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

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Summary

- Why do forest productivity and biomass decline with elevation? To address this question, research to date generally has focused on correlative approaches describing changes in woody growth and biomass with elevation.
- We present a novel, mechanistic approach to this question by quantifying the autotrophic carbon budget in 16 forest plots along a 3300 m elevation transect in Peru.
- Low growth rates at high elevations appear primarily driven by low gross primary productivity (GPP), with little shift in either carbon use efficiency (CUE) or allocation of net primary productivity (NPP) between wood, fine roots and canopy. The lack of trend in CUE implies that the proportion of photosynthate allocated to autotrophic respiration is not sensitive to temperature. Rather than a gradual linear decline in productivity, there is some limited but non-conclusive evidence of a sharp transition in NPP between submontane and montane forests, which may be caused by cloud immersion effects within the cloud forest zone. Leaf-level photosynthetic parameters do not decline with elevation, implying that nutrient limitation does not restrict photosynthesis at high elevations.
- Our data demonstrate the potential of whole carbon budget perspectives to provide a deeper understanding of controls on ecosystem functioning and carbon cycling.

Introduction

Wet tropical montane elevation transects can provide valuable insights into the influence of environmental controls, and in particular temperature, on ecosystem productivity and carbon cycling (Malhi *et al.*, 2010). By providing a strong contrast in environmental conditions in a small biogeographical area and a constant 12-month growing season, they can help us understand the long-term effects of acclimation and community turnover on ecosystem function.

Tropical montane forests have usually been observed to have lower aboveground productivity and biomass than nearby lowland forests (Raich *et al.*, 2006; Girardin *et al.*, 2014a; Spracklen &

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

We present a new dataset and analysis to address this question using a series of measurements of all the major components of

the autotrophic carbon budget of forest ecosystems in a number of forest plots along an elevation gradient in Peru. This requires quantification of the major components of gross primary productivity (GPP, the total photosynthesis per unit ground area), net primary productivity (NPP, the rate of production of new biomass) and autotrophic respiration (R_a, the use of photosynthate by the plant's own metabolism). Such an approach facilitates a quantitative and mechanistic understanding of the relative importance of leaf-, whole plant- and stand-level processes in determining the growth rates and biomass of forest ecosystems. The key components are illustrated in Fig. 1.

From an autotrophic carbon budget perspective, the primary mechanisms that could cause a reduction in growth rates and biomass with increasing elevation are: limitation of rates of photosynthesis and thus declines in GPP; relative increases in R_a and resultant decreases in carbon use efficiency (CUE), which is the ratio NPP : GPP; shifting allocation or storage of NPP away from woody biomass and into canopy or fine roots; or increases in tree mortality rates (decreases in wood residence time) and thus decreases in equilibrium aboveground biomass (Fig. 1). We review each of these potential mechanisms in turn.

Decline in net photosynthesis

A decline in canopy net photosynthesis could result from either a decline in CO_2- and light-saturated leaf photosynthetic capacity, a decline in realized rates of leaf-level photosynthesis below capacity, or through a decline in canopy leaf area. These various declines could occur because of a number of different abiotic drivers, such as decreases in temperature, water availability, atmospheric CO_2, soil nutrient availability and light. Reductions in temperature could decrease metabolic activity and decrease photosynthetic rates below optimum levels; such temperature

dependence is implicit in many ecosystem models. On the other hand, photosynthesis may acclimate to ambient mean temperatures, resulting in little temperature dependence in ecosystem productivity (Lloyd & Farquhar, 2008). The decrease in the partial pressure of CO_2 in air that occurs with increasing elevation could decrease photosynthetic rates; however, research to date suggests that this is offset by the increased diffusivity at high elevations and reduced partial pressure of O_2, resulting in little net sensitivity of photosynthesis to air pressure (Cordell et al., 1998, 1999). High soil water content and low temperatures with increasing elevation can reduce nitrogen mineralization rates and affect plant available nutrients (Benner et al., 2010), leading to decreases in the supply rate of foliar nitrogen and phosphorus necessary for photosynthesis, although this can be confounded by changes in leaf construction costs and lifetime (Cordell et al., 1998; van de Weg et al., 2009; Wittich et al., 2012). Reduced light availability, occurring as a function of frequent cloud cover, can lead to reductions in realised photosynthetic rates below capacity. There is evidence from montane forests that cloud cover, as well as the accompanying leaf wetting events, can result in reduced photosynthesis rates (Letts et al., 2010; Goldsmith et al., 2013). Finally, declines in GPP can also result from decreases in canopy leaf area, which may be a response to nutrient supply limitation (Weaver & Murphy, 1990; Kitayama & Aiba, 2002; Moser et al., 2007).

Changes in carbon use efficiency

Relative increases in R_a at high elevation, and resultant decreases in CUE, may also account for observed decreases in growth and biomass. This could occur if there was increased metabolic investment in processes not directly associated with NPP, such as protection against cold damage, or defence against herbivores or pathogens (although such biotic pressures are expected to decrease with elevation; Metcalfe et al., 2013), or repair of damaged tissues. Although some individual components of respiration have been quantified (e.g. stem respiration; Zach et al., 2009; Robertson et al., 2010), studies of total autotrophic respiration as a function of elevation in tropical forests are exceedingly rare (Leuschner et al., 2013). A common biosphere model assumption is that autotrophic respiration will increase disproportionately with increasing temperature, leading to a decrease in CUE.

Shifting allocation of NPP

Although aboveground NPP has often been observed to decline with elevation (Marrs et al., 1988; Weaver & Murphy, 1990; Girardin et al., 2010; Moser et al., 2011) insights into belowground NPP, and thus total NPP, remain limited. Many studies have noted an increase in root biomass with increasing elevation (Kitayama & Aiba, 2002; Moser et al., 2008; Girardin et al., 2013), but how this relates to root NPP depends on understanding fine root lifetimes. Few studies have quantified root NPP; some have observed no strong patterns with elevation (Girardin et al., 2013) whereas others have observed an increase with
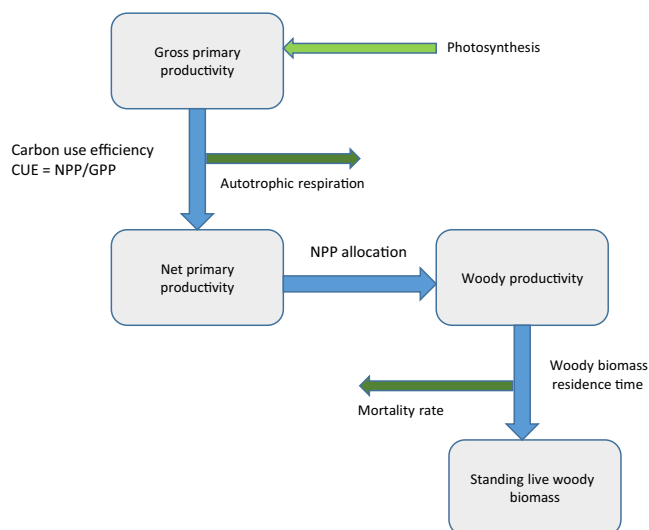

