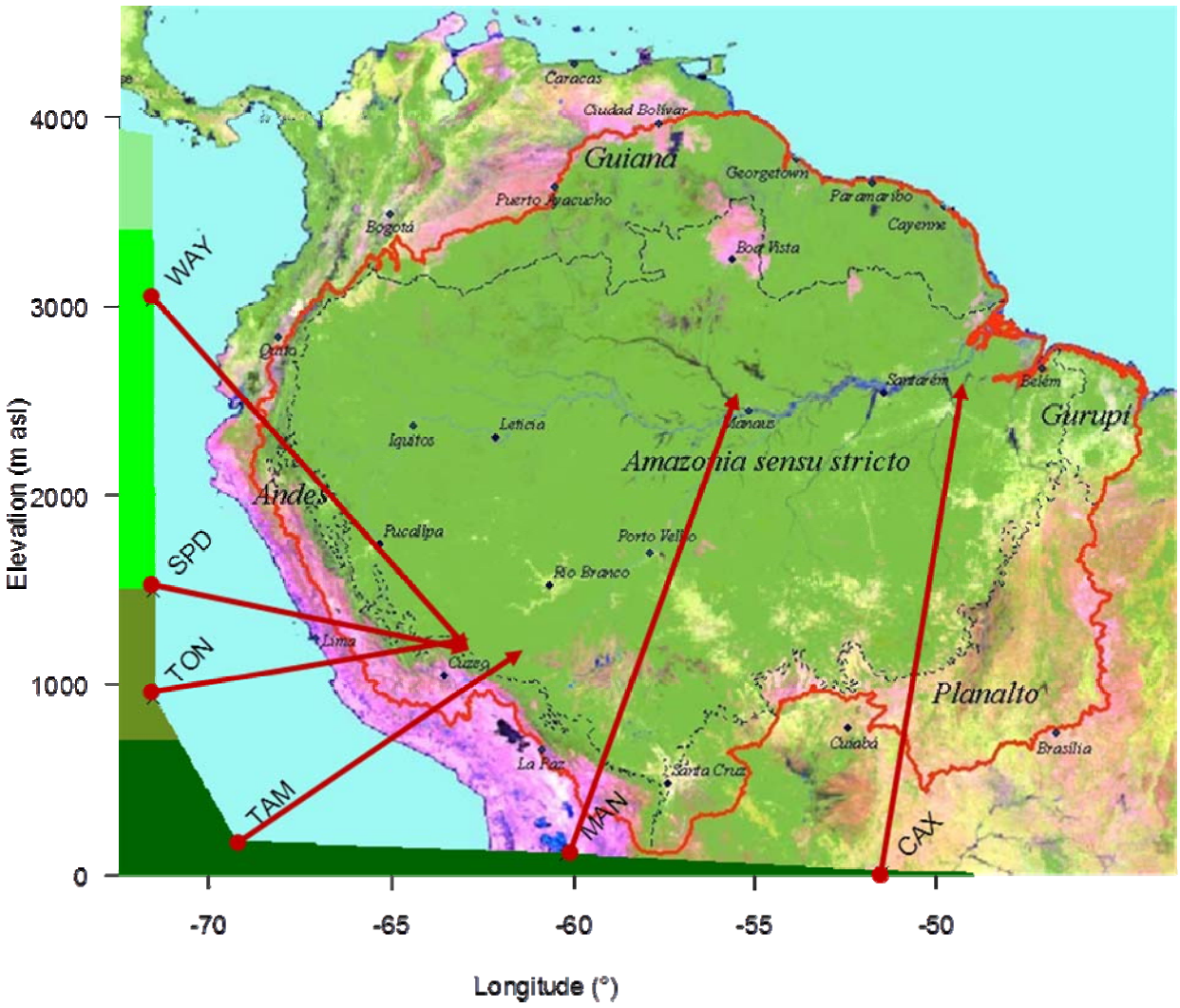
Caracas
Ciudad Bolivar
Guiana
Georgetown
Puerto Ayacucho
Paramaribo
Cayenne
Bogotá
Boa Vista
WAY
Quito
Santarém
Belém
Gurupi
Leticia
Iquitos
Manaus
Amazonia sensu stricto
Andes
SPD
Pucallpa
Porto Velho
Rio Branco
TON
Lima
Cuzco
Planalto
Cuiabá
Brasilia
La Paz
Santa Cruz
TAM
MAN
CAX
Elevation (m asl)
4000
3000
2000
1000
0
-70
-65
-60
-55
-50
Longitude (°)