Fig. 1 The pathway leading from the conversion of photosynthate to standing live woody biomass provides a framework for understanding the processes which can ultimately lead to reduced growth and standing biomass in tropical montane forests as compared with tropical lowland forests. Adapted from Malhi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

elevation (Röderstein *et al.*, 2005; Moser *et al.*, 2011). Nevertheless, it has been hypothesized that declining aboveground NPP is compensated for by a concomitant change in belowground NPP (Leuschner *et al.*, 2007). The observed increase in fine root production along certain elevation transects and the more universal increase for fine root biomass have been proposed as compensation for low nutrient availability.

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

We present a unique dataset where we have conducted intensive monitoring of the carbon cycle for multiple years across a series of 16 plots along a 3300-m elevation transect in Peru. This provides an opportunity to understand how the carbon dynamics of tropical forests vary with elevation, as well as to apply the process-based framework described earlier to generate a quantitative comparison of the relative importance of various factors influencing growth rates and biomass among forests along this elevation transect. These sites are also the location of the CHAMBASA project (Y. Malhi *et al.*, unpublished), which explores the relationships between plant traits and ecosystem function; hence this study presents and explains the benchmark productivity data for various CHAMBASA companion papers (Asner *et al.*, 2016; Bahar *et al.*, 2016; Chavana-Bryant *et al.*, 2016; Goldsmith *et al.*, 2016). It also provides a consistent dataset suitable for testing and aiding ecosystem model development. For this specific paper, for our study system, we ask the following questions: how do key stand-level aspects of the forest carbon cycle, such as GPP, NPP, CUE and NPP allocation to canopy, wood and fine roots, vary with elevation? Is the decline in woody growth rates with increasing elevation in this transect determined by changes in GPP, carbon use efficiency (CUE) or allocation of NPP? Are trends with elevation on this transect linear or is there evidence for abrupt transitions? If the latter, what factors may be causing such an abrupt transition? Are declines in aboveground biomass with elevation on this transect mainly determined by changes in growth rates or changes in mortality rates?

Materials and Methods

Field sites

We collected several years (between 2007 and 2015) of carbon cycling data from 16 1-ha plots along an elevation gradient in Peru, ranging from the high elevation tree line (*c.* 3500 m above sea level, asl), through the cloud forest-submontane transition (1000–1750 m asl) and into the Amazon lowlands (100–220 m asl). Site descriptions are summarized in Table 1 and provided for some sites in more detail in site-specific papers (del Aguila-Pasquel *et al.*, 2014; Girardin *et al.*, 2014a,b; Huaraca Huasco *et al.*, 2014; Malhi *et al.*, 2014). The montane sites are concentrated in the Kosñipata Valley, and the submontane plots either in the adjacent

Tono Valley (TON-01) or in the Pantiacolla front range of the Andes (PAN-02 and PAN-03). These sites have been the subject of on-going, multidisciplinary research by the Andes Biodiversity and Ecosystems Research Group (ABERG: www.andesconservation.org; Malhi *et al.*, 2010). The cloud climatology of this valley is described by Halladay *et al.* (2012) and the water budget has been closed by Clark *et al.* (2014).

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

For eight of these plots, all of the major components of net primary productivity (NPP) and autotrophic plant respiration (R_a) were measured, enabling estimation of gross primary productivity (GPP) and carbon use efficiency (CUE); for the remaining eight, only the major components of NPP have thus far been assessed (Table 2). Data collection dates vary between plots, spanning over 6 yr (2007–2012) in four plots (TAM-05, TAM-06, WAY-01, SPD-02), 4 yr (2009–2012) in four plots (SPD-01, ESP-01, ALP-01, ALP-30), 3 yr (2007–2009) in five plots (TON-01, TRU-03, TRU-04, TRU-07, TRU-08) and 2 yr (2013–2015) in three plots (ACJ-01, PAN-02, PAN-03), representing 61 plot-years of intensive monthly data collection efforts in total (Table 1).

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

Field methods

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

The GEM protocol involves measuring and summing all major components of NPP and autotrophic respiration on monthly or seasonal timescales. For NPP, this includes canopy litterfall (NPP$_{litterfall}$) at biweekly intervals, estimates of leaf loss to herbivory (NPP$_{herbivory}$) from scans of litterfall, aboveground woody productivity of all medium-large (> 10 cm diameter at breast height, DBH) trees in the plot (NPP$_{ACW\geq10\ cm}$) via

Table 1 Environmental characteristics of 1 ha study sites occurring along a 2800 m above sea level (asl) tropical montane elevation transect; na, data not available

	Allpahuayo A	Allpahuayo C	Tambopata V	Tambopata VI	Pantiacolla 2	Pantiacolla 3	Tono	San Pedro 1500 m
RAINFOR site code	ALP11/ALP12	ALP30	TAM05	TAM06	PAN02	PAN03	TON01	SPD02
Latitude	−3.95	−3.9543	−12.8309	−12.8385	−12.64957	−12.6383	−12.9592	−13.0491
Longitude	−73.4333	−73.4267	−69.2705	−69.296	−71.26267	−71.2745	−71.5658	−71.5365
Elevation (m asl)	120	150	223	215	595	848	1000	1527
Slope (°)	1.4	1.5	4.5	2.2	na	na	8	27.1
Aspect (°)	na	196	186	169	na	na	na	125
Solar radiation (GJ m^{-2} yr^{-1})	na	5.22	na	4.80	3.82	na	na	4.08
Mean annual air temperature (°C)	25.2	25.2	24.4	24.4	23.5	21.9	20.7	18.8
Precipitation (mm yr^{-1})	2689	2689	1900	1900	2366	2835	3087	5302
Soil moisture (%)	26.8	10.8	21.8	35.5	na	na	39.8	37.3
Soil type	Alisol/Gleysol	Arenosol	Cambisol	Alisol	Plinthosol	Alisol	Cambisol	Cambisol
P_{total} (mg kg^{-1})	125.6	37.6	256.3	528.8	na	na	751	1630.7
Total nitrogen (N, %)	0.10	0.08	0.16	0.17	na	na	0.42	0.90
Total carbon (C, %)	1.19	1.13	1.51	1.2	na	na	5.01	13.6
Soil C stock (Mg C ha^{-1} from 0 to 30 cm)	93	16	44	38	na	na	79	94
Soil organic layer depth (cm)	12	10	13	37	na	na	35	30

	San Pedro 1750 m	Trocha Union VIII	Trocha Union VII	Trocha Union IV	Esperanza	Wayqecha	Trocha Union III	Açjanaco
RAINFOR site code	SPD01	TRU08	TRU07	TRU04	ESP01	WAY01	TRU03	ACJ01
Latitude	−13.0475	−13.0702	−13.0733	−13.1055	−13.1751	−13.1908	−13.1097	−13.1469
Longitude	−71.5423	−71.5559	−71.5588	−71.5893	−71.5948	−71.5874	−71.5995	−71.6323
Elevation (m asl)	1776	1885	2020	2758	2863	3045	3044	3537
Slope (°)	30.5	38.8	18	21.2	27.3	30	22.4	36.3
Aspect (°)	117	158	n/a	118	302	112	114	104
Solar radiation (GJ m^{-2} yr^{-1})	4.36	3.96	n/a	3.49	n/a	3.51	n/a	4.6
Mean annual air temperature (°C)	17.4	18.0	17.4	13.5	13.1	11.8	11.8	9.0
Precipitation (mm yr^{-1})	5302	2472	1827	2318	1560	1560	1776	1980
Soil moisture (%)	37.6	9.7	15.5	37.3	24.3	23.1	41.5	n/a
Soil type	Cambisol	Cambisol	Cambisol	Umbrisol	Umbrisol	Umbrisol	Umbrisol	Cambisol
P_{total} (mg kg^{-1})	1071.1	496	562.8	746.8	980.8	1413.6	787.3	n/a
Total N (%)	1.20	0.81	1.23	1.99	1.48	0.88	1.55	n/a
Total C (%)	22.7	14.25	28.66	28.33	28.59	19.33	27.22	n/a
Soil C stock (Mg C ha^{-1} from 0 to 30 cm)	75.6	97.1	83.7	289	133.9	231.6	82.4	n/a
Soil organic layer depth (cm)	32	30	80	20	50	36	36	n/a

Table 2 Components of the carbon cycle as measured in 1-ha study sites occurring along a 2800 m tropical montane elevation transect; where appropriate, values are means $\pm$ 1 SE; $NPP_{Herbivory}$, NPP_{ACW}, and $NPP_{BranchTurnover}$ are estimated; all NPP and respiration component measurements are in Mg C ha^{-1} yr^{-1}, NPP allocation fractions are unitless, aboveground biomass values are in Mg C ha^{-1}, and residence time is in years

	Allpahuayo A	Allpahuayo C	Tambopata V	Tambopata VI	Pantiacolla 2	Pantiacolla 3	Tono	San Pedro 1500 m
GPP	39.05 ± 4.59	41.88 ± 4.60	35.47 ± 3.55	34.47 ± 3.53	32.41 ± 4.16	26.90 ± 3.57	28.27 ± 2.58	38.57 ± 4.13
NPP	12.21 ± 0.96	14.27 ± 0.95	14.28 ± 0.83	11.60 ± 0.59	11.34 ± 0.66	9.42 ± 0.64	9.90 ± 0.90	12.08 ± 0.49
CUE	0.31 ± 0.04	0.34 ± 0.04	0.4 ± 0.05	0.34 ± 0.04			0.35 ± 0.05	0.31 ± 0.04
NPP_{Canopy} Allocation	0.38 ± 0.10	0.45 ± 0.07	0.43 ± 0.04	0.49 ± 0.06	0.48 ± 0.04	0.48 ± 0.05	0.55 ± 0.06	0.50 ± 0.03
NPP_{Wood} Allocation	0.37 ± 0.04	0.30 ± 0.03	0.24 ± 0.02	0.33 ± 0.03	0.24 ± 0.02	0.26 ± 0.03	0.21 ± 0.02	0.35 ± 0.03
NPP_{Root} Allocation	0.25 ± 0.03	0.25 ± 0.03	0.32 ± 0.05	0.18 ± 0.02	0.16 ± 0.03	0.14 ± 0.05	0.24 ± 0.08	0.16 ± 0.03
NPP_{Canopy}	4.70 ± 0.86	6.42 ± 0.81	6.15 ± 0.35	5.64 ± 0.41	4.78 ± 0.46	3.97 ± 0.33	5.41 ± 0.36	5.99 ± 0.22
NPP_{Leaf}	2.68 ± 0.66	4.05 ± 0.56	4.03 ± 0.27	3.71 ± 0.39	3.53 ± 0.29	3.04 ± 0.29	3.48 ± 0.21	4.12 ± 0.18
$NPP_{Herbivory}$	0.50 ± 0.12	0.76 ± 0.11	0.76 ± 0.05	0.70 ± 0.07	0.62 ± 0.05	0.53 ± 0.05	0.66 ± 0.04	0.66 ± 0.03
NPP_{ACW}	2.54 ± 0.25	2.76 ± 0.28	2.18 ± 0.22	2.77 ± 0.28	2.78 ± 0.28	2.43 ± 0.24	1.38 ± 0.14	3.04 ± 0.30
$NPP_{Branch\ turnover}$	1.42 ± 0.14	1.01 ± 0.10	0.95 ± 0.10	0.50 ± 0.05	0.65 ± 0.07	0.57 ± 0.06	0.40 ± 0.06	0.52 ± 0.07
$NPP_{Coarse\ root}$	0.53 ± 0.08	0.58 ± 0.08	0.46 ± 0.07	0.58 ± 0.08	0.72 ± 0.04	0.63 ± 0.03	0.29 ± 0.04	0.64 ± 0.09
$NPP_{Fine\ root}$	3.02 ± 0.29	3.50 ± 0.38	4.54 ± 0.71	2.11 ± 0.31	1.80 ± 0.37	1.29 ± 0.48	2.42 ± 0.81	1.89 ± 0.30
R_a	24.92 ± 4.48	27.46 ± 4.51	20.5 ± 3.45	20.27 ± 3.38				26.63 ± 4.11
R_{Leaf}	8.92 ± 3.00	11.35 ± 3.50	8.86 ± 2.84	6.43 ± 2.07				7.06 ± 2.48
R_{Stem}	9.63 ± 3.05	8.11 ± 2.55	5.43 ± 1.77	7.62 ± 2.48				8.91 ± 2.82
$R_{Rhizosphere}$	4.44 ± 0.92	6.38 ± 0.93	5.07 ± 0.61	4.62 ± 0.57				8.79 ± 1.36
$R_{Coarse\ root}$	1.93 ± 0.98	1.62 ± 0.83	1.14 ± 0.59	1.60 ± 0.82				1.87 ± 0.95
Aboveground biomass	130	89	142	112	97	67	92	107
Residence time	51	32	65	40	35	28	66	35