Fig. 1:

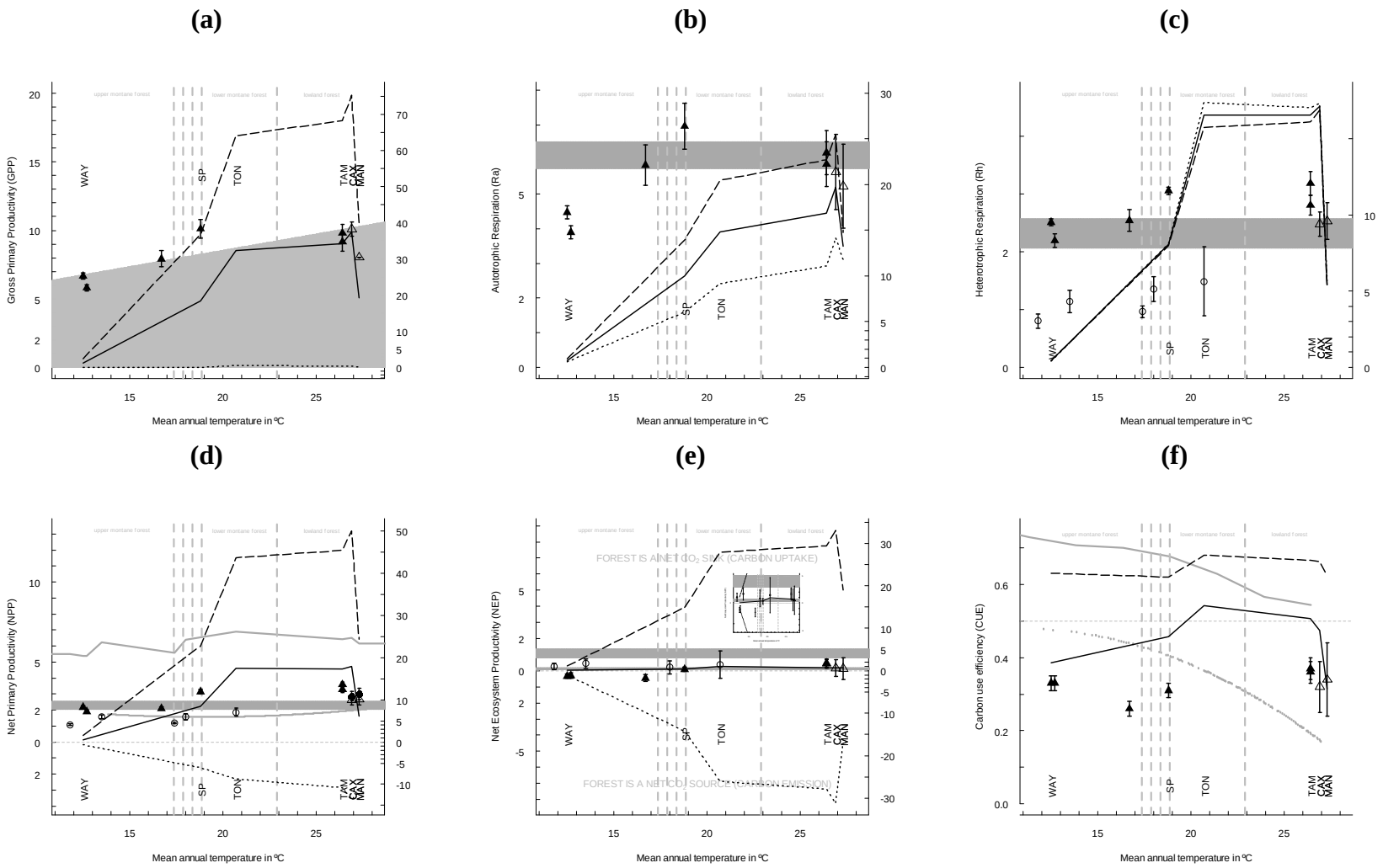
(a)
(b)
(c)
(d)
(e)
(f)
Gross Primary Productivity (GPP)
Autotrophic Respiration (Ra)
Heterotrophic Respiration (Rh)
Net Primary Productivity (NPP)
Net Ecosystem Productivity (NEP)
Carbon use efficiency (CUE)
Mean annual temperature in ºC
upper montane forest
lower montane forest
lowland forest
WAY
SP
TON
TAM
CAX
MAN
FOREST IS A NET CO2 SINK (CARBON UPTAKE)
FOREST IS A NET CO2 SOURCE (CARBON EMISSION)