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

GPP, gross primary productivity; NPP, net primary productivity; CUE, carbon use efficiency. The three allocation variables indicate the fraction of NPP allocated to canopy, wood and fine roots. The various subscripts of NPP indicate the amount of NPP allocated to total canopy, to leaves, lost to leaf herbivory, allocated to ACW (aboveground coarse wood production), to branch turnover, to coarse root production and to fine root production. The various subscripts of R indicate the total autotrophic respiration R_a, and the amounts of this respiration in leaves, the woody stem, rhizosphere and coarse roots.

three-monthly measurement of dendrometers, as well as a full annual census of all trees, woody productivity of small trees (2–10 cm DBH; $NPP_{ACW\ <\ 10\ cm}$) in annually censused subplots, the turnover of branches on live trees ($NPP_{branch\ turnover}$) by conducting three-monthly transect censuses of freshly fallen branch material from live trees, fine root productivity ($NPP_{fine\ root}$) from ingrowth cores installed and harvested every three months, and estimation of coarse root productivity ($NPP_{coarse\ root}$) by applying a multiplying factor to aboveground woody productivity. Leaf area index (LAI) is calculated from photographs taken with a

digital camera and a hemispherical lens and processed with CAN-EYE software (INRA 2010) (Weiss & Baret, 2014) in a subset of the plots (TAM-05, TAM-06, ALP-01, ALP-30, SPD-01, SPD-02, ESP-01, WAY-01) every other month.

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

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

$$CUE = NPP/GPP = NPP/(NPP + R_a) \qquad Eqn\ 1$$

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

Somewhat inevitably, any estimate of NPP may be biased towards underestimation because it neglects several small NPP terms, such as NPP lost as volatile organic emissions, nonmeasured litter trapped in the canopy, or dropped from understorey plants below the litter traps (Clark et al., 2001). At a site in central Amazonia, volatile emissions were found to be a minor component of the carbon budget (0.13 ± 0.06 Mg C ha^{-1} yr^{-1}; Malhi et al., 2009). For belowground NPP, the allocation to root exudates and to mycorrhizae is disregarded. In effect, we treat root exudation and transfer to mycorrhizae as rhizosphere autotrophic respiration rather than as NPP, which could

potentially impact our CUE estimates. Recent estimates from our lowland plots estimate that forests in less fertile sites increased C allocation to the (nonroot) rhizosphere by up to c. 2.2 ± 1.4 Mg C ha^{-1} yr^{-1} compared with fertile sites, an indication that root exudate fluxes are < 7% of GPP (C. E. Doughty et al., unpublished data). Given that these exudates are labile and rapidly respired by mycorrhizae and soil microfauna in the rhizosphere, this exudate NPP term is very similar to fine root autotrophic respiration in terms of carbon cycling.

Many of these measurements have potential systematic uncertainties: we assign sampling or systematic uncertainties to each measurement, and rigorously propagate the uncertainties through our calculations. In particular, it is important to note that our calculation of NPP is based on the summation of four independent measurements (litterfall, tree growth, fine root production and branchfall) and our estimate of GPP is based on the summation of seven independent measurements (the components of NPP, as well as leaf, stem and rhizosphere measurements). Although some of these terms can carry substantial measurement and scaling uncertainties, if the uncertainties are independent for each measurement, these uncertainties propagate by quadrature to result in a manageable uncertainty in the final sum NPP or GPP (Methods S1). For example, although there may be significant uncertainty in our measurement of root productivity or in our scaling of stem respiration, this does not result in unmanageable uncertainties in our estimates of GPP. Hence, a carbon summation measurement comprised of seven independent measurements may potentially be more accurate than an eddy covariance-based estimate comprised of one measurement.

This ecosystem-level approach was complemented by a leaf-level approach to understanding variation in leaf physiological traits. These leaf gas exchange measurements are reported in detail in Bahar et al. (2016) and summarized briefly here. Over the period July–October 2011, measurements were made using a portable photosynthesis system (Licor 6400XT; Li-Cor BioSciences, Lincoln, NE, USA) on 300 canopy trees (c. 1150 sun-exposed leaves) of c. 193 species along the transect, along 12 plots along the full elevation gradient (typically 10–14 species per plot). For each tree, branches were collected from the top canopy position, recut under water to ensure xylem water continuity, before starting gas exchange measurements on the most recently fully expanded leaves. CO_2 response curves of light-saturated photosynthesis ($A \leftrightarrow C_i$ curves) (with PAR at 1800 μmol photons m^{-2} s^{-1}) were performed within 30–60 min of branch detachment, with CO_2 concentrations inside the 6 cm^2 reference chamber ranging in a stepped sequence from 35 to 2000 μmol mol^{-1}. Block temperatures within the chamber were set to 28°C in the lowlands and 25°C in the highlands (ambient mean leaf temperatures at time of measurement ranged between typically 30°C in the lowlands and 23°C in the highest plots). The resultant $A \leftrightarrow C_i$ curves were fitted following the model described by Farquhar et al. (1980) in order to calculate V_{cmax} and J_{max} on a leaf area basis. Rates of CO_2 exchange were corrected for diffusion through the gasket of the LI-6400 leaf chamber (Bruhn et al., 2002) before calculation of V_{cmax} and J_{max}. Any variation in mesophyll conductance is not accounted for in these

estimates. Fitted parameters were scaled to a reference temperature of 25°C using activation energies of 64.8 and 37.0 kJ mol^{-1} for V_{cmax} and J_{max}, respectively (Farquhar *et al.*, 1980). The Michaelis constants of Rubisco for CO_2 (K_c) and O_2 (K_o) at a reference temperature 25°C were assumed to be 404 µbar and 248 mbar, respectively (von Caemmerer *et al.*, 1994); these values were adjusted to actual leaf temperatures assuming activation energies of 59.4 and 36 kJ mol^{-1} for K_c and K_o, respectively (Farquhar *et al.*, 1980. During measurements, RH varied between 60 and 70%. Leaf samples were then dried and analysed for nitrogen and phosphorus content at the Australian National University, Canberra.

Analysis framework

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

$$NPP = GPP \times \frac{NPP}{GPP} \qquad \text{Eqn 2}$$

i.e. NPP = GPP × CUE

$$NPP_{ACW} = GPP \times \frac{NPP}{GPP} \times \frac{NPP_{ACW}}{NPP} \qquad \text{Eqn 3}$$

i.e. NPP$_{ACW}$ = NPP × woody allocation

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

$$AGB = GPP \times \frac{NPP}{GPP} \times \frac{NPP_{ACW}}{NPP} \times \tau_W \qquad \text{Eqn 4}$$

Results

Climate

Figure 2 shows climatic characteristics as a function of elevation. Temperature demonstrates a steady linear decline with elevation, consistent with an adiabatic lapse rate of $-4.4°C$ km^{-1} ($P < 0.001$, $r^2 = 0.99$; Fig. 2a). Total annual precipitation is high along the entire transect (always > 1500 mm) and has a strong peak at mid-elevations (1000–2000 m asl) where night-time cool
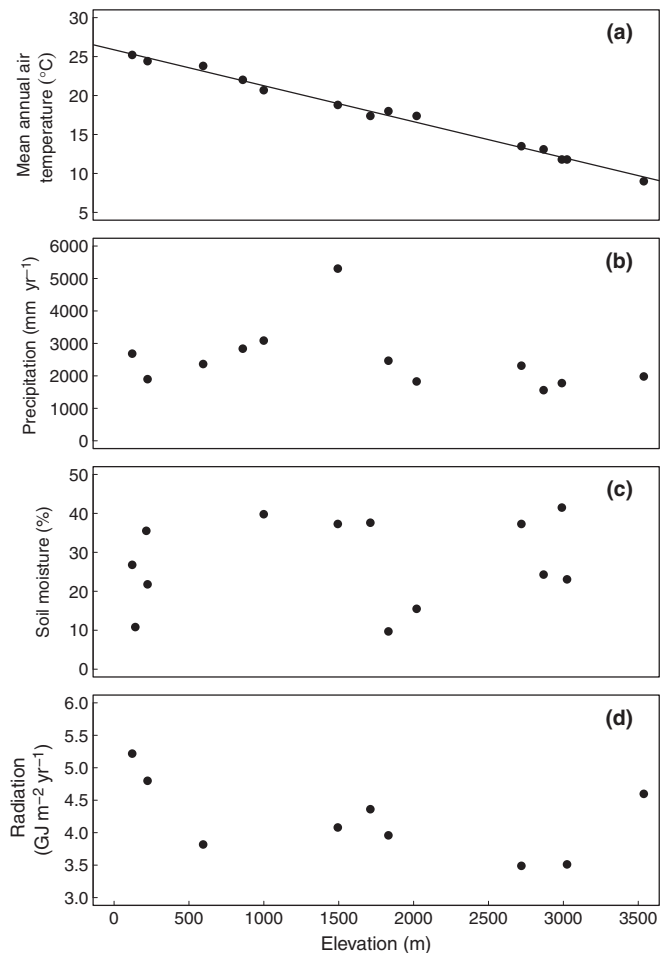

Fig. 2 Variation in climate along the 3300 m above sea level tropical montane elevation transect, including (a) mean annual air temperature, (b) direct precipitation, (c) soil moisture and (d) solar radiation.

katabatic winds from the Andean slopes collide with moist Amazonian air to generate a stationary rainfall front (Killeen & Solorzano, 2008) (Fig. 2b). Soil moisture shows no trend with elevation ($P > 0.05$; Fig. 2c); it is largely aseasonal along the entire transect, with moderate seasonality only observed in two of the lowland plots (TAM-05 and TAM-06; Malhi *et al.*, 2014) and at the uppermost plots (WAY-01 and ACJ-01; Girardin *et al.*, 2014a). In this generally wet transect, spatial variation in annual mean soil moisture content seems to be determined by soil textural properties rather than by variation in precipitation regimes. Solar radiation declines at mid-elevations, associated with a higher frequency of both cloud occurrence and cloud immersion (Halladay *et al.*, 2012), and then rises again at the uppermost, treeline plot (ACJ-01). Cloud immersion is particularly frequent in June–August, the austral winter, when temperatures are slightly lower and the cloud base is lower (Halladay *et al.*, 2012).

Autotrophic carbon budget

The major components of GPP and NPP for the studied plots are shown in Table 2, with key aspects plotted as a function of

elevation in Fig. 3. In all cases, we applied an ANCOVA (response~elevation*location), where location is a categorical variable indicating 'above' or 'below' the zone of transition from submontane to cloud forest at 1600 m asl). We then applied stepwise model reduction and provide the best fit lines for each panel. Thus, the outcomes include lines with different slopes (i.e. interaction), a single line with a slope (i.e. no interaction), or horizontal line(s) at different or the same intercept (i.e. no slope). This approach enabled us to evaluate evidence for a sharp transition at cloud base. We plot all data against elevation as a purely geographical variable free of *a priori* assumptions; in Fig. S2, we plot against temperature as a potential response variable; the resulting significance statistics are almost identical.

We only collected data on autotrophic respiration (and thereby derived GPP) for eight plots. GPP (from the eight-plot dataset) demonstrates a significant linear decline with elevation ($P < 0.01$, $r^2 = 0.62$; Fig. 3a). The plot at 1500 m asl shows values of GPP similar to those of the lowland rainforests, despite being c. 6–7°C cooler, but overall there is no strong statistical support for a break at cloud base. If the overall trend is interpreted as a temperature response alone, the resulting sensitivity of GPP to temperature would be estimated as -1.02 Mg C °C^{-1}.