Fig. 2:

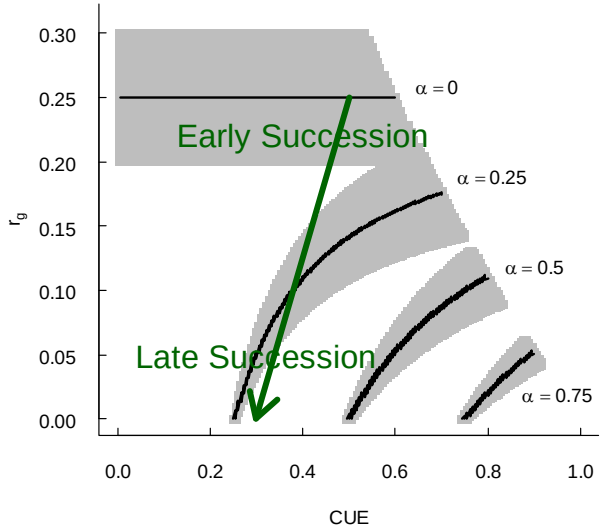
0.30
0.25
0.20
0.15
0.10
0.05
0.00
r_g
α = 0
Early Succession
α = 0.25
α = 0.5
Late Succession
α = 0.75
0.0
0.2
0.4
0.6
0.8
1.0
CUE

Fig. A1:

Table 1:

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_{l0} (g N/g C)	Maximum rate of carboxylation of RuBisCO at 25°C V_{Cmax25} (µmol CO_2/m^2s)	$n_e = V_{Cmax25}/N_{l0}$ (mol $CO_2/m^2s \cdot$ g C/g N)
Wayqecha [n,p,r,t,u]	Intensive census plot WAY-01 (WA_3000) at the Estación Biológica Wayqecha	13º 11' 25.45" S	71º 35' 13.56" W	Cusco, Peru	Cloud forest / upper montane forest	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	13º 2' 56.89" S	71º 32' 12.64" W	Cusco, Peru	Upper/lower montane transition zone	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	12º 57' 16.92" S	71º 33' 12.75" W	Cusco, Peru	Lower montane forest	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	12º 50' 18.59" S	69º 17' 45.65" W	Madre de Dios, Peru	Lowland terra firme forest	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_{l0} (g N/g C)	Maximum rate of carboxylation of RuBisCO at 25°C V_{Cmax25} (µmol CO_2/m^2s)	$n_e = V_{Cmax25}/N_{l0}$ (mol $CO_2/m^2s \cdot$ 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	2º 35' 21.08" S 60º 6' 53.63" W	Amazonas, Brazil	Lowland terra firme forest	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
Caxiuanã Tower plot [a,i,j,k,s]	Intensive census plot CAX-06 at the Estação Científica Ferreira Penna	1º 43' 11.26" S 51º 27' 29.45" W	Pará, Brazil	Lowland terra firme forest	12 [i]	26.9 [j]	2314 [j]	35 [d,j]	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), [f] Quesada (2008), [g] Fyllas *et al.* (2009), [h] Patiño *et al.* (2009), [i] Shuttle Radar Topography Mission (SRTM) elevations from Anderson *et al.* (2009) with canopy height subtracted, [j] 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 m^2/m^2 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 (Mg C ha^{-1} 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) *GPP*	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 Esperanza plot	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]
Trocha Union plot 3 (TRU-03)			3.05±0.47 [e]	4.11±0.26 [e]	1.06±0.73 [e,d]	
Trocha Union plot 4 (TRU-04)			4.31±0.74 [e]	5.98±0.39 [e]	1.67±1.13 [e,d]	
Trocha Union plot 7 (TRU-07)			3.66±0.38 [e]	4.50±0.20 [e]	0.84±0.58 [e,d]	
Trocha Union plot 8 (TRU-08)			5.14±0.80 [e]	5.97±0.73 [e]	0.83±1.53 [e,d]	
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 Amezquita *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)