NPP (from the full 16-plot dataset) shows a significant decline with elevation ($P < 0.001$, $r^2 = 0.61$), and stronger evidence for a transition at 1600 m asl (Fig. 3b). Regression with a break at 1600 m asl ($P < 0.001$, $r^2 = 0.68$) has a lower (better) Akaike
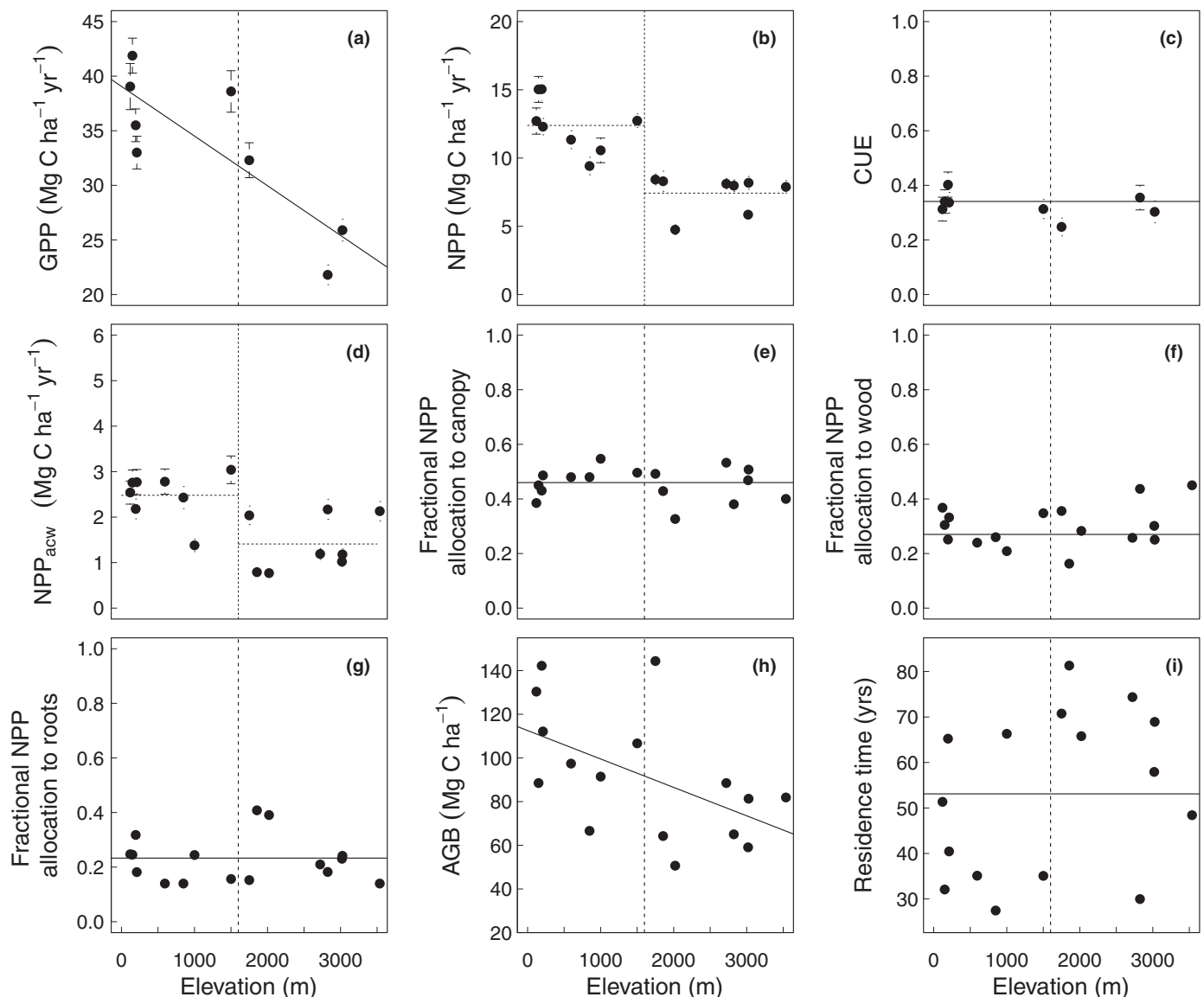

Fig. 3 Variation in carbon cycle characteristics along the 3300 m above sea level (asl) tropical montane elevation transect, including (a) gross primary productivity (GPP), (b) net primary productivity (NPP), (c) carbon use efficiency (CUE), the fraction NPP : GPP, (d) aboveground coarse woody NPP (NPP$_{acw}$), (e) fractional NPP allocation to canopy components, (f) fractional NPP allocation to woody components, (g) fractional NPP allocation to roots, (h) aboveground live biomass (AGB) and (i) woody residence time. The best model fit (according to the Akaike information criterion, AIC) is shown when significant, either a single horizontal line or slope, or two lines split at 1600 m asl (cloud base).

information criterion (AIC) score (66.3) than the simple linear regression (69.6). Above the 1500–1750 m asl transition, there is remarkably no overall trend of NPP with elevation over an elevation range of 1750 m asl (a change of mean temperature of 12–13°C). The same pattern of no trend applies below the 1500 m asl transition, although in this case the lack of trend is strongly driven by the high NPP at a single plot, SPD-02. If this influential plot is removed, there is a significant decline of NPP with elevation in the lowland/submontane plots ($P < 0.001$, $r^2 = 0.79$ for full ANCOVA, Fig. S3).

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

The aboveground coarse woody NPP demonstrates shows substantial site-to-site variation, but a significant linear decline as a function of elevation ($P < 0.02$, $r^2 = 0.28$), with an estimated mean decrease of 0.38 Mg C ha^{-1} yr^{-1} per 1000 m increase in elevation asl (Fig. 3d). However, the best fit model is in two different constant values of NPP$_{acw}$ above and below 1600 m asl (AIC score of 30.1 vs 35.8). This holds true even when the influential plot SPD-02 is removed (Fig. S3). Remarkably, fractional allocation of NPP to canopy, wood and roots demonstrates no significant relationship with elevation and relatively little plot-to-plot variability, nor do plots below 1600 m significantly differ than those above 1600 m asl ($P > 0.1$; Fig. 3d–f). Across the dataset the mean fractional allocations of NPP are $48 \pm 5\%$ to canopy, $29 \pm 4\%$ to wood and $22 \pm 5\%$ to fine roots. Aboveground live biomass (AGB) shows large plot-to-plot variation, but also a significant linear decline with elevation ($P < 0.03$, $r^2 = 0.23$; Fig. 3g). This is strongly associated with a decline in forest stature, rather than a decline in basal area. Biomass residence time (τ_R; calculated as aboveground woody biomass divided by aboveground woody NPP) shows very large plot-to-plot variation and little relationship with elevation, nor do plots at or below 1500 m significantly differ than those above 1500 m asl ($P = 0.3$; Fig. 3h).

Application of analysis framework

We next compare the NPP and respiration components of two upper cloud forest autotrophic carbon budgets against that of the four lowland plots (Fig. 4). The mid-elevation plots are here excluded because of their transitional nature. Woody biomass production rates are 50% lower in the upper montane forests than in the lowlands (Fig. 4a). This decline can be attributed largely to a $36 \pm 7\%$ decline in GPP, together with a moderate ($15 \pm 10\%$) decline in CUE (although in our broader dataset we

see no overall trend in CUE with elevation). There is no significant change in proportional allocation of NPP to woody production, consistent with the larger dataset (Fig. 3). As noted earlier, there is no evidence of an increase in CUE, as might be expected if temperature was a strong positive control on autotrophic respiration.

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

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

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

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

The magnitudes and trends are broadly consistent with those reported by van de Weg *et al.* (2009) for this same elevation gradient. This trend is consistent with results from a fertilisation experiment on the transect, which shows that woody growth rates in plots above 1500 m asl were responsive to N addition
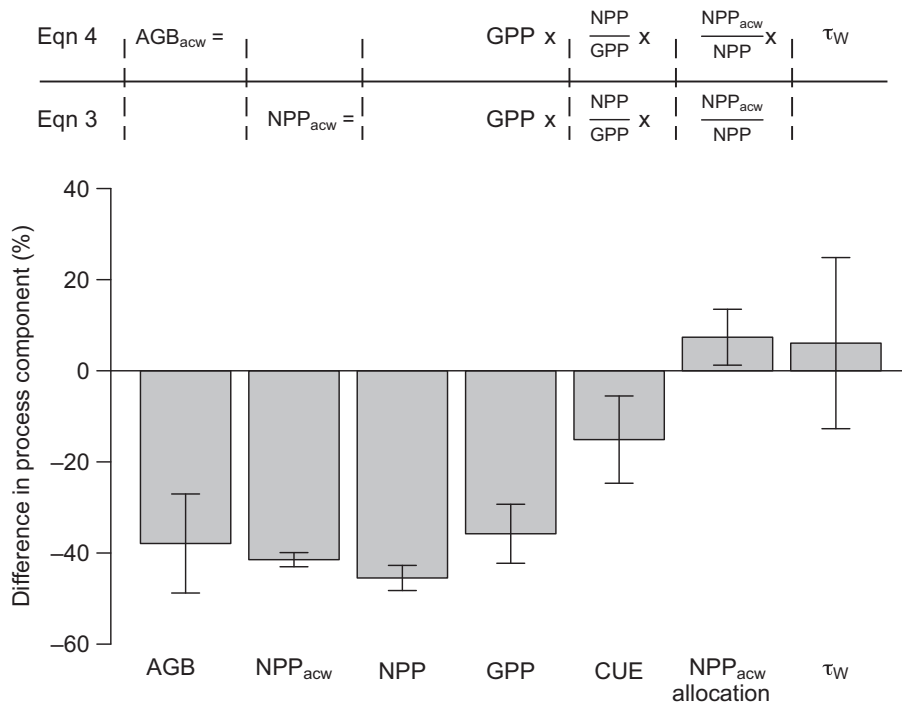
$$\text{Eqn 4} \quad AGB_{acw} = \quad GPP \times \frac{NPP}{GPP} \times \frac{NPP_{acw}}{NPP} \times \tau_W$$

$$\text{Eqn 3} \quad NPP_{acw} = \quad GPP \times \frac{NPP}{GPP} \times \frac{NPP_{acw}}{NPP}$$

Fig. 4 The ratio of key carbon cycle attributes of the two upper montane cloud forest plots (Wayqecha and Esperanza) relative to the four lowland forest plots (Tambopata and Allpahuayo). Error bars indicate ± SE. AGB, aboveground coarse wood live biomass; NPP, net primary productivity; NPP_{acw}, aboveground coarse woody NPP; GPP, gross primary productivity; CUE, carbon use efficiency; τ_W, woody residence time.

(indicating relative limitation of N), and growth rates in plots below 1500 m asl were responsive to P and N combined, indicating some role for P-limitation (Fisher *et al.*, 2013). Overall, the relative availability of these nutrients appears to have no overall effect on the trend of leaf photosynthetic capacity with elevation.

Discussion

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

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

The next question is whether the decline in GPP with elevation is related to a decline in canopy photosynthetic capacity or in rates of actual photosynthesis. Canopy photosynthetic capacity

is a function of canopy leaf area and leaf-level photosynthetic capacity at ambient temperatures. Strikingly, we do not observe any evidence of a decline in photosynthetic parameters under ambient conditions, and only a modest decline in leaf area index (LAI). This suggests that canopy photosynthetic capacity shows only moderate variation with elevation, and that any declines in capacity are manifest through declines in LAI rather than leaf-level properties. The lack of any decline in leaf-level photosynthesis is further supported by the lack of change in leaf nitrogen (N) per unit area with elevation, and the increase of leaf phosphorus (P) per unit area. This suggests that lower temperatures do not lead to lower canopy stocks of key nutrients.

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

A key point to consider is whether the trends in forest properties with elevation are broadly linear, or whether there is an
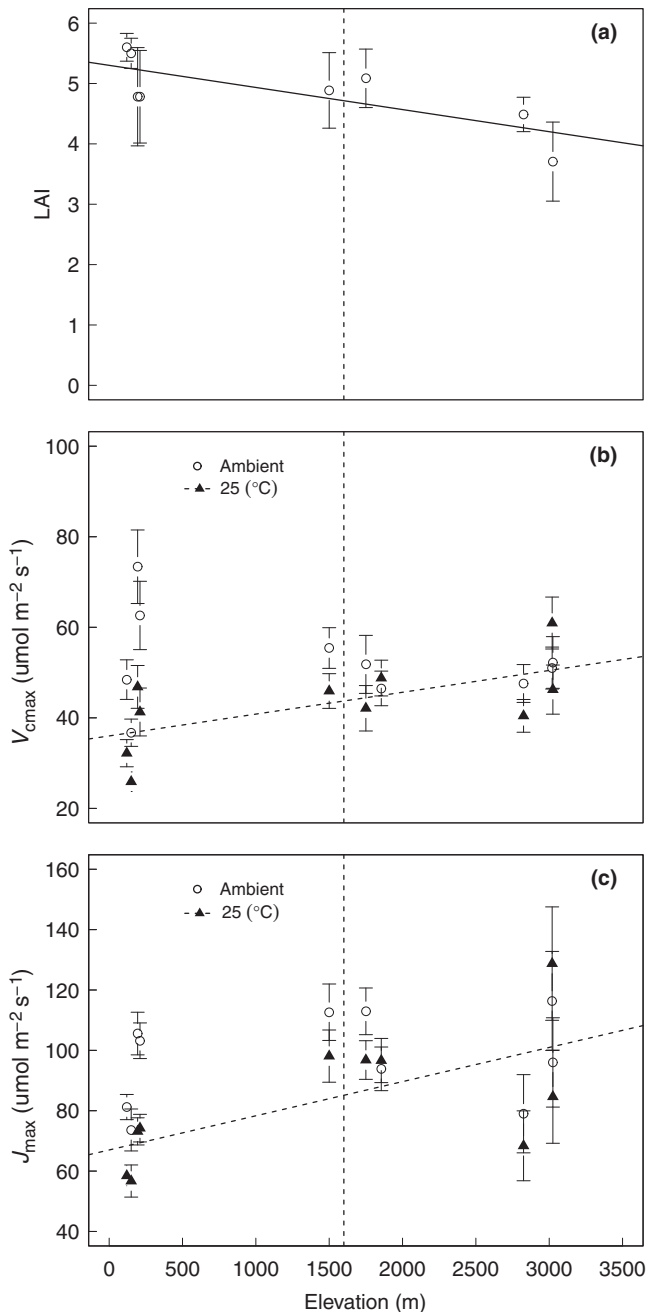
Fig. 5 Variation in key canopy attributes influencing canopy photosynthetic capacity along the 2800 m above sea level (asl) tropical montane elevation transect, including (a) leaf area index (LAI); (b) maximal area-based rates of CO_2 fixation by Rubisco at ambient temperatures (V_{cmax}) and normalized to 25°C ($V_{cmax,25}$); (c) photosynthetic electron transport at ambient temperatures (J_{max}) and normalized to 25°C ($J_{max,25}$). Error bars indicate $\pm$ SE.

such as abundant epiphytic bryophytes (Horwath, 2012), tree ferns and other characteristic cloud forest features and species (W. Farfan Rios, unpublished data), increased leaf waxiness (S. Feakins, unpublished data), shortened canopy stature (Asner *et al.*, 2014) and a changed tree architecture from straight boles (competing for stratified light) to gnarled and twisted boles. This abrupt transition suggests that increase in cloud frequency and particularly cloud immersion drives the decline in GPP, and hence the decline in NPP and woody growth. However, the evidence from the smaller GPP dataset equally supports a simple linear fit as opposed to a step-decline at 1600 m asl, so the support for cloud immersion as a key driver is not conclusive.

In conclusion, we have demonstrated the value of a whole-carbon-budget perspective to provide insight into how and why growth and biomass tend to decline with elevation along a tropical elevation gradient. For this transect, we show that a decline in GPP with elevation is the main determinant of declining growth and biomass, with little trend in CUE, allocation of NPP or biomass residence times. The results could have been very different. For example, for wet–dry gradients in lowland Amazonia, Malhi *et al.* (2015) demonstrated that the observed decline in GPP going from wet to dry forests was offset by increased CUE and increased allocation to woody growth, leading to little trend in woody growth rates with rainfall. The low biomass of dry forests was instead driven by low woody biomass residence times. The other striking result here is the lack of variation in leaf photosynthetic capacity with elevation, with the overall decline of GPP and NPP driven by a transition near cloud base. This suggests that temperature has little direct influence on productivity, with ecosystems acclimating their ecophysiology or shifting in composition to optimize productivity for their particular climate regime. For example, in colder forests, lower rates of nutrient mineralization and uptake are compensated for longer leaf lifetimes and nutrient retention periods, and peak photosynthetic rates are likely optimized to lower temperatures. There is large turnover of tree species between plots; individual species may be constrained by temperature, but the constant changes in species portfolio result in a relatively invariant potential GPP. Such results are consistent with a recent global analysis that suggests NPP is largely determined by stand age and biomass, and not by climate (Michaletz *et al.*, 2014; but note the critique by Chu *et al.*, 2015). Such insights have yet to be incorporated into global vegetation models (Marthews *et al.*, 2012), which tend to predict a high sensitivity of tropical GPP to temperature (Galbraith *et al.*, 2010).

The sensitivity of biomes, and in particular tropical biomes, to warming temperatures is one of the key questions in global change ecosystems research. Although this tropical elevation transect by its nature does not extend to the warmer lowland temperatures of a future warmer world, it does highlight the important processes of acclimation and community turnover that can result in relatively low long-term sensitivity of primary productivity to temperature. Tropical elevation transects are particularly powerful tools for examining temperature relationships, because they do not have the confounding influence of varying length of a dormant winter season (Malhi *et al.*, 2010). However, cloud immersion may confound attempts to use long elevation gradients as

abrupt transition in the elevation region 1500–1750 m above sea level (asl). Figure 3(b) is suggestive of an abrupt decline in NPP around this zone. NPP shows no significant trend with elevation in the range 100–1500 m asl (unless we discount the SPD-02 plot), and no significant trend with elevation in the range 1750–3537 m. The transition zone for NPP (1500–1700 m asl) coincides with the appearance of many typical cloud forest features

proxies for temperature changes alone. In a warming world, the tropical cloud base is like to be rising (Still *et al.*, 1999), and some of the most dramatic responses in carbon cycling and species composition may occur at this cloud immersion ecotone.

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

Author contributions

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

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Relationship between foliar nutrients (nitrogen and phosphorus) and elevation.

Fig. S2 Relationship between primary productivity and temperature.

Fig. S3 Relationship between primary productivity and elevation when the sometimes influential plot SPD-02 is excluded.

Methods S1 Detailed explanation of the measurements and data analysis procedures.

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